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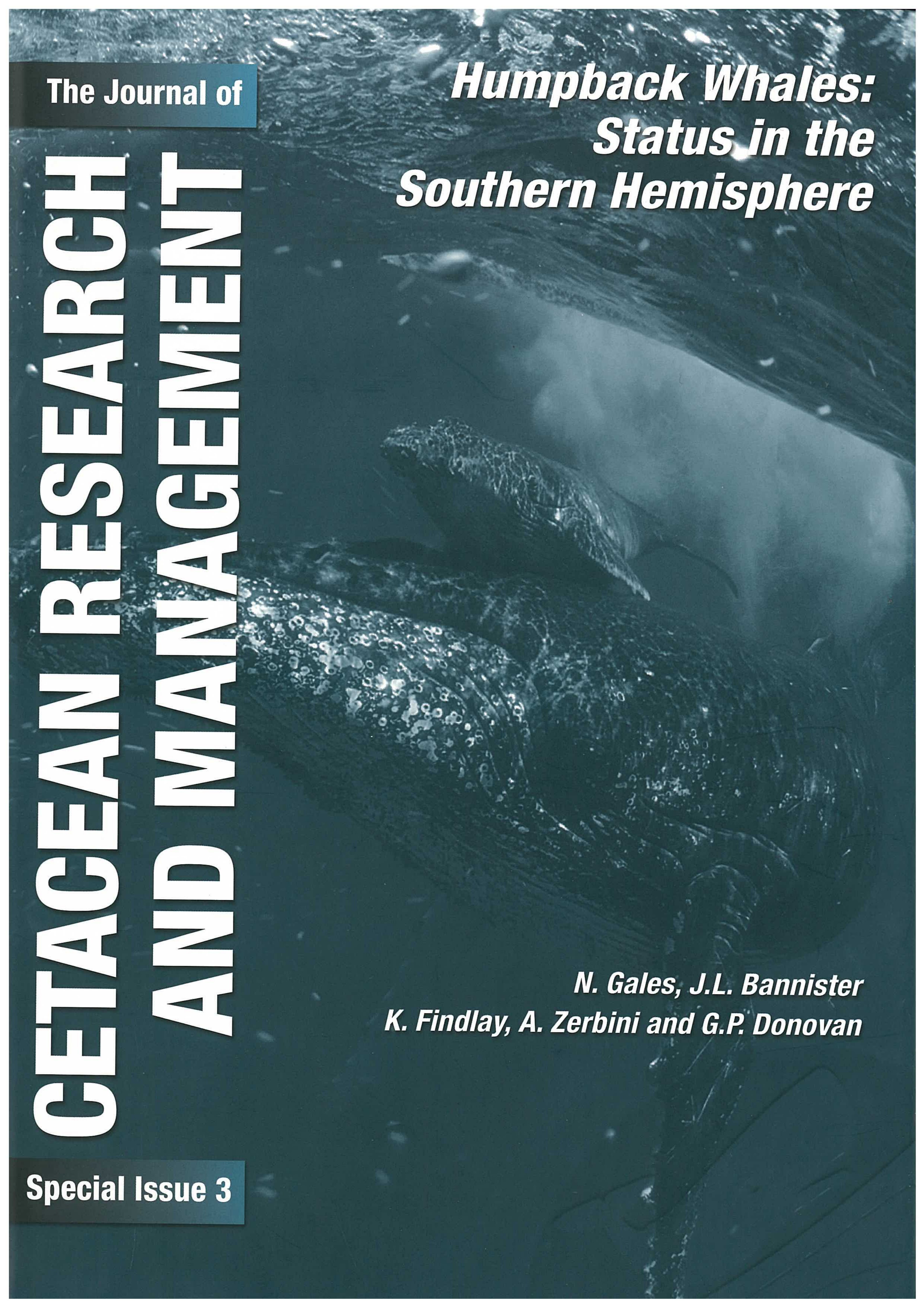
Humpback Whales: Status in the Southern Hemisphere

N. Gales, J.L. Bannister
K. Findlay, A. Zerbini and G.P. Donovan



Humpback Whales: Status in the Southern Hemisphere

Edited by

Nick Gales

Australian Antarctic Division, Australian Centre for Applied Marine Mammal Science,
Channel Highway, Kingston, Tasmania 7050, Australia

John Bannister

Hon Associate, Western Australian Museum, Locked Bag 49, Welshpool DC, WA 6986, Australia

Ken Findlay

96 De Villiers Way, Glencairn 7975, South Africa

Alex Zerbini

Alaska Fisheries Science Center, 7600 Sand Point Way NE, Bldg 4, Seattle, WA 98115-6349, USA

Greg Donovan

International Whaling Commission, The Red House, 135 Station Road, Impington, Cambridge, CB24 9NP, UK

Series Editor

Greg Donovan

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Editorial

Welcome to this volume, the third Special Issue of the *Journal of Cetacean Research and Management*. Special Issues are published from time to time and focus on specific topics. The first and second issues in this series were dedicated to, respectively, Chemical Pollution and Cetaceans (Reijnders *et al.*, 1999) and the Worldwide Status of Right Whales (Best *et al.*, 2001). This issue reports on the status of Southern Hemisphere humpback whales.

The humpback whale (*Megaptera novaeangliae*) is perhaps the most easily recognised cetacean due to its extremely long wing-like pectoral fins, the characteristic shape of the dorsal fin and the presence of many tubercles on the head and flippers. The species is widely distributed in all major oceans including polar, temperate and tropical areas. Most populations migrate between high latitude summer feeding grounds and tropical winter breeding and nursery grounds. Although trans-equatorial movement has been observed for Southern Hemisphere populations (e.g. Pacific coast of Central America), such exchange between populations of the hemispheres is thought to be generally restricted by the 6-month difference in their breeding seasons. As much of the global habitat of humpback whales includes populated coastlines, they have become the modern icon of the whalewatching industry. Their inquisitive nature, large size and spectacular behaviour, which often includes breaching, have helped this expanding industry develop into a multi-billion dollar business.

Historically, humpback whales were commercially important for other reasons. They were a target of open-boat, coastal whalers in the nineteenth century, but it was only after the development of more mechanised forms of whaling (also known as ‘modern whaling’) that the species became the main target of the industry (Tønnessen and Johnsen, 1982). In the Southern Hemisphere, exploitation initially occurred in the early 1900s in coastal areas both in high (e.g. the Antarctic Peninsula and South Georgia) and low (e.g. southern Africa and east and west Australia) latitudes but expanded to pelagic areas primarily after the mid 1920s. In October 1963, the International Whaling Commission protected Southern Hemisphere humpback whales from whaling, but illegal whaling continued thereafter until the early 1970s (Yablokov, 1995). At the time of protection many of the Southern Ocean populations were extremely small. Approximately 210,000 Southern Hemisphere humpback whales were killed by commercial whaling in the twentieth century (Findlay, 2001; IWC catch database).

In 1982, the IWC agreed on a cessation of all commercial whaling (commonly known as ‘the moratorium’), to take effect from 1986. As part of the decision it also agreed that it would undertake a ‘comprehensive assessment’ of the moratorium on whale stocks, although it did not define what this meant at the time (Donovan, 1989). The ‘comprehensive assessment’ was eventually defined by the Scientific Committee as an in-depth evaluation of the status of all whale stocks in the light of management objectives and procedures. It included the examination of: current stock size, recent population trends, carrying capacity and productivity. Of course to do this requires knowledge of population structure and an evaluation of status requires knowledge of the pre-exploitation abundance of the populations. The latter is obtained using population dynamics models in conjunction with the historic catch record (Donovan, 1989). Subsequently, the Committee has been undertaking Comprehensive Assessments (or in-depth assessments) of a variety of species/populations, often, but not always, as a prelude to the *Implementation* process for the Revised Management Procedure.

The Comprehensive Assessment of Southern Hemisphere humpback whales has been on the agenda of the IWC Scientific Committee for many years. At its 1997 meeting, the Committee recognised seven Breeding Stocks (labelled A to G) in the coastal waters of the east coast of South America (A), the west coast of southern Africa (B), the east coast of Africa (C), the west coast of Australia (D), the east coast of Australia and the western Pacific Islands (E), the central south Pacific Islands (F) and the west coast of South America (G), and feeding destinations associated with these stocks (IWC, 1998). In addition, an eighth population in the northern Indian Ocean, then named Breeding Stock X and now referred to as the ‘Arabian Sea Population’, was grouped with the Southern Hemisphere for assessment purposes. Progress had been made on various fronts (e.g. new estimates of abundance and rates of increase were made available for many stocks) after the 1997 meeting, but the assessment was hampered primarily because a reconciled catch series was still needed (IWC, 1997; 1998). Preliminary assessments were conducted between 2000 and 2002 and again in 2004 (IWC, 2001, 2002, 2003, 2005) and their results led to the development of improved catch series and the collection of information on abundance, trends and stock structure that could be used in an full assessment. At the 2005 meeting, the Scientific Committee agreed that it was in a position to initiate the full assessment of Southern Hemisphere humpback whales.

An International Symposium and Workshop on Southern Hemisphere humpback whales was held in Hobart, Tasmania, from 4 to 7 April 2006 under the auspices of the IWC (IWC, 2011a). The meeting was organised by Nick Gales and colleagues from the Australian Antarctic Division, with assistance of Alex Zerbini, Ken Findlay and John Bannister, and was chaired by John Bannister. The meeting attracted 36 scientists from Africa, Asia, Europe, North and South America, and Oceania. Scientists with experience in the assessment of North Atlantic humpback whales (IWC, 2002) also participated.

The goals of the Workshop were to: (1) review the abundance, population structure and status of southern humpback whale breeding stocks and their relationship with feeding grounds in the Southern Oceans; and (2) advance the Comprehensive Assessment of these stocks to near completion using the best available data. A total of 69 papers presented results from recent research on distribution, movements, stock structure, abundance, trends in abundance, estimation of life-history parameters and catch data for Southern Hemisphere humpback whales in their breeding and feeding grounds, or in migratory corridors. Early in the meeting, it became clear that due to the complexity of the stock structure of Breeding Stocks B, C, E and F there were insufficient data to perform an assessment of these stocks and of the Arabian Sea population. Therefore discussion was focused on input data and population dynamic model structure for those stocks (A, D and G) for which an assessment could be conducted at the following IWC annual meeting in St. Kitts and Nevis (i.e. in June 2006). The Workshop also made a number of recommendations for additional data collection and analysis, particularly in relation to improving understanding of stock structure and feeding ground distribution so that catches could be allocated to appropriate populations (IWC, 2011a).

The assessment of Breeding Stocks A, D and G was completed at the end of the IWC annual meeting in 2006 (IWC, 2007). The availability of an absolute abundance estimate for Breeding Stock A (eastern South America), along with data on population trend and relatively unambiguous catch allocations, meant that this assessment was judged by the Committee to be the most precise. The Committee concluded that this population was at nearly 30% of its pre-exploitation size. Breeding Stock D (Western Australia) was estimated to be at 70–80% of pre-exploitation abundance. While estimates of trend and total population size were also available for this stock, inference on current status was possibly influenced by greater uncertainty in catch allocation due to mixing with Breeding Stock E in the Antarctic. Finally, the status of Breeding Stock G (western South America) was much less certain (point estimates varied between 30 and 70% of pre-exploitation size) due in large part to lack of trend information on the breeding grounds and uncertainty in stock structure.

After the completion of the assessment of Breeding Stocks A, D and G, the Committee spent five years (2007–2011) reviewing information and methods required to conduct an assessment of the African humpback whale populations (stocks B and C). The stock structure on these breeding grounds was more complex and allocation of feeding ground catches to the sub-components of the breeding stocks was confounded with very limited movement and mixing data. The Committee concluded that there were at least two genetically distinct populations (referred to as sub-stocks B1 and B2) within the range of Breeding Stock B (western Africa), with partially overlapping distributions in migratory routes and feeding grounds. Because existing data were insufficient to clarify the degree of overlap or mixing of these two sub-stocks, the SC conducted their assessments with both a single and a two-stock model. The former estimated that Breeding Stock B has probably recovered to about half of its pre-exploitation size, but substantial uncertainty was associated with this estimate (IWC, 2011b). The two-stock model suggested that sub-stock B2 was more depleted than sub-stock B1, but it was not possible to assess whether this difference was real or whether this was caused because incomplete sampling coverage precluded an accurate estimation of the population size in sub-stock B2 (IWC, 2011b). The Committee concluded that there could be as many as four sub-stocks within the range of Breeding Stock C (named sub-stocks C1–4; IWC, 2006, 2009) and that data were available to conduct assessments only for sub-stocks C1 (the east African mainland coast) and C3 (Madagascar) (IWC, 2009). Population dynamics modelling suggested that these sub-stocks had recovered to nearly 65–98% (C1) and 76–83% (C3) of their pre-exploitation abundances (IWC, 2010).

With the completion of the assessment of the African stocks, the Committee has turned its attention to Oceania, (Breeding Stocks E [Eastern Australia] and F [South Pacific Islands]). Assessments for these populations will be completed over the next few years.

All of the assessments, at the level of the individual breeding stocks, are compromised to some degree by the paucity of empirical data on which to model mixing patterns. In all likelihood, the nature and extent of mixing will be highly influenced by factors including population density (stage of recovery), environmental variability, and relative density and recovery of other krill predators. Thus historic data derived from Discovery marks and contemporary data acquired from satellite tracking, photo-identification, or genetics may signal very different and potentially highly variable mixing patterns. A circumpolar model, considering all stocks in combination may provide a more precise estimate of the overall status of Southern Hemisphere humpback whales. Whatever approach is taken, it is clear that a great deal remains to be learned about this species in the Southern Hemisphere.

What is evident is that most of the populations have responded extremely well to the protection afforded by the IWC since 1963. Over the next decade we may see a substantial number of the populations return to their estimated pre-whaling abundance. That being said, other populations, such as those around Fiji and the Arabian Sea remain small and highly vulnerable to environmental perturbation or anthropogenic activities.

The overall Comprehensive Assessment, and the eventual recovery patterns of the populations, may also provide a unique insight into how the Southern Ocean ecosystems have changed over the past century. During this period, humpback whales and many other whale and seal populations have moved from high abundance, to near absence and are now on differential recovery trajectories. This volume is an important 'stock take' along these recovery trajectories.

This Special Issue of the *Journal of Cetacean Research and Management* contains the Report of the Workshop in Hobart and peer-reviewed papers, many of which were originally presented to the Workshop and have since been updated. The papers are arranged in a section about general biology and feeding grounds, followed by sections specific to each breeding stock. These papers in large part represent our current state of knowledge on the status of Southern Hemisphere humpback whales.

The editors acknowledge the many colleagues who undertook the review of the papers submitted for publication in this volume. Manuscript review is a time-consuming task, but it is also vital for maintaining the high quality of the work published by this Journal. Reviewers included Scott Baker, John Bannister, Jay Barlow, Peter Best, David Borchers, Trevor Branch, John Brandon, Mark Bravington, Phil Hammond, Jeff Breiwick, Doug Butterworth, Carole Carlson, Justin Cooke, Greg Donovan, Jaume Forcada, Phil Hammond, Scott Kraus, Jeff Laake, Jack Lawson, Christina Lockyer, Tony Martin, David Matilla, Sally Mizroch, Simon Northridge, Charles Paxton, André Punt, Steve Reilly, Jooke Robbins, Vicky Rowntree, Len Thomas, Koen Van Waerebeek, Paul Wade, Hal Whitehead, Judy Zeh and Alex Zerbini.

The Editors also acknowledge the support provided to the Workshop in Hobart by the Government of Australia, by the organising personnel at the Australian Antarctic Division and by the Commission's administrative and publications staff, especially Andrea Cooke, Stella Duff, Jemma Jones, Helen Sharp and Elaine Shield. Their support led to the successful outcome of the Workshop as well as for the publication of this volume.

This Special Issue is dedicated to the memory of Dr. Geoff Kirkwood. Dr. Kirkwood was one of the primary leaders in the field of population modelling within the IWC Scientific Committee and a former Chair of the Revised Management Procedure Working Group and of the IWC Scientific Committee.

Nick Gales, John Bannister, Ken Findlay,
Alex Zerbini, Greg Donovan

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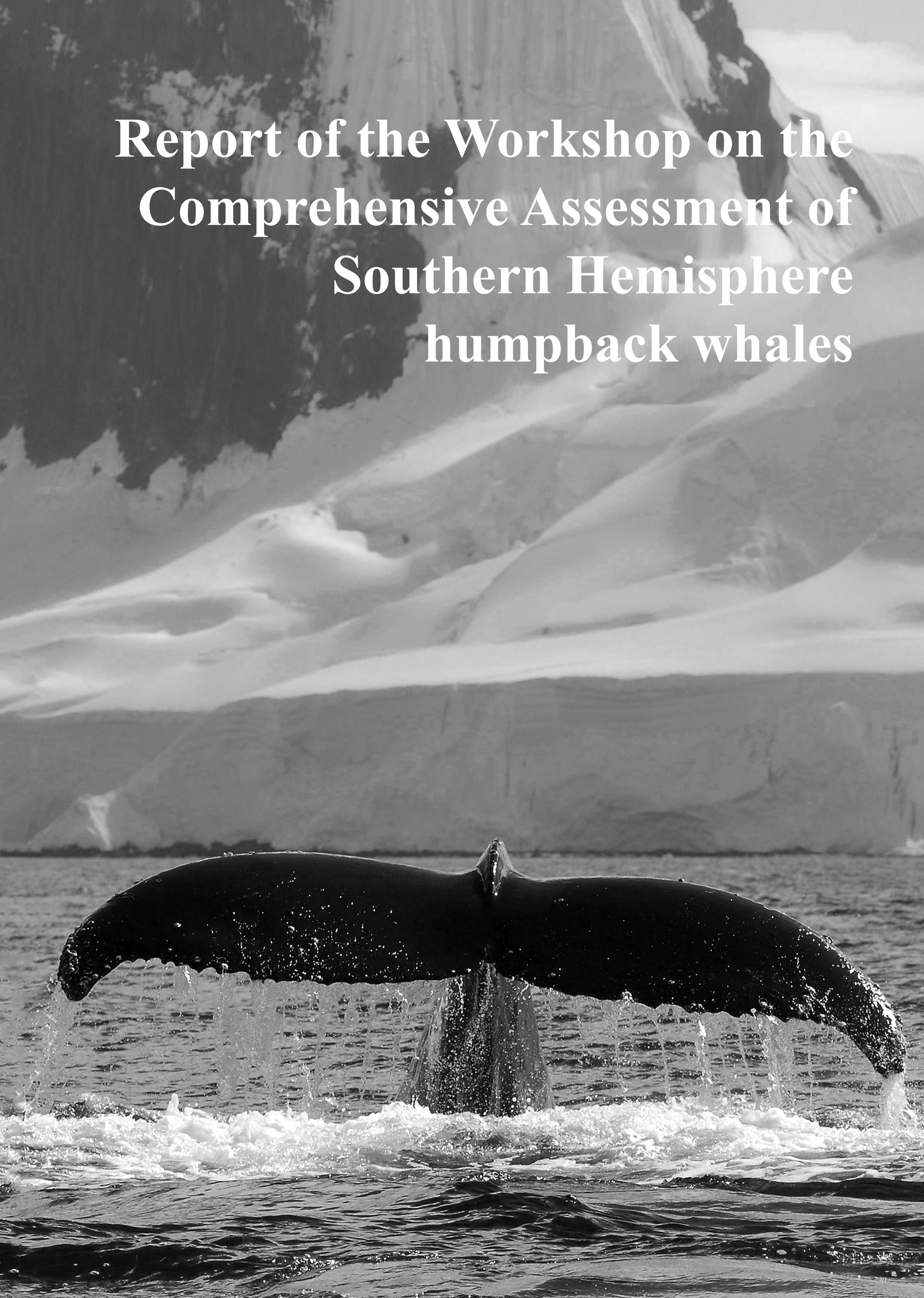
Report of the Workshop on the Comprehensive Assessment of Southern Hemisphere humpback whales



Report: Contents

Photo: © Humpback whale – Antarctic Peninsula. Photo by Emma Newcombe, courtesy of Carlos Olavarría (CEQUA-INACH).

Report of the Workshop on the Comprehensive Assessment of Southern Hemisphere humpback whales

The Workshop was held at the Australian Antarctic Division, Hobart, Tasmania from 4–7 April 2006. The list of participants is given as Annex A.

1. INTRODUCTORY ITEMS

1.1 Welcome and introduction

Gales welcomed the participants to the Workshop. He thanked the steering committee for their assistance in preparations for the meeting, in particular Findlay and Zerbini. He also thanked Bannister and Findlay for producing the summary information and metadata tables that can be found on the IWC website*. For logistical support he thanked Jemma Miller [now Jones] from the IWC Secretariat, and Sarah Robinson and Mandy Denny for local support. Funding for the Workshop came primarily from the Australian Government with additional support being provided by the IWC and the National Marine Fisheries Service (USA).

Donovan welcomed the participants on behalf of the IWC. In particular, he thanked Gales and Robinson for their hard work in providing the excellent facilities and arranging accommodation for the participants.

Donovan had the sad duty to inform the meeting of the recent death of Dr Geoff Kirkwood of Imperial College, London. Geoff had, along with Dr Kay Radway Allen, been one of the primary leaders in the field of population modelling within the Scientific Committee from the mid 1970s when he had been based at CSIRO in Cronulla, Australia and then Hobart. He had been Chair of the Scientific Committee and also chaired the RMP working group until the adoption of the RMP in 1994. He chaired with skill, wisdom and great humour. The meeting held a minute's silence in his honour.

1.2 Terms of reference

In 2005, the Scientific Committee agreed that an Intersessional Workshop be held to advance the Comprehensive Assessment of Southern Hemisphere humpback whales to the point where the process can be completed at the 2006 Annual Meeting.

The agreed Terms of Reference of the Workshop were:

(1) to advance the Comprehensive Assessment of Southern Hemisphere humpback whales to near completion using the best available data; and
(2) to review the abundance, population structure and status of Southern Hemisphere humpback whale breeding populations and their relationship to feeding grounds in the Southern Ocean.

1.3 Election of Chair and appointment of rapporteurs

Bannister was elected Chair. Donovan agreed to co-ordinate the production of the report with the assistance of Butterworth, Childerhouse, Clapham, Findlay, Polacheck and Wade. Final editing of the report was undertaken by Donovan.

1.4 Meeting procedures and time schedule

Gales detailed the practical arrangements for the meeting.

1.5 Adoption of the Agenda

The adopted Agenda is given as Annex B.

1.6 Documents available

The list of documents is given as Annex C. The Workshop also had available the most recent tabulated summaries of information available and metadata available as published on the IWC website*.

1.7 Publication of proceedings

It was agreed that, provided there were sufficient high quality papers, it would be appropriate to publish the report of this workshop and appropriate papers as a Special Issue of the *Journal of Cetacean Research and Management*, similar to that resulting from the earlier work on right whales (Best *et al.*, 2001). An editorial team will be assembled and the usual refereeing policy of the journal will be followed. Authors wishing to have their papers considered for publication were asked to inform Gales and Donovan.

2. ASSESSMENT PROCEDURES

2.1 Model or models to be used – general discussion

It was **agreed** that it would be valuable to have an initial general discussion on the modelling framework(s) that might be considered at this Workshop, in order to focus discussions on subsequent Agenda Items. Initial discussions were held in a Working Group convened by Clapham and its report has been subsumed here.

The primary issues identified were:

(1) allocation of feeding ground catches to breeding stocks, notably when mixing of two or more breeding stocks on a feeding ground is suspected;
(2) treatment of abundance estimates from the feeding grounds when allocation of animals to breeding areas is uncertain;
(3) treatment of possible sub-structure in the breeding grounds; and
(4) incorporation of demographic parameters not typically included in modelling (e.g. depensation).

2.2 Allocation of feeding ground catches to breeding stocks

Care must be taken when allocating feeding ground catches to breeding stocks, particularly when mixing of two or more breeding stocks on a feeding ground is suspected. The extent of this problem may vary with feeding area and breeding stock, as discussed under Item 3. In cases where structure is uncertain, multiple scenarios will need to be examined using different variants of the allocation models (e.g. the updated 'Naïve', 'Fringe' and 'Overlap' models proposed in IWC (2006) – and perhaps others such as the

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* *http://www.iwcoffice.org/documents/sci_com/workshops/Table2.pdf* accessed October 2011.

'Fringe minimum[1]' and 'Fringe maximum[1]') to provide for suitable examination of the effect of uncertainty in catch allocation on assessments.

The need to examine the allocation of catches from land stations on migratory routes where there may be some uncertainty in the migratory destination of some or all animals at those locations (e.g. Tangalooma and Byron Bay in Australia, and all New Zealand coastal stations) must also be considered.

2.3 Use of abundance estimates in the models

The absolute estimates used in the models are those from breeding areas. If used, feeding ground estimates are usually incorporated as a test for consistency; if the model results appear inconsistent with the feeding ground estimates, attempts are made to identify the cause of such differences and to resolve them. The Butterworth-Johnston model typically incorporates estimates from feeding and breeding grounds, although to date this has made little difference to their results (SC/A06/HW22). The Workshop **agrees** that prior to their use in a model:

(1) the suitability or otherwise of all estimates of abundance should be determined and where possible, inconsistencies in estimates for the same putative stock should be resolved prior to their use[2]; and
(2) the suitability or otherwise of trends in abundance from feeding grounds should be determined (given *inter alia* the mixing on the feeding grounds problem).

These issues are considered on a case-by-case basis under Item 5.

2.4 Sub-structure in the breeding grounds

In addition to the question of mixing of breeding stocks on the feeding grounds, the question of possible sub-structure within a breeding ground (e.g. as has been suggested for Breeding Stock E) must be examined and this is dealt with on a case-by-case basis under Item 3.

2.5 Population dynamics variables for inclusion in the model

Current models (e.g. those using the logistic) are relatively simple in the way they incorporate demographic parameters. Incorporation of other factors (e.g. depensation, time lag responses) is desirable and probably practical. Genetic analyses may be used to 'ground-truth' estimates of minimum numbers to which the population was reduced (e.g. current mtDNA data set an absolute lower limit). This would set another prior that allows elimination of certain values for minimum population size (and thereby of certain rates of increase without depensation). Reviews of current biological parameters (e.g. maturity and pregnancy rates) should keep in mind that these may not be the same in declining versus increasing (recovering) populations (see Item 6).

2.6 Other issues

The Workshop **recommends** the following terminology:

(1) for the feeding grounds, the existing management Areas (i.e. Areas I–VI – see Donovan, 1991) be retained; and
(2) for the breeding grounds, Breeding Stocks A–G (Southern Hemisphere) and X (Indian Ocean) be used.

3. REVIEW OF STOCK STRUCTURE, DISTRIBUTION AND MOVEMENTS

In discussing these items, the Workshop attempted to focus initially on what information was available for each postulated breeding stock, to consider seasonal distributions and to finally address stock structure hypotheses. The most recent hypothesised stock structure for the Southern Hemisphere reprinted from IWC (2005, p.236) is shown here (Fig. 1).

3.1 Breeding Stock A (Brazil)

3.1.1 Individual movements

3.1.1.1 DISCOVERY AND OTHER ARTIFICIAL MARKS[3]

Table 1 summarises the artificial mark information for Breeding Stock A (SC/A06/HW33). No marks were recovered showing a link with any feeding grounds but it should be noted that only seven whales were marked in the breeding ground.

3.1.1.2 NATURAL MARKS

Photo-identification data (Freitas *et al.*, 2004) on the breeding grounds have shown that individuals photographed in the Abrolhos Bank area (*ca* 17–19°30'S, 38–40°W) were resighted in other areas, as far north as about 12°S.

The Workshop also considered information on known movements of animals from Breeding Stock A to the Antarctic.

SC/A06/HW44 presented the results of the comparison of 829 animals photo-identified in Brazilian waters with nine individuals marked in December 2004 in the waters of the Scotia Sea. An individual photographed on 4 August 2000 on the Abrolhos Bank was subsequently photographed on 4 December 2004 off Shag Rocks near South Georgia.

SC/A06/HW61 reported on an ongoing comparison of 2,500 animals photographed in Brazil with two animals that were photographed (and biopsied) near South Georgia and 18 animals photographed near the South Sandwich Islands in January 2006. Although the genetic studies and a full comparison are not yet complete, thus far three of the South Sandwich whales have also been photographed in Brazil in 1999, 2001 and 2002.

3.1.1.3 TELEMETRY

Information was presented on movements of individual whales from satellite telemetry. The animals were marked towards the end of the time spent on the breeding grounds and thus provide valuable information on migration routes and destinations but little information on within breeding ground movements.

SC/A06/HW46 summarised the results of satellite telemetry studies conducted off the coast of Brazil. Seven whales tagged on Abrolhos Bank in two different seasons, 2003 (Zerbini *et al.*, 2006) and 2005, migrated to an area east of South Georgia (54°20'S, 36°40'W) and north of the South Sandwich Islands (*ca* 58°S, 21°30W). One whale moved down to the South Sandwich Islands and then moved west.

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[1] In the case of Fringe minimum, core areas in the feeding grounds are allocated with high probability to particular breeding stocks. However, it was noted that in some cases there may be mixing of animals from different breeding areas in even the core area (as is suspected to occur in Area V). The Fringe maximum model allocates to one breeding stock animals from both the core area as well as from a wider region out to the boundary of the core area in the adjacent feeding Area.

[2] This is important, as in some models, the average of widely different estimates is 'used' implying that equal plausibility is given to both estimates.

[3] Annex D provides a brief overview of the artificial mark information presented for humpback whales in the Southern Hemisphere. Artificial marks include Discovery marks, and marks placed under national schemes.

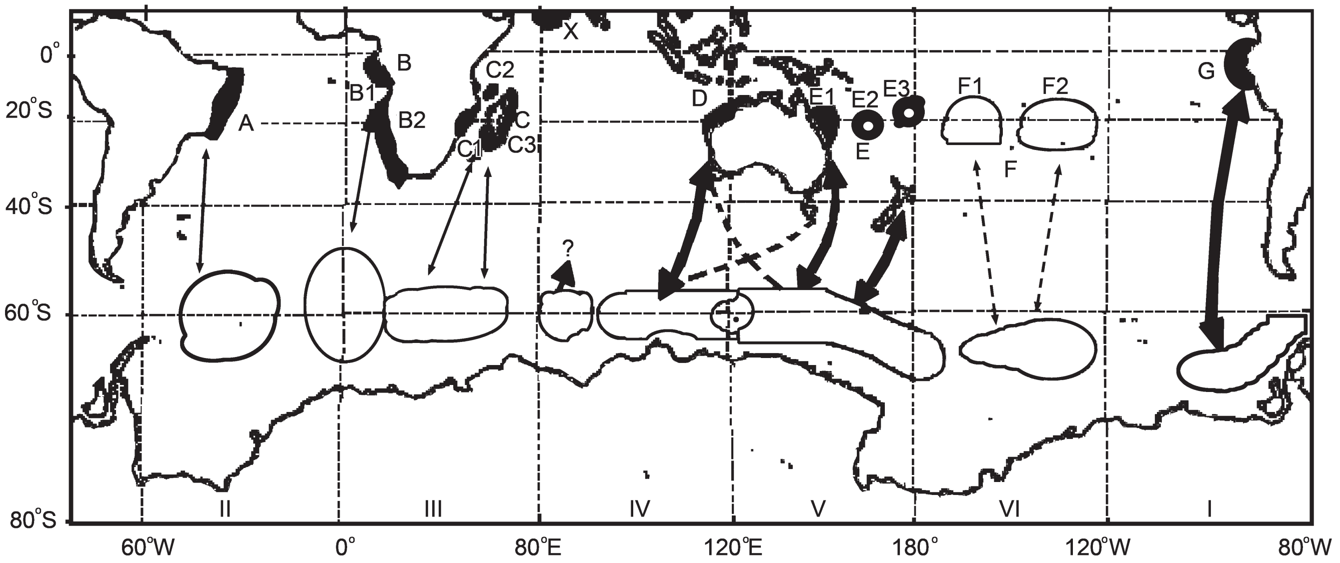

Fig. 1. New hypothetical stock structure for Southern Hemisphere humpback whales. This is for illustrative and discussion purposes only. The areas and sub-areas identified reflect approximate, rather than necessarily exact, boundaries. A dotted line represents hypothetical connection, thin lines represent a small number of documented connections between areas from resights using Discovery marks, photo-id or genetics, or satellite tracked whales, and thick lines represent a large number of documented connections between areas from resights using Discovery marks, photo-id or genetics, or satellite tracked whales.

Of note is that none of these whales migrated south of 60°S or east of 20°W, the current stock boundary of Breeding Stock A in the feeding grounds. These movements are consistent with the current hypothesised connection between Breeding Stock A (Brazil) and Area II. The satellite tagged whales had not migrated to nearer than 300km of South Georgia.

In general discussion, it was noted that in the early whaling years (1904 onwards), many humpback whales were taken within 100km of South Georgia and reference was made to the hypothesis (Perrin, 2001) that the present lack of whales close to South Georgia could be interpreted as suggesting that a population that fed close to South Georgia was extirpated and the cultural memory of feeding grounds close to South Georgia had been lost. However, it was noted that not only was the sample size of whales monitored small but also that the high density of krill in the area where the whales were feeding meant that there was no requirement for them to move into coastal South Georgia waters.

3.1.1.4 OTHER

No information was presented under this Item.

3.1.2 Stock structure

3.1.2.1 GENETIC STRUCTURE

Most of the information considered under this item concerned the links between animals found in Breeding Stock A and those found on the feeding grounds, notably Areas I and II.

SC/A06/HW11 reported on genetic analyses of whales from Abrolhos Bank, Brazil. Mitochondrial DNA control-region sequences were used to investigate genetic diversity and the putative association between Brazilian and Antarctic (Areas I and II) humpback whales to clarify the location of the feeding ground for the Brazilian population. For the Brazilian sample, 57 polymorphic sites were identified, defining 61 haplotypes. For the Antarctic samples, 24 and 21 segregation sites were detected defining 17 and 13 haplotypes for Areas I and II respectively. The high mtDNA diversity (nucleotide and haplotype) observed in the Brazilian sample is in agreement with other breeding areas studied in the Southern Hemisphere and in the North Atlantic. Both Antarctic Areas showed the highest number of shared haplotypes, while a high percentage of exclusive haplotypes (88.5%) occurred in the Brazilian population. Furthermore, in analyses such as AMOVA, pairwise F_{ST} and Φ_{ST}, the two Antarctic Areas could not be statistically differentiated while the Brazilian population was always significantly different from either Area I or Area II.

The authors noted the results showed a greater distinctiveness of the Brazilian population in comparison with the Antarctic Peninsula samples, indicating that Area I and the western portion of Area II (close to the Antarctic Peninsula), do not comprise the main feeding ground of Brazilian humpback whales.

In discussion, it was noted that these results were in agreement with results from satellite tagging and photo-

Table 1

Summary of information from artificial marks for Breeding Stock A.

	Breeding stock A	Putative feeding grounds (Area II)
Humpbacks marked (all marks)	7 (18°S, 38°W)	31
Marks recovered	0	1
Origin of marks recovered	0	2
Movements to other Areas	0	1*
Movements from other Areas	Marked: 62°S,116°W (Area I) Recovered: 28°S, 45°W**	–

*Recovered off Cape Horn in cooker. **Recovered in cooker.

identification (Items 3.1.1.2 and 3.1.1.3). It was also encouraging that genetic studies with relatively low sample sizes can still be useful for excluding some feeding grounds from a connection to a breeding ground. Rosenbaum noted that there were no shared haplotypes between this study and previous studies in the North Atlantic, suggesting that there has been no cross-hemisphere genetic exchange in the Atlantic, in contrast to what is thought to be the case in the Pacific.

3.1.3 Seasonal distribution

3.1.3.1 WINTER

SC/A06/HW02 reported on a series of four aerial surveys (2002–2005) on the Brazilian coastal breeding ground. The surveys covered coastal waters along Brazil within the 500m isobath. Humpback whales were found along most of the coastline covered (from nearly 5 to 23°S). The main area of concentration was the Abrolhos Bank where about 80% of the population was observed; no whales were found south of 23°S. Movements in the wintering grounds are still poorly known. Photo-identification data (Freitas *et al.*, 2004) have shown that individuals photographed in the Abrolhos Bank area were resighted in other areas, as far north as about 12°S. Animals tagged with satellite transmitters in the southern portion of the Abrolhos Bank showed marked individual variation in their movements (Zerbini *et al.*, 2006). Some whales moved south along the coast towards Cabo Frio (23°S) or west towards the outer continental shelf on the Abrolhos Bank. None of these whales moved further north than 16°30'S.

In discussion, it was noted that the information from the aerial surveys was consistent with that from satellite tracking (SC/A06/HW46) which showed that by around 23°S, the seven tagged whales had moved away from the coast on migration.

Clapham noted that both North Atlantic song, and a different song of unknown origin, had been heard from humpback whales near the equator, suggesting that the possibility of some genetic exchange across hemispheres exists in this part of the Atlantic (although see the lack of genetic evidence for this referred to under Item 3.1.2.1).

3.1.3.2 SUMMER

The telemetry information in SC/A06/HW46 revealed that the four whales for which the transmitters worked long enough, arrived on the feeding ground (an area about 250km northeast of South Georgia and 300km north of the South Sandwich Islands) between December and February with one remaining in the area until May. The authors commented that this fitted well with the concentrations of catches by Soviet whalers (Zerbini *et al.*, 2006).

3.1.3.3 MIGRATION

The telemetry information in SC/A06/HW46 suggests that the animals have a relatively narrow migratory corridor (*ca* 600km) from the Abrolhos Bank almost directly to the feeding areas (about 3,500km and taking about 45 days on average). Of the four animals that were tracked as far as the feeding grounds, three left Brazil in October and arrived in December, whilst one left as late as December, arriving in February.

3.1.4 Summary

At least based upon current knowledge (see Table 2 and Fig. 2), Breeding Stock A has a relatively simple structure which links it to the feeding grounds of the western South Atlantic (i.e. part of Area II), notably South Georgia and the South Sandwich Islands. Thus, the situation for this region is that of a single breeding stock (A) connecting with a single feeding ground (Area II). There is no indication that animals feeding off the Antarctic Peninsula migrate up the eastern coast of South America.

Table 2

Evidence for stock structure for breeding stock A. Key: ++ = strongly supports; + = is consistent with; ~ = evidence is ambivalent or uninformative; – = evidence is inconsistent with; – – = contradicts.

Hypothesis	1 (Single stock)	2 (Multiple breeding stocks)
Breeding grounds	1	>1
Rate of increase	~	~
Genetic differentiation	~	~
Acoustics	~	~
Photo-id interchange	+	– –
Discovery marks	~	~
Satellite telemetry	~	~
Catch data	++	—
Sighting data	++	– –
Total evidence	+++	– – –

3.1.5 Recommendations for future work

A consolidated set of recommendations for Breeding Stock A is given in Annex H.

3.2 Breeding Stock B (West Africa)

3.2.1 Individual movements

3.2.1.1 DISCOVERY AND OTHER ARTIFICIAL MARKS

Table 3 summarises the artificial mark information for Breeding Stock B (SC/A06/HW33). No marks had been

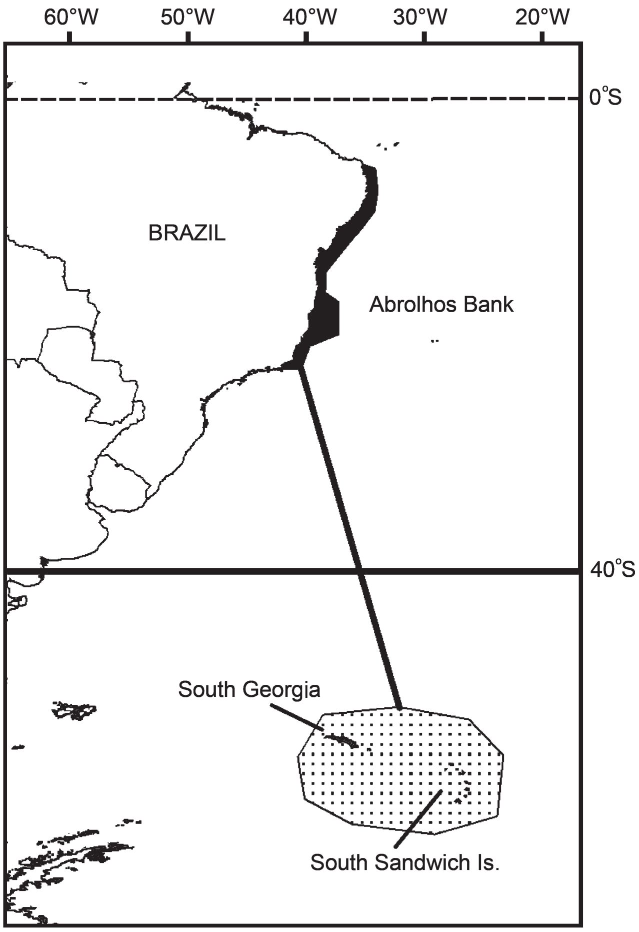

Fig. 2. Map of breeding and feeding grounds for Breeding Stock A, based on current knowledge.

Table 3

Summary of artificial marking information for Breeding Stock B.

Marking	Breeding grounds	Putative feeding grounds (Areas II and III)
Humpback whales marked (all marks)	0	48
Marks recovered	0	0
Origin of marks recovered	0	0
Movements to other Areas	0	2* moved into feeding grounds assigned to Breeding Stock A
Movement from other Areas	0	0

*One found in cooker west of Cape Horn 51°63’S, 33°02’W.

placed in the breeding grounds and no marks have been recovered there. One whale marked on the eastern edge of the putative feeding grounds (62°S, 10°E) was recovered at the southern tip of Madagascar (25°S, 44°E – Breeding Stock C) and the mark from one animal marked at 51°S, 10°W was recovered in a cooker at 51°63’S, 33°02’W.

3.2.1.2 NATURAL MARKS (PHOTO-ID, GENETIC)

It has been postulated that there may be two breeding stocks off west Africa: Breeding Stock B1 which is thought to winter (June–October) along central West African coasts and around the northern islands of the Gulf of Guinea; and breeding stock B2 which is thought to winter off the west coast of South Africa and Namibia, although the northerly extent of this remains undefined.

SC/A06/HW4 considered whales that have been grouped in wintering region B2. Geographically, western South Africa should function as a migration corridor. However, behavioural evidence (feeding and defecation), regular and extended presence of whales during summer (as late as February) and historical catches during this summer season, suggest that the area functions rather as a summer feeding ground. The paper reported on a within-area study of photographs (all years) and microsatellite markers (from 2001 and later). Most photographic effort took place from 2001 onwards. Both tail flukes and left and right dorsal fin photographs (including lateral marks and those on the caudal peduncle) were used for matching. The catalogue contains 266 identified individuals of which 44 were re-sighted at least once. The overall re-sighting rate was high (9.77% between years and 16.54% within and between). The overall sex ratio of animals of known sex ($n = 104$) is near parity but the proportion of females amongst re-sighted animals (64.7%) was higher (although not significantly so) than in whales seen only once (42.9%).

SC/A06/HW10 reported a within-season recapture rate for animals photo-identified off Gabon (Breeding Stock B2) of between 0.5% and 3.3%. Intervals between recaptures were quite variable for data collected between 2001 and 2004, ranging from 3 to 45 days, with means ranging from 9.4 and 15 days. No particular pattern was observed in the recaptures.

SC/A06/HW38 reported two genetic matches found between Gabon (B1) and western South Africa (B2) based on 11 microsatellite markers. These matches involved two females, one of which was accompanied by a calf, when first sighted in September in Gabon; a few months later (December and January) they were seen feeding off the west coast of South Africa. The authors stated that their findings suggest the possibility that pregnant or lactating females from Gabon migrate along the coast and stop to rest and feed in this area. This hypothesis is supported by well described feeding behaviours and female-skewed observed sex ratio for resighted animals off western South Africa.

3.2.1.3 TELEMETRY

SC/A06/HW42 reported the results from satellite tagging of 14 humpback whales (2 mothers with calves, 11 single adults and 1 juvenile) off Gabon (2°S, 9°E) between 29 August and 12 September 2002. Ten of the whales spent the entire time of their tags’ operation in what is believed to be the reproductive winter range. Six whales used the areas north of Gabon into the Gulf of Guinea. Eight of the 14 tagged whales that initially moved north then travelled south of Gabon – six into Angolan waters. Two tagged whales migrated along the same general route (Walvis Ridge) until they reached the Antarctic Convergence, where they diverged. The last received locations showed one animal in Area II and one in Area III, both just either side of the boundary between Areas II and III at 0°.

3.2.1.4 OTHER (e.g. LOST HARPOONS)

No information was provided under this item.

3.2.2 Stock structure

3.2.2.1 GENETIC INFORMATION (POPULATION LEVEL)

SC/A06/HW41 provided a sub-region analysis of mtDNA lineages from humpback whales sampled off the coast of Gabon (B1, $n = 466$) and from Cabinda and the coast of western South Africa (B2, $n = 166$). There was a significant sampling or sex bias toward males in the B1 sample, but an equal sex ratio was found in the B2 sample. Haplotype and nucleotide diversity were high. For the ocean basin AMOVA, significant differences were found among and within the four wintering Regions (A, B, C and X) for both Φ_{ST} and F_{ST}. Significant differences were found in pairwise F_{ST} comparisons between B1 and B2. When samples were partitioned by sex, no significant differences between B1 and B2 were found (only males considered). Using the program MIGRATE (Beerli and Felsenstein, 1999; 2001), a preliminary analysis of gene flow revealed that the interchange between Gabon and western South Africa is very low (approximately $1–2N_em$). Overall, there is clearly significant population differentiation between sub-regions B1 and B2 with some indication of dispersal (either historical or current) based on results from males only and estimates of gene flow. The degree to which whales show significant differentiation and still exhibit gene flow or movements between sub-regions within breeding stocks remains an important question for sub-stock differentiation in this region, and hence management.

SC/A06/HW38 presented a population structure analysis based on 11 microsatellite loci for 493 individuals sampled in Gabon (B1), 12 sampled in Cabinda, Angola (tentatively thought to be B2) and 110 off the west coast of South Africa

(B2). Significant differences were found in the AMOVA only when Cabinda was grouped with Gabon within B1; a significant difference was reported only for pairwise R_{ST} between Gabon and western South Africa. Although the sample from Cabinda was small, current data support a higher similarity between Gabon and Cabinda, than between Cabinda and western South Africa. Estimates of gene flow show that the expected exchange between Gabon and west South Africa is very low (*ca* $1N_em$). Two direct matches between Gabon and western South Africa (see Item 3.2.1.2), suggest that females breeding in B1 may use B2 as a migratory corridor and/or feeding ground.

Pomilla and Rosenbaum (2006) presented information regarding sex ratio and group composition in Gabon. Genetic sexing data collected for 405 individuals resulted in an observed sex ratio of 1.9:1 males to females. Most males were encountered in competitive groups and pairs. Females were more abundant than on other breeding grounds, however mother-calf pairs were under-represented. Of the pairs sampled, 8% were both females, 35% were both males and 57% were mixed sex; two female triads were found, as well as three instances of competitive groups that included two females. These data suggest that the coast of Gabon maintains some characteristics of wintering grounds, i.e. breeding may occur along the coast and extend into the Gulf of Guinea, rather than there being a concentrated breeding ground there.

In discussion, the different implications of the results from the Migrate program and F_{ST} statistics were raised. Pomilla summarised that mtDNA evidence supports a difference between samples off Gabon and South Africa, but the evidence from microsatellites was not as strong. It was also noted that the possible use of the B2 region by B1 females has implications for appropriate choice of grouping of samples.

3.2.2.2 OTHER INFORMATION (e.g. CPUE AND CATCH HISTORY)

Marked difference in crude CPUE indices from Gabon (French Congo) and other land stations off the African west coast were reported by Findlay (2001). While CPUE indices from the Cape, Namibia and Angola declined by 1917 and generally remained low until 1963, CPUE from Gabon showed initial declines by 1917 followed by three series of increases and associated declines between 1917 and 1963. Thus the available CPUE data provide some support for the the presence of more than one breeding stock.

3.2.3 Seasonal distribution

Information in SC/A06/HW53 suggests that some whales remain in low latitudes throughout the year. Findlay noted the differences in timing of catches off the west coast of southern Africa in that the catches from the Gulf of Guinea were during the austral winter, while catches off Namibia in the region of Walvis Bay were made in the austral summer. Animals caught off Namibia during summer were presumed to be feeding within the Benguela upwelling system.

3.2.3.1 WINTER

Available evidence and anecdotal records (e.g. SC/A06/HW10, SC/A06/HW38 and SC/A06/HW42; Rosenbaum and Collins (2006)) suggest a winter distribution for the B1 stock along the coasts of Angola (including Cabinda), Congo, Gabon, Equatorial Guinea (including Bioko), Cameroon, Nigeria, Togo, Benin and Ghana as well as around the offshore islands of São Tomé and Príncipe. Peak abundances are believed to occur in July, August and September although whales remain in the region into December. Throughout much of the Gulf of Guinea, the continental shelf is wide and survey effort has been limited to nearshore waters. Offshore distribution and distribution relative to depth remain unknown. Shore-based effort at Saldanha Bay during July and August of 2001 and 2002 yielded very low sighting rates for humpback whales when compared to summer months.

3.2.3.2 SUMMER

Behavioural evidence (feeding and defecation) along with regular and extended presence of whales during summer (as late as February), as well as the seasonality of historical catches, suggest that the west coast of South Africa (Saldanha Bay) functions as a possible winter migration corridor, but also as a summer feeding ground. This coincides with productivity associated with the Benguela upwelling system. There is no available information for summer abundances in the Gulf of Guinea but a degree of summer presence is suspected (Rosenbaum, pers. comm.). The limited telemetry data (SC/A06/HW42) on two animals showed that one marked near Gabon spent some time near Bouvet Island (*ca* 54°S, 3°E) while the other moved close to the ice edge. The last received locations showed the animals on either side of, but close to, the boundary between Areas II and III at 0°.

The analysis of mtDNA data in Annex E found significant differences between whales sampled from Breeding Stock B and those sampled in Area I (120°W–60°W) but no significant differences with samples from Areas II and III (60°W–70°E).

3.2.3.3 MIGRATION

SC/A06/HW42 revealed that migratory movements of tagged animals showed considerable heterogeneity and unexpected movements in terms of general direction (north vs south) and migration (inshore vs offshore) for both males and females. For the two tags that lasted the longest, both animals migrated along the same general route (but at different times) as far as the Antarctic Convergence, where their paths diverged.

3.2.4 Summary

There is some evidence for stock structure within Breeding Stock B on the African west coast. Some genetic difference between whales from Gabon and Cabinda and off western South Africa has been demonstrated. There is some recent evidence of breeding behaviour from Gabon, Angola, Cabinda, São Tomé, Equatorial Guinea and Congo to the north of the Walvis Ridge, and recent evidence of feeding behaviour, but no breeding behaviour to the south of the Walvis Ridge. Townsend (1935) shows evidence of historical concentrations of humpback whales in the Gulf of Guinea in winter and off Walvis Bay (Namibia) in summer. Satellite telemetry has identified movement from Gabon further northwards to Nigeria and into the Gulf of Guinea as far as Ghana; two animals migrated, primarily offshore, southward to the Antarctic. Summer presence of feeding whales within the Benguela Upwelling System suggests use of this region as a summer feeding ground. Catches of whales with full stomachs (clupeid prey) were made off western South Africa (Olsen, 1914). There is evidence of movement of two female whales (one nursing) from Gabon to western South Africa.

The Workshop **agrees** that, with a B1/B2 border in the vicinity of 18°S (where the Walvis Ridge meets the African

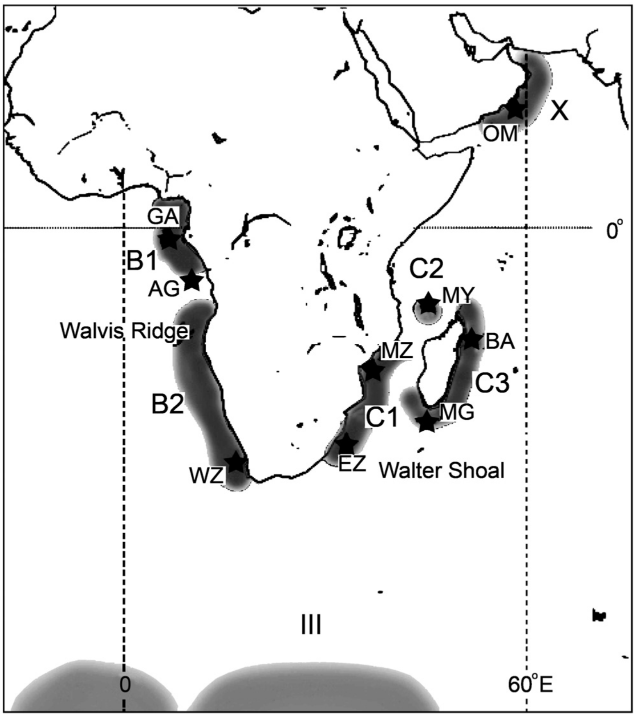

Fig. 3. Map with Breeding Stocks B, C and X and IWC Area III. Key: GA = Gabon; AG = Angola; WZ = western South Africa; EZ = eastern South Africa; MG = southern Madagascar; BA = Antongil Bay, Madagascar; MZ = Mozambique; MY = Mayotte and the Comoros; OM = Oman [taken from SC/A06/HW38].

coast and the Angola Current Benguela Current Front, see Fig. 3):

(1) B1 is a breeding ground; and
(2) B2 is a feeding ground and migration corridor within the productive waters of the Benguela upwelling system.

Some of the whales feeding within B2 breed within B1. The Workshop also noted that it is unclear whether subdivisions exists within B1. There is equivocal evidence for at least two breeding stocks on the western coast of Africa, and one of these clearly breeds in an area (perhaps only a portion) of B1; whether the other breeding stock(s) exist within the bounds of B1 or elsewhere remains unclear. The observed genetic differences among females between B1 and B2 may be explained by the existence of a second breeding stock which is sampled on migration in B2, but this is currently unknown. In order to try to resolve this question, two areas of work are required:

(1) further analysis of genetic samples to detect the signature of multiple breeding stocks (if these exist);
(2) surveys of other portions of B1 (notably off the Angolan coast).

The Workshop **recommends** that this be done (see Item 3.2.5).

3.2.5 Recommendations for future work

A consolidated set of recommendations for Breeding Stock B is given in Annex H.

3.3 Breeding Stock C (East Africa)

Three sub-regions have been postulated for Breeding Stock C: C1 (migrations along the east coast of South Africa up to breeding grounds off Mozambique and Tanzania); C2 (Mayotte Island, the Comoros Islands and other islands and reef systems of the Mozambique Channel); C3 (the coastal waters of Madagascar).

Table 4

Summary of information from artificial marks for Breeding Stock C.

	Breeding grounds	Putative feeding grounds (10°E–50°E)
Humpbacks marked (all marks)	8	249
Marks recovered	2	5
Origin of marks recovered	0	7
Movements to other Areas	0	0
Movement from other Areas	0	0

3.3.1 Individual movements

3.3.1.1 DISCOVERY AND OTHER ARTIFICIAL MARKS

Table 4 summarises the artificial mark information for Breeding Stock C (SC/A06/HW33). Two animals[4] marked in the putative feeding area (10°E–50°E) were recovered in breeding grounds (southern tip of Madagascar). Only eight whales were marked in the winter grounds of Breeding Stock C.

3.3.1.2 NATURAL MARKS (PHOTO-ID, GENETIC)

SC/A06/HW9 reported on mark-recapture studies (using fluke photographs) carried out between 2000 and 2005 in Antongil Bay, northeast Madagascar (C3). Within-year recaptures represented 6–18% of all individuals identified in a particular year. The mean intervals between first and last capture within a year ranged from about 3–8 days, suggesting short residency times within the Bay and high movement rates through the Bay and throughout the region. There were few recaptures between years (2.8% of all individuals within the study period). The timing of recapture of individuals showed marked periodicity such that most individuals were resighted in subsequent years within a few days of the sighting date in the first year.

In discussion, it was noted that the pattern of individual periodicity has important ramifications for both mark-recapture analysis and genetic sampling. Appreciable bias can be introduced if sampling is not temporally bounded so as to provide a representative sample.

SC/A06/HW12 reported on studies in the waters around and neighbouring Mayotte Island in the Comoros Archipelago within the northern Mozambique Channel (C2). Overall, the C2 sub-region is particularly data deficient regarding the occurrence and distribution of humpback whales, in that survey effort has largely been limited to Mayotte and the neighbouring Geyser-Zélée Reef Complex in the waters of the eastern Comoros Archipelago. To date, 113 tissue samples and 699 identification photographs of humpback whales have been collected and contributed to a photographic and genetic archive for C2. A total of 78 whales has been identified genetically and up to 250 photographically. Only four whales (all females) have been photographically or genetically recaptured in multiple years. The majority of humpback whale encounters in the waters surrounding Mayotte and the neighbouring Geyser-Zélée Reef Complex are mother-calf pairs (73%, n = 189), of which only 8% (n = 11) were accompanied by one or more (two) escorts. Competitive activity is rarely observed and

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[4] One at the western edge of this feeding ground at the boundary with the putative feeding area for Breeding Stock B.

there is only one record of a group composed of more than five whales. The photographic and genetic evidence suggests that eight individuals (6 males and 2 females) have moved between C2 and C3 (or *vice versa*) between years. Addressing the issue of differentiation between the C2 and C3 sub-regions will require additional survey and sampling effort across other areas of C2.

SC/A06/HW38 (and see SC/A06/HW12) reported three genetic matches (two females and one male) between Mayotte (C2) and northeast Madagascar (C3) based on 11 microsatellite markers. One additional match (one male) was found between northeast Madagascar and the east coast of South Africa (C1).

3.3.1.3 TELEMETRY

No studies have been carried out in this region.

3.3.1.4 OTHER (e.g. LOST HARPOONS)

The recovery of one harpoon tip (Olsen, 1914) provides evidence of linkage between Durban on the South African east coast (C1 migration stream) and Linga Linga in southern Mozambique (southern C1).

3.3.2 Stock structure

3.3.2.1 GENETIC INFORMATION (POPULATION LEVEL)

SC/A06/HW41 reported *inter alia* on a sub-regional analysis of mtDNA lineages from humpback whales sampled off southern and central Mozambique and eastern South Africa (C1, *n* = 151), from the islands of Mayotte and associated reef systems (C2, *n* = 78), and from the east coast of Madagascar (C3, *n* = 511). There was a significant sampling or sex bias toward males in the C3 sample and towards females in the C2 sample; an equal sex ratio was found in the C1 sample. Haplotype and nucleotide diversity were high. For the ocean basin AMOVA, significant differences were found among and within the four Breeding Stocks (A, B, C and X) for both Φ_{ST} and F_{ST}. Significant differences were found in pairwise F_{ST} comparisons between C1 and C3, and C1 and C2, but not for C2 and C3. When samples were partitioned by sex, no significant differentiation was found between C2 and C3 for males or females based on pairwise F_{ST} comparisons. When only males were considered, no regional sub-structure was found within Breeding Stock C. While still preliminary, the highest degree of effective migrants per generation (as inferred from the program MIGRATE) occurs from C3 to C2 and from C3 and C1. Overall, there is clearly some significant population differentiation between sub-regions C1 and C2 and C1 and C3 with some indication of dispersal (either historical or current) based on results from males only and estimates of gene flow. The lack of significant F_{st} and Φ_{ST} pairwise comparisons for C2 and C3 is consistent with microsatellite analysis and photographic and genetic capture-recaptures between these sub-regions (SC/A06/HW38 and SC/A06/HW12). The number of samples and time of sampling from C2 have been limited. A more complete analysis of whales in the C2 sub-region is needed to better evaluate the degree of connectivity of C2 and C3 sub-regions. The authors noted that the degree to which whales show significant differentiation and still exhibit gene flow or movements between sub-regions within breeding stocks remains an important question for management.

SC/A06/HW38 presented a population structure analysis based on 11 microsatellite loci for more than 800 individuals sampled in C1, C2 and C3. When sub-region partitions were tested, the AMOVA did not identify significant variation and the pairwise comparisons reported significant differences only between Northeast Madagascar (C3) and both sites within C1 (eastern South Africa and Mozambique), and between Mayotte (C2) and eastern South Africa. In contrast with F_{ST} and R_{ST} results, the highest estimate of gene flow (over evolutionary time) was reported between sub-Regions C1 and C3, but exchange of migrants was estimated also across all other boundaries. However, this may reflect the small size of the C2 population. Comparisons of microsatellite data by sex (F_{ST} and assignment indices) show that gene flow within Region C is not strictly male-biased and females may play an important role in mediating gene flow related to Mayotte or the east coast of South Africa. This finding is consistent with functional differences among the sites within this wintering region. The authors suggest that an overview of all the evidence suggests separation of C1, but not between C2 and C3.

Two papers made reference to sex ratio data. Pomilla and Rosenbaum (2006) presented information regarding sex ratio for Antongil Bay (C3). Genetic sexing data collected for 564 individuals resulted in an estimated observed sex ratio of 1 female to 2.4 males. SC/A06/HW12 reported on studies in the waters around the Geyser-Zélée Complex and neighbouring Mayotte Island in the Comoros Archipelago in the northern Mozambique Channel (C2). Of the genetically identified calves (*n* = 8), the sex ratio was 1:1 (*n* = 8), whereas for non-calves (*n* = 69), the sex ratio was 1 males to 3.6 females (reduced to 1 male to 1.87 females if the 26 mothers are excluded).

Genetic (mtDNA) analyses reported in Annex E found significant differences between whales sampled from Breeding Stock C and animals sampled in Area I, but no significant differences with samples from Areas II and III.

3.3.2.2 OTHER INFORMATION (e.g. CPUE AND CATCH HISTORY)

Marked difference exists in crude CPUE indices from (i) Natal and Mozambique and (ii) Madagascar. While the Natal and Mozambique CPUEs declined by 1915, CPUE off Madagascar remained relatively high until the early 1950s (Findlay, 2001).

3.3.3 Seasonal distribution

3.3.3.1 WINTER

Findlay *et al.* (2011) showed concentrations of humpback whales off the coast of Mozambique as far north as Mozambique Island (15°S) in August and September. The distribution of whales to the north of this region remains largely unknown, although incidental sightings of humpback whales are reported as far north as Zanzibar.

Along the east coast of Madagascar (C3), there are reports of whales from Fort Dauphin/Talagnaro in the southeast to Antongil Bay in the northeast (Rosenbaum *et al.*, 2001, SC/A06/HW9). There are concentrations off Isle St Marie (where there is a whalewatching industry) and Antongil Bay (where there has been a 10-year research programme). Concentrations have also been reported in August (the peak breeding season) between Toliara and Fort Dauphin, south of 22°S (Best *et al.*, 1998). There is a question as to whether whales along the east coast represent whales migrating to a final breeding destination or whether the coast represents an extended breeding area. Given the short residency/transience of whales in Antongil Bay (SC/A06/HW9) and concentrations of whales observed in August in the south, it is probable that there are whales distributed along (and continually moving along) the coast throughout the breeding season. On the west coast of Madagascar there are reports of whales from Toliara in the southwest to Nosy Bé in the northwest. Boat-based surveys have documented whales (including competitive groups) off Toliara into late October/early November, well after a decrease in the density of whales in Antongil Bay in the northeast. It is possible that there are concentrations of whales off Toliara, as well as further north up the west coast, for the entire season; however the relationship of these whales to those on the east coast is unknown and requires further research.

There are also winter reports of sightings and historical records from the coasts of the Comoros Archipelago, other island and reef systems in the C2 region, and the Mascarenes (Mauritius and Reunion).

The observed female biased sex ratio and rate at which mother-calf pairs are encountered (SC/A06/HW12) suggests that the eastern portion of the Comoros Archipelago (C2) may be preferentially sought out by pregnant or nursing females, although systematic survey effort in reef lagoon systems has only been possible late in the wintering seasons to reef lagoon systems.

In discussion on winter distribution and the relationship of C3 with C2, it was noted that the several between-year matches between Mayotte (C2) and Antongil Bay (C3), combined with the low rate of recapture between years in Antongil Bay, suggests that there is a strong connection between C2 and C3. The Workshop **recommends** that an analysis of capture probability is undertaken to assess whether there is random exchange between the C2 and C3 regions.

3.3.3.2 SUMMER

There is some indication of humpback whale concentrations on Star Bank and Walter's Shoal (south of Madagascar) in the months of November and December. Rosenbaum *et al.* (2001) reported that mother-calf pairs were prominent in the concentrations on Walter's Shoal. It is unknown whether these are late or non migrators. It could not be confirmed if these whales were engaged in feeding behaviour. There is at least one confirmed sighting of a mother with a calf off the coast of Mozambique in the month of February.

Although there is considerable sightings and catch information from the Antarctic feeding grounds, without better knowledge of the relationship between animals on the feeding and breeding grounds, it is not possible to detail the summer distribution in Antarctic waters (and see Item 3.9).

3.3.3.3 MIGRATION

Findlay reported that humpback whales reach the east African coast as far south as Knysna (33°S) as early as April and move northwards along the east coast of southern Africa to the coastal waters of Mozambique. Migratory behaviour is observed as far north as Cape Vidal (28°S), while incidence of song suggests that breeding behaviour largely begins to the north of this. Humpback whales migrate southward along the east coast of Africa as far south as Knysna in September, October and November.

The meeting noted that there had been little research effort expended on regions to the east of Madagascar. Rosenbaum indicated that the limited survey effort has shown humpback whales in Reunion and Mauritius at times similar to those when whales are seen in Antongil Bay (C3).

3.3.4 Summary

There is evidence of breeding in sub-region C1 from approximately 28°S to possibly as far north as Tanzania/Kenya, while a migratory corridor exists to the south of 28°S. Breeding also occurs off the Comoros Islands and Mayotte (C2), and in the coastal waters of Madagascar, although the relationship between whales on the east and west coasts of Madagascar is unknown. Recaptures of individuals provide potentially extensive connectivity between Mayotte (C2) and Antongil Bay (C3), and to a lesser extent (one individual) between the east coast of South Africa (1) and Antongil Bay. No evidence of connectivity exists for South Africa/Southern Mozambique (C1) and Mayotte (C2). One lost harpoon (Olsen, 1914) provides a link between eastern South Africa (Durban) and Southern Mozambique (Linga Linga). Genetic differentiation has been found between Antongil Bay (C3) and eastern South Africa/Southern Mozambique (C1), and between Mayotte (C2) and East South Africa/Southern Mozambique (C1), while no genetic differentiation is found between Mayotte (C2) and Antongil (C3).

On the basis of what is known of the stock structure of humpback whales off the east coast of Southern Africa, five potential sub-regions were identified.

(1) C1 South (C1-S) including eastern South Africa and Mozambique as far north as Mozambique Island (15°S).
(2) C1 North (C1-N) extending northwards from Mozambique Island to the northern limit of the range (southern Tanzania possibly into Kenya).
(3) C2 including Mayotte Island, the Comoros Islands and the Mozambique Channel.
(4) C3 around Madagascar.
(5) C4 extending across the Mascarene group of islands, including Mauritius and Reunion.

The Workshop **agrees** that delineation between C1-S and C1-N may be a cline rather than a definite line, although given the current deficiency of data to the north of Mozambique Island the border can currently be considered a latitudinal line in the region of Mozambique Island (15°S). The links described above suggest that C2 and C3 may not be separate.

Seven models of stock structure were considered (Fig. 4). The Workshop **agrees** that the most plausible is that linking C1-N and C1-S into one breeding sub-stock and the separate linking of C2 and C3 into another. The next most likely model links (1) C1-N and C1-S and (2) C2 and C3 while including some overlap between the C1-N and the combined C2/C3 sub-stocks.

3.3.5 Recommendations for future work

A consolidated set of recommendations for Breeding Stock C is given in Annex H.

3.4 Breeding Stock X (Indian Ocean)

3.4.1 Individual movements

3.4.1.1 DISCOVERY MARKS

There is no information from Discovery or other artificial marks for this stock.

3.4.1.2 NATURAL MARKS

Recent information on photo-identification is limited to data collected from Oman (SC/A06/HW48). A total of 64 whales was photo-identified in Oman during surveys conducted between 2000 and 2004. Of these, six individuals have been observed on at least two surveys, four on three surveys, one on four surveys and one on five. Individually identified whales were resighted in both the Gulf of Masirah and Dhofar at different times of the year and across survey years, indicating a high degree of residence off the coast of Oman.

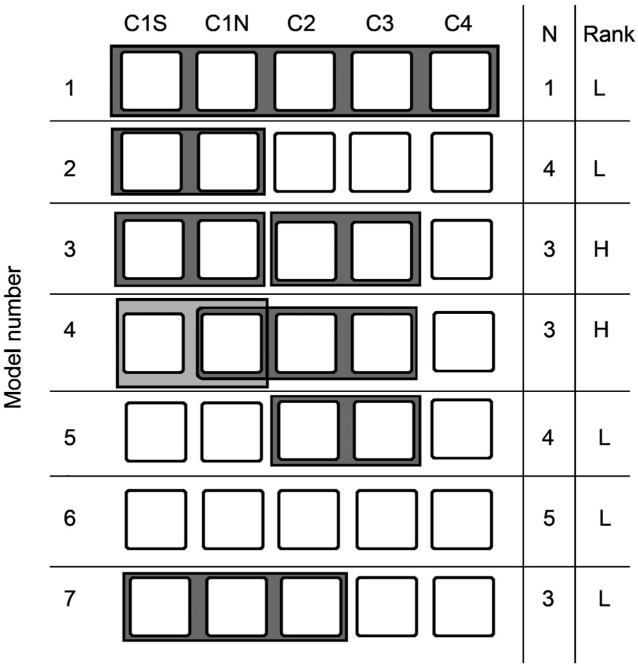

Fig. 4. Schematic diagram showing possible models for stock structure for east Africa. N = number of breeding stocks and Rank: L = low; H = high.

Resightings within surveys are few. Comparison of identified whales in the Oman catalogue with those from Zanzibar (*n* = 7), Madagascar (*n* = 1,104) and Mayotte (*n* = 185) yielded no matches (catalogues from April 2003).

SC/A06/HW38 reported the results of a genetic capture-recapture analysis of 34 individuals sampled off Oman and more than 800 individuals from Breeding Stock C. No matches were found.

3.4.1.3 TELEMETRY

No information was available.

3.4.2 Stock structure

3.4.2.1 GENETIC INFORMATION

SC/A06/HW38 and SC/A06/HW41 examined population structure for animals from Breeding Stocks X and C (its nearest geographical neighbour) using microsatellites and mtDNA, respectively. The results show significant differentiation between the two stocks for both markers, reflected both in the AMOVA and in the pairwise comparisons for F_{ST}, R_{ST} and ϕ_{ST}. Evolutionary gene flow estimated with the program MIGRATE is absent for mtDNA and limited for microsatellites. The program STRUCTURE sorted individuals from X into a separate cluster. All of the evidence suggests isolation of Breeding Stock X from the sampled sites in Breeding Stock C.

SC/A06/HW38 and SC/A06/HW41 also reported reduced genetic diversity within Breeding Stock X compared with reported diversity for other sampling sites for Breeding Stocks A, B and C. The reasons for such reduced diversity, as well as the origin of this stock, will be further investigated by the authors.

Both studies show a lack of gene flow between Breeding Stock X and Breeding Stock C, its nearest neighbour. Breeding Stock X has a strong genetic separation from all other areas to which it has been compared.

mtDNA data were examined to compare animals from Breeding Stock X with samples from feeding Areas I, II and III (Annex E). The significant differences found support the hypothesis that whales from Breeding Stock X do not migrate to southern high latitudes.

In discussion, Baker commented that the strength of the differences between Breeding Stock X and other Breeding Stocks was greater than that seen between other Breeding Stocks.

The Workshop **agrees** that the genetic information showed that animals from Breeding Stock X were reproductively isolated from the Southern Hemisphere Breeding Stocks.

Clapham commented that there were substantial Soviet catches in multiple areas of the Arabian Sea, and that they were probably from an Arabian Sea stock; although the population size in Oman is small and shows little sign of recovery, the lack of studies in other parts of the Arabian Sea prevent a definitive conclusion about whether any significant recovery at the population level has occurred or not.

3.4.3 Seasonal distribution

3.4.3.1 WINTER

Most of the available information (catch history and recent surveys) is limited to Northern Hemisphere winter months (September–March). Mikhalev (1997; 2000) reported on illegal catches of humpback whales across the northern Arabian Sea during October, November and December of 1966–1967. Of these 64 were taken in Oman, 164 in Pakistan and 12 in northwest India. Recent survey efforts have been limited to Oman and divided between two main areas, the Gulf of Masirah (central Oman) and Dhofar (southern Oman).

SC/A06/HW48 reviewed seasonal distribution and population characteristics of humpback whales off Oman. A higher proportion of whales is encountered in the Gulf of Masirah during early winter (September–December), with a shift in abundance to Dhofar during late winter (January–March). The Gulf of Masirah is a presumed feeding area. Sex was determined for 38 of 44 individually identified animals observed between October 2000 and November 2002 in the Gulf of Masirah and a 1:1 ratio of males (19) to females (19) was found.

A high incidence of singers and detected song was recorded in Kuria Muria Bay (Dhofar) in February and March and is consistent with the January–April breeding season predicted by Mikhalev (1997; 2000). Almost all (96%) of whales sampled during recent surveys in Dhofar in February and March were male (*n* = 28).

Observations of mother-calf pairs are sparse. None have been recorded since 2001 and competitive groups were absent. The high proportion of males observed in Dhofar in February–March, compared to the parity of sexes observed in the Gulf of Masirah in October–November, indicates that while the females are present in the Oman/Arabian Sea population, they are elusive or not present in the Dhofar region during February–March. Mikhalev (2000) also noted a paucity of mother-calf pairs in the Arabian Sea and only one mother-calf pair was observed during the hunt. The Soviet catch data do not provide more explicit details of catches by region, so it is impossible to determine whether pregnant females were found in the eastern Arabian Sea as opposed to off the coast of Oman. The ratio of males to females in the Soviet catch neared parity (126:112), so the paucity of mother-calf pairs in recent observations cannot be confirmed by bias in the Soviet catch toward females. It is possible that calving and nursing are taking place predominantly in other areas of the Arabian Sea. A suspected nursery area is the Gulf of Masirah. Weather conditions and logistic constraints have so far prevented planned surveys in the Gulf of Masirah in February and March.

3.4.3.2 SUMMER

Summer months coincide with the seasonal southwest monsoon. The monsoon generates large swells and dense coastal fog, making boat and shore-based observations difficult. It is highly probable that more active and regular feeding takes place between May and September, during the peak of upwelling. There have been few sightings in summer, presumably due to difficult weather conditions.

3.4.3.3 OTHER

The peak calving period is March, which indicates a Northern Hemisphere breeding cycle. However, it is also coincident with the monsoon-driven upwelling season, and calving may be tied more to food availability than to a Northern Hemisphere breeding cycle.

A mother-calf pair was recently reported from the Arabian Sea, in September. This is the first confirmed sighting of a mother and calf in the Arabian Sea since 2001 and is from a region for which no recent records exist. The size of the calf was consistent with a Southern Hemisphere breeding cycle.

3.4.4 Summary

The Workshop **agrees** that the evidence shows this to be an isolated population, resident in the Arabian Sea year round i.e. this is both a breeding and a feeding ground.

3.4.5 Recommendations

A consolidated set of recommendations for Breeding Stock X is given in Annex H.

3.5 Breeding Stock D (western Australia)

3.5.1 Individual movements

3.5.1.1 DISCOVERY MARKS

Table 5 summarises the artificial mark information for Breeding Stock D. A strong link was found between breeding (western Australia) and feeding grounds (Area IV). One animal marked in Area IV was recaptured on the east coast of Australia (Breeding Stock E).

Table 5

Summary of artificial marking information for Breeding Stock D.

Marking	Breeding grounds	Putative feeding grounds (Area IV – 70°E–130°E)
Humpbacks marked (all marks)	333	896
Marks recovered	41	29
Origin of marks recovered	16	42
Movements to other Areas	0	1*
Movement from other Areas	–	12** (approx 9% of whales marked in breeding stock E or Area V) were recovered in Area IV as far west as 113°E.

*Marked in Area IV and recaptured in eastern Australia. **In addition, 1 animal marked in Fiji was reported as recovered at 55°S, 87°E (western Area IV) by Soviet fleet – there is uncertainty surrounding this as it was reported as a fin whale.

3.5.1.2 NATURAL MARKS

Considerable photo-identification data have been collected off western Australia (see the metadata table available on the IWC website*). The Workshop **agrees** that it is extremely important to compare the major photo-identification catalogues from western Australia with catalogues from eastern Australia (see Item 3.5.5).

3.5.1.3 TELEMETRY

Telemetry studies are being undertaken for this area but as yet have not proved successful.

3.5.2 Stock structure

3.5.2.1 GENETIC INFORMATION

SC/A06/HW20 reported on a study involving a sample of 258 whale biopsy samples collected over 2002 and 2003 off North West Cape, Western Australia (along the migration route) which resulted in a male skewed sex ratio in both seasons. This area was selected because whales are in high density on the shelf there, and are therefore accessible for study. No sampling biases (towards sampling more males than females) could be detected from a multivariate test to identify relationships between the proportion of males and cue type, month, year, pod size, speed, sea state, swell, migration direction (including milling, north and south) and the various interactions. Given that measurements of sex ratio in Antarctica have shown evidence of fairly equal sex ratios, the authors suggest that further investigation is critical to ensure accurate estimates of population size are made.

There was considerable discussion within the Workshop as to whether the observed sex-bias (which has been seen on both breeding grounds and elsewhere) is real or just a bias in sampling for various reasons. It was noted that studies in Western Australia have previously found age and sex-structure in the migrating animals, so the timing of sampling could have an influence on the observed sex-ratio in the study presented in SC/A06/HW20. The issue is of particular relevance with respect to abundance estimation and how estimates relate to the total population. The issue is relevant to areas other than off western Australia.

The Workshop **agrees** that sex-bias has a potential to bias abundance estimates and thus inputs to the assessment models. It is less clear how a true skew in sex ratio in areas where catches occurred can be explicitly incorporated into the present assessment model which does not explicitly incorporate sex structure. With respect to the study reported in SC/A06/HW20, the Workshop **agrees** that there is still some uncertainty regarding possible heterogeneity of sexes across the area, given that biopsy sampling was limited to only a proportion of the area. This requires further examination.

The present state of studies using mtDNA data to examine population structure of humpback whales across the South Pacific and eastern Indian Oceans (New Caledonia, Tonga, Cook Islands, French Polynesia (Society Islands), Colombia and western Australia) was briefly summarised in the Workshop. A total of 1,113 sequences (470bp of the mtDNA control region) revealed 115 unique haplotypes based on 71 variable sites. Significant differences were found, at both the haplotype and nucleotide level, among the six breeding grounds ($F_{ST} = 0.033$; $\Phi_{ST} = 0.022$) and between most pair-wise comparisons. With respect to stock structure for Breeding Stock D, although the level of genetic differentiation between the western Australian samples and other areas is not high (due at least in part to the high haplotypic diversity that prevents F_{ST} values from being higher), there are significant genetic differences between western Australia and the areas to the east of Australia with which it was compared. However, whilst noting this

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* *http://www.iwcoffice.org/documents/sci_com/workshops/Table2.pdf* accessed October 2011.

conclusion, the Workshop **agrees** that a major limitation of this study is that no samples from eastern Australia were analysed (see Annex H).

3.5.2.2 OTHER INFORMATION

No additional information was presented.

3.5.3 Seasonal distribution

3.5.3.1 WINTER

It was noted that there were anecdotal records of humpback whales further north in Indonesia at approximately 8–10°S. The Workshop **recommends** that this anecdotal information be formally reported to the Scientific Committee and Bannister agreed to follow this up.

3.5.3.2 SUMMER

SC/A06/HW57 presented the results of JARPA (Japanese Research Programme in the Antarctic) sighting surveys in the waters south of 60°S in Areas IV and V. The research area was covered uniformly by systematic sighting surveys during the 1987/88–2004/05 austral summer seasons. Humpback whales were widely distributed in Area IV. The main concentration was between 80°E and 120°E in both northern and southern strata, i.e. on the eastern side of the Kerguelen Plateau. Apparent habitat expansion (from north to south) of humpback whales was observed in the longitudinal sector of the higher concentration between the first half of the JARPA survey period (1989/90–1996/97) and the second half (1997/98–2003/04). The average latitudinal position of the sightings was 60°30'S and 62°30'S in the two halves respectively. However, in discussion, the Workshop noted that the apparent expansion may reflect a combination of increase in density and some actual movement.

3.5.3.3 MIGRATION

SC/A06/HW21 reported on aerial and vessel based surveys conducted in each of the years 2000–2005 off North West Cape, Western Australia, along the migration route. In 28 aerial surveys and 38 boat surveys, a total of 3,466 humpback whales in 2,340 pods were sighted. Humpback whales were observed to migrate north past the study area during June and July, followed by a transition period in August. The southern migration past the study area occurred from September to November. Peak numbers were present in the study area during the transition period in August when approximately half of the whales observed were migrating either north or south. The majority of northbound whales migrated within the 300m isobath while southbound whales showed a preference for depths less than 200m. During the transition period, whales were most widely distributed over the area, with large numbers of whales observed offshore to the 1,100m isobath.

3.5.4 Summary

Recent information confirms earlier results, e.g. from Chittleborough (1965), with animals migrating northwards during winter from Antarctic Area IV along the west coast of Australia towards a current breeding ground destination as far north as 15°S (Jenner *et al.*, 2001) beyond North West Cape, Western Australia (*ca* 21°50'S, 114°10'E). The southerly migration takes place in late winter/spring. A few early northward migrating animals may reach the coast in April, but the main northbound stream arrives in June. Recent aerial surveys for southern right whales along the south coast between Cape Leeuwin, Western Australia and Ceduna, South Australia have recorded animals moving westwards until August, from as far east as Esperance (33°52'S, 121°54'E), with some stragglers reaching the coast even further east in the Great Australian Bight (Bannister, pers comm.). Catches off the south coast at Albany (35°01'E, 117°53'E) and off the west coast at Carnarvon (24°53'S, 113°40'E) and Point Cloates (22°43S, 113°40E), 1949–63 (Chittleborough, 1965; Dawbin, 1997), showed marked segregation during the northern migration, with sexually immature animals and mature females at the end of lactation in the vanguard, most adult males travelling in the middle of the period, pregnant females in the rear, and non-pregnant females being found throughout. On the southern migration, those first to arrive in warmer waters were the first to depart. Pregnant females, among the last to arrive from the south, having given birth were among the last to leave. Off North West Cape the highest numbers of animals, widely distributed, have recently been found in August at the time of transition between northern and southern migrations (SC/A06/HW21). Off Perth, Western Australia (31°57'S, 115°51'E) southbound animals are found mostly in September and October, with mother-calf pairs most commonly seen in November (Burton, 1991); humpbacks are generally not seen off the south coast after August, i.e. during the southern migration. The Workshop concluded that the question of a possible sex bias in migrating animals still remains to be resolved. In the Antarctic, the area of greatest concentration recently has been east of the Kerguelen Plateau, between 80°–120°E (SC/A06/HW57). There may have been some habitat expansion from north to south in that area in recent years.

3.5.5 Recommendations for future research

A consolidated set of recommendations for Breeding Stock D is given in Annex H.

3.6 Breeding Stocks E (eastern Australia) and F (Oceania)

3.6.1 Individual movements

3.6.1.1 DISCOVERY AND OTHER ARTIFICIAL MARKS

Table 6 summarises the artificial mark information for Breeding Stocks E and F.

There are strong links between Breeding Stock E and feeding grounds in this region. Animals marked in the breeding ground spread more widely in the feeding grounds that for any other breeding stock. Animals marked off eastern Australia were recovered as far west as 113°E in the Antarctic and one was recovered off Carnarvon, Western Australia (Breeding Stock D). There are links to the eastern

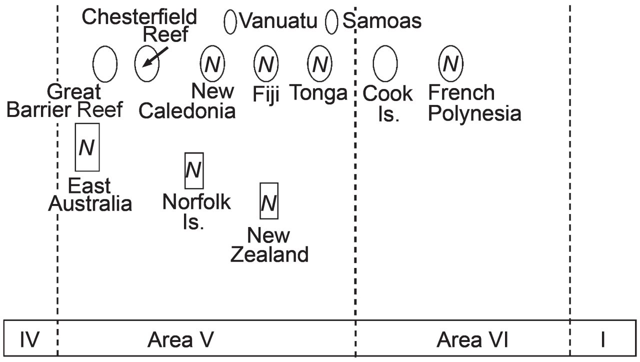

Fig. 5. Schematic map showing putative breeding grounds, migratory corridors and feeding areas of the South Pacific. Area V covers from 130°E to 170°W and Area VI from 170°W to 120°W. *N* = samples available.

Table 6
Summary of artificial marking information for Breeding Stocks E and F.

Marking	Breeding Stock E	Putative feeding grounds (Area V?)
Humpbacks marked (all marks)	2,712	664
Marks recovered	95	26
Origin of marks recovered	97	22
Movements to other Areas	9* (to Area IV), 3** (to Area I)	3 (movement to west to Area IV)
Movement from other Areas	1 movement from Area IV	1 movement from Area VI
Marking	**Breeding Stock F**	**Putative feeding grounds (Area VI?)**
Humpbacks marked (all marks)	7	66
Marks recovered	0	1
Origin of marks recovered	0	2
Movements to other Areas	0	1 movement to eastern Australia
Movement from other Areas	0	0

*1 animal marked in Fiji was reported as recovered at 55°S, 87°E (western Area IV) by Soviet fleet – there is uncertainty surrounding this as it was reported as a fin whale (see Item 3.5.1.1). **2 animals marked in Tonga were recovered at the western edge Area I – one of these marks was recovered from cooker.

Australia migratory corridor and New Zealand (interchange both ways). One whale marked in Fiji was recovered at eastern Australia (Tangalooma).

In contrast, no marks have been recovered linking Breeding Stock F with feeding grounds, but this reflects the very small sample size with only two animals marked on the breeding grounds and a total lack of whaling activity there.

3.6.1.2 NATURAL MARKS (PHOTO-ID, GENETIC)

There is a very considerable amount of photo-identification data for eastern Australia (Breeding Stock E) as indicated in the table of metadata available on the IWC website*. However, discussion at the meeting focused on papers examining photo-identification data from other areas relevant to Breeding Stocks E and F.

SC/A06/HW50 reported on photo-identification of humpback whales in New Zealand waters and their migratory connections to breeding grounds of Oceania. To help document the recovery of humpbacks in New Zealand and improve understanding of their migratory connections, photographs have been obtained opportunistically since 1994 and systematically since 2004. The catalogue of 34 whales has been compared with nearly 1,400 photographically identified individual whales throughout the wintering grounds of Oceania. To date there have been two whales resighted off New Caledonia, one resighted off Tonga and one New Zealand in different years. There have been no resightings from other regions in the same year. The connections with New Caledonia are consistent with recent genetic and song evidence suggesting a close relationship with this breeding ground. However the low rate of resighting in all available catalogues from Oceania (including New Caledonia) suggests that the primary wintering grounds for the New Zealand component of Breeding Stock E have yet to be identified. Systematic matching with a component of individuals identified from eastern Australia is planned for November 2006.

SC/A06/HW55 described the movement of individual humpback whales between winter breeding grounds of Oceania (South Pacific) documented by individual identification photographs collected from 1999 to 2004. The report extends previous comparisons for some of these regions (Garrigue *et al.*, 2002). Photographs were collected with comparable effort across the six years in four primary island breeding grounds: New Caledonia, Tonga (Vava'u) the Cook Islands and French Polynesia (Mo'orea and Rurutu) and with less effort in a few adjacent regions: Vanuatu, Fiji, Samoa, Niue and American Samoa. Catalogues from all regions were compared during annual meetings of the South Pacific Whale Research Consortium. For the six year period, regional catalogues of fluke photographs representing 1,148 annual sightings of 1,021 individual whales from Oceania were compared to investigate interchange between wintering grounds. Most resightings occurred within regions (e.g. see SC/A06/HW51) but 23 individuals were sighted in two regions (mostly adjacent) in different years, including interchange between Breeding Stocks E and F. One individual was resighted during the same year in two regions (Tonga and the Cook Islands), although a second was seen in two subregions of Tonga in the same year (Vava'u and Eau). No individual was sighted in more than two regions during the six years. The documented movement between regions was one-directional except for one individual sighted first in French Polynesia, then in American Samoa and then again in French Polynesia (in different years). No directional trend was apparent in the one-directional movement and movement between regions did not seem to be sex specific (although a sex bias could not be discounted).

SC/A06/HW19 noted that historically, humpback whales migrating through eastern Australia and New Zealand waters, and breeding off northeastern Australia, New Caledonia, Fiji and Tonga were assigned for management purposes to Antarctic Area V. So far within the current Comprehensive Assessment, humpback whales in these regions have been considered to be a part of Breeding Stock E. The paper reports on the relationship between the New Caledonia and Tonga breeding grounds, based on seasonal return and interchange of individual whales (photo-id and genotype-id), as well as population genetic differentiation (the latter is discussed under Item 3.6.2.1). The results showed significantly higher recapture probabilities within each breeding ground compared to the recapture probability between them, using both photo- and genetic-id.

SC/A06/HW49 described the results of an eight-year survey of humpback whales in the Cook Islands (South Pacific). At least 93 humpback whales were individually identified from tail fluke photographs. A separate catalogue uses the dorsal fin, scarring and underwater shots of lateral

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* *http://www.iwcoffice.org/documents/sci_com/workshops/Table2.pdf* accessed October 2011.

pigmentation. Although tail fluke matches have been made with neighbouring countries (7 with Tonga, 1 with French Polynesia, 1 with Niue, east of Tonga and 1 with American Samoa), the relationship of humpbacks in this region to those in adjacent tropical areas remains unclear. There have been no inter-annual re-sightings to date.

SC/A06/HW60 presented the results of research within French Polynesia. Using fluke photographs taken from 1990–2005, Poole identified 416 individual whales; there have been 37 inter-annual re-sights of 34 individuals. Identified whales were compared with those of New Zealand, New Caledonia, Tonga, Niue, the Cook Islands, Columbia, Ecuador and the Antarctic Peninsula. There has been one intra-annual resight between Moorea and the Cook Islands. Two inter-annual matches were found between French Polynesia and American Samoa; five matches with Tonga; and one with New Caledonia.

In discussion, the Workshop **agrees** that is was essential that a full comparison with catalogues for eastern Australia be undertaken as soon as possible. This is discussed further under Item 3.6.5.

3.6.1.3 TELEMETRY

No information is available for either Breeding Stock E or F.

3.6.1.4 OTHER (e.g. LOST HARPOONS)

No additional information was presented.

3.6.2 Stock structure

3.6.2.1 GENETIC INFORMATION (POPULATION LEVEL)

SC/A06/HW19 reported on the relationship between whales on the New Caledonia and Tonga breeding grounds, based on seasonal return and interchange of individuals (see Item 3.6.1.2 above), as well as on population genetic differentiation using mtDNA and microsatellite data. The analysis of mtDNA using samples from both regions after removal of replicates identified by microsatellite genotyping revealed significant differentiation. This was supported by a new analysis of microsatellite loci (up to nine), showing significant differentiation between the two regions. These analyses, and the previous report of demographic and reproductive isolation of New Caledonia (Garrigue *et al.*, 2004), demonstrate significant differentiation within Breeding Stock E. The authors conclude that the current Breeding Stock E must be subdivided into at least three stocks or substocks: one represented by the breeding grounds along eastern Australia (the Great Barrier Reef and perhaps Chesterfield Reef) referred to as E1; a second represented by New Caledonia (E2); and a third by Tonga (E3). They noted that the degree of isolation or interchange between these and other known wintering grounds, such as Vanuatu, Fiji and the Samoas, remains poorly described.

SC/A06/HW31 presented an analysis of the contemporary genetic diversity of New Zealand humpback whales, comparing mtDNA data (a 470bp of the mtDNA control region consensus sequence) with that from breeding grounds across the South Pacific (New Caledonia, Tonga, Cook Islands, French Polynesia and Colombia) and eastern Indian (western Australian) Oceans. A total of 30 samples collected around New Zealand, mostly during the northbound migration, was compared with 1,112 samples from breeding grounds. The analysis revealed 20 haplotypes in the New Zealand samples, all seen before in New Caledonia and some also in other breeding grounds. The New Zealand humpback whale haplotype diversity (h) was 0.97 ± 0.015, and the nucleotide diversity (π) was 2.18% ± 1.14%, similar to those from the compared breeding grounds, but they were significantly different only at haplotype level with the Cook Island, French Polynesia and Colombia breeding grounds. Significant differences were found only at haplotype level with the same three locations when a pair-wise AMOVA was performed. Three breeding grounds (western Australia, New Caledonia and Tonga) did not show significant differences at either nucleotide or haplotype levels. This genetic evidence and the available demographic data suggest a closer relationship of the New Zealand stock with New Caledonia and Tongan whales; however, the authors cautioned that because of the small sample size from New Zealand this should be considered a preliminary finding.

SC/A06/HW60 presented the results of research within French Polynesia. Analyses of sloughed skin (n = 101) resulted in a sex ratio of 1.5 males to 1 females; 22 haplotypes were found, few of which are shared with whales from other regions of the South Pacific. Based on genetic differences between and limited interchange with other regions of Oceania, the author considered that the whales of French Polynesia should be considered a distinct breeding stock, even from those of the Cook Islands, just 1,000km to the west.

Whilst welcoming these papers, the Workshop noted that despite the large number of samples available, there have as yet been no major genetic comparisons of the data from eastern Australia with samples from other parts of the South Pacific. The Workshop **strongly recommends** that such analyses be undertaken as soon as possible, since they are fundamental to understanding stock structure in these regions and in particular, may enable a reduction in the number of hypotheses in Item 3.6.2. This is discussed further under Item 3.6.3.

3.6.2.2 OTHER INFORMATION (e.g. CPUE AND CATCH HISTORY)

The meeting noted that CPUE series were available for certain areas, but considered that these did not provide information on stock structure *per se* for this region.

3.6.3 Seasonal distribution

3.6.3.1 WINTER

SC/A06/HW28 presented the results of a cetacean survey (visual and acoustic) in October in the waters of Independent Samoa in 2001. It revealed that humpback whales, including calves, are present at very low densities in the coastal waters of Samoa in October. The presence of calves and frequent singing indicates this is likely to be a small breeding area or migratory corridor to a breeding area.

SC/A06/HW49 described the results of an eight-year survey of humpback whales in the Cook Islands. Surveys were conducted at Palmerston Atoll, Aitutaki and Rarotonga during the austral winter months (June to October) from 1998 to 2005. Additional observations were made from the islands of Atiu and Mangaia. During 2,911 survey hours (over 563 days at sea), 522 humpback whale groups (846 animals) were recorded. All classes were observed, including singers, mothers and calves, mother/calf/escort trios and competitive groups. Although the Cook Islands region may represent a breeding ground for humpback whales, the low density of animals and the complete lack of inter-annual re-sightings to date suggest that it is not a central breeding location. These waters may well serve as a corridor for migrating humpback whales.

SC/A06/HW60 presented the results of research within

French Polynesia. Whales have been observed near at least 25 islands in all of French Polynesia's five archipelagoes, although sightings of whales in the Marquesas Islands are very rare and sightings within the Tuamotu Islands are not frequent. Calves represented 10% of all network sightings. During the austral winters of 1991–2005, boat surveys were conducted at Moorea in the Society Islands, and from 1999–2005 at Rurutu in the Austral Islands. Calves again represented approximately 10% of all whales. At Moorea, individual whales' residence times were usually limited to three days or less; at Rurutu, residence times for some individuals ranged from 2–6 weeks.

Humpback whales are thus known from at least seven areas in the South Pacific that are or may be breeding grounds: the Great Barrier Reef, Chesterfield Reef, New Caledonia, Tonga, Cook Islands, Samoa and French Polynesia.

3.6.3.2 SUMMER

SC/A06/HW57 presented the results of JARPA sighting surveys in the waters south of 60°S in Areas IV and V. The research area was covered uniformly by systematic sighting surveys from the 1987/88 to 2004/05 austral summer seasons. Humpback whales were widely distributed in Area V. It seems that there may be a boundary in the feeding grounds at around 130°–140°E. This sector is notable in that it includes the minimum distance between the Antarctic Continent and the southern boundary of the Antarctic Circumpolar Current. Whales in Area V were clearly distributed along the Pacific Antarctic Ridge where the southern boundary of the Antarctic Circumpolar Current is observed.

3.6.3.3 MIGRATION

There are three known migratory areas relevant to the currently designated Breeding Stock E: the eastern Australian coast, Norfolk Island and New Zealand. SC/A06/HW49 also suggested that Cook Islands waters may serve as a migratory corridor (and see Item 3.6.3.2).

Childerhouse reported on land-based sighting surveys undertaken during the northward migration in 2004 and 2005 at Tory Channel, Cook Strait in New Zealand over a two week period (18 June–3 July) each year. The purpose of the study was to investigate trends in abundance since whaling had ceased in 1964. Some 140 (2004) and 72 (2005) individuals were estimated to have migrated past during daylight hours; a crude analysis suggested that their numbers were at about 0.23 of the numbers in 1960.

3.6.4 Summary

Table 7 and Fig. 6 summarise the Workshop discussions concerning stock structure for Breeding Stocks E and F.

In discussion, it was noted that certain components of alternate models could not be excluded based on available genetic analyses and photo-identification comparisons.

The Workshop **strongly recommends** (see Item 3.6.5) that future analyses include:

(1) incorporation of samples from eastern Australia;
(2) consideration of possible yearly variation in the different localities;
(3) consideration of possible sex-bias in dispersal; and
(4) consideration of the possibility of replicate sampling of individuals.

With respect to point (4), it was noted that in breeding grounds in Oceania where this has been investigated (e.g. Tonga), it was not found to be a significant problem. Microsatellite genotyping is planned for other areas to ensure that this is not a problem for the rest of Oceania. Olavarria noted that analysis of yearly variation and sex-bias in mitochondrial DNA is underway.

3.6.5 Recommendations for future work

A consolidated set of recommendations for Breeding Stocks E and F is given in Annex H.

3.7 Breeding Stock G

3.7.1 Individual movements

3.7.1.1 DISCOVERY AND OTHER ARTIFICIAL MARKS

Table 8 summarises the artificial mark information for Breeding Stock G (SC/A06/HW33). There was no whaling effort and no whales were marked on the breeding grounds.

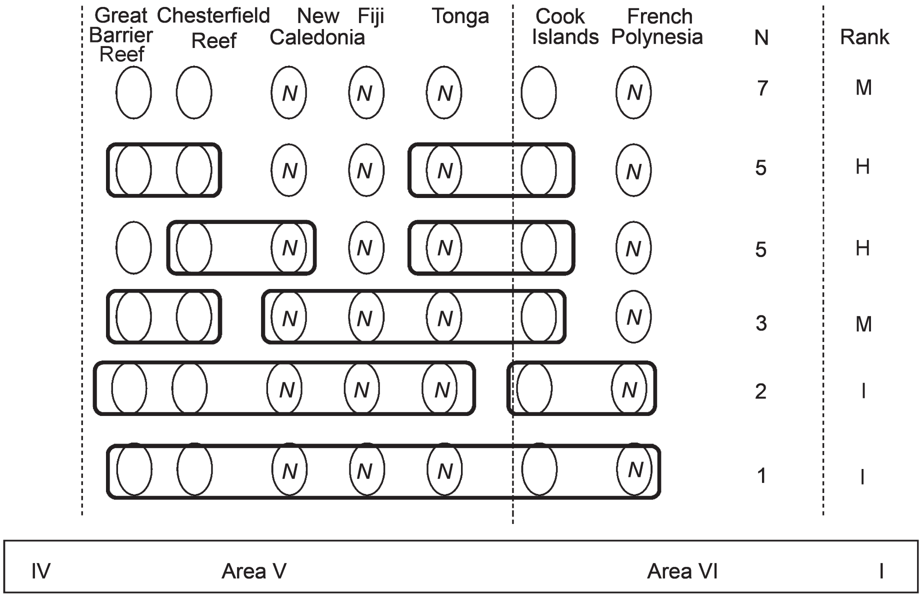

Fig. 6. Schematic diagram showing possible models for stock structure in the South Pacific. N = number of breeding stocks and Rank: L = low; M = medium; H = high.

Table 7a

Models of stock structure for breeding grounds (EA = east Australia [includes Great Barrier Reef except in Model 1]; CR = Chesterfield Reef; NC = New Caledonia; Tg = Tonga; CI = Cook Islands; FP = French Polynesia) of the South Pacific. Key: ++ = strongly supports; + = is consistent with; ~ = evidence is ambivalent or uninformative; – = evidence is inconsistent with; – – = contradicts.

Model	1	2	3	4	5	6
No. breeding grounds	7	5	5	3	2	1
	All separate	{EA-CR}; {NC}; {Tg-CI}; {FP}	{EA}; {CR-NC}; {Tg-CI}; {FP}	{EA-CR}; {NC-Tg-CI}; {FP}	E-F separation	All pooled
Rate of increase	+	+	+	+	– –	– –
Genetic differentiation	+	++	++	–	–	– –
Acoustics	+	+	+	–	–	–
Photo-id return	+	+	+	–	–	– –
Photo-id interchange	–	–	–	+	–	+
Discovery marks	~	~	~	~	–	–

Table 7b

Summary of the evidence used to construct Table 7a.

Rate of increase	There are at least 3 sites that are on migratory corridors for these populations. The east coast of Australia is almost certainly related to whales migrating to the Great Barrier Reef and possibly Chesterfield Reef. It has a 2004 abundance estimate of 7,090 whales and an annual rate of increase of 10.6% (SC/A06/HW27). Norfolk Is. has shown very little sign of recovery with current sighting rates of ~1/30 cf. those in the 1950s (SC/A06/HW36). Similarly, sighting rates from New Zealand are lower than in the 1950s (Childerhouse, pers. comm.). It is not known which breeding population or populations were related to the Norfolk Is. or New Zealand migratory routes although the lack of recovery is similar to that of Fiji.
Genetics	mtDNA differentiation rejects random intermingling of the four primary Oceanic regions, suggesting instead some degree of maternal fidelity (SC/A06/HW42; Olavarria *et al.*, 2006). Comparison with eastern Australia or Chesterfield Reef does not exist but should prove very informative. Nuclear DNA rejects panmixia of NC and Tonga. Information unavailable for other pair-wise comparisons. Paternity inference (gametic recapture analysis) suggests relative reproductive autonomy of New Caledonia – SC/A06/HW19, Garrigue *et al.* (2004); Baker *et al.* (2005) – but see Palsbøll *et al.* (2005).
Photo-id return	Photo-id returns suggest a reasonably high level of fidelity to primary breeding grounds (New Caledonia, Tonga, and French Polynesia) as reflected in relatively small estimates of abundance (SC/A06/HW51, SC/A06/HW52, SC/A06/HW60, Garrigue *et al.*, 2004). Few cases of documented interchange in the same winter season (SC/A06/HW55).
Photo-id interchange	Photo-ids suggest low, but detectable, levels of interchange or dispersal between neighbouring populations in Oceania with very low levels of movement among more distant populations across (SC/A06/HW55, SC/A06/HW60). There are several instances of movements between E and F (e.g. SC/A06/HW55). A very important gap is the lack of comparisons between eastern Australia and elsewhere.
Discovery marks	Discovery marks demonstrate a low level of dispersal among breeding grounds against a background of a higher level of fidelity demonstrated by photo-id. They also display some level of longitudinal movement on the feeding grounds compared with breeding grounds (SC/A06/HW33).
Acoustics	Song recordings demonstrate some similarity between Eastern Australia, New Caledonia and Tonga indicating there is some level of connection (probably inter-year dispersal) between these populations. They also demonstrate differences between these populations that suggest this connection is at a low level. Further investigation required to document rate of change across eastern Australia to Oceania (Helweg *et al*., 1998).

3.7.1.2 NATURAL MARKS

SC/A06/HW08 described a photo-identification study carried out between 1991 and 2004 off Ecuador (1°S, 80°W), during which 1,064 humpback whales were identified. 76 (7.14%) of these were resighted off Ecuador between these years. The longest span between capture and recapture was 11 years for one individual. 61 (5.71%) were individually identified within the same year. The maximum period within season between first and last recapture was 50 days, while the minimum was 1 day.

In discussion, it was noted that Columbia and Ecuador are the main wintering areas along the west coast of South America, and a previous study had provided photo-identification matches between Columbia, Ecuador and Panama (Flórez-González *et al.*, 1998), suggesting there is no differentiation between these areas.

3.7.2 Stock structure

3.7.2.1 GENETIC INFORMATION

SC/A06/HW29 presented the results of an investigation of the genetic (mtDNA control region sequences) relationship between humpback whales from the two summer feeding areas that have been linked to Breeding Stock G, the Antarctic Peninsula and the Magellan Strait. A total of 89 samples from the Antarctic Peninsula and 52 from the Magellan Strait areas were compared using an AMOVA analysis; significant differences were found between these two feeding areas to the haplotype (F_{ST}) and nucleotide (Φ_{ST}) levels. Comparison of these two feeding areas with breeding grounds of the South Pacific and the Indian Ocean revealed significant differences for each pair-wise comparison except for that between Colombia and the Antarctic Peninsula. The authors suggest that the genetic information, allied to that from the photo-identification link between the Antarctic Peninsula and Magellan Strait, reveals heterogeneity in the feeding areas of this Breeding Stock.

3.7.3 Seasonal distribution

3.7.3.1 WINTER

SC/A06/HW15 presented information on a survey (742km) undertaken in the central and southern parts of the Galapagos archipelago (1,000km from mainland Ecuador) between the 31 August and 10 September 2005 aimed at examining humpback whale presence, distribution and relationship to

Table 8

Summary of artificial marking data for Breeding Stock G.

Marking	Breeding grounds	Feeding grounds (Area I)
Humpback marked (all marks)	0	131
Marks recovered	0	4
Origin of marks recovered	0	4
Movements to other Areas	1* marked: 62°S, 116°W (Area I). Recovered: 28°S, 45°W (Stock A)	0
Movement from other Areas	0	2** marked in Tonga (breeding stock E(i)) recovered in Area I (west edge)

*Recovered in cooker and may (anecdotal) have been taken in the South Pacific. **One recovered in cooker.

other stocks in the South Pacific. Only one mother with a newborn calf was seen, giving an encounter rate of 0.27 whales/100km of survey. No sounds were recorded from 25 hydrophone stations. The adult female was biopsied and an mtDNA comparison with six animals from mainland Ecuador and other South Pacific areas undertaken. Four different haplotypes were defined, all previously described only in the Southeastern Pacific population. The Galapagos specimen had a haplotype found in one individual biopsied off Colombia, thus establishing some degree of relatedness with the mainland stock. The authors suggest that while there is evidence that the Galapagos Islands is occupied as a breeding area, the low density recorded suggests that the population is small.

Castro noted reports of cows and calves sighted from naturalists' cruises off Isobela Island in the Galapagos Islands from January to March. The timing of these sightings is unusual here and it was speculated that these may be Northern Hemisphere whales, perhaps connected to Costa Rica and Panama. Genetic studies (Baker *et al.*, 1998) suggest that there has been at least historic (perhaps during the last ice age) exchange between the eastern North and South Pacific humpback whale populations. There is also a match of an individual whale from Magellan Strait to Costa Rica (and back to Magellan Strait) with relatively few photographs from either area, there is thus the possibility that the northernmost whales on the feeding grounds (Magellan Strait) migrate furthest north to Costa Rica, passing through the breeding grounds in Ecuador and Columbia. There is considerable exchange between Ecuador and Columbia (Félix and Haase, 2005; Félix and Haase, 2001).

3.7.3.2 SUMMER

SC/A06/HW29 compared mtDNA control region sequences from 89 samples from the Antarctic Peninsula and 52 samples from the Magellan Strait areas. An AMOVA showed significant differences between the two feeding areas. Genetic and demographic data (based on photo-id) strongly suggest that both feeding areas are related to the same breeding grounds (Columbia and Ecuador) but that heterogeneity exists among the feeding areas, similar to that observed in North Pacific and North Atlantic humpback whale populations.

3.7.4 Summary

The Workshop noted the following.

BREEDING GROUND INFORMATION

(1) Genetic evidence of differentiation of Breeding Stock G (Colombia) from other breeding grounds in the Southern Hemisphere, including its nearest neighbours, A and F.
(2) Photo-id evidence of differentiation of South Pacific (E, F) Breeding Stocks and neighbouring Breeding Stock A (based on lack of movement between E/F and A).
(3) Evidence of historical and current distribution on wintering grounds off Ecuador and Colombia, but also extending north to Panama and Costa Rica.
(4) Some suggestion of differentiation within Breeding Stock G, in northern (Costa Rica/Panama) and southern (Colombia/Ecuador) areas, based on differentiation (photo-id and genetics) between feeding areas (see below).

FEEDING AREA INFORMATION

(1) Historical and current distribution of Breeding Stock G animals in Area I off the west coast of the Antarctic Peninsula, including South Shetland Islands.
(2) Current distribution during summer in the Magellan Strait and adjacent channels and fjords, in south-eastern South America (genetic and photo-id evidence shows strong differentiation between the two feeding areas).
(3) Satellite tagging shows residence off the Antarctic Peninsula during summer season.

MIGRATORY LINKAGE

(1) Some evidence from Discovery marks of movement between Breeding Stock E (Tonga) and the Antarctic Peninsula, but one mark was found in a cooker.
(2) Genetic evidence of a non-significant difference between the Antarctic Peninsula and the Colombian breeding area, but significant differences between it and the South Pacific (Breeding Stocks E, F) and Indian Ocean (D) and South Atlantic (A) breeding grounds.
(3) Genetic evidence shows a significant difference between the Magellan Strait area and the South Pacific (Breeding Stocks E, F and G) and the Indian Ocean (D).
(4) Photo-id analysis shows strong evidence for a linkage between the Antarctic Peninsula and Breeding Stock G and a lack of linkage with the South Pacific (Breeding Stocks E, F) and South Atlantic (A).
(5) Photo-id shows strong evidence for linkage between the Magellan Strait and Breeding Stock G.

CONCLUSION

Although the possibility of modelling the Magellan Strait feeding area as a separate stock was raised, given the lack of strong evidence for this and any information on a link to breeding grounds, the Workshop **agrees** that Breeding Stock G should be modelled as a single stock.

3.7.5 Recommendations for future work

A consolidated list of recommendations for Breeding Stock G is given in Annex H.

Table 9

Evidence for stock structure for breeding stock G.

Hypothesis	1 breeding stock	>1 breeding stocks
Rate of increase	~	~
Genetic differentiation	~	~
Acoustics	~	~
Individual interchange	+	~
Catch data	~	~
Total evidence	+	~

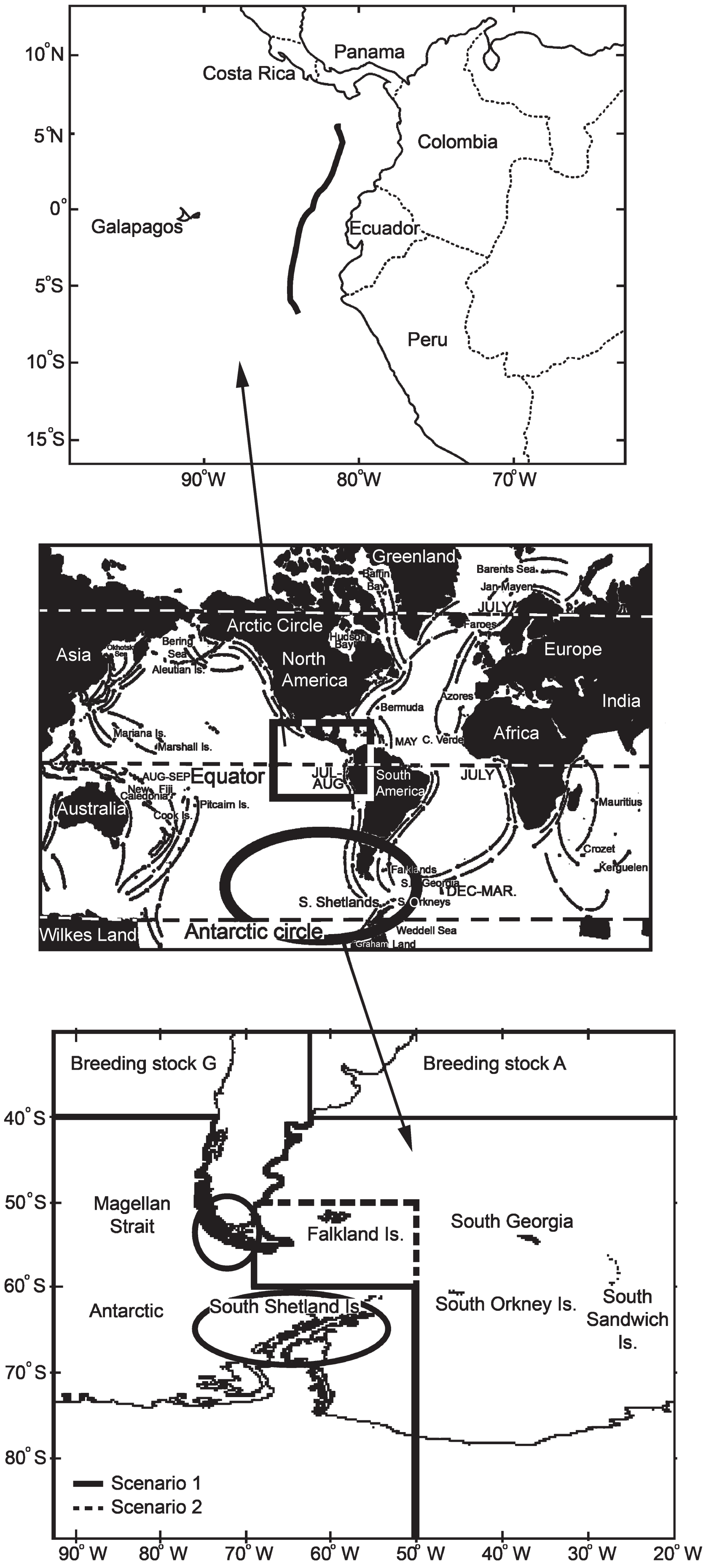

Fig. 7. Map showing possible links with feeding grounds for Breeding Stock A (see text).

3.8 Overall population structuring

3.8.1 Breeding grounds

SC/A06/HW41 presented an mtDNA analysis of humpback whale population structure from Breeding Stocks A, B, C and X. A total of 1,489 individuals was examined (130 of these were not genotyped and may have contained duplicates). Samples were stratified by sex and year for some regions. AMOVA analyses showed significant differences in all strata across all compared regions (A, B, C and X). Most pairwise comparisons using F_{ST} and M_{ST} were also significant. Preliminary analysis using MIGRATE gave the highest degree of migrants from B to A, but interpretation of this remains equivocal. Lack of, or low, gene flow was indicated between C3 and B2, and between C and X (and X and C in the other direction). Overall, the results suggest significant differentiation between breeding stocks in different ocean basins, although there appears to be some overlap between B and C.

SC/A06/HW38 used microsatellites to examine population structure among the same four breeding stocks. A much lower level of structure was found than in the mtDNA analysis, but significant differentiation among regions was found; the differences were bigger between A and B than between B and C. Some evidence was presented to suggest further substructure among B and C, and the suggested divisions did not correspond to the ones currently in use. Assignment indices and F_{ST} estimates for males and females were consistent with a scenario of male-biased dispersal (and therefore gene flow). Estimates of dispersal rates overall suggested high numbers of effective migrants per generation exchanged between adjacent wintering regions, as well as within regions. The detection of movement in genotypically identified individuals further suggests ongoing gene flow across existing stock boundaries.

SC/A06/HW59 presented a preliminary mtDNA analysis using a large sample set (total number of sequences = 2,683) from all recognised regions (i.e. A–G and X), and as such represented the first comprehensive comparison of all Southern Hemisphere humpback whale breeding stocks. AMOVA and F_{ST} comparisons showed significant differences between all regions and sub-regions, except between regions C2 and C3. The latter finding is consistent with other analyses presented at the Workshop, and the overall finding of differentiation elsewhere is broadly in agreement with existing stock structure concepts for Southern Hemisphere humpback whales.

Africa (B and C)

The Workshop considered stock structure for the breeding grounds off Africa (B and C).

With regard to possible links between Breeding Stocks B and C, one individual has been identified and genotypically identified in both areas (Pomilla and Rosenbaum, 2005). It was also noted that there was broad similarity in song between A, B and C (Darling and Sousa-Lima, 2005, Cerchio, unpublished data). Song is regarded by some as an overly sensitive indicator of dispersal in that a relatively small amount of male dispersal across regions can result in similarity, and as a result the utility of song in assessing population differentiation is limited. Furthermore, it is possible that song exchange occurs not by male dispersal across different breeding grounds but through mixing on migration or on a common feeding ground.

Some of the nuclear genetic analyses presented in SC/A06/HW38 do indicate a degree of mixing between B and C. However, given the clear separation shown in (female-mediated) mtDNA, the sex (male) of the one whale known to have moved between regions, and the similarity of (male-mediated) song, the most parsimonious explanation is that exchange between B and C primarily involves males.

Conclusion

It was noted that a very considerable amount of work had gone into producing the genetic data presented at the Workshop, and that some of this information was the result of intensive last-minute analysis. It had not been possible to fully evaluate such a large amount of work in such a short time. It looked forward to receiving a consolidated summary of the analyses at the next meeting of the Scientific Committee, and requested that this also include a table summarising pairwise comparisons between other breeding grounds. It was also suggested that additional analytical methods might be explored to examine structure, such as those being considered by the TOSSM program (IWC, 2007a).

3.8.2 Feeding grounds

SC/A06/HW40 provided the results of a genetic study based on biopsy samples from 411 humpback whales obtained during surveys of the Japanese Whale Research Program under Special Permit (JARPA) and the International Decade for Cetacean Research/Southern Ocean Whale and Ecosystem Research (IDCR/SOWER). The study was conducted to describe the genetic population structure of humpback whales on their Antarctic feeding grounds. Samples were obtained from the feeding grounds in Areas III ($n = 81$), IV ($n = 172$), V ($n = 97$) and VI ($n = 61$), and were examined for (1) sex, (2) the sequence variation of the first 334bp nucleotides of the mtDNA control region and (3) genetic variation at the genotypes of six microsatellite loci. Duplicate samples were excluded from the analysis. The level of genetic diversity in the Antarctic was high for both genomes: the nucleotide diversity at the mtDNA was estimated at 0.0263 and the mean expected heterozygosity at the nuclear loci at 0.7820 for the total samples. In general, results based on both mtDNA and microsatellites were similar and suggest population structure of humpback whales in the Antarctic feeding grounds. These genetic results are consistent with the previous view based on non-genetic data that Areas III, IV, V and VI are occupied by different populations. Marked differences were found between whales in Areas IV and V for both mtDNA and microsatellites, and the same pattern was found for both sexes. Results of the other pair-wise comparisons among Areas showed more subdivisions for females than for males. One explanation for this result is that the difference is due to the lower sample sizes for males in these comparisons. The possibility of intermingling of populations in bordering sectors cannot be discarded yet, and a comprehensive analysis that involves genetic data from low and high latitudes is recommended to resolve this issue. The authors also noted that they could not comment from their data on relationships between feeding and breeding areas, and recommended that a comparison between samples from the two regions should be a high priority for further work.

The Workshop welcomed this analysis from the feeding grounds. In discussion, it was noted that few biopsy samples were collected from the longitudinal sector near the division between Areas IV and V, which also coincides with a gap in sighting distribution (SC/A06/HW57). It was also noted that krill is not abundant in that particular sector.

SC/A06/HW57 provided information from JARPA surveys on the distribution of humpback whales in Areas IV and V, in waters south of 60°S. Humpback whales were widely distributed in both Areas, with a major concentration between 90° and 120°E, and wide dispersal in other parts of Area IV. An apparent habitat expansion was observed between 1989/90–1996/97 and the latter half of the surveys in 1997/98–2003/04. However, in discussion it was noted that the apparent expansion may result from a combination of an increase in density and some actual movement.

Pastene reported a single case of a molecular marker match for a female humpback whale first sampled in the western part of Area V (January 1995) that was subsequently re-sampled in the eastern part of Area IV (January 2000) (Pastene *et al.*, 2000).

A question was raised regarding whether the boundary of Area V (assuming this represents a stock) should be moved to 120°E (from 130°E). It was noted that this was consistent with Discovery mark data, and it was suggested that east Australian whales were indeed moving further to the west than the current boundary of Area V. However, given that the region between 120° and 130°E was identified as a high-density area in the JARPA surveys, it is possible that mixing occurs in this region between whales from Areas IV and V. Omura (1953) examined the distribution of humpback whales in the feeding grounds of Areas IV and V based on catch data. He suggested that two populations occur in these Areas with a boundary around 130°–142°E. He did not discard the possibility of intermingling between these two populations in the feeding grounds. He also examined the pattern of catches by month, and suggested that for the months where more data were available (November–March), the boundary between these two populations changed from 120°–130°E in November to the east of 140°E in December and to 120°–140°E in January.

SC/A06/HW26 presented analyses of mtDNA and microsatellites to address the question of structure and diversity of humpback whales in Areas I, II and III. High diversity was found in all areas in both genomes. Differences were found between Area I and both II and III; the two latter Areas were not easily differentiated, suggesting mixing between them. This conclusion is limited by the current small sample size, and it was suggested that the consequent power of the analysis to discriminate differences in populations was low, and required further work, notably using recently collected samples from IDCR/SOWER cruises. The results suggested substructure even at a fine scale in Area I, and that different breeding populations may mix in Areas II and III.

The Workshop noted that a further 71 biopsy samples were collected from the 2005/2006 SOWER cruise. It **recommends** that IDCR/SOWER samples be made available as soon as practicable. It was subsequently noted that owing to issues with CITES permits, it would not be possible for further analyses to be conducted prior to the 2006 Annual Meeting.

SC/A06/HW29 found significant genetic differences between two feeding areas, one off the western coast of the Antarctic Peninsula and another in the fjords and channels of Chile (the Magellan Strait area).

3.8.3 Linkages between breeding and feeding grounds

An analysis conducted at the Workshop by Loo and colleagues (Annex E) examined genetic differentiation between samples from Breeding Stocks A, B, C and X, and feeding Areas I, II and III. The analysis suggested that animals found in Area I are genetically isolated from Breeding Stocks A, B, C and X. Differentiation of Area I is consistent with the current knowledge that individuals summering in this Area migrate to the western coast of South America, with a lack of evidence of mixing of this population with other southern groups.

Humpback whales wintering in Region X are believed to comprise the only population that does not undertake the characteristic seasonal migration observed in this species. The results of this analysis, depicting a clear lack of gene flow between Breeding Stock X and all feeding areas, supports this hypothesis.

The lack of significant differences for comparisons between animals from Breeding Stocks B and C and Areas II and III suggests that whales feeding in any of these two Areas may use either wintering regions, the degree to which remains uncertain. The data cannot, however, rule out ancestral polymorphism presence, or historical gene flow causing this lack of differentiation.

Animals from Breeding Stock A show conflicting results from different tests with respect to connection to Area II, probably due to the fact that the Area II sample included samples collected around the South Sandwich Islands and Bouvet Island, while previous data so far support connection of Breeding Stock A only to the South Sandwich Islands (Zerbini *et al.*, 2006, SC/A06/HW11). Further work will be conducted to compare Area IIW and IIE samples separately as in SC/A06/HW26. Sub-Region B1 does not show significant differences from Area II, whereas sub-Regions B2 and C1 do not show differentiation from Areas II and III, and sub-Regions C2 and C3 are not significantly differentiated from Area III.

The opportunistic basis of the sample collection on the feeding grounds, as well as the small sample sizes presented, suggest some caution in the interpretation of these results. The authors noted that the results are highly preliminary and more detailed analysis and exploration of scenarios will be explored in a forthcoming paper using mtDNA and 11 microsatellite loci. To increase the power of the analysis, all available IDCR/SOWER samples are needed (see the recommendation under Item 3.8.2).

In summary, the results of this preliminary study support:

(i) significant genetic differentiation between Area I and Breeding Stocks A, B, C and X;
(ii) significant genetic differentiation between Breeding Stock X and Areas I, II and III;
(iii) significant genetic differentiation between Breeding Stock A and Area III, but an uncertain degree of differentiation between Breeding Stock A and Area II, because of the low sample size for Area II (and combining IIE and IIW);
(iv) no significant differentiation between Areas II and III with respect to Breeding Stocks B and C; and
(v) the conclusion that the newly proposed Feeding Area B2 shows no significant differences in pairwise F_{ST} with Area II and III, but a significant difference with Area I.

The genetic analysis in SC/A06/HW29 indicated strong links between the Antarctic Peninsula and Colombia; in contrast, there was no apparent link between the feeding grounds in the Magellan Strait and sampled areas off the west coast of South America. It is possible that the Magellan Strait population is related to animals from the north of Colombia (potentially including Central America), but it is not possible to assess this on current evidence (see Item 3.7).

The Workshop noted the great value in undertaking genetic analyses of animals from both the breeding and feeding grounds. It **recommends** that every effort be made for scientists to share data and carry out such analyses. It noted the positive discussions being held by Baker, Pastene and Rosenbaum in this regard, under the IWC Data Availability Agreement, and looks forward to their successful conclusion and the submission of one or more analyses to the Committee.

Rock *et al.* (2006) examined photographic evidence documenting the movements of three individuals between their breeding grounds on the northeast coast of Australia (Breeding Stock E) and feeding grounds in Area V. Photo-id pictures from low latitude breeding grounds and high latitude feeding grounds (obtained during JARPA surveys) had been submitted to the Antarctic Catalogue. Although these individuals exhibited marked site fidelity to the same low latitude breeding ground, their sightings in high latitude feeding grounds vary by 35° longitude, confirming dispersal of Breeding Stock E whales in the Antarctic feeding grounds of Area V. These results are generally consistent with existing knowledge about the migratory destinations of humpback whales migrating and breeding off the eastern coast of Australia.

Rock *et al.* (2006) also reported the case of one individual photo-identified twice in Antarctic Area VI. The individual was first sighted during an IDCR/SOWER survey (3 January 1991 at 64°56'S; 171°43'W), and again six years later at a similar geographical position during a JARPA survey (1 January 1997 at 65°33'S; 167°29'W).

3.9 Conclusions on stock structure

It was clear from discussions and data presented during the Workshop that the level of confidence associated with stock structure concepts varies considerably across the Southern Hemisphere. In some areas (e.g. Breeding Stock A and Area II) the connections between breeding and feeding grounds and the structure within them are reasonably well understood; in such cases discussion focused largely on the extent to which boundaries should be expanded or contracted in variations of model runs. In others (e.g. Breeding Stocks B, C, E and F), there is considerable unresolved complexity and insufficient data to discriminate among a variety of stock structure hypotheses. There was much discussion of how the boundaries of each stock should be shifted, and accordingly of how the 'core' and 'fringe' areas for some of the stocks should be defined for the purpose of catch allocation.

Stock A

The Workshop **agrees** that the most plausible hypothesis is that of a single breeding stock (A) connecting with a single feeding ground (Area II). Given that the great majority of the catches in Area II were taken at South Georgia and the South Sandwich Islands, catch allocation for the purpose of modelling is thus relatively straightforward (see Fig. 8).

Stocks B and C

The Workshop **agrees** that, at present, the situation for both stocks B and C is too complex and unresolved to allow useful attempts to develop stock structure hypotheses of value for assessment modelling.

Stock D

The Workshop **agrees** that the available information is sufficient to generate a reasonable hypothesis regarding Breeding Stock D and its general connection to the feeding grounds of Area IV. However, there remains the question of how much encroachment/mixing exists with Area V to the east and Area III to the west.

In relation to the discussion on the location for the core feeding grounds for Breeding Stocks D and E the following Discovery mark data support the division between the two stocks is being moved 10° to the west. It was noted that the previously agreed boundaries for the core area of the feeding grounds for Breeding Stock D are from between 80°E to 110°E with the eastern fringe set between 110°E to 130°E.

Of the 132 marks recovered from humpback whales marked in the breeding and feeding grounds associated with Breeding Stock E, 12 whales (approximately 9% of the recoveries) were recorded moving from Area V into Area IV.

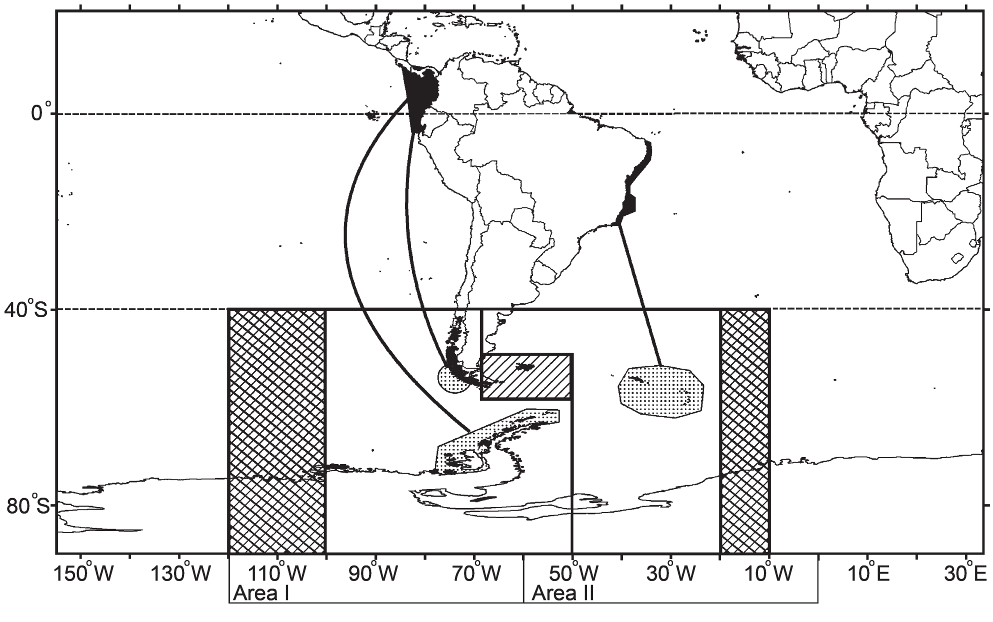

Fig. 8. Map showing the hypotheses to be modelled for Breeding Stocks A and G.

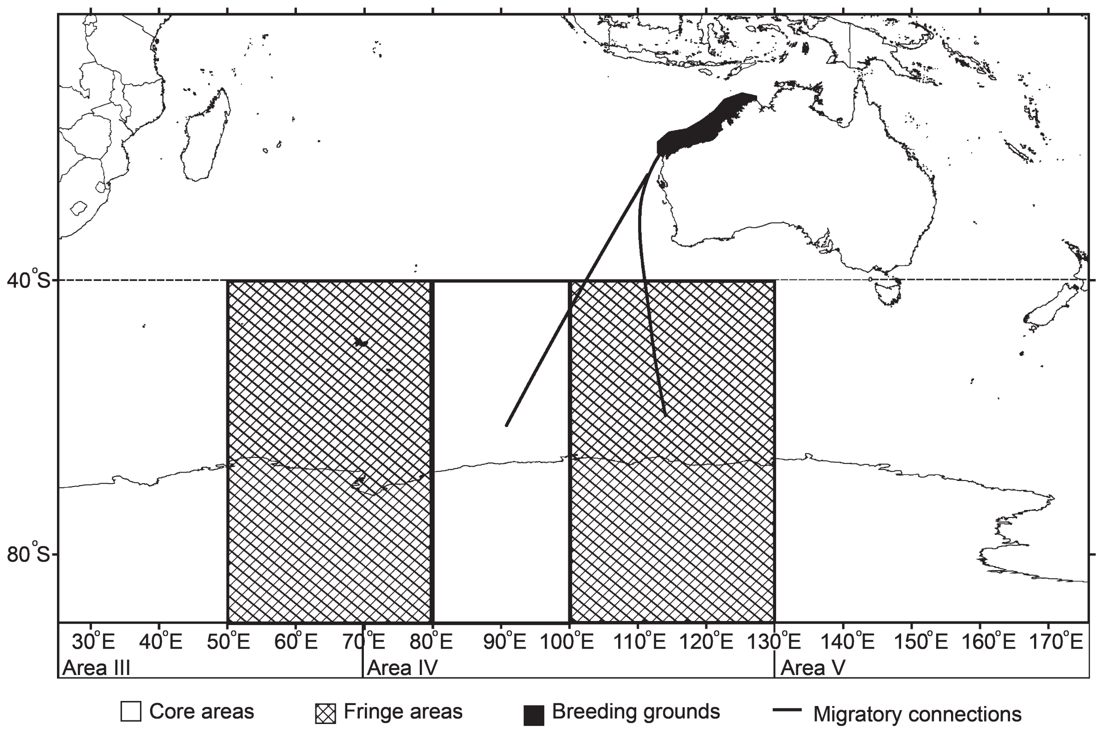

Fig. 9. Map showing the hypotheses to be modelled for Breeding Stock D.

All but two of these animals were recovered at a maximum longitude of 113°E in Antarctic waters. The exceptions are one animal marked in the breeding grounds/migratory corridor on eastern Australia (Breeding Stock E) that was recovered on the breeding grounds/migratory corridor on the west coast (Breeding Stock D) and one animal marked in Fiji which was recorded as recovered at 55°S, 87°E (on the western side of Area IV) by the Soviet whaling fleet (although there is some confusion in relation to this record as the animal was reported as a fin whale).

There is very limited marking data to suggest easterly movement of animals from Breeding Stock D. Only one animal (approximately 2% of all recoveries from Breeding Stock D) was recorded moving from the feeding grounds west of 110°W and to the east coast of Australia.

The Workshop therefore **agrees** that the core area of the feeding grounds for Breeding Stock D should be set at between 80°E and 100°E, with the eastern fringe set as between 100°E to 130°E and the western fringe at 50–80°E.

The agreed options for boundaries for Breeding Stock D are given in Fig. 9.

Stocks E and F

The Workshop **agrees** that the situation for Breeding Stocks E and F is complex and currently unresolved, and therefore that it is impossible to construct stock structure hypotheses for assessment modelling, particularly with respect to the assignment to Breeding Stocks of catches taken on the feeding grounds.

Stock G

As with Stock A, there appears to be a relatively straightforward connection between feeding grounds off the Antarctic Peninsula and the Colombia/equatorial western South America region that is considered as breeding stock G. The issue of where humpbacks feeding in the Magellan Strait breed remains open, but even if these animals bypass equatorial regions and winter in Central America, this remains in the area currently defined as stock G. Since the bulk of catches were taken in the Antarctic Peninsula region, catch allocation to stock G is straightforward. The boundary options for stock G are shown in Fig. 8.

Conclusion

The Workshop **agrees** that while it is possible to discuss modelling options to allow completion of the Comprehensive Assessment for Breeding Stocks A, D and G at the 2006 meeting, this is not possible for the other stocks, given current knowledge.

4. CATCH INFORMATION

4.1 Data sources

4.1.1 Whaling

SC/A06/HW47 summarised the work of Allison and the Secretariat computing department in developing the humpback whale catch database and providing information for assessment work at the Workshop.

There are two primary issues with respect to the catch series:

(1) the completeness of the total catch record; and
(2) allocation of catches in relation to what is known or suspected about stock structure (including alternative hypotheses).

With respect to the first issue, it is believed that the total record is largely without major gaps (although see Item 4.2.1). Before addressing the second issue it is important to consider the nature of the data themselves.

In the best case, individual catch records are available. These provide full information on a wide variety of factors, including operation, date, time, position to the nearest degree (or finer), species, sex and length. There can then be a gradation of data available down to the case where it is suspected that some catches occurred but their magnitude and details are unknown.

For Southern Hemisphere humpback whales, Allison reported that there are reasonable positional data for most catches (either exact position or at least land station in early years). A summary of the data available by year (since 1900) was given that included:

General position: Ocean, Area (e.g. Angola), Operation (Name).

Species: Humpbacks, Unknown, 'Final' humpback.

What is coded (resolution of data): e.g. exact, daily position, sex, length.

Qualifier: e.g. Any doubts over the quality of the data.

Notes: e.g. Discrepancies and how handled including unspecified.

With respect to known problems with data (excluding those related to the falsified Soviet data discussed below), these can be summarised as follows:

No data but some operation known: Angola catches in 1915; catches by the *Saragossa* in April/May 1930; subsistence catches at Tonga (see below) – no correction has been applied.

Unknown species: For some early years at South Georgia and the South Shetlands – this has been 'corrected' by comparison with proportions known for similar operations in the same year or the proportion known for the same or similar operations in surrounding years.

Unsure position: In the late 1920s for some South Shetlands 'pelagic' operations (if no information was available, all were allocated to the South Shetlands although it is known that some could range further) and catches ($n = 941$) by three Japanese pelagic operations in 1941/42 (allocated to same area as other Expeditions that year).

However, by far the greatest source of uncertainty in the database relates to the very large amount of falsified USSR catch data prior to 1972 where the issues are much more complex. Fortunately a small number of Soviet scientists managed to keep many of the original records and from this it has been possible to reconstruct the true catch (Yablokov, 1994; Yablokov *et al.*, 1998) but for some expeditions individual records are not available. In order to make the database as complete as possible, a small intersessional working group (Allison, Brownell, Clapham, Donovan, Mikhalev, Tormosov) met in Cambridge to determine if and how it was possible to assign catches to some level of geographical and temporal resolution. From examination of the data and the recollection of the Soviet scientists on board, it was found that the 'official' cruise tracks submitted by the USSR were generally reliable. For all but about 2.5% of the catch, catches by month were also known and from this it was possible to assign approximate positions of catches. In order to test the applicability of this method, the approach was also used for catches of 'known' positions and was found to be reasonably reliable (although inevitably the allocated catches were more widespread).

For the present meeting, Allison provided data broken down as requested at the 1998 and 2005 Annual Meetings of the Scientific Committee (see Item 4.2.2).

The Workshop thanked Allison and her staff for the considerable amount of work this represented.

The Workshop also considered SC/A06/HW53 that presented information on humpback whales killed by 19th century open-boat whaling. Catch and sighting data from Townsend (1935), Best (1987) and a small sample of logbooks of voyages not included in previous studies were used to describe the extent of humpback whaling in several oceanic regions, excluding the Antarctic. It was estimated that 16,188 humpback whales were taken between 1800 and 1900 in the Southern Hemisphere. The authors concluded that catch data extracted directly from the logbooks confirmed the general pattern of catches seen in the Townsend data, and sightings data from the logbooks revealed a more extensive distribution pattern than shown by catches alone. The catches assigned to humpback whale wintering grounds need to be compared to subsequent catches to determine their significance.

The Workshop **agrees** that in general, the level of the catches pre-1900 confirm its view that it was reasonable to assume that for modelling purposes, populations had recovered by 1900. It also **recommends** that persons having information on 'non-Yankee' humpback whaling should forward this information to the authors of SC/A06/HW53. However, it also **recommends** that for some of the Oceania grounds (notably Tonga), effort should be made to determine the level of undocumented pre-20th century catches to determine if this is a valid assumption.

4.1.2 Incidental catches in fishing gear

There are records of incidental catches in fishing gear and shark nets from several areas in the Southern Hemisphere, including Ecuador, South Africa and Australia. This information is summarised in the table of information included on the IWC website*. It was also noted that scarring patterns provide some information on the likelihood of entanglement events (e.g. SC/A06/HW48) although translating this into removal rates is not simple. The Workshop **agrees** that for modelling purposes, those with information on mortality in fishing gear should attempt to put 'bounds' on the likely extent.

Analysis of suitable caudal peduncle photographs for evidence of entanglement for humpbacks in Oman indicated that between 30–40% of sampled whales had been entangled (SC/A06/HW48). This rate is lower than the 65% estimated for the Gulf of Maine (Robbins and Mattila, 2000), and lower than the 57% estimated for North Atlantic right whales (Kraus, 1990). The Oman estimate is likely to be conservative, as some entanglements may have involved body parts other than the caudal peduncle and some entanglement scarring may have healed or been masked by other types of scars over time. Although documented humpback whale mortalities from entanglement in Oman are low, when viewed in relation to the low population estimates for humpback whales there, this entanglement rate may represent a significant threat, a concern shared with other small or isolated cetacean populations (e.g. Clapham *et al.*, 1999; D'Agrosa *et al.*, 2000; Kraus, 1990).

4.1.3 Ship strikes

The Workshop noted that Van Waerebeek would be presenting a global summary of ship strike information at the 2006 Scientific Committee meeting. It **agrees** to consider this issue further there.

4.2 Development of 'best' and 'alternative' catch/removal series

4.2.1 Total

The Workshop **agrees** that the total catches in the IWC database now reflect the best available data for Southern

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* *http://www.iwcoffice.org/documents/sci_com/workshops/Table2.pdf* accessed October 2011.

Hemisphere humpback whale catches. However, as noted above (Item 4.1.1), the catch data for Tonga are incomplete for the post-1900 period and Baker agreed to try to determine the approximate extent of such catches and provide this information to Allison.

4.2.2 By stock structure hypothesis

The options for Breeding Stocks A, D and G are given under Item 3.9 above. Donovan reported that the IWC database will allocate catches by at least 10° square, using the correction approach discussed above (Item 4.1.1). The data are now available* for Scientific Committee members.

4.3 Catch-per-unit-effort (CPUE)

Catch-per-unit-effort data have two potential uses in the assessment process. The first is to provide a crude check on model outputs and the second is to provide a relative index of abundance for fitting. The Workshop recalled previous discussions within the Committee over the use of CPUE data as a measure of relative abundance (e.g. IWC, 1989). It **agrees** that if CPUE series are to be considered in the second context, authors proposing the use of such data must justify why they consider the data to be suitable.

5. ESTIMATES OF RECENT ABUNDANCE AND OBSERVED TRENDS

A summary of all information on reproductive parameters available by breeding stock is given in the table available on the IWC website*. Given the time constraints, the Workshop **agrees** to consider only issues related to Breeding Stocks A, D and G under this item. Abundance and trend information for the other stocks will be discussed at the 2006 Scientific Committee meeting.

5.1 Review of methods

This item was not discussed owing to lack of time although methodological issues were considered when reviewing presented estimates.

5.2 Available estimates by stock structure hypothesis

5.2.1 Breeding stocks

BREEDING STOCK A

SC/A06/HW2 reported on the monitoring of humpback whales on the Brazilian breeding ground from 2002 to 2005. The objective of the study was to monitor humpback whale abundance to provide information to support the development of future strategies for the conservation of humpbacks off Brazil, particularly given concerns over the potential impact of increasing vessel traffic and shoreline development. A four year series (2002–2005) of aerial surveys was undertaken on the Brazilian breeding ground and abundance was estimated according to standard line-transect methods. The authors presented an estimate of abundance for 2005 that incorporated a value of $g(0)$ calculated in a novel manner as described in SC/A06/HW24. In that paper, the authors stated that none of the traditional methods to estimate $g(0)$ could be used for the Brazilian aerial surveys. They instead developed an estimate based on the ratio between (i) a population size estimate from distance sampling assuming $g(0) = 1$ and (ii) an independent population size estimate based on mark-recapture methods. The estimate they chose to use was the average of a bootstrap sample and accounts for availability and perception bias combined.

There was considerable discussion of this approach. In response to a question as to whether the estimation of $g(0)$ from this method is consistent with an estimate derived from a simple model of surfacing rate, the authors noted that while no direct comparison had been made, they believed that their estimate was consistent with what is known about humpback surfacing behaviour.

The Workshop noted that there are a number of reasons to believe that the estimation of $g(0)$ from the direct comparison of abundance estimates from aerial surveys with mark-recapture estimates may not represent an appropriate procedure (e.g. as the two estimates are generated using different methods, they have different assumptions and strengths and may not be estimating the same population). It was suggested that the method does not really estimate $g(0)$ but rather is a calibration of the line transect technique using mark-recapture. It was observed that estimates of abundance for Hawaii obtained using mark-recapture methods are consistently higher than estimates from line transect surveys for the same time and area (Baker and Herman, 1987). This arises because mark-recapture estimates the population size for all the individuals that occur in the area during the season whereas aerial surveys estimate only the number of whales in the area at the time of the survey. By contrast, even the uncorrected aerial abundance estimate presented in SC/A06/HW2 was higher than the mark-recapture estimate (and correction for $g(0)$ further increases the size of the aerial survey estimate). In response to a suggestion that the mark-recapture estimate be used as the abundance estimate and the aerial survey dataset be used as a relative survey series for modelling, it was noted that the mark-recapture estimate does not apply to the whole breeding area.

The Workshop **agrees** that the above issues and other potential biases associated with this comparison should be addressed in a revised analysis, although the authors present stated that they continued to believe that the method described in SC/A06/HW24 was a valid approach.

In conclusion, the Workshop **agrees** that the uncorrected aerial survey estimate, corrected using the Barlow method (Andriolo *et al.*, 2006) provides the best estimate of abundance for 2005. The resultant estimate is 6,550 (CV = 0.29; 95% CI 3,700–11,400).

STOCK D

SC/A06/HW3 analysed the results of an aerial survey off Carnarvon, Western Australia in 2005, following a series of surveys in the same area since at least 1982. From 1982–1994 aerial surveys in that area had provided evidence of an increase (of 10.15%±4.6%, see Bannister and Hedley, 2001) in Group IV (Breeding Stock D) animals. The next survey, in 1999, had been designed to obtain an estimate of absolute abundance of northward migrating animals, as had the 2005 survey. A new approach was planned in 2005 whereby a land-based component was to be used to 'ground-truth' the aerial results. In the event, poor weather meant that only 11 of the 30 planned flights took place in good conditions and logistical problems caused relocation of the land-based operation to a site where a high proportion of animals was recorded as not moving in any definite direction (i.e. they appeared to be using the area as a 'resting' area). However, the authors developed a method to use the aerial and land-based results to obtain an estimate of $g(0)$ to take account of pods missed by the aircraft and animals not present at the

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* *http://www.iwcoffice.org/documents/sci_com/workshops/Table2.pdf* accessed October 2011.

surface from which they estimated abundance for 2005. The authors highlighted a number of potential problems with the estimate. They also applied the 2005 estimate of *g*(0) to the 1999 results (where despite poor weather more complete coverage over the two-month period had been achieved) to obtain a revised 1999 estimate.

The Workshop welcomed the analysis presented in the paper. However, while it **agrees** that the authors are to be congratulated for developing an ingenious method to try to obtain an estimate for 2005 despite the severe practical problems in the field, the Workshop also **agrees** that it is unable to accept this estimate for a number of reasons, including those listed by the authors themselves. However, for the purposes of modelling, it **agrees** to use the revised figure for 1999 of 10,000 (95%CI 8,000–12,500). However, it notes that caution is needed when applying the estimate of *g*(0) from 2005 to the 1999 survey and **recommends** that the problem be considered further and that an updated paper be presented to the 2006 Annual Meeting.

STOCK G

SC/A06/HW13 used mark-recapture data to estimate abundance for the southeastern Pacific stock. A total of 1,061 individuals were identified between 1991 and 2004 off the coast of Ecuador (2°S, 81°W) The best estimate obtained using the closed Petersen estimator was 2,917 whales (95% CI 1,751–4,859; CV 0.19), pertaining to the period 2003–2004. Estimates with the open Jolly-Seber model were more heterogeneous, even when data were pooled in periods of two years. An estimate of 2,881 whales (95% CI 1,722–4,039) was obtained for 2004 using this approach (assuming constant survival rate and time-specific capture probabilities). Although the authors recognised that several sources of bias probably affected the estimate (especially those related to sex ratio), they believed the estimate to be representative of the Southeastern Pacific migratory population because Ecuador is located in the southern part of the wintering area through which whales are most likely to pass. They noted that a more extensive collaborative effort including other wintering areas further north and the integration of breeding and feeding data would help to increase precision in abundance estimates.

There was some discussion of this paper with respect to mark-recapture assumptions (e.g. see Hammond, 1986). For example, at least one of the sampling periods must comprise a random sample. It was noted that there is consistent effort through the season including a dedicated research component on whalewatching trips, indicating that the later years of the study period met the assumption of a random sample. The later years were also those with the largest sample sizes. Matching with other catalogues in Area A is already underway but not yet completed. It was also noted that there has already been a comparison of Ecuador sightings with the Antarctic catalogue.

The Workshop **agrees** that the Petersen estimate for 2003–2004 (2,920 whales; 95% CI 1,750–4,850; CV 0.19) should be considered the best estimate from the analyses presented in SC/A06/HW13, as the sample size was highest over this period, the sample appeared to be random and it had the lowest CV.

SC/A06/HW54 reported on mark-recapture abundance estimates obtained for the Antarctic Peninsula area using Chapman's two-sample estimator. Photographic samples used in the analyses were collected between the 1994/1995 and the 2001/2002 Antarctic seasons by three different groups: the College of the Atlantic (COA), the Brazilian Antarctic Programme, Projeto Baleias (PROANTAR) and Instituto Antártico Chileno, Proyecto (INACH). The samples used for the estimator were not segregated by time, as is typically the case, since doing so would result in small annual sample sizes, and also because any site fidelity by individual whales to specific feeding sites would result in heterogeneity in inter-annual capture probabilities. Instead, samples were segregated by the three primary groups conducting the sampling. Three estimates were made using the full collections from the three organisations as samples, and two with the COA sample selected to temporally match those obtained by the other organisations. The new estimates ranged from 1,960 (95% CI 900–3,000) to 3,260 (95% CI 2,100–4,500). However, in their discussion, the authors cautioned that most consistent high-use areas for humpback whales near the Peninsula are well known, and are likely to be frequented by the commercial cruise operators and also to be selected as the targets of dedicated research operations, so the areas worked by the three groups are unlikely to be truly independent.

The same authors presented SC/A06/HW56, which gives mark-recapture estimates of abundance for Breeding Stock G humpback whales. They noted that mark-recapture abundance estimates using two samples from the same habitat may be substantially biased, while small sample sizes lead to several other sources of bias. They therefore attempted to minimise such bias by: (a) using samples from different habitats that have independent sources of heterogeneity; and (b) increasing sample sizes by pooling across years. One set of samples was collected from the west coast of South and Central America and the other from the Antarctic Peninsula. Samples were collected between 1991 and 2004 and were pooled over spans from 0–12 years. To account for and estimate the influence of the open-population bias resulting from the pooling of samples, a regression was fitted to the mean of the abundance estimates for each span of time used after filtering the estimates for low-sample bias. From this, the authors estimated the abundance of humpback whales in Group G in 1997 to be 3,850 (95% CI 3,700–4,000).

The Workshop welcomed these papers that incorporated data from the feeding grounds. During discussion, it was noted that there are two apparently separate feeding grounds (Antarctic Peninsula and Magellan Strait) and that including data from the Magellan Strait feeding ground could improve the estimate. The Workshop **agrees** that while the approach described in SC/A06/HW56 appears to be a useful extension of mark-recapture analytical approaches, there is insufficient detail about how the method (and particularly the pooling) has been implemented or the potential sources of bias. It **recommends** that the authors provide more detail and explanation of this work to the 2006 Annual Meeting.

Despite the above, the Workshop **agrees** that for Breeding Stock G modelling purposes, both the estimates provided in SC/A06/HW13 (2,920 in 2003–2004; 95% CI 1,750–4,850) and in SC/A06/HW56 (3,850 in 1997; 95% CI 3,700–4,000) should be used. The Workshop also **recommends** a comparison of photo-id catalogues from Ecuador, Panama and Costa Rica.

5.2.2 Feeding grounds

SC/A06/HW57 reported on current distribution and abundance estimates in Areas IV (70°E–130°E) and V (130°E–170°W) in the waters south of 60°S, based on results obtained by the JARPA programme. This incorporates large-scale line transect surveys and has been carried out in a consistent way (alternating each year between Areas IV and V) since 1987/88. Humpback whales were widely distributed in Areas IV and V. It seemed that there was a distribution boundary around 130°E–140°E related to hydrographic features in keeping with previously noted distribution patterns. Further, it was found that humpbacks were concentrated between 90°E and 120°E in northern and southern strata on the eastern side of the Kerguelen Plateau, but were widely dispersed in other parts of Area IV. In Area IV, abundance estimates ranged from as low as around 2,700 in 1991/92 to as many as 33,000 in 2001/02, while for Area V, the range was from about 1,400 in 1990/91 to as many as 10,000 in 2004/05; CVs ranged from 0.11 to 0.33.

The Workshop welcomed the presentation of this work and thanked the authors. There was considerable discussion of the results. It was noted that similar discussions over the comparison of results from JARPA data and from IWC/IDCR and SOWER data are occurring in the context of abundance estimates for Antarctic minke whales. The Workshop **agrees** that full consideration of this issue is required. To facilitate this at the 2006 Annual Meeting, it **strongly encourages** presentation of the following information:

(1) clearer/enlarged displays of effort and sightings data, in particular to show details of the southern strata and the ice edge;
(2) display/analyses of the temporal distribution of searching effort within-season, particularly with respect to latitude and the ice edge, in order to allow evaluation of any changes over time and to evaluate whether following the path of any migration may be of concern;
(3) a full description of the policy that determines when the vessels steam/transit without sampling/sighting effort, how and when this may change over the course of a survey and displays/analysis of any potential bias that may result from policy decisions;
(4) analyses of sightings cues by *inter alia* area, time, season, sighting distance;
(5) separate analyses of sighting effort for vessels that carry out sightings only (SV) and vessels that also catch whales (SSV);
(6) separate analysis of school size by SV and SSV, taking into account time within a season and area, especially with respect to latitude and ice edge; and
(7) evaluate/display how the fraction/density of whales in the northern and southern areas covered by the vessels may have changed over time (taking into account seasonal differences in timing of effort, etc.).

SC/A06/HW6 presented estimates of abundance for humpback whales in the Southern Ocean in the austral summer based upon the IWC's IDCR-SOWER circumpolar (CP) sighting survey programmes. These have encircled Antarctica three times: 1978/79–1983/84 (CPI), 1985/86–1990/91 (CPII) and 1992/93–2003/04 (CPIII), surveying strata totalling respectively 64.3%, 79.5% and 99.7% of the open-ocean area south of 60°S. Abundance estimates were presented for each survey, for Management Areas I–VI, for longitudinal ranges corresponding to breeding stocks A–G as defined by the 'Naïve' model, and for circumpolar sets CPI–CPIII. Circumpolar estimates with approximate midpoints of 1980/81, 1987/88 and 1997/98 were 7,100 (CV = 0.36), 10,200 (CV = 0.30) and 41,800 (CV = 0.11). When adjusted for unsurveyed northern areas south of 60°S by assuming densities equal to those in the corresponding northern strata surveyed, these estimates become 9,700, 12,500 and 41,600 respectively. As estimates of total abundance, they are negatively biased because they assume that all whales on the trackline are sighted, and because some humpback whales remained north of 60°S during the period of the surveys.

In discussion, it was noted that while there appears to be reasonable agreement between SOWER and JARPA abundance estimates, there are still some large differences in some areas and years, in particular for Area IV in 2002/03. A potential explanation is that the SOWER estimate was generated over a three-year period while the JARPA estimate was derived from a single year survey. Effective strip width and school size have increased over the survey period. The proportion of humpback whales north of 60°S will vary around the circumpolar area and it was suggested that it would be useful to explore what proportion of whales are north of 60°S by each feeding area. That could be achieved through the use of JSV (Japanese Scouting Vessel) data but one potential difficulty is that the JSV data cover the years prior to most of the IWC and JARPA surveys when humpback whales were less abundant; it may not be reasonable to assume that the relative proportions north and south of 60°S have remained the same. It is interesting to note that in the most recent SOWER cruise, more humpback whales were seen north of 60°S than south of 60°S. While it is likely that the abundance estimates from JARPA and SOWER are negatively biased as whales north of 60°S are not being surveyed, it is also possible that extrapolation to the unsurveyed area south of 60°S in the CPI and CPII IDCR surveys may result in a positive bias in some areas if densities fall off monotonically away from the ice edge, and that the latitudinal movement of whales across the 60°S boundary may have resulted in changing proportions of the total abundance south of 60°S being surveyed in different years.

SC/A06/HW37 presented a re-analysis of the sighting data from the 1995/1996 BROKE East survey, to provide an abundance estimate of humpback whales within the survey area encompassed by IWC Area IV. These data had previously been examined by Thiele *et al*. (1998). However, those authors had found a large discrepancy between their estimate (900 animals) and estimates obtained from other surveys in a similar region. The new analysis provided a corrected estimate (10,813) that is more consistent with other survey results. The authors also discussed a strategy to compare the BROKE estimates with other estimates from similar surveys within Antarctic Area IV. Finally, abundance estimates obtained from a preliminary analysis of the latest 2005/2006 BROKE West survey were also presented.

During discussion, it was suggested that density estimates for the common areas surveyed by SOWER, JARPA and BROKE surveys be investigated. The Workshop noted that reanalysis of the SOWER and JARPA data would be very labour intensive. However, the comparison of the three methods could be extremely useful in investigating true variances from each of the surveys. Before this is undertaken it would be worth investigating if the respective datasets will allow for statistically robust comparisons. It was requested that SC/A06/HW37 be updated with a more detailed explanation of methods and results. It was noted that initial analysis of the BROKE survey had yielded an anomalous estimate of abundance, which had consequently raised questions about the reliability of the survey. The Workshop **agrees** that these new results allay such concerns and hence that the BROKE survey can now be considered a useful source of data for investigating humpback abundance. The

Workshop **recommends** that this work be further explored for discussion at the 2006 Annual Meeting.

SC/A06/HW43 reported on ship surveys undertaken by the Projeto Baleias/Brazilian Antarctic Program during the austral summers of 2006. The data were used to estimate abundance in the Gerlache and Bransfield Straits west of the Antarctic Peninsula (the eastern end of Area I). Distance sampling methods were applied. No statistical difference in encounter rate was evident between the Bransfield and Gerlache Straits, although the average was slightly higher for the former. Estimated abundance was 330 (95% CI: 150–700) and 1,700 (95% CI: 1,000–2,600) in the surveyed areas of Gerlache and Bransfield Straits, respectively, with a pooled abundance of 2,000 whales (95% CI: 1,300–3,000) and an extrapolated estimate for the whole Bransfield area of 2,800 (95% CI: 1,800–4,400). The authors note that the estimate is of limited use for stock assessment as it represents only a fraction of Stock G total abundance. The similarity of this estimate to the mark-recapture estimates for the breeding grounds (e.g. SC/A06/HW13) is evidence that the latter are underestimates.

5.3 Relating feeding ground estimates to stock structure hypothesis

SC/A06/HW25 derived estimates of rates of increase from time series of population estimates for humpback whales from the IDCR-SOWER sighting survey series (see Item 5.2.2). Estimates were reported for Management Areas I–VI, for longitudinal ranges corresponding to breeding stocks A–G as defined by the Naïve model, and for circumpolar sets CPI–CPIII. Point estimates were positive for all breeding stocks and were significantly greater than zero for stocks D and E. The circumpolar annual rate of increase was estimated at 9.6%, with a 95% CI of 5.8–13.4%.

In discussion, it was noted that the Naïve model is, by definition, somewhat simplistic and, at least for Breeding Stock E, incorrect. Given this, the results from this paper by breeding stock should be viewed with caution until the appropriateness of the Naïve model is better understood. The Workshop **agrees** that it would be useful to consider using a model (or models) with changing boundaries over time, as krill (and hence probably whale) distribution varies over time. This changing distribution may have implications for interpreting increase rates obtained from the feeding ground surveys; it is quite likely that there will be differences between rates of increase observed on feeding and breeding grounds. Although the available data are limited and exhibit large confidence intervals, the Workshop **agrees** that they may be useful as one of several datasets to be used in the modelling exercise.

5.4 Trend estimates by stock structure hypothesis

The Workshop **agrees** that for all Breeding Stocks, especially A, G and D (which are of immediate priority), there is a need to investigate how much the overall estimate of trend from abundance estimates is being affected by the abundance estimate from the fringe areas. It would be useful to generate abundance estimates for the core and fringe areas independently, or even by 10° longitudinal sector, to see what influence the fringe abundance estimates have on the trend to be used in the naïve model. The Workshop **recommends** that this work be undertaken and presented to the 2006 Annual Meeting.

BREEDING STOCK A

SC/A06/HW45 presented the results of a Bayesian assessment for Breeding Stock A. It provided information about rates of increase, however this did not represent the whole stock but rather the core area of the breeding grounds. The Workshop **agrees** that this information is suitable for use in the modelling exercise. The Workshop **recommends** that a revised modelling paper be submitted to the 2006 Annual Meeting that includes additional exploration (e.g. using a variety of models for *r*) and details clearly the caveats and limitations of the data. Zerbini agreed to undertake this work.

BREEDING STOCK G

Preliminary information for Breeding Stock G was provided in SC/A06/HW54. The Workshop **recommends** that the authors of that paper and all the catalogue holders co-operate and undertake reanalysis of all of the available data to provide further information about trend to the Committee as soon as possible. The Workshop **agrees** that in the interim, the models should be fitted assuming a variety of priors for *r* (and see Item 6.3).

BREEDING STOCK D

The Workshop was informed that there is an ongoing reanalysis of the entire western Australian catalogue that will include the provision of relative abundance estimates; however, this will not be completed in time for the 2006 Annual Meeting. Therefore the most recent trend information is that reported by Bannister and Hedley (2001) for the period 1982–1994 and the Workshop **agrees** that this be used in the modelling exercise.

6. BIOLOGICAL PARAMETERS

A summary of all information on reproductive parameters available by breeding stock is given in the table available on the IWC website*. New information is discussed below.

6.1 Natural mortality rates

It was noted that the models are not particularly sensitive to values of natural mortality rates. Given the time constraints, it was **agreed** not to discuss this item further.

6.2 Age and length at attainment of sexual maturity

SC/A06/HW5 reviewed estimates of the age at sexual maturity, given concerns over earlier calibration of earplug readings. In particular, Chittleborough (1959) and others, including Nishiwaki (1959) had concluded that humpback whales reach puberty at around five years of age. Although there was some support for this value from longitudinal studies of individual whales in the Gulf of Maine (Clapham, 1992), questions remained, given the accepted values for other rorquals of around 10 years. Chittleborough had assumed a biannual accumulation rate of earplug growth layer groups (GLGs), partly from comparison with readings from baleen plates. However, the reliability of baleen plate readings has subsequently been questioned (particularly owing to wear), even for young animals. The authors noted that the ovulation and natural mortality rates estimated on the basis of two GLGs per year now seem too high to be biologically feasible. They concluded that it was not that Chittleborough's readings were in error, but rather his interpretation of their accumulation rate.

The Workshop thanked the authors for this thorough review and encouraged its publication. The potential value of stable isotope studies to evaluate GLG formation in earplugs was noted.

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* *http://www.iwcoffice.org/documents/sci_com/workshops/Table2.pdf* accessed October 2011.

In considering estimates of attainment of sexual maturity from photo-identification studies, the Workshop noted the large difference between the results from the Gulf of Maine (around five years, Clapham, 1992)[5] and those from southeast Alaska (first calving at 8–16 years, Gabriele *et al.*, 2007); the latter are more consistent with an annual GLG formation rate in earplugs (see above). It was noted that these differences may reflect different ecological conditions (including oceanographic productivity, prey bases and length of migration) and that extrapolating from one region to another may not be appropriate, particularly for a 'flexible' parameter such as age at attainment of sexual maturity, which has been shown to change over time within the same population for some species (e.g. Icelandic fin whales – see discussion in IWC, 2007b). The Workshop noted the large number of photo-identification catalogues available for the Southern Hemisphere and **urges** examination of these for obtaining further estimates of age at attainment of sexual maturity.

Further discussion of this issue occurs under Item 6.3 in relation to the maximum plausible rate of increase.

6.3 Reproductive rates

SC/A06/HW23 reported on the resighting histories of 292 female humpback whales identified as mothers along the east coast of Australia from 1984–2005. No animals were observed in every year of the study effort. There were 24 instances of observations in two consecutive years, 24 instances of consecutive three year sightings, and one each of four year and five year consecutive sightings. The mean proportion of sightings of calves was 0.417 (95% CI: 0.381–0.453), which may be taken as an estimate of overall calving rate for this group of females. The mean calving interval for the 72 females known to be mothers, observed over a 22-year period, was 2.39 years (95% CI: 2.20–2.62). Most known mothers ($n = 58$, 67%) had at least one calf in a 2 or 3 year interval of consecutive sightings. There were a number of examples of one-year cycles: 14 two-year sequences in which the mother gave birth in both years; two occasions in which the mother gave birth in each year of a three-year sequence; and one occasion in which the mother gave birth in each year of a five-year sequence.

In discussion, it was suggested that photographing females during the northward migration prior to parturition may result in an overestimation of the calving interval. The Workshop **agrees** that a reanalysis of these data excluding the early migration photographs would be valuable.

Much of the discussion under this item centred on the appropriateness of the value of 12.6% per annum given by Clapham *et al.* (2001) for the upper bound[6] for a maximum plausible increase rate, based on the simple model approach given in Brandão *et al*. (2000). The value had been obtained assuming survival rates for all age classes of 0.99, a pregnancy rate of 0.5 (i.e. a 2-year calving interval on average) and an age at parturition of 5 years (based on the Gulf of Maine). Reported rates of increase of around 10% have been reported for western and eastern Australia (e.g. Bannister and Hedley, 2001; Paterson *et al.*, 2001) and considerably higher estimates from the feeding grounds (SC/A06/HW57) and some doubts have been expressed that the feeding ground estimates represent true rates of increase for total populations.

With respect to calving intervals, it was suggested that an average calving interval of two years was unlikely. In this context there was some discussion on the occurrence of one year calving intervals. There is photo-identification evidence that this can occur from eastern Australia (see SC/A06/HW23), the Gulf of Maine (5% of females with calves) and Hawaii (13%) as well as information from whaling data (e.g. Cerchio, 2003; Chittleborough, 1955; 1959; 1965). However, it should be noted that there is no information on the neonatal survival of these calves (e.g. it may be lower due to nutritional stress in the mother, for example, or she may have been able to calve in consecutive years due to the early mortality of a previous calf). It was noted that the levels of one year calving intervals alone were insufficient to account for the high observed increase rates in some areas.

Following the discussion under Item 6.2, there was additional discussion on the age at first parturition and whether five years was a reasonable value. It was noted that increase rate estimation is highly sensitive to the age at sexual maturity.

In noting that changes in age at attainment of sexual maturity are thought to be one mechanism for density dependence to occur[7], it was suggested that Chittleborough's (revised for annual GLG formation) estimate for the age-at-maturity needed to be considered as applying to whales born before 1950 and hence before the onset of the main catches of humpback whales from Area IV. The estimate may thus apply to a population only slightly reduced from its initial level, and the value may have subsequently decreased in response to the later considerable reduction of the population as a result of catches. However, Clapham pointed out that blue and fin whale populations had already been appreciably reduced by the time Chittleborough's samples were taken, so that these could already at that time have reflected some change in age-at-maturity in response to consequential enhanced krill abundance.

Other information relating to reproductive rates briefly discussed included the possible effects of male biased sex ratios (see Item 3.5.2.1), mating outside the breeding grounds and the possibility of reproductive senescence, which is generally believed to be absent in mysticetes (see review by Marsh and Kasuya, 1986) although some anecdotal evidence was mentioned for the North Pacific.

In conclusion, the Workshop noted that the available information on biological parameters for humpback whales from around the world, such as age at sexual maturity, calving and survival rate, strongly suggested that the values currently used in modelling exercises (a maximum annual rate of increase of 12.6%) seemed biologically implausible. It **recommends** that a review of the available information be undertaken in 2006 that concentrates on examining the existing data in the context of determining a likely bound for *r*. This review should consider *inter alia*:

(1) the possible sources of bias in any existing estimates (including sample size and site);
(2) the likely direction of any such bias and if possible its maximum extent; and
(3) the time period for which the estimate applies and what is thought to be known about the status of the

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[5] SC/A06/HW23 presented information on one animal observed as a calf that was identified as a mother six years later.

[6] The same authors presented a lower bound for the maximum plausible increase rate of 3.9% using the following values: adult survival 0.95; first year survival 0.92; pregnancy rate 0.4; age at parturition 9 years (based on southeast Alaska).

[7] Length at attainment of sexual maturity is thought to be more constant – thus an increase in growth rates as a result of more food being available will result in a decline in the age at attainment of sexual maturity.

population(s) to which the estimate applies. This review should be valuable in providing an appropriate upper bound for *r* in modelling exercises.

At this stage, the Workshop suggested that models be run with a uniform prior for the annual growth rate parameter *r* bounded above not only by 12.6% as in the past, but also by lower values to investigate sensitivity; it was recognised that at this stage, no analyses would be seen as definitive.

7. THREATS

There was insufficient time to discuss this item.

8. ENVIRONMENTAL PARAMETERS

There was insufficient time to discuss this item.

9. ASSESSMENTS AND PROJECTIONS

There was only limited time to review and discuss the papers presented under this item – SC/A06/HW22 and SC/A06/HW45 and issues related to assessment and projection models.

9.1 Inputs for models

The Workshop **agrees** that modelling to be undertaken before the 2006 Annual Meeting should use input parameters based on the decisions taken at this workshop with respect to catch estimates, population abundance estimates and population trends for stocks A, G and D (see above). Results based on these inputs will be the focus of the review of modelling results at the meeting, although exploration of model results based on alternative and/or additional inputs may be undertaken to provide insights into the sensitivity and robustness of the results. In particular, the Workshop noted that the abundance estimates from the feeding grounds for Breeding Stock D from the third circumpolar IDCR and the more recent JARPA surveys are substantially higher than those based only on the breeding ground estimates. This will need to be considered when reviewing the model results. However, the resolution of any such differences will not be straightforward due to confounding issues related to potential stock mixing and the interpretation of the feeding ground abundance estimates.

The Workshop noted that there are other model inputs that are required for one or more of the model implementations, and for which the workshop did not provide an agreed set of values. These include:

(1) Bayesian prior for the intrinsic rate of growth;
(2) estimates of minimum historic population sizes to use as a lower bound in the model; and
(3) Bayesian priors for the mixing matrix to use in multi-stock models (although the workshop did not have sufficient time to consider basic catches and abundance estimates for use in such models or the approach to take for these models).

With respect to the Bayesian prior for the intrinsic rate of growth, the Workshop suggested that models be run with a uniform prior for the annual growth rate parameter *r* bounded above not only by 12.6% as in the past, but also by lower values to investigate sensitivity (see Item 6.3).

It was noted that there are extensive data on length distribution for the commercial catches and more limited data on ages for some Areas. It was suggested that consideration should be given to development of length/age models, particularly with respect to the question of possible transient age structure in relationship to maximum intrinsic growth rates.

Finally, the Workshop **agrees** that where CPUE data have been used (e.g. SC/A06/HW22), results should also be presented where such data are excluded.

9.2 Outputs for models

SC/A06/HW25 reported on simulations conducted to test the robustness of assessment results to certain key assumptions. In particular, the most recent assessment of Breeding Stocks D and E uses a population model that allows for mixing between feeding areas (Johnston and Butterworth, 2005; 2002). The model makes a number of assumptions about whale movement in the feeding areas, the historic catch distribution across the feeding areas and the form of density regulation acting upon the populations. The sensitivity of this model to these assumptions was tested using a simulation approach. Specifically, data were generated from a population model where the assumptions were relaxed in a number of plausible ways and then the model was fitted to the data. Using this approach, the effects of whale movements over a finer spatial scale in the feeding areas, the catch distributions across this sub-area scale and the incorporation of density regulation on the feeding areas were explored. SC/A06/HW25 found that Johnston and Butterworth's model was robust to both whale movements on a fine scale and with catch distributed as per this scale. However, when density regulation was implemented in the form of density dependence on the feeding areas, the model produced estimates that were quite different from those from the simulated population. The authors recommended that the inclusion of density dependence on feeding areas in models that allow for mixing of whales on the feeding grounds be investigated further.

The Workshop welcomed this work. In discussion, it was noted that the results in SC/A06/HW25 may be overestimating the sensitivity of the results to assumptions about density dependence due to choice of parameter values used in the simulations. However, the Workshop emphasised the importance of independent checks of model performance and robustness and it **agrees** that it is important to consider alternative assumptions about density dependence; it **encourages** further model development that would allow the effects of such assumptions to be tested.

The Workshop noted the model outputs presented. It **agrees** that they comprise the basic outputs that should be presented in future assessment results. In addition, it **recommends** that covariance estimates should be presented for the primary output statistics from the assessment models (e.g. *K*, *r*, current depletion) and that the output statistic should include model estimates of minimum population size. The Workshop also **reaffirms** the importance of providing output results which test the sensitivity of the results to alternative values for the key inputs (alternative catch series or abundance estimates).

Finally, the Workshop **recommends** expansions of the assessment models be developed that include a floor on the minimum historical population and depensation, and that assessment results incorporating these be presented at the 2006 Annual Meeting.

10. CONCLUSIONS AND RECOMMENDATIONS TO THE SCIENTIFIC COMMITTEE

10.1 Recommendations for future research

The Workshop **agrees** a number of recommendations and these can be found throughout the report. Consolidated recommendations by Breeding Stock can be found in Annex H. Recommendations relevant to attempting to complete the assessments for Breeding Stocks A, G and D at the 2006 Annual Meeting are considered under Item 10.2.

From the perspective of completing the assessment for the other areas, the highest priority research is for studies of stock structure and movements for Breeding Stocks B, C, E and F, particularly those that will allow appropriate allocation of catches from the feeding grounds to breeding stocks. Information from a variety of sources is important in this regard, especially genetic, photographic, telemetric and acoustic studies. In this regard, the Workshop **strongly recommends** that high priority be given to the following work that can be undertaken using existing samples/catalogues from the breeding grounds:

(1) genetic and photo-identification catalogue (see Items 3.5.5 and 3.6.5) comparisons amongst samples/catalogues from Western Australia, eastern Australia and Oceania and comparisons with samples/catalogues from the feeding grounds.

In addition, the Workshop **agrees** that high priority should be given to comparison of existing samples/photographs from feeding grounds with those from the breeding grounds, and the collection of additional samples/photographs from the feeding grounds. This will be extremely valuable to help elucidate high and low latitude connections and to discriminate among alternative hypotheses concerning mixing on the feeding grounds and should be given high priority. The Workshop therefore **recommends** that:

(1) biopsy sampling and photo-identification of humpback whales remains a high priority for future SOWER cruises;
(2) samples from the 2006 SOWER cruise (Area III, $n = 71$) are transferred as soon as possible to the WCS/AMNH Cetacean Conservation and Research Program for analysis and subsequent transfer back to SWFSC for storage; and
(3) photographs from SOWER cruises continue to be sent to the Antarctic catalogue hosted by the College of the Atlantic;
(4) the existing protocols for access to SOWER biopsy samples and photographs be reviewed to see if modifications are required; and
(5) national programmes (e.g. JARPA II, BROKE) and international programmes (e.g. SO GLOBEC, CCAMLR) operating in the Antarctic, wherever possible, allocate time to the collection of photographs and biopsy samples and that all photographs should be submitted to the Antarctic catalogue.

The Workshop stresses that the value of individual identification data is dramatically increased by the sharing of data amongst research groups. Whilst recognising the rights of data collectors, it **strongly encourages** the development of inclusive regional catalogues (e.g. by Breeding Stock) and the comparison of such catalogues with (a) neighbouring Breeding Stock catalogues and (b) the Antarctic catalogue. Such catalogues also provide a means of obtaining estimates of biological parameters such as age at attainment of sexual maturity and natural mortality rates (see Item 6).

Similar considerations with respect to collaborative studies apply to the comparison of genetic samples. For example, the Workshop noted the great value in undertaking genetic analyses of animals from both the breeding and feeding grounds (Item 3.9). It **recommends** that every effort be made for scientists to share data and carry out such analyses. It noted the positive discussions being held by Baker, Pastene and Rosenbaum in this regard, under the IWC Data Availability Agreement, and looks forward to their successful conclusion and the submission of one or more analyses to the Committee.

The Workshop also **agrees** that for a number of areas, abundance data are lacking and that for most areas trend information is lacking. The most appropriate method for each stock/area needs to be determined: in some cases it may entail mark-recapture (photographic and/or genetic) methods and in other cases distance based methods (aerial, vessel or land-based). Detailed recommendations can be found in each of the individual sections under Item 5. With respect to mark-recapture data, the need to exclude short-period recaptures and to take account of the distribution of recapture effort in analysing such data to infer movement rates was emphasised.

10.2 Work plan before the 2006 Annual Meeting

The Workshop **agrees** that it should be possible to complete the assessments for Breeding Stocks, A, D and G based on the discussions held at the Workshop. With respect to Breeding Stock A, the Workshop **agrees** that **high priority** should be given to the following tasks, which must be conducted before the meeting.

(a) The estimate of rate of increase obtained from sighting per unit of effort data for the period 1995–1998 ($r = 0.055$, $SD[r] = 0.017$, SC/A06/HW46) should be reviewed. Alternative models (including non linear functions) and potential overdispersion in the data should be investigated. Zerbini agrees to undertake this task.
(b) The most recent estimate of abundance (SC/A06/HW2) should be used as an input parameter in the assessment models. However, the $g(0)$ methods applied to correct this estimation for perception and availability bias (SC/A06/HW24) should be reconsidered. It is **recommended** that for the assessment to be conducted at the 2006 Annual Meeting, the $g(0)$ estimated by Andriolo *et al.* (2006) should be used. Kinas and Engel agree to undertake this task.
(c) Considering the new catch allocation hypothesis (Item 3.10), new catch series should be produced from the IWC database and used in the assessment models. Zerbini agrees to consult with Allison and undertake this task.

The Workshop recognised the very considerable amount of work that had gone into producing the genetic data, some of which was the result of intensive last-minute analysis. It had not been possible to fully evaluate this work in the time available and the Workshop **requests** that a consolidated summary of the analyses be presented at the 2006 meeting. This summary should comprise a table summarising pairwise comparisons between breeding grounds.

In examining abundance estimates for Breeding Stock G (see Item 5.2.1), the Workshop notes that the method described in SC/A06/HW56 appears to be a useful extension of mark-recapture analytical approaches but agrees that there is insufficient detail about how the method (and particularly the pooling) has been implemented or the potential sources of bias. It **recommends** that the authors provide more detail and explanation of this work to the 2006 Annual Meeting. Similarly, the Workshop noted that caution was needed in the application of $g(0)$ from one survey to that in another survey in the estimate for Breeding Stock D (see Item 5.2.1) and it **recommends** that this be examined further and an updated version of SC/A06/HW3 be presented to the 2006 Annual Meeting.

With respect to estimates from the feeding grounds and in particular the JARPA surveys, the Workshop noted the ongoing discussions in the Committee of this issue with respect to Antarctic minke whales. It **encourages** provision of the information listed under Item 5.2.2 to assist in this work. The Workshop also **recommends** that the data from the BROKE surveys be explored further for discussion at the 2006 Annual Meeting (see Item 5.2.2).

The Workshop noted the need to review the available information for considering an appropriate value for the maximum rate of increase (*r*) for humpback whales (see Item 6.3). It **recommends** that a review of the available information be undertaken in 2006 that concentrates on examining the existing data in the context of determining a likely bound for *r* as detailed under Item 6.3. In the meantime, it **agrees** that those undertaking modelling exercises should consider examining the sensitivity to using lower values than the currently used annual rate of 12.6% (see Item 9.1).

11. ANY OTHER BUSINESS

No business was raised under this item.

12. ADOPTION OF REPORT

Given the time constraints, there was insufficient time available to review the report in detail at the Workshop. It was agreed that individual participants would send any comments on the available draft to Donovan. In addition, certain individuals agreed to formulate research recommendations for the various Breeding Grounds. Donovan agreed to co-ordinate all the responses and to undertake detailed editorial work on the report. Once completed the report would be circulated to all participants for final comments.

In conclusion, the Chair thanked Gales and his staff for their hospitality, and the rapporteurs and all the participants for their co-operative approach. The participants thanked Bannister for his customary wise Chairmanship.

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Annex A
List of Participants

Scott Baker
Marine Mammal Institute
Hatfield Marine Science Center
2030 SE Marine Science Drive
Newport OR 97365
USA
Email: scott.baker@oregonstate.edu

John Bannister
Hon Associate
Western Australian Museum
Locked Bag 49
Welshpool DC
WA 6986
Australia
Email: bannisj@bigpond.com

Jaco Barendse
Mammal Research Institute
University of Pretoria
32 Disa Avenue
Kommetjie
Cape Town 7975
South Africa
Email: jaco.barendse@gmail.com

Doug Butterworth
Dept. of Mathematics & Applied Mathematics
University of Cape Town
Rondebosch 7701
South Africa
Email: Doug.Butterworth@uct.ac.za

Cristina Castro
Pacific Whale Foundation
PO Box: 17-21-872
Quito
Ecuador
Email: pccastro@interactive.net.ec

Doug Cato
Defence Science and Technology Organisation (DSTO),
PO Box 44 Pyrmont NSW
Australia

and

School of Geosciences, FO9, University of Sydney,
NSW 2006,
Australia.
Email: dcato@usyd.edu.au;
doug.cato@dsto.defence.gov.au

Salvatore Cerchio
WCS/AMNH Cetacean Conservation
and Research Program
Conservation Genomics
American Museum of Natural History
Central Park West at 79th Street
New York, New York 10024
USA
Email: scerchio@wcs.org

Simon Childerhouse
Australian Antarctic Division
Australian Marine Mammal Centre
203 Channel Highway
Kingston
Tasmania 7050
Australia
Email: simon.childerhouse@aad.gov.au

Phillip Clapham
Alaska Fisheries Science Center
National Marine Mammal Laboratory
7600 Sand Point Way NE, Bldg 4
Seattle
WA 98115-0070
USA
Email: phillip.clapham@noaa.gov

Tim Collins
Wildlife Conservation Society
Oceans Giants Program
2300 Southern Boulevard
Global Conservation-Marine
Bronx
New York 10460
USA
Email: tcollins@wcs.org

Greg Donovan
International Whaling Commission
The Red House
135 Station Road
Impington
Cambridge
CB24 9NP
UK
Email: greg.donovan@iwcoffice.org

Márcia Engel
Humpback Whale Institute – Brazil
Instituto Baleia Jubarte (IBJ)/Humpback Whale Institute – Brasil
Base Praia do Forte: Av. do Farol, s/n – Praia do Forte,
Mata de São João, BA, 42700-000
Brazil
Email: marcia.engel@baleiajubarte.org.Br

Ken Findlay
96 De Villiers way
Glencairn 7975
South Africa
Email: kenfin@mweb.co.za

Paul Forestell
Pacific Whale Foundation
300 Maalaea Road, Suite 211
Wailuku , HI 96793
USA
Email: paul.forestell@liu.edu

Nick Gales
Australian Antarctic Division
Australian Centre for Applied Marine Mammal Science
Channel Highway
Kingston
Tasmania 7050
Australia
Email: nick.gales@aad.gov.au

Claire Garrigue
Opération cétacés
BP 12827
98802 Nouméa
Nouvelle-Calédonie
France
Email: op.cetaces@lagoon.nc

Susan Holloway
Dept. of Mathematics & Applied Mathematics
University of Cape Town
Rondebosch
Cape Town 7701
South Africa
Email: Susan.Holloway@uct.ac.za

Jennifer Jackson
British Antarctic Survey,
High Cross,
Madingley Road,
Cambridge
CB1 0ET
Email: jacksonjennifera@gmail.com

Greg Kaufman
Pacific Whale Foundation
300 Maalaea Road, Suite 211
Wailuku , HI 96793
USA
Email: greg@pacificwhale.org

Paul Kinas
Fundação Universdade Federal do Rio Grande (FURG),
Departamento de Matemática
96200-970, Caixa Postal 474,
Rio Grande, RS,
Brazil
Email: dmtkinas@furg.br

Rebecca Leaper
Department of the Environment and Heritage
(Australian Antarctic Division)
203 Channel Highway
Kingston TAS 7050
Australia
Email: rebecca.leaper@aad.gov.au

Koji Matsuoka
Institute of Marine Research
Toyomi Shinko Bldg
4–5 Toyomi-Cho
Chuo-ku
Tokyo 104-0055
Japan
Email: matsuoka@cetacean.jp

David Mattila
Hawaiian Islands Humpback Whale
726 South Kihei Road
Kihei
HI 96753
USA
Email: david.mattila@noaa.gov

Michael Noad
School of Veterinary Science
University of Queensland
St. Lucia
Qld. 4072
Australia
Email: mnoad@uq.edu.au

Carlos Olavarria
Laboratorio de Genética Molecular Marina Ecología de Ecosistemas Marinos Fundación CEQUA
c/o INACH. Plaza Muñoz Gamero 1055
Punta Arenas
Chile
Email: carlos.olavarria@cequa.cl

Luis Pastene
Institute of Cetacean Research
Toyomi Shinko Bldg
4–5 Toyomi-Cho
Chuo-ku
Tokyo 104-0055
Japan
Email: pastene@cetacean.jp

Dave Paton
Reeflection Pty Ltd
PO Box 919
Jamison Centre
ACT, 2614
Australia
Email: dave@blueplanetmarine.com

David Peel
Commonwealth Scientific and Industrial Research Organisation
(CSIRO)
Marine and Atmospheric Lab
GPO Box 1538
Hobart TAS 7001
Australia
Email: david.peel@csiro.au

Tom Polacheck
CSIRO
Castray Esplanade
Hobart
TAS 7162
Australia
Email: tom.polacheck@csiro.au

Cristina Pomilla
American Museum of Natural History, Molecular Lab
79th Street at Central Park West
New York
NY 10024
USA
Email: cristina.pomilla@nyu.edu

Michael Poole
Centre de Recherches Insulaires et Observatoirre de l'Environnement
BP 1013
Papetoai
Moorea
French Polynesia
E-mail: dwwe@mail.pf

Howard Rosenbaum
Wildlife Conservation Society
2300 Southern Boulevard
International Conservation-Marine
Bronx
New York 10460
USA
Email: hrosenbaum@wcs.org

Chandra Salgado Kent
Curtin University
Centre for Marine Science & Technology
School of Science
Building 301 – Physical Sciences
Bentley Campus
GPO Box U1987 Perth,
Western Australia 6845
Email: C.Salgado@cmst.curtin.edu.au

Eduardo Secchi
Prof. Adj.
Lab. Tartarugas e Mamiferos Marinhos
Instituto de Oceanografia
Universidade Federal do Rio Grande/FURG
Rio Grande – RS, Brasil
Brazil
Email: edu.secchi@furg.br

Paul Wade
Alaska Fisheries Science Center
7600 Sand Point Way NE
Seattle
WA 98115-0070
USA
Email: paul.wade@noaa.gov

Alexandre Zerbini
Alaska Fisheries Science Center
7600 Sand Point Way NE
Seattle
WA 98115-0070
USA
Email: alex.zerbini@noaa.gov

Annex B
Agenda

1. Introductory items
    1.1 Welcome and introduction
    1.2 Terms of reference
    1.3 Election of chair and appointment of rapporteurs
    1.4 Meeting procedures and time schedule
    1.5 Adoption of Agenda
    1.6 Documents available
    1.7 Publication of proceedings

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    2.1 Model or models to be used

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    3.1 Breeding Stock A
        3.1.1 Individual movements
            3.1.1.1 Discovery marks
            3.1.1.2 Natural marks (photo-id; genetic)
            3.1.1.3 Telemetry
            3.1.1.4 Other (e.g. lost harpoons)
        3.1.2 Stock structure
            3.1.2.1 Genetic information (population level)

        - 3.1.2.2 Other information (e.g. CPUE and catch history)
    - 3.1.3 Seasonal distribution
        - 3.1.3.1 Winter
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        - 3.1.3.3 Other
    - 3.1.4 Summary
    - 3.1.5 Recommendations for future work
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    - 3.2.2 Stock structure
        - 3.2.2.1 Genetic information (population level)
        - 3.2.2.2 Other information (e.g. CPUE and catch history)
    - 3.2.3 Seasonal distribution
        - 3.2.3.1 Winter
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        - 3.2.3.3 Other
    - 3.2.4 Summary
    - 3.2.5 Recommendations for future work
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        - 3.3.1.1 Discovery marks
        - 3.3.1.2 Natural marks (photo-id; genetic)
        - 3.3.1.3 Telemetry
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    - 3.3.2 Stock structure
        - 3.3.2.1 Genetic information (population level)
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    - 3.3.4 Summary
    - 3.3.5 Recommendations for future work
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        - 3.4.1.3 Telemetry
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        - 3.4.2.2 Other information (e.g. CPUE and catch history)
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        - 3.4.3.2 Summer
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    - 3.4.4 Summary
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        - 3.5.1.1 Discovery marks
        - 3.5.1.2 Natural marks (photo-id; genetic)
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        - 3.5.2.2 Other information (e.g. CPUE and catch history)
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    - 3.5.4 Summary
    - 3.5.5 Recommendations for future work
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        - 3.6.1.1 Discovery marks
        - 3.6.1.2 Natural marks (photo-id; genetic)
        - 3.6.1.3 Telemetry
        - 3.6.1.4 Other (e.g. lost harpoons)
    - 3.6.2 Stock structure
        - 3.6.2.1 Genetic information (population level)
        - 3.6.2.2 Other information (e.g. CPUE and catch history)
    - 3.6.3 Seasonal distribution
        - 3.6.3.1 Winter
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        - 3.6.3.3 Other
    - 3.6.4 Summary
    - 3.6.5 Recommendations for future work
- 3.7 Breeding Stock F
    - 3.7.1 Individual movements
        - 3.7.1.1 Discovery marks
        - 3.7.1.2 Natural marks (photo-id; genetic)
        - 3.7.1.3 Telemetry
        - 3.7.1.4 Other (e.g. lost harpoons)
    - 3.7.2 Stock structure
        - 3.7.2.1 Genetic information (population level)
        - 3.7.2.2 Other information (e.g. CPUE and catch history)
    - 3.7.3 Seasonal distribution
        - 3.7.3.1 Winter
        - 3.7.3.2 Summer
        - 3.7.3.3 Other
    - 3.7.4 Summary
    - 3.7.5 Recommendations for future work
- 3.8 Breeding Stock G
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        - 3.8.1.1 Discovery marks
        - 3.8.1.2 Natural marks (photo-id; genetic)
        - 3.8.1.3 Telemetry
        - 3.8.1.4 Other (e.g. lost harpoons)
    - 3.8.2 Stock structure
        - 3.8.2.1 Genetic information (population level)
        - 3.8.2.2 Other information (e.g. CPUE and catch history)
    - 3.8.3 Seasonal distribution
        - 3.8.3.1 Winter
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    - 3.8.4 Summary
    - 3.8.5 Recommendations for future work
- 3.9 Overall population structuring
    - 3.9.1 Breeding grounds
    - 3.9.2 Feeding grounds

- 3.9.3 Linkages between breeding grounds and feeding grounds
- 3.10 Conclusions on stock structure, including alternative hypotheses if appropriate

4. Catch information
    - 4.1 Data sources (including informal report of intersessional group)
        - 4.1.1 Whaling
        - 4.1.2 Incidental catches in fishing gear
        - 4.1.3 Ship strikes
    - 4.2 Development of 'best' and alternative catch/removal series
        - 4.2.1 Total
        - 4.2.2 By stock structure hypothesis
    - 4.3 Catch-per-unit-effort (CPUE)

5. Estimates of recent abundance and observed trends
    - 5.1 Review of methods
        - 5.1.1 Sightings surveys
        - 5.1.2 Mark-recapture
        - 5.1.3 Other (e.g. genetic, acoustic)
    - 5.2 Available estimates by stock structure hypothesis
        - 5.2.1. Breeding stocks (A, B, C, D, E, F and G)
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    - 5.3 Relating feeding ground estimates to stock structure hypotheses
    - 5.4 Trend estimates by stock structure hypothesis

6. Biological parameters
    - 6.1 Natural mortality rate
        - 6.1.1 Methods
        - 6.1.2 Estimates
    - 6.2 Age and length at attainment of sexual maturity
        - 6.2.1 Methods
        - 6.2.2 Estimates
    - 6.3 Reproductive rates
        - 6.3.1 Methods
        - 6.3.2 Estimates

7. Threats

8. Environmental parameters
    - 8.1 Carrying capacity

9. Assessment and projections
    - 9.1 Inputs for model(s)
    - 9.2 Model outcomes

10. Conclusions and recommendations to Scientific Committee
    - 10.1 Recommendations for future research
    - 10.2 Workplan for SC/58

11. Any other business

12. Adoption of report

Annex C
List of Documents

SC/A06/HW

1. ÁLAVA. J.J. AND FÉLIX, F. Logistic population curves and vital rates of the Southeastern Pacific humpback whale stock off Ecuador. 11pp.

2. ANDRIOLO, A., KINAS, P.G, ENGEL, M.H. AND MARTINS, C.C.A. Monitoring humpback whale (*Megaptera novaeangliae*) population in the Brazilian breeding ground, 2002 to 2005. 12pp.

3. PAXTON, C.G.M., BANNISTER, J.L. AND HEDLEY, S.L. Group IV humpback whales: their status from aerial and land-based surveys off Western Australia 2005. 22pp. (Published in this volume).

4. BARENDSE, J., BEST, P.B. AND THORNTON, M. Preliminary results of photo-identification of humpback whales on the west coast of South Africa. 14pp.

5. BEST, P.B. A note on the age at sexual maturity of humpback whales. 6pp. (Published in this volume).

6. BRANCH, T.A. Humpback abundance south of 60°S from three completed sets of IDCR/SOWER circumpolar surveys. 14pp. (Published in this volume).

7. NO PAPER.

8. CASTRO, C., FÉLIX, F., FORESTELL, P., HAASE, B., KAUFMAN, G. AND SCHEIDAT, M. Site fidelity of humpback whales *Megaptera novaeangliae* in Ecuador between 1991–2004, based on photo-identification. 5pp.

9. CERCHIO, S., POMILLA, C., ERSTS, P., RAZAFINDRAKOTO, Y., LESLIE, M., ANDRIANRIVELO, N., COLLINS, T., DUSHANE, J., MURRAY, A., WEBER, D., AND ROSENBAUM, H.C. Estimation of abundance of breeding stock C3 of humpback whales, assessed through photographic and genotypic mark-recapture data from Antongil Bay, Madagascar. 12pp.

10. COLLINS, T., CERCHIO, S., POMILLA, C., NGOUESSONO, S., MBADINGA, N., DUSHANE, J., MURRAY, A., WEBER, D., ERSTS, P. AND ROSENBAUM, H.C. An estimate of abundance using mark recapture data for breeding stock B1: Gabon. 8pp.

11. ENGEL, M., FAGUNDES, N.J.R., ROSENBAUM, H.C., OTT, P.H., SCHMITT, R., SECCHI, E., DALLA ROSA, L. AND BONATTO., S.L. Mitochondrial DNA variability and evaluation of the likely feeding grounds of the humpback whale (M*egaptera novaeangliae)* population of the Abrolhos Bank, Bahia, Brazil. 15pp.

12. ERSTS, P.J., POMILLA, C., ROSENBAUM, H.C., KISZKA, J. AND VÉLY, M. Humpback whales identified in the territorial waters of Mayotte [C2] and matches to Madagascar [C3]. 7pp.

13. FÉLIX, F., CASTRO, C., HAASE, B., FORESTELL, P., ALAVA, J. AND SCHEIDAT, M. Estimates of the Southeastern Pacific humpback whale stock with mark-recapture models in Ecuador. 7pp.

14. FELIX, F., MUÑOZ, M. AND HAASE, B. Bycatch of humpback whales in artisanal fishing gear in Ecuador during 2005. 5pp.

15. FÉLIX, F., PALACIOS, D.M., CABALLERO, S., HAASE, B. AND FALCONI, J. The 2005 Galápagos humpback whale expedition; a first attempt to assess and characterize the population in the archipelago. 8pp. (Published in this volume).

16. FINDLAY, K.P. AND BEST, P.B. The migrations of humpback whales past Cape Vidal, South Africa, and a preliminary estimate of the population increase rate. 36pp.

17. FORESTELL, P. H., KAUFMAN, G. D. AND CHALOUPKA, M. Abundance estimate of humpback whales in Hervey Bay, Australia, based on CMR profiles, 1988–2002. 15pp.

18. NO PAPER.

19. GARRIGUE, C., OLAVARRIA, C., BAKER, C.S., STEEL, D., DODEMONT, R., CONSTANTINE, R. AND RUSSELL, K. Demographic and genetic isolation of New Caledonia (E2) and Tonga (E3) breeding stocks. 10pp.

20. JENNER, K.C.S., JENNER, M-N., SALGADO KENT, C.P. AND BRASSEUR, M. A preliminary analysis of sampling biases of sex ratio from two seasons of biopsy samples for breeding stock D. 6pp.

21. JENNER, K.C.S., JENNER, M-N., SALGADO KENT, C.P. AND STURROCK, V.J. Recent trends in relative abundance of humpback whales in breeding stock D from aerial and vessel based surveys. 13pp.

22. JOHNSTON, S.J. AND BUTTERWORTH, D.S. Updated assessments of various breeding populations of Southern Hemisphere Humpback whales. 38pp.

23. KAUFMAN, G. D., FORESTELL, P. H., MALO, A. AND LEHMAN, S. Calving rates and intervals for East Australia female humpback whales, based on individual photo-identifications: 1984–2005. 6pp.

24. KINAS, P.G., ANDRIOLO, A. AND ENGEL, M. Integrating photo-identification and aerial surveys to estimate g(0) for humpback whales (*Megaptera novaeangliae*) in the Brazilian breeding ground. 8pp.

25. LEAPER, R., PEEL, S., PEEL, D., BRAVINGTON, M. AND GALES, N. An assessment of the west and east Australian breeding stocks of humpback whales: simulating different mixing and catch allocation on feeding grounds. 26pp.

26. LOO, J., POMILLA, C., BEST, P.B., FINDLAY, K.P. AND ROSENBAUM, H.C. Structure and diversity between feeding aggregations of humpback whales (*Megaptera novaeangliae*) using mitochondrial and nuclear DNA. 15pp.

27. NOAD, M., CATO, D.H. AND PATON, D. Absolute and relative abundance estimates of Australian east coast humpback whales (*Megaptera novaeangliae*). 15pp. (Published in this volume).

28. NOAD.. M., PATON, D.A., GIBBS, N.J. AND CHILDERHOUSE, S.J. A combined visual and acoustic survey of humpback whales and other cetaceans of Samoa. 15pp.

29. OLAVARRIA, C., AGUAYO, A., ACEVEDO, J., MEDRANO, L., THIELE, D. AND BAKER, C.S. Genetic differentiation between two feeding areas of the Eastern South Pacific humpback whale population: [Update on SC/57/SH3] 7pp.

30. NO PAPER.

31. OLAVARRIA, C., CHILDERHOUSE, S., GIBBS, N. AND BAKER, C.S. Contemporary genetic diversity of New Zealand humpback whales and their genetic relationship with Breeding Stocks D, E, F and G. 8pp.

32. PATON, D., BROOKS, L., BURNS, D., FRANKLIN, T., FRANKLIN, W., HARRISON, P. AND BAVERSTOCK, P. First abundance estimate of East Coast Australian humpback whales (*Megaptera novaeangliae*) utilising mark-recapture analysis and multipoint sampling. 11pp.

33. NO PAPER.

34. GIBBS, N., PATON, D., CHILDERHOUSE, S. AND CLAPHAM, P. Assessment of the current abundance of humpback whales in the Lomaiviti Island Group of Fiji and a comparison with historical data. 12pp.

35. PATON, D. AND KNIEST, E. Analysis of data collected during humpback whale sighting surveys at Cape Byron, Eastern Australia, 1998 to 2004. 16pp.

36. PATON, D., OOSTERMAN, A., WHICKER, M. AND KENNY, I. Assessment of sighting survey data of humpback whales (*Megaptera novaeangliae*), Norfolk Island. 9pp.

37. PEEL, D. AND THIELE, D. An estimate of abundance of humpback whales within Antarctic Area IV from the BROKE survey data. 9pp.

38. POMILLA, C., BEST, P.B., FINDLAY, K.P., COLLINS, T., ENGEL, M.H., MINTON, G., ERSTS, P., BARENDSE, J., KOTZE, P.G.H., RAZAFINDRAKOTO, Y., NGOUESSONO, S., MEŸER, M., THORNTON, M. AND ROSENBAUM, H.C. Population structure and sex-biased gene flow in humpback whales from Wintering Regions A, B, C, and X based on nuclear microsatellite variation. 22pp.

39. NO PAPER.

40. PASTENE, L.A., GOTO, M., NISHIWAKI, S., YOSHIDA, H. AND KANDA, N. Genetic characteristics and population structure of humpback whales in the Antarctic feeding ground as revealed by mitochondrial DNA control region sequencing and microsatellite analysis. 13pp.

41. ROSENBAUM, H.C., POMILLA, C.C., LESLIE, M.C., MENDEZ, M.C., BEST, P.B., COLLINS, T., ENGEL, M.H., ERSTS, P.J., FINDLAY, K.P., BONATTO, S., KOTZE, P.G.H., MEŸER, M., MINTON, G., BARENDSE, J., THORNTON, M., RAZAFINDRAKOTO, Y. AND NGOUESSONO, S. Mitochondrial DNA diversity and population structure of humpback whales from their wintering areas (Breeding Stocks) in the Indian and South Atlantic Ocean (Wintering Regions A, B C, and X). 16pp.

42. ROSENBAUM, H.C. AND MATE, B. From North of the Equator to the Antarctic: Unique and unexpected movements for humpback whales off the coast of West Africa and throughout the eastern South Atlantic Ocean. 2pp.

43. SECCHI, E., DALLA ROSA, L., KINAS, P.G., NICOLETTE, R.F. AND AZEVEDO, A., MAIA, Y.G. Abundance of humpback whale, *Megaptera novaeangliae*, in the Gerlache and Bransfield Straits, Antarctic Peninsula region. 11pp. (Published in this volume).

44. STEVICK, P.T., PACHECO DE GODOY, L., MCOSKER, M., ENGEL, M.H. AND ALLEN, J. Movement of a humpback whale from Abrolhos Bank, Brazil to South Georgia. 5pp.

45. ZERBINI. A.N., WARD, E., ENGEL, M.H., ANDRIOLO, A. AND KINAS, P.G. A Bayesian assessment of the Conservation Status of humpback whales (*Megaptera novaeangliae*) in the Western South Atlantic Ocean (Breeding Stock A). 21pp. (Published in this volume).

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50. CONSTANTINE, R., RUSSELL, K., GIBBS, N., CHILDERHOUSE, S. AND BAKER, C.S. Photo-identification of humpback whales in New Zealand waters and their migratory connections to breeding grounds of Oceania. 5pp.

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Annex D
Discovery mark summary

David Paton

SC/A06/HW33 reports on the Discovery marking data associated with the International Marking Scheme (IMS). Between 1932 and 1984, 5,165 humpback whales were reported as marked with Discovery marks in the Southern Hemisphere. Of these 3,111 humpbacks were reported as confirmed hits. Discovery marking was undertaken both on the breeding grounds and the feeding grounds. Concentrated effort in Discovery marking was undertaken within Areas IV and V with a total of 91% of humpback whales marked in the Southern Hemisphere marked within these two regions. Within these two Areas, the Discovery marking effort has been conducted in both the breeding grounds/migratory corridor (65% of confirmed hits) and the feeding grounds (35% of confirmed hits).

The whaling data also show a strong bias towards catch effort in Areas IV and V with 29% and 41% of the total catch for the Southern Hemisphere humpback whale catch between 1947 and 1973 recorded in these Areas respectively. A total of 204 Discovery marks were reported returned under this scheme for the Southern Hemisphere. Areas IV and V recorded the highest percentage of Discovery mark returns, with 34% and 58% respectively.

The Discovery mark data support the original finding of Mackintosh (1942) in relation to the stock structure for Southern Hemisphere humpback whales forming relatively discrete groups with strong linkages associated between breeding grounds within the longitudinal boundaries of the feeding grounds, and relatively low incidence of large-scale movement between areas.

Further analysis is required to assess bias associated with marking and whaling effort. Exclusion of short period recoveries from the analysis is also required.

Table 1
Discovery mark results, by area, for all recoveries under the International Marking Scheme.

Area marked	Area recaptured					
	I	II	III	IV	V	VI
I	4 (80%)	1 (20%)	0	0	0	0
II	0	2 (100%)	0	0	0	0
III	0	0	7 (100%)	0	0	0
IV	0	0	0	58 (98%)	1 (2%)	0
V	1(0.75%)	0	0	12 (9.1%)	119 (90.15%)	0
VI	0	0	0	0	1 (50%)	1 (50%)

REFERENCE

Mackintosh, N.A. 1942. The southern stocks of whalebone whales. *Discovery Rep.* 22: 197–300.

Annex E

Assessment of genetic differentiation between Breeding Stocks A, B, C and X, and Areas I, II and III based on mtDNA

J.C. Loo[5,2,3], C.C. Pomilla[2,3], M.C. Mendez[1,2,4], M.C. Leslie[1,2], and H.C. Rosenbaum[1,2,3,4]

INTRODUCTION

In order to evaluate connections of Breeding Stocks in the Indian and South Atlantic Oceans with Antarctic Feeding grounds for humpback whales, we present an analysis of mtDNA control region sequences for Breeding Stocks A, B, C and X with Areas I, II and III.

METHODS

DNA isolation, purification and sequencing methodologies are detailed in SC/A06/HW41. In order to characterise patterns of genetic variation and gene flow between Breeding Regions B and C and Feeding Areas I, II and III, we followed the same statistical procedures detailed in SC/A06/HW41. This study includes all samples analysed in our previous report and incorporates 92 samples from Areas I, II and III.

RESULTS

Pairwise comparisons at the haplotype and nucleotide levels show significant differences between Breeding Region X and all feeding Areas, and between Feeding Area I and all wintering regions included in this study. In addition, Breeding Region A was significantly different from Area III at the haplotype level. No further differentiation was found between wintering sub-Regions and Areas II and III at both haplotype and nucleotide level.

The exact test of differentiation provided further resolution to that offered by our comparisons using ϕ_{ST} and F_{ST} indices. In addition to what was seen when computing pairwise comparisons using fixation indices, there are significant differences among the following population comparisons: Breeding Region A vs Feeding Areas II and III, Breeding Sub-Region B1 vs Feeding Area III, and Breeding Sub-Region C3 vs Feeding Area II.

DISCUSSION

Our study suggests that Area I is genetically isolated from Breeding Regions A, B, C and X. Differentiation of Area I is consistent with the current knowledge that individuals summering in this Area migrate to the western coast of South America, and with the lack of evidence of mixing of this population with other Southern groups.

Humpback whales wintering in Region X are believed to comprise the only population that does not undertake the characteristic seasonal migration observed in this species. Our results, depicting a clear lack of gene flow between Region X and all Feeding Areas, support this hypothesis.

The lack of significant differences for comparisons between Regions B and C and Feeding Areas II and III suggests that whales feeding in any of these two Areas may use both wintering regions, the degree to which remains uncertain. We cannot, however, rule out ancestral polymorphism presence, or historical gene flow causing this lack of differentiation.

Region A shows conflicting results with different tests as to connection to Area II, probably due to the fact that our Area II sample included samples collected around Sandwich Islands and Bouvet Island, while previous data so far support connection of Region A only to Sandwich Island (SC/A06/HW11). Further work will be conducted to compare Area IIW and IIE samples separately as in SC/A06/HW26. Sub-Region B1 does not show significant differences with Area II, whereas sub-Region B2 and C1 do not show differentiation from Areas II and III, and sub-Regions C2 and C3 are not significantly differentiated from Area III.

The opportunistic basis of the sample collection in the feeding grounds, as well as the small sample sizes presented, suggest some caution in the interpretation of these results. These results are highly preliminary, a more detailed analysis and exploration of scenarios needs to be explored using

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[1] *WCS/AMNH Cetacean Conservation and Research Program, c/o Marine Conservation, Wildlife Conservation Society, 2300 Southern Blvd., Bronx, NY 10460–1099, USA.*

[2] *Molecular Systematics Laboratory and Conservation Genetics Program, American Museum of Natural History, 79th Street and Central Park West, New York, NY 10024, USA.*

[3] *American Museum of Natural History,Center for Biodiversity and Conservation, 79th Street and Central Park West, New York, NY 10024, USA.*

[4] *Columbia University, Department of E3B, New York, New York.*

[5] *Department of Biology, New York University, 1009 Silver Center,100 Washington Square East, New York, NY 10003, USA.*

mtDNA and 11 microsatellite loci. To have the fullest power of the analysis, all available IDCR/SOWER samples are needed.

In summary, our results support:

(1) genetic isolation between Area I and Breeding Regions A, B, C and X;
(2) genetic isolation between Breeding Region X and Areas I, II and III;
(3) genetic isolation between Region A and Feeding Area III, but an uncertain degree of differentiation between Region A and Feeding Area II; and
(4) no significant differentiation between Feeding Areas II and III with respect to Breeding Regions B and C.

Table 1

Sample size (*n*) for each of the sites included in this study.

Site	*n*	Site	*n*
Breeding Stocks		**Feeding areas**	
Stock A (West South Atlantic Ocean)	164	Area I (170ϒW-50ϒW)	
Region B (Southeastern Atlantic Ocean)		Western Antarctic Peninsula	41
B1	466	Area II (50Wϒ–0ϒ)	
B2	119	South to Sandwich Is – South to Bouvet I.	24
Region C (Southwestern Indian Ocean)		Area III (0ϒ–70ϒE)	
C1	151	Off Eastern Queen Maud Land-Off Mac Robertson Land (III)	27
C2	78		
C3	511		
Region X (Northern Indian Ocean)	38		

Table 2

Genetic differentiation between ten sampling sites, including three wintering regions, and three feeding areas. Pairwise ϕ_{ST}-values, F_{ST}-values and *P*-values for the exact test of differentiation are presented. Significant values are in bold ($P<0.05$), as estimated from 10,000 random permutations.

	ϕ- statistics			*F* - statistics			Exact test		
	I	II	III	I	II	III	I	II	III
A	**0.02546**	-0.00078	0.00088	**0.05442**	0.00382	**0.00919**	**0.00000**	**0.03980**	**0.00000**
B1	**0.03081**	-0.00665	0.00748	**0.0476**	-0.00205	0.00503	**0.00000**	0.24565	**0.00335**
B2	**0.02952**	-0.00792	-0.00535	**0.05286**	0.00159	0.00358	**0.00000**	0.18820	0.26250
C1	**0.02046**	-0.00919	0.00174	**0.04791**	-0.00525	–0.00002	**0.00000**	0.56520	0.33150
C2	**0.02756**	-0.00281	-0.00511	**0.05406**	0.00167	–0.0002	**0.00000**	0.05625	0.16580
C3	**0.02658**	-0.00301	0.00045	**0.04860**	0.00075	–0.00486	**0.00000**	**0.02970**	0.54570
X	**0.15396**	**0.08936**	**0.11033**	**0.20128**	**0.15224**	**0.11925**	**0.00000**	**0.00000**	**0.00000**

Annex F
Consideration of observed male-skewed sex ratios in humpback whales

M. Noad, D. Mattila, P. Wade, C. Salgado-Kent, S. Cerchio, C. Garrigue

The study in SC/A06/HW21 led into a discussion of the general issue of the male-skewed sex ratios that are commonly observed on breeding grounds and sometimes in other areas such as on migration routes. Irrespective as to whether this is a real phenomenon or is only due to sampling issues, it may lead to underestimation of abundance, especially with respect to mark-recapture studies. This can be explored in sensitivity analyses to examine whether it has a major effect on assessment models (i.e. increase potentially affected abundance estimates by an assumed amount and investigate the influence of this higher abundance on assessment results). A brief discussion was held on how this possible source of bias could be avoided in sampling schemes, such as having shore-based observers select groups to be sampled and relay this information to boat-based biopsy samplers, but there was insufficient time to discuss this in any detail.

Some evidence for true 50:50 sex ratio on breeding grounds

(1) Catches in Western Australia had a ratio of approximately 1.4:1 and Dawbin (1997) felt that male-biased sex ratios in the catch record were due to selection bias against females by whalers.
(2) Autumn-Winter aerial surveys in the Gulf of Maine showed that all whales departed the feeding grounds to presumably migrate to the breeding grounds.

Mechanisms that could cause biased sex ratio on all or part of a breeding ground

(1) Males reside longer on breeding grounds.
(2) Males may aggregate (the 'floating lek' hypothesis) and so higher density areas are probably male biased.
(3) Some females do not migrate – this seems unlikely as empirical evidence points to growth rates in some populations that are not feasible without all or most females migrating every year to alternately calve and mate.

Sampling problems that could cause bias in the observed sex ratio

(1) Greater detection and subsequent sampling of larger groups that are known to contain more males than females.
(2) Greater boat avoidance by females.
(3) Groups including females may be harder to approach and take more time and effort in order to successfully collect a sample.
(4) Large groups, which are easier to see are likely to contain a higher proportion of males.
(5) More difficulty in sampling pods of one or two animals which are likely to contain females.
(6) Sampling on higher density areas that may be male biased even if the whole breeding area is not.

REFERENCE

Dawbin, W.H. 1997. Temporal segregation of humpback whales during migration in Southern Hemisphere waters. *Mem. Queensl. Mus.* 42(1): 105–38.

Annex G
Considerations for matching large photo-identification catalogues

D. Mattila, S. Cerchio, P. Forestell, C. Garrigue, K. Matsuoka, D. Paton, M. Poole, C. Salgado-Kent

Comparing large photo identification catalogues can be very useful in illuminating a number of demographic parameters identified by this workshop. However, these efforts can be time consuming and/or costly, and may not answer the questions intended. Conversely, it may not be necessary to match all images to sufficiently answer some questions. Therefore, careful thought should be given to the following considerations:

What are the questions being addressed? These might range from:

(1) definition of population structure through exchange rates;
(2) distribution and residency of individuals within habitats;
(3) abundance estimates (e.g. mark/recapture, rates of discovery); and
(4) biological parameters (e.g. reproductive rates, survivorship, social organisation).

Catalogues which are candidates for comparison should be examined for the following:

(1) the area sampled and the likelihood of exchange to another area;
(2) year and season the images were collected;
(3) number of individuals identified in the catalogue;
(4) comparability of body parts used in identification (e.g. fluke, dorsal, lateral marks);
(5) biases associated with sampling for each catalogue (e.g. sampling platform, primary focus of study);
(6) other information associated with identifications (e.g. age, sex, reproductive history, genetics); and
(7) format of the images (e.g. black and white or colour, print or digital).

With regard to the actual process of matching, the following considerations were highlighted:

(1) reduction of the number of images to be matched through elimination of poor quality images is advantageous;
(2) understand resources available (e.g. personnel, funds);
(3) clearly define match criteria; and
(4) decide on appropriate matching process (e.g. pair-wise, stratified, double blind, computer assisted).

The Working Group is aware of several ongoing efforts to improve the efficiency of the image matching process itself as well as quantifying any problems or biases involved.

A sample of the quality screening criteria developed by Cascadia Research Collective was reviewed, and is given as Appendix 1.

Conclusion

The Working Group **agreed** to the following recommendations:

(1) large catalogues should be screened for quality prior to matching, eliminating poor quality images – this will save time and resources and produce a less biased outcome;
(2) the IWC Scientific Committee should clearly identify the highest priority questions to be addressed and the catalogues that would most likely be used to answer those questions;
(3) a standardised quality screening and match criteria should be identified; and
(4) the IWC Scientific Committee should review previous studies and ongoing efforts to improve photo-identification matching techniques and analyses of error and bias.

Appendix 1

CASCADIA RESEARCH COLLECTIVE FLUKE SCREENING CRITERIA

The quality of the photograph is graded based on: the proportion of the fluke that was visible in the photograph, fluke angle (i.e., how perpendicular it is to the water), the lateral angle of the photographer, the sharpness and grain and the photographic quality (lighting, exposure and contrast), as follows:

Proportion of fluke visible
1 – 100%
2 – 75–99%
3 – 50–74% (base of notch still visible)
4 – <50%
5 – right/left side only

Fluke angle:
1 – perpendicular to the water
2 – short of perpendicular but no loss in visibility
3 – short of perpendicular with some loss in quality but ridging easily visible
4 – low angle, ridging only partially visible
5 – low angle, ridging and markings not visible or very distorted

Photographer lateral angle:
1 – straight behind
2 – not directly behind but minimal distortion
3 – angled about 45° to side
4 – angled >45° but markings still visible
5 – angle so extreme most markings obscured

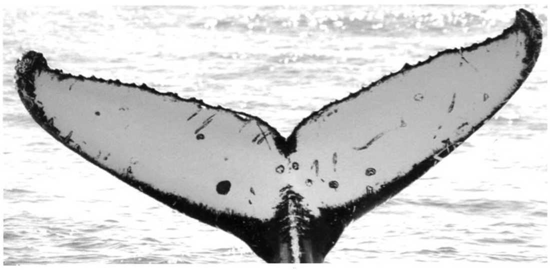
Focus/sharpness:
1 – excellent focus with clear grain
2 – good focus and grain with only minimal loss in quality
3 – okay focus and grain with some loss in ability to discern marks and edges
4 – fair to poor focus in grain with significant loss in clarity
5 – soft focus/grainy with extreme loss in detail

Lighting/contrast/exposure:
1 – excellent lighting and contrast, any marks present would be seen
2 – good but with some loss in contrast on ventral surface
3 – fair, some marks might not be seen at all but most would likely be visible
4 – fair to poor with significant backlighting or exposure problems
5 – poor (e.g. back lit or gray), likely many marks would not be visible

Examples of each grade are given below in Fig. 1.

Proportion visible

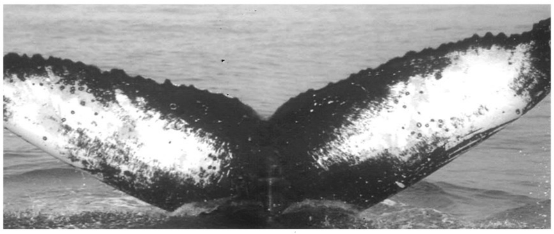
1 = 100%
2 = 75-99%
3 = 50-74%
4 = <50%
5 = partial



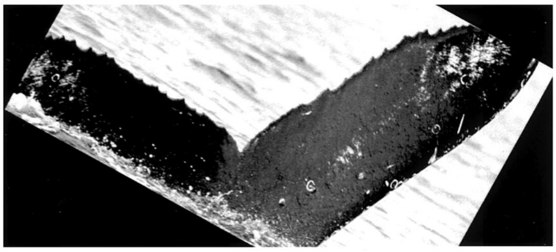
1 = 100%

2 = 75-99%

3 = 50-74% of fluke surface (top of notch still visible)
AND >80% of trailing edge visible.

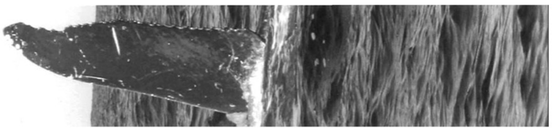


3 = 50-74% of fluke surface (top of notch still visible)
AND >80% of trailing edge visible.



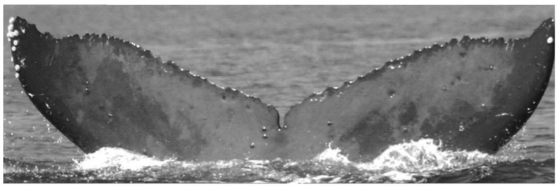
4 = <50% fluke surface OR <80% of trailing edge visible.

4 = <50% fluke surface OR <80% of trailing edge visible.



5 = partial

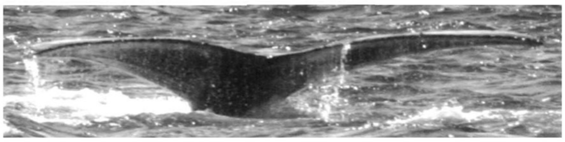
Fluke angle



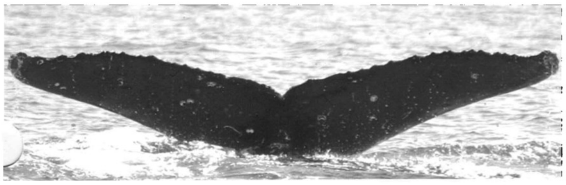
1 = perpendicular to the water

4 = low angle, ridging only partially visible

2 = short of perpendicular but no loss in visibility

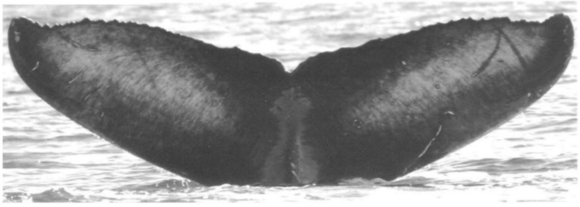


5 = low angle, ridging and markings not visible or very distorted

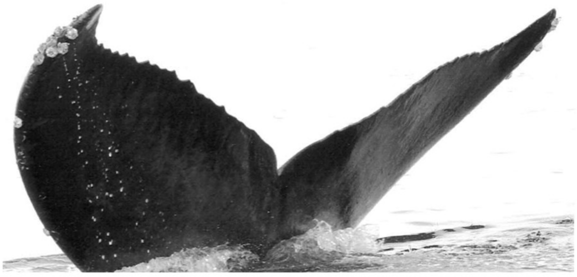


3 = short of perpendicular

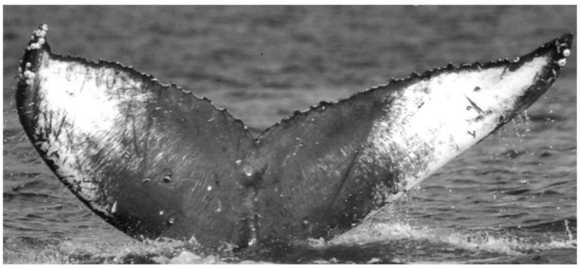
Photographer lateral angle



1 = straight behind

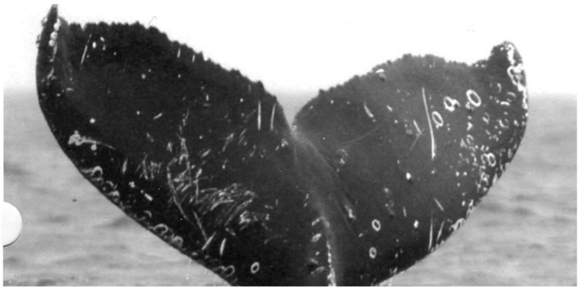


4 = angled >45° but markings still visible



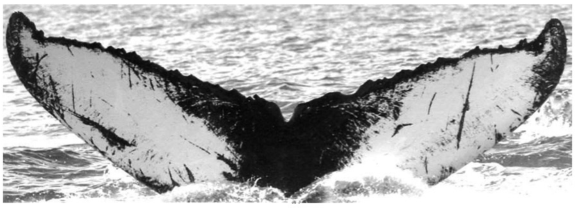
2 = not directly behind but minimal distortion

5 = angle so extreme most markings obscured

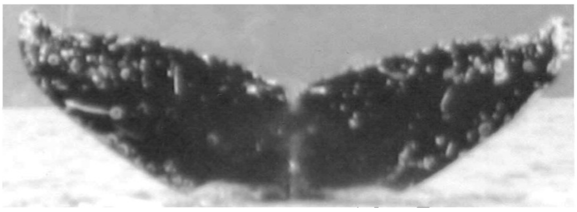


3 = angled about 45° to the side

Focus

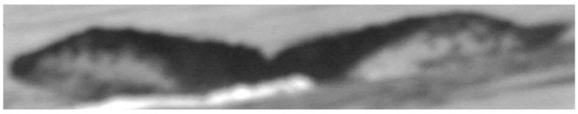


1 = in focus with clear grain



4 = fair to poor focus and grain with significant loss in clarity

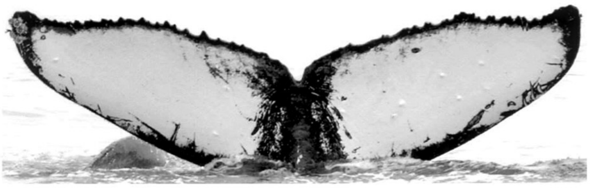
2 = good focus and grain with only minimal loss in quality



5 = soft focus/grainy

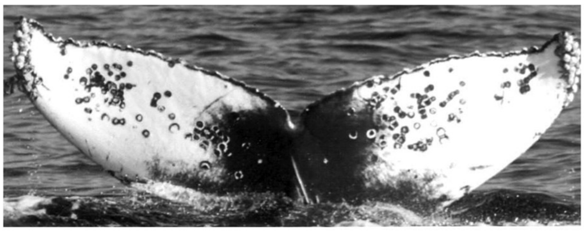
3 = OK focus and grain, some loss in ability to discern marks and edges

Exposure/contrast/lighting (light flukes)

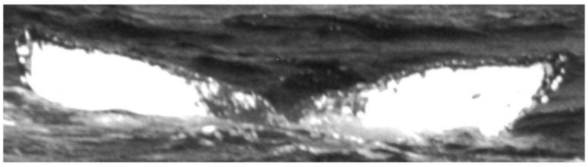


1 = excellent, all marks would be seen

4 = fair to poor with significant backlighting or exposure problems; may be difficult to assign colour category



2 = good but with some loss in contrast on the ventral surface



5 = poor (backlit or grey), likely some marks marks would not be visible; may be difficult to assign colour category

3 = OK, some marks might not be seen

Annex H
Recommendations for each Breeding Stock

Breeding Stock A

Recommendations for work to be completed for the 2006 Annual Meeting are detailed in the main report under Item 10.2. The Workshop **agrees** the following longer term priority recommendations for Breeding Stock A.

(1) Determine whether the northern coast of South America (north and west of 5°S) and oceanic islands off the coast of eastern South America (Fernando de Noronha, São Pedro and São Paulo Archipelago, and Trindade and Martin-Vaz) are areas of regular occurrence of humpback whales and determine their relationship (e.g. through photo-identification, genetic and/or satellite telemetry data) with the main population along the coast of Brazil;

(2) Increase research effort to collect biopsy samples and photo-identification data in the wintering and feeding grounds and migration paths to aid the following objectives:
   (a) investigate whether sub-structuring of the population occurs in the wintering grounds;
   (b) investigate the degree of interchange/isolation within and among wintering and feeding grounds; and
   (c) estimate demographic parameters (e.g. survival, birth rate, age at first parturition).

(3) Satellite telemetry work should continue in the wintering grounds and be initiated in the feeding areas with the following purposes:
   (a) investigate movement across current stock boundaries and possible interchange of individuals with other breeding populations;
   (b) investigate alternative migratory routes and feeding-breeding ground connections;
   (c) identify critical habitat; and
   (d) investigate movements, behaviour and habitat use in relation to oceanographic and biological variables (e.g. distribution and concentration of food).

(4) Compare songs of whales from this breeding stock with others (especially B and G) to better understand the potential cultural connections between these stocks as suggested by preliminary studies (e.g. Darling and Sousa-Lima, 2005).

Breeding Stock B

The Workshop **agrees** to the following recommendations with respect to Breeding Stock B.

(1) Available evidence (satellite tagging, photographic and genetic studies, other reports and whaling data) suggests a region wide presence during the breeding season. The prevailing data presented at the Workshop were restricted largely to the coastal waters of Gabon (B1) and along the west coast of South Africa (B2). The Workshop **recommends** additional systematic boat-based surveys that will yield information on estimates of abundance and occurrence of calves, as well as photo-identification data for life history information and collection of genetic samples from under-surveyed areas in B1 and B2. Specifically survey and collections should occur at:
   (a) west coast of South Africa and Namibia;
   (b) Angola;
   (c) Gabon out to São Tomé and Principe;
   (d) northern Gulf of Guinea and Bioko Island; and
   (e) southern coast of West Africa.

The Workshop **recommends** that survey effort across these regions be concurrent. The relevance of such surveys to the Comprehensive Assessment includes both estimation of abundance from areas for which no abundance estimates are currently available and the strengthening of the understanding of alternative models of stock structure and number of breeding stocks within the Breeding Stock B region.

(2) Genetic results are providing information on structure and interchanges within and between B sub-regions. These include evidence for clearer separation of B1 and B2, and a number of breeding stocks within the B1 region. The Workshop **recommends** that the large-scale genetic analyses be continued and expanded with new approaches to help resolve issues of relationships and population structure within this region, as well as connectivity to feeding grounds.

(3) Small boat surveys at existing field sites are largely focused on the period of July–October (B1), but an out-of-season presence is suspected. The Workshop **recommends** a greater degree of temporal coverage in survey effort.

(4) Telemetry studies in B1 have informed stock structure, migratory routes and destinations for some B1 whales. The Workshop **recommends** that new satellite tagging studies be initiated to identify breeding destinations for whales observed feeding in B2. Tagging should be conducted off:
   (a) west South Africa in both early and late breeding seasons (on either end of migration);
   (b) Angola, southern boundary of B1; and
   (c) upper and/or offshore Gulf of Guinea, northern area of B1.

(5) Additional samples are needed from the Antarctic feeding grounds to help elucidate these high and low latitude connections as well as to discriminate among hypotheses concerning mixing on the feeding grounds.

The Workshop **recommends** that the genetic sampling of humpback whales remains a high priority of SOWER cruises. In order to facilitate this work, the Workshop **recommends** that samples from the 2006 SOWER cruise (Area III, $n = 71$) be transferred as soon as possible to the WCS/AMNH Cetacean Conservation and Research Program for analysis and subsequent transfer back to SWFSC for storage.

(6) Large-scale line transect surveys have the potential to estimate density, abundance and distribution of animals and establish coverage for areas that are difficult to sample comprehensively from shore (i.e. offshore distributions and diverse archipelago systems with humpback whale concentrations). Thus far, no ship-based surveys have taken place in the B region. The Workshop **recommends** that efforts be made to undertake more extensive ship-based surveys throughout the B sub-regions to estimate densities and collect information from areas that are difficult to survey.

The relevance of such surveys to the Comprehensive Assessment is estimation of abundance from areas for which no abundance estimates are currently available and the strengthening of the understanding of overlap of the B1 and B2 sub-populations and number of breeding stocks, through co-incident genetic and natural mark sampling.

(7) The Workshop **recommends** the involvement of scientists from relevant states in the region, and facilitation for future participation in IWC workshops or Scientific Committee meetings.

Breeding Stock C

(1) Based on: (i) un-surveyed areas of humpback whale concentration in northern C1, throughout C2 and in western and southern Madagascar; and (ii) identified C1, C2 and C3 connectivity (SC/A06/HW12), the Workshop **recommends** additional systematic boat-based surveys to gain information on estimates of abundance, as well as other life history information, and collection of genetic samples from under-surveyed areas in northern C1, C2 and in western and southern C3.

Specifically survey and collections should occur at:

(a) Grand Comoro Island, west side of C2;
(b) Mayotte, east side of C2;
(c) Toliara, southwest coast of Madagascar, C3;
(d) Nosy Bé, northwest coast of Madagascar, C3;
(e) Fort Dauphin, southeast coast of Madagascar, C3;
(f) Mascarene Islands;
(g) Pemba coast, northern Mozambique, C1 (initial surveys possibly to start in July 2006); and
(h) Mafia Island, Tanzania, C1.

The Workshop **recommends** that survey effort across these regions be concurrent. The relevance of such surveys to the Comprehensive Assessment includes both estimation of abundance from areas for which no abundance estimates are currently available and the strengthening of the understanding of overlap of the C1, C2 and C3 sub-populations.

(2) Genetic results have yielded valuable information concerning population structure and interchanges within and between C sub-regions. The Workshop **recommends** that the large scale genetic analyses be continued and expanded with new approaches to help resolve issues of relationships and population structure within this region, as well as connectivity to feeding grounds.

(3) Additional samples are needed from the Antarctic Feeding Grounds to help elucidate these high and low latitude connections as well as to discriminate among hypotheses concerning mixing on the feeding grounds. The Workshop **recommends** that the genetic sampling of humpback whales remains a high priority of SOWER cruises. In order to facilitate this work for the next two Annual Meetings, the workshop recommends that samples from the 2006 SOWER cruise (Area III, $n = 71$) be transferred directly to the WCS/AMNH Cetacean Conservation and Research Program for analysis and subsequent transfer to SWFSC.

(4) The satellite telemetry studies in the South Atlantic have greatly helped to identify stock structure and migratory routes and destinations, accordingly the Workshop **recommends** that satellite tagging studies be initiated in as many components of the C sub-region as possible. Tagging sites and times should be chosen to best discern northern and southern migratory movements in C1, distribution and movements throughout C2 and around Madagascar in C3, and interconnections between the 3 sub-regions. Such studies provide relatively rapid and cost effective results to further the understanding of migratory movements within the C region.

(5) Line transect surveys have the potential to estimate densities of animals and establish coverage for areas that are difficult to sample comprehensively (i.e. offshore distributions and diverse archipelago systems with humpback whale concentrations). Thus far only ship-based surveys have taken place in the southern and central C1 sub-regions, although a yacht-based line transect survey has been undertaken across the southern Madagascar region. The Workshop **recommends** that efforts be made to undertake more extensive ship-based surveys throughout the C sub-regions to estimate densities and collect information from areas that are difficult to survey.

These should include:

(a) northward up the coast of Mozambique to Tanzania;
(b) west along the coast of Madagascar and into the Mozambique Channel;
(c) throughout the Comoros Islands; and
(d) south of Madagascar to Walter's Shoal.

The relevance of such surveys to the Comprehensive Assessment is the estimation of abundance from areas for which no abundance estimates are currently available and the strengthening of the understanding of overlap of the C1, C2 and C3 sub-populations, through co-incident genetic and natural mark sampling.

(6) A comprehensive comparison of biological (photographic, genetic and acoustic) data collected in Regions A, B, C, D and X is needed to evaluate the existing preliminary findings of differences and similarities between these regions. The Workshop **recommends** that this work be undertaken and completed in order to finish the Comprehensive Assessment.

(7) Few estimates of population trends are available for Southern Hemisphere humpback whales apart from those arising from the coasts of Australia. The Workshop **recommends** the immediate continuation of the shore-

based surveys at Cape Vidal, South Africa to further the preliminary increase rate provided in SC/A06/HW16. Given the completed series of surveys, it is suggested that this be high priority.

(8) The workshop recommends the involvement of scientists from relevant states in the region, and facilitation for their future participation in IWC workshops or Scientific Committee meetings.

Breeding Stock D

Priority 1 – Genetic analyses

The Workshop noted that only limited genetic comparisons have been made between Breeding Stock D and other breeding areas, especially the Australian coastal areas of Breeding Stock E, despite the existence of relatively large numbers of samples. It **strongly recommends** that further genetic comparisons should be made between western Australia and adjacent breeding areas, particularly coastal eastern Australia (within Breeding Stock E) as soon as possible; this is essential to providing the necessary information on stock structure for the completion of the assessment.

Based on information in the metadata table available on the IWC website* those involved should include Brasseur (Edith Cowan University, Western Australia) and Pastene (ICR) – for samples from Breeding Stock D, both on the breeding and feeding grounds – and Anderson (Southern Cross University, New South Wales), Pastene (ICR), Olavarria (University of Auckland), and Paton (Southern Cross University) – for samples from Australian coastal Breeding Stock E, on breeding and feeding grounds. Given his previous involvement, Baker (University of Auckland) should also participate.

Priority 2 – Photo-identification comparisons

Again, the Workshop noted that despite large sample sizes, there has been no major comparison of photographs from western and eastern Australia. It therefore **strongly recommends** that such a comparison should be conducted as soon as practical, with a primary goal of examining connections between areas and estimating movement rates, both of which are extremely important to the completion of the assessment. From previous experience with comparison of large catalogues, it was **agreed** that rigorous fluke photo quality grading be conducted prior to matching, in order to efficiently allocate research resources and to facilitate efficient matching. Further details are given in Annex G.

Based on information in the metadata table available on the IWC website*, those involved should include, for Breeding Stock D, Jenner (Centre for Whale Research, Western Australia), Burton (Western Whale Research, Western Australia) and Kaufmann (Pacific Whale Foundation), and for Breeding Stock E, at least Franklin (Southern Cross University), Kaufmann (Pacific Whale Foundation), Paton (Southern Cross University) and Pastene (ICR).

Breeding Stocks E and F

Priority 1 – Genetic analyses

The Workshop noted that genetic comparisons have not been made between other breeding grounds and the migratory corridor of eastern Australia or the presumed breeding grounds of the Great Barrier Reef. It **strongly recommends** that genetic comparisons should be made between eastern Australia and the rest of Breeding Stocks E and F, as well as with western Australia (see main report Item 3.5.5); this is essential to providing the necessary information on stock structure for the completion of the assessment.

Priority 2 – Photo-identification comparisons

Again, the Workshop noted that despite large sample sizes, there has been no major comparison of photographs from eastern Australia with those from western Australia and Oceania. It therefore **strongly recommends** that such a comparison should be conducted as soon as practical, with a primary goal of examining connections between areas and estimating movement rates, both of which are extremely important to the completion of the assessment. From previous experience with comparison of large catalogues, it was **agreed** that rigorous fluke photo-quality grading be conducted prior to matching, in order to efficiently allocate research resources and to facilitate efficient matching. Further details are given in Annex G.

Other recommended research include the following.

(1) Filling in gaps in known or suspected regions of known or suspected, past or present high density by vessel-based, aerial or acoustic surveys:
   (a) Great Barrier Reef, including connectivity to eastern Australia migratory corridor and Hervey Bay; and
   (b) Chesterfield Reef, including connectivity to eastern Australia migratory corridor and Hervey Bay.

(2) Maintain or initiate surveys intended for historical comparison to CPUE and model trajectories, particularly in regards to resolving apparent variability in recovery:
   (a) Point Lookout, eastern Australia;
   (b) Cook Strait;
   (c) Norfolk Island; and
   (d) Fiji.

(3) Continue surveys in key location of eastern Australia and Oceania, particularly in regards to evaluating trends in abundance for Oceania:
   (a) eastern Australia: Point Lookout/Byron Bay/Hervey Bay/Whitsundays/Eden;
   (b) New Caledonia;
   (c) Tonga;
   (d) Cook Islands; and
   (e) French Polynesia.

(4) Resolve the degree of demographic and genetic interchange/isolation between eastern Australia migratory corridor and breeding grounds of Oceania by:
   (a) photo-id comparison of eastern Australian catalogues with Oceania (one component of which is planned by Garrigue and others for November 2006);
   (b) analysis of genetic differentiation between eastern Australia and Oceania (migratory corridor and migratory destinations, if possible) using both mtDNA and microsatellites; and
   (c) analysis of song exchange.

(5) Further resolve the degree of demographic and genetic interchange/isolation between eastern Australia's migratory corridor and breeding grounds of Oceania by:
   (a) improved Photo-id analysis for primary regions of Oceania using multi-state, closed or open capture-recapture models;
   (b) further analysis of genetic differentiation among Oceania using both mtDNA and microsatellites by sex and year; and
   (c) analysis of song exchange.

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[*] *http://www.iwcoffice.org/_documents/sci_com/workshops/Table2.pdf* accessed October 2011.

(6) Further investigation of Discovery marking and recovery:
  (a) investigate effort distribution as failing to take this into account can bias perceptions of proportions of whales moving between regions; and
  (b) exclude short period recoveries from analysis of returns.

(7) Initiate satellite tagging to address key questions of migratory destinations:
  (a) in New Zealand to track northward migration to breeding grounds destinations (Fiji?);
  (b) in French Polynesia to track southward migration to feeding area destination (Area VI?); and
  (c) in eastern Australia to track northward migration to breeding ground destinations (GBR).

(8) Further analysis of sex bias to:
  (a) correct (if necessary) shore-based counts from eastern Australia; and
  (b) correct (if necessary) for multi-year sighting/resighting analysis.

(9) Further analysis of migratory connections to feeding grounds (areas) by:
  (a) directed photo-id comparison of eastern Australia and Oceania to IDCR/SOWER, JARPA and other studies (one component of which is under proposal to the Data Availability Group by Garrigue); and
  (b) mtDNA and microsatellite assignment and analysis of differentiation for breeding ground and feeding area samples from IDCR/SOWER (underway by several groups but requires improved access to IDCR/SOWER samples).

Breeding Stock G

The Workshop **recommends** that it is a high priority that existing catalogues from Panama, Costa Rica, Columbia and Ecuador be fully reconciled and compared to catalogues from Antarctica and the Magellan Strait.

Breeding Stock X

Given that the humpback whales of Region X represent an isolated population that has a very low estimate of abundance, the Workshop **strongly recommends** that further research be undertaken that will aid in protection of this stock.

There are whales in unsampled areas between Oman and other study areas in Africa and Western Australia. The Workshop **recommends** that studies should be conducted in these areas.

It **recommends** that further genetic sampling and analysis be completed to more conclusively determine the degree of differentiation for humpback whales of Region X and the timing of its separation from other humpback whale populations.

Distribution of whales in Region X clearly occurs throughout areas of the Arabian Sea but surveys conducted to date have been limited to the coast of Oman. The Workshop encourages more survey effort in other areas to evaluate movements and relationships with whales off the coast of Oman.

Given the seasonal limitations in survey effort and an unresolved degree of movement and connectivity with other concentrations of humpback whales in the Indian Ocean, the Workshop suggests that satellite telemetry studies be initiated.

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Humpback whale abundance south of 60°S from three complete circumpolar sets of surveys

T.A. BRANCH*

MARAM (Marine Research Assessment and Management Group), Department of Mathematics and Applied Mathematics, University of Cape Town, Rondebosch, 7701, South Africa
Contact e-mail: tbranch@uw.edu

ABSTRACT

Austral summer estimates of abundance are obtained for humpback whales (*Megaptera novaeangliae*) in the Southern Ocean from the IWC's IDCR and SOWER circumpolar programmes. These surveys have encircled the Antarctic three times: 1978/79–1983/84 (CPI), 1985/86–1990/91 (CPII) and 1991/92–2003/04 (CPIII), criss-crossing strata totalling respectively 64.3%, 79.5% and 99.7% of the open-ocean area south of 60°S. Humpback whales were absent from the Ross Sea, but were sighted in all other regions, and in particularly high densities around the Antarctic Peninsula, in Management Area IV and north of the Ross Sea. Abundance estimates are presented for each CP, for Management Areas, and for assumed summer feeding regions of each Breeding Stock. Abundance estimates are negatively biased because some whales on the trackline are missed and because some humpback whales are outside the survey region. Circumpolar estimates with approximate midpoints of 1980/81, 1987/88 and 1997/98 are 7,100 (CV = 0.36), 10,200 (CV = 0.30) and 41,500 (CV = 0.11). When these are adjusted simply for unsurveyed northern areas, the estimated annual rate of increase is 9.6% (95% CI 5.8–13.4%). All Breeding Stocks are estimated to be increasing but increase rates are significantly greater than zero only for those on the eastern and western coasts of Australia. Given the observed rates of increase, the current total Southern Hemisphere abundance is greater than 55,000, which is similar to the summed northern breeding ground estimates (~60,000 from 1999–2008). Some breeding ground abundance estimates are far greater, and others far lower, than the corresponding IDCR/SOWER estimates, in a pattern apparently related to the latitudinal position of the Antarctic Polar Front.

KEYWORDS: ABUNDANCE ESTIMATE; ANTARCTIC; BREEDING GROUNDS; DISTRIBUTION; FEEDING GROUNDS; MONITORING; SOUTHERN HEMISPHERE; SOUTHERN OCEAN; SOWER; SURVEY–VESSEL; TRENDS

INTRODUCTION

The International Whaling Commission (IWC) is engaged in a multi-year in-depth assessment of the current status of Southern Hemisphere humpback whales (*Megaptera novaeangliae*). Assessments of the individual Breeding Stocks rely heavily on current estimates of abundance from both their northern breeding grounds and their southern feeding grounds in the Antarctic (Johnston *et al.*, 2011; Zerbini *et al.*, 2011). The IWC currently recognises seven stocks of humpbacks in the Southern Hemisphere that migrate between northerly winter breeding grounds and summer Antarctic feeding grounds, and one (Breeding Stock X) that inhabits the northern Indian Ocean year-round for both breeding and feeding. The simplest way of assigning each Breeding Stock to an Antarctic summer feeding ground is given by the IWC's Naïve model, which assumes that there is no overlap between Breeding Stocks when they are in the Antarctic (IWC, 1998; 2006). The seven Breeding Stocks and their assumed longitudinal range in the Antarctic according to this Naïve model are:

(a) Brazil, especially the Abrolhos Bank (Antarctic: 50°W–20°W);
(b) Central west Africa particularly Gabon (B1) and a separate substock off western Namibia and South Africa (B2) (Antarctic: 20°W–10°E);
(c) Coastal waters of Mozambique (C1), central Mozambique Channel islands (C2) and coastal waters of north and east Madagascar (C3) (Antarctic: 10°E–60°E);
(d) Coastal western Australia, especially 15–16°S (Antarctic: 60°E–120°E);
(e) Coastal eastern Australia, particularly 18–21°S (E1), New Caledonia (E2), and Tonga (E3) (Antarctic: 120°E–170°W);
(f) Cook Islands and French Polynesia (Antarctic: 170°W–110°W);
(g) Coastal waters of western South America between southern Panama and northern Peru (Antarctic: 110°W–50°W).

Abundance estimates are available from most of the breeding grounds, but the only surveys covering the feeding grounds of all Breeding Stocks are the IWC's International Decade for Cetacean Research (IDCR) and Southern Ocean Whale Ecosystem Research (SOWER). The IDCR/SOWER surveys have completely encircled the Antarctic south of 60°S three times while completing circumpolar sets of surveys (CPs): in 1978/79–1983/84 (CPI), 1985/86–1990/91 (CPII) and 1991/92–2003/04 (CPIII). The survey and transit tracklines and positions of humpback sightings are shown in Fig. 1.

Previous humpback whale estimates from the IDCR/SOWER surveys have been based on an incomplete CPIII set of surveys. Branch and Butterworth (2001a) provided circumpolar estimates of 7,100 (CV = 0.36), 9,200 (CV = 0.29) and 9,300 (CV = 0.22) for the three CPs, but the CPIII estimate was based only on surveys up to 1997/98. Subsequent surveys filled in missing longitudinal coverage (140°W–110°W, 80°W–60°W and 80°E–130°E) and also more completely re-surveyed the 130°E–170°W region last surveyed in 1991/92. These recently surveyed longitudinal ranges cover the Antarctic regions where humpback whales are most abundant. Additionally, all

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* Present address: *School of Aquatic and Fisheries Sciences, Box 355020, University of Washington, Seattle, WA 98195, USA.*

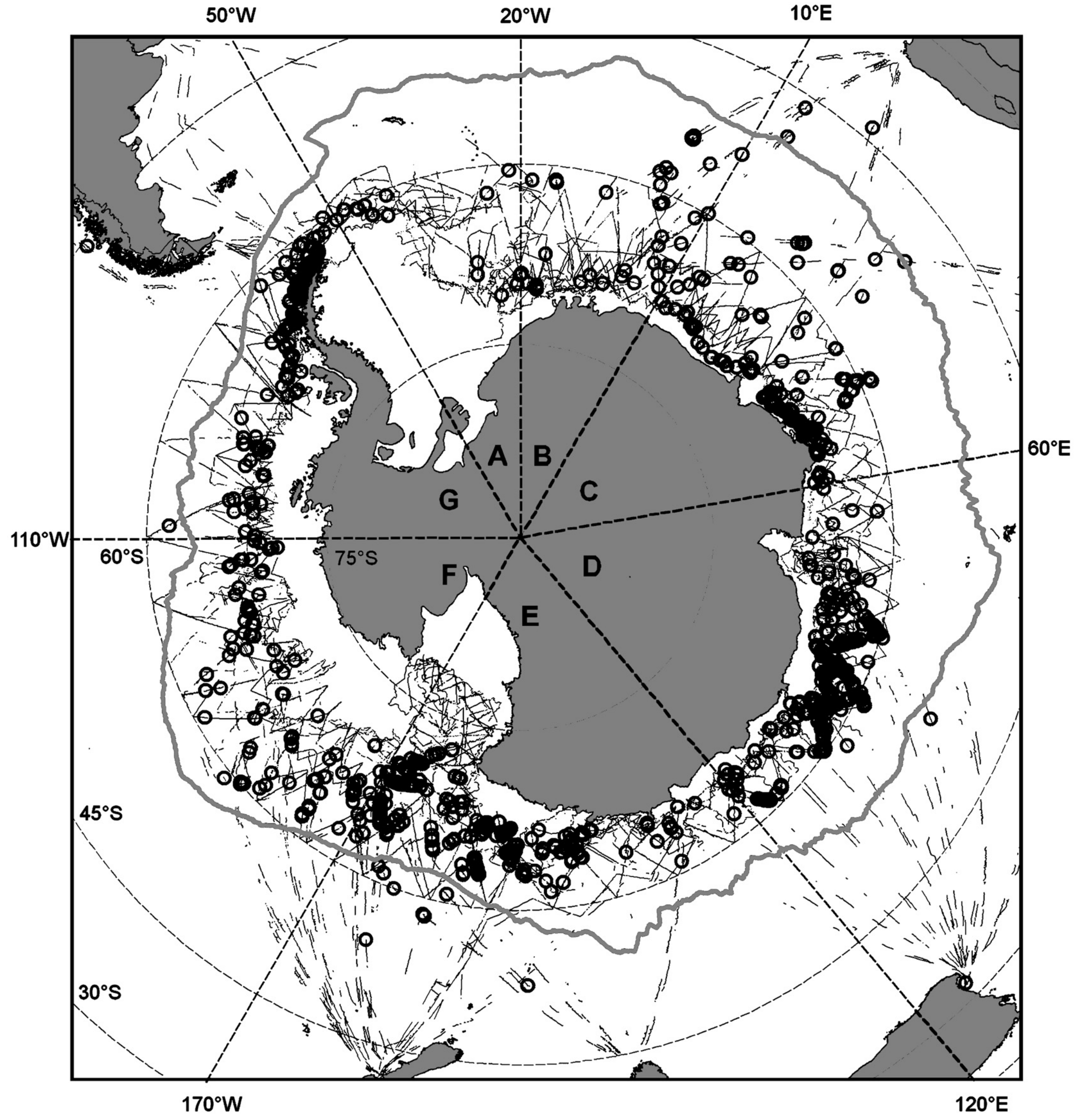

Fig. 1. Primary effort (thin grey lines) and associated sightings (black circles) from the IDCR/SOWER surveys from 1978/79 to 2004/05, including transits to and from the survey regions and survey years (1984/85, 2004/05) devoted primarily to experiments that are not included in the circumpolar estimates. Surveys (as opposed to transits) were normally conducted south of 60°S. The Antarctic Polar Front is represented by a thicker line and is based on data from Moore *et al*. (1999). Dashed lines extending from the South Pole and associated letters A–G represent the assumed Antarctic divisions between Breeding Stocks A–G based on the IWC's Naïve feeding model.

previous estimates were presented only at the circumpolar level and thus could not be used to assess the status of individual Breeding Stocks.

This paper presents updated circumpolar estimates of abundance and estimates for individual surveys, each Management Area (Donovan, 1991), and each of the Breeding Stocks divided according to the Naïve model feeding areas (IWC, 1998; 2006).

METHODS

The standard distance sampling methods used to analyse the IDCR/SOWER surveys have been described in detail in Branch and Butterworth (2001a). A broad overview is provided here together with particulars where methods have been updated from those in Branch and Butterworth (2001a); differences are also summarised in Table 1. Much of the process of data extraction and abundance estimation is automated in the IWC's Database Estimation System Software (DESS, Strindberg and Burt, 2004), although substantial post-DESS manipulation is needed to divide the estimates between Breeding Stocks and Management Areas. DESS version 3.42 dated April 2006 is used in these analyses.

Survey design

Survey cruise tracks and strata have been presented for the earlier surveys (Branch and Butterworth, 2001b; Matsuoka *et al.*, 2003). Important features include that: the first five CPI surveys generally left an unsurveyed region between the northern and southern strata; surveys in CPI and CPII generally left an unsurveyed area between the northern boundary of the survey region and 60°S; in general the CPI tracklines were rectangular while later survey tracklines were zigzag in pattern; and CPI and CPII took six years each while CPIII took 13 years (Figs 2a–c). Finally, individual surveys within CPI and CPII were non-overlapping while in CPIII some longitudinal ranges were surveyed more than once. These features make it difficult to obtain comparable estimates from the three CPs.

Table 1

Summary of changes to the analyses compared to those in Branch and Butterworth (2001a).

Topic	Branch and Butterworth (2001a)	This paper	Implications
Activity codes	BA, BB, BC, BL, BR, SE, BH, BI, BO, BP, BQ, BU, BV	BB renamed to BK	None
Duplicates and triplicates	'Definite' and 'possible' duplicates and triplicates treated as multiple records of a single sighting	Only 'definite' duplicates and triplicates treated as multiple records of a single sighting	No effect on estimates based on surveys up to and including 1997/98 (Branch and Butterworth, 2001a)
Survey legs parallel to ice edge in 1988/89 and 1989/90	Included	Excluded	Increases CPII estimates by a moderate amount, because 1,535.3 n.miles of effort and associated sightings were excluded in 1988/89; and 30.1 n.miles in 1989/90
Area of ES stratum in 1996/97	67,072 n.mile^2	Corrected to 52,534 n.mile^2	Decreases CPIII estimate by 0.1%
EN2 stratum in 1997/98	Treated as if divided into two separate strata each surveyed by one vessel	Treated as one stratum surveyed by two vessels	Negligible effect
Estimated school size	Either regression method or mean within 1.5 n.miles	Regression method unless positive correlation or school size less than one, then mean within 0.5 n.miles	No effect since regression always positive for humpback whales

Data selected for analysis

Survey modes and activity codes

In CPI the surveys were conducted in closing mode only but in CPII and CPIII the vessel alternated between closing mode and independent observer (IO) mode. In closing mode, when a sighting is made the vessel leaves the trackline to confirm the species identity and school size of the sighting. In IO mode (which is a form of passing mode) the vessel does not leave the trackline when a sighting is made, and an additional observer is placed on the IO platform just below the barrel who operates independently from the barrel observers to provide information about the detectability of whales on the trackline. For minke whale analyses, closing mode and IO mode are treated separately (Branch and Butterworth, 2001b), but the paucity of sightings for other species renders this difficult so that closing mode and IO mode data are combined in this paper to obtain abundance estimates for humpback whales. In a sensitivity test conducted on the surveys up to 1997/98, estimates obtained separately from closing and IO mode were similar (Branch and Butterworth, 2001a).

A variety of activity codes have been used over the years in both closing and IO mode. The same codes used in Branch and Butterworth (2001a) are used here (Table 1) except that the 'BB' code has now been renamed 'BK' (and is included) while 'BB' now refers to blue whale research periods (and is excluded).

Species codes

Sightings recorded as code 07 ('humpback whale') are included and code 71 ('like humpback') excluded in obtaining abundance estimates. A sensitivity test conducted by Branch and Butterworth (2001a) revealed that including 'like humpback' sightings increased the abundance estimates by 0.0%, 0.6% and 1.6% for the three CPs respectively, up to 1997/98.

Duplicates and triplicates

During IO mode duplicate (or even triplicate) records can be made of the same sighting from different platforms. Duplicates and triplicates are coded as 'definite', 'possible' or 'remote'. The most recent analysis of humpback whale abundance from these surveys (Branch and Butterworth, 2001a) treated all 'definite' and 'possible' duplicates and triplicates as a single sighting, while 'remote' duplicates and triplicates were treated as sightings of multiple schools. In this paper only 'definite' duplicates and triplicates are treated as single sightings, bringing the methods in line with those used for minke whales (Branch, 2006; Branch and Butterworth, 2001b). A previous sensitivity test for this change for minke whales revealed that abundance estimates changed by less than 1% (Branch and Butterworth, 2001b); a similar minor impact is likely for humpback whales.

Abundance estimation

Abundance estimates were obtained using the standard distance sampling formula (e.g. Buckland *et al.*, 1993):

$$N = \frac{A \cdot \bar{s} \cdot n}{2 \cdot w_s \cdot L} \tag{1}$$

where:

N = abundance estimate
A = area of stratum (n.miles^2)
$\bar{s}$ = mean school size
n = number of schools sighted during primary search effort
w_s = effective search half-width for schools (n.miles)
L = primary search effort (n.miles)

The CV for N is calculated from:

$$CV(N) = \sqrt{\left[CV\left(\frac{n}{L}\right)\right]^2 + \left[CV(\bar{s})\right]^2 + \left[CV(w_s)\right]^2} \tag{2}$$

Effective search half-width

Recorded angle and forward distance data are often rounded, artificially introducing peaks in the distribution of perpendicular distances that do not reflect the true distribution of perpendicular distances. To account for this rounding error, sightings are assumed to be evenly 'smeared' across a particular sector of angles and distances before the distribution of perpendicular distances is calculated. Smearing is conducted using Method II of Buckland and Anganuzzi (1988). The resulting distribution of perpendicular distances is then grouped into 0.1 n.mile bins to the truncation distance of 2.4 n.miles as in Branch and Butterworth (2001a). The detection function is fitted to these data based on perpendicular distance *y*.

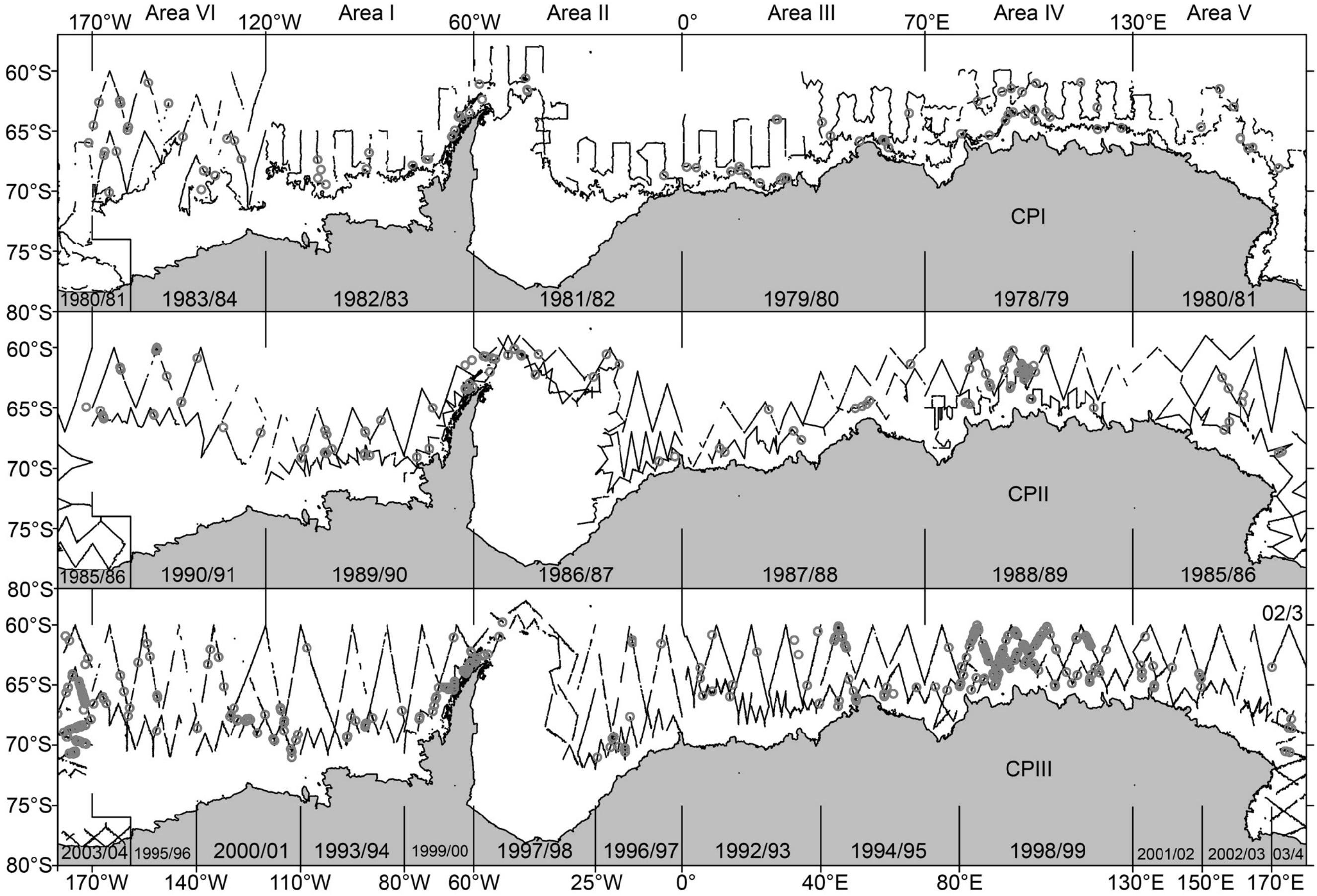

Fig. 2. Primary search effort (solid lines) and associated humpback whale sightings (circles) during each of the surveys included in the three circumpolar sets of surveys (CPI, CPII and CPIII). Vertical lines at the top of each panel show the longitudinal boundaries of the six IWC Management Areas, while vertical lines at the bottom of each panel show the divisions between each survey (six surveys in CPI and CPII, twelve in CPIII).

$$f(y) = f(0)g(y) = f(0)\left[1-\exp\left(-\left[\frac{y}{a}\right]^{-b}\right)\right] \qquad (3)$$

where $g(y)$ is the probability that a school at a perpendicular distance y from the trackline will be sighted and $a \geq 0.0001$ n.miles and $b \geq 1$ are parameters to be estimated. It is assumed that $g(0) = 1$, i.e. that all schools on the trackline are sighted. It is possible in theory to estimate $g(0)$ for humpback whales using the duplicate sightings in IO mode data, but this has proven complicated even for minke whales (Okamura *et al.*, 2003; 2005; 2006) and is beyond the scope of this paper.

Mean school size

School size estimates are obtained from sightings with confirmed school sizes in closing mode only. Closing mode estimates are used because IO mode estimates of school size are negatively biased (IWC, 1987, p.70). Large schools are visible at greater distances than small schools and therefore estimates of school size were corrected for bias using the regression method proposed by Buckland *et al.* (1993), which accounts for changes in the detectability of different school sizes with distance from the vessel.

Pooling to estimate the search half-width and mean school size

Sample sizes were small in most of the surveys (especially CPI and CPII), and therefore search half-width and mean school size could not be estimated separately for each survey; instead, separate estimates for search half-width and mean school size were obtained for each CP set, as in Branch and Butterworth (2001a). Given the higher number of sightings in CPIII, it might be possible to obtain separate estimates of these quantities for the first and second halves of CPIII in future analyses.

Averaging for strata surveyed by two vessels

Where a stratum is surveyed by two vessels the resulting abundance estimates were combined by effort-weighted averaging.

Obtaining CVs for combined stratum estimates

When individual abundance estimates for each stratum (N_i) and associated CVs (CV_i) are combined, CVs are stratum-specific for each n_i/L_i component, but from data pooled over each CP for $\bar{s}$ and w_s. The following procedure is therefore needed to correctly obtain the overall CV for the sum of several strata:

$$X_i = \frac{N_i \cdot w_s}{\bar{s}} = \frac{A \cdot n_i}{2 \cdot L_i} \qquad CV(X_i) = \sqrt{CV(N_i)^2 - CV(\bar{s})^2 - CV(w_s)^2}$$

$$X = \sum_{i=1}^{n} X_i \qquad CV(X) = \sqrt{\sum_{i=1}^{n}\left[X_i \cdot CV(X_i)\right]^2} \Big/ X$$

$$N = \sum_{i=1}^{n} N_i \qquad CV(N) = \sqrt{CV(X)^2 - CV(\bar{s})^2 + CV(w_s)^2}$$

Combining estimates

Abundance estimates for individual strata need to be combined to obtain estimates applicable to the CPs, to Management Areas, to the Breeding Stocks and to each individual survey. Surveys in 1984/85, 2004/05 and 2005/06 are omitted when obtaining abundance estimates for the CPs as these were largely dedicated to experiments. Abundance estimates for CPI and CPII are comparatively easy to obtain because the individual surveys each covered one Management Area, but during CPIII some surveys overlapped, and CPIII surveys sometimes crossed the border between two Management Areas. In general these combinations require omitting some strata or surveys, and splitting other strata (and their associated effort and sightings) into substrata. Where strata are split it is also necessary to re-calculate the new stratum areas, the areas of the unsurveyed regions north of the new strata, and the unsurveyed areas between the northern and southern strata during the first five surveys. More detail is given below.

Stratum areas

When the strata are divided to obtain Management Area and Breeding Stock estimates, survey effort and sightings must be split into the two new strata. Additional calculations are needed to find the area of the two new strata and the area of the unsurveyed region (if any) between the northern strata and 60°S, and between the northern and southern strata in CPI. An *R* script provided by M.L. Burt (pers. comm.) is used to calculate these new survey areas.

Circumpolar abundance estimates

Circumpolar abundance estimates are obtained using the ‘survey-once’ method, i.e. the most recent and most complete survey is preferred when surveys overlap (Branch, 2005; Branch and Ensor, 2004). Key elements are: (1) The 1991/92 survey in Area V is omitted since Area V was re-surveyed more completely and more recently in 2001/02–2003/04; (2) *ad-hoc* strata ENA and ESA in 1999/00 and ESA in 2001/02 are omitted; (3) longitudinal bands are omitted from the 1993/94 (60°W–80°W) and 1996/97 (25°W–30°W) surveys; (4) the entire ES stratum and also EN east of 180° are omitted from the 2002/03 survey; (5) N1 west of 180° in 2003/04 is omitted; and (6) the 2004/05 and later surveys are excluded since these were devoted primarily to experiments and not to abundance estimation.

IWC Management Areas

Management Area estimates are obtained using the ‘survey-once’ method (Branch, 2005; Branch and Ensor, 2004). For CPI and CPII each individual survey covered a single Management Area, but for CPIII surveys exclusions were required as for circumpolar estimates. In addition the 1994/95 strata are split at 70°E, and the 2000/01 strata are split at 120°W. An additional abundance estimate is provided for Area V based on the 1991/92 survey estimate, which is denoted as CPIII* since this survey is excluded under the ‘survey-once’ circumpolar method. This additional estimate is included when estimating the rate of increase of humpbacks in Area V.

Breeding stocks

The assumption was made that the Naïve model used for allocating catches in the feeding areas to the Breeding Stocks (IWC, 1998; 2006) was also appropriate for dividing the abundance estimates among the Breeding Stocks. In addition to the deletions outlined for the circumpolar estimates, many strata had to be split to obtain abundance estimates for these longitudinal regions. Divisions were required at 20°W, 10°E, 60°E, 120°E, 170°W, 110°W and 50°W. It should be noted that under the Naïve model, the currently agreed division between Breeding Stock G and A is at 50°W south of 58°S and either at 50°W or 70°W north of 58°S, whereas other divisions do not change with latitude. An additional estimate (denoted CPIII*) is provided for Breeding Stock E based on the 1991/92 survey combined with a 10° longitudinal section from the 1998/99 survey. This 10° slice of the 1998/99 survey was also included in the other CPIII Breeding Stock E estimate, but contributes less than 200 whales to the total.

Individual surveys

Abundance estimates are provided for each survey used in the CPs and for 1991/92. No longitudinal slices are omitted except for the *ad-hoc* strata ENA and ESA in 1999/00 and ESA in 2001/02.

Comparable-area estimates

The differing nature of the three CPs poses several issues when comparing estimates. Major issues include the different survey design, survey modes, and unsurveyed central regions in CPI, the lack of survey effort northwards to 60°S in most of the CPI and CPII surveys, and the unknown proportion of humpback whales north of 60°S during the survey period. Only the unsurveyed northern areas are taken into account to obtain estimates from ‘comparable areas’. The simple assumption employed by Branch and Butterworth (2001a; 2001b) and Branch (2007) is used here: that the density in the unsurveyed northern areas is the same as in the strata adjacent and south of the unsurveyed strata. If instead the true density in the unsurveyed areas was lower than in the more southerly surveyed areas, this assumption would cause positive bias in estimated whale abundance for CPI and CPII, and negative bias in the estimated increase rate.

In most cases this is straightforward, but for the 1981/82 survey between 40°W and 30°W there was no northern stratum, only a southern stratum (W2S). As densities are expected to be higher near the ice edge in the southern stratum, it was deemed inappropriate to adjust the W2S estimates upwards, and instead the estimate from the adjacent EN stratum (or the western section of EN when EN is split to obtain Breeding Stock estimates) is adjusted upwards. This differs slightly from the methods used previously, where the W1N estimates were adjusted upwards for the unsurveyed region north of W2S in 1981/82 (Branch and Butterworth, 2001a; 2001b).

For this work the areas of the unsurveyed northern regions have been more accurately estimated from the stratum boundaries and these differ slightly from those in previous papers (Branch and Butterworth, 2001a; 2001b).

Estimating the annual rate of increase

To estimate the annual rate of increase for each series of abundance estimates (circumpolar, Management Areas etc), an exponential growth model was fitted to the log of the ‘comparable areas’ abundance estimates:

$$\ln \hat{N}_t = \ln N_0 + rt$$

where

N_0 is the first abundance estimate in the series;

$\hat{N}_t$ is the abundance estimate t years after the first abundance estimate;

r is the annual rate of increase.

The actual distribution of whales within each area is expected to change from year to year, and this variability would not be taken into account if the overall variance accounted only for the sampling variance reported from each individual survey. This missing variability is termed 'additional variability'. When fitting a growth model to interannual estimates, the overall variance comprises both the reported variance for each survey and the additional variance (which is assumed to be the same for all surveys). To obtain maximum likelihood estimates for *r*, the following negative log likelihood is minimised:

$$-\ln L = \sum_t \left[\ln \sqrt{CV_t^2 + CV_{\text{add}}^2} + \frac{\left(\ln N_t - \ln \hat{N}_t\right)^2}{2\left(CV_t^2 + CV_{\text{add}}^2\right)} \right]$$

where

CV_i is the reported coefficient of variation for the abundance estimate in year *t*;

CV_{add} is the coefficient of variation for the additional variance.

Likelihood profiling was used to find the 95% confidence intervals (e.g. Hilborn and Mangel, 1997), i.e. finding the two values of *r* for which the negative log likelihood is 1.92 units higher than the maximum likelihood estimate.

Comparison with breeding ground estimates

Surveys in both the Antarctic and the northern breeding grounds may only incompletely cover the entire Breeding Stocks (this would be indicated by any substantial differences between estimates from the two regions). Northern breeding ground estimates were collated by reviewing abundance estimates presented to the IWC at the Workshop on the Comprehensive Assessment of Southern Hemisphere Humpback Whales, 4–7 April 2006, Hobart Australia, and summarised in other papers (Bannister, 2005; Johnston and Butterworth, 2006; Zerbini *et al.*, 2011). These estimates are generally more recent than the mid-year of the IDCR/SOWER estimates, and it is likely that all Breeding Stocks are increasing. For comparisons, the IDCR/SOWER estimates from CPIII were either assumed to remain constant or projected to the mid-year of the breeding ground estimates by assuming an increase rate of 5% or 10%, which are reasonable rates of increase given a maximum upper bound from life history characteristics of 11.8% (Zerbini *et al.*, 2010).

RESULTS

The IDCR-SOWER surveys covered 64.3% (CPI), 79.5% (CPII) and 99.7% (CPIII) of the region between 60°S and the ice edge, based on updated estimates of the areas of the unsurveyed regions (Table 2). Plots of the primary survey effort and primary sightings during CPI, CPII and CPIII are given in Figs 2a–c. Of particular interest is the absence of humpback whale sightings in the Ross Sea south of 72°35'S despite extensive effort (Fig. 1).

Stratum-specific details of the components of the abundance estimates are presented in Table 3 and estimates of search half width and estimated school size are found in Table 4. Detection function fits to the smeared sightings are plotted in Figs 3a–c for each of the CPs. Search half-width increased substantially from 0.746 n.miles in CPI to 0.924 n.miles in CPII and 1.505 n.miles in CPIII. One further result to note is the high number of sightings recorded directly on the trackline in CPI (Fig. 3a).

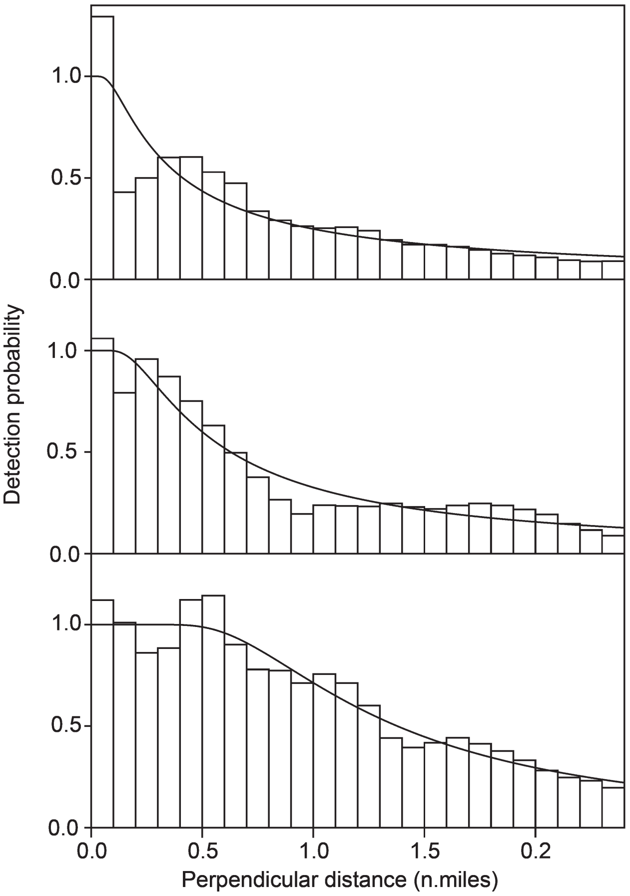

Fig. 3. Fit of the detection function to the smeared and truncated sightings recorded during CPI, CPII, and CPIII.

The crude sighting rate (total primary sightings divided by total primary search effort) for each CP is 1.8, 3.2 and 12.5 schools per 1000 n.miles for CPI, CPII and CPIII respectively. Estimated circumpolar abundance increased 45% from CPI to CPII and increased fourfold from CPII to CPIII (Table 5). The estimated abundance south of 60°S for CPIII is 41,500 (CV = 0.11). Most of this increase in the CPIII abundance comes from Management Areas IV (17,900) and V (13,200), although abundance estimates are also highest in CPIII in Areas I, II and III and similar to CPI and CPII in Area VI (Table 6). When separated into Breeding Stocks, stocks D (18,000) and E (13,300) are estimated to contain the majority of the CPIII abundance, and the CPIII estimates are also similar to or higher than CPI and CPII for all Breeding Stocks (Table 7). Estimates for individual surveys are provided in Table 8; the 1998/99 survey estimate of 17,700 (CV = 0.18) in Area IV accounts for 43% of the CPIII total. During the 1998/99 survey in Area IV alone, 208 primary sightings were recorded within 2.4 n.miles of the trackline, compared to 65 in total from CPI and 111 from CPII. More sightings were also recorded during the 2002/03 (87) and 2003/04 (93) surveys in Area V than from the CPI surveys.

The estimated circumpolar rate of increase is 9.6% per annum (95% CI 5.7%–13.3%), while point estimates ranged from –0.2% to 14.9% for Management Areas and from 1.6% to 14.4% for Breeding Stocks (Table 9). For most Management Areas and Breeding Stocks the confidence intervals were broad and ranged outside the [0%; 11.8%] interval (Zerbini *et al.*, 2010), although the estimated rate of increase was significantly greater than zero for Management

Areas IV and V, for Breeding Stocks D and E, and for the circumpolar estimates.

Abundance estimates from the northern breeding grounds (discussed in depth in the Discussion) varied greatly from the IDCR/SOWER estimates in CPIII (Table 10), even when the IDCR/SOWER estimates were extrapolated to the mid-year of the range of years to which the breeding ground estimates applied. For Breeding Stocks A, B and C, the IDCR/SOWER estimates were far smaller (3–44%) than the northern breeding grounds, for Breeding Stocks D, E and F, the IDCR/SOWER estimates were much higher (135–445%), and for Breeding Stock G the IDCR/SOWER estimates were similar (53%–124%).

DISCUSSION

Circumpolar abundance estimates for humpbacks presented here are the most recent and most complete to date, with strata coverage approaching 100% of the area south of 60°S in CPIII. The CPIII estimates should be adopted as the best available estimates for the summer abundance of humpback whales south of 60°S, and for certain Breeding Stocks arguably provide a better estimate of abundance than northern breeding ground surveys.

Although humpback whale sightings were recorded around the Antarctic, they were absent from the Ross Sea south of about 72°35'S, a pattern that has not previously

Table 2

Estimates of the unsurveyed areas between the northern boundaries of the surveys and 60°S, compared with those in Branch and Butterworth (2001b).

		This paper		Branch and Butterworth (2001b)	
Survey	Stratum	Unsurveyed south of 60°S	Surveyed north of 60°S	Unsurveyed south of 60°S	Surveyed north of 60°S
1978/79	EN	53,181		53,181	
1978/79	W1N	38,645		38,645	
1979/80	WN	255,938		255,938	
1979/80	EN	100,763		100,763	
1980/81	EN	263,267		263,267	
1980/81	WN	91,934		91,934	
1981/82	W1N		74,162	100,005	74,162
1981/82	EN	388,670		288,507	
1982/83	WN	243,507		243,506	
1982/83	EN	178,386		178,386	
1983/84	EN	35,088		35,088	
1985/86	WN		38,306		38,305
1986/87	WS2		12,060		11,992
1986/87	EN	74,342		74,341	
1986/87	WN		10,530		10,596
1987/88	WN	263,936		263,930	
1987/88	EN	58,824		54,823	
1988/89	EN	17,773		17,772	
1988/89	WN	17,773		17,772	
1989/90	WN	249,265		249,265	
1989/90	EN	167,243		167,243	
1990/91	EN	43,860		43,706	
1991/92*	WN	121,361		120,700	
1991/92*	EN	245,043		247,210	
1996/97	WNE	14,691		14,510	
1997/98	WS		13,670		14,040
1997/98	WN		32,548		32,722
CPI		1,649,379	74,162	1,649,220	74,162
CPII		893,015	60,896	888,852	60,893
CPIII excluding 1991/92		14,691	46,218	14,510	46,762

Table 3

Components of abundance estimates for each survey. Indicated for each stratum are the stratum name, vessel, area (A), number of transects (N_L), number of schools sighted after smearing and truncation (n_s), search effort (L), sighting rate (n_s/L), and estimates of abundance in each stratum (N). The strata that were surveyed by more than one vessel are indicated by the same number in the 'Ave' column; resulting abundance estimates are combined using effort-weighted averaging.

Stratum	IWC Area	Year	Vessel	Stratum	A (n.mile^2)	N_L	n_s	L (n.mile)	$n_s/L*10^3$	CV	N	CV	Ave
1	IV	1978/79	T16	EN	156,766	18	5.0	2,155.5	2.32	0.48	398	0.58	
2	IV	1978/79	T16	W1N	39,256	2	0.0	222.2	0.00	0.00	0	0.00	1
3	IV	1978/79	T16	W1S	20,389	5	0.0	200.6	0.00	0.00	0	0.00	
4	IV	1978/79	T16	W2N	153,914	3	1.0	384.7	2.60	0.86	438	0.33	2
5	IV	1978/79	T16	W2S	29,600	12	4.0	1,073.3	3.73	0.49	121	0.59	3
6	IV	1978/79	T18	ES	27,571	16	4.0	1,436.6	2.78	0.40	84	0.52	
7	IV	1978/79	T18	W1N	39,256	6	0.0	685.3	0.00	0.00	0	0.00	1
8	IV	1978/79	T18	W2N	153,914	11	2.4	1,212.5	1.98	0.54	327	0.64	2
9	IV	1978/79	T18	W2S	29,600	4	2.0	393.4	5.08	0.28	165	0.33	3

Cont.

Stratum	IWC Area	Year	Vessel	Stratum	A (n.mile^2)	N_L	n_s	L (n.mile)	$n_s/L*10^3$	CV	N	CV	Ave
10	III	1979/80	K27	ES	41,772	20	4.0	1,346.5	2.97	0.54	135	0.63	
11	III	1979/80	K27	WN	200,724	16	4.0	2,014.9	1.99	0.65	436	0.73	
12	III	1979/80	T11	EN	217,865	20	2.0	2,636.7	0.76	0.60	181	0.69	
13	III	1979/80	T11	WS	33,619	19	7.0	968.2	7.23	0.30	266	0.45	
14	V	1980/81	K27	EN	208,159	14	2.0	877.3	2.28	0.57	519	0.66	
15	V	1980/81	K27	ES	98,766	5	0.0	439.6	0.00	0.00	0	0.00	4
16	V	1980/81	K27	WS	34,164	17	0.0	698.1	0.00	0.00	0	0.00	
17	V	1980/81	T11	ES	98,766	21	1.0	2,133.3	0.47	0.81	51	0.88	4
18	V	1980/81	T11	WN	139,191	15	3.0	1,151.6	2.61	0.75	397	0.82	
19	II	1981/82	SM1	ES	29,633	18	0.0	1,162.9	0.00	0.00	0	0.00	
20	II	1981/82	SM1	W1N	135,504	10	1.0	1,064.9	0.94	0.77	139	0.84	
21	II	1981/82	SM1	W2S	52,096	10	0.0	920.6	0.00	0.00	0	0.00	5
22	II	1981/82	SM2	EN	145,063	17	1.0	1,748.8	0.57	1.01	91	1.06	
23	II	1981/82	SM2	W1S	35,725	9	0.5	872.2	0.57	1.05	24	1.10	
24	II	1981/82	SM2	W2S	52,096	12	0.0	812.4	0.00	0.00	0	0.00	5
25	I	1982/83	SM1	ES	33,050	15	1.9	928.0	2.05	0.54	73	0.63	
26	I	1982/83	SM1	WN	163,926	15	1.0	1,426.1	0.70	0.81	126	0.88	
27	I	1982/83	SM2	EN	149,433	17	3.0	1,054.4	2.85	0.66	465	0.74	
28	I	1982/83	SM2	WS	25,596	19	0.0	1,414.8	0.00	0.00	0	0.00	
29	VI	1983/84	K27	EMS	158,893	5	4.0	1,094.4	3.65	0.59	635	0.68	
30	VI	1983/84	K27	WN	207,721	5	7.9	875.6	9.02	0.33	2,048	0.46	
31	VI	1983/84	SM1	EN	202,108	5	1.0	911.6	1.10	0.85	242	0.91	
32	VI	1983/84	SM2	WMS	156,457	5	2.1	1,309.0	1.60	0.46	273	0.57	
1	V	1985/86	K27	EN	279,611	16	0.0	1,757.7	0.00	0.00	0	0.00	
2	V	1985/86	K27	WS	104,814	28	2.0	1,596.8	1.25	0.53	117	0.57	
3	V	1985/86	SM1	EM	165,912	20	2.0	1,866.4	1.07	0.97	158	0.99	
4	V	1985/86	SM1	WM	166,349	8	2.0	850.0	2.35	0.61	347	0.64	
5	V	1985/86	SM2	ES	107,717	22	0.0	1,737.8	0.00	0.00	0	0.00	
6	V	1985/86	SM2	WN	139,065	10	0.0	1,121.5	0.00	0.00	0	0.00	
7	II	1986/87	K27	ES1	23,142	8	1.0	527.6	1.90	0.82	39	0.84	
8	II	1986/87	K27	WS1	10,270	4	2.0	185.5	10.78	0.65	98	0.20	
9	II	1986/87	K27	WS2	21,143	4	1.0	239.7	4.17	2.09	78	0.20	6
10	II	1986/87	K27	WS3	79,605	15	3.0	1,014.8	2.96	0.42	209	0.47	7
11	II	1986/87	K27	EN	124,057	7	0.0	965.9	0.00	0.00	0	0.00	
12	II	1986/87	SM1	EBAY	15,242	7	0.0	232.2	0.00	0.00	0	0.00	
13	II	1986/87	SM1	ES2	44,975	29	1.0	1,287.8	0.78	0.81	31	0.83	
14	II	1986/87	SM1	WBAY	11,505	3	0.0	166.4	0.00	0.00	0	0.00	
15	II	1986/87	SM1	WN	95,361	6	1.0	516.6	1.94	0.98	164	1.00	
16	II	1986/87	SM2	EM	69,908	9	0.0	1,445.6	0.00	0.00	0	0.00	
17	II	1986/87	SM2	WS2	21,143	3	2.0	234.6	8.53	0.96	160	0.20	6
18	II	1986/87	SM2	WS3	79,605	19	0.0	1,119.8	0.00	0.00	0	0.00	7
19	III	1987/88	SM1	ES	87,677	15	5.9	1,196.0	4.93	0.60	387	0.63	
20	III	1987/88	SM1	WN	148,821	13	1.0	857.3	1.17	1.22	154	1.24	
21	III	1987/88	SM2	EN	168,881	14	1.0	1,086.7	0.92	1.08	138	1.10	
22	III	1987/88	SM2	WS	74,351	21	4.0	1,247.3	3.21	0.52	212	0.56	
23	IV	1988/89	SM1	BS	6,520	4	0.0	231.9	0.00	0.00	0	0.00	
24	IV	1988/89	SM1	EN	181,166	12	2.0	1,116.3	1.79	0.70	288	0.73	
25	IV	1988/89	SM1	WS	58,693	10	5.0	483.5	10.34	0.87	539	0.89	
26	IV	1988/89	SM2	BN	17,486	15	0.0	627.7	0.00	0.00	0	0.00	
27	IV	1988/89	SM2	ES	52,441	9	1.0	554.3	1.80	0.93	84	0.95	
28	IV	1988/89	SM2	WN	156,617	12	29.9	1,431.9	20.88	0.57	2,899	0.61	
29	I	1989/90	SM1	ESBAY	62,594	24	8.0	1,386.7	5.77	0.54	321	0.57	
30	I	1989/90	SM1	WN	168,761	13	7.0	1,167.1	6.00	0.41	899	0.46	
31	I	1989/90	SM2	EN	153,029	14	1.5	1,429.8	1.05	0.73	146	0.76	
32	I	1989/90	SM2	WS	45,128	30	7.0	1,433.1	4.88	0.43	196	0.47	
33	VI	1990/91	SM1	EN	191,954	7	3.0	666.6	4.50	0.49	767	0.53	
34	VI	1990/91	SM1	WS	45,414	14	7.3	950.1	7.68	0.61	311	0.65	
35	VI	1990/91	SM2	ES	108,268	9	1.0	952.9	1.05	0.83	101	0.85	
36	VI	1990/91	SM2	WN	211,788	9	9.0	1,043.4	8.63	0.77	1,622	0.80	
1	V	1991/92	SM1	EN	165,429	17	7.5	1,008.8	7.43	0.26	827	0.26	
2	V	1991/92	SM1	WS	58,643	15	14.0	748.2	18.71	1.00	731	1.00	
3	V	1991/92	SM2	ES	82,039	22	0.0	1,416.4	0.00	0.00	0	0.00	
4	V	1991/92	SM2	WN	137,734	9	2.0	655.3	3.05	1.25	281	1.25	

Cont.

Stratum	IWC Area	Year	Vessel	Stratum	*A* (n.mile^2)	N_L	n_s	*L* (n.mile)	$n_s/L*10^3$	CV	*N*	CV	Ave
5	III	1992/93	SM1	ES	23,207	23	1.0	893.4	1.12	0.85	17	0.85	
6	III	1992/93	SM1	WN	210,035	15	0.0	1,404.5	0.00	0.00	0	0.00	8
7	III	1992/93	SM1	WS	61,527	3	1.0	143.0	6.99	0.67	288	0.06	9
8	III	1992/93	SM2	EN	150,547	9	1.0	1,101.2	0.91	0.97	91	0.97	
9	III	1992/93	SM2	WS	61,527	31	3.0	1,774.6	1.69	0.79	70	0.79	9
10	III	1992/93	SM2	WN	210,035	1	0.0	134.2	0.00	0.00	0	0.00	8
11	I	1993/94	SM1	WS	50,596	23	10.0	1,068.3	9.36	0.49	316	0.49	
12	I	1993/94	SM1	EN	293,196	22	2.0	1,581.8	1.26	0.70	248	0.70	
13	I	1993/94	SM2	WN	251,735	16	1.0	1,134.0	0.88	0.85	148	0.85	
14	I	1993/94	SM2	ES	72,249	20	4.5	1,076.4	4.18	0.36	202	0.37	
15	III	1994/95	SM1	WS	51,938	23	14.0	919.6	15.22	0.49	528	0.50	
16	III	1994/95	SM1	EN	146,681	15	1.0	1,154.5	0.87	1.01	85	1.01	
17	III	1994/95	SM2	WN	148,803	14	16.0	921.6	17.36	0.54	1,726	0.54	
18	III	1994/95	SM2	ES	60,046	17	3.0	899.2	3.34	0.52	134	0.52	
19	III	1994/95	SM2	PRYD	21,096	8	0.0	414.2	0.00	0.00	0	0.00	
20	VI	1995/96	SM1	WS	34,051	19	4.0	738.9	5.41	0.56	123	0.56	
21	VI	1995/96	SM1	EN	242,073	21	7.5	1,045.3	7.17	0.60	1,162	0.60	
22	VI	1995/96	SM2	WN	97,945	9	2.0	528.5	3.78	0.84	248	0.84	
23	VI	1995/96	SM2	ES	72,349	19	1.0	1,068.5	0.94	0.94	45	0.94	
24	II	1996/97	SM1	ES	52,534	38	5.8	1,229.2	4.72	0.58	166	0.58	
25	II	1996/97	SM1	WN	113,687	10	2.9	463.9	6.25	1.62	469	1.63	
26	II	1996/97	SM2	EN	241,928	32	3.0	1,260.4	2.38	0.73	385	0.73	
27	II	1996/97	SM2	WS	23,028	15	2.0	384.5	5.20	0.37	80	0.37	
28	II	1997/98	SM1	WS	32,620	17	8.6	490.3	17.54	0.83	381	0.83	
29	II	1997/98	SM1	EN1	84,726	12	0.0	581.1	0.00	0.00	0	0.00	
30	II	1997/98	SM1	ES2	10,451	9	0.0	226.3	0.00	0.00	0	0.00	
31	II	1997/98	SM1	EN2	80,013	4	0.0	202.1	0.00	0.00	0	0.00	10
32	II	1997/98	SM2	WN	52,135	8	1.0	493.3	2.03	1.37	71	1.37	
33	II	1997/98	SM2	ES1	47,036	16	0.0	741.5	0.00	0.00	0	0.00	
34	II	1997/98	SM2	EN2	80,013	4	0.0	330.8	0.00	0.00	0	0.00	10
35	IV	1998/99	SM1	WS	42,605	26	46.9	850.0	55.18	0.25	1,571	0.26	
36	IV	1998/99	SM1	EN	169,387	25	44.5	1,136.1	39.17	0.41	4,433	0.42	
37	IV	1998/99	SM2	WN	105,396	18	100.4	637.2	157.56	0.19	11,095	0.20	
38	IV	1998/99	SM2	ES	70,193	50	16.0	1,241.6	12.89	0.19	604	0.20	
39	IV	1998/99	SM1	ES	70,193	2	0.0	52.5	0.00	0.00	0	0.00	
40	I	1999/00	SM1	WS	20,506	13	5.2	446.9	11.64	0.52	160	0.53	
41	I	1999/00	SM1	EN	57,309	11	3.0	417.7	7.18	0.67	275	0.67	
42	I	1999/00	SM2	WN	110,906	11	0.0	664.4	0.00	0.00	0	0.00	
43	I	1999/00	SM2	ES	23,632	11	32.2	298.0	108.05	0.30	1,704	0.31	
44	VI	2000/01	SM1	WN	252,078	12	2.0	514.0	3.89	0.67	655	0.67	11
45	VI	2000/01	SM1	WS	43,916	16	2.0	446.5	4.48	1.07	131	1.08	12
46	VI	2000/01	SM2	WN	252,078	21	7.0	710.3	9.85	0.22	1,660	0.23	11
47	VI	2000/01	SM2	WS	43,916	16	5.0	311.5	16.05	0.34	471	0.35	12
48	I	2000/01	SM1	EN	127,789	19	2.0	700.8	2.85	0.83	244	0.84	13
49	I	2000/01	SM2	EN	127,789	2	2.0	37.3	53.62	0.07	4,578	0.09	13
50	I	2000/01	SM2	ES	29,080	20	9.0	542.7	16.58	0.34	322	0.34	
51	V	2001/02	SM1	WS	34,886	21	9.0	550.4	16.35	0.29	381	0.29	
52	V	2001/02	SM1	ES	26,099	11	0.0	292.9	0.00	0.00	0	0.00	14
53	V	2001/02	SM2	WN	46,333	7	0.0	438.5	0.00	0.00	0	0.00	
54	V	2001/02	SM2	EN	83,082	8	3.0	486.4	6.17	0.84	342	0.84	
55	V	2001/02	SM2	ES	26,099	3	1.0	131.2	7.62	0.82	133	0.06	14
56	V	2002/03	SM1	ES	126,870	24	14.0	1,018.0	13.75	0.25	1,166	0.26	
57	V	2002/03	SM1	EN	135,038	6	1.0	183.9	5.44	0.60	491	0.61	15
58	V	2002/03	SM1	W2N	101,237	11	20.6	459.1	44.87	0.58	3,037	0.58	16
59	V	2002/03	SM1	W1S	22,128	12	11.0	352.0	31.25	0.30	462	0.31	
60	V	2002/03	SM2	EN	135,038	23	2.0	861.6	2.32	0.58	209	0.58	15
61	V	2002/03	SM2	W2S	21,327	27	29.8	526.0	56.65	0.29	807	0.30	
62	V	2002/03	SM2	W1N	75,395	13	5.0	466.0	10.73	0.41	541	0.41	
63	V	2002/03	SM2	W2N	101,237	4	4.0	43.8	91.32	0.27	6,181	0.06	16
64	V	2003/04	SM2	N1	123,227	13	1.0	489.1	2.04	0.65	168	0.66	
65	V	2003/04	SM1	N2	95,445	18	38.2	587.2	65.05	0.38	4,147	0.38	
66	V	2003/04	SM1	N3	14,598	4	0.0	153.0	0.00	0.00	0	0.00	
67	V	2003/04	SM1	ROSS	56,444	23	0.0	544.6	0.00	0.00	0	0.00	17
68	V	2003/04	SM2	ROSS	56,444	15	0.0	556.7	0.00	0.00	0	0.00	17
69	V	2003/04	SM1	MID	131,782	18	37.7	707.3	53.30	0.47	4,689	0.47	18
70	V	2003/04	SM2	MID	131,782	23	16.0	881.5	18.15	0.36	1,594	0.36	18

been noted. No sightings were recorded despite extensive effort both on the IDCR/SOWER surveys (Fig. 1) and during JARPA surveys (Matsuoka *et al.*, 2011). A similar absence is evident for fin whales in the JARPA surveys, and contrasts with the presence of blue whales and high densities of minke whales in the Ross Sea (Branch, 2006; 2007; Branch *et al.*, 2007; Matsuoka *et al.*, 2005). The absence of humpbacks from the Ross Sea could be due either to extirpation from whaling, or because they never have inhabited the Ross Sea. The IWC catch database (provided by C. Allison, IWC) includes 21 expeditions listed as 'Ross Sea' during 1923–29. Catches from these expeditions included 9,330 blue whales, 1,451 fin whales and 890 humpback whales, i.e. humpback whales constituted about 8% of the total. These totals could, however, have come from the pack ice north of the entrance to the Ross Sea. A published account of the 1928/29 Larsen expedition to the Ross Sea reveals that all of the 13 humpback catches in the IWC catch database were taken in the pack ice outside the Ross Sea and not inside the Ross Sea (Marshall, 1930), thus it is possible that even during industrial whaling, humpback whales rarely entered the Ross Sea. Two hypotheses are proposed for the absence of

Table 4

Estimates of search half-width (w_s), estimated school size ($E[s]$) and their associated CVs for each circumpolar set. Estimates differ slightly for each category of the CPIII estimates due to slight changes in how the strata were divided and which strata were included to obtain the estimates.

Surveys	w_s	CV	$E[s]$	CV
CPI all	0.746	0.327	1.63	0.049
CPII all	0.924	0.193	1.64	0.067
CPIII circumpolar	1.504	0.055	2.02	0.031
CPIII IWC areas	1.504	0.055	2.02	0.031
CPIII breeding stocks	1.511	0.055	2.01	0.033
CPIII individual surveys	1.525	0.051	2.04	0.029

Table 5

Estimates of abundance obtained from each circumpolar set of surveys, and the associated CVs and 95% confidence intervals obtained using the method of Buckland (1992). CPIII estimates exclude the 1991/92 survey.

		Circumpolar estimates			Adjusted simply for equal areas		
Circumpolar set	Mid-year	N	CV	95% CI	N	CV	95% CI
CPI	1980/81	7,058	0.36	(3,500; 14,100)	9,701	0.36	(4,900; 19,300)
CPII	1987/88	10,233	0.30	(5,700; 18,300)	12,488	0.30	(7,000; 22,300)
CPIII	1997/98	41,505	0.12	(33,000; 52,200)	41,344	0.11	(33,000; 51,700)

Table 6

Estimates of abundance for each IWC Management Area. Estimates from Area V in CPIII were obtained from complete coverage south of 60°S in 2001/02–2003/04 but incomplete coverage in 1991/92 (denoted by CPIII*).

					Estimates		Comparable areas	
IWC Area	CP set	Seasons	Long. range	Mid-year	*N*	CV	*N*	CV
Area I	CPI	1982/83	60	1982/83	663	0.64	1,405	0.66
(120°W–60°W)	CPII	1989/90	60	1989/90	1,561	0.37	3,048	0.41
	CPIII	1993/94	30					
		1999/00	20					
		2000/01	10	1997/98	3,549	0.20	3,549	0.20
Area II	CPI	1981/82	60	1981/82	254	0.69	421	0.92
(60°W–0°)	CPII	1986/87	60	1986/87	550	0.38	464	0.40
	CPIII	1996/97	25					
		1997/98	35	1997/98	1,178	0.39	1,005	0.38
Area III	CPI	1979/80	70	1979/80	1,017	0.49	1,657	0.56
(0°–70°E)	CPII	1987/88	70	1987/88	890	0.46	1,212	0.56
	CPIII	1992/93	40					
		1994/95	30	1993/94	2,504	0.40	2,504	0.40
Area IV	CPI	1978/79	60	1978/79	968	0.45	1,102	0.46
(70°E–130°E)	CPII	1988/89	60	1988/89	3,809	0.52	4,167	0.53
	CPIII	1994/95	10					
		1998/99	50	1997/98	17,938	0.18	17,938	0.18
Area V	CPI	1980/81	60	1980/81	957	0.59	1,876	0.60
(130°E–170°W)	CPII	1985/86	60	1985/86	622	0.50	622	0.50
	CPIII*	1991/92	60	1991/92	1,838	0.46	3310	0.34
	CPIII	2001/02	20					
		2002/03	20					
		2003/04	20	2002/03	13,246	0.20	13,246	0.20
Area VI	CPI	1983/84	50	1983/84	3,198	0.47	3,240	0.47
(170°W–120°W)	CPII	1990/91	50	1990/91	2,801	0.53	2,976	0.51
	CPIII	1996/96	30					
		2000/01	20	1998/99	3,098	0.27	3,098	0.27

Table 7

Estimates of abundance for each breeding group of humpback whales, obtained from the feeding areas by assuming that the Naïve model is correct. Estimates of abundance for CPIII* include a 10 degree longitudinal section from the 1998/99 survey that is also included in the CPIII estimate.

					Estimate		Comparable areas	
Breeding group	CP	Seasons	Long. range	Mid-year	*N*	CV	*N*	CV
A (50°W–20°W)	CPI	1981/82	30	1981/82	98	0.96	45	0.88
	CPII	1986/87	30	1986/87	336	0.55	259	0.62
	CPIII	1996/97	5					
		1997/98	25	1997/98	168	0.61	200	0.64
B (20°W–10°E)	CPI	1979/80	10					
		1981/82	20	1980/81	246	0.85	692	0.84
	CPII	1986/87	20					
		1987/88	10	1986/87	70	0.63	70	0.63
	CPIII	1992/93	10					
		1996/97	20	1995/96	595	0.51	595	0.51
C (10°E–60°E)	CPI	1979/80	50	1979/80	720	0.53	1,043	0.62
	CPII	1987/88	50	1987/88	700	0.46	926	0.57
	CPIII	1992/93	30					
		1994/95	20	1993/94	2,391	0.41	2,391	0.41
D (60°E–120°E)	CPI	1978/79	50					
		1979/80	10	1978/79	1,033	0.44	1,219	0.46
	CPII	1987/88	10					
		1988/89	50	1988/89	3,869	0.52	4,202	0.52
	CPIII	1994/95	20					
		1998/99	40	1997/98	17,959	0.17	17,959	0.17
E (120°E–170°W)	CPI	1978/79	10					
		1980/81	60	1980/81	995	0.58	1,913	0.60
	CPII	1985/86	60					
		1988/89	10	1985/86	622	0.50	622	0.50
	CPIII*	1991/92	60					
		1998/99	10	1992/93	2,012	0.43	3,484	0.33
	CPIII	1998/99	10					
		2001/02	20					
		2002/03	20					
		2003/04	20	2001/02	13,300	0.20	13,300	0.20
F (170°W–110°W)	CPI	1982/83	10					
		1983/84	50	1983/84	3,198	0.47	3,240	0.47
	CPII	1989/90	10					
		1990/91	50	1990/91	2,801	0.53	2,976	0.51
	CPIII	1995/96	30					
		2000/01	30	1997/98	3,852	0.22	3,852	0.22
G (110°W–50°W)	CPI	1981/82	10					
		1982/83	50	1982/83	683	0.63	1,452	0.65
	CPII	1986/87	10					
		1989/90	50	1989/90	1,505	0.34	2,817	0.38
	CPIII	1993/94	30					
		1997/98	10					
		1999/00	20	1996/97	3,337	0.21	3,310	0.21

humpback whales from the Ross Sea. First, their body shape with long flippers may be unsuited for heavy pack ice concentrations, unlike the more ice-adapted minke whales (e.g. Ainley *et al.*, 2007), and they tend to avoid regions where they could encounter high ice concentrations. Second, the dominant krill species north of about 73°S in the Ross Sea is Antarctic krill (*Euphausia superba*), but south of 73°S, ice krill (*E. crystallorophias*) is dominant (Sala *et al.*, 2002). Perhaps humpback whales have an aversion to ice krill.

The pattern of an increase in search half-width from CPI to CPII to CPIII is a general feature of the IDCR-SOWER surveys and has been previously noted for blue, fin, minke, sperm, humpback, killer and southern bottlenose whales (Branch and Butterworth, 2001a). This change is reflected in a wider shoulder in the hazard-rate model fit to the sightings of these species (Branch and Butterworth, 2001a) and appears to reflect a real change in the searching pattern of observers, with less effort directed to searching directly ahead of the vessel over time. The pronounced peak in sightings in CPI that were exactly on the trackline, and slightly lower sightings at small distances from the trackline, likely reflects substantial rounding of small sighting angles to zero degrees in those earlier surveys, as was evident for other species in CPI (Branch and Butterworth, 2001a).

Previous analyses have shown that humpback estimates from the IDCR-SOWER surveys are relatively insensitive to the following analytical choices: choice of truncation distance; inclusion of like humpback sightings; excluding mixed schools; treating possible and definite duplicates and triplicates as a single sighting; and obtaining separate abundance estimates from closing and IO mode (Branch and Butterworth, 2001a).

Table 8

Estimates of abundance for each IWC survey.

Year	Area/s	Longitudes	*N*	CV
1978/79	IV	70°E–130°E	968	0.45
1979/80	III	0–70°E	1,017	0.49
1980/81	V	130°E–170°W	957	0.59
1981/82	II	60°W–0	254	0.69
1982/83	I	120°W–60°W	663	0.64
1983/84	VI	170°W–120°W	3,198	0.47
1985/86	V	130°E–170°W	622	0.50
1986/87	II	60°W–0	550	0.38
1987/88	III	0–70°E	890	0.46
1988/89	IV	70°E–130°E	3,809	0.52
1989/90	I	120°W–60°W	1,561	0.37
1990/91	VI	170°W–120°W	2,801	0.53
1991/92	V	130°E–170°W	1,838	0.46
1992/93	III	0°E–40°E	194	0.53
1993/94	I	110°W–60°W	915	0.31
1994/95	III+IV	40°E–80°E	2,473	0.40
1995/96	VI	170°W–140°W	1,579	0.47
1996/97	II	30°W–0	1,099	0.75
1997/98	II	60°W–25°W	451	0.73
1998/99	IV	80°E–130°E	17,703	0.18
1999/00	I	80°W–60°W	2,139	0.27
2000/01	VI+I	140°W–110°W	2,294	0.18
2001/02	V	130°E–150°E	764	0.41
2002/03	V	150°E–170°W	6,545	0.26
2003/04	V	170°E–170°W	7,288	0.27

Table 9

Estimates of the annual rate of increase for humpbacks in each Management Area, for each breeding stock and for the circumpolar estimates as a whole.

Region	Rate of increase	95% CI
Area I	0.046	(–0.029; 0.123)
Area II	0.065	(–0.026; 0.152)
Area III	0.033	(–0.072; 0.133)
Area IV	0.149	(0.100; 0.197)
Area V	0.128	(0.067; 0.174)
Area VI	–0.002	(–0.072; 0.068)
Breeding stock A	0.053	(–0.083; 0.214)
Breeding stock B	0.031	(–0.255; 0.285)
Breeding stock C	0.066	(–0.048; 0.171)
Breeding stock D	0.144	(0.096; 0.192)
Breeding stock E	0.137	(0.067; 0.185)
Breeding stock F	0.016	(–0.055; 0.086)
Breeding stock G	0.046	(–0.034; 0.129)
Circumpolar	0.096	(0.057; 0.133)

Circumpolar estimates for CPI and CPII are similar to previous estimates but the CPIII estimate of 41,500 is substantially greater than the previous estimate for CPIII (then incomplete) of 9,300 based on 1991/92–1997/98 (Branch and Butterworth, 2001a). This increase is explained by the high estimated abundance in Area IV, which was only surveyed in 1998/99, and by the re-surveying of Area V in 2001/02–2003/04. Most of the estimated abundance (75%) in CPIII is in Area IV and V. The Area IV estimate (17,938) is within the range of recent JARPA estimates (Matsuoka *et al.*, 2011) (Fig. 4). Although the Area V estimate (13,246) is above the highest reported JARPA estimate of 9,342, the confidence intervals around these estimates are wide and the differences are not statistically significant (Fig. 4).

The three CPs differ in substantial ways: survey design, primary effort mode, and unsurveyed regions all changed from one CP to the next. Previously, sensitivity analyses have shown that survey design and primary effort mode only had a minor impact on humpback abundance estimates (Branch and Butterworth, 2001a), but it is important to account for the unsurveyed area south of 60°S in CPI and CPII. To obtain comparable estimates from the CPs it was assumed that the density in the unsurveyed northern strata was the same as in the adjacent northern strata, an assumption that has been made for previous estimates based on the IDCR/SOWER data (Branch, 2006; Branch, 2007; Branch and Butterworth, 2001a; 2001b). Data from the IDCR/SOWER surveys provide some support for this assumption: humpback whale density is highest close to the pack ice, and lower further away, but density is fairly similar for distances of more than 60 n.miles from the ice edge (Kasamatsu *et al.*, 2000). If instead, density is lower in the northern unsurveyed areas, then the ‘comparable areas’ estimates for CPI and CPII will be too high compared to those for CPIII, and the estimated rate of increase will be negatively biased.

Estimated rates of increase are subject to the comparability of CPI, CPII and CPIII surveys, especially given that CPI and CPII surveys did not cover the most northerly areas. JARPA surveys in recent years have found high densities of humpback whales near 60°S in Area IV (Matsuoka *et al.*, 2011). However, given the magnitude of the increase from CPII to CPIII it is unlikely that a different method for comparability would alter the general conclusion that humpback whales have increased dramatically in numbers. According to the ‘comparable-areas’ estimates, circumpolar abundance estimates are increasing at 9.6% per annum (95%

Table 10

Comparison of abundance estimates for each breeding stock based on surveys and mark-recapture methods from the northern breeding grounds in austral winter (references provided in the text), and from the IDCR/SOWER CPIII surveys in the Antarctic in the austral summer. For comparability, the CPIII estimates are projected to the mid-year of the relevant breeding ground estimate by assuming an annual rate of increase (ROI) of either 0% (no increase), 5% or 10%. The ratio of the CPIII to breeding ground estimates is also given.

Breeding stock	Breeding ground estimates		CPIII projected estimates			Ratio of CPIII to breeding ground
	Year	Estimate	ROI = 0%	ROI = 5%	ROI = 10%	
A	2008	9,300	168	285	481	0.02–0.05
B	2004–06	7,600	595	956	1,538	0.08–0.20
C	2000–06	13,000	2,391	3,844	6,182	0.18–0.48
D	2005	12,800	17,959	26,131	38,020	1.40–2.97
E	1999–05	9,000	13,300	13,637	13,982	1.48–1.55
F	2003–07	1,350	3,852	5,071	6,676	2.85–4.95
G	2006	6,504	3,337	5,366	8,628	0.51–1.33
Total	1999–08	59,584	41,602	55,290	75,507	0.70–1.27

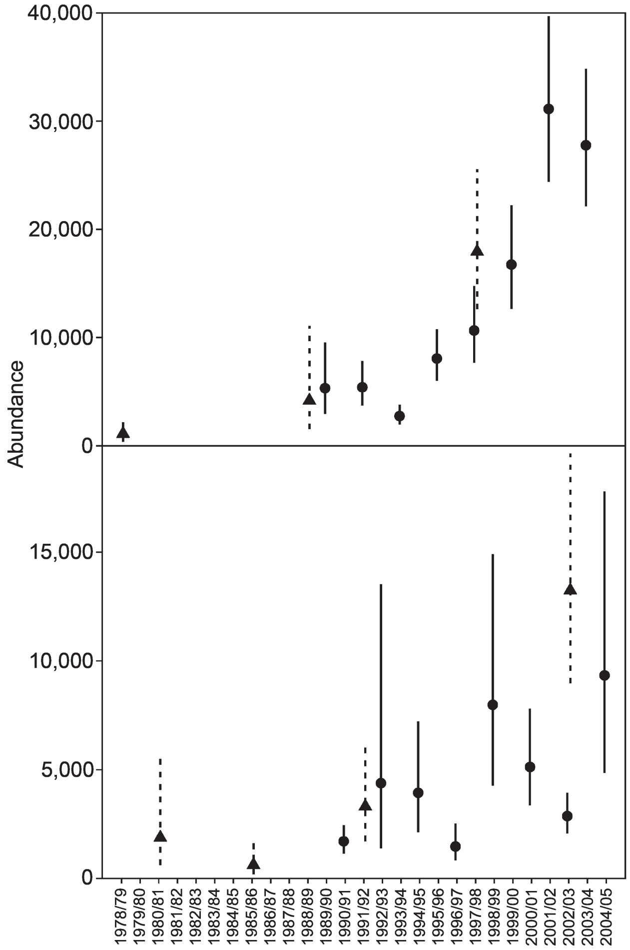

Fig. 4. Comparable-area IDCR/SOWER abundance estimates (triangles, dashed lines) and JARPA abundance estimates (circles, solid lines) for IWC management Area IV (top panel) and Area V (bottom panel). JARPA estimates were obtained from Table 3 of Matsuoka *et al*. (2011).

CI 5.8–13.4%), a rate that is significantly greater than zero. Estimated rates of increase for Area IV and V and Breeding Stocks E and F are at or greater than the estimated biological maximum of 11.8% (Zerbini *et al*., 2010). JARPA surveys in Area IV also show an increasing trend at greater than 10.1% per year (Matsuoka *et al*., 2005), mirroring the estimates here. An increasing rate is to be expected for large baleen whales recovering from depletion since intraspecific competition should be lower, and indeed this pattern has been observed in many other baleen whale populations (Best, 1993; Branch *et al*., 2004), including humpback whales off the eastern and western coasts of Australia. Additionally, however, there is some variability around the circumpolar estimates and wide variation in the range of estimated rates of increase for different areas and Breeding Stocks, likely due to the small number of IDCR/SOWER abundance estimates for each group (3–4), high associated CVs, changes in the survey design between the circumpolar sets of surveys and year-to-year variability in the distribution of humpback whales.

No attempt was made to constrain either the point estimate or the confidence interval to a biological maximum of 11.8% (Zerbini *et al*., 2010). Due to the limited number of abundance estimates in each area, and the wide confidence intervals associated with each abundance estimate, it is expected that some estimated rates of increase will be much smaller than the true rate, and others much larger, and that the confidence intervals around the estimated rates of increase will be broad.

Comparison of breeding ground and feeding ground estimates

Abundance estimates in the Antarctic differ greatly from those in the temperate breeding grounds. A suggested current abundance for each Breeding Stock is listed in this section, and compared with feeding ground estimates in Table 10.

Breeding stock A

For Breeding Stock A, a fixed-wing aircraft survey off Brazil estimated an abundance of 9,330 (CV = 0.16) for 2008 (Wedekin *et al*., 2010). The projected CPIII estimate is only 2–5% of this estimate (Table 10). Satellite tagging data have demonstrated that humpback whales from this Breeding Stock travel to feeding grounds near South Georgia and the South Sandwich Islands, but no tracked whales have yet travelled south of 58°S (Zerbini *et al*., 2006; Horton *et al*., 2011), and high densities were also recorded north of 60°S in the JSV database between 25°W and 5°E during summer (Miyashita *et al*., 1995), thus the IDCR/SOWER surveys likely cover only a very small fraction of the total stock. The IDCR/SOWER-estimated rate of increase of 5.3% (95% CI –8.3 to 21.4%) is accordingly not very applicable to this Breeding Stock. For Breeding Stock A, estimates of abundance and rates of increase should therefore be taken from the breeding grounds: abundance 9,330 (CV = 0.16) (Wedekin *et al*., 2010); rate of increase: 7.4% (95% CI 0.6–14.5%) (Ward *et al*., 2011).

Breeding stock B

For the B1 substock in Gabon, genotypic mark-recapture abundance was estimated to be 7,134 (CV = 0.23) in 2004–06 (Collins *et al*., 2010). For the B2 substock, a photographic catalogue from 2001–05 contained 260 individuals with a high inter-annual resighting rate of 16.5% that suggested a small population (Barendse *et al*., 2006). Assuming that the B2 substock was ~500, the total for Breeding Stock B was ~7,600 in 2004–06. The projected CPIII estimate is just 8–20% of this total (Table 10). During transits to and from the IDCR/SOWER surveys, relatively high numbers of humpback whale sightings were recorded (Fig. 1) north of 60°S in the 20°W to 10°E region. JSV data revealed high densities of humpback whales north of 60°S in the summer between 25°W and 5°E (Miyashita *et al*., 1995). Finally, the 2005/06 IDCR/SOWER survey (not included in these abundance estimates), conducted fin whale research in the 55°S–61°S and 5°E–20°E region and recorded a large number (149) of humpback whale schools, nearly all north of 60°S (Ensor *et al*., 2006). It is therefore likely that most humpback whales from this Breeding Stock do not migrate south far enough (to 60°S) to reach the region covered by the IDCR/SOWER surveys, and therefore the breeding ground abundance estimate of ~4,300 should be preferred. Rates of increase have not been estimated from the breeding grounds and the IDCR/SOWER estimate (3.1%) has broad 95% confidence intervals (–25.5% to 28.5%) and applies only to a portion of the population, thus current trends in Breeding Stock B are not well defined.

Breeding stock C

For the C1 substock, a ship-based line-transect survey estimated abundance to be 5,965 (CV = 0.17) in 2003 (Findlay *et al*., 2011). For the C2 substock, a total of 250 individuals were photo-identified from the eastern Comoros Archipelago but no abundance estimate was calculated (Ersts *et al.*, 2006). For C3 at Antongil Bay, Madagascar, photographic and genetic mark-recapture techniques provided estimates ranging from 4,936 (CV = 0.44) to 8,169 (CV = 0.44) for 2000–2006 (Cerchio *et al.*, 2009). The total for Breeding Stock C was therefore approximately 13,000 in 2000–06. The extrapolated CPIII abundance estimate is only 18–48% of the total breeding ground estimate (Table 10). In the applicable Antarctic region (10°E–60°E), numerous sightings of humpback whales were made during transits north of 60°S (Fig. 1) and (as summarised above) during fin whale research on the 2005/06 IDCR/SOWER survey (Ensor *et al.*, 2006). It is therefore likely that the greatest portion of this Breeding Stock does not migrate south far enough to be included in the IDCR/SOWER surveys, and thus the breeding ground estimates summing to about 12,000 are more relevant for this stock than the IDCR/SOWER estimates. The best estimated rate of increase (9.0% or 12.3%) for this stock comes from shore-based counts at Cape Vidal, South Africa (Findlay and Best, 2006).

Breeding Stock D

In the breeding grounds, an aerial survey estimated that there were 12,800 humpback whales (95% CI 7,500–44,600) in Breeding Stock D in 2005 (Paxton *et al.*, 2011). This population has been increasing steadily at 10.15% (SE = 4.6%) per year (Bannister and Hedley, 2001). At this rate of increase, the CPIII estimates would have increased to about 38,000, i.e. 2.89 times the breeding ground estimate in 2005 (Table 10), only just below the upper confidence interval of the breeding ground estimate of 44,600. JARPA estimates for Management Area IV of 31,134 (CV = 0.123) in 2001/02 and 27,783 (CV = 0.115) in 2003/04 come from a similar longitudinal range (70–130°E vs. 60–120°E) and are also more than double the breeding ground estimates (Matsuoka *et al.*, 2011). Despite substantial effort during IDCR/SOWER transits, few humpback whales have been sighted north of the IDCR/SOWER survey region (Fig. 1), suggesting that the majority are inside the IDCR/SOWER survey region. If the feeding ground estimates provide a more complete survey of the entire Breeding Stock, this would imply that either the breeding ground survey does not cover the full distribution of this Breeding Stock or that a substantial portion of these humpback whales do not migrate to the west coast of Australia each year. An examination of the sightings from the breeding ground survey showed high numbers of sightings even in the northernmost survey leg (Paxton *et al.*, 2011), so it is possible that a portion of the breeding ground was not surveyed. Some support for non-migration comes from the male-biased sex ratio on the west coast of Australia: 194 males and only 64 females were sampled migrating past the North West Cape in 2002–03, and the authors suggested that the missing whales may overwinter near the feeding grounds instead of migrating (Jenner *et al.*, 2006). It is tentatively suggested that the feeding ground estimates from IDCR/SOWER and JARPA provide a more complete abundance estimate than the breeding ground survey, and hence the current abundance of Breeding Stock D is >30,000. Rates of increase from both IDCR/SOWER and JARPA surveys are above biologically plausible levels and have wide confidence intervals; therefore the more precise 10.15% annual rate of increase from the feeding grounds should be preferred for this Breeding Stock (Bannister and Hedley, 2001).

Breeding stock E

For substock E1 a shore-based survey at Point Lookout estimated abundance to be 7,090 (95% CI 6,459–7,782) in 2004 (Noad *et al.*, 2011), and a multi-point mark-recapture estimate of 7,041 (95% CI 4,075–10,008) was obtained for the east coast of Australia for 2005 (Paton *et al.*, 2011). Mark-recapture methods from 1999–2004 gave estimates of 383 (CV = 0.35) using photographs and 804 using genotypes for New Caledonia (substock E2); similar methods yield estimates of 1,168 (CV = 0.16) from photographs and 1,840 using genotypes for Tonga (substock E3) (Constantine *et al.*, 2010). The total breeding region abundance for Breeding Stock E is therefore ~9,000 during 1999–2005. The projected CPIII estimate is 1.48–1.55 times greater than this total (Table 10) and is also higher than the JARPA estimates in recent years (2,700–9,800 during 1998/99–2004/05) in Area V (Fig. 4). All sources have estimated a high rate of increase for this population, IDCR/SOWER: 13.7% (95% CI 6.7–18.5%), JARPA: 6.4% (CV = 0.71) (Matsuoka *et al.*, 2005), the Point Lookout shore survey: 10.6% (95% CI 10.1–11.1%) (Noad *et al.*, 2011), Byron Bay: 11.0% (95% CI 2.3–20.5%) (Paton and Kniest, 2011), and Hervey Bay: 13.4% (95% CI 11.6–15.2%) (Forestell *et al.*, 2011). The IDCR/SOWER and JARPA estimates probably include most of the Breeding Stock given that few humpback whales are sighted north of the survey region during IDCR/SOWER transits (Fig. 1). Humpback whales migrating past the east coast of Australia have a male-biased sex ratio of 2.4:1 (Brown *et al.*, 1995), suggesting that not all females leave the feeding grounds in winter (Paton and Kniest, 2011). It is not clear whether to prefer estimates from the breeding or feeding regions, although these estimates are broadly similar, suggesting that the total abundance of Breeding Stock C is probably in the range of 8,000–13,000. The Point Lookout survey provides the most precise estimate of the rate of increase: 10.6% (95% CI 10.1–11.1%) per year (Noad *et al.*, 2011).

Breeding Stock F

During 1998–2005, 93 individuals were identified (no interannual resightings) in the Cook Islands (substock F1), implying a small substock (Hauser and Clapham, 2006). In French Polynesia (substock F2), photographic mark-recapture methods provided breeding ground abundance estimates ranging from 853 (CV = 0.24) to 1,849 (CV = 0.16) during 2003–2007 (Albertson-Gibb *et al.*, 2009). The projected CPIII estimate is 2.84–4.94 times greater than the center of this range of breeding ground estimates (Table 10). There are several reasons to suspect that this estimate refers to only a portion of Breeding Stock F. First, no abundance estimate is available for the Cook Islands (Hauser and Clapham, 2006). Second, the French Polynesia estimate was based on two islands with the highest densities of humpback whales, but sightings have also been reported around 23 other islands (Poole, 2006). Third, the sex ratio in French Polynesia is male biased (1.5:1) (Poole, 2006), and therefore some females may remain near the feeding grounds in the winter. For these reasons, the IDCR/SOWER estimates (3,852, CV = 0.22) seem more appropriate for this Breeding Stock. The estimated rate of increase from the IDCR/SOWER is 1.6% (95% CI –5.5% to 8.6%), suggesting that this population could be increasing, stable or decreasing.

Breeding Stock G

A photographic mark-recapture study in Ecuador provides a breeding ground abundance estimate of 6,504 (95% CI 4,270–9,907) in 2006 (Félix *et al.*, 2011). The projected

CPIII estimate is similar (0.51–1.33) to this estimate (Table 10), and to an alternative feeding ground estimate from a CCAMLR survey in East Antarctica of 6,991 (CV = 0.32) in 2001 (Hedley *et al.*, 2001). The estimated rate of increase from IDCR/SOWER is 4.6% (95% CI –3.4% to 12.9%), while the breeding ground estimates are increasing rapidly during 1997–2006 (Félix *et al.*, 2011). It seems reasonable to conclude that Breeding Stock G numbers 5,000–8,000 and is increasing at 5–10% per year.

Summary of breeding stocks

Estimates for Breeding Stocks A, B and C are far lower than from the feeding grounds, while those for Breeding Stocks D, E and F are far higher. These differences may just be due to inherent uncertainty in the survey estimates. However, it is interesting to note that the ratio between the two appears linked to the position of the Antarctic Polar Front (Fig. 1). In regions where this front is far to the north, the breeding ground estimates are higher than the IDCR/SOWER estimates (suggesting that many humpback whales are further north and outside the IDCR/SOWER survey region), while in regions where the front is further south, breeding ground estimates are similar or lower than the IDCR/SOWER estimates. Differences in the estimates may also be due to the use of the Naïve model (IWC, 1998; 2006) to place longitudinal divisions between the Breeding Stocks in the Antarctic. In reality, the divisions between the Breeding Stocks are not fixed: there is some mixing of the Breeding Stocks in the Antarctic, but it is unlikely that most humpback whales from Breeding Stocks A, B and C actually migrate to the Antarctic regions assumed to be inhabited by Breeding Stocks D, E and F.

Total Southern Hemisphere abundance

The sum of all available abundance estimates from the northern breeding grounds is 60,000; whereas the corresponding totals for the IDCR/SOWER surveys are 42,000, 55,000 and 76,000 for assumed rates of increase of 0% (which is unlikely), 5% and 10% respectively (Table 10). Both IDCR/SOWER and feeding ground estimates are negatively biased. In the IDCR/SOWER surveys, some humpback whales on the trackline are missed (i.e. $g(0)<1$). Humpback whales produce very visible cues, thus this bias is probably small: an estimate of 10% was obtained from the eastern North Pacific (Calambokidis and Barlow, 2004). A more substantial negative bias comes because some humpbacks do not migrate southwards far enough to reach the IDCR/SOWER survey region. For Breeding Stocks A, B and C, where the Antarctic Polar Front is further north, the sum of the breeding region estimates is about 30,000 but the projected IDCR/SOWER estimates are only 3,000–8,000. The sum of the breeding ground estimates is probably also negatively biased because not all breeding grounds have been surveyed. For these reasons it is fairly safe to conclude that there are more than 55,000 humpback whales in the Southern Hemisphere.

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A note on the age at sexual maturity of humpback whales

Peter B. Best

Mammal Research Institute, University of Pretoria, c/o Iziko South African Museum, PO Box 61, Cape Town, 8000 South Africa
Contact e-mail: pbest@iziko.org.za

ABSTRACT

The conclusion of researchers in the 1950s that humpback whales reached sexual maturity at about age five was largely influenced by their interpretation of baleen tracings, and to achieve consistency with these tracings the accumulation rate of ear plug laminations (growth layer groups: GLGs) was assumed to be two per year. However, ovulation and natural mortality rates calculated by these researchers under the same assumption produced estimates that are difficult to reconcile with other biological data or with more recent estimates using individual re-sighting data. Such disparities are reduced or disappear when an annual accumulation rate is used, in which case their ear plug data would have indicated a mean age at sexual maturity of 9–11 years. Recent estimates of the age of female humpback whales at first calving using longitudinal studies of photo-identified individuals have produced conflicting results, some (from southeastern Alaska) being compatible with the earlier age-determination studies, others (from the Gulf of Maine) suggesting a much younger age.

KEYWORDS: HUMPBACK WHALE; GROWTH; AGE DETERMINATION; AGE AT SEXUAL MATURITY; PHOTO-ID

INTRODUCTION

The potential for using laminations in the ear plug of mysticetes for age determination was discovered in the mid 1950s (Laws and Purves, 1956; Purves, 1955). Prior to this, biologists had relied heavily on the pattern of transverse ridges and grooves in baleen plates, a technique first suggested by Scoresby (1820) but only taken up seriously by Ruud (1940; 1945) and Tomilin (1945). While counting the ear plug laminations was more straightforward than trying to interpret the ridging on baleen plates, and problems of wear did not arise, there was still a need for calibration of the rate of lamina accumulation. This was really only established (for fin whales, *Balaenoptera physalus*) in 1967 (Roe, 1967), and for sei whales (*B. borealis*) in 1974 (Lockyer, 1974), in both cases at one growth layer group (GLG, or one dark plus one light lamination) per year.

Chittleborough published his classic works on the biology of southern humpback whales (*Megaptera novaeangliae*) between 1954 and 1965, thus overlapping the period of the discovery of ear plug age determination but pre-dating its calibration. His finding (Chittleborough, 1959), and that of Nishiwaki (1959), that humpback whales reached puberty around age five, later received some support from longitudinal studies of individual humpback whales first sighted as calves in the Gulf of Maine, in which 12 females reached sexual maturity between the ages of five and seven (Clapham, 1992). Despite this apparent confirmation of Chittleborough and Nishiwaki's findings, scepticism has remained, largely because their conclusions flew in the face of conventional thinking about the age of other rorquals at puberty (generally taken to be at around age ten). There have even been moves to organise a humpback whale ear plug reading exercise, ideally involving Chittleborough himself, to attempt to reconcile the apparent paradox (Bannister *et al.*, 2000).

This note was prompted by a paper received for review (since published as Gabriele *et al.*, 2007), in the course of which some of the original publications were revisited.

REVIEW OF PAPERS

Chittleborough (1959)

This paper presents the results of reading ear plugs from 657 humpback whales and also includes photographs of 12 plugs from eight whales, bisected for reading, as well as the resultant counts. Apart from two examples of unreadable plugs, a comparison of the photographs with Chittleborough's counts makes it clear that what he considered a lamination was identical to what would be called a GLG today and his description in the text of the laminations and how he interpreted them confirms this. It seems extremely unlikely that Chittleborough interpreted plugs any differently from the majority of present-day readers, and he gives the number of laminations at puberty in 290 females as ranging from 5–14 with a mean of close to nine.

Chittleborough's conclusion that the age at puberty was five (and the rate of lamination accumulation thus two per year) was based on the results of his interpretation of tracings from baleen plates. Illustrations of such tracings that he gives show how difficult their interpretation must have been, particularly as there did not seem to be any neonatal baseline from which to start counting. Although wear at the tip was supposed to make the allocation of ages to whales more than six years old unreliable, there seems no objective means of establishing when wear started and how fast it occurred. The omission of the portion of the baleen plate below the gum must also have influenced age readings. Perhaps because of these difficulties, there has never been adequate calibration of this technique for age determination. Stable isotope analyses of bowhead and right whale baleen has shown that (for balaenids at least) annual periodicity in baleen growth can be identified (Best and Schell, 1996; Schell *et al.*, 1989) and could theoretically provide a means for calibrating baleen growth in humpback whales. In comparable analyses of minke whale baleen, however, only one or two periods could be identified, even in the largest animals (my interpretation of figures in Hobson *et al.*, 2004). The latter authors concluded that if minke whale baleen grows at the same rate as bowhead baleen (17–25cm year^{-1}), then the baleen plate may represent only the last year of life. They did not mention that at the southern right whale rate of baleen growth (25–60cm/year), the plates would represent even less than that.

Nishiwaki (1959)

By plotting the total number of ovarian corpora against the number of ear plug laminations in about 100 females, Nishiwaki showed that the first ovulation occurred around an age of 9–12 laminations in the ear plug, concluding that sexual maturity is reached when 11 laminations have accumulated. He then simply stated 'Since two laminations are formed in a year, the whale just reaching to the sexual maturity is five years old or slightly old than that'. No supporting data or reference is given for the conclusion that lamina formation is bi-annual.

Dawbin (1959)
Two marked humpback whales caught in Cook Strait, New Zealand, had been at large for 12 months and 18 months respectively, but baleen and ear plugs were only recovered from the latter animal. This whale was estimated at 36ft in length at marking (so clearly not a calf) but proved to be only 34ft 7in when killed. Despite the obvious error in size-estimation at marking, it was estimated to be at least in its second year and therefore when killed would have had a minimum age of three years. Baleen tracings showed three zones and there were five distinct and two indistinct laminations in the ear plug, while histological analysis of the testes indicated that the whale was still sexually immature. This was taken as supporting evidence of a bi-annual rate of lamina accumulation. However as the whale's age was actually unknown, and the baleen tracing analysis only consistent with the minimum age assigned, the evidence is inconclusive.

Chittleborough (1960b; 1962)
The recapture of two marked humpback whales and the collection of ear plugs and reproductive organs (and in the one case baleen plates) from them were used to provide evidence in confirmation of a bi-annual rate of lamina accumulation. The whales were a male 36.75ft long and a female 39ft long at death, and both had been at large for almost five years after marking. The male had 12 laminations in the ear plug and the testes weighed 1kg each. The size, number of laminations and testes weight were all consistent with an individual approaching puberty, but the age from baleen plate tracings was given as 'at least 5 years' (as Chittleborough (1959) stated that ages of six or more were impossible to separate using baleen tracings, this qualification is quite significant). The female had ten laminations in the ear plug and one corpus albicans in the ovaries. Chittleborough posited that the whale must have become mature one year earlier, but there is no indication that the whale was lactating and so it is possible that the whale had become mature at least two years previously (i.e. it had completed one full reproductive cycle). It is important to note that, despite the title of one of the papers, neither of these was an individual of known age, and both were described at marking as yearlings approximately 30ft long. Estimates of whale length at sea can be very inaccurate (errors of 15% or more in either direction were observed for Antarctic minke whales (Best, 1984)), and the reasons for their assignation as yearlings are unknown (but would certainly not include individual identification). As evidence of a bi-annual rather than annual rate of lamina accumulation, the data from these whales must be considered equivocal.

OTHER IMPLICATIONS OF ASSUMING A BI-ANNUAL RATE OF EAR PLUG LAMINA ACCUMULATION

Chittleborough (1959), Nishiwaki (1959) and Symons and Weston (1958) regressed the number of ovarian corpora against age as determined from ear plug laminations for humpback whales off Australia, the Ryukyu Islands in the North Pacific, and Antarctic Area I respectively. The regression coefficient so obtained for the Australian data was 0.558 ovulations per lamination, for the Antarctic data 0.59 per lamination, and although the coefficient for the Japanese data was not given, it can roughly be estimated from the illustrated slope of the regression as 0.50. Under the assumption of a bi-annual rate of lamina formation, these translate into annual ovulation rates of between 1 and 1.18 per year. If these are compared with annual pregnancy rates of 0.37 (Chittleborough, 1965) and 0.40 (derived from data in Nishiwaki, 1959), it suggests that only one in 2.5–3 ovulations was successful, and that presumably a high proportion of females must have undergone a post-partum ovulation. However, examination of the ovaries of females killed in Tonga shortly after parturition failed to reveal such a phenomenon (Chittleborough, 1965), implying that the frequency of ovulation at the start of each reproductive cycle must be much higher than the 1.2 observed (Chittleborough, 1959). Chittleborough's explanation of this discrepancy was that some of the ovulations at the start of the reproductive cycle must have been 'missed' because their corpora lutea had regressed so much they were not recognised as being from the current cycle. However, if the rate of lamina accumulation was assumed to be annual rather than bi-annual, the ovulation rates would be halved and it would be unnecessary to postulate major ovulation failure (or 'missing' corpora albicantia).

Chittleborough (1965) also estimated the natural mortality rate of humpback whales assuming two ear plug laminations accumulated per year. For the Area IV population off Western Australia, coefficients for adult males and females were estimated as 0.086 (SE 0.14) and 0.087 (SE 0.129) respectively, while for the Area V population off East Australia, an estimate of 0.097 was considered to be representative of natural mortality in adult males (Chittleborough, 1960a; 1965). More recently, estimates of annual survival in humpback whales have been obtained from re-sightings of naturally marked individuals. In the Gulf of Maine (North Atlantic), Buckland (1990) estimated annual survival as 0.951 (95% CI: 0.929, 0.969), and Barlow and Clapham (1997) non-calf survival at 0.96 (SE 0.008). In the central North Pacific, Mizroch *et al*. (2004) estimated adult survival at 0.963 (95% CI: 0.944, 0.978). Although the populations, time periods and methods involved are all different, the Northern Hemisphere estimates imply substantially lower annual mortality rates than those calculated by Chittleborough. However, if an annual rather than bi-annual rate of lamina accumulation had been adopted, the mortality rates for Australian humpback whales would have been halved and would essentially be not significantly different from those for the Northern Hemisphere.

CONCLUSIONS

This review indicates that it was an assumption of a bi-annual rate of lamina accumulation, rather than a different interpretation of what constituted a growth layer group in the ear plug, that led to estimates in the late 1950s of the age of humpback whales at sexual maturity of around five years. In this assumption, researchers were mainly guided by the results of baleen plate tracings, a technique that seemed to involve a high degree of subjectivity in its interpretation, was only applicable to animals in the first few years of life and was never calibrated adequately. Estimates of ovulation and natural mortality rates made under the assumption of a bi-annual rate of lamina accumulation now seem too high to be biologically feasible.

The conclusions of the 1950s studies on the age of humpback whales at sexual maturity were seemingly supported by later longitudinal studies of individually identified animals in the Gulf of Maine (Clapham, 1992). However, further such studies in southeastern Alaska have revealed ages at first calving in humpback whales of 8–16 (average 11.8) years, more consistent with the results of age determination studies assuming an annual rate of lamina formation in the ear plug (Gabriele *et al.*, 2007). The reasons for this discrepancy between the two photo-identification studies remain to be resolved.

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Abundance estimates and trends for humpback whales (*Megaptera novaeangliae*) in Antarctic Areas IV and V based on JARPA sightings data

Koji Matsuoka, Takashi Hakamada, Hiroshi Kiwada, Hiroto Murase and Shigetoshi Nishiwaki

The Institute of Cetacean Research, 4–5, Toyomi-cho, Chuo-ku, Tokyo 104-0055, Japan
Contact e-mail: matsuoka@cetacean.jp

ABSTRACT

Sighting survey data from the Japanese Whale Research Program under Special Permit in the Antarctic (JARPA) are analysed to obtain abundance estimates for humpback whales (*Megaptera novaeangliae*) south of 60°S. The surveys were conducted during the 1989/90–2004/05 austral summer seasons (mainly in January and February); the survey areas alternated between Area IV (70°E–130°E) and Area V (130°E to 170°W) each year. Primary sighting effort totalled 293,811 n.miles over 6,188 days. Abundance estimates are obtained using standard line transect analysis methods and the program DISTANCE. Estimated densities of humpback whales were highest east of the Kerguelen Plateau (80°E–120°E). Abundance estimates for Area IV range from 2,747 (CV = 0.153) in 1993/94 to 31,134 (CV = 0.123) in 2001/02, while those for Area V range from 602 (CV = 0.343) in 1990/91 to 9,342 (CV = 0.337) in 2004/05. The estimates are similar to those obtained from the International Whaling Commission's IDCR-SOWER surveys, which were conducted in Area IV (in 1978/79, 1988/89 and 1998/99) and in Area V (in 1980/81, 1991/92 and 2001/02–2003/04). Estimated annual rates of increase for Area IV (16.4%; 95% CI = 9.5–23.3%) and Area V (12.1%; 95% CI = 1.7–22.6%) are also similar to those obtained from the IDCR-SOWER surveys. The total abundance in Areas IV and V based on the most recent JARPA surveys (2003/04 and 2004/05 combined) is 37,125 (95% CI = 21,349–64,558); the confidence interval incorporates estimated additional variance. Results of several sensitivity tests are presented that suggest that estimates of abundance and trends are not appreciably affected by factors such as different approaches to deal with survey coverage (which in some cases was poor or included gaps). Changes in the order in which survey strata were covered and potential effects are investigated using a nested GLM approach; a QAIC model selection criterion suggests a preference for not attempting to adjust for such changes. Under various sensitivity approaches, the point estimates of increase rates are not greatly affected for Area IV. Although they drop by typically a half for most approaches for Area V, they nevertheless remain within the confidence limits of the base case estimate of 12.1% per year (95% CI = 1.7–22.6%). The presented results thus suggest that the estimated abundance of humpback whales in Area IV has increased rapidly. Although there is also an increase indicated for Area V, it is neither as rapid nor as precisely estimated. Taking these results together with the similar rates of increase estimated from coastal surveys off western and eastern Australia for Breeding Stocks D and E respectively, and given demographic limitations on the increase rates possible for closed populations of humpback whales, the hypothesis is advanced that whales from Breeding Stock E may have shifted their feeding distribution westward as their numbers have increased, perhaps to take advantage of the higher densities of krill to be found to the west.

KEYWORDS: ABUNDANCE ESTIMATE; ANTARCTIC; HUMPBACK WHALE; JARPA; SURVEY-VESSEL; TRENDS

INTRODUCTION

There are several genetic stocks (genetically differentiated populations within a species) of humpback whales in the Southern Hemisphere. The International Whaling Commission Scientific Committee (IWC SC) has hypothesised a total of at least seven Breeding Stocks, which it has called Stocks 'A', 'B', … 'G' (IWC, 2005) and is still working to refine this. The population named Breeding Stock D has its breeding grounds in the waters off western Australia and in summer is believed to be found mainly in Area IV, south of 60˚S. Breeding Stock E which has its breeding grounds in the waters off eastern Australia and some of the south Pacific islands, is believed to be found mainly in Area V south of 60˚S in summer.

Humpback whales were heavily over-exploited during the last century. Allen (1980) estimated that at the end of commercial whaling, the stocks of this species had been reduced to 2% of an original population of 130,000 animals. More recent evaluations as part of the IWC Scientific Committee's Comprehensive Assessment are ongoing, but results reported to date, when summed over the seven Breeding Stocks, suggest an original abundance of about 125,000 whales reduced to a minimum of about 4% of that number by the mid-1960s (e.g. IWC, 2009; Jackson *et al.*, 2008; Johnston *et al.*, 2011; Johnston and Butterworth, 2005; Johnston and Butterworth, 2007; Zerbini *et al.*, 2011). Fortunately, signs of recovery are now evident for many, although not all, of these stocks. In particular, the abundance of Breeding Stocks D and E have been estimated, based on data from off Australia, to be increasing at annual rates of around 10%–10.2%, SE = 4.6% by Bannister and Hedley (2001) and at 10.6%, SE = 0.5% by Noad *et al.*, (2011). In addition to the conservation value for continued monitoring of the abundance and trends of these stocks, continued monitoring is also important because the stocks provide an excellent opportunity to improve understanding of the dynamics of baleen whale populations recovering from low levels.

There are two major sources of systematic sightings data in the Antarctic; one of these is the IWCs IDCR/SOWER cruises (e.g. see Matsuoka *et al.*, 2001), which are considered later in this paper. The other and the focus of the present paper, is the sighting component of the JARPA (Japanese Whale Research Program under Special Permit in the Antarctic) programme. The stated objectives of the JARPA programme were: (a) elucidation of the stock structure of the Antarctic minke whale (*Balaenoptera bonaerensis*) to improve stock management; (b) estimation of biological parameters of the Antarctic minke whale to improve the stock management; (c) elucidation of the role of whales in the Antarctic marine ecosystem through whale feeding ecology; and (d) elucidation of the effect of environmental change on cetaceans (Government of Japan, 1987; 1996). In order to address these four objectives, JARPA comprised a combination of sighting and lethal sampling surveys. This programme took place each year from 1987/88 to 2004/05 during the austral summer. JARPA was designed to alternate surveys in Antarctic Areas IV and V in each of the sixteen years of the full-scale research period.

Sightings data collected by the SVs (dedicated sighting vessels) and SSVs (sighting and sampling vessels) during JARPA have been used to estimate abundance and abundance trends of blue whales (Branch *et al.*, 2004) and other large whale species (Kasamatsu *et al.*, 2000; Matsuoka *et al.*, 2005a; Matsuoka *et al.*, 2005b). Abundance estimates for Antarctic minke and humpback whales have also been presented to annual and intersessional meetings of the IWC Scientific Committee (e.g. Hakamada *et al.*, 2006; Matsuoka *et al.*, 2006) including the recent review of the JARPA programme (IWC, 2008). During these meetings, concerns were expressed on certain aspects of the work, particularly the potential effect of the sampling component (of Antarctic minke whales) of the JARPA surveys on the abundance estimates of this and other species of whales (e.g. Wade, 2008). The review Workshop recommended further work and made a number of specific suggestions (Table 1).

The primary objective of this paper is to present analyses of the humpback whale sightings data in Antarctic Areas IV and V that take into account relevant recommendations of the IWC Scientific Committee. To facilitate understanding of the estimation procedures and the interpretation of results, some details of the JARPA survey procedures are provided below, with further details set out in appendix 1 of Hakamada *et al*. (2007).

A secondary objective of this study is to compare JARPA abundance estimates in the feeding grounds of Areas IV and V with those in the breeding grounds and migratory corridors in the waters off both sides of Australia. (Bannister and Hedley, 2001; Paxton *et al.*, 2011) and eastern Australia (Noad *et al.*, 2011).

In addition, the paper will compare abundance estimates in Areas IV and V obtained by JARPA with those obtained by the IWCs IDCR (International Decade for Cetacean Research) and SOWER (Southern Ocean Whale and Ecosystem Research) research programmes. Under these programmes, dedicated sighting surveys (primarily aimed at Antarctic minke whales) have been conducted by the IWC in the Antarctic annually from 1978/79 to 1995/96 (IDCR) and then from 1996/97 (SOWER). An overview of IDCR/SOWER surveys is given in Matsuoka *et al*. (2003). One of the features of JARPA is that, unlike the IDCR/SOWER programmes, surveys have been repeated in the same area and in similar months every second season over a long period. The JARPA surveys can thus facilitate estimation of trends and the extent of inter-year variability in local abundance.

SURVEY DESIGN AND DATA COLLECTION

As noted above, JARPA comprised a combination of sighting and lethal sampling surveys. In order to try to obtain biological samples representative of the Antarctic minke whale population, a random sampling method was adopted within a line transect sighting survey design. The sighting and sampling surveys were conducted by two or three SSVs proceeding along predetermined tracklines. A dedicated SV was introduced from the 1991/92 season. The JARPA surveys have been conducted in a generally consistent way since 1989/90. This paper incorporates data from the eight full-scale surveys in Area IV (1989/90, 1991/92, 1993/94, 1995/96, 1997/98, 1999/00, 2001/02 and 2003/04), and the eight in Area V (1990/91, 1992/93, 1994/95, 1996/97, 1998/99, 2000/01, 2002/03 and 2004/05). Details of the surveys' design and some modifications over time are given in Nishiwaki *et al*. (2006) and in appendix 1 of Hakamada *et al*. (2007). Implications of some of these modifications for the results for abundance and abundance trends are discussed later.

Research area

The research area and geographical sub-divisions are shown in Fig. 1. Although JARPA covered the Antarctic sector between 35˚E and 170˚W south of 60^{o}S, the analyses in this paper focus on IWC management Areas IV (70^{o}E–130^{o}E) and V (130^{o}E–170^{o}W) since this allows them to be restricted to data collected in the same months (January–February) over the full set of cruises. Areas IV and V were divided into two sectors (western and eastern) that were further divided into northern (60˚S to 45 n.miles from the ice edge) and southern (from the ice edge to 45 n.miles away) strata. The western sector of Area IV includes a separate Prydz Bay stratum. For this sector, north and south strata were divided at 66^{o}S. The eastern sector of Area V includes the Ross Sea; for this sector the north and south strata were divided at 69°S.

Monthly coverage

Although the JARPA research period ranged from the end of November to March in each season, regular research in Areas IV and V was concentrated in January and February (Fig. 2). This coincides with the peak migration period of humpback whales to Antarctic feeding grounds (Kasamatsu *et al.*, 1996).

Table 1

List of recommendations for improvements to estimates of abundance of humpback whales from the JARPA surveys from the IWC Scientific Committee (IWC, 2008) and priority assigned by the Advisory Group.

Tasks	Priority	Remarks
1. Estimation of detection function (re-estimate in the cases where the number of detection is small)	H	Addressed; Table 6a, 6b (Abundance); Table 7 (Trend)
2. Investigation of sensitivities to pooling all vessels to estimate effective strip width and mean school size	M	For humpback whales, data had already been pooled for all vessels
3. Variance estimation from the SSV data	M	To be addressed in future work
4. Sensitivity analysis with appropriate weighting and/or bootstrapping	M	Addressed; Tables 6a, 6b and 7
5. Abundance estimates treating as if abundance in gaps between two strata were 0	L	Addressed; Table 6a, 6b and 7
6. Extrapolation of density into unsurveyed areas were surveyed	H	Addressed; Table 6a,
8. Estimation of additional variance	M	Partially addressed; Table 7 and 9b, Future analyses will utilize GLM
9. Revised estimates of annual increase rate and its CV following suggestions 1–8	M	Addressed; Table 7 and 9b

Research vessels

Relevant information on the vessels used is given in Table 2. *Kyo-maru No.1* (K01)*, Toshi-maru No.25* (T25) and *Toshi-maru No.18* (T18) operated as SSVs for the surveys from 1989/90 to 1997/1998. *Kyosin-maru No.2* (KS2) engaged exclusively in sighting surveys (SV) from 1995/96. *Yusin-maru* (YS1) was used from the 1998/1999 cruise replacing the T18 and *Yusin-maru No.2* (YS2) was used from the 2001/2002 cruise replacing the T25.

Order of the surveys

The order in which strata were surveyed within the main survey period (January–February) is shown in Figs 3a and 3b for Areas IV and V respectively. Abundance estimates are based on single coverage of the blocks shown in Fig. 3 in the season concerned.

Trackline design

The trackline was designed to cover the whole research area and was followed consistently throughout the JARPA

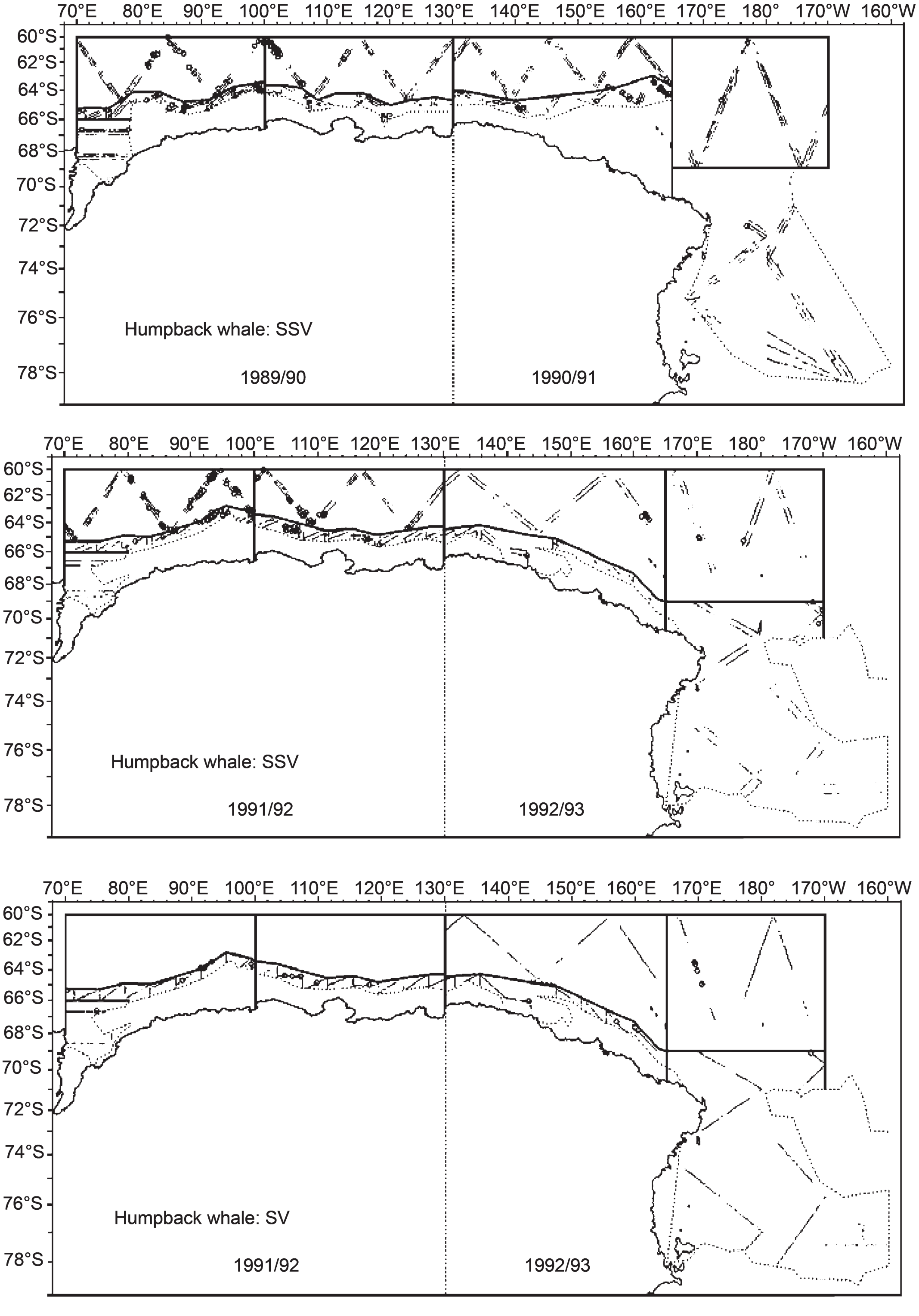


Fig. 1. Primary searching effort (thin lines) and associated primary sightings (circle) of humpback whales in Areas IV and V with the ice edge line (dotted) during the 1989/90 to 2004/05 JARPA surveys. The areas not surveyed in the 1995/96, 1999/00, 2001/02 and 2003/04 seasons are shaded grey. SSV = Sighting and sampling vessels, SV = Dedicated sighting vessel.

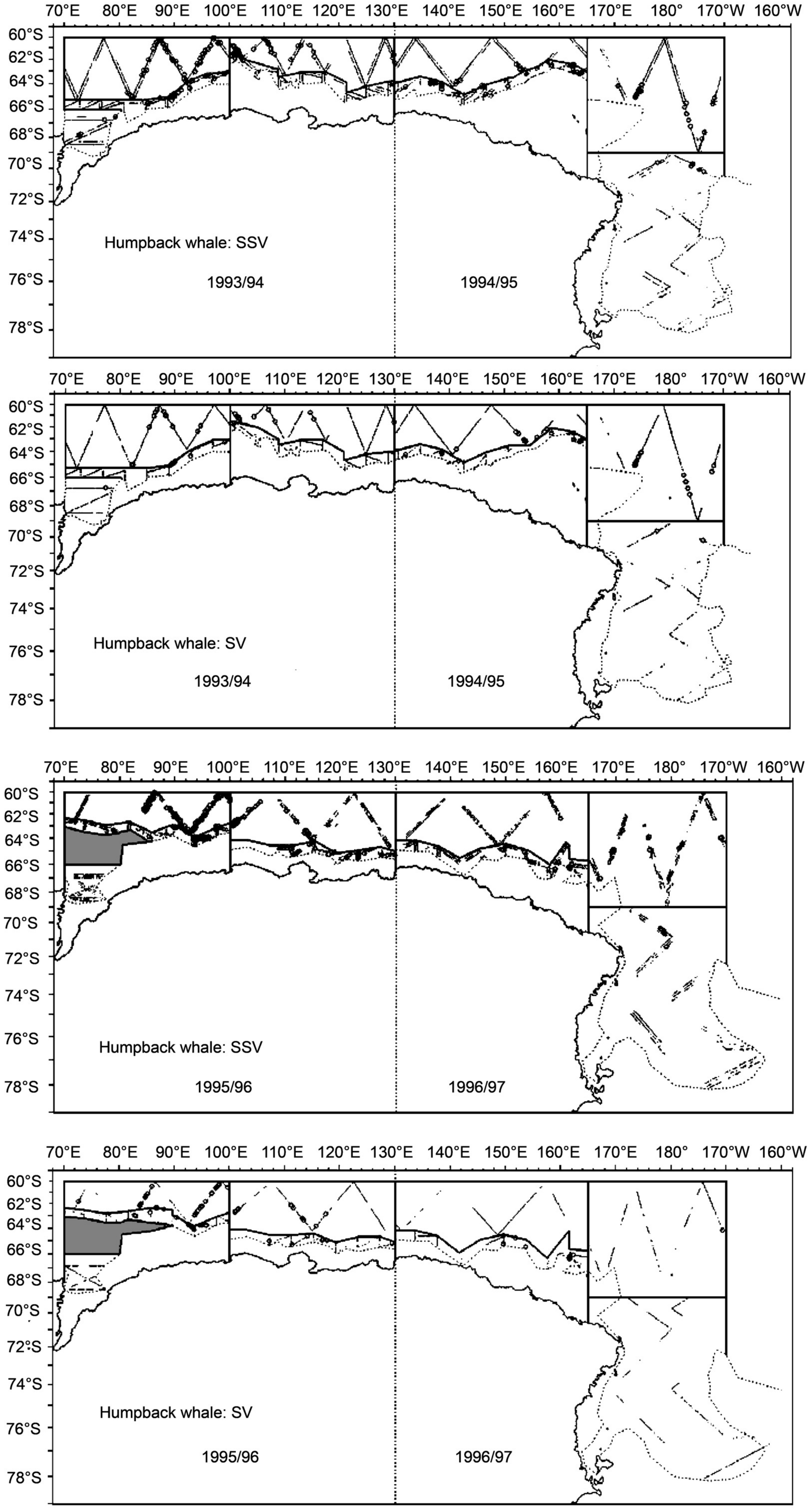
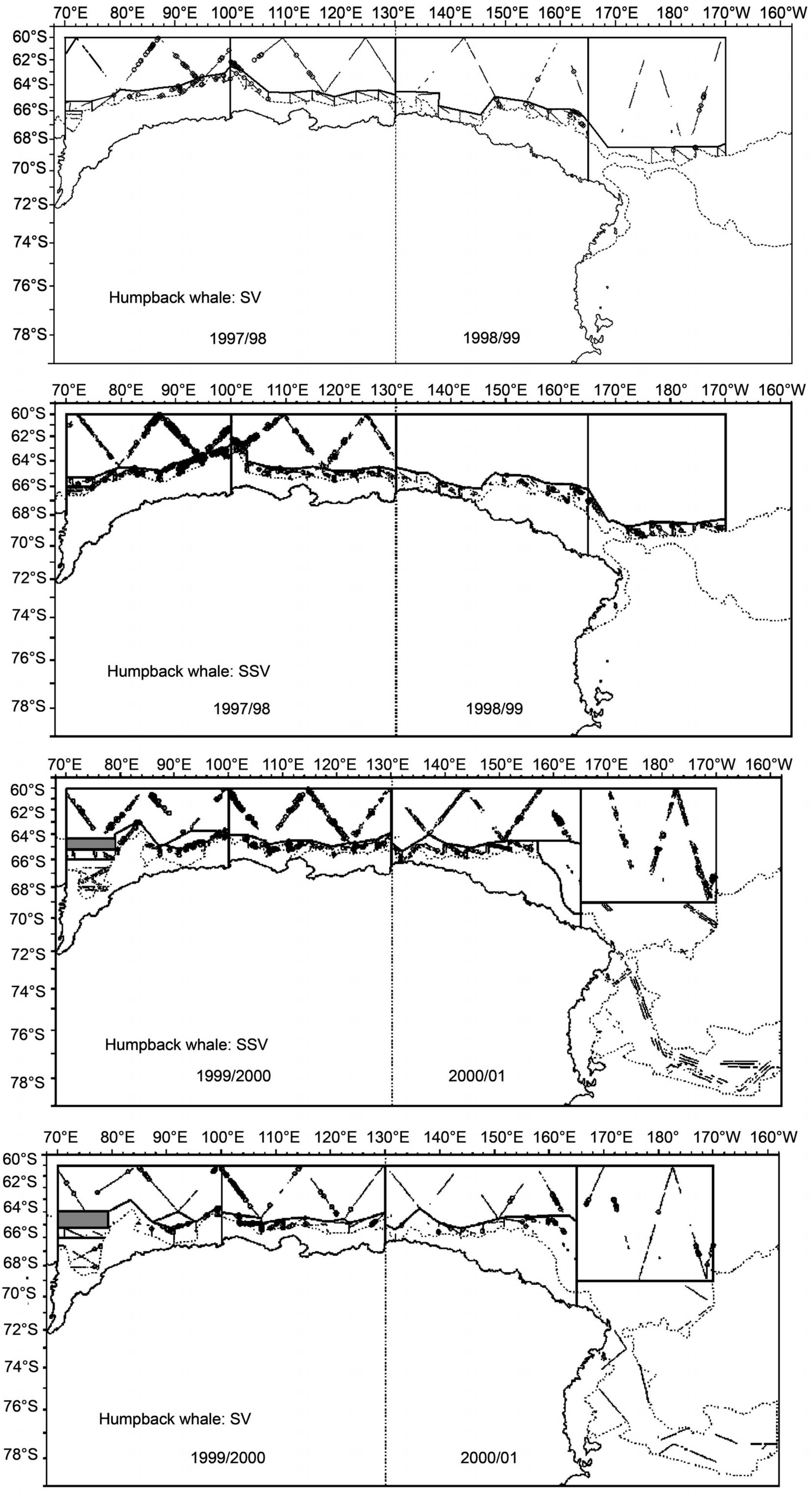

70°E
80°E
90°E
100°E
110°E
120°E
130°E
140°E
150°E
160°E
170°E
180°
170°W
160°W
60°S
62°S
64°S
66°S
68°S
70°S
72°S
74°S
76°S
78°S
Humpback whale: SSV
1993/94
1994/95
Humpback whale: SV
1993/94
1994/95
Humpback whale: SSV
1995/96
1996/97
Humpback whale: SV
1995/96
1996/97

Fig. 1 (part 2).


70°E
80°E
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120°E
130°E
140°E
150°E
160°E
170°E
180°
170°W
160°W
60°S
62°S
64°S
66°S
68°S
70°S
72°S
74°S
76°S
78°S
Humpback whale: SV
1997/98
1998/99
Humpback whale: SSV
1997/98
1998/99
Humpback whale: SSV
1999/2000
2000/01
Humpback whale: SV
1999/2000
2000/01

Fig. 1 (part 3).

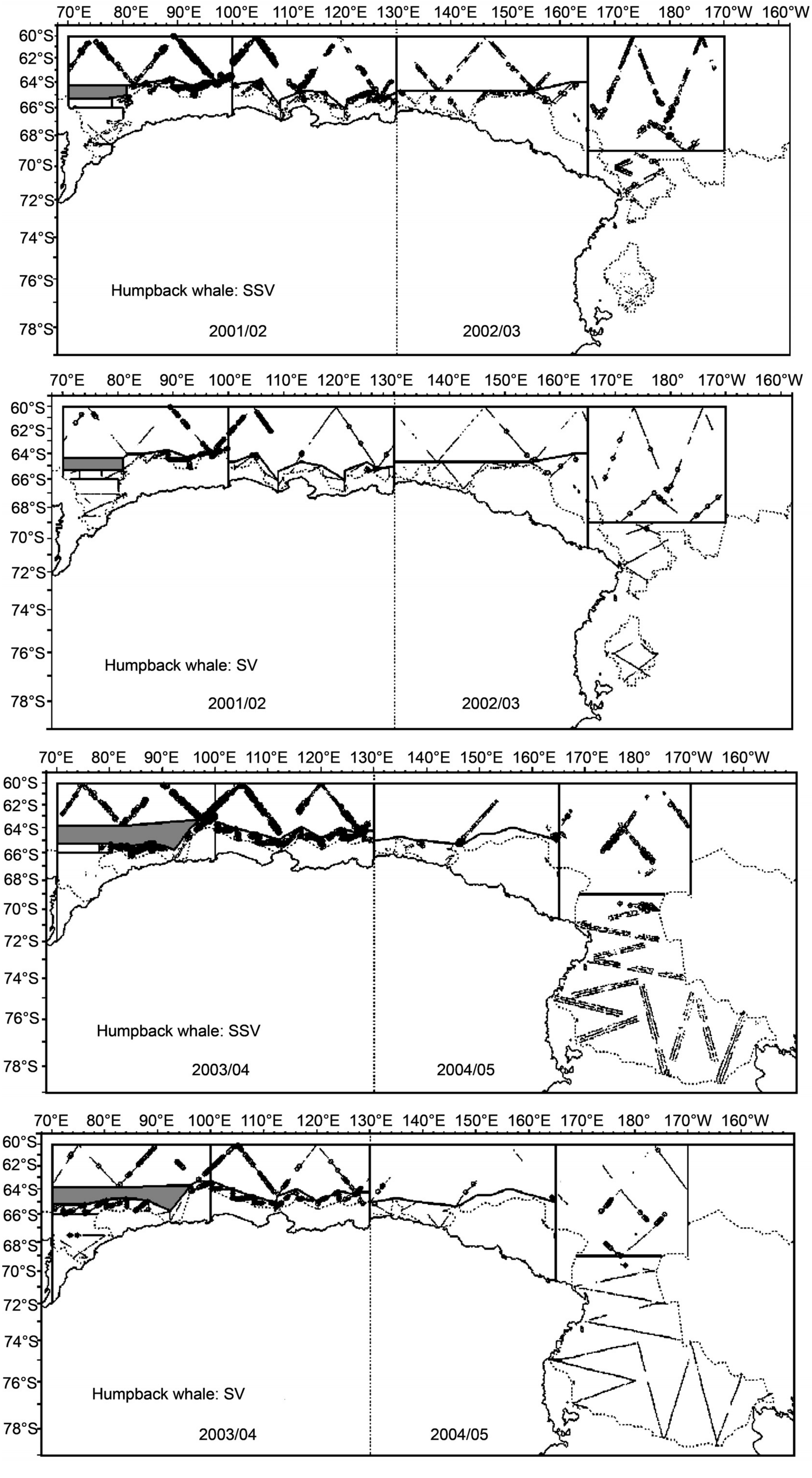

70°E 80°E 90°E 100°E 110°E 120°E 130°E 140°E 150°E 160°E 170°E 180° 170°W 160°W
60°S 62°S 64°S 66°S 68°S 70°S 72°S 74°S 76°S 78°S
Humpback whale: SSV
2001/02
2002/03
Humpback whale: SV
2001/02
2002/03
Humpback whale: SSV
2003/04
2004/05
Humpback whale: SV
2003/04
2004/05

Fig. 1 (part 4).

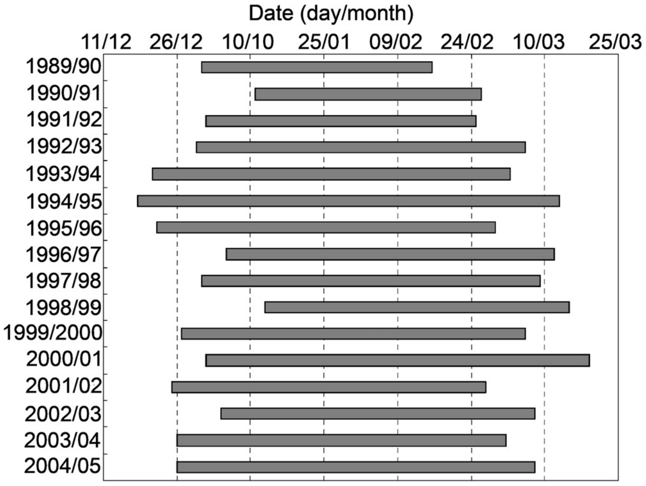


Fig. 2. Start and end dates of JARPA surveys for abundance estimation of humpback whales in Areas IV and V.

surveys (Figs 1 and 4). The saw-tooth type trackline for the southern strata was chosen to allow for a wide area coverage. The starting points of the trackline were selected at random from 1 n.mile intervals on lines of longitude. Trackline way points were systematically set on the ice edge and on the locus of points 45 n.miles from that edge in southern strata, and on this locus and the 60°S latitude line in northern strata. Nishiwaki *et al*. (2006) provides more details.

Sighting survey procedure

Two or three SSVs travelled in parallel (7 n.miles apart) on each predetermined trackline. The SSVs surveyed at a standard speed of 11.5 knots. The survey was conducted under what were considered optimal research conditions for Antarctic minke whales (i.e. when visibility was over 2 n.miles and the wind speed was <25 knots in the southern strata, <20 knots in the northern strata).

The SSVs interchanged tracklines each day to avoid possible bias associated with a fixed location in the pair or triplet of tracklines. Sightings of whales were classified into primary and secondary sightings. Primary sightings were those made under normal searching mode; secondary sightings were those made under other modes (e.g. during closing or chasing modes or off effort). In effect, the sighting surveys by the SSVs were conducted under normal closing mode (NSC in IDCR-SOWER notation as described in Nishiwaki *et al*., 2006) i.e. after a sighting was made the vessels approached a school of whales to confirm species and school size; this mode is denoted as SSV hereafter.

One of the three SSVs behaved as a SV from the 1991/92 to 1994/95 cruises. From 1995/96 three SSVs and an additional SV (KS2) operating in closing mode (i.e. NSC as above but without lethal sampling of whales) were allocated to the survey. From 1998/99, the SV (KS2) introduced the passing mode option (NSP in IDCR-SOWER notation) i.e. the vessel did not approach the whale after the sighting was made and searching from the barrel continued uninterrupted, except that in some special cases, such as sightings of blue whales, closure was effected once the vessel came abeam of the whale. During a 12-hour survey day, the observers alternated between normal closing mode (4 hours) and passing modes (8 hours). For the SV these modes are denoted as SVC and SVP hereafter. The SSVs followed the SV at a distance of over 12 n.miles to avoid any influence of sampling activities on the SV's sighting survey.

A researcher on board recorded all the information on the whales sighted. The sighting record included the date and the time of the sighting, the position of the vessel, a classification of survey mode and sighting (primary or secondary), the angle and distance from the vessel of the initial sighting, the species and school size, the estimated body length and other information as for the IDCR-SOWER cruises. More details of these procedures are given in Nishiwaki *et al*. (2006).

ANALYTICAL PROCEDURE

The procedure applied here to analyse the sightings data is similar to that used for the IWC/IDCR-SOWER surveys by Branch and Butterworth (2001a; 2001b). To provide 'base case' estimates of abundance:

(1) distances and angles are corrected for possible bias by using the results of the distance and angle estimation experiments;
(2) the sighting rate is obtained for each day;
(3) smearing parameters are obtained by Buckland and Anganuzzi's (1988) method II;
(4) $g(0)$ is assumed to be 1; and
(5) sightings data are pooled each season and across strata to the extent necessary for reliable estimation of the effective search half-width (w_s, using either a hazard rate or half-normal model) and the mean school size ($E(s)$), based on standard line transect analysis methods using the program DISTANCE (Thomas *et al*., 2005).

The sections below set out further assumptions made to obtain base case estimates, followed by descriptions of sensitivity tests in which one or more of the base case specifications and assumptions are varied.

Data selected for the analysis

Size of the research area

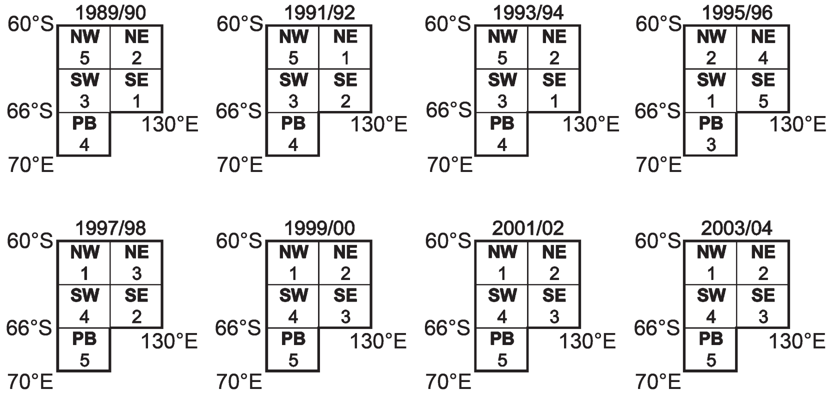
The surveys covered the region between the ice edge and 60°S, The open water area for each stratum for each survey

Table 2

Specifications of the research vessels used for the JARPA surveys.

	Kyo-maru No.1	*Toshi-maru No.25*	*Toshi-maru No. 18*	*Yushin-maru*	*Yushin-maru No.2*	*Kyoshin-maru No.2*
Call sign	JKNG	8JCG	JPMQ	JLZS	JPPV	JFHR
Register length (m)	69.15	68.37	63.20	69.61	69.60	68.18
Molded breadth (m)	10.30	9.90	9.90	10.40	10.80	10.80
Gross register tonnage	812.08	739.92	758.33	720.00	747.00	372.00
Barrel height (m)	18.00	18.00	18.00	18.00	18.00	17.00
IOP height (m)	–	–	–	13.50	13.50	10.50
Upper bridge height (m)	10.00	10.00	10.00	10.00	10.00	8.00
Bow height (m)	6.40	6.00	6.20	6.50	6.50	–
Maximum continuous output (hp)	5,000	3,600	3,500	5,280	5,280	2,100

(a) Area IV



(b) Area V

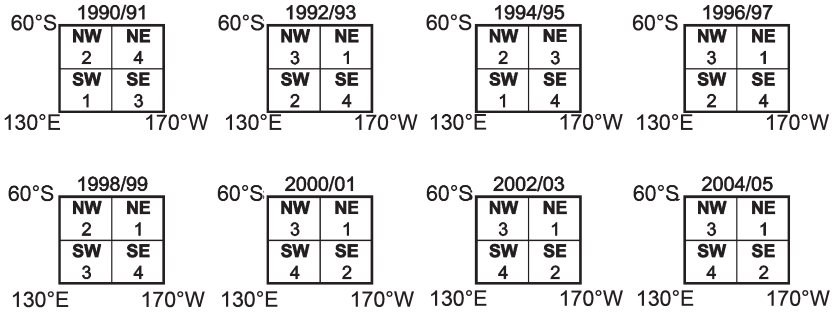


Fig. 3. Survey order by strata. (a) Antarctic Area IV of JARPA survey from the 1989/90 to 2003/04 seasons. (b) Antarctic Area V of JARPA survey from the 1990/91 to 2004/05 seasons. Key: NW = North-West, NE = North-East, SW = South-West, SE = South-East (Ross Sea), PB = Prydz Bay.

was calculated using the *Marine Explore* Geographical Information System version 4 (Environment Simulation Laboratory Co, Ltd, Japan). The ice edges and hence boundaries between the northern and southern strata differed for SVs and SSVs because their surveys were not completely synchronous, so that the ice edges they encountered differed. This results in slightly different stratum areas for the two. For abundance estimates developed combining data over the SSV and SV modes, the averages of the two area sizes for each stratum are used.

Unsurveyed area

Some small parts of Area IV were unsurveyed on four of the cruises, with the proportions not surveyed listed in Table 3. These 'gaps' (see Fig. 1) arose because of the retreat of the ice edge after survey of the more northerly of the two strata concerned had been completed, necessitating re-location of the trackline for the more southerly stratum. For base case abundance estimates, these gaps are treated as having the same density as the more northerly stratum. This is because densities tend to be higher closer to the ice edge, and these gap regions are more typical of areas more distant from the ice. Note that such 'gaps' differ from instances where coverage of a survey was poor or incomplete because of shortage of time and/or bad weather. The consequences for abundance estimates of each of these effects are addressed further below under 'Sensitivity Tests'.

Survey modes

Sightings data collected under SSV, SVC and SVP modes were combined for the estimation of the mean school size and effective search half-width for schools. Although separate estimates are obtained for each of these modes in the case of Antarctic minke whales (Hakamada *et al.*, 2007), data were pooled here. This is because the limited number of sightings made of humpback whales required the inclusion of as many sightings as possible, as in the case of the IDCR-SOWER based abundance estimates for species other than the Antarctic minke whale (Branch, 2011; Branch and Butterworth, 2001a).

ABUNDANCE ESTIMATION

The methodology used for abundance estimation is described in Branch and Butterworth (2001a) and has been accepted by the IWC Scientific Committee in the past. The program DISTANCE (Thomas *et al.*, 2002) was used to implement this. The basic formula is;

$$P = \frac{AE(s)n}{2wsL} \qquad (1)$$

where,

P is the estimated abundance in numbers in the stratum,

A is the open ocean area of the stratum,

$E(s)$ is the estimated mean school size,

n is the number of primary sightings of schools,

w_s is the effective strip half-width for schools, and

L is the primary search effort.

The CV of P is calculated using the approximate formula:

$$\mathrm{CV}(P) = \sqrt{\{\mathrm{CV}\left(\frac{n}{L}\right)\}^2 + \{\mathrm{CV}(E(s))\}^2 + \{\mathrm{CV}(w_s)\}^2} \qquad (2)$$

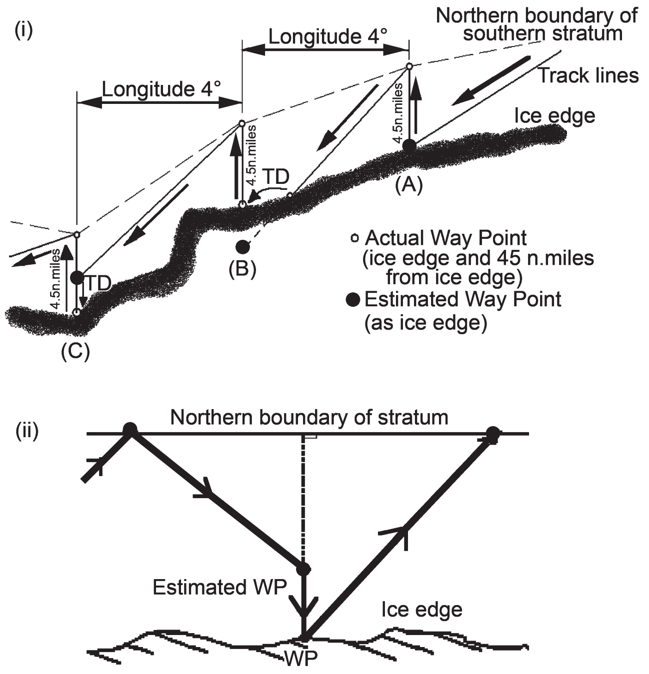


Fig. 4. Trackline design in southern strata. (i) (A): saw tooth shape trackline with intervals of four degrees longitude. Southern way points (WPs) were set on the ice-edge and northern WPs (northern boundary) were set on the locus of points 45 n.miles from the edge. (B): When the ice edge was encountered before reaching a planned southern WP (estimated WP), the research vessels stopped surveying and moved to the next four degree longitudinal interval line along the ice edge (in TD – topman down – mode). Then the research vessels reversed direction and resumed the survey (BC in NSC and BP in NSP modes) northward. (C): When the ice edge was not encountered on reaching a planned southern WP, the research vessels stopped surveying and moved south (in TD – topman down – mode) on the longitudinal line through the WP until the vessels encountered the ice edge. Then the research vessels reversed direction and resumed the survey (BC in NSC and BP in NSP modes) northward. (ii) In the case of surveys in the Ross Sea, survey was continued on a bisector line after reaching an estimated southern WP. If the time elapsed from the estimated WP to the true WP on the ice edge was over two hours, a revised trackline was set from the true WP to the next WP on the northern boundary.

Under the assumption of distribution log-normality, 95% confidence intervals for the abundance estimates are calculated as (P/C, CP) where C is given by:

$$C = \exp(Z_{0.025}\sqrt{\log_e[1+\{\mathrm{CV}(P)\}^2]}) \qquad (3)$$

and

$Z_{0.025}$ represents 2.5-percentage point of a standard normal distribution. More details of the analysis methods may be found in Buckland *et al*. (2001) and Branch and Butterworth (2001a; 2001b).

Correction of the estimated angle and distance
To be able to detect and if necessary correct for biases in angle and distance observations, experiments using a radar reflecting buoy were conducted by each vessel during each cruise as is the case for the IDCR/SOWER cruises (the experimental methodology is described in Nishiwaki *et al*., 2006). Linear regression models were used to examine possible differences between observed and true (obtained from radar) distances for each platform for each cruise (Table 4a). In order to correct for such biases, the estimated distance was divided by the estimated slope of a regression through the origin if this slope differed significantly from 1 at the 5% level. A similar approach was used for angles. More details of the methodology may be found in Branch and Butterworth (2001b).

Table 3
The percentages of the open ocean area not surveyed in Area IV surveys.

Season	Percentage of area not surveyed
1989/90	–
1991/92	–
1993/94	–
1995/96	9.2
1997/98	–
1999/00	4.5
2001/02	2.7
2003/04	10.0

Truncation distance
The conventional truncation distance for perpendicular distances of sightings estimated for Antarctic minke whales is 1.5 n.miles (Branch and Butterworth, 2001b). However, because of their larger body and blow sizes, humpback whales can be seen much further from vessels than Antarctic minke whales. The approximation advocated in Buckland *et al.* (2001) to truncate such that about 5% of the data are excluded, has therefore been applied as in Branch and Butterworth (2001a), with results rounded to the nearest 0.3 n.miles. Accordingly the perpendicular distance distributions were truncated at 2.7 n.miles.

Smearing parameters
Smearing parameters were calculated for each cruise to make allowance for errors in estimates of distances and angles following Branch and Butterworth (2001a). The sightings data are smeared before their truncation to give n, and then used in the estimation of the effective search half-width (w_s) and the mean school size ($E(s)$) for input to equation (1). Radial distance and angle data were smeared in the conventional manner by using Method II of Buckland and Anganuzzi (1988) and then grouped into intervals of 0.3 n.miles for estimating w_s values. For Antarctic minke whales, smearing parameters are conventionally estimated separately for each stratum from the data. However, due to the lower numbers of sightings of humpback whales, some pooling was necessary here to obtain robust estimates from the Buckland and Anganuzzi method. The smearing parameter values reported in Table 4b were thus obtained from pooled sightings (including sightings with both confirmed and unconfirmed school size) separately for each cruise.

Effective search half-width
The smeared and truncated sighting data for schools were grouped into intervals of 0.3 n.miles to estimate the detection function. A hazard rate model with no adjustment terms and a half-normal model were considered as potential detection functions. The better model was selected by AIC in each case; $g(0)$ was assumed to be 1 (i.e. no schools present on the trackline were missed).

Mean school size
The method regressing the logarithm of school size against the detection $f(y)$, as described by Buckland *et al.* (2001) was used to estimate mean school size ($E(s)$). If the regression coefficient was not significant at the 15% level, the mean of the observed school size was input to equation (1). Note that pooling across survey modes means use of school size estimates for SVP mode which may bias the estimate of $E(s)$

Table 4a

Estimated observer bias (expressed as multiplicative correction factors) in distance and angle estimation for JARPA surveys from 1989/90 to 2004/05.

		Platform			
		Barrel		Upper bridge	
Season	Vessel	Distance	Angle	Distance	Angle
1989/90	K01	n.s.	0.930	n.s.	0.872
	T18	n.s.	1.047	n.s.	n.s.
	T25	1.099	n.s.	1.075	n.s.
1990/91	K01	n.s.	1.051	0.953	1.064
	T18	n.s.	n.s.	n.s.	n.s.
	T25	0.882	n.s.	0.961	n.s.
1991/92	K01	0.930	n.s.	n.s.	0.950
	T18	n.s.	n.s.	0.960	n.s.
	T25	n.s.	n.s.	1.070	n.s.
1992/93	K01	n.s.	0.942	1.083	0.941
	T18	n.s.	n.s.	n.s.	n.s.
	T25	n.s.	1.056	n.s.	1.082
1993/94	K01	0.863	n.s.	n.s.	n.s.
	T18	n.s.	n.s.	n.s.	n.s.
	T25	n.s.	n.s.	n.s.	1.057
1994/95	K01	n.s.	n.s.	n.s.	0.933
	T18	n.s.	n.s.	0.934	n.s.
	T25	0.940	n.s.	0.902	n.s.
1995/96	K01	n.s.	n.s.	n.s.	n.s.
	T18	n.s.	n.s.	1.110	0.956
	T25	0.889	n.s.	0.905	1.040
	KS2	n.s.	0.905	n.s.	0.898
1996/97	K01	0.822	n.s.	0.844	n.s.
	T18	0.711	n.s.	n.s.	n.s.
	T25	0.799	n.s.	0.773	1.036
	KS2	0.789	0.951	0.662	1.050
1997/98	K01	0.842	n.s.	0.746	n.s.
	T18	0.902	n.s.	0.788	n.s.
	T25	0.729	n.s.	0.914	n.s.
	KS2	0.876	n.s.	0.788	n.s.
1998/99	K01	0.902	n.s.	0.956	1.057
	T25	n.s.	1.053	n.s.	1.065
	YS1	0.923	n.s.	0.968	n.s.
	KS2	0.928	0.950	n.s.	n.s.
1999/2000	K01	n.s.	n.s.	1.050	n.s.
	T25	n.s.	1.081	n.s.	n.s.
	YS1	n.s.	n.s.	n.s.	n.s.
	KS2	n.s.	0.930	n.s.	n.s.
2000/2001	K01	n.s.	1.051	n.s.	n.s.
	T25	n.s.	n.s.	1.062	n.s.
	YS1	n.s.	n.s.	n.s.	n.s.
	KS2	n.s.	n.s.	n.s.	0.861
2001/2002	K01	0.957	0.921	0.957	n.s.
	T25	0.951	n.s.	0.960	n.s.
	YS1	n.s.	n.s.	n.s.	n.s.
	KS2	n.s.	n.s.	n.s.	n.s.
2002/2003	K01	1.073	n.s.	n.s.	n.s.
	YS1	1.051	1.037	1.058	0.938
	YS2	1.050	n.s.	n.s.	n.s.
	KS2	n.s.	n.s.	n.s.	1.088
2003/2004	K01	0.957	0.921	0.957	n.s.
	YS1	0.951	n.s.	0.960	n.s.
	YS2	n.s.	n.s.	n.s.	n.s.
	KS2	n.s.	n.s.	n.s.	n.s.
2004/2005	K01	1.113	1.096	1.044	n.s.
	YS1	1.029	0.939	1.024	0.919
	YS2	1.102	1.061	n.s.	n.s.
	KS2	1.084	0.966	1.064	n.s.

*n.s. indicates not significant at 5% level.

Table 4b

Smearing parameters for each stratum used in abundance estimation. Units for angles are degrees, while for distances the values given are proportions.

	Area IV			Area V	
Season	Angle	Distance	Season	Angle	Distance
1989/90	4.978	0.308	1990/91	3.963	0.257
1991/92	6.589	0.266	1992/93	4.616	0.396
1993/94	5.821	0.356	1994/95	6.411	0.206
1995/96	5.742	0.273	1996/97	7.732	0.214
1997/98	5.612	0.231	1998/99	8.710	0.281
1999/2000	6.769	0.233	2000/01	6.559	0.307
2001/02	5.289	0.233	2002/03	4.106	0.174
2003/04	7.180	0.188	2004/05	6.486	0.250

downwards. Only sightings for which school size was confirmed were used to obtain these estimates.

Population rate of increase

To estimate rate of increase in an Area, an exponential trend was assumed with the following error structure:

$$P_y = \beta \exp(\alpha y) + v_y,\ \ \hat{P}_y = P_y + u_y, \qquad (4)$$

where

P_y and $\hat{P}_y$ are the true and survey estimated abundances in an Area in season y,

α is the instantaneous increase rate,

β is abundance for season $y = 0$,

u_y reflects survey sampling error, and

v_y is the error associated with additional variance, which arises from an inter-annual variation in the proportion of whales in the surveyed area at the time of the survey.

In order to take the additional variance of abundance estimates (CV_{add}) as well as the survey sampling CV into account, the negative log-likelihood function minimised to estimate is:

$$l(\alpha,\beta,CV_{add}) = \frac{1}{2}\sum_y \log\left[CV(\hat{P}_y)^2 + CV_{add}^2\right] + \sum_y \frac{\left(\log(\hat{P}_y) - \log(\beta) - \alpha y\right)^2}{2\left[\left\{CV(\hat{P}_y)\right\}^2 + CV_{add}^2\right]} \qquad (5)$$

Estimates of standard errors for and CV_{add} were obtained from the associated Hessian (Information matrix), with CI estimates assuming a *t*-distribution with 6 degrees of freedom.

Sensitivity tests

Alternative estimates of effective search half-width

The base case selects between the hazard rate and half-normal models for the detection function for cruise-stratum/set-of-strata combinations. For sensitivity tests, either all forms are set to half-normal or all to hazard rate.

Inclusion of tracklines that followed the contours of the ice edge

In practice, some of the tracklines obtained where the saw-tooth type trackline design approach was used, were nearly parallel to the ice edge (e.g. SW and SE strata in Area IV).

This could lead to overestimation of abundance because of possible higher density close to the ice edge. As sensitivity tests to examine the effect of tracklines that followed the contours of the ice edge, two datasets were developed: one that excluded portions of tracklines that followed the contours of the ice edge (Option B), and the other one that excluded all tracklines not parallel to lines of longitude (Option C). Given the small number of sightings in the SW and SE strata in Area IV on earlier cruises, only seasons from 1997/98 onwards were considered.

Unsurveyed areas and incomplete coverage

Two approaches have been taken to attempt to bound the uncertainty associated with the treatment of ‘gaps’ in coverage as defined above for the base case estimates:

(1) the abundance contributions from these gaps are set to zero (i.e. whales in such gaps at the time of surveying the more southerly strata are considered as ones already effectively counted in the earlier surveying of the more northerly strata, as these whales would subsequently likely have moved further south); and
(2) the density in a gap is assumed to be the same as the higher density in the stratum immediately to the south, rather than that immediately to the north as in the base case.

The implications of incomplete to poor coverage of certain strata as a result of time shortage or weather factors also need consideration. Selection of potentially more serious cases to examine was guided by inspection of the cruise track plots in Fig. 1, and instances where a review by Wade (2008) suggested coverage to be ‘low’ in the sense of less than about 50%. However, because for humpback whales, the data for SSV and SV surveys are combined, only cases where coverage was incomplete or poor for both these two survey modes were considered further. Further, following consideration of the extent of the poor coverage together with the contribution from the stratum concerned to the abundance estimate for the complete Area for that cruise, sensitivity to instances of poor or incomplete coverage in Area V for the SE stratum in 2002/03 and the SW stratum in 2004/05 was deemed likely to be slight and further calculations for those cases were not pursued.

For the remaining cases, the approach followed to examine sensitivity was as follows. For the base case estimates of abundance, the extrapolated density for the (nearly) unsurveyed portion of a stratum is taken to be the same as that in the surveyed portion of the stratum. For an alternative to this, the average of the ratio of the densities in these two portions of the stratum on other cruises was evaluated (in the case of this humpback analysis this amounts to considering the ratio of sighting rates, as values of other inputs to the calculation of density are common), and this was used instead to extrapolate the density in the surveyed to that for the (nearly) unsurveyed portion for the season in question. The development of such averages did not include data from every other cruise, as consideration was also given to similarities of ice-edge configurations between the cruises. The strata for which such alternative computations were conducted, together with the other cruises used to develop the average ratio required shown in parenthesis, were as follows:

Area IV: 1995/96 SE over 100˚–108˚E (1989/90; 1991/92; 1997/98; 1999/00; 2003/04)

Area V: 1990/91 SE over 69˚–71˚S (1992/93; 1994/95; 1996/97; 2004/05)

Area V: 1992/93 NE over 68˚–69˚S (2002/03; 2004/05)

Area V: 2000/01 SE over 69˚–71˚S (1992/93; 1994/95; 1996/97; 2004/05)

Area V: 2004/05 NW over 130˚–148˚E (1998/99; 2000/01; 2002/03)

The effect of survey modes and survey timing

To investigate the extent of effects of the survey modes (i.e. SSV, SVC and SVP) and timing of the survey conducted in each stratum (which differed in some years because of differences in the order in which the strata were surveyed) on estimates of population increase rates, GLM analyses were undertaken. In the Prydz Bay stratum in Area IV and the SE stratum in Area V, no sightings of humpback whales were made for some of the cruises. Hence a Poisson error structure was assumed for the GLMs. A hierarchy of such models was evaluated for each Area. As discussed in Hakamada *et al.* (2007), because stratum areas vary from season to season as a result of different ice edge locations, it is not immediately obvious whether such approaches should be based on the density or on the abundance in a stratum, and arguments can be offered to support either approach. However density is perhaps the more obvious choice and furthermore Hakamada *et al.* (2007) found little difference in results for the two approaches for minke whales. Accordingly the analyses here are based only on density.

$$\text{Model (i):}\quad \log E\left[n_{obs}(y,a)\right] = \log\left(\frac{2w_{y,a}L_{y,a}}{E_{y,a}(s)}\right) + \log(D_{true}(0,a)) + \alpha y \tag{6a}$$

$$\text{Model (ii):}\quad \log E\left[n_{obs}(y,a)\right] = \log\left(\frac{2w_{y,a}L_{y,a}}{E_{y,a}(s)}\right) + \log(D_{true}(0,a)) + \alpha y + M \tag{6b}$$

$$\text{Model (iii):}\quad \log E\left[n_{obs}(y,a)\right] = \log\left(\frac{2w_{y,a}L_{y,a}}{E_{y,a}(s)}\right) + \log(D_{true}(0,a)) + \alpha y + M + T \tag{6c}$$

$$\text{Model (iv):}\quad \log E\left[n_{obs}(y,a)\right] = \log\left(\frac{2w_{y,a}L_{y,a}}{E_{y,a}(s)}\right) + \log(D_{true}(0,a)) + \alpha y + M + a*T \tag{6d}$$

Where:

y is the season,

a is the stratum,

$E[n_{obs}(y,a)]$ is the expected number of sightings in stratum a in season y,

$w_{y,a}$ is the effective search half-width for season y and stratum a,

$L_{y,a}$ is the primary searching distance for season y and stratum a,

$E(s)_{y,a}$ is the estimated mean school size for season y and stratum a,

$D_{true}(y,a)$ is the unbiased (i.e. free from the survey mode effect) density for season y and stratum a,

α is the population's exponential rate of increase,

M is the mode factor for SSV and SVC surveys standardised to SVP,

T is a categorical variable related to survey timing that is defined below, and

$a*T$ is an interaction between the stratum a and timing T factors.

The first term on the right-hand-side as known as the offset. It uses values of w_s and $E(s)$ pooled over modes, so that all inputs required are listed in Tables 5a and 5b. The approach used here makes the assumption that the variances of w_s and $E(s)$ are relatively small compared to the variance associated with the observed number of sightings. Additional variance has not been considered in these analyses.

The middle day of the survey period in each stratum was calculated and categorised into groups as a basis to specify T for models (iii) and (iv) above. The groups in bold letters below are included in the intercept of the alternative models considered (i.e. the effect of those groups is set to zero in the calculations). Because the estimate of α seemed to be sensitive to the definition of T for Area IV in particular, five groupings were considered:

(1) T = 1: Dec 15–31; T = 2: Jan 1–15; T = **3: Jan 16–31**; T = 4: Feb 1–15; T = 5: Feb 16–29; and T = 6: Mar 1–15 (Grouping $T1$)

Table 5a

Abundance estimates for humpback whales in Area IV (south of 60°S) from the 1989/90 to 2003/04 JARPA cruises. A= size of research area; n= number of schools sighted on primary effort (truncated at a perpendicular distance of 2.7 n.miles after smearing); L= primary searching distance; w_s= the effective search half width (hazard rate model estimate, or half normal if shown in italics); $E(s)$= mean school size; D=estimated density (individuals/100 n.miles^2); P=estimated abundance.

Season	Stratum	A (n.mile^2)	n	L (n.mile)	n/L *10^2	CV	w_s (n.mile)	CV	$E(s)$	CV	D (ind.)	P (ind.)	CV
1989/90	NW	222,563	21.2	1,987.6	1.067	0.297	0.996	0.226	2.000	0.093	1.071	2,383	0.331
	NE	219,245	20.0	1,964.4	1.018	0.448	0.727	0.426	1.750	0.082	1.225	2,687	0.522
	SW	35,878	10.4	2,518.3	0.411	0.391	0.937	0.201	1.804	0.056	0.396	142	0.412
	SE	41,143	1.0	1,362.2	0.073	0.732	0.937	0.201	1.804	0.056	0.071	29	0.761
	PB	36,488	2.0	831.9	0.240	0.482	0.937	0.201	1.804	0.056	0.231	84	0.526
	Total	555,317	54.6	8,664.4	0.630	0.215	–	–	–	–	**0.959**	**5,325**	**0.302**
1991/92	NW	219,713	41.7	2,482.7	1.680	0.231	1.052	0.202	1.929	0.062	1.540	3,383	0.265
	NE	216,299	16.0	2,173.9	0.736	0.300	*1.005*	*0.143*	1.803	0.049	0.661	1,429	0.317
	SW	37,191	19.7	2,237.5	0.880	0.350	*1.379*	*0.172*	1.680	0.082	0.536	199	0.368
	SE	39,732	17.0	2,281.7	0.745	0.378	0.746	0.327	1.870	0.051	0.905	360	0.424
	PB	36,569	1.0	607.5	0.165	0.730	*1.379*	*0.172*	1.680	0.082	0.100	37	0.755
	Total	549,504	95.4	9,783.3	0.975	0.150	–	–	–	–	**0.984**	**5,408**	**0.188**
1993/94	NW	233,289	43.7	4,160.7	1.050	0.191	*1.220*	*0.122*	1.614	0.068	0.694	1,619	0.208
	NE	163,982	30.5	3,175.1	0.960	0.290	*1.874*	*0.171*	1.774	0.079	0.454	744	0.310
	SW	39,755	24.8	2,377.7	1.043	0.338	*1.381*	*0.157*	1.571	0.070	0.597	237	0.354
	SE	41,353	7.0	2,258.9	0.310	0.315	*1.381*	*0.157*	1.571	0.070	0.179	74	0.334
	PB	34,506	4.0	1,077.0	0.371	0.688	*1.381*	*0.157*	1.571	0.070	0.211	73	0.701
	Total	512,885	110.0	13,049.4	0.843	0.138	–	–	–	–	**0.536**	**2,747**	**0.153**
1995/96	NW	149,107	122.2	3,530.5	3.461	0.171	*1.126*	*0.070*	1.543	0.037	2.347	3,611	0.176
	NE	230,473	45.8	2,979.7	1.537	0.280	*1.076*	*0.119*	1.826	0.079	1.304	3,007	0.289
	SW*	89,825	54.5	2,851.2	1.911	0.318	*1.468*	*0.118*	1.909	0.050	1.293	1,100	0.336
	SE	33,980	27.6	2,039.9	1.353	0.246	*1.248*	*0.154*	1.893	0.087	1.029	348	0.267
	PB	25,970	0.0	1,321.8	–	–	–	–	–	–	–	0	–
	Total	529,354	250.1	12,723.1	1.966	0.123	–	–	–	–	**1.524**	**8,066**	**0.142**
1997/98	NW	217,645	191.6	3,367.2	5.690	0.200	1.829	0.071	1.870	0.035	2.924	6,365	0.204
	NE	219,602	107.2	3,622.7	2.959	0.367	*1.681*	*0.085*	1.658	0.040	1.465	3,217	0.369
	SW	31,615	171.3	3,432.5	4.991	0.157	*1.533*	*0.064*	1.767	0.030	2.944	931	0.161
	SE	34,374	25.2	3,195.9	0.789	0.218	*1.549*	*0.168*	1.555	0.090	0.395	136	0.239
	PB	4,407	2.0	490.0	0.408	0.758	*1.533*	*0.064*	1.767	0.030	0.204	9	0.761
	Total	507,643	497.3	14,108.3	3.525	0.123	–	–	–	–	**2.099**	**10,657**	**0.166**
1999/2000	NW*	229,368	54.7	2,825.3	1.936	0.193	*1.347*	*0.113*	1.532	0.066	1.098	2,519	0.204
	NE	226,272	160.7	3,550.8	4.525	0.208	0.828	0.170	1.538	0.032	4.203	9,510	0.228
	SW	44,862	106.3	2,336.7	4.549	0.245	0.579	0.222	1.710	0.039	6.839	3,068	0.274
	SE	34,175	165.1	2,704.3	6.105	0.191	*1.447*	*0.068*	2.183	0.054	4.613	1,576	0.195
	PB	21,288	3.0	1,244.7	0.241	0.610	0.579	0.222	1.710	0.039	0.369	78	0.651
	Total	555,964	489.8	12,661.8	3.868	0.110	–	–	–	–	**3.013**	**16,751**	**0.143**
2001/02	NW*	222,449	252.2	3,043.6	8.286	0.191	1.259	0.071	1.941	0.035	6.371	14,171	0.196
	NE	244,921	238.2	3,271.6	7.281	0.206	1.286	0.061	1.754	0.032	4.937	12,093	0.209
	SW	32,199	386.8	2,321.8	16.658	0.176	1.201	0.053	1.870	0.027	13.164	4,239	0.178
	SE	35,955	63.5	2,885.2	2.201	0.257	*1.090*	*0.097*	1.672	0.057	1.755	631	0.266
	PB	28,472	0.0	1,033.7	–	–	–	–	–	–	–	0	–
	Total	563,995	940.7	12,555.9	7.492	0.104	–	–	–	–	**5.520**	**31,134**	**0.123**
2003/04	NW*	243,849	241.2	3,236.6	7.452	0.249	*1.334*	*0.051*	1.680	0.026	4.728	11,529	0.248
	NE	218,072	278.9	3,738.5	7.460	0.137	*1.495*	*0.050*	1.666	0.025	4.152	9,053	0.140
	SW	38,976	389.3	2,275.2	17.111	0.112	1.417	0.063	1.886	0.021	11.315	4,410	0.117
	SE	38,952	448.2	3,633.2	12.336	0.139	*1.489*	*0.039*	1.643	0.019	6.911	2,692	0.134
	PB	37,537	2.0	508.5	0.393	1.294	1.417	0.063	1.886	0.021	0.261	98	1.296
	Total	577,386	1359.6	13,392.0	10.152	0.077	–	–	–	–	**4.812**	**27,783**	**0.115**

*Including area not surveyed as indicated in Table 3.

Table 5b

Abundance estimates for humpback whales in Area V (south of 60°S) from the 1990/91 to 2004/05 JARPA cruises. The notation is as for Table 5a.

Season	Stratum	A (n.mile^2)	n	L (n.mile)	$n/L*10^2$	CV	w_s (n.mile)	CV	$E(s)$	CV	$\boldsymbol{D}$ (ind.)	$\boldsymbol{P}$ (ind.)	CV
1990/91	NW	239,688	1.0	2,726.8	0.037	1.096	*1.189*	*0.163*	1.303	0.087	0.020	48	1.111
	NE	348,822	0.0	2,498.9	–	–	–	–	–	–	–	–	–
	SW	64,431	21.7	1,635.0	1.328	0.369	*1.189*	*0.163*	1.303	0.087	0.728	469	0.387
	SE	188,136	1.0	1,670.0	0.060	0.961	*1.027*	*0.138*	1.546	0.070	0.045	85	0.973
	Total	841,077	23.7	8,530.7	0.278	0.343	–	–	–	–	**0.072**	**602**	**0.343**
1992/93	NW	325,648	5.0	2,299.3	0.217	1.428	*0.712*	*0.156*	2.000	0.083	0.305	993	1.435
	NE	348,822	9.0	1,661.5	0.542	0.858	*0.712*	*0.156*	2.000	0.083	0.761	2,654	0.868
	SW	59,450	5.0	1,907.4	0.262	0.485	*0.712*	*0.156*	2.000	0.083	0.367	218	0.506
	SE	210,194	4.0	2,256.3	0.177	0.644	*0.712*	*0.156*	2.000	0.083	0.249	523	0.653
	Total	944,113	23.0	8,124.5	0.283	0.482	–	–	–	–	**0.465**	**4,388**	**0.623**
1994/95	NW	209,990	14.0	3,229.4	0.433	0.747	1.793	0.083	1.658	0.055	0.200	420	0.749
	NE	314,697	26.1	2,554.1	1.022	0.411	*1.320*	*0.147*	2.000	0.115	0.774	2,437	0.430
	SW	39,911	41.6	2,469.0	1.687	0.200	1.793	0.083	1.658	0.055	0.789	315	0.210
	SE	173,180	5.0	1,293.0	0.386	0.519	*1.320*	*0.147*	2.000	0.115	0.293	507	0.531
	Total	737,778	86.7	9,545.5	0.909	0.200	–	–	–	–	**0.499**	**3,678**	**0.307**
1996/97	NW	288,197	1.0	2,784.6	0.036	1.679	*1.520*	*0.194*	1.632	0.117	0.019	55	1.694
	NE	337,779	14.0	3,133.4	0.446	0.356	*1.381*	*0.190*	1.700	0.062	0.274	926	0.375
	SW	53,960	17.5	3,124.4	0.560	0.369	*1.520*	*0.194*	1.632	0.117	0.286	162	0.394
	SE	187,983	6.0	2,098.5	0.286	0.500	*1.381*	*0.190*	1.700	0.062	0.176	331	0.515
	Total	867,919	38.5	11,140.9	0.345	0.230	–	–	–	–	**0.170**	**1,474**	**0.274**
1998/99	NW	314,708	2.0	997.0	0.201	0.660	0.639	0.419	1.684	0.078	0.264	832	0.786
	NE	328,037	4.9	652.8	0.751	0.669	0.575	0.560	0.773	0.074	0.505	1,655	0.876
	SW	48,333	30.8	2,333.5	1.320	0.431	0.639	0.419	1.684	0.078	1.740	841	0.500
	SE	25,709	34.9	1,561.0	2.233	0.145	*1.046*	*0.128*	1.787	0.082	1.892	504	0.167
	Total	716,787	72.6	5,544.3	1.309	0.202	–	–	–	–	**0.535**	**3,831**	**0.430**
2000/01	NW	271,089	43.2	3,751.9	1.153	0.389	*1.368*	*0.128*	1.762	0.074	0.741	2,016	0.396
	NE	348,535	44.3	3,941.1	1.124	0.293	*1.668*	*0.132*	1.956	0.071	0.659	2,297	0.305
	SW	79,594	30.5	3,152.9	0.968	0.224	0.780	0.418	1.645	0.072	1.035	815	0.362
	SE	148,828	0.0	3,320.2	–	–	–	–	–	–	–	–	–
	Total	848,046	118.1	14,166.1	0.833	0.189	–	–	–	–	**0.605**	**5,128**	**0.215**
2002/03	NW	266,687	12.0	2,777.2	0.432	0.393	1.291	0.126	1.548	0.094	0.259	691	0.404
	NE	345,003	58.0	5,077.1	1.142	0.181	1.902	0.087	1.672	0.050	0.502	1,732	0.188
	SW	79,376	18.8	2,209.8	0.852	0.331	1.291	0.126	1.548	0.094	0.510	406	0.342
	SE	69,872	3.0	2,111.9	0.142	0.489	1.902	0.087	1.672	0.050	0.062	44	0.493
	Total	760,938	91.8	12,176.0	0.754	0.144	–	–	–	–	**0.378**	**2,873**	**0.157**
2004/05	NW	278,281	19.5	970.0	2.015	0.780	*1.688*	*0.199*	2.050	0.075	1.223	3,405	0.791
	NE	336,130	85.8	3,381.8	2.537	0.196	*1.295*	*0.080*	1.583	0.460	1.551	5,214	0.309
	SW	51,373	16.0	856.7	1.873	0.235	*1.437*	*0.232*	1.686	0.099	1.099	564	0.270
	SE	212,181	10.0	8,158.7	0.123	0.575	*1.295*	*0.080*	1.583	0.460	0.075	159	0.629
	Total	877,965	131.4	13,367.2	–	–	–	–	–	–	**1.064**	**9,342**	**0.337**

(2) T = 1: Dec 15–Jan 15; T = **2: Jan 16–31**; T = 3: Feb 1–15; and T = 4: Feb 16–Mar 15 (Grouping *T*2)

(3) T = 1: Dec 15–Jan 15; T = **2: Jan 16–Feb 15;** and T = 3: Feb 16–Mar 15 (Grouping *T*3)

(4) T = 1: Dec; T = **2: Jan**; T = 3: Feb; and T = 4: Mar (Grouping *T*4)

(5) T = **1: Dec and Jan** and T = 2: Feb and Mar (Grouping *T*5)

QAIC (Burnham and Anderson, 1998) rather than AIC was used to select amongst these models and alternatives for specifying T because it can be applied to GLMs with over-dispersed Poisson errors. QAIC is defined here as

$$QAIC = -\frac{2\log(L)}{\hat{c}} + 2p \tag{7}$$

where L is likelihood of the model without over-dispersion, $\hat{c}$ is the estimated over-dispersion parameter and p is the number of estimable parameters including the over-dispersion parameter.

RESULTS

Distribution of humpback whale sightings

Fig. 5 shows the distribution of the primary searching effort (grey lines) and positions of humpback whale primary sightings during the 1987/88–2004/05 JARPA cruises. The primary searching effort covered the research area quite thoroughly. Humpback whales were widely distributed in Areas IV and V, and were more frequently sighted in Area IV. They were rarely found in the Prydz Bay and the Ross Sea, but were observed in southern strata as far south as the ice edge. Estimated densities were highest between 80˚E and 120˚E in both the northern and southern strata; this area corresponds to the eastern side of the Kerguelen Plateau. There were relatively few sightings in the longitudinal sector between 130˚E and 145˚E.

Abundance estimates

Tables 5a and 5b show abundance estimates (P) of humpback whales in Areas IV and V respectively, by season and stratum. The tables also show the total number of the primary sightings after truncation (n), open ocean area (A), primary searching effort (L), n/L, effective search half width (w_s),

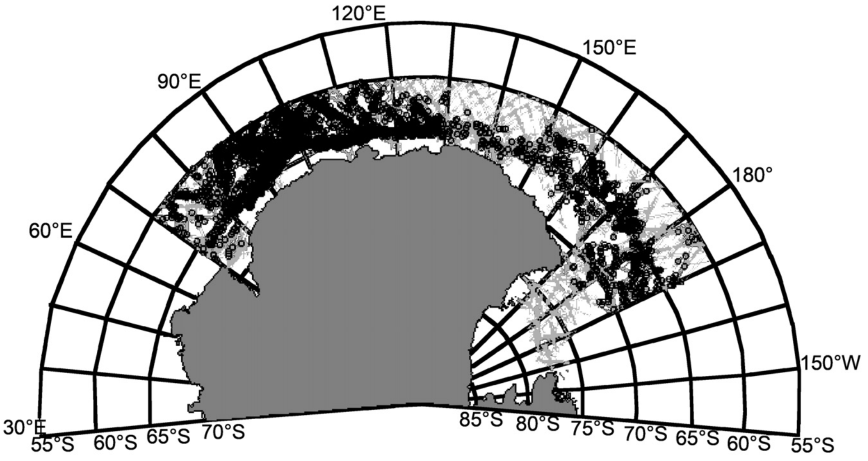


Fig. 5. Distribution of the primary searching effort (grey lines) and associated humpback whale primary sightings during the 1989/90–2004/05 JARPA surveys in Areas IV and V which are used in the analyses of this paper.

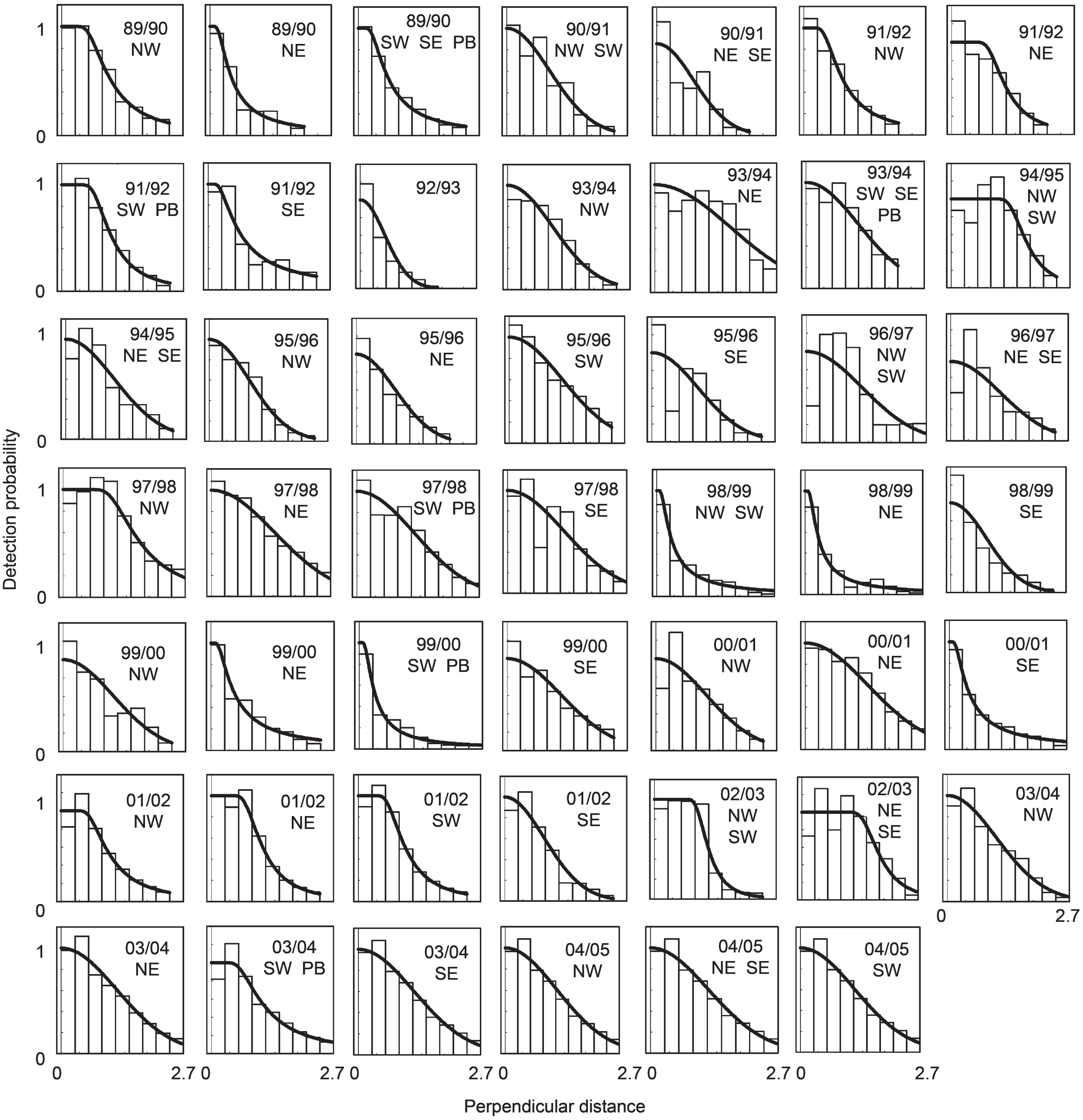


Fig. 6. Estimated detection probability functions (AIC-based selection between hazard rate and half-normal forms) for humpback whales for the 1989/90 to 2004/05 JARPA surveys. These results are for data combined across the SSV, SVC and SVP survey modes.

estimated mean school size (*E(s)*), estimated whale density (*D:* whales/100 n.miles^2) and the CVs for each estimate. The primary effort and associated primary sightings of humpback schools whales used for these estimates are plotted in Fig. 1. Abundance estimates in Area IV range from 2,747 (CV = 0.153) for the 1993/94 season to 31,134 (CV = 0.123) for the 2001/02 season (Table 5a). In Area V, abundance estimates range from 1,474 (CV = 0.274) for the 1996/97 season to 9,342 (CV = 0.337) for the 2004/05 season (Table 5b). The most recent abundance estimate for Areas IV (2003/04 season) and V (2004/05 season) combined is 37,125 (CV = 0.288, where this computation also takes account of the estimates of additional variance). Fig. 6 shows the detection probability functions in relation to perpendicular distance from the trackline in nautical miles that were used for the analyses by cruise and stratum (or combination of strata); there are no obvious indications of model mis-specification, nor of any trend towards distributions with sharper peaks near the trackline in the earlier years.

Abundance trends

Fig. 7 shows the abundance estimates in Areas IV and V plotted against survey season; for comparative purposes, estimates obtained using IDCR-SOWER data (Branch, 2011) are also shown. An increasing trend in abundance is evident for both Areas IV and V, more clearly so for the former. Annual rates of increase estimates from the JARPA surveys using equation (5) are 16.4% (95% CI = 9.5–23.3%) for Area IV over the 1989/90 to 2003/04 cruises, and 12.1% (95% CI = 1.7–22.6%) for Area V over the 1990/91 to 2004/05 cruises. The estimate for Area IV is clearly significantly positive; the result for Area V is also significantly above zero, but not as clearly so as that for Area IV. The additional CVs are estimated as 0.309 and 0.437 for Areas IV and V respectively (Table 7).

Sensitivity tests

Alternative estimates of effective search half-width

The effects on abundance estimates at the Area level, and also on annual rates of increase, compared to the base case for these and the following two sets of sensitivity tests are shown in Table 6a and 6b, with differences in estimates of precision and the associated additional variance shown in Table 7.

There are occasional instances of a large difference, but viewed overall the average change in the abundance estimates from the base case never exceeds 5%, and any alteration to the rate of increase estimate is below 1%.

Inclusion of tracklines that followed the contours of the ice edge

These tests apply only to Area IV, and are somewhat restricted because of insufficient data to allow them to be conducted for the first four seasons of surveys there. For the subsequent seasons, these alternative treatments make little difference on average to abundance estimates (Table 6a), and also have little impact on the estimated abundance trend (Table 7). Thus there is no definitive indication that including tracklines that followed the contours of the ice edge in estimating humpback whale abundance and trends introduces substantial bias.

Unsurveyed areas and incomplete coverage

Results for these sensitivity tests mirror those for the use of alternative functional forms to estimate effective search half-width: the average change in the abundance estimates from the base case and any alteration in the rate of increase estimate are small (Table 6a, 6b and 7).

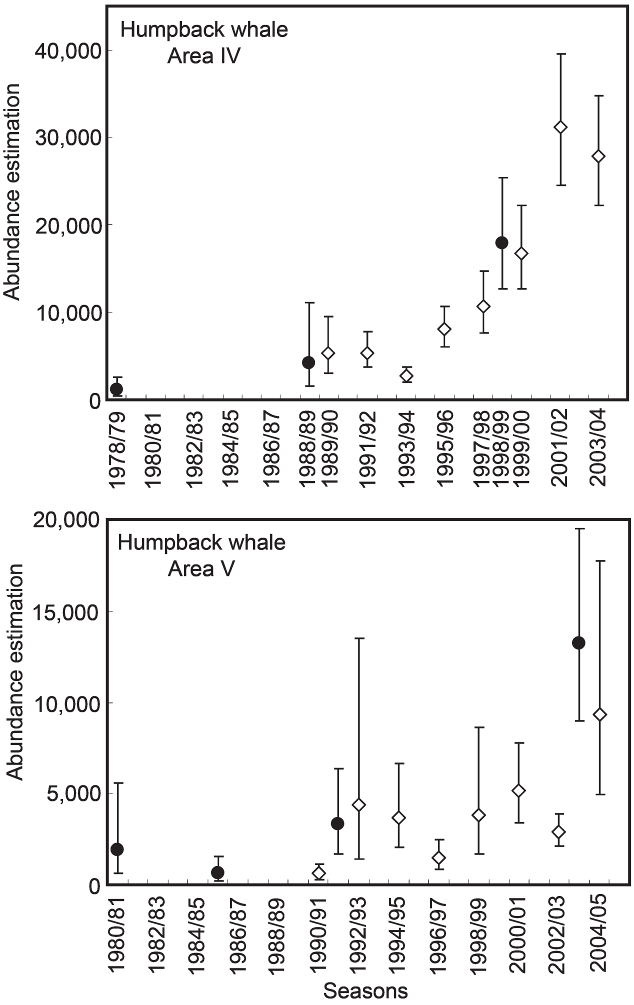


Fig. 7. Abundance estimates for humpback whales in Areas IV and V (south of 60°S), which were surveyed primarily during January to February, from the JARPA surveys from 1988/89 to 2004/05. Estimates from the IDCR-SOWER surveys (Branch, 2011) are shown by the filled circles. Vertical lines show 95% confidence intervals.

The effect of survey modes and survey timing

Table 8a shows the observed number of sightings SSV, SVC and SVP surveys, as used for input to the GLM models of equation (6), by season and stratum. Table 8b shows the QAIC for each model and estimated instantaneous annual rates of increase for Areas IV and V with their 95% confidence intervals. Comparison of the abundance trend estimates in Table 6a, shows broad agreement for Area IV – all point estimates are high and in the 16–20% range. However, this is not the case for Area V, for which most point estimates in Table 8b are less than half that for the base case. Nevertheless, all the Table 8b estimates fall within the CIs for the corresponding base case estimates in Table 7. QAIC selects the more parsimonious models, choosing only survey mode amongst the covariates considered, and then only for Area IV. This does not necessarily mean that survey timing or the order in which the strata were surveyed has no effect on estimates, but rather that there is insufficient information content in the data to reveal such an effect. For Area IV, even if the (changing) order of surveying strata is taken into account, although the

Table 6a

Abundance and annual rate of increase (ROI) estimates for Area IV for the base case and sensitivities.

Season	1989/90	1991/92	1993/94	1995/96	1997/98	1999/00	2001/02	2003/04	Average % of change	ROI (%)	Change from base case (%)
Base case	5,325	5,408	2,747	8,066	10,657	16,751	31,134	27,783	–	16.4	–
	–	–	–	–	–	–	–	–	–	–	–
Hazard rate model	5,325	5,666	2,331	8,051	10,537	17,233	31,108	25,818	–	16.1	–0.3
	0%	5%	–15%	0%	–1%	3%	0%	–7%	–2%	–	–
Half–normal model	4,041	5,183	2,747	8,066	11,205	12,632	32,844	27,708	–	17.2	0.8
	–24%	–4%	0%	0%	5%	–25%	5%	0%	–5%	–	–
Trackline Option B*	5,325	5,408	2,747	8,066	10,705	14,685	30,713	29,376	–	16.4	0.0
	–	–	–	–	0%	–12%	–1%	6%	–2%	–	–
Trackline Option C	5,325	5,408	2,747	8,066	11,034	14,146	30,484	34,224	–	17.1	0.7
	–	–	–	–	4%	–16%	–2%	23%	2%	–	–
Gap abundance=0**	5,325	5,408	2,747	7,467	10,657	16,479	30,359	24,924	–	15.9	–0.5
	–	–	–	–7%	–	–2%	–2%	–10%	–5%	–	–
Gap abundance=stratum below**	5,325	5,408	2,747	8,578	10,657	18,145	31,730	31,905	–	17.2	0.8
	–	–	–	6%	–	8%	2%	15%	8%	–	–
Poor coverage corrections***	5,325	5,408	2,747	8,279	10,657	16,751	31,134	27,783	–	16.4	0.0
	–	–	–	3%	–	–	–	–	3%	–	–

*Due to the small number of sightings, there were insufficient data to evaluate options B and C for the 1989/90 to 1995/96 seasons; the averages quoted for these sensitivities refer to the 1997/98 to 2003/04 seasons. **1995/96, 1999/00, 2001/02 and 2003/04 seasons. ***SE stratum in 1995/96 season.

Table 6b

Abundance estimates and annual rates of increase for Area V for the base case and sensitivities.

Season	1990/91	1992/93	1994/95	1996/97	1998/99	2000/01	2002/03	2004/05	Average % of change	ROI (%)	Change from base case (%)
Base case	602	4,388	3,678	1,474	3,831	5,127	2,873	9,342	–	12.1	–
	–	–	–	–	–	–	–	–	–	–	–
Hazard rate model	523	5,396	3,592	1,460	3,994	4,734	2,873	9,067	–	12.2	0.1
	–13%	23%	–2%	–1%	4%	–8%	0%	–3%	0%	–	–
Half–normal model	602	4,388	3,785	1,474	2,302	4,824	3,415	9,342	–	12.5	0.4
	0%	0%	3%	0%	–40%	–6%	19%	0%	–3%	–	–
Poor coverage corrections*	770	4,386	3,678	1,474	3,831	5,518	2,873	11,466	–	12.0	–0.1
	28%	0%	–	–	–	8%	–	23%	15%	–	–

*SE stratum in 1990/91, NE stratum in 1992/93, SE stratum in 2000/01, NW and SW strata in 2004/05 seasons.

Table 7

Estimated annual instantaneous rates of exponential increase, together with their standard errors and 95% confidence intervals, for base case and other detection function selections for Areas IV and V, respectively. α is the instantaneous rate of increase. CV_{add} is the CV corresponding to the additional variance associated with abundance estimates.

	α	SE(α)	95%CILL	95%CIUL	CV_{add}	SE(CV_{add})
Area IV						
Base case	0.164	0.028	0.095	0.233	0.309	0.102
Hazard rate	0.161	0.033	0.082	0.241	0.374	0.114
Half–normal	0.172	0.027	0.105	0.238	0.296	0.097
Opt B	0.164	0.028	0.096	0.233	0.304	0.102
Opt C	0.171	0.028	0.103	0.239	0.302	0.103
Gap abun=0	0.159	0.028	0.089	0.228	0.313	0.103
Gap abun=below	0.172	0.028	0.103	0.241	0.306	0.103
Poor coverage corrections	0.164	0.028	0.095	0.233	0.309	0.102
Area V						
Base case	0.121	0.043	0.017	0.226	0.437	0.167
Hazard rate	0.122	0.045	0.012	0.232	0.469	0.181
Half–normal	0.125	0.040	0.028	0.222	0.386	0.168
Poor coverage corrections	0.120	0.043	0.014	0.225	0.440	0.162

best estimate of the rate of increase drops, the lower 95% confidence limit remains at or above 10% as for the base case. For Area V the results in Table 8b do barely admit the possibility of no increase within their 95% CI's, but with one exception, taking survey ordering into account increases estimates of the rate of increase compared to the QAIC-selected model.

Under QAIC, inclusion of survey mode as a factor is selected only for Area IV, but the change to the estimated rate of increase is negligible, and the mode factor estimates themselves suggest SVC and SSV density estimates only slightly (and not significantly) greater than those for SVP. For Area V, a likely reason for non-selection of these factors, which suggest somewhat lower densities in SVC and SSV modes compared to SVP, is their associated high estimated standard errors.

Table 8a (part 1)

Observed numbers of sightings (truncated at 2.7 n. miles perpendicular distance after smearing) by survey mode used for input to the GLMs of equation (6) in Area IV.

Area IV by SSV		Area IV SVC		Area IV SVP	
Stratum	n_{obs}	Stratum	n_{obs}	Stratum	n_{obs}
1989/90					
NW	21.2				
NE	20.0				
SW	10.3				
SE	1.0				
PB	2.0				
1991/92					
NW	42.0				
NE	16.0				
SW	13.5	SW	6.8		
SE	9.9	SE	5.7		
PB	0.0	PB	1.0		
1993/94					
NW	33.5	NW	10.0		
NE	16.9	NE	11.0		
SW	17.3	SW	6.9		
SE	6.0	SE	1.0		
PB	3.0	PB	1.0		
1995/96					
NW	101.4	NW	20.7		
NE	33.0	NE	13.0		
SW	34.7	SW	19.6		
SE	20.6	SE	7.0		
PB	0.0	PB	0.0		
1997/98					
NW	149.9	NW	28.7	NW	8.7
NE	80.2	NE	24.6	NE	1.0
SW	129.8	SW	17.7	SW	20.9
SE	17.9	SE	5.0	SE	1.0
PB	2.0	PB	0.0	PB	0.0
1999/2000					
NW	40.6	NW	4.0	NW	10.0
NE	93.9	NE	23.0	NE	43.0
SW	76.5	SW	8.0	SW	21.4
SE	86.2	SE	21.3	SE	58.0
PB	0.0	PB	0.0	PB	3.0
2001/02					
NW	195.0	NW	16.0	NW	41.0
NE	178.9	NE	18.0	NE	40.0
SW	261.1	SW	29.9	SW	96.6
SE	52.3	SE	1.0	SE	10.0
PB	0.0	PB	0.0	PB	0.0
2003/04					
NW	174.9	NW	33.0	NW	33.0
NE	198.8	NE	27.7	NE	52.6
SW	293.8	SW	31.7	SW	64.3
SE	280.2	SE	38.8	SE	128.3
PB	0.0	PB	1.0	PB	1.0

DISCUSSION

Distribution of humpback whales

Humpback whales were widely distributed in Areas IV and V, with higher concentrations in Area IV, although they were rarely found in Prydz Bay and the Ross Sea. There were relatively few sightings in the longitudinal sector from 130˚E to 145˚E, which coincides with a gap in krill distribution (Murase *et al.*, 2006). However, the development of a quantitative approach to the comparison of humpback whale distribution to krill distribution and oceanographic features in the research area is beyond the scope of the present paper. It will be investigated in the future.

Table 8a (part 2)

Observed numbers of sightings (truncated at 2.7 n. miles perpendicular distance after smearing) by survey mode used for input to the GLMs of equation (6) in Area V.

Area V by SSV		Area V SVC		Area V SVP	
Stratum	n_{obs}	Stratum	n_{obs}	Stratum	n_{obs}
1990/91					
NW	1.0				
NE	1.0				
SW	21.7				
SE	1.0				
1992/93					
NW	5.0	NW	0.0		
NE	3.0	NE	6.0		
SW	1.0	SW	4.0		
SE	3.0	SE	1.0		
1994/95					
NW	6.0	NW	8.0		
NE	10.0	NE	17.0		
SW	26.6	SW	15.0		
SE	3.0	SE	2.0		
1996/97					
NW	1.0	NW	0.0		
NE	12.9	NE	1.0		
SW	8.0	SW	8.6		
SE	6.0	SE	0.0		
1998/99					
NW	2.8	NW	4.7	NW	3.6
NE	16.8	NE	4.5	NE	0.0
SW	15.6	SW	3.0	SW	11.7
SE	30.1	SE	0.0	SE	4.0
2000/01					
NW	29.3	NW	5.0	NW	8.9
NE	23.6	NE	8.0	NE	12.2
SW	11.8	SW	3.6	SW	14.9
SE	0.0	SE	0.0	SE	0.0
2002/03					
NW	6.0	NW	1.0	NW	5.0
NE	39.6	NE	3.0	NE	14.9
SW	15.0	SW	1.6	SW	2.0
SE	2.0	SE	0.0	SE	1.0
2004/05					
NW	8.6	NW	5.7	NW	5.0
NE	46.0	NE	7.2	NE	22.8
SW	15.0	SW	0.0	SW	2.0
SE	9.0	SE	0.0	SE	1.0

Abundance estimates and abundance trend based on JARPA data

As noted earlier, the IWC Scientific Committee has made several suggestions to improve abundance estimation of Antarctic minke (and by inference humpback) whales from JARPA surveys during previous meetings, particularly at the recent review Workshop (IWC, 2008). Table 1 shows the recommended work by the workshop and how these suggestions have been addressed in the analyses of this paper. It shows that all high priority items have been considered as have most medium priority items. We believe that these few remaining medium priority items seem unlikely to greatly effect the estimates of abundance and trend presented here, although they will be considered in the future.

Although the information content of the data to determine inter-mode differences is poor, the results of sensitivity analyses undertaken here provide no basis to question the pooling of the data across survey modes (SSV, SVC and SVP) for the base case abundance estimation. The same conclusion follows for the effect of including data from

Table 8b

QAIC and estimated annual instantaneous rate of exponential increase in Areas IV and V. is the estimated over-dispersion parameter. The line in **bold** indicates the model selected by QAIC.

Model	$\hat{c}$	QAIC	ΔQAIC	α	SE(α)	α 95%LL	α 95%UL
Area IV							
(i)	13.76	119.89	1.03	0.199	0.017	0.166	0.233
(ii)	**14.35**	**118.86**	**0.00**	**0.201**	**0.018**	**0.165**	**0.237**
(iii) with T1	14.44	124.05	5.19	0.199	0.019	0.161	0.237
(iii) with T2	14.24	121.85	2.99	0.203	0.018	0.166	0.239
(iii) with T3	14.20	120.29	1.42	0.202	0.018	0.166	0.238
(iii) with T4	14.14	123.03	4.17	0.195	0.018	0.159	0.231
(iii) with T5	14.10	121.01	2.15	0.201	0.018	0.165	0.236
(iv) with T1	13.72	140.11	21.25	0.159	0.029	0.101	0.218
(iv) with T2	13.46	138.06	19.20	0.159	0.029	0.101	0.217
(iv) with T3	13.28	131.34	12.47	0.176	0.025	0.127	0.225
(iv) with T4	13.63	163.61	44.75	0.172	0.021	0.130	0.215
(iv) with T5	13.68	127.65	8.78	0.177	0.021	0.135	0.219
Area V							
(i)	**11.08**	**78.29**	**0.00**	**0.066**	**0.034**	**–0.001**	**0.134**
(ii)	10.58	82.25	3.96	0.056	0.035	–0.015	0.126
(iii) with T1	9.24	97.91	19.62	0.050	0.036	–0.022	0.122
(iii) with T2	9.89	90.89	12.60	0.046	0.035	–0.023	0.116
(iii) with T3	9.82	89.44	11.15	0.045	0.035	–0.024	0.115
(iii) with T4	9.01	96.03	17.74	0.054	0.035	–0.016	0.124
(iii) with T5	10.85	82.57	4.28	0.057	0.037	–0.016	0.130
(iv) with T1	4.97	138.14	59.86	0.167	0.053	0.061	0.273
(iv) with T2	5.21	131.09	52.80	0.161	0.050	0.061	0.261
(iv) with T3	5.77	118.01	39.72	0.158	0.051	0.056	0.260
(iv) with T4	7.24	112.24	33.95	0.088	0.046	–0.004	0.180
(iv) with T5	10.07	91.96	13.68	0.062	0.048	–0.034	0.158

tracklines that followed the contours of the ice edge in the analyses. The impacts on overall estimates of abundance and trend of the choice of functional form for the detection function, and of some instances of survey gaps and poor coverage, are small.

The greater differences between the base case and GLM estimates of rates of increase for Area V than for Area IV is not altogether surprising. It is readily evident from inspection of Fig. 7 that while the data for Area IV give broadly consistent indications of a steady increase, for Area V the estimate from the final 2004/5 survey is highly influential in determining any point estimate for rate of increase (a feature also of the IDCR-SOWER results for this Area). The point estimates themselves are high given the estimate of Clapham *et al*. (2006) of a maximum demographically plausible annual increase rate for humpback whales of 10.6%. However, it should be noted that the lower 95% CIs for this rate for the base case and sensitivities in Table 7 are all below this bound, although only barely so for some cases. The possibility of immigration and changes in distribution (see Conclusion) warrants further investigation.

Comparison with IDCR-SOWER estimates

A comparison of the list of JARPA and IDCR-SOWER estimates of abundance in Table 9a, and the corresponding plot in Fig. 7, shows the results from the two sets of surveys to be entirely consistent.

The rates of increase in Areas IV and V, as estimated from JARPA and IDCR-SOWER results are also similar (Table 9b). Rates of increase estimated from JARPA data are 16.4% (95% CI = 9.5–23.3%) in Area IV and 12.1% (95% CI = 1.7–22.6%) in Area V, which compare with rates estimated from IDCR-SOWER data of 14.9% (95% CI = 10.0–19.7%) and 12.8% (95% CI = 8.7–16.9%) for those two Areas respectively (Branch, 2011). However Branch's estimates of precision are based on estimates of additional variance of zero. Importantly the greater frequency of the JARPA surveys makes realistic (and reasonably precise – Table 7) estimates of additional variance achievable – something that is scarcely possible for the lesser numbers of IDCR-SOWER surveys, and this has important implications for reliable estimation of precision. If the estimates determined in this paper are used, although the IDCR-SOWER estimates change only slightly, their CIs do expand (Table 9b). They

Table 9a

Comparison of JARPA and IDCR-SOWER (Branch, 2011) abundance estimates of humpback whales in Areas IV and V.

	JARPA		IDCR/SOWER	
Season	Estimate	CV	Estimate	CV
Area IV				
1978/79	–	–	1,102	0.46
1988/89	–	–	4,167	0.53
1989/90	5,325	0.302	–	–
1991/92	5,408	0.188	–	–
1993/94	2,747	0.153	–	–
1995/96	8,066	0.142	–	–
1997/98	10,657	0.166	–	–
1998/99	–	–	17,938	0.18
1999/00	16,751	0.143	–	–
2001/02	31,134	0.123	–	–
2003/04	27,783	0.115	–	–
Area V				
1980/81	–	–	1,876	0.60
1985/86	–	–	622	0.50
1990/91	602	0.343	–	–
1991/92	–	–	3,310	0.34
1992/93	4,388	0.623	–	–
1994/95	3,678	0.307	–	–
1996/97	1,474	0.274	–	–
1998/99	3,831	0.430	–	–
2000/01	5,127	0.215	–	–
2002/03	2,873	0.157	–	–
2003/04	–	–	13,246	0.20
2004/05	9,342	0.337	–	–

Table 9b

Comparison of JARPA and IDCR-SOWER (Branch, 2008) rates of increase estimates in Areas IV and V. The values marked IDCR-SOWER are as estimated by Branch (2008), whose estimates of CV_{add} were zero for both these Areas; those marked IDCR-SOWER revise Branch's results by incorporating the base case estimates of CV_{add} obtained for each of these Areas from the analyses in this paper (see Table 7).

Programme	Period (D/M/Y)	Estimate	95%CILL	95%CIUL
Area IV				
JARPA	31/12/89–01/03/04	0.164	0.095	0.233
IDCR-SOWER	28/12/78–22/02/99	0.148	0.081	0.215
Area V				
JARPA	01/11/91–08/03/05	0.121	0.017	0.226
IDCR-SOWER	17/12/80/–28/02/04	0.122	0.053	0.191

nevertheless still reflect somewhat greater precision than do the JARPA estimates. The reason for this is that the IDCR-SOWER surveys extend over a longer period of time.

Comparison with western and eastern Australia estimates

The abundance estimate of humpback whales off western Australia based on an aerial survey conducted in 2005 is 13,145 (95% CI = 4,984–38,726 – Paxton *et al.*, 2011). The annual rate of increase for this population has been estimated at 10.15% (SE = 4.6%, see Bannister and Hedley, 2001). Off eastern Australia the abundance estimate based on data collected in 2004 is 7,090 (SE = 660) and the rate of increase is estimated at 10.6% (SE = 0.5%) (Noad *et al.*, 2011). These quite high estimates of rates of increase are consistent among surveys conducted in breeding areas and migratory corridors and those carried out in Antarctic feeding areas (IDCR-SOWER and JARPA).

Estimates of abundance in absolute terms off western and eastern Australia are lower than the estimates for Antarctic Areas IV and V. One possible explanation is that the surveys at low latitudes are conducted in specific migratory corridors which may not cover all the adults migrating. Furthermore, recent studies conducted in the Western Antarctic Peninsula region (McKay *et al.*, 2004) and in the North Atlantic (Smith *et al.*, 1999) have suggested that some portions of humpback population do not return to their breeding grounds every year. The possibility of sex-biased migration to breeding grounds has been suggested (Jenner *et al.*, 2006), which also would imply that surveys in migratory corridors do not cover complete populations; this warrants further investigation. Therefore the lesser abundance estimates in lower latitude surveys off western and eastern Australia compared with those obtained for the Antarctic feeding grounds of Areas IV and V do not necessarily indicate inconsistency.

CONCLUSION

In summary, humpback whales in Area IV are increasing at an apparently high rate. Although there is also an increase indicated for Area V, it is neither as rapid nor as precisely estimated. Given that coastal surveys indicate that Breeding Stocks D and E are both increasing at an annual rate of about 10%, which is close to the maximum possible demographically, the greater rates of increase (from both the JARPA and IDCR-SOWER surveys) estimated for the Area IV feeding grounds compared to Area V may reflect a distributional shift of the increasing numbers of Breeding Stock E humpbacks towards Area IV, perhaps to take advantage of higher concentrations of krill there.

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A description and summary of the Antarctic Humpback Whale Catalogue

JUDITH ALLEN*, CAROLE CARLSON*^ AND PETER T. STEVICK*,+

Contact e-mail: jallen@coa.edu

ABSTRACT

The Antarctic Humpback Whale Catalogue (AHWC) is an international collaborative project investigating movement patterns of humpback whales in the Southern Ocean and corresponding lower latitude waters. The collection contains records contributed by 261 researchers and opportunistic sources. Photographs come from all of the Antarctic management areas, the feeding grounds in southern Chile and also most of the known or suspected low-latitude breeding areas and span more than two decades. This allows comparisons to be made over all of the major regions used by Southern Hemisphere humpback whales. The fluke, left dorsal fin/flank and right dorsal fin/flank collections represent 3,655, 413 and 407 individual whales respectively. There were 194 individuals resighted in more than one year, and 82 individuals resighted in more than one region. Resightings document movement along the western coast of South America and movement between the Antarctic Peninsula and western coast of South America and Central America. A single individual from Brazil was resighted off South Georgia, representing the first documented link between the Brazilian breeding ground and any feeding area. A second individual from Brazil was resighted off Madagascar, documenting long distance movement of a female between non-adjacent breeding areas. Resightings also include two matches between American Samoa and the Antarctic Peninsula, documenting the first known feeding site for American Somoa and setting a new long distance seasonal migration record. Three matches between Sector V and eastern Australia support earlier evidence provided by Discovery tags. Multiple resightings of individuals in the Antarctic Peninsula during more than one season indicate that humpback whales in this area show some degree of regional feeding area fidelity. The AHWC provides a powerful non-lethal and non-invasive tool for investigating the movements and population structure of the whales utilising the Southern Ocean Sanctuary. Through this methodical, coordinated comparison and maintenance of collections from across the hemisphere, large-scale movement patterns may be examined, both within the Antarctic, and from the Antarctic to breeding grounds at low latitudes.

KEYWORDS: HUMPBACK WHALE; SOUTHERN HEMISPHERE; PHOTO-IDENTIFICATION

INTRODUCTION

The Antarctic Humpback Whale Catalogue (AHWC) is an international collaborative project investigating movement patterns of humpback whales (*Megaptera novaeangliae*) in the Southern Ocean and corresponding lower latitude waters. College of the Atlantic (COA) has maintained a collection of humpback whale identification photographs from the Antarctic since 1987 with initial contributions coming primarily from collaborating scientists and opportunistic sources from South America and the Antarctic Peninsula. Early resightings confirmed migration of humpbacks between the Peninsula and the western coast of South America (Stone *et al.*, 1990). Since 1998, the International Whaling Commission (IWC) has provided support for the expansion of this catalogue to include dorsal fins and for the development of a searchable online database.

The collection has grown substantially in size and geographic scope. It now contains records of individual whales from throughout the Southern Ocean Sanctuary, in all of the Antarctic management areas, the feeding grounds in southern Chile and also in most of the known or suspected low-latitude breeding areas, allowing comparisons to be made over all of the major regions used by Southern Hemisphere humpback whales and spanning more than two decades. The collection has been internationally collaborative; 261 researchers and opportunistic sources have contributed photographs to these analyses.

The AHWC sets out to:

(1) compile identification photographs of the ventral fluke and the left and right flanks of humpback whales collected by collaborating researchers or from opportunistic sources;
(2) create and maintain relational databases for associated field data;
(3) scan and archive all images and link these to the databases;
(4) report to contributors on completion of photo comparison and work with these collaborators to disseminate findings; and
(5) provide online access to the photographic collection. In this paper the organisation and maintenance of the AHWC and the statuses of these collections is reported on.

METHODS

Photograph processing and archive

Photographs have been submitted as prints, slides, negatives or in electronic format. All catalogued photos were digitised and stored electronically. Images not submitted electronically were scanned at 300dpi and stored in TIFF format to avoid losses in quality resulting from image compression. Electronic submissions were archived in their original format; copies of these were cropped and adjusted as required and these copies used for analysis. A unique serial number was assigned to each image. The individual identification number and serial number served as a file name, linking each photograph to all related database records. The best images of each individual were additionally stored in an *iMatch* database that was used for image comparison analysis.

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* *College of the Atlantic, 105 Eden Street, Bar Harbor, ME 04609, USA.*
+ *Aquatic Systems Group, University of Southern Maine, 350 Commercial St, Portland, ME 0410, USA.*
^ *Princetown Center for Coastal Studies, 115 Bradford St., Provincetown, MA 02657, USA.*

Photographs to be included on the web page were additionally stored at 100dpi in JPG format. This resolution is adequate for on-screen resolution, but not for reproduction, providing data security for collaborators, while the small file size resulting from the compressed format and low resolution facilitates web operations. The low-resolution images used on the website were stored in a *Filemaker Pro* database on a web server to make these available to the web page. All electronic images and databases were stored on a network file server and backed up to a remote tape drive daily.

Photographic collections

Individual humpback whales were identified by natural markings and permanent scars. Humpback whales may be identified by features on several areas of the body. The most commonly used are the shape and markings of the ventral side of the flukes or the dorsal fin and flank (Katona and Whitehead, 1981). Photographs of three body regions, the fluke, the left side of the dorsal fin and flank, and the right side of the dorsal fin and flank, were maintained separately within the catalogue.

Photographic comparison was conducted following the model developed by Katona and Beard (1990) modified for use with electronic images. The best photographs of each individual were stored in the *iMatch* database, which was continually updated as better photographs were received. The image management software *iMatch* allowed the user to assign categories, subcategories and properties to images. Assigned categories include geographic area, ventral fluke pattern type (five categories, 1–5, ranging from all white to all black) with subcategories within types indicating specific arrangement of pigmentation, and categories indicating presence of features such as orca scars, barnacle scars and injuries. Categories may be viewed alone or in combination. While area sighted may be used as a search criterion, new animals were compared to catalogued whales from all other regions without regard to anticipated population structuring or distance between sighting locations. Data such as the years that an individual was sighted may be associated with images as properties. Combined, categories and properties provide convenient and flexible means to view specific sub-sets of the collection without compromising comprehensive comparison.

New photographs were either printed for comparison with the on-screen catalogue, or the new image was displayed on a separate monitor allowing catalogue images to be displayed in full-screen format. Before comparison commenced each whale represented by a fluke photograph was assigned a pattern type. This individual was then compared to all of the individuals in the collection that had been assigned the same pigment type and to those assigned one type darker and one type lighter. Previously, new individuals had been compared to all individuals in the catalogue without regard to pigment type. With the increasing size of the collection and resulting time required for comparison of each new individual this became impractical and, with the ease of sorting allowed by the *iMatch* software, the comparison with the most dissimilar types was discontinued. While an individual assigned a type of 3, for example, is very unlikely to be categorised from a different photograph as a type 5 or a type 1, this procedure slightly increases the risk of false negative errors in identification. The dorsal fin collections are not yet large enough to require this type of selection and each new individual was compared to all individuals currently in the catalogue. A system for grouping animals with similar dorsal fin appearance using characteristics such as fin shape or flank pigmentation could easily be developed if the collection became large enough that one were needed.

All new photographs were compared to the collection twice by different technicians. Photographs that matched a previously identified whale was assigned that catalogue identification number; photographs which represent a new animal were assigned a new identification number, added to the catalogue and included in all future comparisons. The *iMatch* software allows new photographs to be added to the catalogue immediately upon completion of photo-comparison, further speeding analysis.

Photographic quality was coded by methods developed by Friday *et al.* (2000). As inclusion of poorer quality photographs increases the probability of errors in identification and resulting biases in analyses (Friday *et al.*, 2008; Stevick *et al.*, 2001) as well as substantially increasing the time required to make comparisons. The minimum quality of photographs accepted into the catalogue has been made more restrictive, and some photographs that show identifiable markings and may be included in the collections of collaborators were excluded from the catalogue.

Databases

Accompanying data for all photographs are stored in a relational database (*MS FoxPro*). The fluke and dorsal/flank collections are combined in a single data file but the area of the body represented in the photograph is distinguished by use of a data field indicating fluke or dorsal type (right or left), to facilitate analysis of the three collections independently. Where photographs of more than one body region were obtained from an individual during the same sighting, and identified as such by the contributor, the same identification number was applied to all photographs of that animal for convenience. However, analyses were only conducted by one body area; no attempt was made to integrate these in specific investigations. Additional information stored included the identity of the contributor, date and location to the degree of precision provided by the contributor, roll and frame (or contributor's image file name for electronic images), any id number supplied by the contributor corresponding to their cataloguing system and photographic quality code. Images and data accessed by the web page were stored in a *Filemaker Pro* database, hosted on a local web server.

Reporting

A standardised data report was issued to all contributors on completion of cataloguing of submissions. The report included the catalogue number assigned and the data submitted with the photographs as it is recorded in the file. The year and region are provided for any previous sighting history along with the contributor. Contact information for contributors of these previous sightings was provided to facilitate further communication between the contributors, allowing them to exchange additional data if they chose to do so. To assist collaborators in sharing significant findings, periodic updates of sightings histories were provided, along with reports of potentially important resightings of whales previously submitted. AHWC personnel also assist collaborators in presenting and publishing these findings.

Online access

In order to facilitate access by contributors to the collection, an online Antarctic Catalogue web page was developed (. Both fluke and dorsal fin/flank collections are currently available, although a search criterion allowing the user to specify dorsal fin/flank has not yet been added. Users are able to log in and search by pigmentation pattern, geographic area, or catalogue number. Only those photographs for which permission has been received to publish electronically are included in the online collection. Images displayed are identified by catalogue number and the contact organisation for the contributor. No additional data are available online. Photos submitted by the IWC, Allied Whale researchers, and opportunistic sources are accessible to the general public. A login-security system restricts access to the remainder of the collection to contributors only. Access to photographs submitted by other contributors is restricted unless otherwise indicated. Users are advised of the security protocol of the project, whereby they are not permitted to share their password with others or reuse photographs or other information without permission. Instructions including the website address, login and password are sent to contributors with the data report. Users may search either a public database or a secure contributor-only database. Before accessing either database, users must agree to terms of use (see Appendix 1) which include not publishing or reproducing information without written consent.

RESULTS

Photographic collections

The AHWC contained 7,107 photographs as of May 2010. Each photograph is included in one of three collections: fluke; right dorsal fin/flank; or left dorsal fin/flank. The fluke photographic collection consists of 6,083 photographs of 3,665 individual whales. Of the >4,000 fluke photographs maintained in the *iMatch* database and used for photographic comparison, 4.6% were coded as the poorest quality (3–), with 9.5% coded as 3+ (Friday *et al.*, 2000). While these poor quality photographs make it more difficult to correctly identify an individual, leading to more potential for false-positive errors in identification (Stevick *et al.*, 2001) and potential biases in estimation of population parameters if they are included in calculations (Friday *et al.*, 2008), they contain adequate information to make unambiguous identification from an appropriate corresponding photograph, and are therefore retained for their use in documenting movement of individual animals. The right dorsal fin/flank collection consists of 521 photographs of 413 individuals. The left dorsal fin/flank collection consists of 503 photographs of 407 individuals.

Photographs submitted from high-latitude feeding areas include IWC Antarctic Areas II, III, IV, V and VI and coastal water of Chile, as well as the Antarctic Peninsula (which spans both Sectors I and II). Photographs submitted from low-latitude breeding regions include areas off South America (Peru, Ecuador, Colombia and Brazil), Central America (Costa Rica), Africa (Gabon), Australia and Oceania (Table 1, Fig. 1). As of May 2010, there were 310 individuals resighted in more than one year and 128 individuals resighted in more than one region (Table 2).

Resightings between regions document movement along the western coast of South America and movement between the Antarctic Peninsula and western coast of South America between Peru, Ecuador, Colombia, Panama and Costa Rica (16 matches) (Rasmussen *et al.*, 2007; Stevick *et al.*, 2004; Stone *et al.*, 1990). The matches to Costa Rica (Rasmussen *et al.*, 2007) mark the first documentation of Northern and Southern Hemisphere populations of humpback whales using the same breeding and calving ground during different seasons. Resightings to the Antarctic Peninsula differed dramatically between eastern and western South America (Stevick *et al.*, 2004). No individuals from Brazil were resighted in either the Antarctic Peninsula or off western South America. A single individual from Brazil however was

Table 1

Fluke and dorsal photographic collections, by region. Individual whales that have been identified in multiple regions are listed in each region, so the total number of individuals listed may not be the same as the column totals.

	Fluke		Right dorsal		Left dorsal	
Region	Photos	No. whales	Photos	No. whales	Photos	No. whales
Antarctic Peninsula	1,924	995	50	34	42	34
Antarctic II–VI total	478	296	145	110	169	125
Sector II*	30	22	–	–	–	–
Sector III	196	117	16	13	26	15
Sector IV	168	108	82	59	72	63
Sector V	67	40	30	26	53	37
Sector VI	11	7	17	12	18	12
Gabon	94	78	–	–	–	–
St. Helena	3	2	–	–	–	–
Ghana	1	1	–	–	–	–
South Africa	11	7	–	–	–	–
Brazil	1,524	888	2	2	5	5
Chile	83	77	–	–	–	–
Peru/Ecuador/Colombia/ Panama/Costa Rica	1,075	767	72	30	64	26
American Samoa	265	159	–	–	–	–
Tahiti	1	1	–	–	–	–
New Zealand	2	1	–	–	–	–
Tonga	24	18	–	–	–	–
French Polynesia	2	2	–	–	–	–
Madagascar	247	226	–	–	–	–
E Australia	34	27	1	1	2	1
W Australia	317	242	251	236	221	213
Totals	6,083	3,665	521	413	503	407

*Antarctic Peninsula includes individuals identified along the coast of the AP and South Shetland Islands as far to the east as the South Orkney Islands (45°W). Area II includes individuals identified east of the South Orkney Islands to 0° (see Stevick, 2005).

Table 2

Number of individual whales identified by fluke photographs in each region, the number of individuals resighted in each region in more than one year, and the distribution of resightings between regions.

			Between region re-sightings			
Region	No. whales	Between year resightings	Pe/Ec/Co/Pa/CR	AP	Sector II	Sector V
Antarctic Peninsula	995	121	–	–	–	–
Sector II	22	–	–	1	–	–
Sector III	117	–	–	–	–	–
Sector IV	108	–	–	–	–	–
Sector V	40	–	–	–	–	–
Sector VI	7	–	–	–	–	–
Gabon	78	–	–	–	–	–
Ghana	1	–	–	–	–	–
South Africa	7	–	–	–	–	–
Saint Helena	2	–	–	–	–	–
Brazil	888	42	–	–	1	–
Chile	77	5	7	–	–	–
Peru	2	–	–	–	–	–
Peru/Ecuador/Colombia/ Panama/Costa Rica	767	63	–	95	–	–
American Samoa	446	1	–	2	–	–
Tahiti	1	–	–	–	–	–
Tonga	18	–	–	–	–	–
New Zealand	1	–	–	–	–	–
French Polynesia	1	–	–	–	–	–
Madagascar	226	–	–	–	–	–
E Australia	7	3	–	–	–	3
W Australia	242	5	–	–	–	–

resighted off South Georgia (Sector II), representing the first documented photo-id link between the Brazilian breeding ground and any high-latitude feeding area (Stevick *et al.*, 2006). A second individual was resighted off Madagascar, demonstrating long distance movement of a female between two widely separated breeding areas, a minimum distance of almost 10,000km and the longest documented movement by a mammal (Stevick *et al.*, 2010). Two individuals from American Samoa were resighted in the Antarctic Peninsula, documenting the first known feeding area for this central South Pacific Ocean stock. One of these individuals was identified twice in the Antarctic Peninsula setting a round trip seasonal migration record of almost 19,000km, spanning 108 longitudinal degrees (Robbins *et al.*, 2011). Resightings also include three matches between Antarctic Area V and eastern Australia (Rock *et al.*, 2006), supporting earlier evidence provided by Discovery tags linking these two areas (Dawbin, 1966).

DISCUSSION

The AHWC provides a powerful non-lethal and non-invasive tool for investigating the movements and population structure of the whales utilising the Southern Ocean Sanctuary. Through methodical, coordinated comparison and maintenance of collections from across the hemisphere, large-scale movement patterns may be examined, both within the Antarctic, and from the Antarctic to breeding grounds at low latitudes. Effort continues to stimulate submission of opportunistic data from the International Association of Antarctica Tour Operators (IAATO) cruise ships in the Southern Ocean and directed samples from research organisations and expeditions working throughout the Southern Hemisphere.

The catalogue has expanded dramatically in recent years. As all new individuals are added to the growing catalogue, the temporal as well as the geographic scope of the

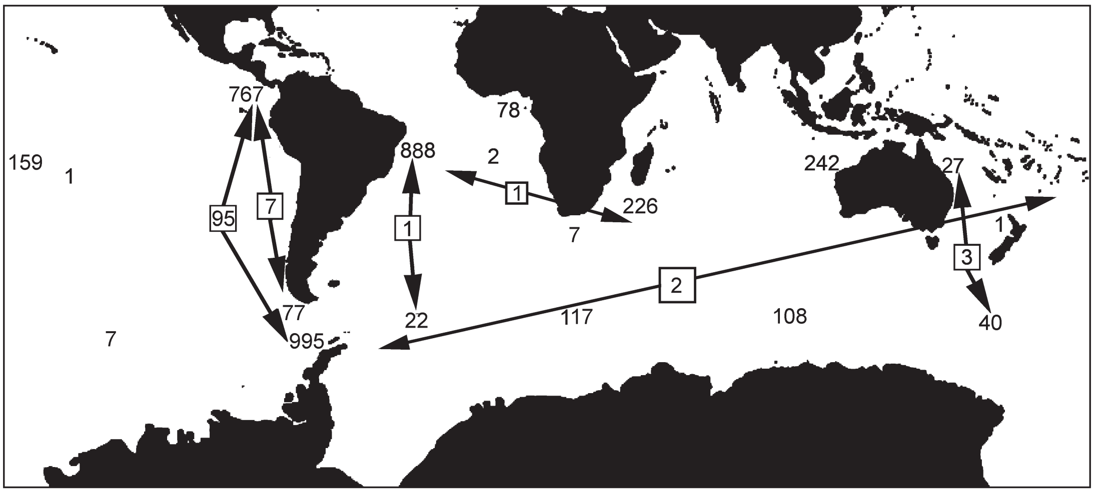

Fig. 1. Distribution of individual humpback whales identified by fluke photographs contained in the AHWC. Arrows and corresponding boxed figures represent the number of individuals resighted between habitats.

collections continues to grow. Increasing awareness of the project among research organisations, tour operators and other organisations has widened the scope of the collection; research efforts in areas that had not previously been sampled have extended the geographic coverage. In addition, the collections of several long-term contributors have expanded substantially, accounting for significant additions of photographs. Thus, the catalogue has almost doubled in size over recent years.

The AHWC is a valuable tool for the facilitation of international collaboration in humpback whale research. With continued expansion, the collection can make substantial contributions towards and understanding of the population ecology of humpback whales in the Southern Hemisphere through examination of broad-scale movements.

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Appendix 1

TERMS OF USE AGREEMENT

By accepting this document and using the Antarctic Humpback Whale Catalogue (AHWC) the User agrees to the following.

(1) Not to use data contained in the Antarctic Humpback Whale Catalogue (AHWC) in any publication, product, or commercial application without prior written consent of the original data provider.

(2) To cite both the data provider and the Antarctic Humpback Whale Catalogue (AHWC) appropriately after approval of use is obtained.

(3) Not to hold the Antarctic Humpback Whale Catalogue (AHWC) liable for errors in the data. While we have made every effort to ensure the quality of the database, we cannot guarantee the accuracy of the data.

The importance of a seasonal ice zone and krill density in the historical abundance of humpback whale catches in the Southern Ocean

CÉDRIC COTTÉ AND CHRISTOPHE GUINET

Centre d'Études Biologiques de Chizé, Centre National de la Recherche Scientifique, 79360 Villiers en Bois, France
Contact e-mail: cecotte@cebc.cnrs.fr

ABSTRACT

Humpback whale populations in the Southern Hemisphere were dramatically reduced by the whaling industry. A comprehensive whaling dataset was used in an analysis of circumpolar abundance of humpback whale catches relative to contemporary densities of its preferred prey, Antarctic krill, and to a major dynamic feature of the marine ecosystem, the summer seasonal ice zone (SSIZ) derived from southernmost whaling locations. The circumpolar abundance of catches derived only from pelagic data, i.e. about 30% of the total humpback whale catches in the Southern hemisphere, was found to be only marginally related to krill density. However, the total abundance of catches – from pelagic operations and land stations, from high and low latitudes – was found to be more related to SSIZ than to krill density, especially when excluding the highly dynamic west Atlantic region where the circulation probably drives the ecosystem. A large SSIZ is likely to provide a favourable feeding ground for humpback whales, given their high energy requirements and because of its predictability and the prey aggregation processes occurring there.

KEYWORDS: HUMPBACK WHALE; SOUTHERN OCEAN; WHALING; CATCH ABUNDANCE; ICE; EUPHAUSIIDS; SOUTHERN HEMISPHERE

INTRODUCTION

The humpback whale (*Megaptera novaeangliae*) is the most studied whale species of the Southern Hemisphere, due to its typical seasonal migration between winter breeding grounds in tropical/sub-tropical areas and summer feeding grounds in Antarctic waters (e.g. Paton and Clapham, 2006; Stevick *et al.*, 2004; Zerbini *et al.*, 2006). In contrast with other large balaenopterids, humpback whales breed in delimited coastal breeding grounds, which has resulted in the identification of seven geographically defined stocks (IWC, 1998; Rice, 1998), each associated with supposed feeding grounds (Donovan, 1991; IWC, 1998). The predictability and the availability of humpback whales has made them accessible to the modern whaling industry since the beginning of the 20th century, before the exploitation of the larger baleen whales such as blue and fin whales (Brown and Lockyer, 1984), and until the cessation of humpback whaling in the Southern Hemisphere in 1963 (although the Soviet whaling fleet was active until 1973). Based on catch records corrected for illegal Soviet whaling, a total of more than 200,000 humpback whales was killed in the Southern Hemisphere from 1904 to 1980 (Clapham and Baker, 2001).

Tynan (1998) suggested that the heterogeneous distribution exhibited by the higher trophic-level populations in the marine environment, including whales, is influenced by the Southern Boundary of the Antarctic Circumpolar Current. She suggested that the circumpolar distribution of whales reflects the non-uniform high-latitude penetration of the typical water mass of the Antarctic circumpolar current. Sea ice has also been recognized as a major driving force of the Southern Ocean, playing a crucial role in primary production and also in population dynamics and recruitment of Antarctic krill (Atkinson *et al.*, 2004; Loeb *et al.*, 1997), the chief prey of humpback whales (Kawamura, 1994; Laws, 1977). Indeed sea ice seems to be important for large krill-eating whales (Nicol *et al.*, 2000; Thiele *et al.*, 2000) since the pelagic whaling industry was created to catch whales at the ice edge where both whales and krill concentrate (Brierley *et al.*, 2002). In this paper the relationship between sea ice extent, available estimates of krill density, and the abundance of humpback whale catches longitudinally in the Antarctic, is investigated.

MATERIALS AND METHODS

Whales, krill and environmental data

Whaling catch data were provided by the International Whaling Commission (IWC). Humpback whale catch data from industrial floating factory operations in the Southern Ocean from 1913 to 1973 (including Soviet catches) were calculated. Catches from land stations, taken early in the 20th century, were also considered. Land station catches from colder waters (south of 40°S latitude including data from South Georgia and the South Shetland Islands), and land station catches in waters north of 40°S latitude (including data from Southern Africa, America, Australia and New Zealand) were pooled. The IWC has recognised that catch allocation to breeding/feeding ground is important because it has to take into account mixing of two or more stocks. The extent of the problem varies with feeding area and breeding stock. For the circumpolar analyses, catches from land stations and from low latitudes (i.e. breeding grounds) were allocated to the corresponding feeding grounds in the Southern Ocean according to known migration patterns between breeding and feeding grounds and stock structure models developed by IWC (2005). These were established from documented connections using several methods such as returns of Discovery tags, photo-identification and genetic marks, or satellite tracking (Chittleborough, 1965; Mackintosh, 1942; Pomilla and Rosenbaum, 2005; Zerbini *et al.*, 2006). Total catches in each breeding area were divided by the number of 10° sectors and allocated equally among them according to available information on migration patterns. For cases where connections were uncertain, a weighted allocation of catches was used (e.g. the updated 'Fringe' models proposed in IWC (2006) when two neighbouring areas are likely to overlap) to provide for suitable examination of the effect of uncertainty in catch allocation on assessments. The weighted allocation taking this uncertainty into account was calculated such that for the 10° sectors corresponding to ‘fringes’, half of the catches from land stations and breeding grounds were attributed to each of the two putatively overlapping feeding areas.

Hjort *et al*. (1933) introduced the concept of ‘catch per boat per day’ and used the expression ‘catcher’s days work’ in measuring effort. Omura (1973) summed effort from 1931 to 1972 by 10° squares of latitude and longitude. In this paper effort has been summed for the same 10° longitude squares to estimate circumpolar effort over the pelagic whaling period (1931 to 1972) although it should be noted that whaling was banned in the sector between 70°W and 160°W in 1938 and again in 1947–1955, and permitted for only four days each season in the 1950s.

Sea ice extent was derived from the whaling catch data for each month from December to February and averaged over the 1931–1960 period. From 1904 to 1930 whales were taken in areas surrounding land stations, for which there is no information on sea ice extent. From 1931, the location of the ice edge, where the pelagic fleets concentrated their effort, was calculated as the mean latitude of the southernmost catch positions of all large whale species (more details are given in Cotté and Guinet, 2007). Thus, only pelagic catcher data were used in this historical definition of sea ice extent. The mean latitudes of the 10 southernmost whale catch positions were calculated for 36×10° longitudinal circum-Antarctic sectors; for a given sector, month and year, catch positions more than 3° north of the southernmost catch position were excluded. Across all years, the mean summer seasonal ice zone (SSIZ) was defined as the area delimited by the maximum summer (December) and the minimum summer (February) sea ice extent (Parkinson, 2004).

Global estimates of krill biomass were extracted from the compilation by Atkinson *et al*. (2004) of historical krill densities in the Southern Ocean. These data were derived from the Discovery expeditions (Foxton, 1966; Marr, 1962), during the summers of 1926–39. They were obtained from archived net sampling logs, original tables and an electronic krill database. Most of the Discovery net samplings were carried out with a 1m ringnet.

Data analysis

The Southern Ocean was divided into 36 sectors of 10° where the longitudinal abundance of whale catches, krill density and SSIZ were averaged. This sector size corresponds to the longitudinal resolution of sea ice extent from the analysis of Cotté and Guinet (2007). Generalised Additive Model (GAM, Hastie and Tibshirani, 1990) analysis was used to investigate relationships, possibly non-linear, between SSIZ and krill densities and the longitudinal variability of whale catches. In order to take into account the

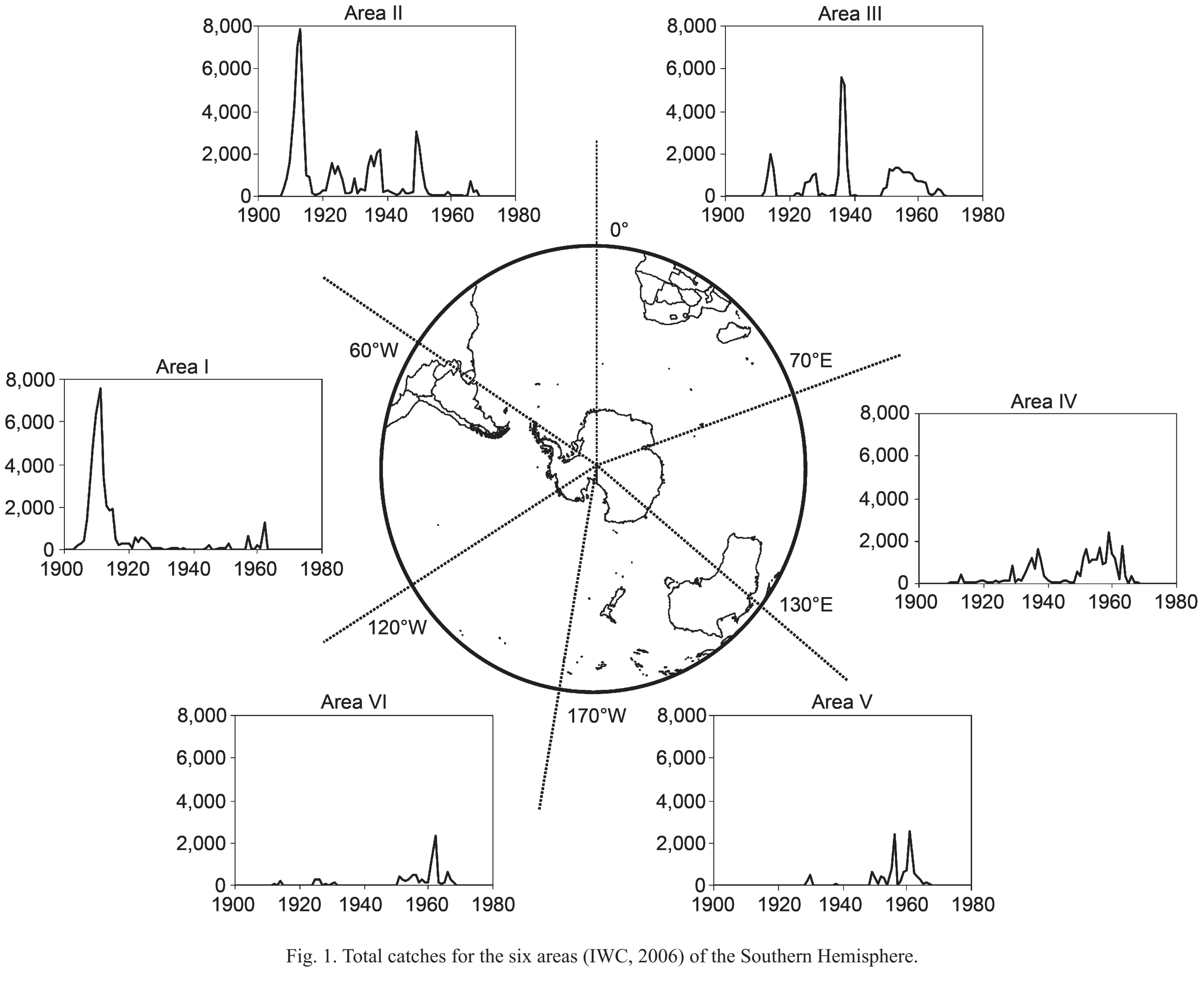

Fig. 1. Total catches for the six areas (IWC, 2006) of the Southern Hemisphere.

spatial structure of the catches, an autocorrelation term was added to the model:

$$\text{Catch abundance} = \beta_0 + \text{s(SSIZ)} + \text{s(krill densities)} + \text{s(autocorrelation)} \qquad (1)$$

Since data were not normally distributed (Shapiro-Wilk tests, all $P<0.05$), a log-link function and a negative binomial distribution were used.

The analysis was first performed with pelagic whaling data only. Subsequently analyses were carried out with the land station data included in the catch dataset. Further analysis excluded the sectors from the Antarctic Peninsula to the South Sandwich Islands, i.e. between 75°E and 15°E, where an advection process is suspected to be the main factor driving krill and whale distribution (Trathan *et al.*, 2007). Indeed, the krill population in the West Southwest Atlantic area has been shown to be especially driven by advection, where the process is known as the ‘krill conveyor belt’ (Fach and Klinck, 2006; Murphy *et al.*, 1998).

RESULTS

Circumpolar exploitation of humpback whales occurred over approximately six decades, from the beginning of the 20th century until the 1960s. Fig. 1 shows intensive early exploitation in Areas I and II prior to the introduction of pelagic operations. Whaling occurred throughout the period for Areas II and III, with later exploitation in Areas IV, V and VI. Population productivity should be thus taken into consideration in areas where catches are lower but extend over a longer period. Despite lack of knowledge of the rate of productivity of circumpolar humpback whale populations (varying with population level), it could be reasonably suggested that this productivity is well below total catch levels during this intensive whaling period.

Whaling effort, represented as ‘catcher’s day’s work’ (Fig. 2), reveals a heterogeneous circumpolar pattern, with considerably more time spent in the Atlantic and Indian Oceans than in the Pacific. Such differences could be attributed to the cessation of whaling in Pacific waters for about ten years. However, effort south of the eastern Australian and Kerguelen-Heard regions was similar, despite a lack of regulation. Regulation is thus not the main driver of the effort pattern. Indeed, the pattern is very similar to that for catches (Figs 3 and 4). Moreover, the reason why this parameter was not used to explain catch abundance is that the main targets of pelagic whaling driving the effort pattern were blue and fin whales rather than humpback whales.

The SSIZ is large in the east Atlantic and west Indian sector and north of the Ross Sea (Fig. 3b). Krill were abundant in the Atlantic Ocean and also in the East-Indian sector, i.e. around 90°E (Fig. 3c). Circumpolar catch abundance from pelagic whaling in the Southern Ocean also exhibited a marked heterogeneous circumpolar pattern (Figs 3a, 4b). Most catches were in the West Atlantic and East Indian sectors, in the Ross Sea, and south of South Africa. The addition of land station data from polar waters incorporated catches mainly from the southwestern Atlantic, while land station data in subtropical/tropical waters increased the catch data available mainly between 15°W and 180°W, i.e. in the African and Australian sectors (Fig. 4c).

The GAM analyses showed that circum-Antarctic krill densities were not associated with SSIZ ($P = 0.45$). Since they are statistically independent, these two explanatory variables were included in the models (Table 1). Catch distribution from pelagic data was explained only partially by krill densities. Circumpolar catch abundance in the Southern Hemisphere (from pelagic and land station data), was related to SSIZ. Excluding western Atlantic sectors (between 75°E and 15°E), krill densities were still not associated with SSIZ ($P = 0.15$) and SSIZ is the major explanatory variable for the longitudinal abundance of humpback catches. Using large longitudinal sectors of 30º no relationship was obtained for pelagic data only when the total circumpolar catches of whales was linked to both krill and SSIZ, either when including the West Atlantic area (krill and SSIZ, $P<0.01$) or excluding the West Atlantic area ($P = 0.01$).

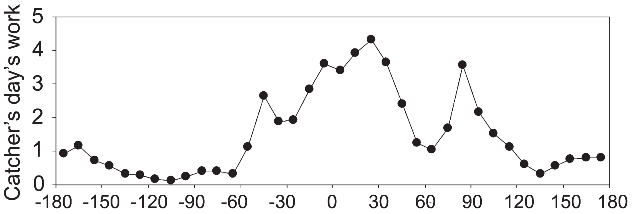

Fig. 2. Longitudinal pelagic whaling effort, summed from 1931 to 1972, as ‘catcher’s days work’ (from Omura, 1973)

DISCUSSION

Several biases occurred when attempting to quantify proxies for humpback whale circumpolar abundance such as whaling effort, rate of productivity and regulation of catches (spatially, in the western Pacific from 70° to 160°W in 1939 and from 1948 to 1955, and temporally such as the four day season in the 1950s). Despite these biases, pelagic catches taken in the Southern Ocean are the most relevant data for approximation of circumpolar abundance of humpback whales. However, pelagic whaling constituted only 30% of the total humpback whaling conducted and it was thus necessary to add the large amount of low latitude catches and data from high latitude land station to provide a more realistic assessment of the circumpolar abundance of humpback whales. This was particularly the case for Areas I and II where most whales were caught prior to pelagic whaling (1930). The assessment relies upon knowledge of the migration pattern of humpback whales between breeding and feeding grounds in order so as to correctly allocate catches from low latitudes. Some connections, for example between Breeding Stock A off Brazil and feeding grounds in Area II, are now relatively well understood through satellite tracking, confirming the feeding ground from the Antarctic Peninsula to the South Sandwich Islands (Zerbini *et al.*, 2006), although Discovery marks show that whales can cross the Drake passage (Paton and Clapham, 2006). Uncertainties still exist over the specific migratory destinations of some populations and care needs to be taken when allocating breeding ground catches by feeding areas. Despite migration corridors in a relatively straight north–south line, the humpback whale has been shown to be a mobile species possibly travelling longitudinally to extended feeding grounds and limited breeding grounds see IWC (2005; 2006). The hypothesis of discrete groups in relation to Southern Hemisphere stock structure (Mackintosh, 1942) is supported by Discovery mark data, suggesting relatively discrete longitudinal fidelity and low incidence of large scale movement between areas. Furthermore, as total catch is only a proxy measure of abundance and does not give absolute abundance, it is important to take into account how long the

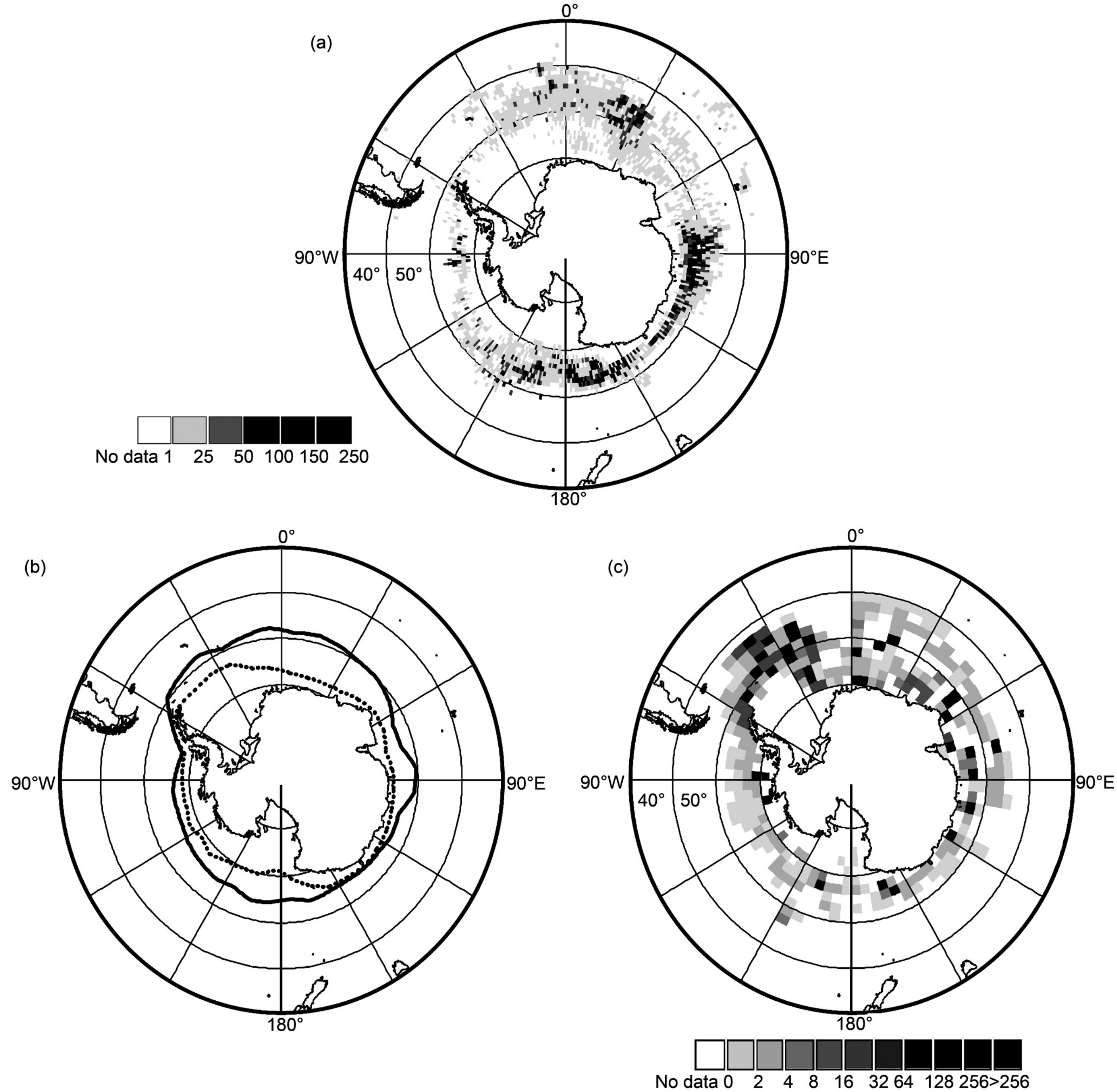

Fig. 3. Whales, SSIZ and krill distribution. (a) Pelagic catches. (b) Early (December, continuous line) and late (February, dotted line) summer ice extent. (c) Global krill distribution (number of krill per m^{-2}) (from Atkinson *et al.*, 2004)

catches were taken for and the level of final depletion. It is difficult to assess this level on a stock by stock basis and, while there is currently an increase in humpback whale abundance in several areas, post-whaling abundance from the 1970s suggests that a large proportion of the total whale population was caught. Areas with exploitation spread over a period of time, such as Areas II and III, can exhibit some recovery in numbers, while short and intense exploitation gives a snapshot of the situation. Although some recovery could lead to an overestimate of the abundance of humpback whales where exploitation was consistently spread over time, it can be assumed that 'whale production' is less than total catches, especially in Areas II and III, and thus should not influence the analysis.

From pelagic catch records, the east Indian and south African sectors exhibit high humpback whale abundance, while land station data from the southern feeding grounds add many catches, mainly in the Atlantic sector where humpback whaling began owing to the accessibility of animals close to islands. The whole pattern, reconstructed from pelagic, southern (feeding) land stations and northern (breeding) catches, is very similar to the circumpolar patterns of blue and fin whale catches (Branch *et al.*, 2007). The slight relationship between catch abundance from pelagic data only and krill density does not seem to be reliable since the circumpolar abundance of whale catches is largely underestimated, particularly in the sector from the west Atlantic to the west Indian Ocean. In considering the circumpolar abundance of all catches, SSIZ is the dominant parameter, especially when the southwest Atlantic sector is excluded. Indeed the increase of the SSIZ in explaining whale catch abundance when excluding this area, where high densities of krill were reported, shows that this parameter is especially important in the other areas. On the basis that

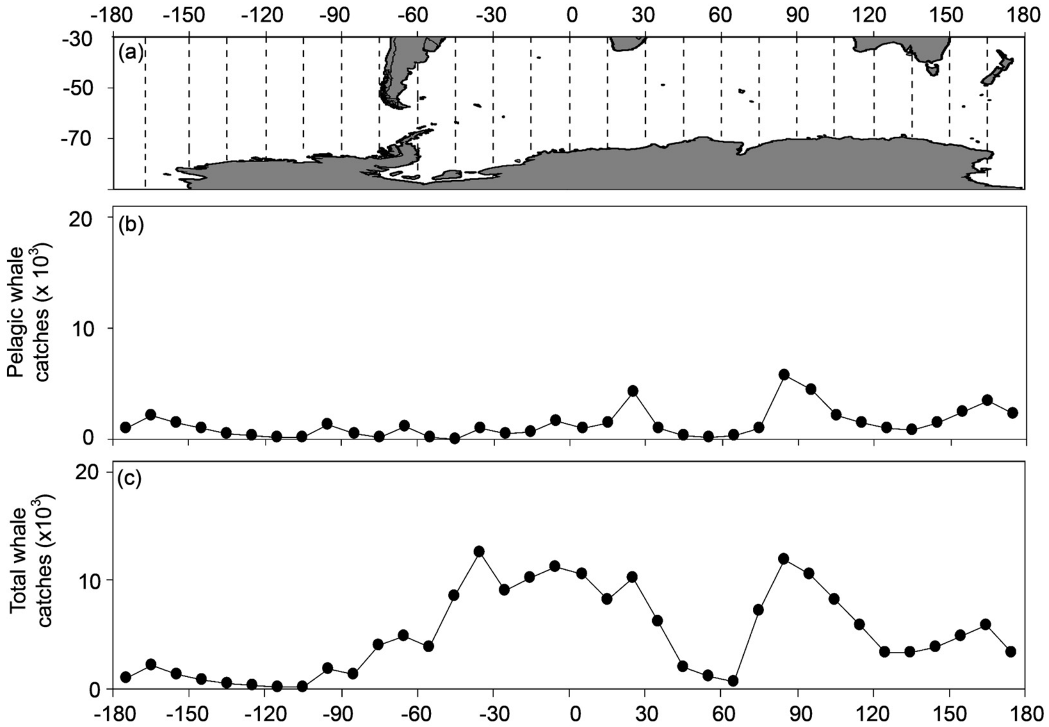

Fig. 4. (a) Study area. (b) Circumpolar abundance of whales from pelagic catches. (c) Circumpolar abundance of whales from pelagic and land station data. Catches from high latitude land stations were allocated to longitudinal sectors according to known migration patterns between breeding and feeding grounds and stock structure.

longitudinal movements within each stock (Paton and Clapham, 2006) could confuse the analysis, i.e. catches would be more representative of whaling effort than a proxy of whale abundance, the same analysis was done at a coarser scale using 30° sectors. Although whale catch abundance was correlated with both krill densities and SSIZ, the results using 10° and 30° seem to be relatively robust to any noise in the analysis resulting from possible movements.

The marginal relationship with krill in the 10° sector analysis may be influenced by the strong densities of both whale catches and krill in the west Atlantic sector. This region is highly dynamic and krill distribution and abundance are believed to be driven by the complex circulation between the Antarctic Peninsula (corresponding to Area I), and South Georgia (corresponding to Area II) (Murphy *et al.*, 1998). However, circumpolar catch abundance is more definitely related to the large SSIZ from the east Atlantic to west Indian Ocean and in the eastern Indian Ocean. As the humpback whale is one of the largest krill predators in the Southern Ocean, undertaking long migrations to consume large amounts of krill, it was not expected that whale catch abundance would be less related to krill than to the SSIZ. Such a result could be either an artefact due to the lack of an accurate assessment at a circumpolar scale (Smetacek and Nicol, 2005), or reflect the importance of SSIZ in affecting krill biomass and thus the accessibility of these prey to whales feeding in the vicinity of the sea-ice edge.

The results in relation to the SSIZ suggest that humpback whales mainly targeted krill in relation to sea-ice habitat, and not simply in relation to the overall prey abundance. Whales are known to follow the receding ice edge, followed by the whaling fleets (Hjort *et al.*, 1933), where large densities of krill could be found. Indeed, abundant krill were found just south of the ice edge (Brierley *et al.*, 2002). Although krill are able to track the receding ice edge, the rapid melting of pack ice through summer removes this protective shield from air-breathing predators (Lizotte, 2001). Krill are then available in large and dense swarms allowing highly efficient foraging by large whales (Nemoto, 1970). However, rich aggregations of krill are of little interest for whales if they are not autocorrelated in time and space (Simard and Lavoie, 1999). The patchiness of whale prey could therefore be a key factor for the attractiveness of the Antarctic area, with the SSIZ acting as a major predictable feature influencing krill abundance and distribution. A large SSIZ ensures an efficient

Table 1

Results of the GAM analyses of summer seasonal ice zone (SSIZ), and krill explaining the variability of the different datasets of southern humpback whale catch abundance.

	Explanatory variables	*F*	*df*	*P*
Pelagic data	SSIZ	2.58	1	0.12
	Krill	3.03	1.78	0.06
Total circumpolar data	SSIZ	4.17	1	0.05
	Krill	2.03	1.61	0.15
Circumpolar data without western Atlantic sectors	SSIZ	13.87	1	<0.01
	Krill	2.75	1	0.11

feeding ground as the ice sheet decays over summer. The sea ice habitat is important for krill, especially because of sea ice algae, which provide the only suitable food for krill larvae, the most sensitive feeding stage in the krill life cycle (Ross *et al.*, 2000).

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Encounter rates and abundance of humpback whales (*Megaptera novaeangliae*) in Gerlache and Bransfield Straits, Antarctic Peninsula

EDUARDO R. SECCHI*+, LUCIANO DALLA ROSA*#, PAUL G. KINAS^, RAQUEL F. NICOLETTE^, ANNE M. N. RUFINO^ AND ALEXANDRE F. AZEVEDO~

Projeto Baleias/Brazilian Antarctic Programme (PROANTAR)
Contact email: edu.secchi@furg.br

ABSTRACT

During the austral summer of 2006, the Projeto Baleias/Brazilian Antarctic Program (PROANTAR) conducted ship surveys for estimating whale encounter rates and abundance in Gerlache and Bransfield Straits, westward of the Antarctic Peninsula (edge between IWC Areas I and II). The encounter rate was higher in the Bransfield Strait (0.32 groups n. mile–1; 95% CI: 0.26–0.39) than in the Gerlache Strait (0.24 groups n. mile–1; 95% CI: 0.13–0.44), though the difference was not statistically evident. An abundance estimate using conventional distance sampling methods was computed only for the Bransfield Strait. The perpendicular distance data was best fitted by the half-normal model without adjustments. Derived abundance for the surveyed area was 865 humpback whales (95% CI = 656–1,141; CV = 14.13). This area represents only a small fraction of the Stock G feeding ground.

KEYWORDS: HUMPBACK WHALE; ABUNDANCE; ENCOUNTER RATE; ANTARCTICA; SOUTHERN HEMISPHERE; SURVEY-VESSEL

INTRODUCTION

The humpback whale, *Megaptera novaeangliae*, is a cosmopolitan species and occurs in all major ocean basins from tropical to polar waters (e.g. Clapham and Mead, 1999; Dawbin, 1966; Mackintosh, 1965). The species was extensively hunted historically, resulting in global population decline to a very low level (Gambell, 1973). In the Southern Hemisphere, seven breeding stocks are recognised by the International Whaling Commission (IWC, 1998). Both stocks wintering off South America (i.e. Stock G – eastern South Pacific and Stock A – western South Atlantic) were heavily exploited from coastal stations and by the pelagic fleets (e.g. Chittleborough, 1965; Findlay, 2001; Gambell, 1973) and are among the least known breeding stocks. Despite evidence from photo-identification data that whales feeding around the Antarctic Peninsula are part of Stock G (Stevick *et al.*, 2004), controversy remains regarding the feeding ground of whales from Stock A, believed to migrate to somewhere around both the Antarctic Peninsula and South Georgia (e.g. IWC, 1998; Slijper, 1965). Frequent matches between individuals from the Antarctic Peninsula and the eastern South Pacific wintering grounds, as well as the lack of matches between the Peninsula and the western South Atlantic breeding grounds (Acevedo *et al.*, 2007; Dalla Rosa *et al.*, 2004; Rasmussen *et al.*, 2007; Stevick *et al.*, 2004) suggest that the Antarctic Peninsula is a feeding ground for Stock G only and that Stock A feeds elsewhere to the east. Recent findings by Zerbini *et al.* (2011; 2006) show that the migratory destination of Stock A humpback whales is nearby South Georgia and the South Sandwich Islands. These new findings contribute to elucidating the issue concerning the stock structure which is crucial for proper stock assessment. However, other relevant information are necessary for a comprehensive assessment of the current status of humpback whale stocks in the Southern Hemisphere, in particular abundance estimates. Several surveys to estimate whale abundance have been conducted in vast areas of the Southern Ocean, e.g. IWC/IDCR, SOWER or Japanese scouting vessel surveys (Branch and Butterworth, 2001; Reilly *et al.*, 2004) as well as in some breeding grounds (e.g. Bannister and Hedley, 2001; Felix *et al.*, 2005; Findlay *et al.*, 1994; Freitas *et al.*, 2004; Zerbini *et al.*, 2004). Estimates of abundance or any related index (e.g. density or encounter rates) in important concentration areas might be useful for monitoring temporal trends and to compare with corresponding feeding or breeding grounds. Gerlache and Bransfield Straits are important feeding areas for Stock G, where very high encounter rates (Secchi *et al.*, 2002; 2001; Thiele *et al.*, 2004) and site fidelity have been reported (Dalla Rosa *et al.*, 2008; 2001).

Current abundance estimates of humpback whales in the Bransfield Strait are presented and encounter rates between this area and the Gerlache Strait are compared.

MATERIAL AND METHODS

Study Area and Survey design

The Bransfield (approximately 62°S to 63°45'S) is a wide strait (approximately 50 n. mile wide) between western Antarctic Peninsula and the South Shetland Islands. In comparison, the Gerlache Strait (ca. 63°45'S to 65°00'S) is a narrow corridor (approximately 5 to 8 n.miles wide or more

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* *Laboratório de Tartarugas e Mamíferos Marinhos/Instituto de Oceanografia, Universidade Federal do Rio Grande (FURG), Cx.P. 474, Rio Grande-RS, Brazil, 96201-900.*

+ *Laboratório de Mamíferos Marinhos, Museu Oceanográfico 'Prof. Eliezer C. Rios', FURG, Cx.P. 379, Rio Grande-RS, Brazil, 96200-970.*

^ *Laboratório de Estatística Ambiental/Instituto de Matemática e Física, FURG, Cx.P. 474, Rio Grande-RS, Brazil, 96201-900.*

~ *Laboratório de Mamíferos Aquáticos (MAQUA), Departamento de Oceanografia, Universidade do Estado do Rio de Janeiro, Brazil, 20550-013.*

Marine Mammal Research Unit, University of British Columbia, Vancouver BC, Canada.

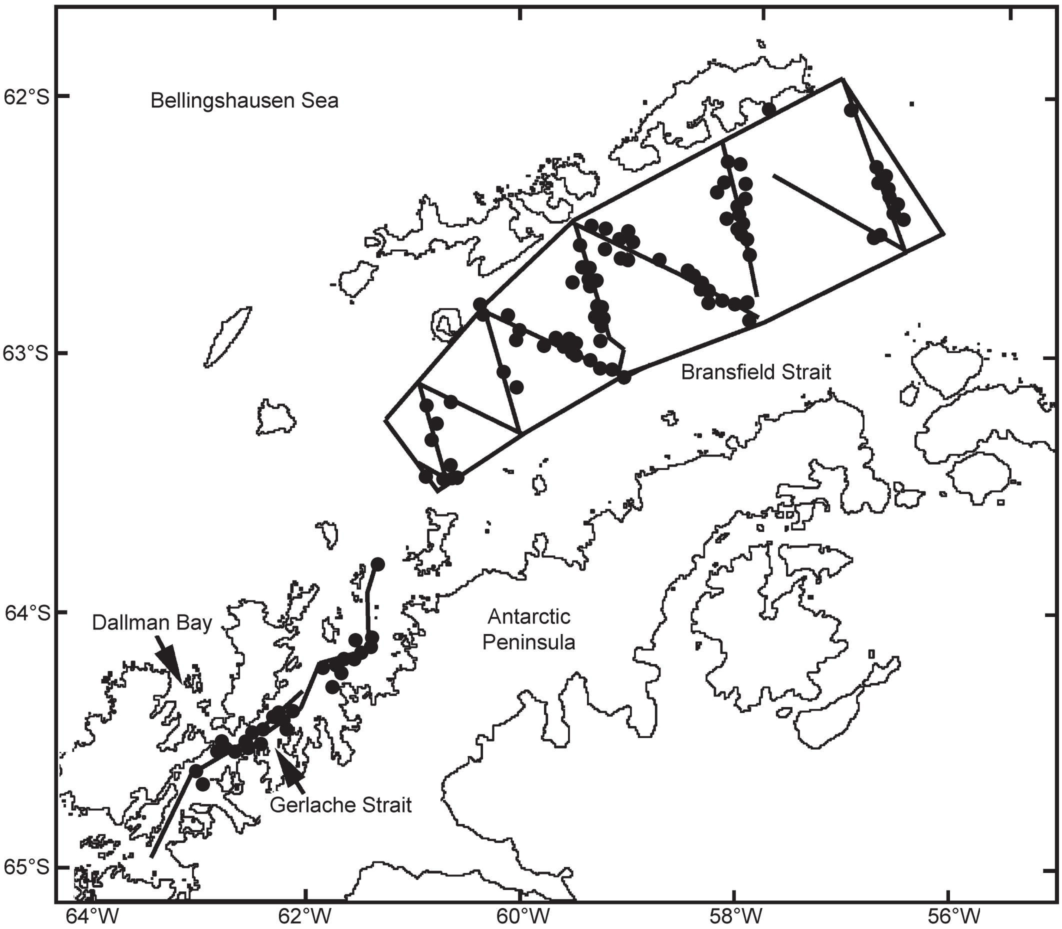

Fig. 1. Survey design and plots of sighting positions in the Gerlache and Bransfield Straits.

in front of large bays) between Brabant and Ansvers Islands and the western Antarctic Peninsula. Its relatively calm waters make cetacean observation easy (Fig. 1).

During the austral summer of 2006, the Projeto Baleias/PROANTAR conducted ship surveys for cetacean sightings in the Gerlache and Bransfield Straits, Antarctic Peninsula region (the boundary between IWC management areas I and II (see Donovan, 1991). In Bransfield, surveys followed nine zig-zag transect lines from the South Shetland Islands towards the Peninsula and back. The start point of the survey in the Bransfield was chosen at random. Areas of poor bathymetry were avoided. This resulted in an unsurveyed strip about 15 n.mile wide westward of the Peninsula. In Gerlache, the tracklines ran along the strait. Tracklines in both Gerlache and Bransfield Straits are shown in Fig. 1. Surveys were conducted in passing mode onboard the Brazilian Navy 75m long Oceanographic and Supply Vessel (NApOc) '*Ary Rongel'*.

Survey protocol

Surveys were conducted between 24 January and 9 February. The observation platforms were the exterior wings of the bridge, approximately 12m above sea level. One observer at each board of the ship, one data recorder and one person resting rotated their positions every 30min. The data recorder and occasionally the person on rest helped the observers to identify species and to estimate group size whenever the animals were very far so the observers could keep on scanning the area. Each observer covered one side of the vessel's trackline forward of the beam (90° quadrant). Searching effort was higher towards the trackline. The searching area of the two observers overlapped approximately 10° on each side of the trackline. Logistics made independent observation impractical and as a result, observers could hear each other whenever a sight was reported to the data recorder. Whales were searched for with 7×50 reticled Fujinon binoculars over 80% of the time and by naked eye. Slight variations in the time observers used the binocular were expected. Ship speed varied around 10 knots, depending on the number of growlers and icebergs in the vicinity. Search effort was restricted to sea conditions ranging from Beaufort scale 0 to 5 (inclusive) to reduce its effect on sighting probability. Although visibility and sea state categories tend to be subjective and may vary among observers, their final classification was defined on a common sense basis. Completely clear sky was considered as an excellent visibility condition. When fog was slightly limiting the observer's sight of the horizon, the visibility was classified as moderate. An approximate control of the observer's limit of visibility was obtained whenever possible by using the ship's radar to read distances from growlers and icebergs. Observation effort was halted when visibility was poor (i.e. below 3 n.mile) and sea state was above Beaufort 5.

For each sighting, the data recorder collected information on species, group size (minimum, best and maximum counting), position, date, time, navigation and environmental conditions. Information regarding sightings, navigation, environmental conditions and effort were stored in the computer using the program *Logger* (IFAW, 1994). The computer was connected to the ship's navigation system, allowing for real-time GPS position storage. The true heading of the ship, the number of binocular reticles between the animal(s) and the horizon and the radial angle between the group and the trackline were recorded immediately after sighting. Detailed checks of the sightings were made during and after the searching effort to identify and exclude probable double counts. Observers were instructed to avoid rounding in both reticle and horizontal angle readings. This information was used to calculate perpendicular distancess of animals to the trackline (e.g. Buckland *et al.*, 2001, p.258; Lerczak and Hobbs, 1998). Lerczak and Hobbs (1998)[1] provided equations for calculating the radial distance from reticle numbers when horizon is obstructed by land. On such occasions, it was necessary to know the distance between the observer and the land blocking the view to the horizon at the exact angle of that sighting. This approach was used to calculate the perpendicular distance of some of the sightings in Gerlache Strait.

Data analysis

Only data obtained during searching effort are considered in the analysis (i.e. crew and researcher sightings made 'off effort' were not included).

The encounter rate, defined as the number of whales sighted per nautical mile surveyed, was used as a simple index of humpback whale density, allowing for comparisons between the Gerlache and Bransfield Straits and with previous studies in these areas. The number of sightings in the Bransfield Strait was sufficient for estimating the detection probability.

Abundance ($\hat{N}$) was estimated using distance sampling methods. Its variance and confidence intervals were obtained using the empiric equation of Buckland *et al.* (2001, p.115).

$$\hat{N} = \frac{A \cdot n \cdot \hat{E}(s)}{2 \cdot L \cdot ESW \cdot \hat{g}(0)}$$

where:

A is the survey area;

n is the number of sightings;

$\hat{E}(s)$ is the estimated mean group size of observed groups;

L is the total trackline length;

ESW is the estimated effective strip width; and

$\hat{g}(0)$ is the estimated detection probability on the trackline (assumed to be 1).

Data analysis was performed using the software *Distance* 5.1 (Thomas *et al.*, 2006). Perpendicular distances were truncated at 3 n.mile and the effective search width was estimated by fitting half-normal and hazard-rate models to the data. Cosine and hermite polynomial series expansions for half-normal function, and cosine and simple polynomial adjustments for hazard-rate were also considered in the set of candidate models. Beaufort sea state was included as a covariate aiming at assessing its potential effects of on the detection probability. The Bayesian Information Criterion (BIC) and Goodness of fit tests were used to select the model that best fit the data.

RESULTS

Encounter rate

Total observation effort was 140.11 n.mile in the Gerlache Strait and 313.80 n.mile in the Bransfield Strait. Encounter rate was higher in the Bransfield Strait (n = 100; 0.32 groups n.mile^{-1}; 95% CI: 0.26–0.39) than in the Gerlache Strait (n = 33; 0.24 groups n.mile^{-1}; 95% CI: 0.13–0.44), though the difference was not statistically evident due to the complete overlap of confidence intervals. Mean group size for the Bransfield Strait (1.87; SE = 0.09) was slightly higher than for the Gerlache Strait (1.67; SE = 0.19). Modal group size was two individuals in both areas.

Table 1

Estimated model parameters: *ESW* = effective strip width (in n.miles); *n/L* = encounter rates; DS = density of groups (groups n.mile^{-2}); *E*(*S*) = mean group size; D = density of individuals (whales n.mile^{-2}); *N* = abundance in the Bransfield Strait.

Parameter	Point estimate	SE	%CV	95%CI
f(0)	0.61	0.05	8.35	0.52–0.72
ESW	1.65	0.14	8.35	1.40–1.94
n/L	0.32	–	10.24	0.26–0.39
DS	0.10	0.01	13.21	0.07–0.13
E(*S*)	1.87	0.09	5.02	1.69–2.07
D	0.18	0.03	14.13	0.14–0.24
N	865	–	14.13	656–1,141

Abundance

The half-normal model without adjustments resulted in the best fit to perpendicular distance data (χ^2 = 5.95; d.f. = 6; p = 0.428). The distribution of perpendicular distances and the fitted detection function are presented in Fig. 2. Abundance was estimated at 865 (95% CI = 656–1,141; CV = 14.13) humpback whales in the Bransfield Strait. Model parameters, density and abundance estimates are shown in Table 1.

DISCUSSION

Encounter rate

Encounter rates of humpback whales were high in both the Gerlache and Bransfield Straits. Surveys were conducted during humpback whale peak density in the region (see Secchi *et al.*, 2001). Despite some intra and interannual variation, humpback whale density is always relatively high in the Gerlache Strait (Secchi *et al.*, 2002; 2001). These authors found that encounter rates of humpbacks whales in this area were higher than in any other of the surveyed areas in the vicinity of the Antarctic Peninsula. Nevertheless, the encounter rate of humpback whales in the Gerlache Strait in this survey was similar to those obtained during years of suspected lower density of the species in this area (see Dalla Rosa *et al.*, 2005; Marques, 2003; Secchi *et al.*, 2001). Photo-identified individuals have been re-sighted on several

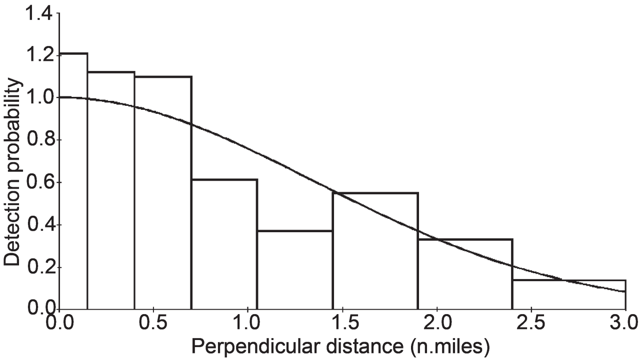

Fig. 2. Half-normal model without adjustment fit to perpendicular distances of humpback whales.

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[1] Errata. 1998. *Mar. Mammal Sci*. 14(4):903

occasions, both within and between seasons in the Gerlache Strait (Dalla Rosa *et al.*, 2004; 2001). One of two humpback whales satellite tagged in the area in the 2004 austral summer remained in the Gerlache area, including the adjacent Dallman Bay, for more than two months, until the tag batteries probably failed (Dalla Rosa *et al.*, 2008). This provides evidence that the Gerlache Strait is an important feeding ground for humpback whales in the Antarctic Peninsula area. The northern part is generally more productive and the humpback whale density is higher than the southern part of Gerlache Strait (Dalla Rosa *et al.*, 2005). Four whales tagged in the summer of 2006 moved from the Gerlache Strait to the Bransfield Strait within a week (Dalla Rosa *et al.*, 2008), which coincides with the higher encounter rate in the Bransfield Strait. The close proximities of the northern Gerlache and Bransfield Straits might suggest that environmental factors influence both areas similarly. These two areas are influenced by cold deep water masses from the Weddell Sea and warmer waters from the Bellingshausen Sea. Zooplankton sampling around the Antarctic Peninsula found the highest krill biomass in Gerlache and Bransfield Straits (Montu *et al.*, 1994). The seasonal input of nutrients and minerals coincides with blooms of phytoplankton in these areas (Bathmann *et al.*, 1997; Loescher *et al.*, 1997).

Abundance

No previous abundance estimates were available for the Bransfield Strait as it was the first time a good proportion of the strait could be surveyed within the PROANTAR expeditions. Although the Bransfield Strait is an important concentration area and perhaps, together with the Gerlache Strait, is among the most important humpback whale feeding grounds around the Antarctic Peninsula (see Secchi *et al.*, 2001), the abundance estimate presented here represents probably a very small fraction of breeding Stock G. Because of navigational restrictions, part of the Bransfield Strait was not surveyed. The density was extrapolated only to a surveyed area of approximately 4,780 n.mile^2. The total Bransfield area is almost twice as large as the surveyed area (approximately 8,085 n.mile^2). The detection probability, assumed to be one, might have caused a slightly underestimation of local abundance as some individuals could have been undetected. Detection probability from ship-based surveys was suggested to be very close to one for humpback whales (e.g. Barlow, 1997). The potential under-detection of animals was minimised by allocating higher observation effort in and near the trackline and by using binoculars most of the time. Only 3% of the sightings were made by naked-eye. Beaufort sea state was considered as a covariate to assess its effect in the detection probability, however no improvement was obtained (increased BIC and small reduction in the CV of $f(0)$).

Although there is some evidence that humpback whales are not very abundant eastward of the Peninsula (e.g. Secchi *et al.*, 2001), they seem to be fairly abundant further south of the Gerlache Strait towards Marguerite Bay, in the Bellingshausen Sea (Secchi *et al.*, 2001; Thiele *et al.*, 2004). A humpback whale satellite tagged in the Gerlache Strait in the 2004 austral summer moved north to the Bransfield Strait (near Deception Island) and then made a long southward movement in the Bellingshausen Sea until the tag stopped transmitting, when the whale was in the vicinity of Marguerite Bay (Dalla Rosa *et al.*, 2008). Another whale tagged in the 2006 austral summer in the Gerlache Strait also moved to the Marguerite Bay area after spending some time in the Bransfield Strait (Dalla Rosa *et al.*, 2008). Although it is assumed here that humpback whales feeding off the Antarctic Peninsula region represent only individuals from Breeding Stock G, their distribution range in the feeding ground is poorly known, therefore, the size of the unsurveyed fraction remains to be determined. Furthermore, there is recent evidence that a small proportion of Stock G does not migrate to the Antarctic, remaining in the Magellan Strait and Fuegian Channels, considered an alternative feeding ground for part of Stock G (Acevedo *et al.*, 2007). Likewise, abundance estimates for Stock G in its breeding grounds are restricted to relatively small areas (e.g. Castro and González, 2002; Felix *et al.*, 2005; Scheidat, 2001). Consequently, the total abundance of Stock G remains unknown. More comprehensive surveys westward of the Peninsula including the eastern Bellingshausen Sea, Gerlache-Bransfield areas and Marguerite Bay are therefore recommended.

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Migration and summer destinations of humpback whales (*Megaptera novaeangliae*) in the western South Atlantic Ocean

Alexandre N. Zerbini[*, +], Artur Andriolo[*, #], Mads Peter Heide-Jørgensen[^], Sergio C. Moreira[*], José Luis Pizzorno[*], Ygor G. Maia[*], Glenn R. VanBlaricom[~] and Douglas P. DeMaster[++]

Contact e-mail: alex.zerbini@noaa.gov

ABSTRACT

Southern Hemisphere humpback whales (*Megaptera novaeangliae*) migrate from wintering grounds in tropical latitudes to feeding areas in the Antarctic Ocean. In 2003 and 2005, satellite transmitters were deployed on humpback whales on their wintering grounds off the eastern coast of South America (Breeding Stock A). Seven whales were tracked for a period of 16 to 205 days travelling between 902 and 7,258km. The tracks of these whales provided partial or full information on the migratory schedule, migration routes and location of the feeding ground in the Southern Oceans. Whales departed from the coast of Brazil from late October to late December between 20˚ and 25˚S and gradually moved away from the South American coast as they moved towards high latitudes. They followed a somewhat direct, linear path, with an approximate geographic heading of 170˚. Satellite telemetry data indicated that the migratory corridors are restricted to a relatively narrow (~500–800km) strip in the South Atlantic Ocean. Migration speed to the feeding grounds averaged 80.2km/day and lasted from 40–58 days. Four individuals arrived at the feeding ground located to the north of the South Sandwich Islands, where they were tracked up to 102 days. Movements in this area were erratic at a mean travelling speed of 22.3km/day. Satellite telemetry data indicate that the main feeding grounds for the population wintering off eastern South America lie between 22˚W and 33˚W and in the southern South Atlantic Ocean south of the Antarctic Convergence but north of 60˚S. This is only partially consistent with the currently proposed stock boundaries for this population on the feeding grounds.

KEYWORDS: HUMPBACK WHALE; MOVEMENTS; MIGRATION; FEEDING GROUNDS; SATELLITE TELEMETRY; SOUTH ATLANTIC OCEAN; SOUTHERN HEMISPHERE

INTRODUCTION

Seasonal migration between winter/breeding and summer/feeding areas is typical of humpback whales (*Megaptera novaeangliae*) (Clapham and Mead, 1999). In the Southern Hemisphere most populations migrate from coastal, low-latitude regions where mating and calving occur, to Antarctic waters for feeding (e.g. Dawbin, 1966; Mackintosh, 1942). The stock inhabiting the western South Atlantic Ocean (WSA) has been termed Breeding Stock ‘A’ (BSA) by the International Whaling Commission (IWC, 1998). The wintering grounds of this population are relatively well known; whales occur in the winter and spring off the coast of Brazil between the northeastern tip of the South American continent (~5˚S) south towards Cabo Frio (23˚S) (Andriolo *et al.*, 2010; Martins *et al.*, 2001; Pizzorno *et al.*, 1998; Zerbini *et al.*, 2004b). Despite this relatively wide latitudinal range, nearly 85% of the population is concentrated in the Abrolhos Bank (~18˚30’S, 38˚30’W) (Andriolo *et al.*, 2010; Siciliano, 1995).

The migration routes and feeding grounds of BSA are poorly known. Until recently, there was no evidence of the migratory destinations of whales wintering off eastern South America. Historically, it was suggested that this population migrated to areas near the Antarctic Peninsula (AP) (~60˚S, 64˚W) and/or South Georgia (SG) (54˚20’S, 36˚40’W) and the Scotia Sea, in the Antarctic sector of the Atlantic Ocean (Mackintosh, 1965; Slijper, 1962; 1965; Slijper and Utrecht, 1959). Studies involving Discovery marks, sighting surveys, photo-identification and molecular genetics conducted on the presumed feeding grounds of BSA (e.g. Moore *et al.*, 1999; Rayner, 1940; Rosenbaum *et al.*, 2000; Stevick *et al.*, 2004), were unable to provide evidence that whales using these regions actually migrated to eastern South America. The first migratory connection between wintering and summering grounds of whales from BSA was obtained in 2003/04 when two individuals monitored by satellite telemetry migrated from the coast of Brazil to offshore waters to the northeast of SG and to the South Sandwich Islands (SSIs) (Zerbini *et al.*, 2006). Subsequently, individuals photo-identified near Shag Rocks (53˚33’S, 42˚02’W), to the west of SG, and near the SSI, were matched with whales wintering off Brazil (Engel and Martin, 2009; Stevick *et al.*, 2006).

In 2005, new satellite transmitters were deployed off the coast of Brazil. This paper combines data from the 2003 and 2005 satellite tagging seasons and provides additional information on the migratory routes and summer destinations of humpback whales in the western South Atlantic Ocean.

METHODS

Field work was conducted in October 2003 and 2005 off the eastern coast of Brazil, in the southern portion of the Abrolhos Bank. In 2003 and 2005, tagging operations were carried out, respectively, from Conceição da Barra (18˚30’S, 39˚30’W), Espírito Santo State (ES), and from Nova Viçosa (17˚53’S, 37˚22W), Bahia State (BA). Daily searches for humpback

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[*] *Projeto Monitoramento de Baleias por Satélite, Instituto Aqualie, R. Edgard Werneck 428/32, Rio de Janeiro, RJ, 22763-010, Brazil.*

[+] *National Marine Mammal Laboratory, Alaska Fisheries Science Center, NOAA Fisheries, 7600 Sand Point Way NE, Seattle, WA, 98115-6349, USA.*

[#] *Departamento de Zoologia, Instituto de Ciências Biológicas, Universidade Federal de Juiz de Fora, MG, Brazil.*

[^] *Greenland Institute of Natural Resources, Box 570, DK-3900 Nuuk, Greenland.*

[~] *Washington Cooperative Fish and Wildlife Research Unit, School of Aquatic and Fishery Sciences, University of Washington, Box 355020, Seattle, WA, 98195-5020, USA.*

[++] *Alaska Fisheries Science Center, NOAA Fisheries, 7600 Sand Point Way NE, Seattle, WA, 98115-6349, USA.*

whales were undertaken during good weather conditions (Beaufort Sea state ≤3) from a 10m-long fibreglass speedboat and two inflatable boats. Transmitter models and configurations differed between the two seasons. In 2003, 'can' ($n = 7$) and 'implantable' ($n = 4$) version of the Wildlife Computers (WC) SPOT 3 transmitters were used (Zerbini *et al.*, 2006). In 2005, only implantable versions of the WC SPOT 5 transmitter were available in two configurations: the 'short implantable' ($n = 13$), with the same dimensions as for the transmitters used in 2003 and a 'long implantable' ($n = 2$), which accommodated an additional AA-cell. Deployment of the tags, biopsy sample collection, and data analysis followed the methods described by Heide-Jørgensen *et al.* (2006) and Zerbini *et al.* (2006). Biopsies were used for DNA extraction and sex determination of each individual as described by Bruford *et al.* (1992) and Bérubé and Palsbøll (1996).

Locations were obtained from Service Argos, Inc. (ARGOS, 1990). Location quality (LC) was coded A, B, 0, 1, 2 or 3 in increasing order of position accuracy. Positions 1 to 3 are presumably of higher accuracy. Service Argos (1990) predicts that 68% of classes 1, 2, and 3 are within 1.0, 0.35, and 0.15km, respectively. Argos does not provide error predictions for location classes 0, A, and B, but errors may range from 3.8km (LC 0) to 23km (LC B) (e.g. Boyd *et al.*, 1998). Distance and rate of travel for each whale was calculated using daily average positions as described in Zerbini *et al.* (2006). Movement was monitored after tag deployment while whales were still on the wintering grounds, but in this paper, only data from whales tracked during part of or the total spring migration, and while on the summer feeding grounds are included. Table 1 summarises information on transmitter configuration and duty cycling for these individuals.

The regions where whale locations were received are categorised by 'wintering ground', 'feeding grounds' and 'migratory corridors'. The wintering ground is defined as the area within the continental shelf (depth <200m) along the Brazilian coast north of 25°S, while the feeding ground is defined as the habitat south of the northern limit of the Antarctic Convergence in the South Atlantic Ocean (~50°S) (e.g. Deacon, 1984). The migratory corridor connects the wintering and the feeding ground.

RESULTS

Seven humpback whales had their migration or partial migration monitored through satellite telemetry (Table 1). Sex identification was obtained through molecular methods for two individuals and was inferred based upon role within the observed group of whales for another five. A total of 1,148 locations were received, tracking days for the whales ranged from 16 to 205 days, and distance travelled varied from 902 to 7,258km (Table 1).

Tracks of the seven individuals monitored during the migration are shown in Fig. 1. Two individuals were monitored for about one quarter to one third of their migration (whales Id no. 27259 [03] and No.26712 [05]). Another (whale Id no. 37274 [05]) was monitored through half of the migration while the remaining four individuals were tracked to the feeding grounds. The migratory path was remarkably consistent among all individuals, irrespective of their departure time and sex. Whales departed from the wintering ground from 19 October to 26 December (Table 1) between the latitudes of 20–25°S. Individuals gradually moved away from the coast of the South American continent as they moved toward higher latitudes. All individuals followed a relatively direct, linear, path with an average geographic heading of 170°. Despite different departure times from the wintering grounds (from late October to late December), some individuals followed almost the same route to their feeding destinations. For example, whale Id no. 10946 (05) left the Abrolhos Bank area nine days before whale Id no. 24641 (05), but their tracks greatly overlapped for nearly half of their migration. Movement rate was also relatively consistent during the migration. Whales travelled at an average rate of 80.2km/day (range = 62.7–92.6km/day) and the migration was completed in an average of 50 days (range = 40–58 days) (Table 2).

Four individuals were tracked to the feeding ground some 3,700km southeast of the wintering grounds (Fig. 1). Arrival was inferred by a change in swimming speed and behaviour in which the linear direction and relatively fast rate of movement was replaced by a slower, more erratic movement pattern. The average speed of travel (22.3km/day, range = 18.0–29.1km/day, Table 2) of whales tracked on the feeding grounds was much lower than in the migratory corridor. This change in behaviour occurred when humpback whales were just south of 50°S, a region regarded to correspond to the northern boundary of the Antarctic Convergence (Deacon, 1984). Whales remained in offshore waters 250–750km northeast of SG and 300km north of the SSIs, in a region bounded by the 51° and the 55°S parallels and the 22° and the 33°W meridians (Fig. 1). Whale Id no. 21810 (03) was tracked for only six days (late December and early January) after its arrival on the feeding grounds, but the remaining individuals were monitored for another 36–102 days. Whale

Table 1

Whales tracked through satellite telemetry in the western South Atlantic Ocean in 2003/04 and 2005/06.

Whale ID no. (year)	Sex	Duty cycling	Daily transmission allowance	Transmission time	Tagging date	Tag longevity (days)	No. of locations received	Distance traveled (km)
21810 (03)	M	eod[2]	300	6–21hr	18 Oct 2003	76	84	4,383
24642 (03)	F[1]	eod	300	6–21hr	27 Oct 2003	205	624	7,258
27259 (03)	M	none	300	6–21hr	19 Oct 2003	39	51	2,315
10946 (05)	F[1]	Oct/Nov – eod, Dec/Jul – e4d[3]	300	7–22hr	19 Oct 2005	80	150	4,895
24641 (05)	F[1]	Oct/Nov – none Dec/Jul – e4d	300	7–22hr	19 Oct 2005	112	185	5,023
26712 (05)	F[1]	Oct/Nov – none Dec/Jul – e4d	300	7–22hr	11 Oct 2005	16	27	902
37234 (05)	F[1]	Oct/Nov – eod, Dec/Jul – e4d	300	0–23hr	19 Oct 2005	32	27	3,445
Total						560	1148	28,221

[1] Assumed to be a female because it was the adult individual in a cow-calf pair; [2] eod = every other day; [3] e4d = every fourth day.

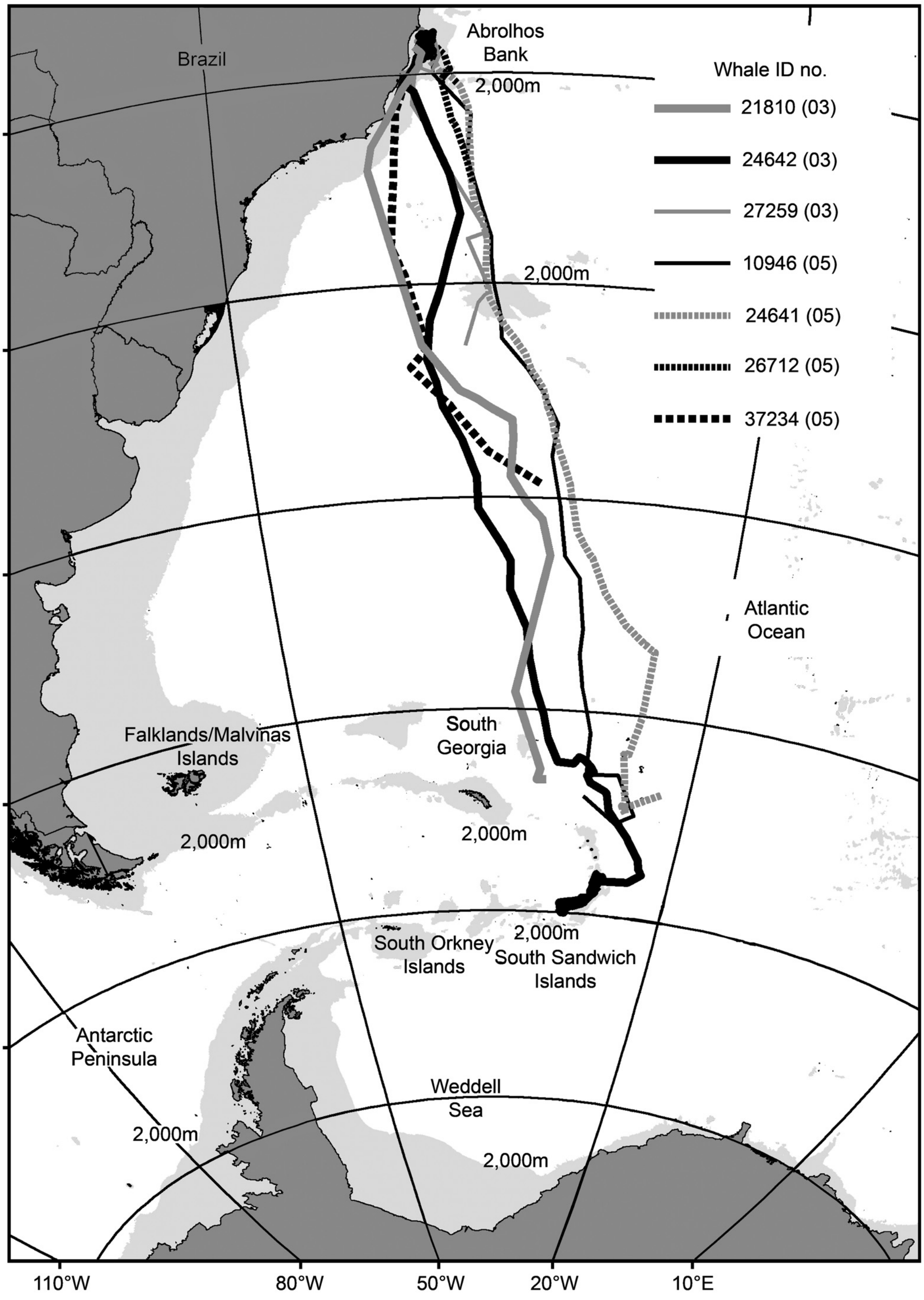

Fig. 1. Southbound migratory routes and summer destinations of humpback whales in the western South Atlantic Ocean.

Id no. 10946 (05) and Id no. 24641 (05) stayed in the same general area, to the north of the SSIs, for the period they were tracked (36–44 days) in the months of December, January and February. Whale Id no. 24642 (03) remained in this same area for about 35 days, after its arrival in February. Subsequently, in March, it moved southeast, and finally moved back west towards the SSIs. This individual remained in the southern sector of the Islands for about 68 days (from mid March to mid May), until transmissions ceased.

DISCUSSION

Migratory schedule, routes and summer destination of whales monitored during the 2003–2004 season were described by Zerbini *et al.* (2006), but sample size was relatively small. The migration of three new individuals was monitored in 2005–2006, but only two were tracked until they reached the feeding ground. The partial or full migration of the additional whales reported here is consistent with and strengthen the conclusions of the previous study. Results confirm that departure from the wintering grounds occur when whales move south of the Abrolhos Bank and along the southeastern coast of Brazil between 20° and 25°S. Despite within-season differences in the onset of the southbound migration, the migratory schedule, path and destination was remarkably consistent among individuals. Departure dates from the wintering ground ranged over a period of two months and none of the whales monitored

Table 2

Travelling distances and movement speed of humpback whales on their migratory routes and feeding grounds in the southwest Atlantic Ocean.

	Migratory corridor				Feeding grounds			
Whale ID no. (year)	Departure date	Distance travelled (km)	Days monitored	Average speed	Arrival date	Distance travelled (km)	Days monitored	Average speed
21810 (03)	31 Oct 2003	3,639	58	62.7 km/day	28 Dec 2003	108	6	18 km/day
24642 (03)	26 Dec 2003	3,733	44	84.8 km/day	8 Feb 2004	2,376	102	23.3 km/day
27259 (03)	9 Nov 2003	1,507	18	83.7 km/day	–	–	–	–
10946 (05)	23 Oct 2005	3,691	40	92.3 km/day	2 Dec 2005	1,048	36	29.1 km/day
24641 (05)	30 Oct 2005	3,692	57	64.8 km/day	26 Dec 2005	817	44	18.6 km/day
26712 (05)	19 Oct 2005	727	9	80.7 km/day	–	–	–	–
37234 (05)	23 Oct 2005	2,317	25	92.6 km/day	–	–	–	–
Average				80.2 km/day				22.3 km/day

travelled together. However, their tracks intersected to a great extent, never being more than 800km apart, and usually much less (300–500km). Migration occurred through deep offshore waters in the WSA and the direction of migration (geographic bearing) and rate of travel were also relatively similar across all whales.

Migratory routes between wintering and feeding grounds of BSA humpback whales remained questionable for nearly 100 years. Two main hypotheses were previously proposed: (1) whales migrated to/from the Antarctic Peninsula (AP) and perhaps the Falkland Islands from/to the eastern coast of South America using coastal waters over the continental shelf (Slijper, 1962; Slijper and Utrecht, 1959); and (2) whales migrated through deep waters from/to tropical latitudes off eastern South America to/from feeding grounds near SG and SSIs (Mackintosh, 1965; Slijper, 1962; 1965). Migratory connections had been proposed based on the coincidental collapse of humpback whaling in the AP, SG and eastern South America in the early 1900s (IWC, 2005) and as an analogy with other Southern Hemisphere humpback whale populations, which seemed to migrate to feeding areas located directly south of their wintering grounds (Dawbin, 1966; Mackintosh, 1942).

Results of telemetry studies were consistent with hypothesis (2) above. Individuals monitored through satellite telemetry migrated to offshore areas in the WSA and the four individuals tracked while in the feeding grounds arrived and remained in waters near SG and the SSI (Zerbini *et al.*, 2006, see Results). This migratory connection was subsequently supported by photo-identification studies. Stevick *et al.* (2006) reported that a whale photographed in December 2004 near Shag Rocks, west of SG, had been previously recorded in August 2000 in the Bank of Abrolhos. In addition, three individuals photographed near the SSIs in January 2006 had also been seen in Brazil, one in each of the years 1999, 2001 and 2002 (Engel and Martin, 2009). Existing data provided little support for the hypothesis that humpback whales wintering off Brazil migrate through coastal waters to the AP. In fact, extensive photo-identification and genetic studies have shown that whales feeding near the Peninsula migrate to the western coast of South America (Olavarria *et al.*, 2007; Rasmussen *et al.*, 2007; Stevick *et al.*, 2004). In addition, humpback whales are rare in coastal waters over the continental shelf south of the wintering grounds in Brazil (e.g. Zerbini *et al.*, 2004a), or in Uruguay and Argentina (Bastida and Rodriguez, 2005; Lichter, 1992).

Certainly, SG was an important historical feeding ground (see Findlay, 2001; Tønnessen and Johnsen, 1982). Humpback whales were heavily exploited in the vicinities of the island (over 25,000 individuals were taken there between 1904 and 1916, Allison, 2006), causing a rapid collapse of this population. Contemporary data indicate that the species has not recovered on the former whaling grounds in coastal waters near SG (Moore *et al.*, 1999, A.R. Martin, pers. comm.). This contrasts with the relatively high abundance of humpback whales off Brazil and provides additional evidence that whales from this population migrate elsewhere, as shown by satellite telemetry. Reasons for low densities of humpback whales in the former whaling grounds of SG are not known, but may be related to complete extirpation of the population using those nearshore waters, competition with other krill predators and/or shifts in distribution resulting from temporal changes in environmental conditions in nearshore waters off SG (Clapham *et al.*, 2008; Zerbini *et al.*, 2006).

All the individuals monitored to the feeding ground migrated to open ocean waters in a region located to the northeast of SG and north of SSI (between approximately 51–55˚S, 22–33˚W; Fig. 1). Whales remained in this area between December and February. Geographical and monthly distribution of these individuals overlapped with existing Soviet catch data from the late 1960s (Mikhalev, 1998; Zemsky *et al.*, 1995) and with sighting data from the 1980–2000s (Hedley *et al.*, 2001; Kasamatsu *et al.*, 1996; Reilly *et al.*, 2004). Consistency among catch, sighting and telemetry data provides strong evidence that the primary feeding ground of humpback whales wintering off Brazil is located to the north of the SSIs from December to February. Except for one individual, locations were not received from whales later in the summer and therefore information on whether whales remain in this area or move to other possible feeding areas explored by whales from BSA is relatively limited. Interestingly, the only whale tracked during late summer and part of autumn (Whale Id no. 24642 [03]) left the area to the north of SSIs in early March, moving southwest and then east towards the South Sandwich Archipelago, where it stayed until May (Fig. 1). This whale departed from the wintering ground (in late December) and arrived on the feeding ground much later (in early February) than the other three individuals. It is unclear what caused this shift in habitat, but one possibility is that foraging opportunities further north are reduced later in the season, forcing whales to look for areas closer to the ice edge, where food availability may be greater.

Despite being monitored for 35–102 days while on the feeding ground, none of the whales moved further south than 60˚S. This suggests that most individuals of this population do not venture into the Weddell Sea and adjacent areas. This is further supported by contrasting estimates of abundance on the feeding grounds south of 60˚S and those obtained on wintering grounds. The abundance in 1997/98 south of 60˚S was estimated to be 200 (CV = 0.64) whales on the feeding ground presumed to be occupied by BSA whales (3rd circumpolar survey of the IDCR/SOWER surveys; Branch, 2011). If a growth rate of ~7%/year is assumed for this stock (Ward *et al.*, 2011), the population size south of 60˚S in 2005 should be nearly 350 whales. This number does not match the much higher abundance estimate of 6,400 (CV = 0.12) whales on the wintering ground off the Brazilian coast (Andriolo *et al.*, 2010), indicating that the majority of the population is likely distributed further north.

Understanding movements and habitat use of whales is important to better define stock structure. The IWC Scientific Committee proposed a number of core feeding grounds associated with the various Southern Hemisphere humpback whale breeding stocks for management and catch allocation purposes (IWC, 1998; 2006). The northern and southern boundaries of these feeding grounds are the 40˚S parallel and the Antarctic continent, respectively. Longitudinal boundaries are vertical lines placed at different meridians. Originally, longitudinal boundaries of the feeding grounds associated with BSA corresponded to the 70˚W meridian in the west and the 20˚W meridian in the east (IWC, 1998). These boundaries encompassed former humpback whaling grounds in the AP, Weddell Sea and the Scotia Sea (SG, SSIs and the South Orkney Islands). The western boundary was shifted to 60˚W once it became clear that humpback whales feeding along the Antarctic Peninsula used the breeding grounds in the eastern South Pacific (Breeding Stock G-BSG) (IWC, 2001; Stevick *et al.*, 2004). Subsequently, it was shown that whales photographed west of 55˚S were also associated with the AP (Dalla Rosa *et al.*, 2004; Stevick, 2005) and the western boundary was changed to its current position at 50˚W (IWC, 2006).

Information presented in this study partially supports the current boundaries of the feeding grounds associated with BSA. Telemetry data indicated that humpback whales wintering off Brazil migrated to the eastern Scotia Sea and remained between the latitudes of 54˚S and 60˚S and the longitudes of 22˚W and 33˚W for the period they were monitored (Fig. 1). This is consistent with an eastern boundary of 20˚W (IWC, 1998; 2006), but provides little evidence to support a western 50˚W boundary. Perhaps more importantly, however, was the finding that no whales moved south of 60˚S, suggesting that humpback whales from BSA may not venture into the higher latitudes of the Antarctic Ocean and Weddell Sea. Results from satellite telemetry were further corroborated by photo-identification. Photographic matches also indicated whales from BSA were using the SSIs during the summer (Engel and Martin, 2009). In addition, the re-sighting of a whale previously seen in Brazil and later photographed near Shag Rocks (53˚33'S 42˚02'W) (Stevick *et al.*, 2006) indicated that at least some individuals from BSA also occurred west of SG, but still nearly 500km to the east of 50˚W. Photo-identification and telemetry studies also indicated that some individuals summering near the AP (BSG) ventured into waters near or west of the current western boundary of BSA (Dalla Rosa *et al.*, 2004; 2008). A whale photographed to the southeast of the South Orkney Islands (at the position 61˚50'S, 38˚48'W) was observed a year later just to the northeast of the Antarctic Peninsula (at the position 62˚11S, 52˚51'W) (Dalla Rosa *et al.*, 2004; 2008). In addition, an individual tagged off the western AP (Gerlache Strait, ~64˚S, 61˚W) moved northeast to the pack-ice in the Weddell Sea (~63˚S) close to the 50˚W meridian (Dalla Rosa *et al.*, 2008).

Although additional studies are clearly needed due to relatively low research effort and small sample sizes, the above data provide preliminary evidence that a review of the boundary between the feeding grounds associated with BSA and BSG (50˚W) is needed (see also discussion by Dalla Rosa *et al.*, 2008). In addition, and perhaps more importantly, these data indicate the potential for a latitudinal separation of whales from these two stocks. Whales from BSA were not photographed or tracked south of ~60˚S, whereas individuals from the AP moving into the Weddell Sea area were only seen south of ~62˚S. Further studies will allow a better description of the areas used by whales from BSA and BSG in their feeding grounds and a more precise description of stock structure in the Antarctic sector of the South Atlantic Ocean.

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Exploring the assumptions of multi-stock assessment models for humpback whales (*Megaptera novaeangliae*) in the Southern Hemisphere: using Breeding Stocks D and E as an example

REBECCA LEAPER*#, SAMANTHA PEEL*, DAVID PEEL+ AND NICK GALES*

Contact e-mail: rebecca.leaper@utas.edu.au

ABSTRACT

There is potential value in exploring multi-stock models to address situations where humpback stocks are mixing. However, sensitivity to the assumptions underlying these models has yet to be fully explored. Using a simple simulation approach, the assumptions of a population model that allows for mixing of humpback whale (*Megaptera novaeangliae*) stocks D and E on feeding areas has been explored by relaxing the assumptions of the original Johnston and Butterworth model in a number of plausible ways. First the ability of the model to estimate parameters was checked for a situation where simulated data are generated from an underlying model of exactly the same form for which the actual values of these parameters are known (Scenario 1). Then the ability of the model to estimate these parameters when alternative forms and assumptions were used for the underlying model generating the data was investigated. Specifically, stocks were allowed to mix non-uniformly across each feeding area and catch was non-uniformly distributed across each feeding area (Scenario 2). The consequences of density dependence implemented on feeding rather than breeding areas (Scenario 3) were also examined. The original mixing model was robust to alternate mixing and catch allocation scenarios in all but one of the simulations, but when density dependence acted at the level of the feeding rather than the breeding areas, the model produced estimates that were quite different from the underlying population. It is recommend that the inclusion of density dependence on feeding areas in models that allow for mixing of whales on these grounds be investigated further.

KEYWORDS: HUMPBACK WHALE; ASSESSMENT; MIXING; CATCH ALLOCATION; DENSITY DEPENDENCE; SIMULATION; MODELLING

INTRODUCTION

The IWC Scientific Committee (SC) has been involved in the Comprehensive Assessment (CA) of Southern Hemisphere humpback whales (*Megaptera novaeangliae*) each year since 2000 (IWC, 2001). To date, assessments have been based on an age-aggregated production model (IWC, 1998) using either maximum likelihood estimation (e.g. Findlay *et al.*, 2000), or more recently Bayesian estimation (e.g. Zerbini, 2005). In addition, assessments have been based on breeding rather than feeding stocks (IWC, 1998), of which there are currently seven putative stocks termed A to G (IWC, 2005; fig. 1 of IWC, 2011, p.3) and have proceeded on the basis of alternative plausible scenarios of catch allocations to these breeding areas (e.g. Johnston and Butterworth, 2004).

In an effort to complete the CA of Southern Hemisphere humpback whales, an intersessional meeting was held in 2006 to review and update the historical catch record, as well as reviewing stock structure information and stock specific abundance and trend estimates. An important task was to consider how this new information could be used to parameterise the age-aggregated production model currently used for the assessment of each breeding stock and whether this model would require modification with respect to the following issues: (1) the allocation of feeding area catches to breeding stocks, notably when mixing of two or more breeding stocks on a feeding area is suspected; (2) the treatment of abundance estimates from the feeding areas when allocation of animals to breeding areas is uncertain; (3) the treatment of possible substructure in the breeding areas; and (4) the incorporation of demographic parameters not typically included in modelling (e.g. depensation).

The review revealed that the knowledge and level of confidence associated with humpback whale stock structure concepts varies considerably across the Southern Hemisphere. In some areas (e.g. Breeding Stock A and Area II), the connections between breeding and feeding areas and the structure within these is reasonably well understood. Here a single breeding stock is connected with a single feeding area. In others (e.g. Breeding Stocks B, C, E and F), there is considerable unresolved complexity and insufficient data to discriminate among a variety of stock structure hypotheses. At one extreme there is substantial substructure within breeding areas (i.e. stocks B and C) and there is also mixing of stocks on feeding areas but probably little exchange between breeding areas (i.e. stocks D and E); at the other extreme there is both substructure within a breeding stock, and mixing of stocks on both feeding and breeding areas (i.e. stocks E and F). Under any one of these stock structure scenarios, it is virtually impossible to provide reliable data (e.g. absolute abundance estimates, abundance trends and historical catch) for assessment models, and model runs based on alternative plausible scenarios for input data have, as yet proved unsatisfactory (IWC, 2011). The issue of how the assessment can best be completed, given such complex stock structure therefore remains an outstanding task.

One possible approach to this problem is to adopt a framework that allows for some degree of stock complexity

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* *Australian Marine Mammal Centre, Australian Antarctic Division, Department of Sustainability, Environment, Water, Population and Communities, 203 Channel Highway, Kingston 7050, Tasmania, Australia.*

Institute of Marine and Antarctic Studies, University of Tasmania, Private Bag 49, Hobart, TAS 7001, Australia.

+ *CSIRO Mathematical and Information Sciences, GPO Box 1538, Hobart, Tasmania 7001, Australia.*

in the model itself. In the North Atlantic, where humpback whales feed in discrete aggregations but mix on breeding areas, multi-stock models have already been used for assessment (Friday *et al.*, 2001). For Southern Hemisphere humpback whales, a similar multi-stock approach has been used to assess stocks D and E (West and East Australia) (Johnston and Butterworth, 2002; Johnston and Butterworth, 2005a; Johnston and Butterworth, 2005b), but these models have not yet been fully explored under the CA. In part this reflects the ongoing debate as to the extent to which stocks D and E mix on their feeding areas. Thus further exploration of multi-stock models and the underlying assumptions of such models may at the very least inform further model development, and at most, hopefully advance the assessment of populations with more complex stock structures. As a first step towards this goal, the assumptions underlying the model framework used by Johnston and Butterworth (2002) to assess Breeding Stocks D and E, are explored in this paper using a simple simulation approach. The sensitivity of the Johnston and Butterworth (2002) mixing model to its assumptions is explored when these are relaxed in a number of plausible ways, and in particular explore the consequences of alternate mixing, catch allocation and density dependence scenarios. The aim is not to present an assessment of Breeding Stocks D and E, but simply to use these stocks as a case study to explore the consequences of these alternative assumptions.

The Johnston and Butterworth mixing model and its underlying assumptions

The multi-stock model developed by Johnston and Butterworth (2002) is an extension of the basic age-aggregated production model (IWC, 1998) used in the single stock case. It allows two breeding stocks to mix on feeding areas such that catches taken in the feeding areas are apportioned to each breeding stock relative to the numbers present in that feeding area. The model makes a number of assumptions: (1) mixing of two breeding stocks occurs uniformly within two feeding areas; (2) historic catch is distributed uniformly within these two feeding areas; and (3) density dependence impacts whales on the breeding areas. Data from Breeding Stocks D and E were used as inputs to the model, having been updated for subsequent model runs (Johnston and Butterworth, 2005a; 2005b).

Humpback whales that breed close to the west (stock D) and the east coast (stock E) of Australia are thought to restrict their feeding to IWC Management Areas IV (70°E–130°E) and V (130°E–170°W) respectively (Fig. 1). However, evidence from a variety of sources suggests that the stocks mix in these feeding areas. Analysis of catch returns taken in areas IV and V throughout the 1950s, supplemented by recoveries of Discovery marks, suggests an exchange of whales across both feeding areas, especially a movement of whales from Breeding Stock E to the feeding areas east of 115°E in Area IV (Chittleborough, 1959; 1965; Dawbin, 1966). More recently, genetic data have lent support this idea, given an instance of a mark-recapture biopsy first sampled in the western part of Area V subsequently re-sampled in the eastern part of Area IV (IWC, 2002). Clues to the historic distribution of humpback whales in Areas IV and V come from the recently updated IWC catch data series (Allison, 2006). It is clear from these data (Figs 1a–c) that the catch for Areas IV and V is not uniformly distributed across these management areas. Sightings data from both the IDCR/SOWER circumpolar cruises and JARPA sightings surveys also suggest that whales are currently encountered more frequently at 20°–40°E, 80°E–100°E, 150°E–180E° and 40°W–70°W (IWC, 2006).

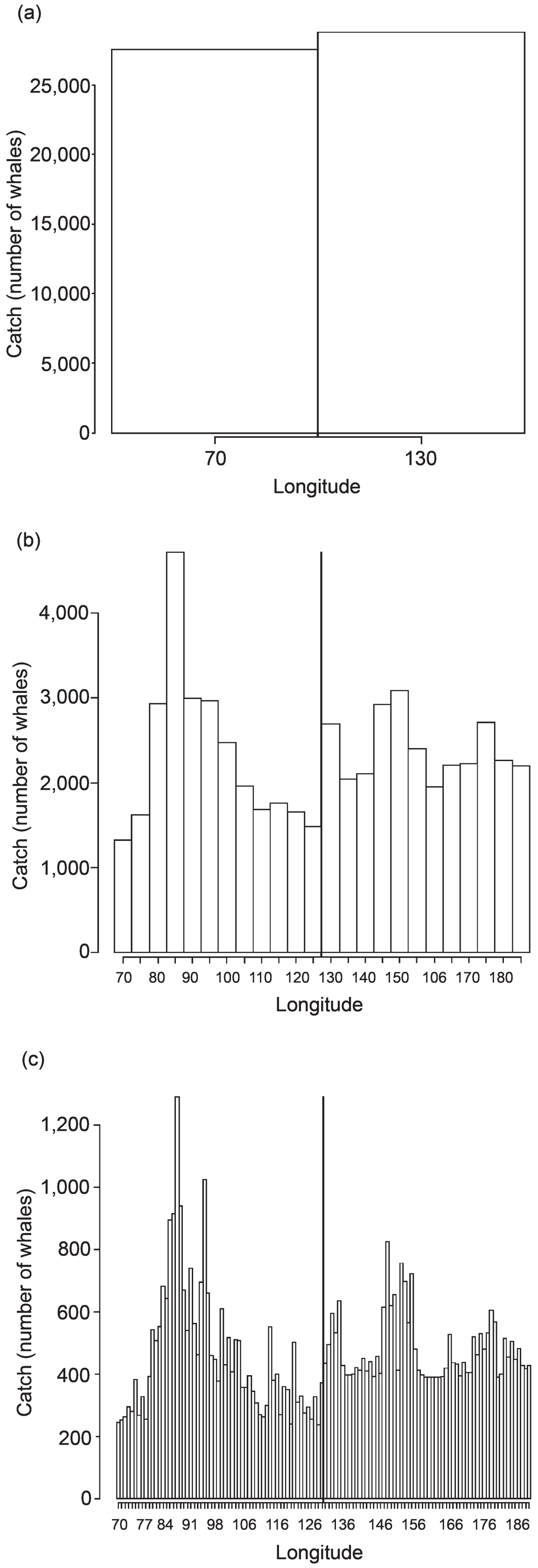

Fig. 1. The distribution of historic catch south of 40ºS by longitude across IWC management areas IV and V, for (a) 2 sub-areas (b) 24 sub-areas and (c) 120 sub-areas.

Alternative specifications for density dependence (e.g. on feeding areas rather than breeding areas) are especially important to consider in cases of models that allow stocks to mix. Under a scenario where only a single stock is being considered (or a scenario when there is no mixing between two stocks), then feeding area density dependence will be equivalent to breeding area density dependence. Furthermore, if the mixing across feeding areas is constrained to be fixed over time then feeding area density dependence will again be no different to breeding area density dependence. However, when the proportions of a stock that move are not fixed through time, breeding area density dependence and feeding area density dependence will not be equivalent. This can be demonstrated by a simplified example. When two stocks (that mix) are both at carrying capacity on a feeding area (i.e. zero net growth) and a large catch is taken from the feeding area of one of the stocks, then under the assumption of feeding area density dependence, both stocks will show an increase the following year. Conversely, when breeding area density dependence is assumed, then only the stock that has a large catch will show an increase as the other stock will still be at carrying capacity. Implementing feeding area density dependence is problematic as it is intrinsically tied to the underlying process of mixing on the feeding area; in the absence of empirical data on whale foraging and movement there may be several plausible hypotheses for the process of mixing. For example, there is evidence to suggest site philopatry on feeding areas for humpback whales where calves learn their feeding ground by accompanying their mothers (IWC, 2002); here mixing is a function of individual whale behaviour. Conversely, whales may have a random probability of feeding in particular areas and hence mixing may be a function of any one of a whole suite of mechanisms related to resource availability and/or foraging strategies.

Objectives

Scenario 1

In order to test sensitivity of estimates from the Johnston and Butterworth (2002) mixing model to alternate mixing, catch allocation and density dependence, a 'base case model' was developed that matched the original model assumptions (Scenario 1). Input data for the Johnston and Butterworth (2002) mixing model were generated using known selected values for the underlying parameters; these values were then compared with estimates obtained by fitting the model to the data generated (Fig. 2). The ability of the model to estimate these parameters from real input data (where the parameter values are unknown) can also then be measured. If comparisons between the simulated 'true population' and that estimated by the Johnston and Butterworth (2002) model outputs are good, it seems that the base case scenario provides a robust benchmark with which to assess alternate scenarios. Because this is a first step towards investigating model assumptions, a full scale simulation approach (i.e. add noise to the input data) was not adopted. Rather, the aim was simply to investigate how well the (Johnston and Butterworth, 2002) mixing model performed, if in 'reality' the population behaved in a more complex way on the feeding areas. Therefore the assessment of alternate scenarios is qualitative only. On this basis a further two different scenarios were examined.

Scenario 2

The original assumption of uniform mixing of two breeding stocks in two feeding (IWC management) areas is relaxed so that stocks now mix non-uniformly across each feeding area. This is implemented by simply: (a) increasing the number of feeding (sub-) areas from 2 to a further 6, 12, 24, 60 or 120 sub-areas across the two (IWC) management areas; and (b) specifying a mixing proportion for each sub-area based on one of two theoretical distributions, defined here as either gamma or highend (see Figs 3a and 4b). The catch is allowed to be distributed non-uniformly across these six sub-areas, again with one of two mixing distributions, either gamma or highend. The combined effect of non-uniform mixing and non-uniform catch produces quite different underlying catch allocations amongst the breeding stocks than Scenario 1 or the Johnston and Butterworth (2002) model.

Scenario 3

In contrast to the Johnston and Butterworth (2002) model, density dependence acts at the level of the feeding areas. Stock mixing and catch allocation are as defined for the original (i.e. base case) model, where mixing and catch are uniformly distributed across two sub-areas.

DATA AND METHODS

Catch data

Stocks D and E were assumed to feed exclusively in both Antarctic feeding areas IV (70ºE–130ºE) and V (130ºE–170ºW), with no humpback whales from other breeding areas feeding in these management Areas. However, the IWC allocation of catch for these stocks (Naïve hypothesis) (IWC, 1998, p.181) corresponds to 60ºE–120ºE (most of Area IV) and 120ºE–170ºW (most of Area V). For each scenario examined, exactly the same catch data as detailed in Johnston and Butterworth (2006) was used, where an *ad hoc* adjustment was made to these catches to make allowance for the extra 10 degrees of the latter set of catches which should correspond to the Area IV catch (see Appendix 1).

Only ~75% of catches in the IWC dataset were however, resolved to the level of individual whale catch location ('individual data'), the remainder being summarised at a much coarser spatial scale ('summary data'). Hence, for the scenario where the two feeding areas were divided into further sub-areas, 'summary data' catches were allocated evenly across the all sub-areas.

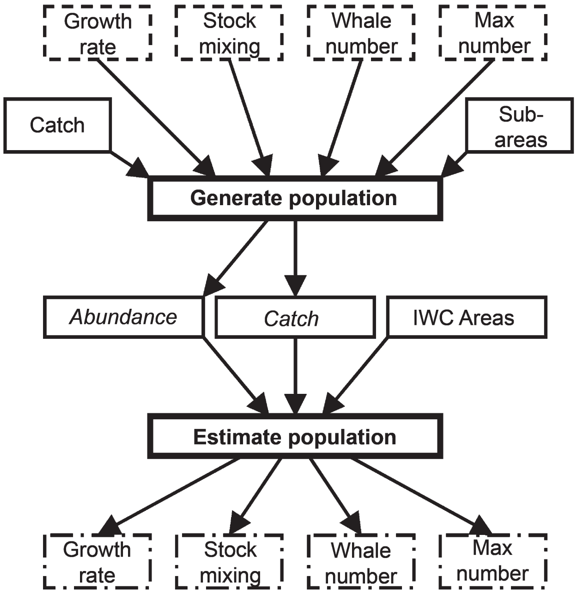

Fig. 2. A schematic of the model simulation process used for the base case and two test scenarios. Values in the dashed boxes are selected by the user and the values in the dot-dashed boxes are model estimates.

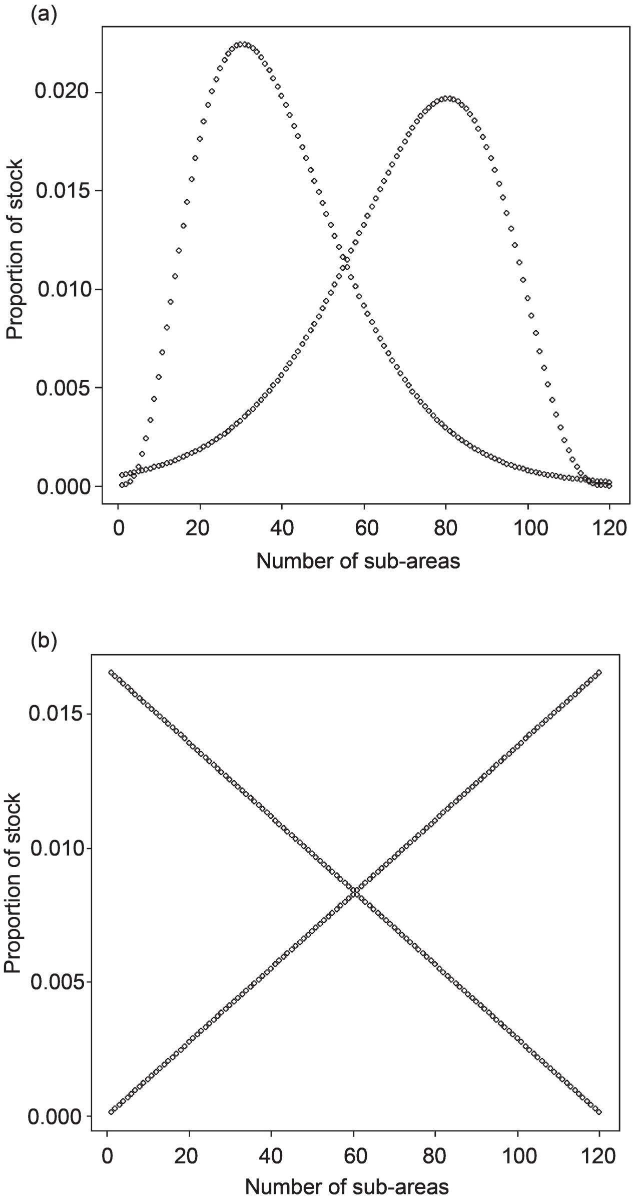

Fig. 3. Spatial distribution of mixing of both stocks in the feeding areas (i.e. proportion of stock in each sub-area) based on (a) gamma distribution and (b) highend distribution.

Population dynamics models

The Johnston and Butterworth (2002) population dynamics model allows for mixing of breeding populations in feeding areas, it takes as input data:

(1) historical catch data for the breeding and feeding areas;
(2) relative abundance estimates for the breeding and feeding areas; and
(3) absolute abundance estimates for the breeding grounds.

The stock growth rates, pre-exploitation abundance (carrying capacity) and proportions (the parameters alpha (α) and beta (β) that drive the mixing across feeding areas) were most recently estimated within a Bayesian framework (Johnston and Butterworth, 2005a; 2005b). For the purposes of this paper the most recent model formulation and fitting procedure, i.e. Johnston and Butterworth (2005a) was used. The likelihood function is given by equation 13 in Johnston and Butterworth (2005a). Data were generated for the years 1900 to 2051.

General mixing model

The population dynamics equation for the general mixing model, a generalisation of the mixing model described in Johnston and Butterworth (2005a), is:

$$N_{y+1,s} = N_{y,s} + r_s N_{y,s}\left(1-\left(\frac{N_{y,s}}{K_s}\right)^{\mu}\right) - C_{y,s} \qquad (1)$$

where:

$N_{y,s}$ is the abundance of breeding stock s in year y;

r_s is the intrinsic growth rate of stock s;

K_S is the carrying capacity of stock s;

μ is the 'degree of compensation' parameter (conventionally assumed to be 2.39 by the IWC/SC); and

$C_{y,s}$ is the number of stock s caught in year y.

In this model, the common feeding ground of the breeding stocks is divided into equal areas. Note that for practical purposes, the value of should be chosen so that these areas evenly overlay the existing IWC management areas. For example, for stocks D and E that are assumed to feed jointly in management areas IV and V, n is even so that areas $1,\ldots,\frac{n}{2}$ are equivalent to management area IV and areas $\frac{n}{2}+1,\ldots,n$ are equivalent to management area V. If the common feeding ground was to be divided into only the management areas IV and V, then use $n = 2$ (as in Johnston and Butterworth, 2005a).

The mixing of the breeding stocks ($s = 1, \ldots, S$) in a common feeding ground is described by:

$$N_{y,A} = \sum_{s \in S} p^{N}_{s,A} N_{y,s} \qquad (2)$$

where:

$N_{y,A}$ is the number of whales in feeding area A in year y; and

$p^{N}_{s,A}$ is the proportion of stock that feeds in feeding area A.

The overall catch from each breeding stock is:

$$C_{y,s} = C^{B}_{y,s} + \sum_{A=1}^{n} C^{F}_{y,s,A} \qquad (3)$$

where:

$C_{y,s}$ is the number of stock s caught in year y;

$C^{B}_{y,s}$ is the number of stock s caught in the breeding ground in year y; and

$C^{F}_{y,s,A}$ is the number of stock s caught in feeding area A in year y.

Using the assumption in Johnston and Butterworth (2005a) that catches of stocks in a feeding area are in the same ratio as the numbers of each stock present there, the numbers of each stock caught in a feeding area can be calculated from:

$$\frac{C^{F}_{y,s,A}}{C^{F}_{y,A}} = \frac{p^{N}_{s,A} N_{y,s}}{N_{y,A}} \qquad (4)$$

where:

$C^{F}_{y,A}$ is the number of whales caught in feeding area A in year y, i.e. $\sum_{s \in S} C^{F}_{y,s,A}$.

Base case model

The base case model comprises the general mixing model with two breeding stocks (i.e. = $\{D, E\}$) and two feeding areas within the common feeding ground (i.e. $n = 2$). These feeding areas are equivalent to the two management areas IV and V. Eighty per cent of breeding stock D is set to feed in management area IV and 80% of breeding stock E is set to feed in management area V, for all years. Thus, the mixing proportion of the breeding stock within the feeding ground is:

$$p^N_{s,A} = \begin{bmatrix} 0.8 & 0.2 \\ 0.2 & 0.8 \end{bmatrix} \tag{5}$$

Non uniform mixing and catch allocation model

The non-uniform mixing and catch allocation model uses the general mixing model with two breeding stocks (i.e. $S = \{D,E\}$) and a number of feeding areas within the common feeding ground (see Table 1 and Appendix 2). The mixing of the stocks within the feeding ground is distributed non-uniformly using separate functions for each stock. That is:

$$N_{y,A} = \sum_{s \in S} f_s(y, A) \tag{6}$$

where f_s is as specified in Table 1. The catch of each stock within the feeding ground is determined using the available spatial catch information on an annual scale.

Feeding area density dependence model

The population dynamics equation for the feeding area density dependence model is:

$$\begin{aligned} N_{y+1,s,A} &= N_{y,s,A} + r_s N_{y,s,A}\left(1 - \left(\frac{N_{y,A}}{K_A}\right)^{\mu}\right) - C_{y,s,A} \\ N_{y+1,s} &= \sum_{A=1}^{n} N_{y+1,s,A} \end{aligned} \tag{7}$$

where:

$N_{y,s,A}$ is the abundance of stock s in feeding area in A in year y;

r_s is the intrinsic growth rate of stock s;

K_A is the carrying capacity of feeding area A;

μ is the 'degree of compensation' parameter (conventionally assumed to be 2.39 by the IWC/SC); and

$C_{y,s,A}$ is the number of stock s in feeding area in A caught in year y.

The initial numbers of each breeding stock that feeds in each feeding area in year 0 is calculated as:

$$N_{0,s,A} = p^N_{s,A} N_{0,s} \tag{8}$$

where p^N and $N_{0,s}$ are as described for the base case mixing model. In this scenario p^N refers to the initial state at year zero only, as the subsequent yearly mixing proportions are allowed to change.

The catch from each stock in each feeding area is

$$C_{y,s,A} = C^B_{y,s,A} + C^F_{y,s,A} \tag{9}$$

where:

$C^B_{y,s,A}$ is the number of stock s that feed in feeding area A caught in the breeding ground in year y; and

$C^F_{y,s,A}$ is the number of stock s caught in feeding area A in year y.

$C^B_{y,s,A}$ is unknown but can be estimated in the same manner as $C^F_{y,s,A}$ in the general mixing model, i.e.

$$C^B_{y,s,A} = C^B_{y,s} \frac{N_{y,s,A}}{N_{y,s}} \tag{10}$$

where:

$C^B_{y,s}$ is the number of stock s caught in the breeding ground in year y; and

$N_{y,s}$ is the number of stock s in year y.

Model performance under the different scenarios

For each of three different scenarios, the performance of the 'True' simulated population with that estimated by the (Johnston and Butterworth, 2005a) model, 'Estimated' by reporting the normalised mean square error (NMSE) was qualitatively assessed between the two population trajectories across all years.

The 'True' and 'Estimated' parameters 'K' (the number of whales at the start of the simulation) and 'r' (the intrinsic rate of increase) are also reported. Table 1 summarises the parameter values used in the simulations for the three scenarios.

Table 1

Parameter values for the simulations of the three test scenarios.

Parameters	Scenario 1	Scenario 2	Scenario 3
Number of areas	Management Areas IV and V	2, 6, 12, 24, 60 and 120 sub areas within the common feeding area	Management Areas IV and V
Catch - feeding area (S 40°S)	Appendix 1	Appendix 1 with spatial information where available	Appendix 1
Catch - breeding area (N 40°S)	Naïve	Naïve	Naïve
Stock mixing strategy	Uniformly distributed across Management areas IV and V	Distributed using a: (1) gamma function, one for each stock; and (2) high-end function, one for each stock	Uniformly distributed within Management areas IV and V
Catch distribution strategy	Uniformly distributed across Management areas IV and V	Distributed into sub-areas according to spatial information on an annual scale	Uniformly distributed within Management areas IV and V
Population dynamics model	Mixing with density dependence acting on the breeding areas	Mixing with density dependence acting on the breeding areas	Mixing with density dependence acting on the feeding areas
Carrying capacity (K)	Initial breeding stock number	Initial breeding stock number	Initial breeding stock number

RESULTS

Base case

There was little difference between the model fit and the underlying simulated population for the base case model. Hence it was possible to reliably gauge the sensitivity of estimates from the Johnston and Butterworth model to the mixing and catch allocation scenarios and changed density dependence (Scenarios 2 and 3). Table 2 details the results of the base case simulation and Fig. 4 shows the population trajectories for (a) stock D and (b) stock E.

Non uniform mixing and catch allocation model

A difference was found between the model fit and the underlying simulated population for only one of the simulation runs (shown in bold in Table 2); for stock D with a gamma mixing distribution and 120 sub areas (Fig. 5a). The population *K* for the estimated population was higher, ~32,500 animals, than the 20,000 for the true population. Whilst both populations followed the same trajectory of decline and recovery, the estimated population recovered to a *K* higher by 2050. The estimated intrinsic growth rate (*r*) for the estimated population was lower, 0.05, as compared to 0.1 for the true population and the NMSE value was 0.0726 (Table 2).

There was little difference between the model fit and the underlying simulated population for all other simulations, an example of which is shown in Fig. 5b (stock E, gamma mixing and 120 sub-areas).

Feeding area density dependence model

There was a substantial difference between the model fit and the underlying simulated population for both stocks when density dependence was implemented on the feeding areas (Figs 6a and 6b, Table 2). For stock D, the initial population (i.e. *K*) for the estimated population was lower, ~16,800 animals, than the 25,000 for the true population. Population trajectories were most similar through a period of decline (1950–63) and recovery (1964–98), but where the estimated population reached initial *K* (~16,800 animals) by about 2020, the true population, did not recover to an initial *K* of 25,000 animals, and remained at a population size of ~7,500 from 2000–50 (Fig. 6a). The estimated intrinsic growth rate (*r*) was lower, ~0.066, than the 0.1 for the true population and the NMSE value was 0.415 (Table 2).

In contrast to stock D, the initial population (i.e. *K*) for the estimated population of stock E was higher, ~48,000 animals, than the 30,000 for the true population. Population trajectories were most similar throughout the period 1950–2050, but where the estimated population reached initial *K* (~48,000 animals) by about 2020, the true population reached the same *K* as the estimated population (Fig. 7b). The estimated intrinsic growth rate (*r*) for the estimated population was lower, ~0.072, than the 0.1 for the true population and the NMSE value was 0.1788 (Table 2).

DISCUSSION

In the base case scenario, the ability of the (Johnston and Butterworth, 2005a) model to estimate the population parameters from generated input data where the parameters values were unknown, was good. Therefore it was possible to gauge the sensitivity of the model to the mixing, catch allocation and density dependence scenarios with confidence. The Johnston and Butterworth (2005a) model was tested for alternate mixing and catch allocation on the feeding grounds on the basis of real data on whale movement and individual catch location, but found that the model was robust to more realistic specifications of these parameters in all but one simulation scenario. It would appear that whilst the combined effect of non-uniform mixing and non-uniform catch can produce a quite different underlying catch allocation than that specified in the Johnston and Butterworth (2005a) model, this introduces very little bias in the estimated population trajectory.

Alternative specifications for density dependence are especially important to consider in cases of models that allow

Table 2

Parameter estimates for 'True' and 'Estimated' populations and associated NMSE values for population trajectories for the three test scenarios.

Scenario 1										
Sub-areas	**Uniform mixing and catch**									
Stock D	**True K**	**Est K**	**True r**	**Est r**	**NMSE**					
2	25,000	24,952	0.1	0.101	0.00012					
Stock E	**True K**	**Est K**	**True r**	**Est r**	**NMSE**					
2	30,000	30,069	0.1	0.099	0.00001					
Scenario 2										
Sub-areas	**Gamma mixing and catch**					**Highend mixing and catch**				
Stock D	**True K**	**Est K**	**True r**	**Est r**	**NMSE**	**True K**	**Est K**	**True r**	**Est r**	**NMSE**
2	25,000	25,023	0.1	0.099	0.00016	25,000	24,984	0.1	0.101	0.00005
12	25,000	25,002	0.1	0.099	0.0001	25,000	24,700	0.1	0.11	0.001
24	25,000	26,374	0.1	0.084	0.0056	25,000	24,688	0.1	0.11	0.001
60	25,000	24,996	0.1	0.1	0.009	25,000	24,659	0.1	0.112	0.002
120	**25,000**	**32,598**	**0.1**	**0.05**	**0.0726**	25,000	24,661	0.1	0.11	0.002
Stock E	**True K**	**Est K**	**True r**	**Est r**	**NMSE**	**True K**	**Est K**	**True r**	**Est r**	**NMSE**
2	30,000	30,480	0.1	0.099	0.00018	30,000	29,935	0.1	0.1	0.00002
12	30,000	29,866	0.1	0.1	0.00007	30,000	29,300	0.1	0.99	0.0055
24	30,000	30,003	0.1	0.099	0.00005	30,000	29,143	0.1	0.1	0.0074
60	30,000	29,682	0.1	0.1	0.0003	30,000	29,163	0.1	0.09	0.0102
120	30,000	30,000	0.1	0.1	0.00003	30,000	29,008	0.1	0.1	0.009
Scenario 3										
Sub-areas	**Uniform mixing and catch**									
Stock D	**True K**	**Est K**	**True r**	**Est r**	**NMSE**					
2	25,000	16,825	0.1	0.066	0.41552					
Stock E	**True K**	**Est K**	**True r**	**Est r**	**NMSE**					
2	30,000	48,842	0.1	0.072	0.17888					

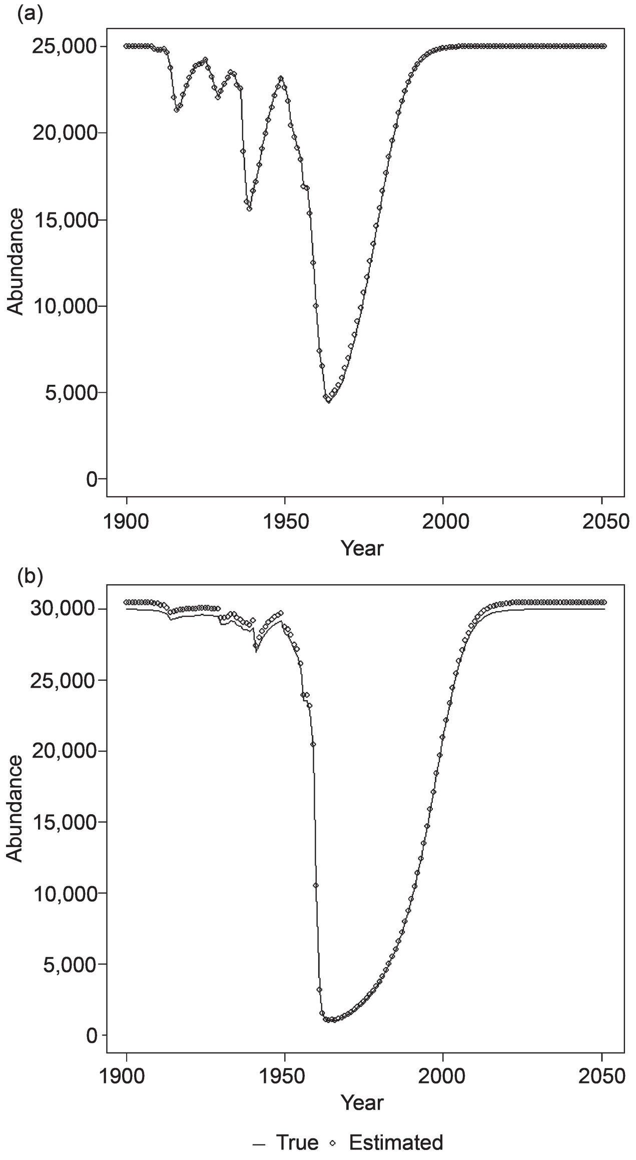

Fig. 4. Population trajectories ‘True’ versus ‘Estimated’ populations for (a) stock D and (b) stock E for the base case model. Note with initial populations = (25,000, 30,000 respectively) for both simulations.

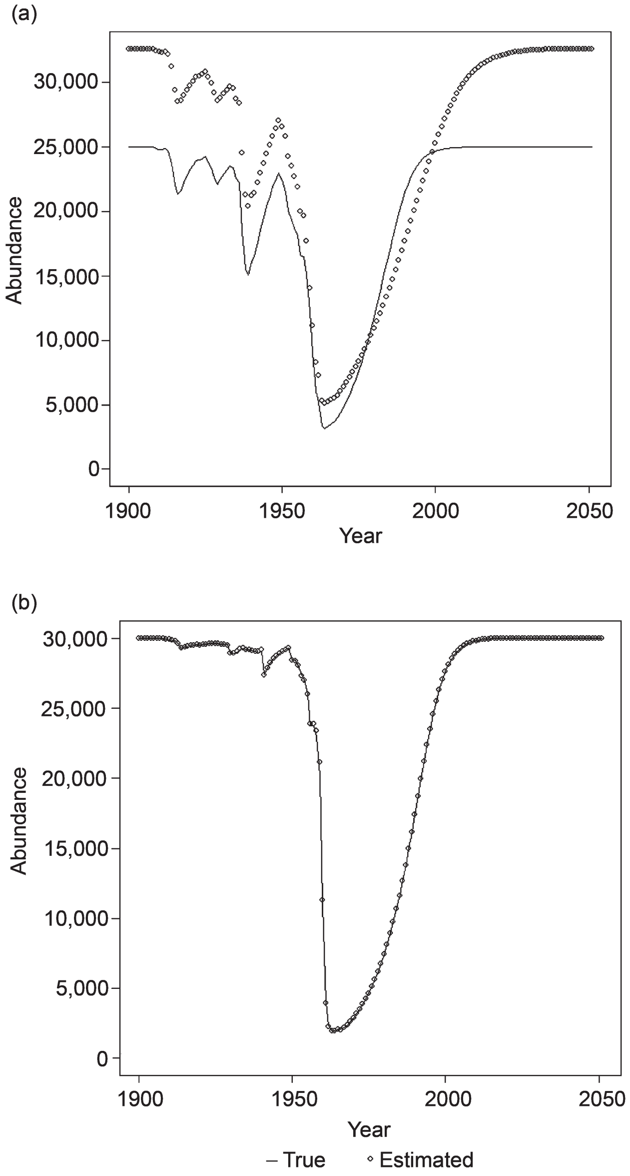

Fig. 5. Population trajectories ‘True’ versus ‘Estimated’ populations for (a) stock D with gamma mixing and 120 sub-areas and (b) stock E under gamma mixing and 120 sub-areas. Note with initial populations = (25,000, 30,000 respectively) for both simulations.

stocks to mix, in that density dependence does not now act on breeding stocks independently. In this scenario, *K* depends on the sum of the two population sizes and does not change between pre- and post-exploitation. Under the feeding area density dependent scenario, the Johnson and Butterworth model estimator performs poorly. In the case of stock D, the model underestimates initial *K* and overestimates recovery. In the case of stock E, initial *K* is overestimated as equal to final *K*.

By the 1960s both stock D and E were drastically reduced so their rate of increase at the cessation of whaling would have been close to *r*. However, stock D was reduced to lower numbers than stock E. Under the density dependence scenario and initial population abundance values used here, stock D cannot increase as fast as stock E and so the latter ends up accounting for the larger fraction of the total *K* and stock D is forced to be smaller. This seems to clearly illustrate a case of changing carrying capacity for each stock, but there is no way the trajectories estimated from the Johnson and Butterworth model used can reflect this. The simulations suggest that there may be differential recovery potential for two depleted stocks when density dependence operates on the feeding grounds and these two stocks mix on these feeding areas. Because the implementation of feeding area density dependence is intrinsically tied to the underlying process of mixing on the feeding area, there may be several plausible hypotheses for the process of mixing that have not been explored here.

Aside from the complexities of modelling feeding area density dependence when stocks are mixing, it is certainly plausible that after severe exploitation and subsequent recovery, whale populations (in the single stock case) may not return to their original level. For example, the North East Pacific stock of gray whales (*Eschrichtius robustus*), considered to be commercially extinct since the end of the 19th century, is now believed to be approaching a level that may be higher than its historical *K* (Moore *et al.*, 2001; Rugh *et al.*, 2005). In contrast, the Antarctic blue whale (*Balaenoptera musculus intermedia*) stock, also depleted to a small fraction of its original level, seems to have only

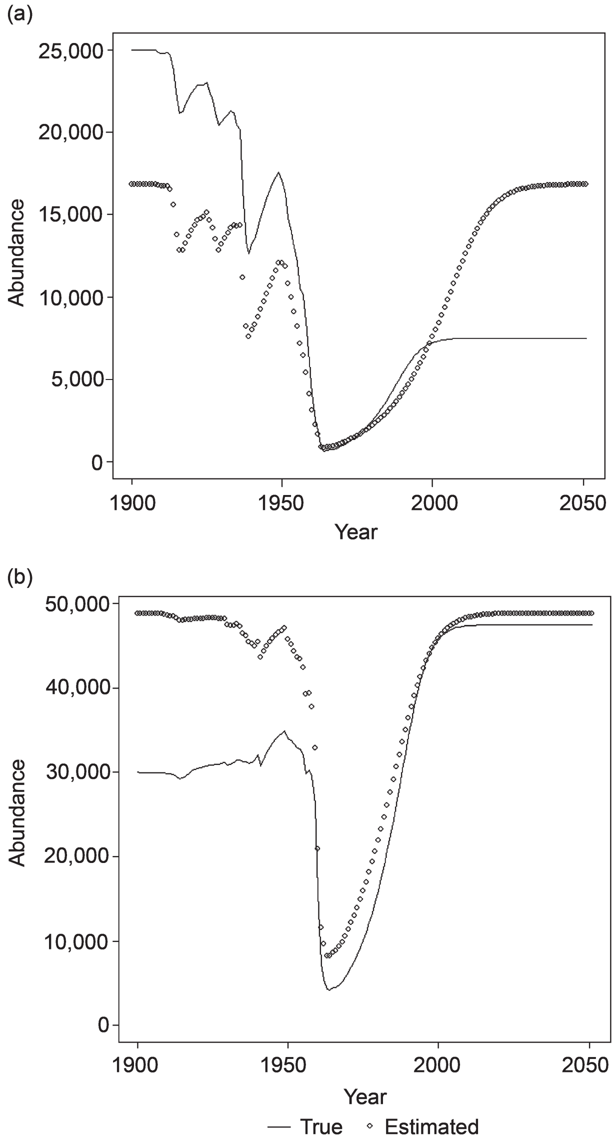

Fig. 6. Population trajectories 'True' versus 'Estimated' populations for (a) stock D with density dependence on the feeding areas and (b) stock E with density dependence on the feeding areas under uniform mixing and 2 sub-areas. Note with initial populations = (25,000, 30,000 respectively) for both simulations.

recovered to approximately 3% of its pre-exploitation level (Branch *et al.*, 2007). In both these cases the notion that *K* is fixed through time and never changes is open to debate.

The IWC has protected Southern Hemisphere humpback whale stocks since 1966, and blue whale stocks since 1965, but these species (and even different populations of the same species, i.e. humpback whales) have appeared to recover at very different rates. Baleen whale populations in the Southern Ocean are likely regulated by resource availability in their feeding areas rather than the breeding areas (unless they have very specific requirements). As just one component of a much larger predator guild, the recovery of whale populations will be influenced by the potential to interact trophically with other species.

In summary, the simulation approach taken here was conducted for illustrative purposes only, but served to demonstrate how alternative specifications for density dependence (e.g. on the feeding grounds rather than the breeding grounds) may be important to consider when stocks are mixing. Given that at least five of the seven putative stocks of humpback whales currently recognised in the Southern Hemisphere may mix on either feeding or breeding areas (or both), further exploration of multi-stock models is recommended.

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Appendix 1

SOUTHERN HEMISPHERE HUMPBACK WHALE CATCHES TO THE SOUTH OF 40°S APPORTIONED TO THE TWO FEEDING AREAS IV AND V

Year	IWC IV (West)	IWC V (East)
1900	0	0
1901	0	0
1902	0	0
1903	0	0
1904	0	0
1905	0	0
1906	0	0
1907	0	0
1908	217	0
1909	118	0
1910	83	0
1911	0	0
1912	0	0
1913	0	0
1914	0	0
1915	0	0
1916	0	0
1917	0	0
1918	0	0
1919	0	0
1920	0	0
1921	0	0
1922	0	0
1923	0	0
1924	0	0
1925	0	0
1926	16.4	65.6
1927	3.2	12.8
1928	14.4	13.6
1929	166	620
1930	74	188
1931	161	0
1932	82	0
1933	601	0
1934	1,343	0
1935	940.8	3.2
1936	1,435	0
1937	842.4	25.6
1938	844.6	38.4
1939	0	0
1940	478.8	1,915.2
1941	0	0
1942	0	0
1943	0	0
1944	0	0
1945	0	0
1946	0	0
1947	1	0
1948	0	0
1949	878.4	813.6
1950	1,149.2	136.8
1951	1,018.2	472.8
1952	296.4	413.6
1953	261.8	11.2
1954	214	752
1955	1,639.6	1898.4
1956	0	0
1957	1,953	176
1958	4,092	1,652
1959	2,731.6	9,890.4
1960	2,497.2	7,388.8
1961	677.2	1,256.8
1962	1,806.6	378.4
1963	415.8	227.2
1964	106.2	68.8
1965	163.8	283.2
1966	133.2	44.8
1967	88.8	27.2
1968	1.2	0.8
1969	0	0
1970	0	0
1971	0	0
1972	0.4	1.6
1973	0	0
1974	0	0
1975	0	0
1976	0	0
1977	0	0
1978	0	0
1979	0	0

Appendix 2

SIMULATION DATA AND MODEL SETTINGS

All test scenarios	**Value for stock D**	**Value for stock E**
Initial breeding stock numbers[1]	20,000	30,000
Intrinsic growth rate	0.1	0.1
Time period[2]	1900 to 2050	1900 to 2050
Each simulation	**Value**	
Number of areas	Management Areas IV and V	
Number of stocks	Stocks D and E	
Number of iterations	100,000	
Catch – breeding ground	Naïve	
Catch – feeding area	Naïve (For Scenario 3, the finer scale spatial data is summed across the sub-areas within each management area to return it to the right format for input into the model)	
Absolute (target) abundances	Size of simulated population in 1999 for each stock (each with coefficients of variation set to 0.00001)	
Relative abundance – breeding ground	5% of simulated population in the same years (as Table 1 of Johnston and Butterworth, 2005b)	
Relative abundance – feeding area	70% of simulated population in the same years as JARPA data (Johnston and Butterworth, 2005b)	
Comparison abundance	IWC/IDCR-SOWER estimates (Johnston and Butterworth, 2005b)	

[1] The initial breeding stock numbers were chosen so that all scenarios could be run without causing the catch to exceed the available stock in a given sub-area/area for all years. Note that Scenarios 2 and 3 are particularly sensitive to this problem. [2] 1900 refers to austral summer season 1900/01 and so on.

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A Bayesian assessment of the conservation status of humpback whales (*Megaptera novaeangliae*) in the western South Atlantic Ocean

ALEXANDRE N. ZERBINI[*,+,#] ERIC J. WARD[*], PAUL G. KINAS[^], MÁRCIA H. ENGEL[~] AND ARTUR ANDRIOLO[**,#]

Contact e-mail: alex.zerbini@noaa.gov

ABSTRACT

The population of humpback whales (*Megaptera novaeangliae*) wintering off the eastern coast of South America is referred to by the International Whaling Commission as 'Breeding Stock A' (BSA). This population was heavily exploited in 20th century modern commercial whaling operations. After more than 30 years of protection, its present status remains unknown. A deterministic sex and age-aggregated population dynamics model was used to estimate the pre-exploitation population size (K), the maximum net recruitment rate (r_{max}), the maximum depletion level (N_{min}/K), and other quantities of interest of BSA. Input data included modern whaling catch series, absolute estimates of abundance, observed growth rates and indices of relative abundance. A Bayesian statistical method was used to calculate probability distributions for the model parameters. Prior distributions were set on r_{max} – an uninformative (Uniform [0, 0.106]) and an informative (Normal [0.067, 0.04^2]) – and on the population size in 2005 – N_{2005} (Uniform [500, 22,000]). A total of 10,000 samples were used to compute the joint posterior distribution of the model parameters using the Sampling-Importance-Resampling algorithm. Sensitivity of model outputs to the priors on r_{max}, a genetic constraint, data inclusion and catch allocation scenarios was investigated. Medians of the posterior probability distributions of quantities of interest for the base case scenario were: $r_{max} = 0.069$ (95% probability intervals [PI] = 0.013–0.104), $K = 24{,}558$ (95% PI = 22,791–31,118), $N_{min}/K = 2\%$ (PI = 0.31%–12.5%), $N_{2006}/K = 27.4\%$ (PI = 18.3%–39.5%), $N_{2020}/K = 61.8\%$ (PI = 23.8%–88.6%), and $N_{2040}/K = 97.3\%$ (PI = 31.6%–99.9%). Despite apparent recovery in the past three decades, the western South Atlantic humpback whale population is still low relative to its pre-exploitation size and requires continued conservation efforts.

KEYWORDS: HUMPBACK WHALE; POPULATION ASSESSMENT; BAYESIAN STATISTICS; MODELLING; MANAGEMENT; SOUTH ATLANTIC; ANTARCTIC

INTRODUCTION

Southern Hemisphere humpback whales (*Megaptera novaeangliae*) were extensively hunted in both coastal and pelagic areas (Best, 1994; Gambell, 1973; Tønnessen and Johnsen, 1982). Protection against whaling was warranted in the late 1960s by the International Whaling Commission (IWC), but the species continued to be taken illegally by the Soviet fleet up to 1973 (e.g. Yablokov *et al.*, 1998). It is estimated that nearly 200,000 whales were taken in the Southern Hemisphere after 1900, causing the declines of populations to small fractions of their pre-exploitation levels (Allison, 2006; Findlay, 2001).

In the western South Atlantic Ocean (WSA), humpback whales occur in wintering grounds off the eastern coast of South America (~5–25°S) from June to December (Andriolo *et al.*, 2006a; 2006b; Martins *et al.*, 2001; Zerbini, 2004) with the majority of the population being concentrated in the Abrolhos Bank (Andriolo *et al.*, 2006a; 2006b). Additional winter records have been reported to the north and to the west of 5ºS (Furtado-Neto *et al.*, 1998) and near oceanic islands off the coast of Brazil (Lodi, 1994), but it is unclear whether these areas correspond to the typical range of the species. This population is referred to as the 'Breeding Stock A' (BSA) by the IWC (IWC, 1998; 2005). Contemporary data suggest that the summering grounds of this stock are located near the Scotia Sea in the Antarctic Sector of the Southwest Atlantic Ocean. Individuals monitored with satellite telemetry migrated to feeding grounds in offshore areas to the northeast of South Georgia and to the South Sandwich Islands (Zerbini *et al.*, 2006; 2011), within the IWC Management Area II. In addition, one individual photo-identified in Brazil was re-sighted near Shag Rocks, to the west of South Georgia (Stevick *et al.*, 2006).

The WSA humpback whale population was hunted since the 17th century. Before the 1900s, whaling operations were of relatively small scale and occurred mainly in low latitude wintering grounds off Brazil (Ellis, 1969; Lodi, 1992; Smith *et al.*, 2006). The introduction of modern whaling techniques and the expansion of the whaling activities to high-density areas in feeding grounds in the early 1900s increased annual catches to several thousand whales and quickly caused the collapse of this population (Findlay, 2001; Tønnessen and Johnsen, 1982).

Previous assessments conducted in the early 2000s suggested that the WSA humpback whale population was still low relative to its pre-exploitation size (Findlay and Johnston, 2001; Findlay *et al.*, 2000; Johnston and Butterworth, 2004; Johnston *et al.*, 2001; Zerbini, 2004; 2005). Since then, additional data on stock identity and migratory connections (IWC, 2006; Rosenbaum *et al.*, 2006; Stevick *et al.*, 2006; Zerbini *et al.*, 2006; 2011), absolute and relative abundance (Andriolo *et al.*, 2006b; Freitas *et al.*,

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[*] *School of Aquatic and Fishery Sciences, University of Washington, Box 355020, Seattle, WA 98195-5020, USA.*
[+] *National Marine Mammal Laboratory, Alaska Fisheries Science Center, NOAA Fisheries, 7600 Sand Point Way NE, Seattle, WA 98115-6349, USA.*
[#] *Projeto Monitoramento de Baleias por Satélite, Instituto Aqualie, R. Edgard Werneck 428/32, Rio de Janeiro, RJ 22763-010, Brazil.*
[^] *Laboratório de Estatística, Departamento de Matemática, Fundação Universidade Federal do Rio Grande, Rio Grande, RS, Brazil.*
[~] *Instituto Baleia Jubarte/Humpback Whale Institute, Rua Barão do Rio Branco, 26, Caravelas, BA, Brazil.*
[**] *Departamento de Zoologia, Instituto de Ciências Biológicas, Universidade Federal de Juiz de Fora, MG, Brazil.*

2004; Martins *et al.*, 2001; Ward *et al.*, 2011; Zerbini *et al.*, 2004), population rate of increase (Ward *et al.*, 2011) and an updated catch series (Allison, 2006) have become available. In this study, a Bayesian assessment of the WSA humpback whale population is provided using a sex and age aggregated population dynamics model. The sensitivity of model outputs to different prior distributions, catch allocation hypotheses and input data is investigated.

METHODS

The data

Catch data

Humpback whales were caught in wintering grounds off the eastern coast of South America since the 17th century, but catches were of relatively small scale and records are poorly known (Ellis, 1969; Lodi, 1992; Smith *et al.*, 2006). Therefore, in this study, only whales killed by modern whaling (post-1900) are considered.

For the purpose of allocation of historic catches, the IWC Scientific Committee (IWC SC) defined boundaries for the Southern Hemisphere humpback whale breeding stocks in the wintering (areas to the north of 40˚S) and feeding grounds (south of 40˚S) (IWC, 1998). Wintering ground catches are allocated to BSA if they were taken south of the Equator, north of 40˚S and west of 20˚W. These included individuals taken in the 20th century by catcher boats operating from whaling stations in Costinha (~7˚S, 35˚W) and Cabo Frio (~23˚S, 42˚W), in Brazil (Williamson, 1975), and by a Soviet pelagic fleet in the Abrolhos Bank Area (~18˚30'S, 38˚30'W) and in offshore areas (~30–32˚S, 33–36˚W) along the central South American coast (e.g. Allison, 2006; Zemsky *et al.*, 1996).

Feeding ground catches were more difficult to assign to breeding stocks because wintering-feeding ground connections were not yet clear and because mixing may occur in the Southern Ocean. Therefore, the IWC SC developed alternative catch allocation hypotheses (named 'Naïve', 'Fringe' and 'Overlap') to account for possible uncertainties in the feeding ground boundaries (IWC, 1998). These boundaries were subsequently reviewed for some stocks (BSA, BSD and BSG) in light of additional information on migratory connections between low and high latitudes and the former Naïve hypothesis was modified and named 'Core' (IWC, 2011). In this study, catch allocation followed the proposed hypotheses described in Table 1 and illustrated in Fig. 1. Catches included whales taken at South Georgia (54˚30'S, 36˚30'W), South Sandwich Islands (56˚20–59˚40'S, 21˚30'W), South Orkney Islands (60˚35'S, 45˚30'W), Falkland Islands (59˚30'S, 51˚45'W), the Antarctic Peninsula (~65˚S, 60˚W for the Overlap model only), and pelagic operations in Antarctic waters (Allison, 2006). Sensitivity of catch allocation hypotheses to model parameter estimates was investigated (see below).

Abundance and trend data

Multiple estimates of abundance were computed for WSA humpback whales. Mark-recapture estimates were obtained only in the wintering grounds (Freitas *et al.*, 2004; Kinas and Bethlem, 1998). Because these estimates corresponded to only a portion of the wintering grounds, they should not be assumed to represent total stock size. Their use as indices of relative abundance was proposed in a preliminary assessment of the BSA (Zerbini, 2004), but the estimated trend obtained from these data (Freitas *et al.*, 2004) was considered unreliable (IWC, 2005). For this reason, mark-recapture-based estimates of population size are not considered further in this study.

Line transect surveys have been conducted in both wintering (Andriolo *et al.*, 2006a; 2006b; Zerbini *et al.*, 2004) and feeding grounds (Branch, 2011; Branch and Butterworth, 2001). Wintering ground estimates were obtained from ship surveys conducted in 1999 and 2000 off the northeastern coast of Brazil (5–12˚S) (Zerbini *et al.*, 2004) and from aerial surveys conducted during 2001 to 2005 (Andriolo *et al.*, 2006a; 2006b). Only the most recent estimate (year 2005), derived from the aerial surveys off Brazil (N_{2005} = 6,251, CV = 0.17) (Andriolo *et al.*, 2006b), covered the entire stock range and therefore is considered the most current and reliable estimate of the size of BSA (IWC, 2011). This figure is therefore assumed to represent an estimate of absolute abundance when fitting the population dynamics model. Estimates from aerial surveys conducted from 2002 to 2004 (Table 2) were obtained using comparable methodology and covered the same portion of the range of the stock (12–21˚S) in the wintering grounds during the same season (Andriolo *et al.*, 2011). These estimates were therefore used here as an index of relative abundance (hereafter called the 'wintering ground index of abundance', WGIA).

Estimates in the feeding grounds associated to BSA were obtained as part of the IWC International Decade of Cetacean Research/Southern Ocean Whale and Ecosystem Research (IDCR/SOWER) circumpolar program (CP), usually south of 60˚S in the Antarctic Ocean (Branch, 2011; Branch and Butterworth, 2001). Because there is evidence that a large component of the population remains north of 60˚S (Reilly *et al.*, 2004; Zerbini *et al.*, 2006) the numbers provided by these surveys should not be used as estimates of total stock size. In this study estimates of abundance from CP surveys of the IDCR/SOWER computed for comparable areas in the feeding grounds linked to BSA (50˚W–20˚W, south of 60˚S) (Table 2; Branch, 2011) were assumed to correspond to another index of abundance (the 'feeding ground index of abundance', FGIA).

Sighting and effort data were collected in the Abrolhos Bank from 1992 to 1998 to investigate the distribution and habitat use of whales off Brazil. Systematic surveys, using comparable methodology, were only conducted from 1995 to 1998 (Martins *et al.*, 2001). Data for this four year period were used to estimate the growth rate of the humpback whale population wintering in the Abrolhos Bank by Ward *et al.* (2011). The estimate from their best model (= 7.4%/year, SD

Table 1

Summary of allocation of catches in the feeding ground (south of 40°S) as specified in IWC (1998, 2006a, 2006b) and Allison (2006).

Core hypothesis	Falkland catches	Fringe hypothesis	Overlap hypothesis
Catches between 70–20°W of longitude and 40–50°S of latitude, plus catches from 50–20°W to the south of 50°S, excluding the Falkland catches	Core catches plus catches taken from 70–50°W between 50 and 58°S	90% of the catches from the Core allocation hypothesis and 10% from a 'Fringe Area' between 20 and 10°W	80% from Core and 10% from) 20°W–10°E (the Naïve allocation hypothesis for BSB) and 10% from 100–50°W (the Core allocation hypothesis for BSG)

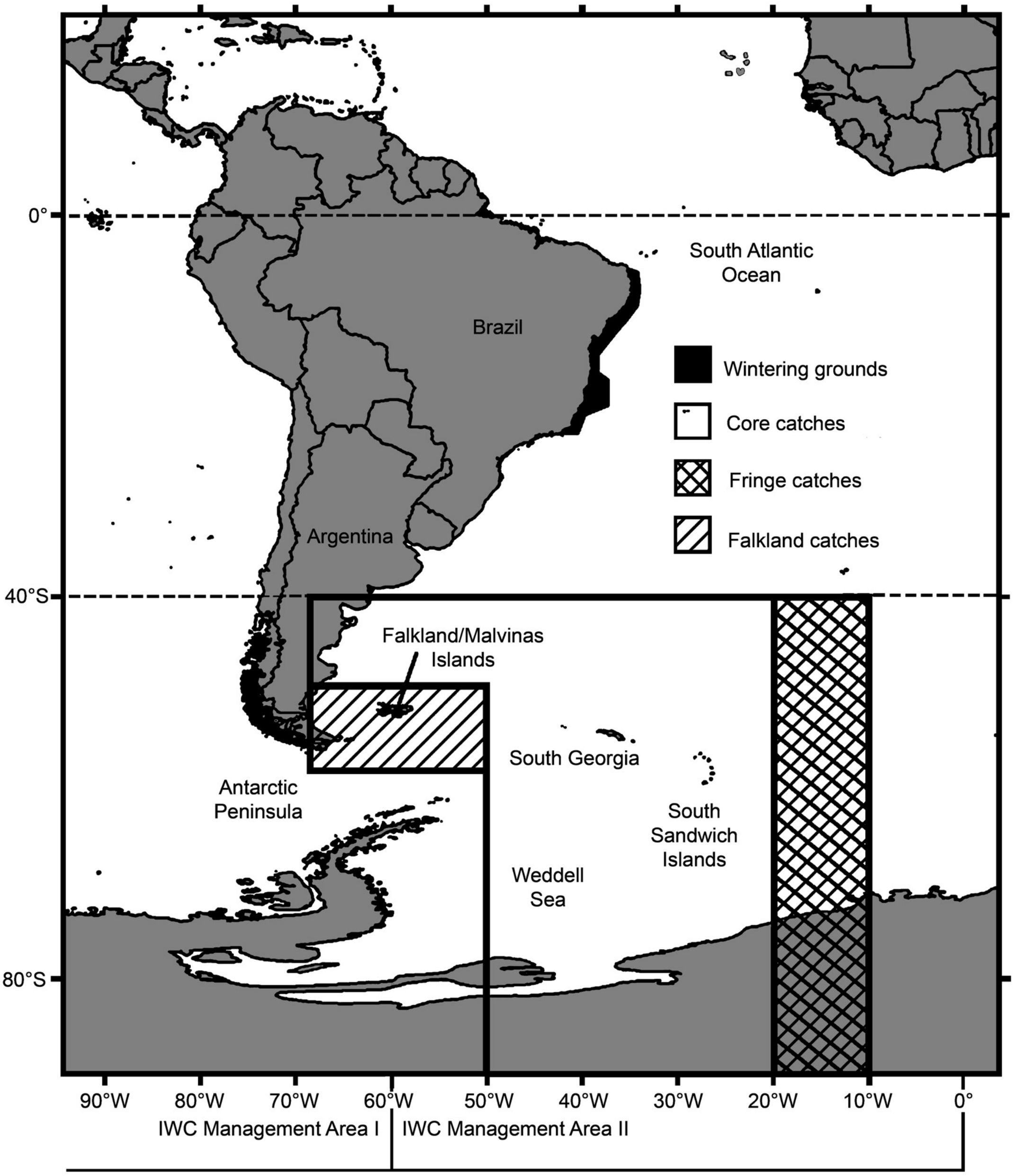

Fig. 1. Breeding stock range in the wintering grounds and feeding ground catch allocation hypotheses.

= 3.3%) was used as the 'observed' growth rate when fitting the population dynamics model in this study.

Modelling techniques

In this study, a Bayesian statistical framework was used to estimate model parameters and quantities of interest (e.g. Gelman *et al.*, 1995; Punt and Hilborn, 1997). Methods were similar to those described and applied to assess the status of the population wintering off the western coast of South America (Breeding Stock G) (Johnston *et al.*, 2011).

Population dynamics model

The density dependent, sex and age-aggregated generalised logistic equation (e.g. Pella and Tomlinson, 1969) was used to model the dynamics of the humpback whale population. The model is deterministic and is represented as:

$$N_{t+1} = N_t + N_t \cdot r_{\max} \cdot \left[1 - \left(\frac{N_t}{K} \right)^z \right] - C_t \qquad (1)$$

where:

N is the population size, in numbers, at time 't' or 't + 1', in years;

r_{max} is the maximum net recruitment rate;

K is the pre-exploitation population size;

z is the parameter that determines the population size where productivity is maximum (also known as shape parameter). This is set here at a value of 2.39, which corresponds to a maximum sustainable yield level of 0.6K (e.g. Butterworth and Best, 1994; Punt and Butterworth, 1999), as conventionally assumed by the IWC SC.

C_t is the harvest, in numbers, in year 't'.

Estimation of the predicted growth rate

A predicted growth rate ($r^{pred}_{1995-1998}$) was computed for comparison with the 'observed' growth rate provided by Ward *et al.* (2011) using the model predicted abundances

Table 2

Indices of relative abundance in the feeding and breeding grounds of western South Atlantic humpback whales (from Andriolo *et al.*, 2006b and Branch, 2008).

Feeding ground index of abundance (FGIA)				Wintering ground index of abundance (WGIA)		
Year	Cruise	N	CV	Year	N	CV
1981/82	CPI	45	0.91	2002	2,305	0.20
1986/87	CPII	259	0.59	2003	2,539	0.19
1997/98	CPIII	200	0.64	2004	3,615	0.19

over the period 1995–1998. The predicted rate assumed an exponential growth and was calculated as:

$$r^{pred}_{1995-1998} = \frac{\sum_{t=1995}^{1997} \ln\left(\frac{N^{pred}_{t+1}}{N^{pred}_{t}}\right)}{3} = \frac{\ln\left(N^{pred}_{1998}\right) - \ln\left(N^{pred}_{1995}\right)}{3} \qquad (2)$$

where:

N^{pred} is the model predicted population size, in numbers, at time '*t*' or '*t* + 1', in years.

Estimation of scaling parameters

The feeding (FGIA) and wintering ground (WGIA) indices of abundance were scaled to the model predicted population size in year *i* by the scale coefficient '*q*', assuming a log-normal distribution for their residuals. A separate *q* was estimated for each index of abundance under the assumption that the same proportion of whales is assumed to occupy the survey areas during the survey period. To consider all forms of uncertainty, we initially allowed each *q* to be a free parameter in our Bayesian models; this approach proved unsuccessful, however, due to the small sample size for each index ($n = 3$), and high CVs of the FGIA estimates (0.59–0.91), which proved not informative with respect to *q*. As an alternative approach, we treated each *q* as a nuisance parameter, and estimated them analytically according to equation (3) below for each index of abundance *j*.

$$q_j = e^{\left(\frac{\sum_{i=1}^{n} \frac{\ln\left(\frac{IA^{obs}_{ij}}{N^{pred}_{i}}\right)}{\sigma^2_{IA^{obs}_{ij}}}}{\sum_{i=1}^{n} \frac{1}{\sigma^2_{IA^{obs}_{ij}}}}\right)} \qquad (3)$$

where:

IA^{obs}_{ij} is the observed index of abundance *j* (FGIA or WGIA) in year *i*;

N^{pred}_{i} is the model predicted population size in year *i*;

n is the number of data points for each index of abundance;

$\sigma_{IA^{obs}_{ij}} = \sqrt{\ln(1+CV^2_{IA^{obs}_{ij}})}$, where CV is the coefficient of variation of the estimated index of abundance *j* for year *i*.

The analytical solution above corresponds to an approximate Bayesian procedure that involves a reduction in the number of parameters over which to integrate (and therefore a reduction in computational time) by replacing the numerical integration of q_j by their maximum likelihood estimates. It has been shown that this approach does not differ from the strictly Bayesian procedure if the prior on *q* is uniform on a logarithmic scale (Punt and Butterworth, 1996; Walters and Ludwig, 1994).

Statistical framework

A Bayesian analysis involves integrating the product of prior distributions of parameters and the likelihood functions that links the probability of the observed data to the model predicted parameters. In this study, the generalised logistic model is fit to as many as four sources of data: the absolute abundance estimate (N_{2005}), the observed growth rate over the period 1995–1998 ($r^{obs}_{1995-1998}$), and two indices of abundance (FGIA and WGIA). We used data from additional surveys (1994–1998) to develop an informative prior for the growth rate. The rationale for using an informative prior based on external data is that when a uniform prior is placed on r_{max}, the output is generally non informative because parameters r_{max} and *K* are highly correlated in the logistic model (e.g. high values of *K* and low values or r_{max} may be equally likely to low values of *K* and high values of r_{max}).

Likelihood functions

The error distribution of the total stock size and the indices of relative abundance were assumed to be log-normally distributed. The negative of the logarithm of the likelihood the absolute stock size (N_{2005}) is:

$$-\ln(L) = \ln(\sigma_{N_{2005}}) + \ln(N_{2005}) + 0.5 \cdot \frac{\left(\ln(N^{pred}_{2005}) - \ln(N_{2005})\right)^2}{\sigma^2_{N_{2005}}} \qquad (4)$$

where:

N^{pred}_{2005} is the model predicted abundance in 2005

N_{2005} is the observed abundance in 2005

$$\sigma_{N_{2005}} = \sqrt{\ln(1 + CV^2_{N_{2005}})}$$

The negative of the logarithm of the likelihood of the indices of abundance is given by:

$$-\ln(L) = \sum_{i=1}^{n}\sum_{j=1}^{m}\left[\ln(\sigma_{IA^{obs}_{ij}}) + \ln(IA^{obs}_{ij}) + 0.5 \cdot \frac{\left(\ln(q_j \cdot N^{pred}_{i}) - \ln(IA^{obs}_{ij})\right)^2}{\sigma^2_{IA^{obs}_{ij}}}\right] \qquad (5)$$

where:

N^{pred}_{i} is the model predicted abundance in year *i*;

IA^{obs}_{ij} is the observed index of abundance *j* in year *i*;

q_j is the estimated scale parameter for index of abundance *j*;

$$\sigma_{IA^{obs}_{ij}} = \sqrt{\ln(1 + CV^2_{IA^{obs}_{ij}})}$$

The error of the growth rate estimates is assumed to be normally distributed. The negative of the logarithm of the likelihood of the growth rate is given by:

$$-\ln(L) = \ln(\sigma_{r^{obs}_{1995-1998}}) + 0.5 \cdot \left(\frac{r^{pred}_{1995-1998} - r^{obs}_{1995-1998}}{\sigma_{r^{obs}_{1995-1998}}} \right)^2 \qquad (6)$$

where:

$r^{pred}_{1995-1998}$ is the model predicted growth rate between 1995–1998 (from equation 2);

$r^{obs}_{1995-1998}$ = 7.4%/year (from Ward *et al.*, 2011);

$\sigma_{r^{obs}_{1995-1998}}$ = 3.3%/year (from Ward *et al.*, 2011).

Thus, the total negative logarithm of the likelihood is the sum of equations (4), (5) and (6), where (5) = 0 and (6) = 0 when the indices of abundance and the observed growth rate, respectively, are not present in the model.

The integration of the prior distributions of the parameters and the likelihood function was approximated by the Sampling-Importance-Resampling (SIR) algorithm as implemented by McAllister *et al.* (1994). This implementation is a special case of the SIR algorithm in which the importance function is set to the prior. In SIR, a large number of independent sets of parameters is randomly drawn from the prior distributions, their likelihood is evaluated given the observed data and each set of data is stored in proportion to their likelihood. In the present study, a total of 10,000 samples were obtained with the SIR algorithm to compute the posterior distribution of parameters and quantities of interest.

Priors

In Bayesian statistical models probability is used as a measure of uncertainty. Within this paradigm, unknown model parameters have probability distributions based on previous knowledge (the priors), which are then updated using the data to derive the posterior distributions, the keystone of Bayesian inference. Priors can be either uninformative or vague, when they carry no substantial knowledge about the parameter of interest, or informative, when they contain relevant information from previous studies. In this study, prior distributions were specified for r_{max} and N_{2005}. There is no need to specify a prior for the pre-exploitation population size (*K*) because it is implicit in the combination of the population model, the catch history and the other priors (Butterworth and Punt, 1995).

Two priors were specified for r_{max}: a uniform prior, and an informative prior. The latter originated from a Bayesian hierarchical meta-analysis of growth rates of eight formerly depleted whale populations (Branch *et al.*, 2004). This prior has a normal distribution with mean 0.067 and standard deviation 0.04. Prior distributions of r_{max} were bounded. The lower boundary of was set to zero because negative maximum net recruitment rates are biologically implausible and the upper boundary corresponds to the maximum growth rate for the species computed from a range of life history parameters observed for several humpback whale populations (10.6%/year, Clapham *et al.*, 2006; IWC, 2007a).

The prior distribution on N_{2005} was uniform (U[500, 22000]). The lower and upper bounds were fixed to a value thought to be greater than the greatest possible value in the posterior probability distribution, but small enough to limit computational time (e.g. Wade, 2002). Although the choice of these bounds may seem arbitrary, their values were assessed not to be important, as they do not influence the results.

Population projection

The population was projected using the 'backwards' method of Butterworth and Punt (1995). The prior distributions of the current absolute abundance (N_{2005}) and the maximum net recruitment rate (r_{max}) are sampled and then used to determine the unique value of the population in 1901 (assumed to correspond to *K*) that corresponds to the value drawn from the prior for N_{2005}, given r_{max} and the applied catch series. This process is accomplished by using a bisection method (Butterworth and Punt, 1995). In this study, the population is projected into the future (2006 to 2040) assuming that non-natural mortality has not taken place since whaling for this stock ceased.

Quantities of interest, modelling scenarios and sensitivity analyses

Posterior probability distributions were calculated for the following parameters and quantities of interest: r_{max}, *K*, Minimum population size (N_{min}), population in 2006 (N_{2006}), maximum depletion level (N_{min}/K), and depletion levels in 2006 (N_{2006}/K), in 2020 (N_{2020}/K) and in 2040 (N_{2040}/K).

The base case scenario

The base case scenario (BC) comprises the following prior, data and catch allocation hypothesis:

Prior distribution on r_{max}: Uniform distribution;

Observed growth rate: $r^{obs}_{1995-1998}$ = 7.4%/year (SD = 3.3%);

Absolute abundance: N_{2005} = 6251 (CV = 0.17);

Catch allocation: Core hypothesis.

Sensitivity analyses

The sensitivity of the BC to the specification of different prior distributions, to the inclusion of various sets of data and to the different catch allocation hypotheses was investigated. The analyses are divided into four different sets of model runs: *Choice of Prior on r_{max}*, *Genetic Constraint*, *Data Inclusion* and *Catch Allocation*. A summary of the proposed scenarios is presented in Table 3.

CHOICE OF PRIOR ON R_{MAX}

The uniform prior presented in the BC was replaced by the informative (Meta-analysis) prior of Branch *et al*. (2004).

GENETIC CONSTRAINTS

Jackson *et al.* (2006) suggested that a genetic constraint be used in the assessment of South Pacific humpback whale populations given the observed genetic diversity. This idea had previously been discussed by Baker and Clapham (2004), who advocated that demographic and genetic approaches should be integrated to better describe whale population dynamics.

The same approach was used here to determine a minimum population size of humpback whales from BSA, given their observed genetic diversity. Baker and Clapham (2004) suggested that the number of extant haplotypes sampled in a population which has undergone a recent bottleneck provides an absolute minimum bound on the number of mature females in the population at the time of the bottleneck (Patenaude, 2002). Jackson *et al.* (2006) proposed a correction factor of 4 to scale the number of sampled haplotypes (minimum number of mature females) to the total (census) population size when the population was at its minimum. The rationale behind this correction factor is that the number of haplotypes must be multiplied by two

Table 3

Summary of the Base Case and sensitivity analysis used in the assessment of humpback whales in the western South Atlantic Ocean.

Scenario	Base Case	Baleen whale meta-analysis r_{max}
Prior on r_{max}	Uniform [0.00, 0.106]	Normal [0.067, 0.04^2]
Observed growth rate present	Yes	Yes
Indices of abundance	–	–
Genetic constraint	–	–
Catch allocation	Core	Core
Scenario	Genetic constraint	FGIA
Prior on r_{max}	Uniform [0.00, 0.106]	Uniform [0.00, 0.106]
Observed growth rate present	Yes	Yes
Indices of abundance	–	FGIA
Genetic constraint	Minimum population = 264	–
Catch allocation	Core	Core
Scenario	WGIA	FGIA + WGIA
Prior on r_{max}	Uniform [0.00, 0.106]	Uniform [0.00, 0.106]
Observed growth rate present	No	Yes
Indices of abundance	–	FGIA + WGIA
Genetic constraint	–	–
Catch allocation	Core	Core
Scenario	No observed growth rate, FGIA + WGIA	Falkland catches
Prior on r_{max}	Uniform [0.00, 0.106]	Uniform [0.00, 0.106]
Observed growth rate present	No	Yes
Indices of abundance	FGIA + WGIA	–
Genetic constraint	–	–
Catch allocation	Core	Core + Falkland catches
Scenario	Fringe catches	Overlap catches
Prior on r_{max}	Uniform [0.00, 0.106]	Uniform [0.00, 0.106]
Observed growth rate present	Yes	Yes
Indices of abundance	–	–
Genetic constraint	–	–
Catch allocation	Fringe catches	Overlap catches

to account for the male population (assuming an even sex ratio) and also by two to correct the minimum effective population size to a lower estimate of census population size (Nunney, 1993; Roman and Palumbi, 2003). Jackson *et al.* (2006) pointed out that this correction factor is conservative, but useful to provide a minimum census population number. Including this constraint in our models can be seen as part of the prior (bounds are commonly used in priors on positive quantities, such as variance parameters), and not additional data.

The total number of mtDNA haplotypes found in whales from BSA was estimated at 66 (Rosenbaum *et al.*, 2006), resulting in a minimum population of 264 whales. Therefore, all population trajectories resulting in a minimum abundance lower than 264 individuals were penalised by having their likelihood set to zero.

DATA INCLUSION

A total of four scenarios were proposed to investigate the sensitivity of the BC to the inclusion/removal of different data in the fit of the model (Table 3). The objective of scenarios FGIA, WGIA and FGIA + WGIA in Table 3 was to investigate whether the inclusion of the indices of relative abundance (FGIA, WGIA, or both) provided additional trend information and how these input data influenced the model outputs. In the fourth scenario (‘no observed growth rate, FGIA + WGIA’ in Table 3), the observed growth rate was removed from the model fit (but the indices of abundance, FGIA and WGIA, were retained) in order to assess how informative this rate was for computation of model outputs.

CATCH ALLOCATION

The sensitivity of the model outputs to the different hypotheses for feeding ground catch allocation was also investigated. The ‘Fringe’ and ‘Overlap’ catch allocations were compared to the ‘Core’ hypothesis used in the Base Case. In addition, because it is not clear whether individuals taken in the Falkland Islands (59˚30’S, 51˚45’W) belonged to BSA, the present assessment investigates the sensitivity of their inclusion in the analyses. The catch series used in the proposed scenarios were provided by Allison (2006) and are presented in Table 4.

RESULTS

Posterior distribution of model parameters for all scenarios investigated in this study (Table 5) were obtained from 10,000 unique parameter vectors of the SIR algorithm.

Base case

The posterior distribution of the parameters and quantities of interest for the BC scenario are presented in Table 5 and illustrated in Fig. 2. The point estimate (median of the posterior probability distribution) on r_{max} is 0.069 (95% probability interval [PI] = 0.013–0.104, Fig. 2A). The

Table 4

Catch series for the allocation scenarios used in the assessment of western South Atlantic humpback whales (from Allison, 2006).

Year	Core catches	Falkland catches	Fringe catches[1]	Overlap catches	Year	Core catches	Falkland catches	Fringe catches[1]	Overlap catches
1904	180	0	180	144	1939	2	0	2	2
1905	288	0	288	233	1940	36	0	92	53
1906	240	0	240	242	1941	13	0	13	10
1907	1,261	0	1,261	1,045	1942	0	0	0	0
1908	1,849	6	1,849	1,605	1943	4	0	4	3
1909	3,391	66	3,391	2,870	1944	60	0	60	48
1910	6,468	49	6,468	5,434	1945	238	0	238	190
1911	5,832	12	5,832	4,892	1946	30	0	31	24
1912	2,881	6	2,881	2,472	1947	35	0	36	30
1913	999	5	999	974	1948	48	0	67	51
1914	1,155	8	1,155	1,054	1949	83	0	212	116
1915	1,697	0	1,697	1,396	1950	698	0	712	614
1916	447	0	447	373	1951	45	0	102.5	84
1917	121	0	121	116	1952	34	0	50.5	49
1918	129	0	129	124	1953	140	0	155.5	124
1919	111	0	111	113	1954	44	0	70	71
1920	102	0	102	97	1955	96	0	137.5	94
1921	9	0	9	7	1956	167	0	199.5	210
1922	364	0	364	310	1957	61	2	77.5	61
1923	133	0	133	116	1958	16	0	19	28
1924	266	0	266	223	1959	15	36	18.5	40
1925	254	0	254	220	1960	27	0	29	45
1926	7	0	7	16	1961	13	4	13	132
1927	0	1	0	0	1962	24	1	26	53
1928	19	0	19	17	1963	12	22	12	12
1929	51	0	56	42	1964	0	0	0	0
1930	107	0	120	92	1965	52	0	69	133
1931	18	0	19	15	1966	0	0	0	15
1932	23	0	24	20	1967	189	0	192	226
1933	132	0	151	114	1968	0	0	0	0
1934	57	0	64	49	1969	0	0	0	0
1935	48	0	149	68	1970	0	0	0	0
1936	105	0	149	109	1971	0	0	0	0
1937	242	0	275	213	1972	2	0	2	2
1938	0	0	0	0	**Total**	**31,170**	**219**	**31,847**	**27,334**

[1] Fractional catches occur under the 'Fringe' hypothesis because of proportional allocation of catches between areas (see IWC, 1998).

posterior median of K indicates that the size of the humpback whale population wintering off the western coast of South America was nearly 24,600 individuals (95% PI = 22,791–31,118) before exploitation by modern whaling (Fig. 2B).

The population trajectory (Fig. 3) shows that the population was severely depleted after a period of intense exploitation between 1905 and 1920 and remained low for the following 40 years, a period which it sustained small catches. BSA reached its lowest numbers in the late 1950s, when nearly 500 (95% PI = 159–3,943) individuals existed in the population. This number corresponds to a depletion level of nearly 2% of K (95% PI = 0.7%–12.5%) (Fig. 2C). In the early 1960s this population started to recover and, despite the several hundred individuals taken by the Soviet whaling, it has continued to grow. The population size in 2006 was estimated to be about 6,800 whales (95% PI = 4,902–9,567), which corresponds to a depletion level of 27% of the pre-exploitation population size (95% PI = 18.3–39.5%) (Fig. 2D). Assuming no human-induced mortality occurs in the future, it is predicted that BSA will reach 62% of K (95% PI = 23.8–88.6%) in 2020 (Fig. 2E) and will be nearly recovered in 2040 (95% PI = 36.5–99.9%) (Fig. 2F).

Sensitivity to choice of prior

Posterior probability distributions for model outputs are presented in Fig. 2. The use of the 'baleen whale meta-analysis' prior had very little effect on the model outputs (Table 5), except that it provided slightly more precise estimates of model parameters. Yet, posterior distributions of model outputs between this and the BC scenario overlapped to a great extent (Fig. 2).

Sensitivity to the genetic constraint

The addition of a genetic constraint prevented the population trajectory from reaching values lower than 264 individuals. This resulted in a small decrease in the posterior median of r_{max} (from 0.069 down to 0.062) and a small increase in K (from 24,600 to 25,000). The posterior median of the minimum populations for this scenario (629 individuals) was greater than the one estimated with the BC scenario, resulting in a greater maximum depletion level (from 2% to 2.4%, Table 5). Posterior medians of the status of the population in 2006, 2020 and 2040 were more pessimistic than the BC scenario. Despite these changes, the posterior probability distributions between the genetic constraint and the BC scenario overlapped to a great extent (Fig. 2).

Sensitivity to data inclusion

The inclusion of the FGIA resulted in a small increase in precision but posterior distributions of model parameters were similar to the BC scenario (Table 5, Fig. 4). In contrast, the addition of the WGIA resulted in an increase in the posterior median of r_{max} and current status, and consequently, a decrease in K and the maximum depletion level. Figs 5A and 5B show the fit of the population dynamics model to each of these indices of abundance. When both FGIA and WGIA were included in the analysis greater precision and

Table 5
Posterior medians, means and 95% probability intervals of model parameters estimated for the assessment of western South Atlantic humpback whales.

	Base case				Baleen whale meta-analysis r_{max} prior			
	Median	Mean	2.5%	97.5%	Median	Mean	2.5%	97.5%
r_{max}	0.069	0.066	0.013	0.104	0.069	0.068	0.022	0.103
K	24,558	25,110	22,791	31,118	24,514	24,846	22,844	28,955
N_{min}	503	850	159	3,943	490	710	168	2,680
N_{2006}	6,808	6,929	4,902	9,567	6,851	6,947	4,942	9,529
Max Depletion	0.020	0.031	0.007	0.125	0.020	0.027	0.007	0.092
Depletion in 2006	0.274	0.278	0.183	0.395	0.277	0.281	0.191	0.394
Depletion in 2020	0.618	0.601	0.238	0.886	0.628	0.615	0.287	0.879
Depletion in 2040	0.973	0.879	0.316	0.999	0.975	0.908	0.444	0.999
	Genetic constraint				FGIA			
	Median	Mean	2.5%	97.5%	Median	Mean	2.5%	97.5%
r_{max}	0.062	0.059	0.011	0.092	0.068	0.066	0.017	0.103
K	24,959	25,548	23,344	31,851	24,600	25,010	22,832	30,198
N_{min}	612	987	278	4,222	511	788	163	3,351
N_{2006}	6,895	6,994	4,947	9,659	6,840	6,947	4,906	9,498
Max Depletion	0.024	0.036	0.012	0.133	0.021	0.030	0.007	0.111
Depletion in 2006	0.272	0.276	0.179	0.397	0.275	0.280	0.186	0.395
Depletion in 2020	0.574	0.562	0.226	0.861	0.617	0.605	0.258	0.882
Depletion in 2040	0.951	0.855	0.284	0.999	0.972	0.892	0.365	0.999
	WGIA				FGIA + WGIA			
	Median	Mean	2.5%	97.5%	Median	Mean	2.5%	97.5%
r_{max}	0.075	0.071	0.020	0.104	0.074	0.071	0.023	0.104
K	24,229	24,670	22,786	29,348	24,274	24,655	22,796	28,817
N_{min}	426	674	153	2,887	437	652	158	2,622
N_{2006}	6,866	6,975	4,931	9,546	6,836	6,943	4,885	9,541
Max Depletion	0.018	0.026	0.007	0.098	0.018	0.025	0.007	0.091
Depletion in 2006	0.280	0.284	0.190	0.400	0.279	0.283	0.191	0.399
Depletion in 2020	0.663	0.638	0.279	0.894	0.653	0.635	0.291	0.890
Depletion in 2040	0.985	0.915	0.411	0.999	0.983	0.919	0.458	0.999
	No observed growth rate, FGIA + WGIA				Falkland catches			
	Median	Mean	2.5%	97.5%	Median	Mean	2.5%	97.5%
r_{max}	0.065	0.062	0.006	0.104	0.069	0.067	0.013	0.104
K	24,790	25,620	22,802	33,849	24,746	25,271	22,996	31,318
N_{min}	562	1,095	160	5,131	542	862	161	3,883
N_{2006}	6,809	6,905	4,893	9,421	6,842	6,923	4,872	9,521
Max Depletion	0.023	0.039	0.007	0.152	0.022	0.032	0.007	0.123
Depletion in 2006	0.270	0.273	0.173	0.390	0.272	0.276	0.182	0.392
Depletion in 2020	0.588	0.573	0.203	0.884	0.620	0.601	0.241	0.884
Depletion in 2040	0.961	0.834	0.233	0.999	0.973	0.882	0.312	0.999
	Fringe catches				Overlap catches			
	Median	Mean	2.5%	97.5%	Median	Mean	2.5%	97.5%
r_{max}	0.069	0.066	0.014	0.103	0.069	0.066	0.014	0.104
K	24,602	25,171	22,847	31,363	20,969	21,495	19,444	26,997
N_{min}	515	840	162	3,800	566	922	162	3,885
N_{2006}	6,844	6,938	4,893	9,556	6,816	6,928	4,909	9,557
Max Depletion	0.021	0.031	0.007	0.120	0.027	0.040	0.008	0.143
Depletion in 2006	0.275	0.278	0.182	0.395	0.321	0.325	0.210	0.466
Depletion in 2020	0.623	0.604	0.243	0.886	0.692	0.664	0.273	0.925
Depletion in 2040	0.974	0.882	0.324	0.999	0.983	0.902	0.362	1.000

therefore more informative results were obtained. Finally, the removal of the observed growth rate resulted in greater uncertainty in parameter estimates, a slightly lower estimate of r_{max} and a slightly more pessimistic estimate of current population status (Table 5). Despite all these differences, the posterior probability distributions of all depletion parameters in the data inclusion scenarios were relatively consistent with those obtained in the BC scenario (Fig. 4).

Sensitivity to catch allocation hypothesis

The posterior medians of the model parameters estimated with the Fringe and the Falkland Island catches were similar between the BC scenario (the Core catches) and the Fringe catches (Table 5, Fig. 6), suggesting almost no difference in results between these catch allocation hypotheses. In contrast, the scenario with the Overlap catch allocation hypothesis produced lower and higher posterior medians of

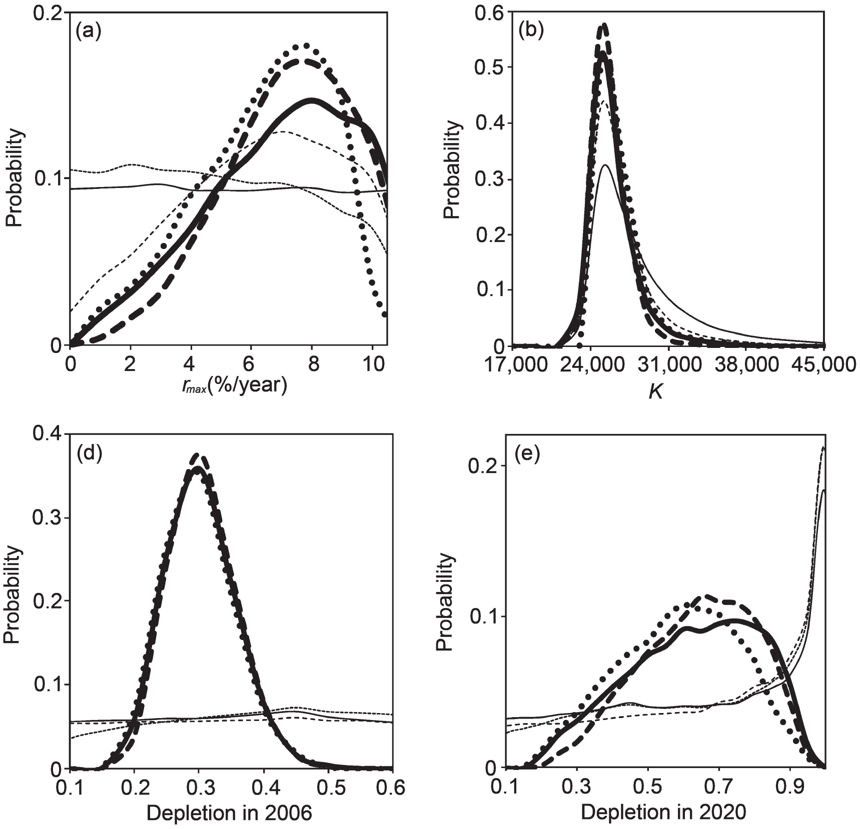

Fig. 2. Posterior (thick lines) and realised prior (thin lines) probability distributions of model parameters and other quantities of interest for the 'Choice of Prior' and 'Genetic Constraint' sensitivity analyses (solid lines = base case; dashed line = baleen whale meta-analysis prior; and dotted line = genetic constraint).

K and of the current (2006) status, respectively. The posterior distribution of *K* between the Overlap and the other catch allocation hypothesis showed very little overlap (Fig. 6B). Also, the Overlap scenario produced more optimistic projections of the recovery of the WSA humpback whale population (Fig. 6).

DISCUSSION

In this study, multiple scenarios were presented to assess the status of the humpback whale population wintering off the eastern coast of South America. They include the use of a different prior distribution for the maximum net recruitment rate, model adjustment to different sets of data and catch allocations. While some variation in the model outputs existed depending on the prior/data used, consistency was observed in almost all scenarios.

The use of an informative prior on r_{max} (the baleen whale on population growth rates hierarchical meta-analysis) (Branch *et al.*, 2004) had very little effect in the model outputs relative to the base case. The posterior median was the same and the posterior distribution was slightly more precise. Gain in precision is a result of the use on a more informative prior relative to the uniform distribution used in the base case, but because the informative prior itself had a relatively low precision (CV = 0.6), the gain is negligible.

Adding a genetic constraint resulted in small changes in the posterior median of the model outputs. The maximum depletion level was greater and the depletion parameters were less optimistic than the BC scenario. The purpose of adding a genetic constraint was to prevent the model from reaching a minimum population size (264 individuals) that was unrealistic given the known genetic diversity of the population. This resulted in eliminating predicted population trajectories with high growth rates as illustrated in Fig. 2 and Table 5, where the posterior median and the upper boundary of r_{max} are lower than those estimated by the base case. Although lower values of r_{max} also resulted in slightly more pessimistic posterior medians of the depletion parameters, their posterior distribution overlapped to a great extent (Fig. 2).

Inclusion of the indices of abundance resulted only in small differences in posterior medians and slightly more precise estimates of model outputs. The main reason for that

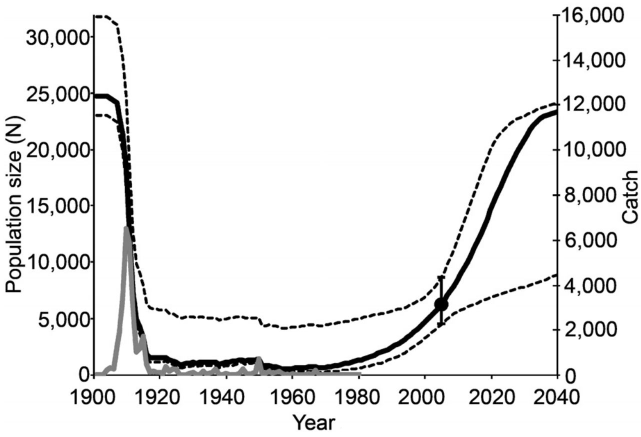

Fig. 3. Population trajectory and fit of the model to the absolute abundance in 2005 of the Base Case scenario. The solid line correspond to the posterior median, dashed lines to the 95% probability intervals, error bars to the 95% confidence intervals of the abundance estimate and the grey line to the Core catch series.

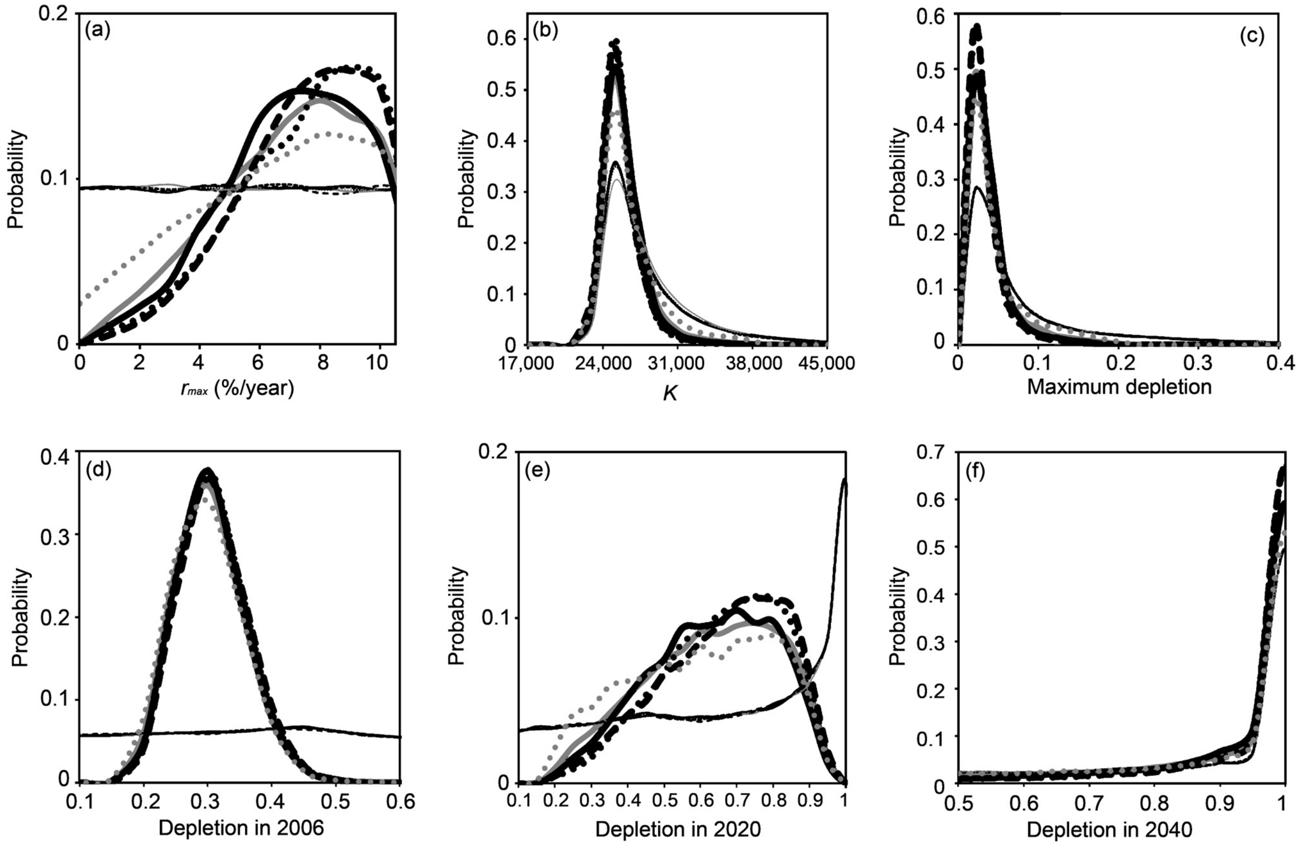

Fig. 4. Posterior (thick lines) and realised prior (thin lines) probability distributions of model parameters and other quantities of interest for the 'Data Inclusion' sensitivity analyses (solid line = FGIA; dashed line = WGIA; and dotted line = FGIA + WGIA). The posterior and prior distributions for the base case scenario are illustrated as a thick gray line for comparison.

is that the indices of abundance used in this study are not very informative. The estimates of abundance from the IDCR/SOWER surveys, despite covering a relatively large period of time (1981/82–1997/98) have poor precision (CVs = 0.59–0.91). The WG estimates of relative abundance, in contrast, have better precision (CVs = 0.19–0.2), but cover only three consecutive years, which is a short period of time to accurately estimate trends in abundance. The removal of the observed growth rate did not result in significant changes in the posterior medians, but it did result in greater uncertainty. Loss of precision occurred because the observed growth rate was informative for the estimation of the maximum intrinsic growth rate despite its relatively large CV (0.48).

Uncertainty in catch allocation in the feeding grounds was tested using four catch allocation scenarios. The use of Core (Base Case), Fringe and Falkland Catches allocation scenarios resulted in similar posterior distributions for model parameters and other quantities of interest. This resulted because the catch series among these scenarios were similar. Only 600 more catches were included in the Fringe hypothesis, a difference of less than 2% relative to Core. These catches originated in the Fringe area between BSA and BSB in the central south Atlantic, where not many humpback whales were taken historically. In addition, only 219 more whales were taken in the Falkland Islands relative to Core. Only the use of the Overlap allocation hypothesis resulted in substantial differences in the posterior distribution of model parameters. These differences were a result of the much lower (nearly 4,000 less) catch allocated to BSA under the Overlap relative to the Core hypothesis. The posterior median of *K* was nearly 20% lower and, consequently, the status parameters were more optimistic than the Base Case scenario. The Overlap scenario assumed that 10% of the catches corresponded to whales caught in the feeding grounds associated with BSG and another 10% in the feeding grounds associated to BSB. Because catches in these feeding grounds were much lower (nearly 15,000 and 5,000 whales, respectively) than those from BSA (over 29,000 whales), the resulting total catch series under the Overlap hypothesis is lower. Contemporary information from photo-identification, genetic and satellite telemetry data do not support an overlap of whales from Brazil with the feeding grounds associated with BSG (the Antarctic Peninsula) (Dalla Rosa *et al.*, 2008; Olavarria *et al.*, 2000; Rosenbaum *et al.*, 2000; Stevick *et al.*, 2004; Stevick *et al.*, 2006; Zerbini *et al.*, 2006; 2011). Therefore it is possible that the overlap between whales from the two wintering grounds may not be realistic, indicating that results obtained with the Overlap scenario should be viewed with caution.

There was great uncertainty in estimating r_{max}, across all sensitivity scenarios. This is illustrated by the relatively broad shape of the posterior probability distribution of this parameter (Figs 1A, 3A and 4A). However, the posterior distribution does indicate that r_{max} for the humpback whale BSA is on the higher end of possible values. The posterior median ranged from 6.2–7.5%/year and there was high probability that it falls between 6–10%/year. These results are consistent with other estimates of the maximum net recruitment rate of humpback whales in both the Northern and Southern Hemispheres. For example, Stevick *et al.* (2003) fit a generalised logistic model to a time series of abundance estimates of humpback whales in the North Atlantic and estimated that r_{max} was 0.078 (8.1%/year) and

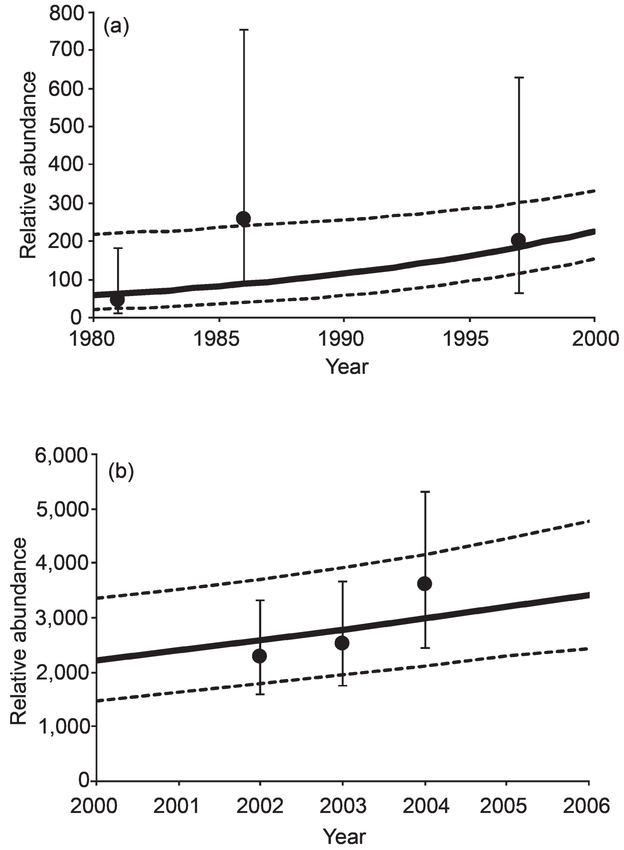

Fig. 5. Fit of the model to the indices of relative abundance in the feeding grounds (A, FGIA scenario) and wintering grounds (B, WGIA scenario). Solid lines correspond to the posterior median, dashed lines to the 95% probability intervals and error bars to the 95% confidence intervals of individual relative abundance estimates.

Johnston *et al.* (2011) have estimated that the r_{max} posterior medians for the Southern Hemisphere humpback whale stock wintering off the western South American coast (BSG) ranged from 6–7%/year, depending on the modeling scenario considered.

The models predicted that if no human-induced mortality occurs, BSA should be near 60% of *K* within the next 15 years and should be nearly recovered by 2040. However, predictions of the population status in the future are highly uncertain as revealed by their wide probability intervals. In addition, these predictions are likely unrealistic because this population has been subject to non-natural mortality due to incidental catches in fishing nets, habitat degradation, and possibly to the development of the oil and gas industry in part of the species habitat (e.g. Engel *et al.*, 2004; Siciliano, 1987; Zerbini and Kotas, 1998). Current levels of human-induced mortality are not known and therefore it is difficult to predict what impact they might have in the recovery of this population. However, if population parameters such as reproductive rates and/or survival are reduced due to anthropogenic factors, a longer period will be required before this stock reaches carrying capacity.

The catch data had the highest impact on the estimate of *K* and therefore misallocation of catches or underreporting should cause bias in the estimate of the status parameters. Zerbini (2004) showed that an increase (as an example to simulate for missing catches) or a reduction (another example to simulate for misallocation) of 20% in the catches, resulted, respectively, in an increase or decrease in nearly 20% in the estimated posterior median of *K*. This positive correlation between the total catch and the estimate of *K* is also clearly visible in this study (e.g. by comparing results obtained for the Core and Overlap models). Underreporting of catches is likely an issue for the WSA humpback whale population. For example, the coastal whaling station in Costinha, northeastern Brazil, operated from 1910 to 1915, closed from 1915 to 1923, and operated again from 1924 to 1985 (da Rocha, 1983; Williamson, 1975), but catches were not reported in 1910 and between 1929 and 1946. Because humpbacks whales were the only species taken previously to this period and were regularly taken in subsequent years it is very likely that they were also taken during the period for which catches are missing. Underreporting of catches will cause an upward bias in the estimate of the current status. The magnitude of the bias is unknown as its estimation depends on the number of whales killed but not reported. However, because catches off Brazil have consistently been low (less than 400 individuals in any given year (Williamson, 1975)) and because the 1929–1946 catches from Costinha correspond to a period in which the population had already been severely depleted (Findlay, 2001), it is possible a small number of catches is missing.

The BC estimated that the WSA humpback whale population is at 27% of its pre-exploitation population size, but the actual status of this population is possibly some unknown number lower than this figure. In addition, for the purpose of the analyses presented here, it is assumed that the population was at carrying capacity before catches were taken in the early 1900s. However, humpback whales were likely caught off the coast of Brazil since at least the 17th century (Ellis, 1969; Lodi, 1992; Smith *et al.*, 2006). The catch history is not known because records were not kept. However, Lodi (1992) indicated that around 50 whales were taken every year. If catches were indeed of this magnitude, it is likely that population was close but not quite at *K* at the beginning of modern whaling.

The present study provides the first assessment of the humpback whale population wintering off Brazil. This analysis was relatively straightforward, mainly as a consequence of data limitation. For example, the model used is a relatively simple population dynamics model. Alternative models (e.g. age-structured) applied in the assessment of other whale species (e.g. bowhead whales [Brandon *et al.,* 2007; Punt and Butterworth, 1999] and gray whales [Wade, 2002]) could not be used in this study because life-history parameters (e.g. survival, fecundity) and age structure of the catches are not available for the population wintering off Brazil. Lack of other proposed models precludes an assessment of the impact of model uncertainty in this analysis. In addition, it is important to note that additional sources of uncertainty were not included in the analysis. For example, the variances associated to the likelihood equations are assumed to be known, resulting in posterior distributions with lighter tails than would be obtained if these parameters were also estimated (e.g. were given prior distributions). In addition, the population dynamic model ignores process variation and assumes a deterministic trajectory of population size, precluding the use of the true-likelihoods as described in de Valpine (2002). This author showed examples for which the use the true likelihoods improves maximum likelihood estimation over procedures that ignore process noise. The impact of omitting these other sources of uncertainty in the Bayesian inference presented here will be dependent on the balance of information between the priors and the data and should be further investigated in assessment models of

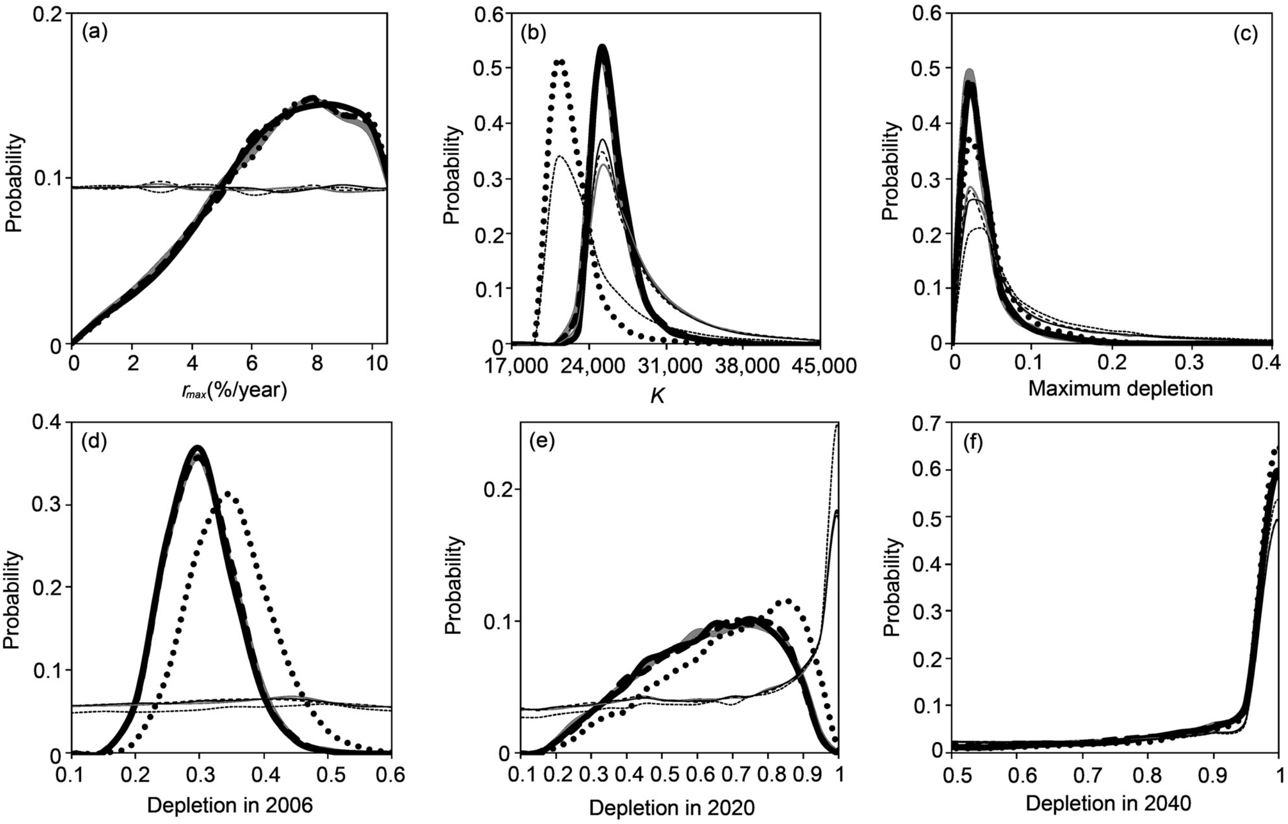

Fig. 6. Posterior (thick lines) and realised prior (thin lines) probability distributions of model parameters and other quantities of interest for the 'Catch Allocation' sensitivity analyses (solid lines = Falkland catches, dashed lines = Fringe hypothesis; dotted line = Overlap hypothesis). The posterior and prior distributions for the base case scenario are illustrated in gray for comparison.

humpback whales. This should be made in conjunction with improvements of the present assessment as more data become available.

CONCLUSION

Despite the uncertainty in estimating r_{max}, estimates of *K* and the status parameters were relatively robust across most scenarios presented in this assessment. Results show high posterior probabilities that:

(1) *K* is within 22,000–28,000 whales;
(2) The population was depleted to less than 4% of its pre-exploitation size in the late 1950s;
(3) The current abundance is between 26 and 32% of *K*.

The results were encouraging as they showed that the humpback whale population in the west South Atlantic has been recovering during the past three decades, after being dramatically reduced by whaling in the early 1900s. However, potential underreporting of catches may have resulted in optimistic estimates of depletion levels. The current estimates indicate that this population is still low relative to historical levels and therefore it requires continued conservation efforts.

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Estimates of population growth rates of humpback whales (*Megaptera novaeangliae*) in the wintering grounds off the coast of Brazil (Breeding Stock A)

Eric Ward[*], Alexandre N. Zerbini[*,+,#], Paul G. Kinas[^], Márcia H. Engel[++] and Artur Andriolo[+,~]

Contact e-mail: warde@u.washington.edu

ABSTRACT

Humpback whales wintering off the eastern coast of Brazil were heavily exploited by commercial whaling in the Southern Hemisphere. During recent years, clear signs of recovery have been observed, but few estimates of population growth rate exist. In this study, quantitative estimates of rates of population increase are obtained from sighting per unit of effort data (1995–98) using generalised linear models and maximum likelihood estimation. The error distributions considered for the models were Poisson and negative binomial. Predictors of the number of sightings included the year, month and 2-week periods during which the sightings were made. Predictors were treated as factors or numeric variables. For the numeric variables, quadratic dependence was also considered for each predictor to allow for possible non-linear relationships. Using Akaike Information Criterion (AICc) as a model selection criterion, the best model included year and month as continuous predictors. The data indicated strong support for the negative binomial over the Poisson models, but did not support models based on a finer temporal scale than month. Assuming year to be a linear predictor, the best estimate of the growth rate for the population wintering off Brazil was 7.4% per year (95% CI = 0.6–14.5%) during the period 1995–98. This estimate provides additional quantitative evidence that this population has been increasing and is consistent with the observed growth rates of other humpback whale stocks.

KEYWORDS: HUMPBACK WHALE; INDEX OF ABUNDANCE; MODELLING; TRENDS; BREEDING GROUNDS; SOUTH ATLANTIC

INTRODUCTION

Humpback whales (*Megaptera novaeangliae*) are present along the eastern coast of Brazil during winter and spring, where breeding and calving takes place (e.g. Andriolo *et al.*, 2010; Martins *et al.*, 2001; Zerbini *et al.*, 2004). By late spring, whales migrate through offshore areas to the Scotia Sea in the southern South Atlantic Ocean (Zerbini *et al.*, 2006) and concentrate in feeding grounds near South Georgia and the South Sandwich Archipelago (Stevick *et al.*, 2006; Zerbini *et al.*, 2011a; Zerbini *et al.*, 2006). This population is referred to as 'Breeding Stock A' (BSA) by the International Whaling Commission (IWC, 1998; 2005).

Individuals from this population were hunted by coastal and small scale offshore operations in the wintering grounds off the coast of Brazil from at least the 17th century (Ellis, 1969; Lodi, 1994). The introduction of modern whaling techniques in the early 1900s increased catches in the wintering grounds but, most importantly, promoted the expansion of whaling to high density areas in feeding grounds in the Antarctic Ocean (e.g. Findlay, 2001; Tønnessen and Johnsen, 1982; Williamson, 1975). The bulk of the feeding ground catches of BSA whales occurred around South Georgia, where approximately 27,000 whales were taken between 1904 and 1920 (Allison, 2006; Findlay, 2001). This substantial catch severely reduced the population to a point where humpback whales became rare in the South Atlantic Ocean. Protection from whaling was imposed by the IWC in the late 1960s, but some whales were taken by the Soviet fleet in both the feeding and the wintering grounds in subsequent years (e.g. Yablokov *et al.*, 1998).

Contemporary studies of humpback whales off the coast of Brazil commenced in the late 1980s. Research initially focused on the Abrolhos Bank area (~18º30'S, 38º30'W) (Martins *et al.*, 2001; Siciliano, 1995; 1997), which is considered the main breeding ground for the species in the western South Atlantic Ocean (Andriolo *et al.*, 2010). However, studies expanded to other areas along the Brazilian coast as the population expanded its distribution to historical wintering habitats (e.g. Andriolo *et al.*, 2010; Zerbini *et al.*, 2004).

During the past 20 years, the population of humpback whales breeding off the coast of Brazil has shown clear signs of recovery. Sightings, strandings and occasions when whales were seen interacting with fisheries have become more common (Pizzorno *et al.*, 1998; Siciliano, 1987; Zerbini and Kotas, 1998) and whales have been observed reoccupying historical areas of distribution (e.g. the northeastern coast of Brazil), (Zerbini *et al.*, 2004) after being nearly absent for several decades (Antonelli *et al.*, 1987). Despite that, the rate at which recovery is occurring is poorly known. Freitas *et al.* (2004) estimated that the annual growth rate of this population was 30.6% (95% CI = 2.6–60.0%) from a time series (1996–2000) of mark-recapture abundance estimates. While the precision is low and the point estimate is well above the maximum plausible for humpback whales (11.8% per year) (Zerbini *et al.*, 2010), this estimate provides additional evidence that the population is increasing.

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[*] *School of Aquatic and Fishery Sciences, University of Washington, Box 355020, Seattle, WA, 98195-5020, USA.*

[+] *Projeto Monitoramento de Baleias por Satélite, Instituto Aqualie, R. Edgard Werneck 428/32, Rio de Janeiro, RJ, 22763-010, Brazil.*

[#] *National Marine Mammal Laboratory, Alaska Fisheries Science Center, NOAA Fisheries, 7600 Sand Point Way NE, Seattle, WA, 98115-6349, USA.*

[^] *Laboratório de Estatística, Departamento de Matemática, Fundação Universidade Federal do Rio Grande, Rio Grande, RS, Brazil.*

[++] *Instituto Baleia Jubarte/Humpback Whale Institute, Rua Barão do Rio Branco, 26, Caravelas, BA, Brazil.*

[~] *Departamento de Zoologia, Instituto de Ciências Biológicas, Universidade Federal de Juiz de Fora, MG, Brazil.*

In this study, general linear models (GLMs) are applied to sighting data collected in the Abrolhos Bank (Martins *et al.*, 2001) in an attempt to estimate the growth rate of the population between 1995 and 1998. This estimate provides additional quantitative information on the growth rate of this stock to be incorporated in population assessment models (Zerbini *et al.*, 2011b).

METHODS

The data

Sighting and effort data were gathered to investigate the distribution, seasonality and habitat use of whales in the Abrolhos Bank from June to November over the period from 1992 to 1998. However, this information was collected in a systematic and comparable fashion only over the period from 1995 to 1998, as described by Martins *et al.* (2001). Cruises were conducted for four days each week, with searches carried out by a team of three observers under relatively good weather and sea conditions (wind speed <20 knots). The ship followed pre-determined transects in the Abrolhos Bank area at an average speed of nine knots. When a group of whales was sighted, the vessel deviated from the trackline to conduct photo-identification and biopsy sampling for as much as 30 minutes, after which it returned to the previous course. On some occasions, when the density of whales in the area was high, the trackline would be abandoned for the day in order to allow photo-identification and biopsy sampling from other whale groups. Martins *et al.* (2001) stratified the data into two-week periods each year, resulting in a total of eight periods per year (Table 1).

Modelling framework and data analysis

The sightings-per-unit-of-effort (SPUE) data were analysed using a GLM framework, which extends the standard linear model by assuming a non-Gaussian error structure, and utilises a 'link' function that transforms non-linear data to fit the assumptions of linear models (McCullagh and Nelder, 1989; Venables and Ripley, 2002). The GLM framework has seen widespread applications in ecology, particularly for problems involving count data (Link and Sauer, 2002). The simplest GLM for count data customarily assumes a Poisson error distribution, and a logarithmic link function. This model has also been termed a log-linear regression model, because the logarithm of the Poisson parameter (u) is taken to be a linear function of the parameters and data:

$$\log\left(u\right) = \beta_0 + \beta_1 X_1 + \beta_2 X_2 + X_3$$

where u represents the mean number of humpback sightings, B_0, B_1, and B_2 are regression coefficients, X_1 and X_2 are covariates, and X_3 represents an optional offset term (or covariate with a coefficient of 1.0) to account for unequal search effort between sampling occasions (e.g. Coronado and Hilborn, 1998).

One problem with assuming that error is Poisson distributed is that the error variance is constrained to be equal to the mean (u). An alternative to the Poisson model is the negative binomial model (Hilborn and Mangel, 1997). The negative binomial distribution is more flexible than the Poisson distribution because it allows the variance to be a function of both the mean and an additional overdispersion parameter (θ). The negative binomial is often better suited to ecological data because many such data sets may include correlated observations, or an excess of zeros ('zero-inflated') (Hilborn and Mangel, 1997). The overdispersion parameter of the negative binomial distribution allows for the aggregated distribution of individuals (such as those encountered in the Abrolhos Bank area), whereas the Poisson distribution assumes individuals to be randomly distributed.

In this analysis, both Poisson and negative binomial models were applied to the sighting data from the humpback whales wintering in the Abrolhos Bank (Table 1). Covariates considered as predictor variables of humpback sightings included Year and either Month or Period (the 2-week block during which the sighting was made). Month, Period and Year were considered both as continuous variables and factors (Month = 7–12; Period = 1–10; Year = 1995–98), but the Month and (two-week) Period were not allowed to act as predictors in the same model to avoid redundancy. To determine whether there was evidence for a non-linear relationship between sightings and temporal variables, possible quadratic dependence was also explored. As the total number of observations was relatively small (n = 40, 20 records from each period), Akaike Information Criterion corrected for small sample sizes (AICc) was used as a model selection criterion to indicate the most appropriate model (Burnham and Anderson, 2002). Addressing model selection in a statistical framework allowed evaluation of which hypotheses about predictor variables and error structures are best supported by the data.

The ultimate objective of this study was to quantify the annual rate of increase or Year effect of the SPUE data over the period 1995–98, so that this information might be incorporated into the stock assessment of BSA, assuming that it reflects the growth rate of the whole population

Table 1

Sighting and search effort data collected on the Abrolhos Bank, which is a wintering ground for humpback whales from breeding stock A (BSA), from 1995–98 (after Martins *et al.*, 2001).

	1995		1996		1997		1998	
Period	No. of sightings	Effort (hr)	No. of sightings	Effort (hr)	No. of sightings	Effort (hr)	No. of sightings	Effort (hr)
1–15 Jul.	31	15.4	35	21.3	83	56.6	72	50
16–31 Jul.	78	38.9	44	37	74	38.9	91	42.4
1–15 Aug.	44	37.8	106	41.5	118	66	127	68.6
16–31 Aug.	142	69.75	153	55.6	177	63	211	106.3
1–15 Sep.	60	26	71	26.1	89	29.3	62	26.6
16–30 Sep.	108	66.3	121	42.75	127	46.7	54	23.25
1–15 Oct.	36	29.5	43	22.1	89	68	121	56.1
16–31 Oct.	59	51.3	72	42.1	36	25.25	24	8.16
1–15 Nov.	30	36.1	34	36.1	25	29.1	25	22.5
16–31 Nov.	4	7.75	22	30.1	53	41.5	12	9.9
Total	**592**	**378.8**	**701**	**354.65**	**871**	**464.35**	**799**	**413.81**

wintering off eastern South America. The annual growth rate from one year to the next is defined as:

$$\lambda = \frac{N_{t+1} - N_t}{N_t}$$

with the instantaneous rate of change (r) as estimated by the GLM transformed into an annual rate by the relationship: $\lambda = \exp(r) - 1$. Additional objectives were to address: (1) whether there is evidence for over-dispersion in the Abrolhos Bank humpback whale data (whether the negative binomial is favoured over the Poisson distribution); (2) whether there is evidence for quadratic dependence on the Year variable rather than linear dependence; (3) whether Period or Month is a better predictor of the number of sightings; and (4) whether there is evidence for quadratic dependence on either the Period or the Month variable.

RESULTS

A large number of GLMs were evaluated for the full data set (the best fitting model and several related models appear in Table 1). The model of humpback whale sightings with the lowest AICc score was one that assumed a negative binomial error distribution, treated the Year variable as a linear predictor and assumed quadratic dependence on the Month variable (Fig. 1). This model suggested that the humpback whale population wintering off Brazil increased by 7.4% per year (95% CI = 0.6–14.5% per year) from 1995 to 1998. The results for other models (Table 2) are presented in terms of the AICc values relative to the lowest score (this difference being denoted by ΔAICc). As a general rule of thumb, models with ΔAICc values that are less than two should be given consideration in addition to the selected model, while models with ΔAICc values that are more than ten should receive little consideration (Burnham and Anderson, 2002).

The first question addressed by the analysis was whether there was more support for the negative binomial error distribution or the Poisson error distribution. For all models considered, the negative binomial model consistently performed better, resulting in lower AICc scores when compared to the corresponding Poisson GLM. The negative binomial models had AICc scores that were at least 30 units better than their Poisson counterparts, indicating that they were strongly preferred by the data. Across models that treated Year as a linear predictor, accepting the negative binomial model resulted in maximum likelihood estimates of the annual growth rate parameter (Year effect) that were 30–50% larger than their Poisson counterparts (Table 2). A second important result was that the standard errors of the Year effect were nearly twice as high for negative binomial models compared to Poisson models, reflecting that the latter's ignoring of correlations between sightings leads to overestimation of precision. Although the autocorrelation between standardised residuals was small for both models, another difference between the negative binomial and Poisson models was that the Poisson models had slightly higher autocorrelation (–0.15 compared to 0.015 for the negative binomial; Fig. 2).

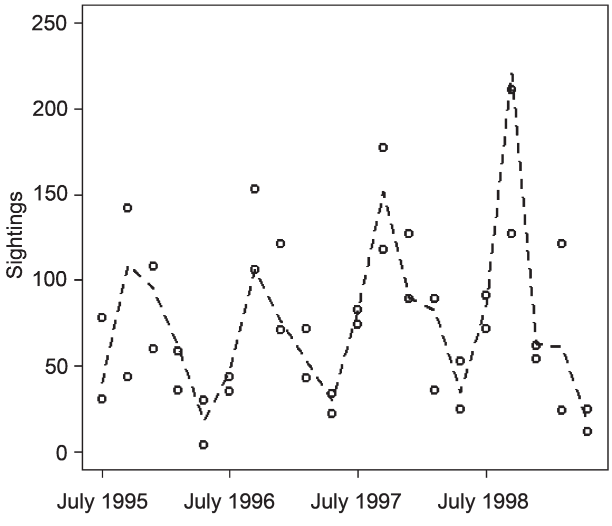

Fig. 1. Plot showing the observed data (Table 1) and the fit from the model with the lowest AICc (Model 1, Table 2). In addition to the Year effect, this model assumes count to be a quadratic function of month. For simplicity, the dashed line has been drawn to show the mean model-predicted number of sightings for each month.

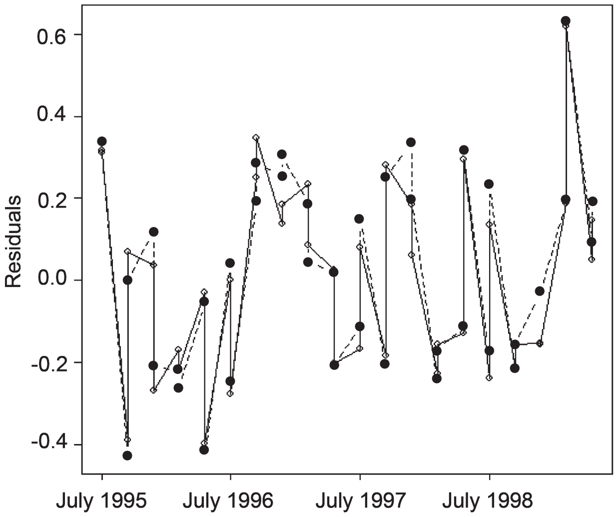

Fig. 2. Standardised residuals for two selected models in Table 2. The open circles and solid line correspond to the model with negative binomial error structure (Model 1, Table 2), whereas the dashed line and closed circles represent the corresponding model with a Poisson error structure (Model 7, Table 2). In addition to the Year effect, these models assume abundance to be a quadratic function of month. The residual with the largest magnitude occurred in the latter half of 1998 surveys.

The second issue investigated was whether there was greater support for a model that treated the Year dependence as quadratic. For a negative binomial GLM with quadratic dependence on Month, adding a quadratic term for Year resulted in a ΔAICc value of 0.51, relative to the model that assumed the Year effect was linear, so that the latter was preferred.

As the SPUE data have been broken down into 2-week blocks as well as by month, it was also important to investigate whether either of these predictor variables should be treated as a factor or as a continuous variable. When Month was used alongside Year as a predictor variable, a GLM that considered quadratic dependence on Month performed better than a GLM that considered Month as a factor (Table 2, ΔAICc = 3.3). Regardless of whether Month was treated as a factor or continuous variable, the overall trend was similar (Fig. 3). The same result was found for the 2-week Period variable – assuming a quadratic dependence on Period resulted in better performance than treating Period as a factor (Table 2, ΔAICc = 12.2). Although the factor model was not favoured over quadratic dependence in either case, it did perform better than models that assumed linear dependence on Month or Period. Unlike the comparison between the Poisson and negative binomial distributions, the

Table 2

Poisson and negative binomial models of humpback whale sightings, using year, month, and (two-week) period as predictor variables. Month and Period may be factors (F), or continuous variables (N) upon which the count depends quadratically. For each model, the estimated Year effect expressed as an annual increase rate and the associated 95% confidence interval (CI) are included. The best model according to the AICc criterion is highlighted in bold.

Model	Error	Number of parameters	Year effect	95% CI	Month	Period	ΔAICc
1	**Negative Binomial**	**5**	**7.4%**	**0.6 – 14.5%**	**N**	**–**	**0**
2	Negative Binomial	7	7.4%	0.8 – 14.3%	F	–	3.29
3	Negative Binomial	5	7.4%	0.4 – 14.8%	–	N	3.79
4	Negative Binomial	12	7.4%	1.4 – 13.6%	–	F	16
5	Poisson	11	5.7%	2.2 – 9.2%	–	F	47.03
6	Poisson	6	5.5%	2.1 – 9.1%	F	–	50.97
7	Poisson	4	5.0%	1.6 – 8.6%	N	–	55.73
8	Poisson	4	4.7%	1.3 – 8.2%	–	N	57.24

choice of predictor variables appeared to have little influence on the Year effect, with all annual growth rate estimates being ~7.4% (Table 2).

DISCUSSION

This analysis explored alternative GLM models of humpback whale sighting data, with the aim of finding a model that was best supported by the data. The model that received the most support was a negative binomial GLM that assumed linear dependence on Year and quadratic dependence on Month (Model 1, Table 2). The estimated Year coefficient was 0.071 (SE = 0.033), suggesting that over the period 1995–98, humpback whale sightings off Abrolhos Bank increased at 7.4% annually. This estimated annual trend for the corresponding Poisson GLM with a linear Year effect (Model 7, Table 2) was lower (~5% per year), however the data did not support the Poisson model assumption.

The negative binomial model with the lowest AICc score treated Month dependence as quadratic, rather than as a factor variable. The trend in the estimated Month effect is similar, regardless of the model chosen; sightings increase from July to September and then proceed to decrease from summer to late autumn. This is consistent with the seasonal variation in abundance observed for this population off Brazil (Siciliano, 1997). A further question concerning intra-annual trends addressed in this study was whether use of a finer temporal scale (the two-week Period) was a better explanation of the variation in the data compared to a coarser scale (Month). The analysis suggested the latter was to be preferred, probably because the observation error associated with the count data may be too high to detect a fine scale temporal trend (e.g. the number of whales in Abrolhos Bank over the course of a particular month).

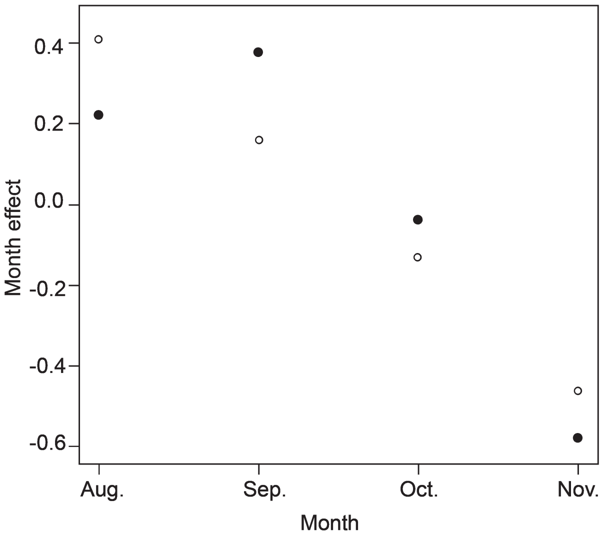

Fig. 3. Estimated Month effects for a model that treats the Month variable as a factor (solid circles; Model 2, Table 2), and a model that assumes quadratic dependence on Month (open circles; Model 1, Table 2).

Ideally, the output from the analysis presented here will be incorporated into the current assessment of this humpback whale stock (Zerbini *et al.*, 2011b). Although sighting data from Abrolhos Bank are not absolute indices of abundance, it is possible to include the annual growth rate (related to the Year effect in these GLMs) into the likelihood as the observed growth rate over the period 1995–98. It should be noted that there are important tradeoffs in assuming a negative binomial error structure over a Poisson error structure on the estimate of the Year effect. The Year coefficient in the negative binomial model is approximately 45% larger (7.4% compared to 5%) than that for the Poisson model, but the associated standard error for the Poisson model is approximately half that for the negative binomial model.

The Year effect estimated by the selected model is taken to correspond to the rate of increase of humpback whales wintering off the coast of Brazil between 1995 and 1998. This estimate (7.4% per year, 95% CI = 0.6–14.5%) presents additional quantitative evidence that humpback whale populations are increasing in the western South Atlantic Ocean. In addition, it provides a point estimate for annual growth rate that is realistic from a biological standpoint, when compared to the previous estimate reported by Freitas *et al.* (2004), 30.6% (95% CI = 2.6–60.0%). While the two confidence intervals overlap, the latter has much poorer precision and the point estimate is well above what is considered plausible for humpback whale populations (e.g. Zerbini *et al.*, 2010).

Sighting surveys conducted by Martins *et al.* (2001) covered the central portion of the Abrolhos Bank. This region includes most of the population of humpback whales wintering off the coast of Brazil and is considered the optimum habitat for the species on its breeding grounds. Because whales on their wintering grounds concentrate first on finding optimal habitat, the estimate of growth rate presented here could be downwardly biased. Once this area becomes full (saturated), the rate of growth would decrease and further whales would move to other, non-surveyed and previously uninhabited regions, which would show a greater rate of growth. The actual population rate of increase would be a combination of the growth in the optimal habitat and the rate of expansion to more peripheral areas.

The rates of increase presented here are consistent with those observed for other humpback whale populations. In the North Atlantic, North Pacific and elsewhere in the Southern Hemisphere, growth rate estimates for humpback whale stock varied between 3% and 15% per year (e.g. Bannister, 1994; Best, 1993; Clapham *et al.*, 2003; Mizroch *et al.*, 2004; Sigurjónsson and Gunnlaugsson, 1990; Stevick *et al.*, 2003).

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Line transect estimates of humpback whale abundance and distribution on their wintering grounds in the coastal waters of Gabon

Samantha Strindberg*, Peter J. Ersts⁺, Tim Collins*, Guy-Philippe Sounguet# and Howard C. Rosenbaum*⁺^

Contact e-mail: sstrindberg@wcs.org

ABSTRACT

There have been few recent estimates of abundance for humpback whales (*Megaptera novaeangliae*) in the eastern South Atlantic Ocean. The first distance sampling survey of the coastal waters of Gabon was conducted in 2002. The difficult logistics of covering a large survey region with limited time, effort and refuelling opportunities required a line transect survey design that carefully balanced the theoretical demands of distance sampling with these constraints. Inshore/offshore zigzag transects were conducted to a distance of up to approximately 50 n.miles from the coast of Gabon corresponding to the 1,000m depth contour, from the border with Equatorial Guinea to a point south of Mayumba, near the Congo border representing 1,488 n.miles of survey effort. Seventy-nine different groups of humpback whales were observed throughout the survey area comprising a northern (Equatorial Guinea to Cap Lopez) and southern (Cap Lopez to Gamba) survey stratum. Relatively large numbers of whales were encountered throughout the southern stratum; encounter rates and densities were considerably lower in the northern stratum. The initial abundance estimate from a distance sampling analysis suggests that more than 1,200 humpback whales were present in Gabon's coastal waters during the survey period. This estimate does not account for either availability or perception bias. In addition, this instantaneous snapshot of the number of whales occupying Gabon's coastal waters is likely to correspond to only a portion of the population that uses these waters over time. However, the abundance estimate derived from the aerial survey are consistent with those based on photographic and genetic capture-recapture techniques. A continuing research programme in this area will help refine estimates of humpback whale abundance and using genetic and photographic data also establish the relationships between this and other populations. This is important given the potential overlap of humpback whales in large numbers throughout this region and the current extent and continued expansion of hydrocarbon exploration and extraction activities throughout the Gulf of Guinea.

KEYWORDS: ABUNDANCE ESTIMATE; SURVEY–AERIAL; AFRICA; ATLANTIC OCEAN; SAMPLING STRATEGY; G(0); MODELLING; HUMPBACK WHALE

INTRODUCTION

Early last century populations of Southern Hemisphere humpback whales declined markedly as a result of intense whaling on both the Antarctic feeding and tropical breeding grounds (Townsend, 1935). The first substantial recorded catches of humpback whales in the Southern Hemisphere date back to the 18th and 19th Century American pelagic whaling period (Mackintosh, 1942; Starbuck, 1878). Modern commercial whaling began in 1904 and terminated in 1963, although substantial illegal catches occurred after the 1963 moratorium (Yablokov, 1994). It is estimated that humpback whales were severely depleted, and reduced to perhaps as little as 5% of their original population sizes, during the last century (Chapman, 1974; Findlay, 2000). Though substantially depleted, these populations now appear to be undergoing recovery on certain wintering grounds.

The Gulf of Guinea and neighbouring waters experienced extensive whaling activity during the 18th and 19th centuries. In addition, the West Coast of Africa was host to an intensive episode of humpback whaling in the early 20th Century (the population in this region is currently termed Breeding Stock B[1] by the IWC). Shore based stations and factory ships moored at sites along the coast, including Saldanha Bay, South Africa and Cap Lopez, Gabon, caught an estimated 17,000 humpback whales between 1909 and 1914 (Best, pers. comm.; Findlay, 2000). Annual catches tended to be larger nearer the equator (Findlay, 2000) with a peak in catch in late July/early August, whereas at the southernmost whaling stations in Africa there were two clear peaks about four months apart. This catch pattern is indicative of a northern migration in autumn and a southern migration in spring (Budker and Collignon, 1952).

Several cycles of intense commercial exploitation during the middle of the 20th century also contributed to the depletion of this stock (Findlay, 2000). The humpback whale fishery in this region reopened in 1949 at Cap Lopez, Gabon, with an initial catch level of 1,356 whales, which had plummeted to only 264 whales when the fishery was abandoned in 1952 (Aguilar, 1985). Only 160 whales were caught during a failed attempt to restart the fishery in 1959. During this period mean humpback whale length declined substantially according to catch records (Budker and Roux, 1968; Tønnessen and Johnsen, 1982), both cited in Aguilar (1985). The abandonment after only one year of a commercial fishery initiated in São Tomé, and the reduction of the artisanal catch on the island of Annobón (Pagalu), are further evidence that the Gulf of Guinea stock had been greatly depleted (Aguilar, 1985).

A series of small boat-based, limited aerial surveys, and some shore-based studies have been conducted along the west coast of South Africa, Angola, and Gabon and have

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* *Wildlife Conservation Society, Global Conservation, 185th Street and Southern Blvd., Bronx, NY 10460, USA.*

⁺ *Center for Biodiversity and Conservation, American Museum of Natural History, 79th Street and Central Park West, New York, NY 10024, USA.*

\# *Aventures Sans Frontière, B.P. 7248, Libreville, Gabon.*

^ *Sackler Institute for Comparative Genomics, American Museum of Natural History, 79th Street and Central Park West, New York, NY 10024, USA.*

[1] Within Breeding Stock B, there are currently two sub-stocks termed B1 and B2. The boundary dividing these two sub-stocks currently lies in Angola, and is being re-evaluated (Pomilla *et al.*, 2006; Rosenbaum *et al.*, 2009).

been published (Walsh *et al.*, 2000) or reported to the IWC's Scientific Committee (Best *et al.*, 1999; 1995; Collins *et al.*, 2010; 2006; Pomilla *et al.*, 2006; Rosenbaum and Collins, 2006; Rosenbaum *et al.*, 2009). Beginning in 2001, pilot surveys were undertaken off Gabon with the objective of obtaining data for genetic and photographic mark-recapture estimates of abundance for humpback whales wintering off its coast (Collins *et al.*, 2010; 2006). In 2002, an extensive and systematic set of aerial line transect surveys were flown off Gabon's coast in order to provide the first seasonal abundance estimate for the Southern Hemisphere humpback whale breeding assemblage in wintering sub-Region B1. The estimate generated from these aerial surveys, as well as those reported in Collins *et al.* (2010; 2006) should provide a basis for evaluating future trends in the population migrating to this region.

METHODS

Description of the study area and survey design

The study area included the entire coastline of Gabon, approximately 486 n.miles, which extends from Equatorial Guinea (1°N) to the Republic of Congo (4°S), and a section of the Congolese coastline until just beyond Conkouati lagoon mouth. The coastal waters of Gabon are characterised by a continental shelf 50–60 n.miles wide that gently slopes to 100m depth with a rapid depth increase thereafter. The 1,000m depth contour was used as a guideline in defining the outer limit of the study area to permit the observation of humpback whale distribution with respect to considerable changes in bathymetry and at varying distances from the coast, while still being feasible in terms of the available survey effort. The inner limit was defined by the coastline; large river inlets were excluded, as were areas in the vicinity of Libreville and Port Gentil to avoid air traffic in those areas.

The study area was split into two strata, namely a northern and southern stratum of 4,706 n.miles^2 and 12,868 n.miles^2, respectively (Fig. 1). This was done to permit the estimation of separate abundance estimates by stratum and due to the survey logistics given available refueling stations in Libreville, Port Gentil, Iguela, Omboué and Gamba. The northern stratum was delimited by the border with Equatorial Guinea and the tip of Cape Lopez; the southern stratum extended south from Cap Lopez until just beyond Conkouati lagoon mouth. Due to persistent fog, the last seven transects legs in the southern stratum were only partially completed in unfavourable sighting conditions. The observations and effort associated with these transect legs were excluded during analysis and the southern stratum was redefined to exclude the partially surveyed region, reducing this stratum to 9,667 n.miles^2.

The definition of two separate survey strata also facilitated the survey design process, as their shape characteristics allowed for a zigzag design, giving an efficient survey plan with no off-effort time between transects (except that required to travel to and from transects at the start and end of each survey day). In addition, it made it possible to orient

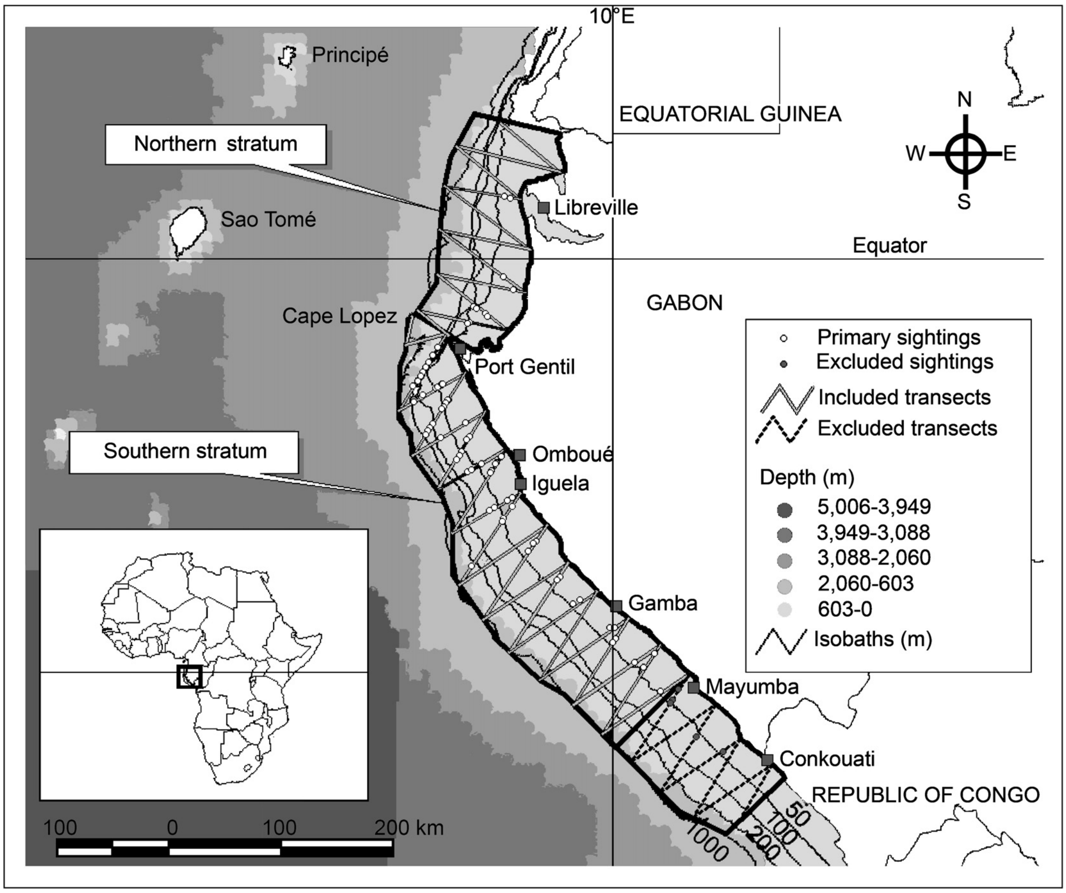

Fig. 1. The study region (bold line) off the Gabon coast delimited by the 1,000m depth contour. The completed line transects in the northern and southern survey stratum are shown as a double line (transects only partially completed and excluded from the analysis are shown as dotted lines). The observations of humpback whale groups made along the survey transects are also shown. The redefined southern stratum that excludes the transects only partially completed due to fog with their five associated observations can also be seen.

Table 1

Details of the study area, survey design with the number of planned/surveyed line transects (k) and planned effort (L_p), as well as the number of observations before truncation (n_{bt}). Also shown are the number of observations (n), the amount of effort (L) and the estimate of encounter rate (n/L) for each stratum with the corresponding standard error (SE), percent coefficient of variation (%CV) and 95% confidence interval (95% CI).

Region	Area (n.m^2)	k	L_p (n.m)	n_{bt}	n	L (n.m)	n/L (n.m^{-1})	SE	(%CV)	95% CI
Study area	14,373	33	1,488.20	74	53	1,348.45	–	–	–	–
Northern stratum	4,706	11	468.83	10	5	446.62	0.011	0.005	44.63	(0.004 – 0.029)
Southern stratum	9,667	22	1,019.37	64	48	902.83	0.053	0.013	24.94	(0.032 – 0.089)
Excluded	3,201	7	298.96	5	–	–	–	–	–	–

the transect legs approximately perpendicular to a suspected density gradient running out from the coast in order to minimise variation in encounter rate and improve the precision of the density estimate. A design axis was used to orientate the line transects and its bearing was defined with respect to an x-axis running in an east-west direction. To orientate the transect legs of the zigzag design approximately perpendicular to the coastline and parallel to the suspected gradient in density, the design axis was set at an angle of 65 and 135 degrees in the northern and southern stratum, respectively.

The automated survey design component of the *Distance* 4 software (Thomas *et al.*, 2010) was changed to produce an amended version of the systematic 'Equal Spaced Zigzag' design with a random start (Strindberg and Buckland, 2004a; 2004b). The amendment to the design included generating the line transects within each survey stratum rather than within a convex hull of each of the survey strata. Given the shape of the strata this led to a more efficient design without any discontinuity in the line transects, which would not have been the case if the usual convex hull were used when generating the transects. It also provided fairly even coverage probability (i.e. the probability of sampling any location in the study area) for this particular survey area, which avoided potentially biased estimates through uneven sampling intensity as described below (Strindberg, 2001). For some other non-convex regions this design might lead to inaccessible areas with zero coverage probability within the study region; whether or not this is the case can be investigated via a coverage probability simulation. When there are inaccessible areas one can revert back to using the convex hull based design. There was insufficient information to attempt an improvement in precision by allocating effort approximately in proportion to abundance in each stratum. Thus, the same equal spacing of 10 n.miles was used to generate the amended 'Equal Spaced Zigzag' designs in each of the strata thereby allocating effort in proportion to stratum size.

The spacing of 10 n.miles in conjunction with the orientation of the design axis was chosen to ensure sufficient replicate transects per stratum for the purposes of estimating variance in encounter rate. The survey design originally comprised 40 transect legs for a combined length of 1,787.16 n.miles with 11 legs (468.83 n.miles) covering the northern stratum and 29 legs (1,318.33 n.miles) covering the southern stratum. The removal of the seven southernmost legs from this analysis, due to the unfavourable survey conditions near the Congolese frontier, resulted in a total survey length of 1,488.2 n.miles with only 22 legs (1,019.37 n.miles) covering the southern stratum. A Transverse Mercator projection was used while generating the design and when calculating the surface areas and line transect lengths (the design is shown in Fig. 1 and details are given in Table 1).

The trade-off between theoretical rigour and difficult logistical constraints

By using an automated survey design algorithm to randomly locate the line transects, a key assumption underlying distance sampling was fulfilled, namely that transects are located randomly with respect to the distribution of the animals (see Thomas *et al*. (2007) for another example of automated survey design use). A random design that also gives even coverage probability is crucial for valid statistical inference using a standard distance sampling analysis. If standard analysis methods are applied when coverage probability is uneven, then biased density estimates may result. To avoid this potential problem when differences in coverage probability are extreme, the Horvitz-Thompson-like (or other) estimator that allows coverage probability to vary by observation can be applied, even if this is likely to lead to an increase in the variance of the estimator (Strindberg, 2001; Strindberg and Buckland, 2004b).

The random zigzag survey design used for this survey was generated by passing the zigzag through equally spaced points on opposite sides of the stratum boundary. This type of design does not provide completely even coverage probability (Strindberg, 2001; Strindberg and Buckland, 2004b). However, the height[2] of the survey strata does not vary dramatically with respect to the design axis used to randomly locate and orientate the zigzag in each survey stratum (the variation in height across each transect causes the potential unevenness in coverage probability). Thus, the variation in coverage probability will also be limited and the design a reasonable alternative to a more complex zigzag design (Strindberg and Buckland, 2004b). This was confirmed by simulating the design 1,000 times over the locations of the sightings and using a χ^2 goodness-of-fit test to examine whether the coverage probability was even at these points (Strindberg, 2001)[3].

A zigzag survey design is an efficient systematic design, as no flight time is wasted moving between survey legs, which was critical for this survey due to limited refuelling opportunities. In addition, with systematic designs, the line transects are evenly spread throughout the study area. Even spatial spread of sampling units tends to improve estimator precision; it ensures that a more representative sample is selected from the population giving less variable estimates (Strindberg, 2001). During aerial surveys, systematic parallel transects are frequently used. Although the latter design gives a more even spatial spread than a zigzag design, it was not an option given the vast extent of the survey area and the limited survey effort available.

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[2] The height of the survey stratum at any point is the length of the line that runs perpendicular to the design axis and is delimited by the points at which this line intersects the survey stratum boundary.

[3] The index-of-dispersion used for this purpose (Strindberg, 2001) had a value of 75.10, which did not exceed the value of the distribution with 78 degrees-of-freedom at the 5% significance level, namely 104.98. Thus the null hypothesis of even coverage probability was accepted.

Executing the surveys

The aerial survey was conducted in a single-engine Cessna 182 provided by the Wildlife Conservation Society (WCS). During the survey the aircraft flew at an average altitude of 740ft at an average speed of 104 knots/hr. A data collector was located in the co-pilot seat and primary observers on each side of the plane made observations by scanning an area perpendicular and forward of the plane. Once a sighting was made, a clinometer measurement to the centre of the group, GPS location of the aircraft and altitude reading were taken as the animals passed abeam. The clinometer reading and altitude were used to calculate the perpendicular distance to each observation, except for four of the observations included in the analysis where it was not possible to obtain a clinometer reading (a GPS location of the group was recorded instead in order to estimate perpendicular distance to the transect line). After passing the sighting, the aircraft left the transect line and circled until the two backseat observers and the front seat recorder were each able to independently identify the species and estimate group size. Each person made three estimates of group size: minimum; maximum; and best.

The aerial survey took place between 5–9 August 2002 (excluding the bad weather survey days), corresponding to a likely peak in the migration and abundance in Gabonese coastal waters, as inferred from field surveys (Collins *et al.*, 2010; 2006) and historical catch information (Budker and Roux, 1968; Townsend, 1935). The line transects were completed from north to south in an attempt to minimise systematically double counting individual humpback whales migrating northwards and artificially inflating the estimate of density and abundance.

Statistical analyses

In line transect distance sampling observers traverse lines of aggregate length L. The number n of animals of interest are counted and the perpendicular distance to each is recorded. If the animals of interest occur in groups, as humpback whales do, then the perpendicular distance to the centre of the group is recorded instead. If all animals located on the line were detected with certainty, then the density of humpback whale groups in the study area surveyed (D_s) is estimated as (Buckland *et al.*, 2001):

$$\hat{D}_s = \frac{n\hat{f}(0)}{2L} \tag{1}$$

where $f(0)$ is the probability density function of the perpendicular distances evaluated at zero. Thus density estimates are obtained from estimates of $f(0)$ and encounter rate (n/L). $f(0)$ can be interpreted as $\frac{1}{\mu}$, where μ is referred to as the effective strip half-width and corresponds to the perpendicular distance from the transect line within which the number of undetected groups is equal to the number of groups detected beyond it. Twice the effective strip half-width multiplied by L gives the effective area surveyed. Humpback whale density is obtained by multiplying the estimated whale group density by the estimated expected group size $\hat{E}(s)$. The densities of groups or individual whales are multiplied by the surface area of the study area or survey stratum to obtain the corresponding abundance estimate.

The Distance software was used to analyse the data (Thomas *et al.*, 2010). A number of different groupings of and truncation points for the observational data, as well as different combinations of key function (Half-normal, Uniform, Hazard rate) and series expansion (cosine, simple polynomial, hermite polynomial) were considered as candidate models when estimating the detection function. During analysis the data were grouped and also right truncated to improve model fit, as it is difficult to obtain accurate clinometer measurements, especially at larger distances where a small change in angle relates to a large change in distance. To account for the fact that observers were not able to see directly beneath the aircraft a left truncation distance for the data was selected by inspecting a histogram of detection frequencies plotted against distance from the transect line. Subsequently only data at distances greater than the left truncation distance were used to fit the detection function, which was then extrapolated back to distance zero. Akaike's Information Criterion (AIC) (Akaike, 1973) was used for model selection. The variance of encounter rate was estimated empirically using the replicate transect lines as samples, while maximum likelihood methods were used to estimate the variance of the effective strip width.

An estimate of expected group size $\hat{E}(s)$ was obtained by pooling all the data and calculating the mean of the average best group size estimated independently by the observers for each detection. Group size was regressed against detection distance to determine whether there was any indication of size bias in the group size estimate.

The estimates of whale or whale group density or abundance are clearly negatively biased, as some animals on the line (or at the left truncation distance) are not detected (i.e. $g(0) \neq 1$). This is an unavoidable consequence of the fact that these species spend the majority of their time underwater, where they are difficult or impossible to detect from the air. The risk of biased estimates is particularly hard to quantify in wintering areas such as the coast of Gabon, where detection probabilities are largely unknown and may vary significantly across group types with different behavioural characteristics. This availability bias is compounded by a perception bias that is due in part to the relatively high speed at which the observers are travelling during an aerial survey by plane, but also influenced by observer fatigue, experience or changing weather conditions (Fleming and Tracey, 2008; Marsh and Sinclair, 1989). Given that survey specific data to apply independent observer methods (Laake and Borchers, 2004) for estimating $g(0)$ were not available, the correction factor proposed by Barlow *et al.* (1988) for aerial surveys of harbour porpoise was used. The probability that an animal is visible given that it is on the transect line is given by:

$$\hat{g}(0) = \frac{t+v}{t+d} \tag{2}$$

where t is the average time an animal stays on the surface, v is the amount of time the animal is within the observer's visual range and d is the average time the animal spends submerged while diving. Unlike some of the independent observer methods that account for availability and perception bias, this method accounts for the former type of bias, but does not permit the estimation of the proportion of groups available for detection that were missed. One of the implicit assumptions is that animals who surface have a $g(0)$ of 1 (if $v > d$, then on average this happens at least once during the time they are under observation). The corrected density estimate of humpback whales is then obtained as follows:

$$\hat{D} = \frac{n\hat{f}(0)\hat{E}(s)}{2L\hat{g}(0)} \tag{3}$$

The estimation of $g(0)$ was based on a small sample of 14 humpback whale groups observed off Iguela in a small sub-region within the aerial survey study area in September 2003. Data on the surfacing, ventilation and dive patterns were recorded by observing groups for as close as possible to 60min each during boat-based surveys. The correction factor was calculated by using the mean values for average surface time t and dive time d, or the lower or upper extreme of their 95% confidence interval (95% CI) ranges (note that the method uses means rather than full distributions and there is no way to evaluate variance or to take account of the patterns of animal availability).

RESULTS

A total of 1,488 n.miles of survey effort consisting of 33 individual transect legs were completed. Combining the northern and southern stratum, the total study area consisted of 14,373 n.miles^2 (see Table 1). Across all strata, average conditions on the Beaufort scale equalled two; however higher Beaufort conditions were encountered in the northern stratum compared to the southern stratum. A total of 74 on-effort group sightings were made across both strata, but the majority of the sightings ($n = 64$) were made in the southern stratum, which covers the region from Cap Lopez to areas south of Gamba (Fig. 1).

The data were left truncated at 450m (0.243 n.miles) from the transect line (Fig. 2). The data were right truncated at 2,350m (1.269 n.miles), pooled across both survey strata and grouped to estimate detection ($\hat{f}(0) = 2.106$ (n.miles^{-1}), percent coefficient of variation (%CV) of 16.38, and a 95% CI = 1.519–2.919) and the effective strip width ($\hat{ESW} = 0.475$ n.miles and a 95% CI = 0.343–0.658), while the analysis was stratified for encounter rate (Table 1). The encounter rate was considerably higher for the southern stratum compared to the northern stratum (0.053 n.miles^{-1} vs. 0.011 n.miles^{-1} with a corresponding %CV of 25% vs. 45%, respectively).

Using AIC for model selection, a half-normal model with no adjustment terms was selected. The AIC value for the selected model was 219.43, while the difference in AIC values for the uniform with a cosine adjustment term and the hazard-rate with no adjustment terms that were ranked second and third was 0.16 and 2.46, respectively. The density estimates of the half-normal and uniform model with cosine adjustment terms were identical to the second decimal place, and the fit of the former model was marginally better; hence it was selected as the final model. The detection function for the half-normal model fit to the grouped observation data is shown in Fig. 2 (according to the goodness-of-fit test, the probability of a χ^2 greater value, $p = 0.97099$). The estimates of humpback whale group density and abundance for the northern and southern stratum, as well as the study area as a whole are given in Table 2. The global density estimate was calculated by taking the mean of the stratum estimates weighted by stratum area. The estimate of humpback whale group density over the entire study area was 0.041 n.miles^{-2} with an abundance of 597 (95% CI = 342–1,042). Although the detection probability in the northern stratum may have been somewhat decreased due to an increase in Beaufort sea state, there were clear differences in densities between the strata.

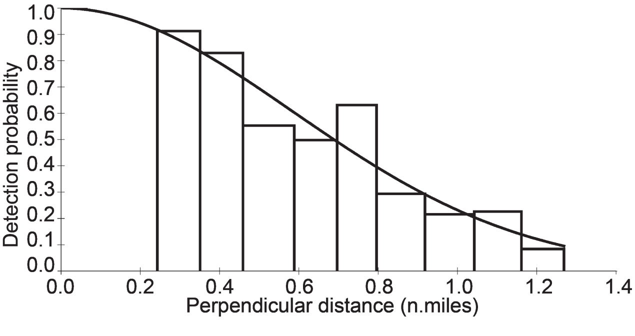

Fig. 2. Detection function for the half-normal model fit to the perpendicular distances of observations of humpback whale groups. Observations with a perpendicular distance of less than 450m (0.243 n.miles) or greater than 2,350m (1.269 n.miles) from the transect line where truncated. To improve model fit the data were grouped for analysis to deal with inaccuracies in the clinometers measurements and the interval cutpoints were also selected to deal with some potential heaping in the data.

The estimate of expected group size $\hat{E}(s)$ was 2.109 with a %CV of 6.86 and a 95% CI of 2.074–2.143. Percentage distribution of estimated group size[4] from one to seven is 30.82, 42.77, 11.95, 7.55, 4.40, 1.89, 0.63, respectively. Using detections beyond 450m from the transect line and only those sightings whose distances had been obtained by means of a clinometer reading, the estimate of group size did not vary significantly from that obtained by regressing group size against detection distance (the p-value was equal to 0.321).

The estimates of humpback whale density and abundance for the northern and southern stratum, as well as the study area as a whole, were calculated using $\hat{E}(s)$. The overall humpback whale density was estimated as 0.09 n.miles^{-2} with a resulting abundance for the study area of 1,259 whales with a 95% CI of 710–2,333 (see Table 2). The stratified estimates of humpback whale density and abundance are also shown in Table 2.

The average surface and dive time were calculated for each of the 14 groups[5] and then the overall averages were calculated across all groups to obtain the mean surface time t and dive time interval d of 2.58 and 3.25 minutes with 95% CIs of 1.77–3.40 and 2.15–4.37, respectively. The smallest clinometer readings taken during the survey were 3 degrees, which at an average altitude of 740ft implies that the observers were scanning for whales out to a distance of approximately 2.3 n.miles. Given that the aircraft flew at an average speed of 104 knots hr^{-1}, this distance would be covered in about 1min, thus this is the time value used for v. The correction factor was calculated by using the mean values for t and d, or the lower or upper extreme of their 95% CI ranges resulting in values between 0.45 and 0.79 with a value of 0.61 using the means (Table 3). Adjusting the overall abundance estimate of 1,259 humpback whales using these extreme values for $\hat{g}(0)$ would alter the result considerably, giving estimates that range between 1,594 and 2,798 with 2,064 corresponding to the value of 0.61. The estimate of availability bias should be interpreted with caution, as it was not possible to collect data at the time of the survey and hence the group size, composition and behaviour might have been different than for those in the area at the time of the survey. Dive times are likely to vary by group type and behaviour, with larger groups or groups displaying certain types of behaviour (e.g. competitive behaviour, repeated breaching, tail lobbing) being on the

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[4] Includes all group size estimates made independently by the observers for those sightings where group size was recorded.

[5] There were 4 mother-calf pairs, 3 other pairs, 5 singletons (3 of which were singing) and 2 other groups (of which one was an unusually large group of about 12 whales that split into four groups of 6, 3, 2, and 1 individual(s) about 18 minutes into the 50 minute observation period).

Table 2

Global (area weighted mean of the stratum estimates) and stratified estimate of humpback whale group density ($\hat{D}_s$) in numbers per n.m^2 and abundance ($\hat{N}_s$), as well as humpback whale density ($\hat{D}$) in numbers per n.m^2 and abundance ($\hat{N}$), with the corresponding standard error (SE), percent coefficient of variation (%CV) and 95% confidence interval (95% CI). These are the unadjusted results that do not account for $g(0)<1$.

Region	Area (nm^2)	Group estimates		SE	(%CV)	95% CI	Individual estimates		SE	(%CV)	95% CI
Study area	14,373	$\hat{D}_s$	0.042	0.012	28.24	(0.024–0.073)	$\hat{D}$	0.088	0.025	29.06	(0.049–0.155)
		$\hat{N}_s$	597	168.59		(342–1,042)	$\hat{N}$	1,259	365.87		(710–2,233)
Northern stratum	4,706	$\hat{D}_s$	0.012	0.006	47.54	(0.004–0.031)	$\hat{D}$	0.025	0.012	48.04	(0.009–0.067)
		$\hat{N}_s$	55	26.15		(21–147)	$\hat{N}$	117	56.20		(44–314)
Southern stratum	9,667	$\hat{D}_s$	0.056	0.017	29.84	(0.031–0.101)	$\hat{D}$	0.118	0.036	30.62	(0.064–0.216)
		$\hat{N}_s$	541	161.42		(300–977)	$\hat{N}$	1,142	349.64		(623–2,091)

Table 3

The estimated values for $\hat{g}(0)$ given a range of values (mean, lower and upper limit of their 95% confidence intervals) for the average time (in minutes) an animal stays on the surface (t) and the average time the animal spends submerged diving (d), assuming the amount of time the animal is within the observer's visual range (v) is approximately 1 minute.

t	d	$\hat{g}(0)$
2.58	3.25	0.61
1.77	3.25	0.55
3.40	3.25	0.66
2.58	2.15	0.76
1.77	2.15	0.71
3.40	2.15	0.79
2.58	4.37	0.52
1.77	4.37	0.45
3.40	4.37	0.57

surface for a larger proportion of time or more visible. Availability for detection is also likely to be different from the air versus from the boat used to collect data to compute ventilation and dive patterns (for example, individual singing males tend to spend more time underwater and are thus less available for detection during an aerial survey).

Humpback whale distribution was negatively associated with increasing water depth (see Fig. 1). Observations were predominantly made in shallow waters of less than 50m depth (52 observations, including all 10 observations made in the northern stratum and most of the observations in the southern portion of the southern stratum). In the northern portion of the southern stratum only a single sighting was made beyond the 200m depth contour, while 12 observations fell in the 50–100m depth range (spread across different transects) and 14 fell in the 100–200m depth range[6] (occurring just south of Cape Lopez where the depth contours are close together due to the precipitous slope of the continental shelf). Thus, 65.82%, 15.19%, 17.72%, 1.27% of the observations were made within the depths ranges 0–50m, 50–100m, 100–200m, 200–1000m, respectively, corresponding to 35.23%, 18.13%, 13.30%, 33.33% of the surface area of the study region[7]. These results are based on fairly coarse GEBCO Digital Atlas[8] (GEBCO Digital Atlas, 2003) bathymetry data, so should be interpreted with some caution.

DISCUSSION

Even with the uncorrected conservative abundance estimate of 1,259 whales (%CV = 29.06; 95% CI = 710–2,333), the results indicate that the humpback whale population utilising the coastal waters of Gabon has undergone some degree of recovery following the cessation of whaling in the 1960s. Correcting for animals on or near the line that are not seen increases estimates of abundance. The estimate of $g(0)$ gives some indication of how the abundance estimate might change. However given that it was not possible to account for perception bias these numbers are still likely to be negatively biased.

Another contributor to the potentially negatively biased abundance estimates is the fact that these surveys provide only an instantaneous snapshot of the number of whales occupying Gabon's coastal waters. There are reports of humpback whales in other areas throughout the region from west South Africa to the Bight of Benin (Best *et al.*, 1999; Van Waerebeek *et al.*, 2001) with some proportion of the population potentially visiting localities in the region where humpback whales are know to congregate, including São Tomé, Bioko and the coasts of Equatorial Guinea, Cameroon, Congo and Angola (Aguilar, 1986; Best *et al.*, 1999; Pomilla *et al.*, 2006; Rosenbaum and Collins, 2006; Rosenbaum *et al.*, 2009; Van Waerebeek *et al.*, 2001). This indicates that the wintering grounds for humpback whales in the Gulf of Guinea extend beyond the coastal waters of Gabon, and thus the likelihood that all whales in the population or populations[9] of interest will occupy these waters at the same time is low. In addition, certain classes of animals such as calving females are likely to have different occupancy periods based on reproductive condition. Recent evidence suggests that some animals (particularly females and juveniles) may not even make the full migration to equatorial waters every year (Corkeron and Connor, 1999). From satellite tagging results of 15 whales in 2002, there is clearly differential use and movement of humpback whales through Gabon's waters (Rosenbaum and Mate, Submitted), demonstrating that this area is an important wintering ground in the Gulf of Guinea.

These considerations suggest that the number of humpback whales actually using Gabon's coastal waters at some point in their life cycle is probably larger than indicated by the transect estimates presented here. Determining exactly how much larger, especially with a corrected estimate that ranges between 1,594 and 2,798, will require additional surveys at different time periods and also using other methods for estimating abundance, such as those described in Collins *et al.* (2010). Following 277 days of boat-based survey effort off the coast of Gabon (primarily in the

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[6] Nine of these observations where made almost exactly along the 200m contour as the third transect south of Cape Lopez followed this contour unlike other transects that tended to cut across all depth contours (see Fig. 1).

[7] Not surprisingly, a test that combines the last two depth categories, due to the single sighting in the 200–1000m depth range, gives $p < 0.001$.

[8] Contours compiled and digitized from the International Bathymetric Chart of the Central Eastern Atlantic (Sheets 1.08–1.12) published by the Service Hydrographique et Oceanographique de la Marine (Paris, France) at a scale of 1:250,000 (datum WGS84).

[9] See Section 3.2.4 of IWC (2011b).

southern stratum), between 2001 and 2006, 1,323 different individuals were identified photographically from tail flukes and 1,404 different individuals were identified from genotyped biopsy samples. Capture-recapture analyses from the photographic identification and genetic studies yield a consistent set of abundance estimates of 4,300–7,200 individuals (Collins *et al.*, 2010; 2006)[10]. As the capture-recapture abundance estimates are carried out through a large portion of the breeding season and likely include animals moving through Gabon's waters to other areas in the Gulf of Guinea, the abundance estimate derived from the distance sampling is consistent with a substantial portion of the entire population being encountered during this period.

The 1,000m depth contour was chosen as the outer limit of the survey region because of both safety and refuelling limitations of the aircraft, in addition to expectations of whale distribution being negatively associated with increasing water depth for this species on their breeding grounds. As the waters on the continental shelf have relatively uniform depths, but depth progressively increases toward the shelf edge, there was some appreciable decrease in encounter rate as the observers approached the 1,000m depth contour along most transects. Consistent with patterns observed in other breeding grounds where humpback whales tend to spend most of their time in coastal waters over the continental shelf, with very limited occurrence in deeper waters (Andriolo *et al.*, 2006; Best *et al.*, 1996; Ersts and Rosenbaum, 2003; Findlay *et al.*, 1994; Zerbini *et al.*, 2004; Zerbini *et al.*, 2006), the vast majority of observations were made on the continental shelf out to a depth of approximately 200m.

The abundance estimates presented here and the distribution of the observations suggest that large numbers of humpback whales use the inshore waters between Cap Lopez and the Congo Frontier (southern survey stratum) during the austral winter breeding season. Given the overlap between this important breeding habitat for humpback whales and extensive ongoing and planned hydrocarbon activities, risks to this population need further investigation. The scientific and conservation community has expressed concern about the negative effects of noise exposure on whale populations and other cetaceans (Clark *et al.*, 2009; IWC, 2011a); seismic surveys occurring in breeding grounds, feeding regions, and restricted migratory corridors may have a negative impact on critical life functions of these species (Cerchio *et al.*, 2010; IWC, 2007). Potential impacts to whales include acoustic disturbance due to geophysical seismic surveys (Cerchio *et al.*, 2010; Di Iorio and Clark, 2010), as well as disturbance associated with vessel traffic and oil production operations (Richardson *et al*., 1995; IWC, 2007; NRC, 2005). In addition, industrial activities within and pollution of the marine environment in Gabon are also causes for some general concern (Findlay *et al.*, 2004). On several occasions during this aerial survey, oil slicks were seen to be emanating from oil production facilities and were relatively large, stretching a kilometre or more from their source across the water's surface.

Given that Gabon's coastal waters are probably a significant wintering area for humpback whales in the southeastern Atlantic Ocean, additional measures for protection and mitigation of impacts to this population on their breeding grounds should be considered.

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Distribution and abundance of humpback whales, *Megaptera novaeangliae*, off the coast of Mozambique, 2003

Ken Findlay*, Michael Meÿer[×], Simon Elwen[#], Deon Kotze[×], Ryan Johnson[~], Pieter Truter[^], Celestino Uamusse[++], Samuel Sitoe[++], Chris Wilke**, Sven Kerwath**, Stephen Swanson[+], Linda Staverees[+] and Jan van der Westhuizen**

Contact e-mail: kenfin@mweb.co.za

ABSTRACT

Humpback whales within the southwestern Indian Ocean undertake annual migrations from summer Antarctic/Southern Ocean feeding grounds to winter breeding grounds in the tropical and sub-tropical coastal waters of Mozambique, Madagascar and the central Mozambique Channel Islands. Little is known of the inter-relationship of humpback whales on each of these wintering grounds, or the inter-relationship of these wintering grounds with the summer Antarctic feeding grounds.

A line-transect survey of cetacean species was carried out in Mozambique coastal waters between Cabo Inhaca (26°00'S, 33°05'E) and just north of Mozambique Island (14°26'S, 40°53'E) and between the 20 and 200m isobaths, over the period 26 August to 7 September 2003. The majority (98.1%) of 951.8 n.miles of search effort carried out on this survey was in passing mode due to the high densities of whales encountered. Humpback whales were the only large whales to be identified and the distribution of 691 sightings of an estimated 1,130 individual humpback whales and 132 sightings of an estimated 154 large unidentified whales show distribution throughout the survey region. Two sightings of individual small whales were made in the region of Inhambane.

In general, higher than expected sighting densities (based on survey effort) were recorded in the region between Cabo Inhaca and Xai-Xai, and in the region of the Pantaloon and David Shoals to the north east of Quelimane. Lower than expected sighting densities were recorded over the Sofala Banks. No distribution trends could be ascribed to environmental parameters, apart from whales being distributed in waters of higher salinities than expected, possibly due to turbidity associated with low salinity water arising from river input. Groups containing a cow and calf pair were distributed across the entire region surveyed.

Analyses of unstratified data result in a total abundance estimate of 6,808 (CV = 0.14) humpback and unidentified whales in the 14,029.5 n.mile^2 area surveyed. As a result of the differences in width of the coastal shelf area along the coast of Mozambique, the line transect survey data were further analysed in four strata. Pooling of estimates over these four strata results in a total abundance of 6,664 whales (CV = 0.16), with highest densities in the southernmost stratum and the lowest densities in the narrow shelf region across the Sofala Banks. Similar analyses of humpback whales only resulted in abundance estimates of 5,930 (CV = 0.15) (unstratified data) and 5,965 whales (CV = 0.17) (data analysed by four strata). Although not directly comparable due to differing survey platforms, these estimates indicate the population to have increased since previous surveys in the early 1990s.

KEYWORDS: HUMPBACK WHALE; SOUTHERN HEMISPHERE; MOZAMBIQUE; ABUNDANCE; DISTRIBUTION

INTRODUCTION

The annual migrations of Southern Hemisphere humpback whales (*Megaptera novaeangliae*) from summer Antarctic or Southern Ocean feeding grounds to winter breeding grounds in shallow tropical and sub-tropical waters is known from the seasonality of whaling catches (Harmer, 1928; 1931; Mackintosh, 1942; Matthews, 1938; Olsen, 1914; Risting, 1912), from natural mark and tag returns (Chittleborough, 1965; Dawbin, 1956; 1966; Gill and Burton, 1995; Rayner, 1940) and from satellite telemetry studies (Zerbini *et al.*, 2006). Seven feeding grounds have been identified within the Southern Ocean (IWC, 1998; Mackintosh, 1942; Omura, 1973), each of which has been linked to a breeding ground in the coastal waters of South America, Africa (including Madagascar), Australia, New Zealand or the islands of the southwestern Pacific Ocean (IWC, 1998; Kellogg, 1929; Mackintosh, 1942; Rayner, 1940). En route between breeding and feeding grounds, humpback whales appear to utilise the coastal waters of Southern Hemisphere continents as migratory corridors, a factor which made them particularly susceptible to land-based whaling operations (Findlay, 2001). Historical catch records have indicated two general migration corridors in southern African waters. The west coast corridor takes whales as far north as breeding grounds off Gabon (Budker, 1954; Budker and Collignon, 1952; Townsend, 1935), although Tønnessen and Johnsen (1982) suggest that catches off Angola and Gabon arose from different stocks. The east coast corridor conveys whales to breeding grounds off Mozambique (Best, 1993; Findlay *et al.*, 1994; Olsen, 1914), Madagascar (Angot, 1951; Ersts and Rosenbaum, 2003) and the central Mozambique Channel Islands (Angot, 1951; Best *et al.*, 1998).

Populations of Southern Hemisphere humpback whales declined markedly during the 20th century as a result of severe modern whaling on both the Antarctic feeding and tropical breeding grounds (Findlay, 2001). Humpback whaling in South Africa started in 1908 in Durban (~30°S) and continued until October 1963. Catches were predominantly made prior to 1918, although subsequent to 1913 humpback whales no longer formed the major

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* *Oceanography Department, University of Cape Town, Private Bag, Rondebosch 7701, South Africa.*

[×] *Oceans and Coasts, Department of Environmental Affairs, PO Box 52126, Victoria and Alfred Waterfront 8002, South Africa.*

** *Department of Agriculture, Forestry and Fisheries, P Bag X2, Roggebaai, Cape Town 8012, South Africa.*

[+] *Formerly Marine and Coastal Management, Private Bag X2, Roggebaai 8012, South Africa.*

[#] *Mammal Research Institute, University of Pretoria. c/o Iziko: SA Museum, PO Box 61 Cape Town 8000, South Africa.*

[~] *Oceans Research, PO Box 1767, Mossel Bay 6500, South Africa* and *Department of Zoology and Entomology, University of Pretoria, Pretoria 0002, South Africa.*

[^] *Research Diving Unit, Oceanography Department, University of Cape Town, Rondebosch 7701, South Africa.*

[++] *Department of Biology, Universidade Eduardo Mondlane, Maputo, Mozambique.*

component of the Durban whaling ground catch (Best, 1994). Limited catches of presumably western Indian Ocean humpback whales were recorded off the southern Cape coast (Plettenberg Bay and Mossel Bay) between 1911 and 1916 (Best, 1994), and Best and Ross (1996) suggested that these animals migrate along the east coast of southern Africa. Modern whaling occurred in Mozambique waters between 1910 and 1923, with a floating factory operating off the Bazaruto Archipelago in 1910, a land station and two floating factories operating independently at Linga-linga (Inhambane) between 1911–1915 and 1912–1923 respectively, a land station operating in Delagoa Bay between 1912–1913, and floating factories operating at Quelimane in 1912 and at Angoche (16°S) between 1911–1912 (Tønnessen and Johnsen, 1982). Humpback whales dominated this catch, although Tønnessen and Johnsen (1982) noted that only 3,360 whales were taken in the Mozambique whaling grounds in this era, with the highest catches recorded off Linga-linga, and catches to the north of Quelimane being generally poor.

Certain Southern Hemisphere populations of humpback whales appear to be undergoing considerable recovery from whaling in certain wintering grounds including those that migrate through the southwestern Indian Ocean. Although the time period of surveys was too limited to provide any estimate of population trend, the shore-based surveys carried out off Cape Vidal between 1988 and 1991 (Findlay and Best, 1996a; Findlay and Best, 1996b) suggest that the population has undergone some recovery since the cessation of humpback whaling in the region in October 1963. Assessments of humpback whale populations off the east and west coasts of Australia have shown population increase rates of about 10% per annum (Bannister *et al.*, 1991; Bryden *et al.*, 1990; Hedley *et al.*, 2011; Paton and Kniest, 2011), and based on preliminary results from shore-based surveys off Cape Vidal, South Africa, between 1988 and 2002 (Findlay *et al.*, in press) a similar increase is expected for the Mozambique population.

Migrations in the southwestern Indian Ocean being suggested by Best *et al.* (1998) comprise three principal migratory streams, including:

(a) an East African corridor taking whales to and from the coastal waters of Mozambique, hereafter termed the C1 ground after IWC (1998);
(b) a Madagascar Ridge corridor taking animals through Walters Shoal, to and from the coastal waters of Madagascar (termed the C3 ground); and
(c) a Central Mozambique Current corridor taking whales to and from the coastal waters of the central Mozambique Channel Islands of Aldabra, the Comores Islands and Mayotte, or to the coastal waters of Mozambique to the north of 18°S (termed the C2 ground).

However the complete migratory destinations and routes and inter-relationships between the three wintering grounds of Mozambique, Madagascar and the Central Mozambique Channel Islands are relatively unknown. Ersts *et al.* (2006) reported on movements of individual humpback whales between Antongil Bay, Madagascar and Mayotte. This paper reports on a cruise undertaken in Mozambican waters (Fig. 1) to estimate the abundance of humpback whales utilising the C1 breeding grounds, and to investigate their distribution. Little or no survey of humpback whales on their Mozambique breeding grounds has been carried out since 1991, when Findlay *et al.* (1994) surveyed the southern and central coastal waters of Mozambique. The survey reported

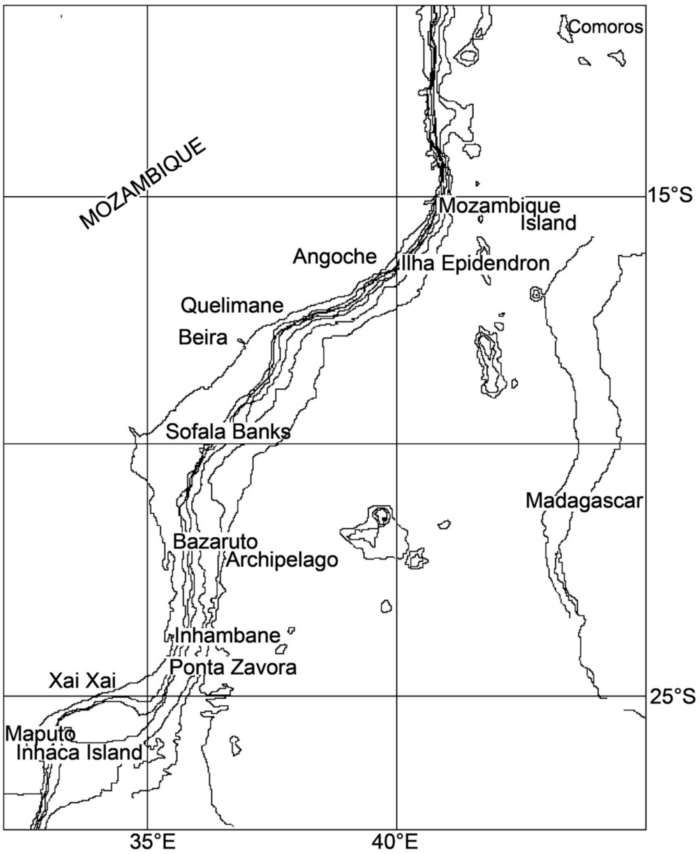

Fig. 1. The coastal waters of the Mozambique Channel showing localities referred to in the text.

here extends the coverage of Mozambique waters by some 300 n.miles north of the area surveyed by Findlay *et al.* (1994). Timing of the cruise was selected to coincide with maximum expected abundance of humpback whales within the study area.

METHODS AND MATERIALS

Field survey

Line-transect survey

A line-transect survey of all cetacean species was carried out between Cabo Inhaca (26°00’S, 33°05’E) and to the north of Mozambique Island (14°26’S, 40°53’E), between the 20 and 200m isobaths from 26 August to 7 September 2003. Limited search effort was also carried out both inshore and offshore of this area.

The survey was carried out between 0700 and 1700 each day in suitable weather conditions (i.e. adequate visual conditions with a clear visible horizon, sea conditions < Beaufort 5 and wind speed of <24 knots). All survey was on predetermined transects (Table 1) at a speed over ground of between 8 and 11 knots depending on current conditions. Searching was undertaken by two rotating teams (of a minimum of five seated observers each) from a specially constructed observation platform on the vessel’s upper bridge at 12m above sea level. Searching was carried out using both wide-angle binoculars (7 × 35) and the naked eye. All searching activity was recorded as search effort and environmental conditions (wind speed and direction, cloud cover, Beaufort Sea State, swell height) were logged by observers during each hour of observation. An automated system recorded the vessel position, speed through the water, speed over the ground, heading and depth as well as environmental parameters (barometric pressure, wind speed and direction, sea surface temperature and salinity) on each minute of the cruise.

The survey was planned in both passing and closing modes. In closing mode, the vessel diverted from the survey trackline to intercept the observed cetacean groups to confirm group size and species identity. On completion of the interception the vessel resumed searching on a new trackline directly to the next way-point. All closing activity from the time of diversion until resumption of survey effort on the new trackline was considered as off survey effort and all sightings made during this time were considered secondary sightings. No diversions from the trackline were made in passing mode. However, the high densities of whales encountered resulted in almost all survey being carried out in passing mode, due to both the difficulty in tracking groups of whales in view during closing mode, and the high incidence of secondary sightings made during closing mode. Consequently observers carried out species identification and estimated group composition (i.e. the presence or absence of a calf) and group size from the trackline, usually at the closest distance when the whales were abeam of the vessel. Group size and composition were recorded as confirmed only when observers were certain of the size and composition of intercepted groups (or groups which passed close to the vessel in passing mode). In passing mode all sighted groups were tracked through the observation area by at least one observer, until they were abeam, so as to ensure that groups were not double counted.

Table 1

Positions and survey coverage of transects searched during the line transect component of the cruise.

				Total distance searched (n.m.)		
Leg	Start position	End position	Total planned distance (n.m.)	Passing mode	Closing mode	Total
1	26° 00 S, 33° 05 E	25° 28 S, 33° 09 E	32.20	29.3	0	29.3
2	25° 28 S, 33° 09 E	25° 22 S, 33° 43 E	31.29	21.48	0	21.48
3	25° 22 S, 33° 43 E	25° 01 S, 34° 12 E	33.61	0	0	0
4	25° 01 S, 34° 12 E	25° 30 S, 35° 01 E	52.96	0	0	0
4A	25° 37 S, 34° 12 E	24° 36 S, 35° 13 E	75.44	61.31	14.89	76.2
5	25° 30 S, 35° 01 E	24° 36 S, 35° 13 E	55.08	0	0	0
6	24° 36 S, 35° 13 E	24° 11 S, 35° 37 E	33.21	34.46	0	34.46
7	24° 11 S, 35° 37 E	23° 31 S, 35° 36 E	40.01	39.82	0	39.82
7A	23° 31 S, 35° 36 E	23° 31 S, 35° 29 E	6.42	7.7	0	7.7
8	23° 31 S, 35° 29 E	22° 59 S, 35° 42 E	34.16	33.95	0	33.95
9	22° 59 S, 35° 42 E	22° 28 S, 35° 34 E	31.87	31.02	0	31.02
10	22° 28 S, 35° 34 E	21° 56 S, 35° 36 E	32.05	30.68	0.4	31.08
11	21° 56 S, 35° 36 E	21° 31 S, 35° 32 E	25.27	26.68	0	26.68
12	21° 31 S, 35° 32 E	21° 00 S, 35° 41 E	32.11	31.36	0.16	31.52
13	21° 00 S, 35° 41 E	20° 34 S, 35° 26 E	29.54	29.52	0	29.52
14	20° 34 S, 35° 26 E	20° 13 S, 36° 07 E	43.79	35.11	0	35.11
15	20° 13 S, 36° 07 E	19° 33 S, 35° 34 E	50.63	45.01	2.14	47.15
16	19° 33 S, 35° 34 E	19° 40 S, 36° 39 E	61.63	50.22	0	50.22
17	19° 40 S, 36° 39 E	18° 50 S, 36° 30 E	50.72	51.35	0	51.35
18	18° 50 S, 36° 30 E	18° 38 S, 37° 16 E	45.19	44.82	0.19	45.01
19	18° 38 S, 37° 16 E	18° 00 S, 37° 10 E	38.42	36.13	0	36.13
20	18° 00 S, 37° 10 E	17° 51 S, 37° 50 E	39.11	20.87	0	20.87
21	17° 51 S, 37° 50 E	17° 25 S, 38° 07 E	30.63	29.41	0	29.41
22	17° 25 S, 38° 07 E	17° 25 S, 38° 42 E	33.40	34.58	0	34.58
23	17° 25 S, 38° 42 E	17° 04 S, 39° 12 E	35.52	38.07	0	38.07
24	17° 04 S, 39° 12 E	16° 46 S, 39° 40 E	32.27	23.47	0	23.47
25	16° 46 S, 39° 40 E	16° 24 S, 40° 02 E	30.47	29.71	0.16	29.87
26	16° 24 S, 40° 02 E	15° 58 S, 40° 24 E	33.50	33.52	0.04	33.56
27	15° 58 S, 40° 24 E	15° 32 S, 40° 39 E	29.74	28.06	0	28.06
28	15° 32 S, 40° 39 E	15° 00 S, 40° 53 E	34.73	34.33	0.02	34.35
29	15° 00 S, 40° 53 E	14° 26 S, 40° 53 E	34.00	21.87	0	21.87
Total			1,168.99	933.81	18.00	951.81

On making a sighting of any cetacean observers immediately estimated the radial distance to the sighting, and angle of the sighting from the bow of the ship. Angles were measured using angle boards (to the nearest degree), while radial distances were estimated using a photographic measurement of the group relative to the horizon (after Gordon, 1990). This required the horizon and target group to be immediately photographed after sighting with a fixed focal length lens (300mm) from the known upper bridge height. At the same time distances were estimated by eye using hand held reticules. Calibration of the reticule and the photographic techniques were carried out in a trial where measurements were made co-incidentally with radar measurements over a 5 n.mile approach to a radar-reflective small boat.

Analyses

All sightings of whales unidentified to species were assigned to species on a pro rata basis of sightings of identified whales. As humpback whales were the only large whale species recorded during the survey, all unidentified whales have been assigned as humpback whales. Absolute abundances are estimated for both humpback whales and humpback and unidentified whales combined.

Relative abundance

Effort (miles searched), frequency of observations and expected observation frequency were calculated by half degree square and by environmental parameter interval. Expected observation frequencies were calculated from the total number of whales sighted apportioned to the particular interval by the distance searched in that interval. Environmental parameters analysed included wind speed (in 5kt intervals), Beaufort Scale (1 to 5), and swell height (0 to 3m, in 0.5m intervals) (all of which possibly influence sighting probabilities), water depth intervals (0–20m, 20–50m, 50–100m, 100–200m and >200m intervals), sea surface temperature (20˚C to 26+˚C in 1°C intervals), sea surface salinity (33.7ppt to 35.3ppt, in 0.1ppt intervals) and current speed (0kt to 6kt, in 1kt intervals). Problems at certain times throughout the survey with the automated depth-finder, resulted in depths being read after the survey from 1:300,000 bathymetric charts in 0–20m, 20–50m, 50–100m, 100–200m and >200m depth intervals. Malfunction of the thermo-salinograph from 1100 on 30 August to 1500 on 31 August meant that no sea surface temperature and salinity data were collected over this period. Current speeds were calculated as the absolute difference of vessel speed through the water and speed over the ground averaged by 10 minute interval.

Absolute abundance

Radial distances from the research vessel, the *FRS Algoa*, to each sighting were calculated using a modification of Gordon's (1990) photographic method. Distances between the horizon and the whale on an image taken with a 300mm focal length lens were used to calculate the dip angle between the horizon and the whale group and consequently the angle between the whale group and the vertical. (With the low swell heights recorded during this cruise, the angle between the vertical and the horizon is constant from any given height). Image distances were measured on a binocular microscope, and radial distances from the vessel to whale were computed (after Buckland *et al.*, 1993; Gordon, 1990) incorporating a correction factor derived from the radar calibration experiment.

Perpendicular distances of groups from the trackline were calculated for all sightings as d.sin(θ), where d and θ are the radial distance and the sighting angle respectively. The programme *Distance Version 5 Release 2* (Thomas *et al.*, 2006) was utilised to fit a hazard-rate model (Buckland *et al.*, 1993),

$$g(y) = 1 - \exp[-(y/a)^{1-b}]$$

to the perpendicular distances grouped into 0.2 n.mile intervals and truncated at 3.6 n.miles to give the probability density function *f*(0) and its variance V[*f*(0)]. No measure of the group detectability on the trackline, *g*(0), was made and it was assumed to be one (i.e. that every whale on the trackline was seen). The abundance estimate (*N*) of whales in the area surveyed (*A*) was given by

$$N = [A.n.s.f(0)]/[2L.g(0)]$$

where *n* is the total number of groups sighted on primary effort, *s* is the mean group size of confirmed groups, and *L* is the total length of the search track.

The variance on this estimate ($V(N/N^2)$) was calculated using the delta method,

$$V(N/N^2) = V[f(0)]/[f(0)]^2 + V[s]/s^2 + V[n_i/l_i]/[n/L^2].$$

V[*ni*/*li*] was the variance on transect sighting rates, where n_i and l_i were the number of sightings and the search effort of transect (*i*) respectively.

Inclement weather encountered on 26 August resulted in the initial survey effort (of 15.61 n.miles) on 27 August being carried out in deep water outside of the planned survey area and both this effort and its associated fifteen sightings have been excluded from the abundance estimation. The inshore and offshore limits of the area surveyed (A) were selected from the inshore and offshore transect way points, and intermediate points between them on the 20 (inshore) or 200m (offshore) isobaths, to provide the minimum area delineated by the survey transects.

On the basis of the relatively broad shelf area between Cabo Inhaca and Ponta Zavora, the narrow shelf area between Ponta Zavora and Cabo Bazaruto, the Sofala Banks between Cabo Bazaruto and Epidendron Island, and the relatively narrow shelf region between Epidendron Island and the northern limit of the survey, abundance estimation was also carried out on the data stratified into these four regions.

RESULTS

A total of 951.8 n.miles was searched during the line transect survey component of the cruise (Tables 1 and 3, Fig. 2). The weather encountered during the survey period was very good with only 18.6% of survey lost to inclement weather. High winds encountered off Xai Xai necessitated slight modification to the planned survey effort (Table 1), while all remaining transects were completed largely as planned. Although the survey was planned between the 20 and 200m isobaths, limited search effort was carried out in both shallower and deeper waters.

The high densities of humpback and unidentified large whales encountered during the survey effort resulted in only limited closing mode survey (18 n.miles) being carried out, and 933.8 n.miles of the survey were carried out in passing mode. Closing mode was compromised in that tracking of primary and secondary sightings was almost impossible once the vessel heading had altered. The total search effort of 951.8 n.miles covered 81.4% of the planned 1,170 n.miles of search effort. Mean vessel speed (measured as speed over ground by GPS logger each minute of the survey) during the survey was 9.90 (SD±1.12) kt. The majority of search effort

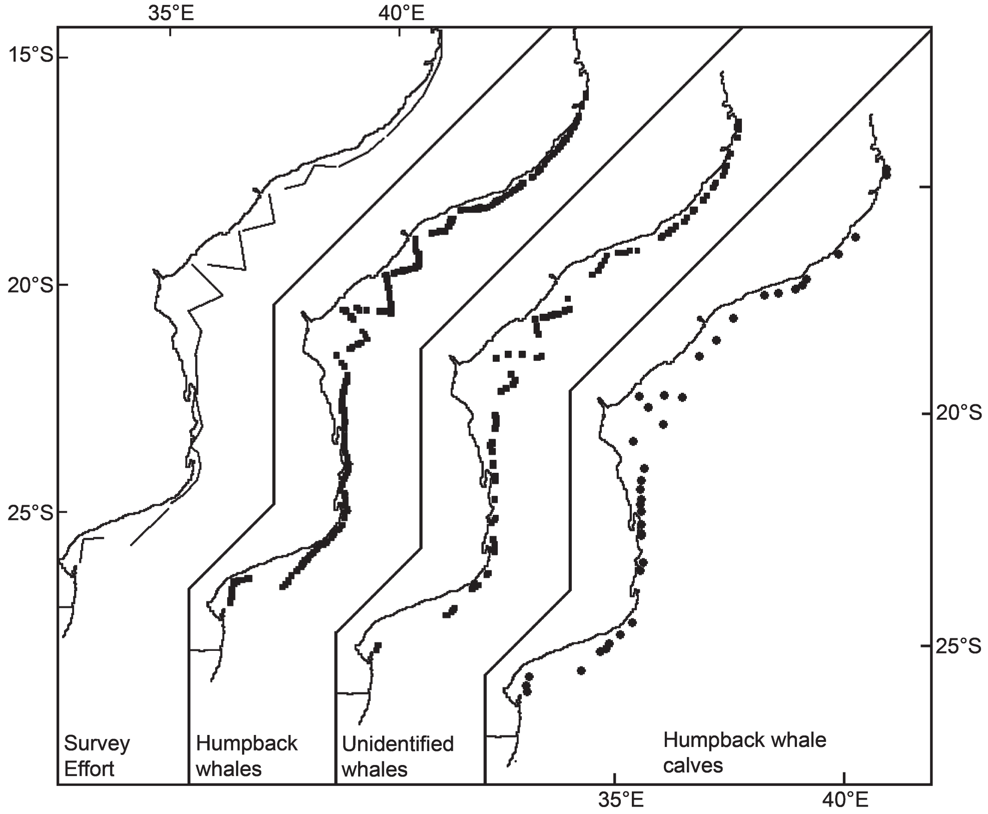

Fig. 2. The distribution of search effort carried out, and sightings of humpback whales, unidentified whales and humpback whale calves made during the line transect survey off Mozambique, 26 August to 7 September, 2003.

was carried out in excellent sighting conditions, in wind speeds of less than 15kt, swell heights of less than 1m and Beaufort Sea condition of 3 or less. The low correlation between wind speed and Beaufort Sea condition ($r^2 = 0.36$; $p > 0.05$; $n = 6{,}365$) possibly reflects Beaufort Sea condition being recorded on an hourly basis, rather than on a minute basis as for wind speed. Sea surface temperatures recorded during the survey ranged between 21ϒ and 26ϒC (with an increasing northward cline in temperatures), while salinities were recorded between 33.7 and 35.2ppt, with lowest salinities being recorded over the Sofala Bank region, offshore of the Zambezi River Mouth. Current speeds recorded over the survey ranged between 0.03 and 5.78kt.

A total of 884 groups of an estimated 2,187 individual cetaceans of at least four species were recorded during the survey effort (Table 2). Sightings of large whales were recorded only on full search effort during passing and closing modes and during confirmation of groups during closing mode, as numbers of whales in the region were too high to record during off-effort periods. Few secondary sightings of large whales were recorded during interception of primary sightings during closing mode, and during periods of effort carried out when weather conditions were unacceptable for full search effort (on 26 August and 5 September). The majority of large whale sightings were cued by blows (Fig. 2), while all sightings of small cetaceans were cued by sight

Table 2

Cetaceans sighted during primary and secondary search effort during the line transect survey off Mozambique, 26 August to 7 September 2003. Secondary sightings are those made during confirmation of primary sightings or under effort in unacceptable weather conditions.

		Primary sightings		Secondary sightings	
Species	Group size confirmation	Groups	Individuals	Groups	Individuals
Humpback whales	Confirmed group size	258	503	20	28
	Un-confirmed group size	379	552	34	47
Unidentified large whales	Confirmed group size	–	–	–	–
	Un-confirmed group size	129	151	3	3
Unidentified small whales	Confirmed group size	1	1	–	–
	Un-confirmed group size	1	1	–	–
Bottlenose dolphin	Confirmed group size	3	13	1	4
	Un-confirmed group size	13	100	–	–
Spinner dolphin	Confirmed group size	4	121	3	62
	Un-confirmed group size	12	289	2	107
Risso's dolphin	Confirmed group size	1	2	–	–
	Un-confirmed group size	–	–	–	–
Unidentified dolphin	Confirmed group size	–	–	–	–
	Un-confirmed group size	18	197	2	6
Total		819	1,930	65	257

Table 3

Parameters analysed in estimation of abundance of humpback and large unidentified whales sighted during the line transect survey off Mozambique, 26 August to 7 September, 2003.

Stratum	Area (A)	Effort (total L)	Transects	Primary sightings (n)	f(0) (SE)	ESW (SE)	Density of groups (SE)	Mean group size (SE)	Density of whales (SE)	N (%CV)
Cabo Inhaca to 14°20.5'S	14,029	936.19	28	734	0.67416 (0.038)	1.4833 (0.083)	0.26428 (0.037)	1.8363 (0.060)	0.48528 (0.069)	6,808 (14.22)
Cabo Inhaca to Ponta Zavora	1,587.63	105.63	3	123	0.65770 (0.055)	1.5205 (0.127)	0.39537 (0.061)	1.9734 (0.156)	0.78024 (0.135)	1,239.0 (17.32)
Ponta Zavora to Cabo Bazaruto	1,243.64	204.41	7	180	0.48543 (0.033)	2.0600 (0.142)	0.22203 (0.067)	2.5050 (0.219)	0.55619 (0.175)	692.00 (31.44)
Cabo Bazaruto to Epidendron Island	10,001.94	455.26	12	293	0.74998 (0.086)	1.3334 (0.153)	0.25040 (0.059)	1.6254 (0.673)	0.40701 (0.097)	4,071.0 (23.97)
Epidendron Island to 14°20.5 S	1,196.26	170.89	6	115	0.89253 (0.122)	1.1204 (0.153)	0.30292 (0.094)	1.8291 (0.144)	0.55407 (0.177)	663.00 (31.98)
Pooled stratified estimate										6,664.0 (15.67)

of body or splashes. A total of 691 groups of humpback whales was sighted during the effort component of the line transect survey of which 637 groups were primary sightings (Table 2), while 132 groups of unidentified whales were sighted during the on effort component of the line transect survey, of which 129 groups were primary sightings. The distribution of these 691 sightings of an estimated 1,130 individual humpback whales and 132 sightings of an estimated 154 large unidentified whales show individuals to occur throughout the survey region (Fig. 2). Two sightings of two single unidentified small whales, were made in the region of Inhambane.

The high densities of whales encountered (mean of 8.87 groups per hour) necessitated that once sighted, groups were visually tracked through the observation area until they were abeam of the vessel, so as not to be recorded as new sightings. Diversion of the vessel from the trackline during closing mode resulted in confusion between previous primary sightings and new secondary sightings, and the survey was therefore carried out predominantly in passing mode. However, given the high densities of sightings, confirmations of group size could be carried out on a relatively large sample within acceptable distance ranges, usually as the group was at it's closest to the observation platform when abeam of the vessel. The sizes of 284 groups of humpback whales were confirmed (37%) providing a mean group size of 1.89 whales per group. Mean group sizes recorded during the 1991 survey (Findlay *et al.*, 1994) ranged by stratum between 1.80 and 2.16 whales per group. Species identity was carried out only on confirmation of the animal's body. Given that the only identified species of large whale on the survey were humpback whales, the assumption that all unidentified whales were humpback whales appears reasonable (the only other large whale species to be expected in the region, would be low densities of southern right whales in the extreme south of the survey area). Comparison of confirmed and unconfirmed group size estimates (Fig. 3) of humpback and unidentified large whales show the unconfirmed group sizes to be smaller ($\chi^2 = 388.7$; $df = 6$; $p < 0.0001$), possibly due to the underestimation of distant groups. Consequently only confirmed group sizes have been utilised in the calculation of the mean size of humpback whale groups of 1.90 (SD±1.09; $n = 284$) individuals. Group sizes of all sightings of unidentified whales remained unconfirmed. Age or sex composition of groups remained undetermined, although all groups containing calves were assumed to include a cow-calf pair. A total of 47 groups of humpback whales containing a calf were recorded throughout the survey area (Fig. 2). Thirty-eight of these calves were recorded within 278 groups of confirmed group size (13.7%), while a further nine calves were recorded in groups of unconfirmed group size.

The direction of travel of humpback whales was non-random over the four cardinal quadrants ($\chi^2 = 21.7$; $df = 3$; $p < 0.0007$), with fewer than expected whale groups observed travelling in a northwesterly direction (Fig. 3). Travel in a northwesterly direction was probably influenced by the orientation of the Mozambique coastline in a general northeasterly/southwesterly direction. Despite long-shore movement of animals, no directed northward or southward migration of animals were believed to bias encounter rates.

Relative abundance of humpback whales within the surveyed area

Expected densities of humpback whales were calculated as a function of search effort. Whales were not randomly distributed by half degree square ($\chi^2 = 145.0$; $df = 43$; $p < 0.0001$), with higher than expected sighting frequencies in the regions between Cabo Inhaca and Xai-Xai, between Ponta Zavora and Bazaruto and in the region of the Pantaloon Shoals to the north east of Quelimane, and lower than expected sighting frequencies over the Sofala Banks. The relative abundances of humpback whales and large unidentified whales were analysed by comparison of observed and expected densities across environmental parameters (Fig. 4). A significant difference ($\chi^2 = 10.4$; $df = 4$; $p < 0.035$) was found between the observed and expected frequencies of whale groups recorded by Beaufort Sea state (Fig. 4), although this is possibly a reflection of the sightability of whales in different sea states. Lower than expected frequencies were recorded in both Beaufort Sea state 1 and 4, and higher than expected frequencies were recorded in Beaufort Sea states 2 and 3, reflecting (as with wind speed) both the visibility of sighting cues and whale behaviour. Wind speed appeared to have a significant influence on sighting probability ($\chi^2 = 29.6$; $df = 6$; $p < 0.00005$) between observed and expected frequencies by wind speed (Fig. 4). Lower than expected frequencies were recorded during both light (<5knots) and strong winds (>15knots), with higher than expected frequencies recorded at intermediate wind speeds (5–10knots). The lower than expected sighting probabilities under light weather conditions is ascribed to both whale behaviour and the visibility of cues under such conditions.

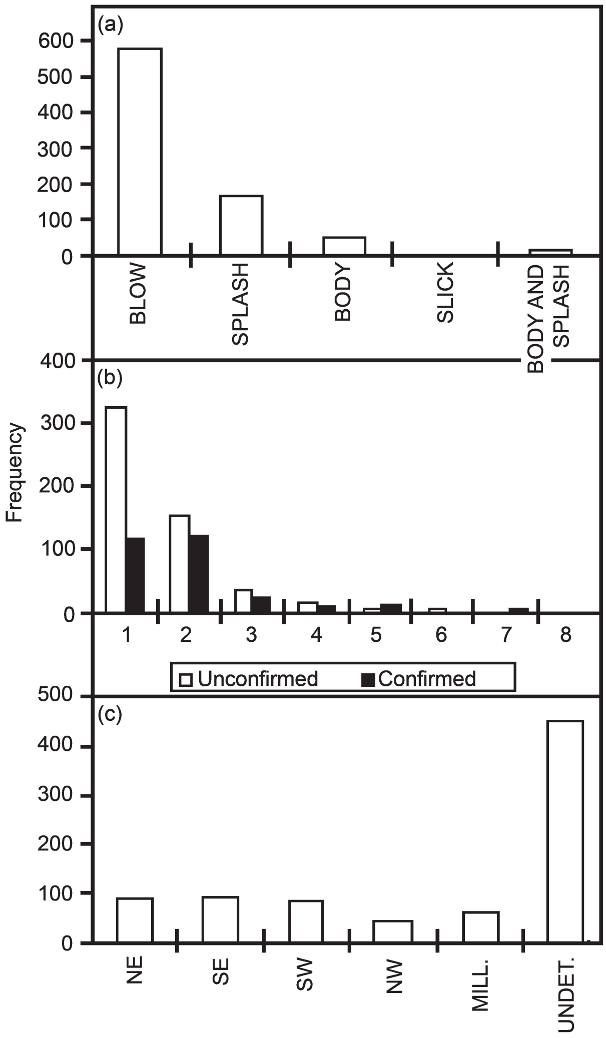

Fig. 3. Frequencies of sighting cues (a), confirmed and unconfirmed size estimates (b) and direction of travel (c) of groups of humpback and unidentified large whales sighted during the line transect survey.

No trend was evident in sighting rates by swell height (Fig. 4). Whales were observed at significantly different depths to those expected from a random distribution with respect to effort ($\chi^2 = 11.6$; $df = 4$; $p < 0.020$) (Fig. 4), with higher than expected frequencies recorded in the 100–200m depth interval and lower than expected densities recorded in both shallow and deeper water depth intervals. Although a significant difference ($\chi^2 = 12.2$; $df = 4$; $p < 0.02$) was found between observed and expected frequencies of whales by sea surface temperature interval (Fig. 4), no trend in distribution by sea surface temperature was evident. Humpback whale distribution was significantly related ($\chi^2 = 46.7$; $df = 15$; $p < 0.00004$) to sea surface salinity (Fig. 4), with possible avoidance of lower salinity waters. Although a significant difference between observed and expected sighting frequencies were recorded by current speed (distributed ($\chi^2 = 13.6$; $df = 55$; $p < 0.018$), whales were not distributed in faster or slower currents (Fig. 4).

Line transect survey

The relationship between photographically-determined distances to the small boat and radar measured distances recorded during the distance calibration experiment is shown in Fig. 5. Distances to 477 groups of whales were obtained from 579 photographs taken, the remaining 102 images being duplicates or blurred to the point that the group was indistinguishable within the image. Photographic distances were corrected for the error calculated from the radar calibrations ($y = 0.3462e^{0.8501x}$, $r^2 = 0.9725$, $p < 0.05$, $n = 35$, where x = photo distance and y = radar distance). Distances to the remaining 289 groups were determined from hand held reticule measurements converted to distance based on the results of the calibration experiment ($y = 2.9854e^{03423x}$, $r^2 = 0.9602$, $p < 0.05$, $n = 35$, where x = reticule distance and y = radar distance, Fig. 6).

Unstratified data

HUMPBACK AND UNIDENTIFIED WHALES COMBINED

The 734 groups of humpback and unidentified whales sighted within 3.6 n.miles of the ship during the 936.19 n.miles of acceptable survey effort resulted in an encounter rate of 0.784 groups per n.mile (SE (ni/li) ± 0.099). The frequency of perpendicular distance estimates from the trackline is provided in Fig. 7. The hazard-rate model fitted to the perpendicular distances truncated at 3.6 n.miles resulted in an estimated sighting probability density function at zero $f(0)$ of 0.67416 (SE±0.038) (Table 3). On the assumption that $g(0) = 1$, this leads to an estimated density of 0.265 groups per square nautical mile and an estimate of 0.485 whales per square nautical mile. Such densities result in an abundance estimate of 6,808 whales (CV = 0.14) over the surveyed area of 14,029.49 n.miles^2 (Table 3).

HUMPBACK WHALES

A total of 618 groups of humpback whales were sighted within 3.6 n.miles of the trackline during 936.19 n.miles of acceptable on effort survey. Frequencies of groups sighted with distance from the trackline are shown in Fig. 9. On the assumption that $g(0)$ equals 1, the hazard rate model applied to these frequencies resulted in an estimated sighting probability density function at zero $f(0)$ of 0.69354 (SE ± 0.037) and an effective search width of 1.4419 (SE ± 0.078) (Table 4). Densities of encountered groups and whales were estimated at 0.22891 (SE ± 0.033) and 0.42268 (SE ± 0.062) per n.mile^2 respectively, leading to an abundance estimate of 5,930 (CV = 0.15) across the surveyed area of Mozambican waters (Table 4).

Data stratified by coastal region

HUMPBACK AND UNIDENTIFIED WHALES

Totals of 123, 180, 293 and 115 primary sightings of humpback and unidentified whales were made during 105.63, 204.41, 455.26 and 170.89 n.miles of search effort in Strata 1 to 4 respectively (Table 3). The frequencies of perpendicular distance estimates from the trackline of sightings in each stratum are provided in Fig. 8. Hazard rate models were fitted to the perpendicular distances truncated at 3.6 n.miles in each of these strata and resulted in the sighting probability density function values at zero shown in Table 3, along with other results of analyses of abundance estimation in each of these four strata. A significant difference was found in mean group size by stratum (Table 5, $F = 6.26$, $p < 0.005$, $n = 252$). A pooled total of 6,664 (CV = 0.16) whales was estimated in the area surveyed (Table 3), with highest densities in the southernmost stratum and the lowest densities across the Sofala Banks.

HUMPBACK WHALES

Totals of 113, 160, 253 and 92 primary sightings of humpback and unidentified whales were made within 3.6 n.miles of the trackline during 105.63, 204.41, 455.26 and 170.89 n.miles of search effort in Strata 1 to 4 respectively

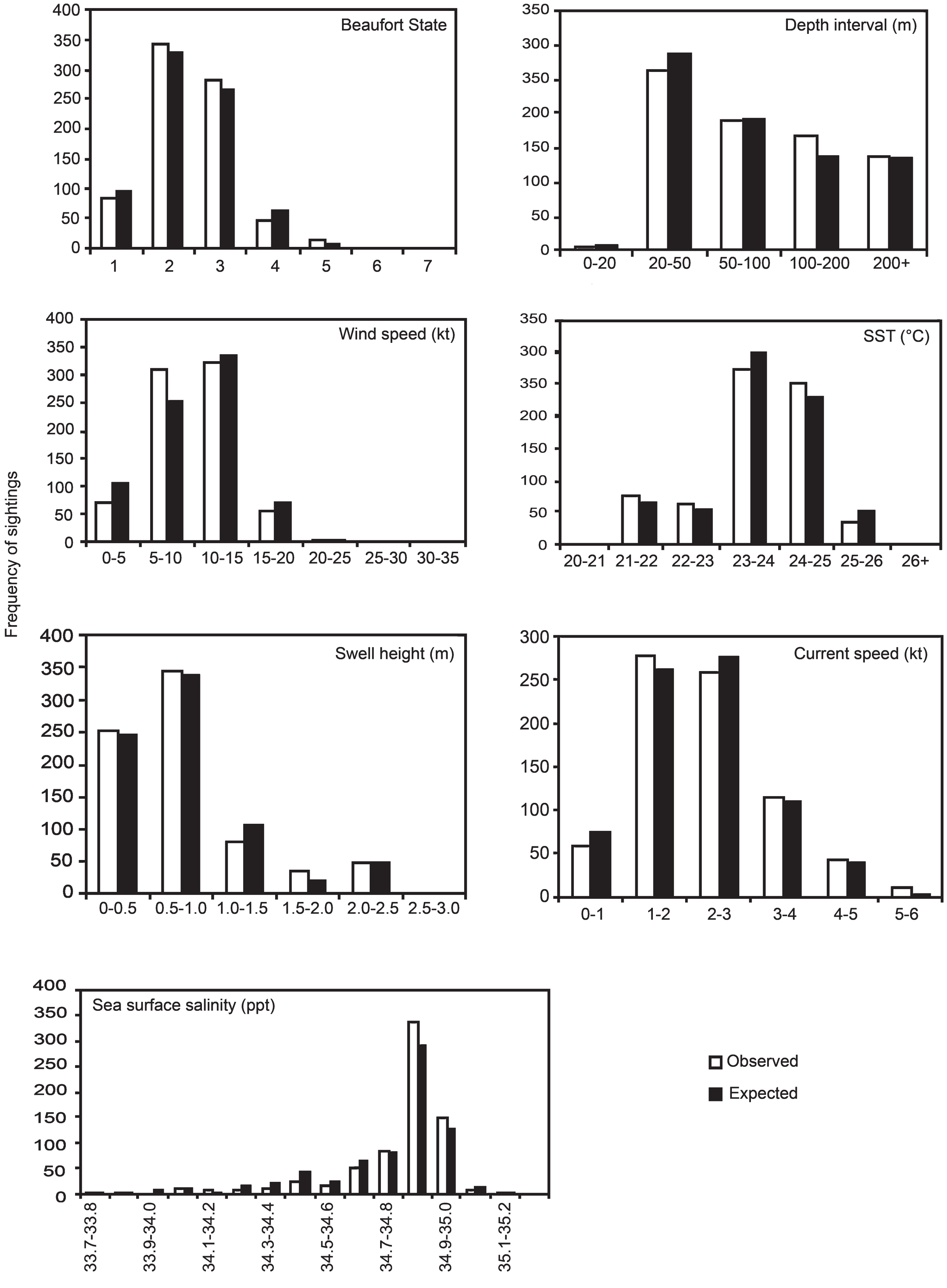

Fig. 4. Observed and expected numbers of humpback and large unidentified whale groups sighted by Beaufort State, wind speed, swell height, water depth, sea surface temperature, sea surface salinity and current speed interval during the line transect survey off Mozambique, 26 August to 7 September 2003. Expected numbers were calculated under the assumption that sighting densities are determined by relative search effort.

(Table 3). Frequencies of sightings with distance from the trackline (in 0.2 n.mile distance bins) are shown in Fig. 10. Application of the hazard rate model to these frequencies resulted in sighting probability density function values at zero, and on the assumption of $g(0)$ equalling 1 resulted in effective search widths of between 1.23 and 1.96 (see Table 4). Densities calculated in the four strata showed (as with the combined analyses of humpback and unidentified whales) densities to be lowest across the Sofala Banks and highest in the southern stratum between Inhaca and Ponta Zavora.

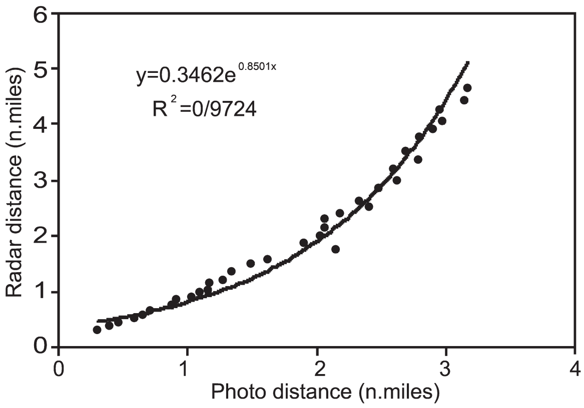

Fig. 5. Relationship between distance measurements to an inflatable small boat target measured by the photographic distance measurement (after Buckland *et al.*, 1993; Gordon, 1990) and by radar during the distance calibration experiment.

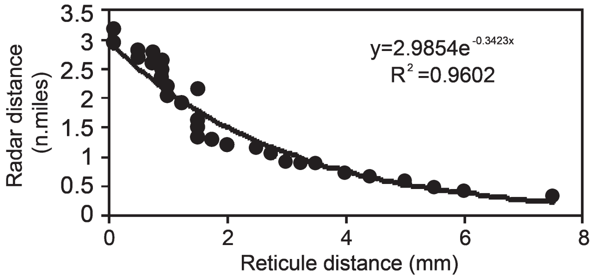

Fig. 6. Relationship between distances measured to an inflatable small boat by hand-held reticules and by radar during the distance calibration experiment.

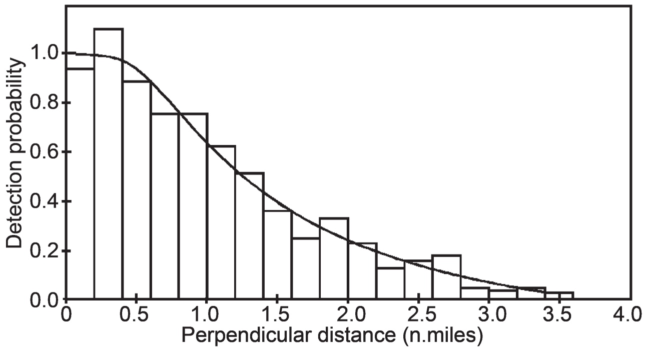

Fig. 7. Frequency of groups of humpback and unidentified whales sighted at perpendicular distances from the trackline during primary search effort over the line transect survey off Mozambique, 26 August to 7 September 2003.

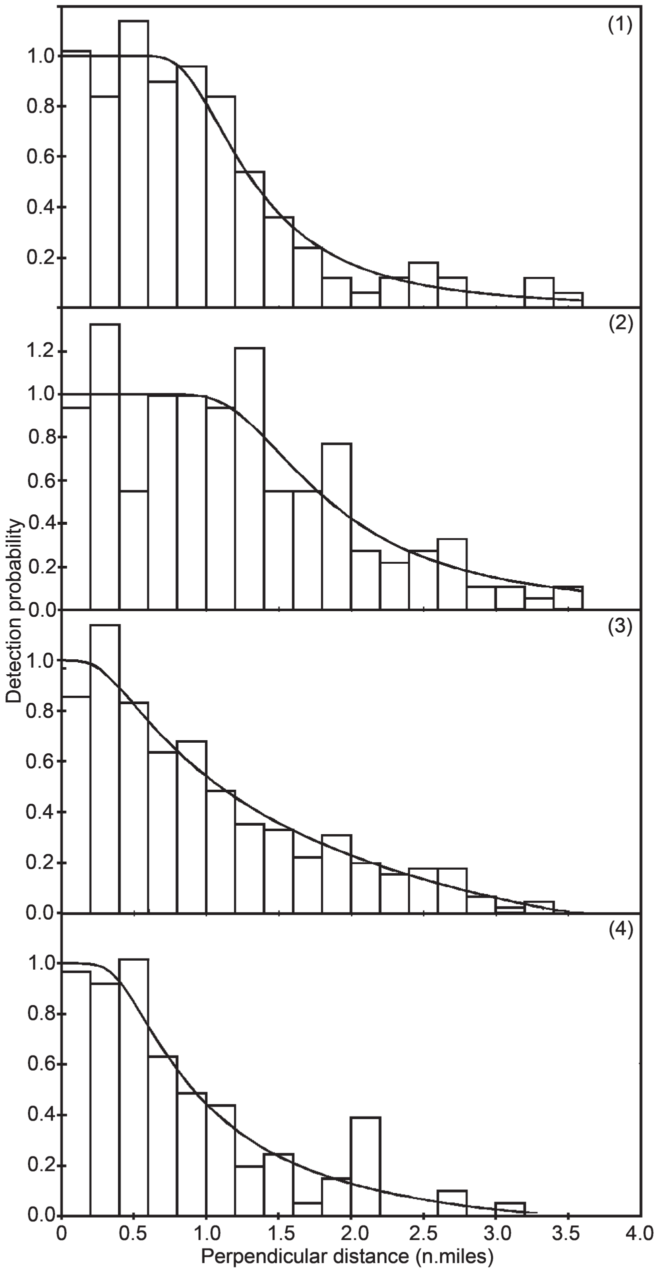

Fig. 8. Frequency of groups of humpback and unidentified whales sighted at perpendicular distances from the trackline in each of the four strata during primary search effort over the line transect survey off Mozambique, 26 August to 7 September 2003. (Stratum 1, Cabo Inhaca to Ponta Zavora; Stratum 2, Ponta Zavora to Cabo Bazaruto; Stratum 3, Cabo Bazaruto to Epidendron Island, and Stratum 4, Epidendron Island to 14°20.5'S).

Pooled stratum estimates resulted in an abundance estimate of 5,965 whales (CV = 0.17).

DISCUSSION

Townsend's (1935) charts of the positions of 19th Century open-boat whale-ships on days on which humpback whales were taken, show high catches in the region of 14°–15°S on the east coast of Africa, and few or no catches elsewhere on the Mozambican coast. Given that humpback whales migrate throughout coastal waters of this region, Findlay *et al.* (1994) believed this to be an error on Townsend's part in attributing catches from the coast of Mozambique to the town of Mozambique. However, Townsend's (1935) charts also show high localised catches in the region of Baie d'Antongil (15°30'S) in the north east of Madagascar, where Ersts and Rosenbaum (2003) have described a humpback wintering ground. Sightings recorded during the current survey were across the survey area and do not support the clumping of catches in the 14°–15°S region of the coast as indicated by Townsend (1935). Although such clumping may result from selection of anchorages or other logistic aspects, the availability of both sheltered sites and catches of other species indicated by Townsend (1935) elsewhere along this coast (for example, the catch of southern right whales on the Delagoa bay grounds off Maputo in southern Mozambique) suggest some anomaly in the distribution of catches shown by Townsend (1935). Rørvik (1980) and da Silva (in litt.)

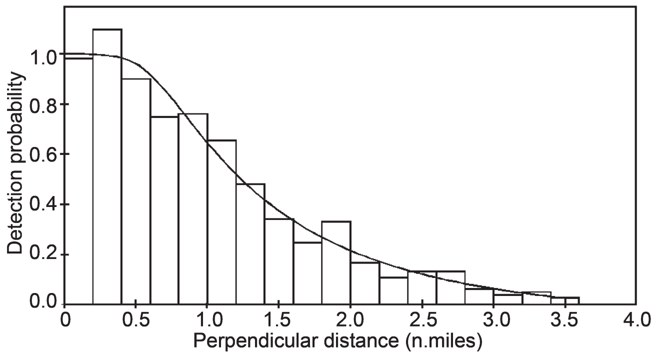

Fig. 9. Frequency of groups of humpback whales sighted at perpendicular distances from the trackline during primary search effort over the line transect survey off Mozambique, 26 August to 7 September 2003.

[see Findlay *et al.,* 1994] record sightings of humpback whales made in Mozambique waters, but neither sets of data have associated effort and no overall distribution patterns can be determined. However it should be noted that Rørvik (1980) recorded no sightings to the north of Angoche. Similarly, Tønnessen and Johnsen (1982) noted that catches to the north of Quelimane were generally poor. Despite few sightings within southern Tanzania, it was believed that the planned transects of this survey would extend beyond the northern limit of the wintering ground, and that sighting rates would decline in the north of the survey.

The timing of the 2003 survey was selected to maximise the abundance of humpback whales on the wintering ground. Olsen (1914) reported on the seasonality of humpback whale catches in the Durban whaling grounds over the period 1910 to 1912, and although Best *et al.* (1998) suggests that the 1912 data may be compromised, the seasonality of catches in both 1910 and 1911 show bimodal peaks in the last 10 days of July and in mid- to late September. Further bimodal seasonality of catches and sightings off Durban were reported by Matthews (1938) and Bannister and Gambell (1965) respectively. Sightings of humpback whales made by the Union Whaling Company's spotter aircraft in the Durban whaling grounds between 1972 and 1975 were too few to describe any seasonal abundance patterns (Findlay, 1989). Catches from Linga-linga, Mozambique, were unimodal in seasonal abundance with peak catches in August or July (Lea, 1919; Olsen, 1914). Bermond (1950) analysed catches off Madagascar in the 1938, 1939 and 1949 seasons by 10 day period and found a marked bimodal seasonality in 1938 and 1939 (peaks in July and late August/early September), but a less pronounced bimodal seasonality in 1949. Angot (1951) provided a more detailed analysis of the 1949 data and showed a bimodal seasonality with peaks in late July and early September (Table 1). Findlay (1994) and Findlay and Best (1996a; 1996b) provided the results of shore based monitoring of the migration of humpback whales off Cape Vidal, northern KwaZulu-Natal between 1988 and 1991, and found the northward migration to occur between July and August and the southward migration to occur in September and October. Although direction of movement of groups recorded during the 2003 survey was not random over the four cardinal quadrants of the compass (possibly due to the orientation of the coastline limiting movement in a north westerly direction), there was no difference in direction of movement between northerly and southerly direction which might have biased counts. Furthermore the southward migration is thought to commence in late August/early September so that any population movement would have been expected against the northward direction of the survey (thus limiting bias of the vessel following the migration).

Sighting conditions encountered during the cruise were generally very good with only 18.5% of survey lost to inclement weather. Relative sighting rates were marginally lower under calm conditions (wind speed of less than 5 knots or sea state of 1) probably as a result of reduced cues from less surface active behaviour under these conditions or from reduced visibility of blows against calm sea conditions. However, such calm conditions formed a relatively small component of the survey and relative differences are not believed to bias overall sighting rates. On the basis of observed versus expected frequencies of sightings, humpback and large unidentified whales were not randomly distributed by area, with lower than expected sighting frequencies over the Sofala Bank region. The most marked difference between the observed and expected sighting frequencies by environmental parameter was by sea surface salinity, where whales were distributed in higher salinities than expected. The lowest salinity waters were recorded in the Sofala Banks region (possibly corresponding to the outflow of the Save, Zambezi, and Pengue Rivers in this region). Avoidance of turbid waters by humpback whales has been noted during observations off Cape Vidal in South Africa and it is possible that turbid freshwater river outflow influenced whale distribution over the Sofala Banks.

A yacht-based survey of humpback whales carried out in Mozambique waters in 1991 (Findlay *et al.*, 1994), found

Table 4

Parameters analysed in estimation of abundance of identified humpback whales sighted duringthe line transect survey off Mozambique, 26 August to 7 September, 2003.

Stratum	Area (A)	Effort (total L)	Transects	Primary sightings (n)	f(0) (SE)	ESW (SE)	Density of groups (SE)	Mean group size (SE)	Density of whales (SE)	N (%CV)
Cabo Inhaca to 14°20.5'S	14,029	936.19	28	618	0.69354 (0.037)	1.4419 (0.078)	0.22891 (0.033)	1.8465 (0.060)	0.42268 (0.062)	5,930.0 (14.68)
Cabo Inhaca to Ponta Zavora	1,587.63	105.63	3	113	0.69726 (0.0613)	1.4342 (0.126)	0.37295 (0.069)	1.9795 (0.156)	0.73825 (0.148)	11,72.0 (20.14)
Ponta Zavora to Cabo Bazaruto	1,243.64	204.41	7	160	0.51120 (0.038)	1.9562 (0.146)	0.20006 (0.060)	2.4862 (0.217)	0.49738 (0.155)	619.00 (31.19)
Cabo Bazaruto to Epidendron Island)	10,001.94	455.26	12	253	0.81445 (0.088)	1.2278 (0.133)	0.22631 (0.056)	1.6341 (0.068)	0.36980 (0.093)	3699.0 (25.20)
Epidendron Island to 14° 20.5'S	1,196.26	170.89	6	92	0.80234 (0.097)	1.2464 (0.150)	0.21597 (0.064)	1.8398 (0.148)	0.39733 (0.122)	475.00 (30.75)
Pooled stratified estimate										5,965.0 (16.62)

Table 5

Mean group sizes of confirmed groups recorded by survey stratum off Mozambique, 26 August to 7 September 2003.

Stratum[1]	Average	SD	n
1	1.916667	1.126722	48
2	2.436364	1.607432	55
3	1.701754	0.739885	114
4	1.714286	0.825029\	35

[1] Stratum 1, Cabo Inhaca to Ponta Zavora; Stratum 2, Ponta Zavora to Cabo Bazaruto; Stratum 3, Cabo Bazaruto to Epidendron Island, and Stratum 4, Epidendron Island to 14° 20.5'S

whales distributed over the entire region surveyed, although whale densities were highest in the southern region between 33°E and 35°30'E (Maputo to Ponta Zavora) a region of shallow banks where the southerly Mozambique Current flowed further offshore. A high proportion of cow and calf pairs were sighted on the Sofala Banks during the 1991 survey (Findlay *et al.*, 1994), and compared favourably with proportions of cow and calf pairs sighted on other presumed calving grounds. As with the 1991 survey, highest densities of whales were recorded in the southern region between Cabo Inhaca and Ponta Zavora. Surprisingly however, cow calf groups were distributed throughout the survey area suggesting a possible expansion of the area utilised by lactating females.

The abundance of whales estimated from this survey ranged between 6,808 (CV = 0.14) humpback and unidentified whales and 5,930 humpback whales (unstratified analyses) and 6,664 humpback and unidentified whales (CV = 0.16) and 5,965 humpback whales (CV = 0.17) (data analysed across the four coastal strata). The abundance estimate of 5,965 (CV = 0.17) whales is a marked increase over the estimate made in 1991 of 1,954 (CV = 0.38) by Findlay *et al.* (1994) or the estimate of 1,776 made during shore-based surveys on the northern KwaZulu Natal coast in 1991 (Findlay and Best, 1996b). However, comparison of these estimates requires considerable caution and no attempt has been made to estimate increase rates from these surveys. Firstly, the survey limits are not directly comparable in distribution or extent. The 1991 area surveyed by Findlay *et al.* (1994) extended from Maputo Bay (25°45'S) to 18°S and between the 10 and 100 fathom (or 18.3 and 183m isobaths) (a total area of 12,591 n.miles^2), while the current survey extended from Cabo Inhaca (26°00'S) and 14°20.5'S from inside the 20m isobath to immediately outside the 200m isobath (a total area of 14,029 n. miles^2). Although both the 1991 and the 2003 surveys assumed that all whales on the trackline were sighted (that $g(0)$ was 1) the distribution of sightings from the trackline may have differed between the two survey platforms, as the sighting probabilities of five observers at 12m above sea level on the more stable *FRS Algoa* platform would be expected to be considerably higher than those of two observers at 10m on a yacht mast.

Furthermore, the population abundance estimated during this survey must be considered minimal for the Mozambique population for a number of reasons.

(1) Although the timing of the survey was planned to coincide with maximal expected abundance on the Mozambique grounds, numerous sightings made in transit between Richard's Bay, South Africa and Cabo Inhaca suggest that a considerable proportion of the population was to the south of the surveyed area during the survey.

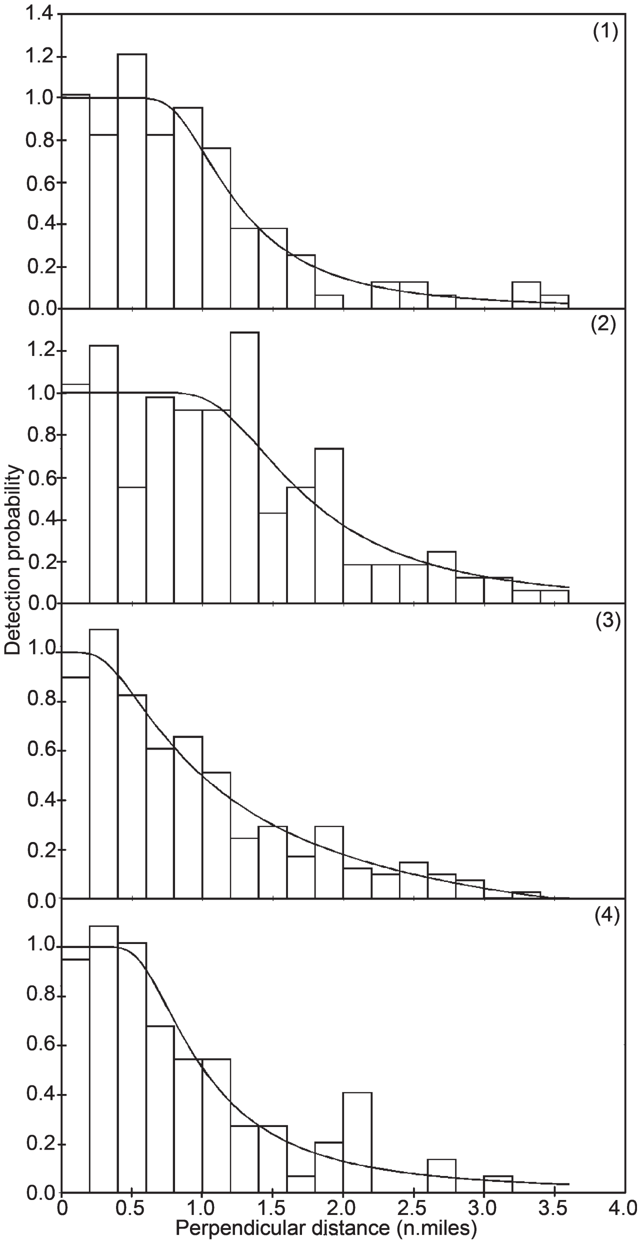

Fig. 10. Frequency of groups of humpback whales sighted at perpendicular distances from the trackline in each of the four strata during primary search effort over the line transect survey off Mozambique, 26 August to 7 September 2003. (Stratum 1, Cabo Inhaca to Ponta Zavora; Stratum 2, Ponta Zavora to Cabo Bazaruto; Stratum 3, Cabo Bazaruto to Epidendron Island, and Stratum 4, Epidendron Island to 14°20.5'S).

(2) The definition of the survey area between the 20 and 200m isobaths was selected on the basis of distributions and historical catches of humpback whales in coastal waters in breeding grounds across the Southern Hemisphere. However the sightings on this survey during limited effort in water depths of over 200m suggest that some unknown proportion of the population was offshore of the major area surveyed.

(3) The high encounter rates on the northernmost transects of the area surveyed suggest that it is probable that the northern limits of the breeding grounds were not surveyed.

(4) The assumption of $g(0)$ being one over all sighting conditions encountered likely biases the abundance estimate downwards.

Although not directly comparable to the yacht based survey of Mozambican waters carried out in 1991 (Findlay *et al.*,

1994) or shore based surveys off northern KwaZulu-Natal in 1990 and 1991 (Findlay and Best, 1996a) these estimates suggest the population of humpback whales off Mozambique has increased since the early 1990s. However, no increase rates have been calculated due to the marked differences in survey procedures, design and area.

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Density, group composition and encounter rates of humpback whales (*Megaptera novaeangliae*) in the eastern Comoros Archipelago (C2)

PETER J. ERSTS*, JEREMY KISZKA+,#,^, MICHEL VÉLY~ AND HOWARD C. ROSENBAUM++,*

Contact e-mail: ersts@amnh.org

ABSTRACT

The Comoros Archipelago is an assemblage of oceanic islands, banks and offshore reef systems that longitudinally span the northern Mozambique Channel. The greater Comoros Archipelago has been designated by the IWC as Wintering sub-Region C2 for humpback whales and is currently considered data deficient. Since 1997, annual marine mammal surveys of varying length and objective have been carried out in the waters surrounding Mayotte, the eastern most island in the Comoros Archipelago. The humpback whales component of these surveys focused effort in and around the lagoon surrounding Mayotte. While it is expected that humpback whales can found throughout Comoros Archipelago it still remains unknown as to what degree humpback whales utilise specific banks and offshore reef systems within this area. Surveys conducted in 2002 and 2003 included passing mode and closing mode components intended to examine the density, group composition and encounter rates of humpback whales in an offshore reef complex and a bank adjacent to the lagoon surround Mayotte. The densities of humpback whales, out to one nautical mile from the surveyed transects, ranged from 0.027 to 0.618 whales/n.mile^2 across three study sites. Females with calves were the most frequently encountered group type. Encounter rates ranged from 0.98 to 2.36 groups per hour of search effort. These results, while exploratory in nature, indicate that the eastern region of the Comoros may be an important area for humpback whales during the late austral winter months and that additional, more intensive systematic research is warranted.

KEYWORDS: HUMPBACK WHALE; BREEDING GROUNDS; CONSERVATION; SURVEY-VESSEL; SOUTHERN HEMISPHERE

INTRODUCTION

During the austral winter, humpback whales (*Megaptera novaeangliae*) undertake an annual migration from the cold waters of Antarctic feeding grounds to the warm waters of low-latitude wintering regions where breeding and calving take place. The International Whaling Commission (IWC) recognises seven major low-latitude wintering regions (A-G) for management of Southern Hemisphere humpback whale populations (IWC, 2000; 2004). The southwestern Indian Ocean has been designated Wintering Region C and is currently further partitioned into three smaller units; Wintering sub-Region C1, C2, and C3. These sub-regions largely correspond to the termini of three migratory streams postulated to exist within the southwestern Indian Ocean (Best *et al.*, 1998). One of the proposed migratory streams is thought to carry humpback whales northward through the centre of the Mozambique Channel to the Comoros Archipelago; designated by the IWC as Wintering sub-Region C2. Despite their close proximities, aggregations of whales in the Comoros Archipelago are differentiated from aggregations found along the eastern coast of South Africa and Mozambique (C1) (Findlay and Best, 1996; Findlay *et al.*, 1994) and from aggregations found along eastern and southern coast of Madagascar (C3) (Best *et al.*, 1998; Best *et al.*, 1996; Rosenbaum *et al.*, 1997); however recent evidence has shown that individual humpback whales utilise both C1 and C2 (Ersts *et al.*, 2011).

The Comoros Archipelago is an assemblage of oceanic islands, banks and offshore reef systems that longitudinally span the northern Mozambique Channel between Madagascar and Mozambique. Elsewhere in the world, humpback whales are frequently observed in near-shore waters of low-latitude island chains where movement among close, adjacent islands and banks has been well documented through photographic analysis (Baker and Herman, 1981; Baker *et al.*, 1986; Balcomb and Nichols, 1982; Calambokidis *et al.*, 2001; Cerchio *et al.*, 1998; Darling and Morowitz, 1986; Garrigue *et al.*, 2002; Garrigue *et al.*, 2000; Mattila and Clapham, 1989; Mattila *et al.*, 1989; Mattila *et al.*, 1994; Urban and Aguayo, 1987; Whitehead and Moore, 1982). Satellite telemetry data has also demonstrated that humpback whales show a strong preference for shallower waters than for deeper inter-island channels and that animals can quickly move through an entire archipelago (Mate *et al.*, 1998). To date, limited systematic effort has been applied toward understanding humpback whales in Wintering sub-Region C2 (Rosenbaum *et al.*, 2001) and little published data are available (Kiszka *et al.*, 2007). While it is expected that humpback whales can found throughout C2, it still remains unknown as to what degree humpback whales utilise specific banks and offshore reef systems within this area.

Récif du Geyser (Geyser Reef) and Banc de la Zélée (Zélée Bank) form an isolated offshore reef complex on the eastern edge of the Comoros Archipelago. This complex along with the Banc de l'Iris (Iris Bank), a bank of similar size and structure adjacent to the island of Mayotte, possess environmental conditions that have been broadly described as those sought by humpback whales during their stay in the low-latitude wintering regions (Balcomb and Nichols, 1982;

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*Center for Biodiversity and Conservation, American Museum of Natural History, Central Park West at 79th Street, New York, New York, 10024 USA.

+ Observatoire des Mammifères Marins. Office National de la Chasse et de la Faune Sauvage and Direction de l'Agriculture et de la Forêt. BP 103. F-97600 Mamoudzou, Mayotte (France).

LIENSS (Littoral, Environnement et Sociétés). UMR 6250 CNRS-Université de La Rochelle. 2, rue Olympe de Gouges. 17000 La Rochelle, France.

^ Direction de l'Environnement et du Développement Durable. Conseil Général de Mayotte. BP 101, 97600 Mayotte (France).

~ Association MEGAPTERA, 23, rue Alexandre Dumas, 75011 Paris, France [Current address: *Route Royale, Tamarin, Mauritius*].

++ Wildlife Conservation Society, Ocean Giants Program, 2300 Southern Blvd., Bronx, NY 10460-1099, USA.

Dawbin, 1966; Ersts and Rosenbaum, 2003; Smultea, 1994; Whitehead and Moore, 1982). However, due to the relative inaccessibility of the Geyser-Zélée Complex, the presence of humpback whales and other marine mammals has previously only been known from a few anecdotal reports by fisherman and charter boat captains.

Since 1997, annual marine mammal surveys of varying lengths and objectives have been carried out in the waters surrounding Mayotte. These surveys focused their effort in and around the lagoon surrounding Mayotte. Surveys conducted in 2002 and 2003 included an exploratory component intended to examine the density and group composition of humpback whales and other marine mammals utilising the Geyser-Zélée Complex. This paper presents the results from these exploratory surveys along with a comparison of sighting data collected during the same time period on Iris Bank. Wintering sub-Region C2 is particularly data-deficient for humpback whales (Rosenbaum *et al.*, 2001) and these results, while exploratory in nature, represent much needed data to help describe this region and guide future research initiatives.

METHODS

Study area

Mayotte (12°50'S, 45°10'E), a territorial collectivity of France, is a small island in the northern Mozambique Channel (Fig. 1). Iris Bank (12°34'S, 44°59'E) is adjacent to the northern extent of the 437 n.mile^2 lagoon surrounding Mayotte (Fig. 2). Iris Bank covers an area of approximately 65 n.mile^2 with a mean depth of 30m (max 80m).

Geyser Reef and Zélée Bank (12°24'S, 46°25'E), form an isolated complex 80 n.mile northeast of the island of Mayotte (Fig. 3). This complex sits atop what is presumed to be a seamount of volcanic origin (Quod *et al.*, 2000; UNEP and IUCN, 1988), and is composed of two distinct areas separated by a 4.5 n.mile wide channel that exceeds 600m in depth.

Geyser Reef is approximately 120 n.mile^2 in area while Zélée Bank is smaller, covering approximately 70 n.mile^2. Depths on this complex range from 1m near the reef crest to 40m in the interior regions. The edge of the complex is characterised by near vertical walls that rapidly drop to depths of over 1,000m within as little as 500m of their shallowest points. The complex remains completely submerged at low tide, with the exception of a partially emergent western rim of the Geyser Reef.

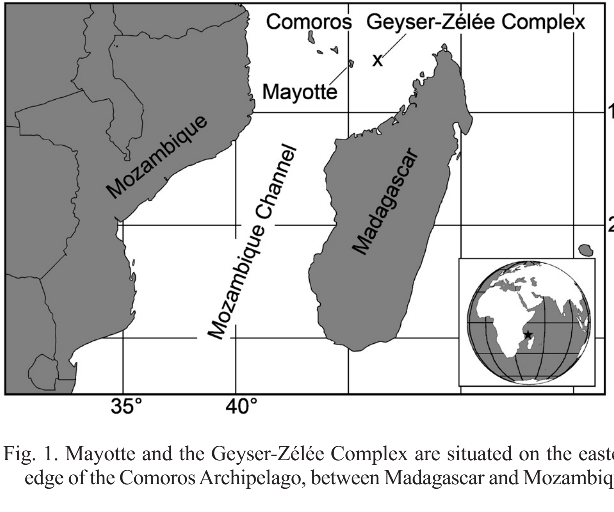

Fig. 1. Mayotte and the Geyser-Zélée Complex are situated on the eastern edge of the Comoros Archipelago, between Madagascar and Mozambique.

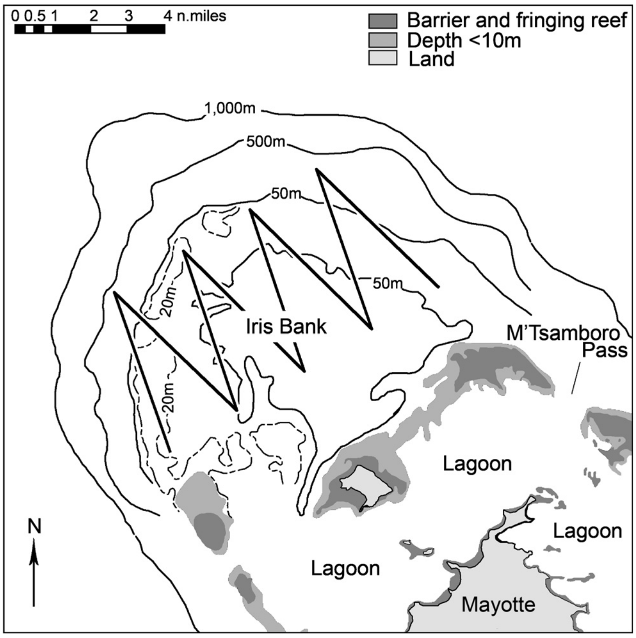

Fig. 2. Iris Bank.

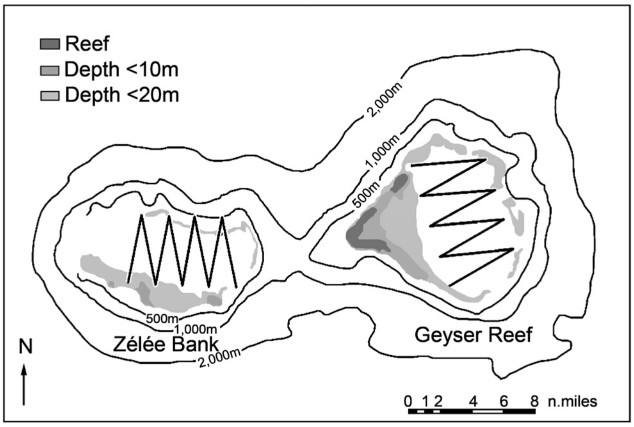

Fig. 3. Geyser-Zélée Complex.

Surveys

The initial survey of the Geyser-Zélée Complex was conducted in September 2002. When an opportunity occurred to return to the Geyser-Zélée Complex in October of 2003, the 2002 surveys were replicated for reason of comparability even though alternative survey designs were proposed after the 2002 experience.

Closing mode surveys for humpback whales were conducted in the waters surrounding Mayotte during the days and weeks immediately preceding and following the surveys of the Geyser-Zélée Complex. Tables 1 and 2 summarise survey effort applied during 2002 and 2003. As indicated in Table 1, survey objectives of 2002 included applying closing mode effort on Iris Bank as well as in the interior of the lagoon surrounding Mayotte. Data collected in the interior of the lagoon in 2002, however, are not reported here nor are they included in this analysis; only sighting data collected on Iris Bank were used for this analysis.

Passing mode

Line transect distance sampling methods (Buckland *et al.*, 2001) were applied during surveys in the interior of Geyser Reef, Zélée Bank and Iris Bank (Figs 2 and 3) to determine

Table 1
Summary of surveys conducted in 2002 and 2003.

Start date	End date	Location	Survey methods
27/08/02	08/09/02	Lagoon surrounding Mayotte* + Iris Bank	Closing mode only
09/09/02	14/09/02	Geyser Reef + Zélée Bank	Passing mode + Closing mode
15/09/02	25/09/02	Lagoon surrounding Mayotte* + Iris Bank	Closing mode only
23/09/03	01/10/03	Iris Bank	Closing mode only
05/10/03	08/10/03	Geyser Reef + Zélée Bank	Passing mode + Closing mode
09/10/03	10/10/03	Iris Bank	Passing mode only
11/10/03	16/10/03	Iris Bank	Closing mode only

*Data collected in the interior of the lagoon in 2002 are not reported here nor included in this analysis.

diversity and density of marine mammals. Pre-determined saw-tooth transects were uploaded to the navigational computer aboard the survey vessel, a 17.5m catamaran chartered out of Mayotte. Transects were completed at eight knots with all aspects of navigation along the transects being controlled by the navigational computer (i.e. auto-pilot) aboard the survey vessel. A transect was composed of eight, 4.5 n.mile long legs with 2 n.miles between the apex of each saw-tooth. The same design was used on each of the three locations, although the orientation of each transect was different in order to maximise coverage.

Observations for marine mammals were carried out by two teams of four observers from the roof of the cabin, approximately 4.5m above the water surface. Each team actively observed for four legs or approximately two hours at a time. When not on watch, team members remained below decks to minimise fatigue and potential observational bias. Each team consisted of a starboard and port side primary observer and data collector. The starboard and port observers worked independently observing in an arc from the trackline to perpendicular with the trackline on their respective side. Observers searched by naked eye and with binoculars. Starboard and port side teams were allowed to communicate with one another when a sighting was recorded near the trackline or at the apex of a saw-tooth in an attempt to minimise duplicate observations. The survey vessel did not deviate from the pre-determined transect at any time to attempt photographic identification or genetic sampling.

Data collectors recorded time (hour, minutes, seconds), estimates of group size (min, max, best), cue (i.e. blow, breach), bearing and estimated distance to each sighting and geographic position at the time of initial detection. Where species determination was not possible, sightings were simply recorded as ‘whale-like’ or ‘dolphin-like’.

Perpendicular distance estimates were calculated using a method based on spherical geometry as outlined in Ersts *et al.* (2008). This spherical method involves finding the intersection between two great-circles and requires the geographic location of the survey platform, a detection or radial distance, and the bearing to the sighting at the initial time of detection. This method was chosen because the configuration of the cabin roof did not allow for the use of angle boards. Bearings to sightings were obtained with hand-held nautical sighting compasses. Bearings were recorded to the nearest degree and post-corrected to account for magnetic declination. The most experienced member of the observation team estimated the distance from the survey platform to the sighting at the time of initial detection. When possible, photographs were taken of each sighting; however, photographic techniques for estimating distance were not used in this analysis. Positional data were collected using either a hand-held Garmin *eTrex Venture* or *Garmin Geko 201*. Positional data were recorded in decimal degrees and stored with six or more significant digits so as not to introduce additional inaccuracies.

Closing mode

A closing mode methodology was employed in which the survey vessel would leave a previously determined search track in order to close on the group of whales or dolphins. The survey vessel would return to the search track once the group of whales or dolphins had been completely sampled or the maximum time limit (90 minutes) was reached. Maximum time limits were conservatively imposed to minimise any short-term alterations to behaviour or movement of the animals. Search tracks were designed to maximise spatial coverage but were not rigidly defined or followed. Consequently, only group size estimates from the closing mode data were used in the subsequent analyses of distribution and density.

When a group of marine mammals was encountered, the initial and last positions of the group were recorded in addition to descriptive attributes and photographs of tail flukes and dorsal fin features. Humpback whales were the

Table 2
Summary of closing mode effort, identified individuals, and encounter rates.

	Geyser-Zélée Complex		Iris Bank	
	2002	2003	2002	2003
Searching effort (hours)*	7.20	5.69	19.17	17.33
Total closing mode effort (hours)**	19.28	13.71	29.90	30.45
Groups	17	9	13	17
Identified individuals (flukes/ dorsal)	7/19	6/14	9/16	4/27
Dorsal only	13	9	7	23
Flukes only	1	1	–	–
Dorsal and flukes	6	5	9	4
Groups/hour (searching effort)	2.36	1.58	0.68	0.98
Identified individuals/hour (searching effort)	0.97/2.64	1.05/2.46	0.47/0.83	0.23/1.56
Groups/hour (total effort)	0.88	0.66	0.43	0.56
Identified individuals/hour (total effort)	0.36/0.99	0.44/1.02	0.30/0.54	0.31/0.87

*Searching effort refers to time spent actively searching for cetaceans. **Total closing mode effort includes time spent actively searching and sampling cetaceans, acoustic watches, acoustic recording, processing samples etc., but not time spent in transit.

primary focus of these surveys, thus behavioural information was not collected for other cetacean species and photographic data of other species were only collected for species confirmation. Groups of humpback whales were classified into one of seven classes (mother-calf pairs, mother-calf-escort, pairs, competitive groups, non-competitive, singers and singletons), based on observed attributes or behavioural characteristics previously described for this species (Baker and Herman, 1984; Clapham *et al.*, 1992; Tyack and Whitehead, 1983). Acoustic watches were not systematically undertaken to search for singing whales. When solitary humpback whales with extended (> 15 minutes) but regular dive intervals were encountered they were checked for singing periodically throughout the encounter when possible and the presence or absence of other humpback whales within sight of the survey vessel was also noted.

Humpback whales were photographed using a *Nikon D1* digital camera fitted with an 80-200mm 2.8f lens. Individual humpback whales were identified using photographs of the ventral side of their tail flukes (Katona and Whitehead, 1981), dorsal fins (Blackmer *et al.*, 2000) and other natural markings.

Density calculation

Group densities were calculated with the same basic equation used in similar surveys throughout the West Indies (Mattila and Clapham, 1989; Mattila *et al.*, 1994):

$$Density = \frac{N_W}{(D \times 2 \times W)}$$

where N_W is the number of sightings up to W n.miles from the track line and D is the length of the trackline in nautical miles. Due to the exploratory nature of these surveys and the limitations of the survey vessel, detection functions were not fit to the observations and no attempt was made to correct for biases associated with weather, detection distance estimates, or observer experience. Whale density was calculated by multiplying the group density by the average group size determined from encounters made during closing mode surveys. This method for calculating density makes the assumption that group types encountered during closing mode surveys are representative of the group types observed during passing mode surveys. For added interpretability, passing mode data and their subsequent analysis are presented in three distance bins: 0.5, 1.0 and 1.5 n.miles. All sightings made beyond 1.5 n.miles were discarded.

Spatial calculations

A spherical method (Ersts *et al.*, 2008) for computing perpendicular distances estimates was chosen in part because of the inability to use angle boards, but also because it could be directly used with the geographical coordinates (i.e. longitude and latitude) and standard compass bearings. This spherical method also generates the geographical coordinates of each sighting which can be used in other broad scale spatial analyses.

The geographic mean longitude and latitude of the minimum bounding rectangle for each transect was used to produce both an east-west and north-south subdivision. A coarse examination of distribution of sighting made during passing mode was undertaken by tallying the number of sightings in both the east-west and north-south subdivision for each of the three survey sites using all available sightings out to 1.5 n.miles from the transect. The latitudinal or longitudinal mean can be used to divide a rectangular region into two parts of equal area regardless of the north-south or east-west orientation of the rectangle. However, together, latitudinal and longitudinal means will only provide four subdivisions of equal area when the rectangular area has an exact north-south or east-west orientation.

RESULTS

Humpback whale group composition

Humpback whales were the only large whale species encountered during closing mode surveys in the Geyser-Zélée Complex and on Iris Bank (Table 3). A total of 56 groups of humpback whales were encountered. No competitive groups were encountered during closing mode, however, two competitive groups were observed during passing mode surveys on the Geyser-Zélée Complex in 2003. Acoustic watches were neither performed on a regular basis nor in a systematic fashion, thus the number of singers is likely to be negatively biased. Nonetheless, single whales were infrequently encountered. Mean group size was 1.96 for both the Geyser-Zélée Complex and Iris Bank (n = 26, SD = 0.34 and n = 30, SD = 0.49 respectively).

Females with calves were the most frequently encountered group type on both the Geyser-Zélée Complex and Iris Bank (69.23%, n = 18 and 70.00%, n = 21 respectively). Pairs accounted for the second most frequently encountered group type on the Geyser-Zélée Complex and Iris Bank (23.08%, n = 6 and 16.66%, n = 5 respectively). Assuming an equal probability of encountering a pair, single animal, or female with a calf, the proportion of females with calves

Table 3

Number of encounters by species and humpback whale group type recorded during closing mode surveys on the Geyser-Zélée Complex and Iris Bank.

	Geyser-Zélée Complex		Iris Bank	
	2002	2003	2002	2003
Humpback whale	17	9	13	17
Mother-calf	11	6	6	12
Mother-calf-escort	1	–	–	3
Pair	4	2	4	1
Singleton	1	–	2	1
Singer	–	1	1	–
Spinner dolphin	1	2	4	3
Pantropical spotted dolphin	–	–	–	1
Spinner and pantropical spotted dolphin	2	1	2	2
Indo-Pacific bottlenose dolphin	–	–	1	1
Melon-headed whale	–	–	–	1

was significantly higher for the 2002 survey of the Geyser-Zélée Complex ($\chi^2_2 = 11.41$, $p < 0.01$), and the 2003 survey of Iris Bank ($\chi^2_2 = 23.06$, $p < 0.001$). There was no significant difference in the proportion of pairs, single animals, or females with calves encountered during the 2002 survey of Iris Bank ($\chi^2_2 = 1.07$, $p > 0.5$) nor for the 2003 survey of the Geyser-Zélée Complex ($\chi^2_2 = 4.66$, $p > 0.096$). The sample size was too small to examine pair-wise comparisons of group type frequency by year and location.

Individually identified humpback whales

A total of 26 humpback whales were identified over the course of these surveys using photographs of tail flukes (Table 2). Alternatively, 76 humpback whales were identified using photographs of dorsal fins from the left side of the animal. Whales that were only represented by photographs of dorsal fins from the right side were not included in this analysis. Individuals identified by dorsal fins are presented as an alternative expression for the number of individuals encountered because of the infrequency at which the animals encountered in this region have fluke-up dives (Ersts, pers. obs).

Encounter rates and sightings per unit of closing mode effort were higher for the Geyser-Zélée Complex than Iris Bank (Table 2). While there was a substantial decrease in group encounter rate and total closing mode effort between 2002 and 2003 on the Geyser-Zélée Complex, there was a slight increase in the rate of identified individuals per hour. Conversely, there was only a marginal increase in total closing mode effort between 2002 and 2003 on Iris Bank, but a noticeable increase in both the group encounter rate and rate of identification by dorsal fin.

With the exception of three mother-calf pairs, all individuals identified on the Geyser-Zélée Complex and Iris Bank were only encountered once. One mother-calf pair was encountered on three consecutive days in the interior of Geyser Reef during the 2002 survey. On Iris Bank, one mother-calf pair was observed twice during the 2002 surveys with four days between sightings. Two additional multi-day sighting of mother-calf pairs were recorded during the 2003 season (one with four days between consecutive sightings and the other with five days between consecutive sightings).

Humpback whale density

Since no other species of large whales were encountered during closing mode surveys and only two additional encounters with two other large species of cetacean (sperm whale [*Physeter macrocephalus*] and blue whale [*Balaenoptera musculus*]) have been documented for the waters surrounding Mayotte in recent years (Kiszka *et al.*, 2007), all observations made during passing mode that were labelled as 'whale-like' were subsequently considered to be humpback whales and used in the estimation of whale density (Table 4). Of all humpback whale and 'whale like' sightings, blows were the most observed cue (47%, $n = 63$). Body and body parts (i.e. tail flukes, dorsal and pectoral fins) were the second most frequently observed cues (29%, $n = 39$) and breaches accounted for 24% ($n = 32$) of the observed cues.

Whale density was calculated by multiplying the group density by the mean group size of encounters recorded during closing mode surveys on Iris Bank and in the Geyser-Zélée Complex. Considerable variation was found among each passing mode survey (Table 4). Sightings from each transect were examined for differential distribution among the transect legs for each of the three strip widths using chi-squared tests assuming an equal sighting probability on any given leg of the transect. With the exception of the 8 October survey, the distribution of sightings among transect legs did not significantly deviate from the expected frequencies for any transect and the deviation observed on the 8 October survey was only marginally significant ($\chi^2_2 = 14.45$, $p = 0.044$).

The close proximity of the transect legs caused observational overlap between adjacent legs; the amount of which is proportional to the strip width under consideration and to the survey vessels proximity to the start or end of any given leg. This overlap, in addition to the mobility of the animals under consideration, introduced the possibility that certain groups of animals may have been double counted, introducing a positive bias to the density estimation. The influence from these possible double captures was examined by independently calculating density estimates derived from non adjacent legs and comparing them to the density estimate derived from all legs, for each time the transect was surveyed using the Wilcoxon matched-pairs signed-ranks test. The null expectation would be that no difference should be observed

Table 4

Upper half of the table provides the frequency of number of sightings made during passing mode surveys on Geyser Reef, Zélée Bank and Iris Bank. Values in square brackets indicate the number of sightings within 0.5 n.mile, 1 n.mile, and 1.5 n.miles of the transect respectively. The lower half of the table provides the number of sighting within the indicated strip width and the resulting whale density is provided in parentheses.

	Geyser Reef			Zélée Bank			Iris Bank	
	12/09/02	06/10/03	07/10/03	13/09/02	05/10/03	08/10/03	09/10/03	10/10/03
Humpback whale	23 [18, 20, 21]	11 [7,9,10]	3 [3,5,5]	16 [13,15,15]	15 [9,13,14]	10 [7,8,9]	5 [3,4,5]	2 [1,1,1]
'Whale-like'	4 [3,3,4]	4 [1,1,1]	8 [1,2,5]	3 [2,2,2]	8 [2,3,3]	17 [4,8,12]	3 [0,0,0]	0 [0,0,0]
'Dolphin-like'		1	1	2	3	1	2	
Stenella spp.			1				1	
Melon-headed whale							1	
Transect distance (n.miles)	36.53	36.6	36.79	34.75	35.31	35.38	36.54	36.55
Obs. to 0.5 n.mile (whale density)	21 (1.129)	8 (0.429	4 (0.214)	15 (0.864)	11 (0.612)	11 (0.610)	3 (0.161)	1 (0.054)
Obs. to 1 n.mile (whale density)	23 (0.618)	10 (0.268)	7 (0.187)	17 (0.479)	16 (0.445)	16 (0.444)	4 (0.107)	1 (0.027)
Obs. to 1.5 n.mile (whale density)	25 (0.448)	11 (0.196)	10 (0.178)	17 (0.320)	17 (0.315)	21 (0.388)	5 (0.089)	1 (0.018)

between the densities calculated from all legs compared to non-adjacent legs. For each survey, the density estimates derived using all legs of a transect were bounded on both sides by the density estimates derived using non-adjacent legs. Consequently, the results of the Wilcoxon matched-pairs signed-ranks test were the same for both density comparisons (T = 125, n = 24, $p > 0.48$) and the null expectation was not rejected in either situation. Even though a positive bias was likely introduced, the density estimates generated here are not being used for population estimation where the implications would be an overestimate of population size.

Humpback whale distribution

Understanding of the Geyser-Zélée Complex was limited to general environmental descriptions (Quod *et al.*, 2000; UNEP and IUCN, 1988) and coarse bathymetric data interpreted from nautical charts. It was assumed that the areas being surveyed were generally environmentally featureless relative to the size of a humpback whale. Therefore animals were expected to be evenly distributed. To broadly determine if distribution was uniform, sightings out to 1.5 n.miles were pooled for Iris Bank ($n = 7$), Geyser Reef ($n = 46$) and Zélée Bank ($n = 55$) then analysed with respect to the longitudinal and latitudinal mean for each of the three transects. Few sightings were made during passing mode surveys on Iris Bank, yet they were all made on the western half of the bank. On Geyser Reef, sightings (70.0%) were found to be concentrated on the eastern half of the area surveyed without notable differences in north-south concentrations (52.2% and 47.8% respectively). Sighting on Zélée Bank showed both a concentration on the eastern (67%) and southern zones (65%). While the orientation of the transect on Zélée Bank had a very slight northwest-southeast orientation, sightings on this bank can be broadly interpreted as being concentrated in the southeastern quadrant of the area surveyed.

Other species observed

Spinner dolphins (*Stenella longirostris*) and Pantropic spotted dolphins (*S. attenuata*) were the second most commonly observed species and were frequently encountered together in mixed groups (Table 3). Two groups of Indo-Pacific bottlenose dolphin (*Tursiops aduncus*) were encountered on the Iris Bank. A group of approximately 600 melon-headed whales (*Peponocephala electra*) was encountered on the eastern edge of Iris Bank on 27 September 2003 during closing mode surveys and a smaller group of 30-40 individuals was later observed on 9 October during one of the passing mode surveys. The sighting on 27 September is best described as a super-group, stretching well over a nautical mile, comprised of distinct subgroups containing 30 to 60 individuals.

DISCUSSION

The results from these short, exploratory surveys of the Geyser-Zélée Complex and the subsequent comparison to Iris Bank provide much needed data on humpback whale encounter rates and densities in Wintering sub-Region C2 (IWC, 2011; Rosenbaum *et al.*, 2001). Overall, the results indicate that the eastern region of the Comoros Archipelago is an important area for humpback whales during the late austral winter months and that additional, more intensive systematic research is warranted. It is necessary to reiterate that during computations of animal densities, detection functions were not fitted to the observations and no attempt was made to correct for biases associated with weather, detection distance estimates, or observer experience. Consequently, calculations of population size were not attempted and the resulting observed densities should only be considered general estimates. Regardless of the limitations and any potential biases that may exist in the observed density calculations, these results provide much-needed data on humpback whale distribution and encounters for a region in which no other data of this type are currently available.

Whale density

The densities of humpback whales, out to one nautical mile from the transect, ranged from 0.027 to 0.618 whales n.miles^{-2} across the three survey areas (Table 4). As expected, whale density decreased with each subsequent distance bin (0.5, 1.0 and 1.5 n.miles) due to a decreasing detection probability with increasing distance from the trackline (Buckland *et al.*, 2001). The close proximity of the legs of each transect and the mobility of the animals under consideration introduced the possibility that certain groups of animals may have been double counted. Given that the density estimate derived from all legs of a transect was bounded on both sides by the density estimates derived from non-adjacent legs, the density estimates reported may be considered the median estimates of observed animal density for each survey. While it is highly likely that instances of double counting occurred, it was not possible to definitively quantify the degree of double counting and no attempts were made to derive population estimates using these data.

The apparent decrease from 2002 and 2003 in observed densities on the Geyser-Zélée Complex can be largely attributed to seasonality. Both the 2002 and 2003 surveys were conducted during the latter portion of the migratory cycle, but the 2003 surveys were conducted almost a full month later than the 2002 surveys. The magnitude of variation observed within the 2003 surveys in the Geyser-Zélée Complex is interesting but not wholly unexpected. A medium sized commercial fishing vessel had been working in and around the Geyser-Zélée Complex several days prior to and during the 2003 surveys. Additionally, on 4 October 2003, two large charter boats departed Mayotte on route to Geyser Reef to film whales. Consequently, a total of four large boats (> 12m) and several smaller fishing boats (< 8m) were present in Geyser Reef within the survey area during the 6 October and 7 October surveys. In contrast, only a few small open boats were observed on Geyser Reef in 2002. No other boats were observed on Zélée Bank in 2002 or 2003. The co-occurrence of variation observed within the 2003 surveys in the Geyser-Zélée Complex and increase in boat traffic merits further investigation, but cannot be quantified from these data. Any potential displacement of humpback whales from these banks due to anthropogenic activities is a considerable conservation and management concern.

Group composition and encounter rates

During the closing mode component of these surveys a total of 56 groups of humpback whales were approached. Significantly more females with young were encountered than pairs or single animals. No groups with more than four whales were encountered and competitive behaviour was only observed from afar on two occasions during passing mode surveys. There was no *a priori* knowledge or expectation in the frequency each group type may be encountered, thus each group type encountered was considered to have an equally probability of being observed. Based on these data alone, the greater propensity of encountering females with young is attributed to the late-season timing of these surveys.

With no prior knowledge of the degree to which humpback whales used the offshore banks and reef systems throughout C2, the encounter rates for the Geyser-Zélée Complex were higher than anticipated, especially given that the surveys were conducted during the end of migratory cycle. Both the densities and the encounter rates seem to indicate that there are greater concentrations of animals on the Geyser-Zélée Complex than are found on the Iris Bank. However, several factors regarding the encounter rates must be considered. The survey platform used during closing mode surveys on Geyser-Zélée Complex offered a much higher vantage point than the platform used on Iris Bank. This undoubtedly had a positive influence on the ability to locate animals. Secondly, these surveys were notably short and the resulting encounter rates could be greatly influenced by an especially good or poor day on the water. Finally, drawing upon previous survey experiences of Iris Bank, whales encountered on Iris Bank can be exceedingly evasive. This evasiveness can result in unidentified whales, negatively impacting encounter rates for identified individuals.

Localised distribution

Based on the limited bathymetric data available, the interior regions of the Geyser Reef and Zélée Bank appear to be relatively uniform. Therefore it was expected that the distribution of humpback whales in the interiors of the complex would therefore also be relatively uniform and the same was expected for Iris Bank. Uniform distribution, however, was not evident. Instead, the sighting localities derived from observations made during passing mode surveys were found to be concentrated in the western half of Iris Bank, the southeast corner of Zélée Bank and in the eastern half of Geyser Reef.

The apparent differential distribution observed cannot fully be explained with the data from these short surveys alone. Fine scale habitat-relationship models could not be built from sighting localities due to the lack of detailed bathymetric data and the possible geographic inaccuracies resulting from the estimated detection distances. These results can only highlight coarse patterns in geographic distribution. As these three survey sites are small and featureless relative to the size of humpback whales, future surveys should examine which, if any, factor has its greatest influence on distribution, e.g. physical environment, social organisation, proximity to other humpback whales or proximity to anthropogenic activity.

Conservation and management concerns

The Geyser-Zélée Complex is currently less impacted by human activities, such as fishing and nature-based tourism, than Iris Bank due to its relative inaccessibility. Polunin and Frazier (1974) were the first to qualitatively note that the Geyser-Zélée Complex showed little evidence of anthropogenic impact in the early 1970s. Quod *et al*. (2000) found that Geyser-Zélée Complex began to be regularly exploited by fisherman as early as 1989, a trend that continues today. As resources have become depleted in the waters immediate adjacent to Mayotte and neighbouring islands (e.g. Anjouan and Madagascar), subsistence fisherman undertake risky, multi-day voyages to the Geyser-Zélée Complex and similar near by banks aboard small (< 8m), open boats. Furthermore, Mayotte is being heavily promoted as an underdeveloped tourist destination and the newest concern is that the Geyser-Zélée Complex will be targeted as an attractive new destination for multi-day diving, fishing and, to a lesser extent, whalewatching trips or as a stopover point for charters running between Mayotte and Madagascar.

While the relative isolation of the Geyser-Zélée Complex has afforded humpback whales and other marine mammals some degree of solitude in the past, the complex remains unmonitored and poorly understood. To date the governing administration has not adopted any official conservation or management policies concerning the Geyser-Zélée Complex even though recent trends in fishing and charter boat activity are increasing. Conversely, Iris Bank and the waters surrounding Mayotte are easily accessible to recreational boaters and whalewatching operators. Marine mammals are protected in the waters surrounding Mayotte, but enforcement and monitoring are largely insufficient due to lack of personnel and poor communication between departments within the administration.

Currently, there are no applicable estimates of the direct energetic costs to humpback whales associated with displacement (Baker and Herman, 1989) or demonstrations of permanent, large-scale population-level effects (Corkeron, 2004) associated with vessel traffic. Given the group types observed in the survey areas, their proximity to human activity and time-scales for which any chronic and large-scale population-level effects are likely to be measured (Bejder *et al.*, 2006), a precautionary management approach (Robinson, 2006) is recommended in the absence of these data. Collection of adequate baseline data should be initiated to monitor trends through time and this effort should start before there are significant increases in nature based tourism or in the promotion of nature based tourism.

CONCLUSION

These results, while exploratory, indicate that humpback whales are found in varying concentrations in offshore reef systems and on banks in Wintering sub-Region C2. Generally, the marine mammals in the waters of Mayotte and the Geyser-Zélée Complex remain poorly understood and face a potential increasing exposure to anthropogenic noise and disturbance from human activities. The conservation and management challenges Mayotte and the Geyser-Zélée Complex face are not unique in the sense that they face many of same threats and pressures as other marine environments around the world. These initial results will hopefully serve as a catalyst for further research and highlight the potential of this largely under-studied region. At the 2006 Workshop on the Comprehensive Assessment of Southern Hemisphere Humpback Whales convened in Hobart, Australia, it was recommended that efforts be made to undertake more extensive ship-based surveys throughout Wintering Region C (IWC, 2011). The collection of adequate data with the ability to discern temporal differences will require a considerable resource commitment and highlights the need for better international and regional cooperation.

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Seasonal distribution, abundance, habitat use and population identity of humpback whales in Oman

G. Minton*,+, T. Collins*,^, K. Findlay#, P. Ersts~, H. Rosenbaum**, P. Berggren++ and R. Baldwin^*

Contact e-mail: gianna.minton@gmail.com

ABSTRACT

Previously published data on the occurrence of humpback whales (*Megaptera novaeangliae*) in the Arabian Sea suggests that the region hosts a non-migratory population that adheres to a Northern Hemisphere breeding cycle. In order to investigate the distribution and abundance of this population, twelve small boat surveys were conducted in three main locations off the coast of Oman between February 2000 and November 2004. Humpback whales were observed during surveys in Dhofar and Gulf of Masirah on Oman's Arabian Sea coast, but not during surveys in the Muscat region in the Gulf of Oman. An even ratio of males to females was observed and sampled during surveys in the Gulf of Masirah, which was surveyed in October and November ($n = 38$), while almost all whales sampled in Dhofar in February/March were male ($n = 28$). Song was detected frequently in the bay surrounding the Halaniyat Islands (formerly known as the Kuria Muria Bay) in February/March, but observations of mother-calf pairs were sparse, and competitive groups were absent. Feeding was observed in both October/November and February/March, but behavioural and environmental observations indicate that the Gulf of Masirah is primarily an important feeding ground, while the Dhofar region, particularly the Halaniyat Bay, may be a breeding area. However, limited survey effort and a lack of recent observations of mother-calf pairs or competitive groups raises the possibility that the primary mating, calving and nursing areas are yet to be identified. Sixty-four individual whales were identified using photographs of dorsal fins or tail flukes. A high rate of re-sightings between years and between survey areas at different times of the year indicates year-round residence off the coast of Oman. A Chapman's modified Petersen estimator was applied to various data pairings to calculate abundance. All pairings yielded estimates of less than 100 individuals, but sample sizes were small and there were various sources of possible bias. Analysis of scarring on the caudal peduncle region of identified individuals in Oman indicates that between 30 and 40% are likely to have been involved in entanglements with fishing gear. Comparison of the Oman photo-identification catalogue with those from Zanzibar, Antongil Bay (Madagascar) and Mayotte and the Geyser Atoll (Comoros Archipelago), yielded no photographic matches. These data are consistent with the hypothesis of a discrete population. The distribution of fluke pigmentation rankings from the Oman catalogue, which varied significantly from those of Madagascar and Mayotte, provides further evidence for this theory. The evidence presented here provides a strong underpinning for the recent IUCN Red List classification of the Arabian Sea sub-population of humpback whales as Endangered. In light of ongoing coastal development and other threats to this population's habitat and future survival, urgent research and conservation measures are recommended.

KEYWORDS: HUMPBACK WHALE; ARABIAN SEA; OMAN; MARK-RECAPTURE; BREEDING GROUNDS; FEEDING GROUNDS; DISTRIBUTION; ENTANGLEMENT; PHOTO-ID; GENETICS; NORTHERN HEMISPHERE

INTRODUCTION

Humpback whales (*Megaptera novaeangliae*) are known to undertake seasonal migrations between high latitude summer feeding grounds and tropical winter breeding grounds (e.g. Chittleborough, 1965; Clapham and Mead, 1999; Dawbin, 1966). Feeding and breeding cycles in Northern and Southern Hemisphere populations are typically six months out of phase (Lockyer, 1984). Although some circumstantial evidence exists for limited interbreeding between hemispheres, particularly off the South American coast of the central Pacific Ocean, (Acevedo-Gutiérrez and Smultea, 1995; Caballero *et al.*, 2001; Flórez-González *et al.*, 1998; Hazevoet and Wenzel, 2000; Stone *et al.*, 1990), genetic evidence supports traditional stock definitions originally described from distributions observed by whaling fleets and marking data (Breiwick, 1983). These stocks or sub-populations typically demonstrate high fidelity to well defined breeding areas and seasons, and little mixing occurs between populations (Baker *et al.*, 1998; Baker and Medrano-González, 2001; Baker *et al.*, 1990; Medrano-Gonzalez *et al.*, 2001).

Early records of humpback whales from the Arabian Sea region in the Northern Hemisphere include whaling data and observations collected from merchant vessels (Brown, 1957; Slijper *et al.*, 1964; Wray and Martin, 1983). No feasible migration routes can link this population to the high latitude Northern Hemisphere regions, and most observers suggested these animals belonged to Southern Hemisphere stocks (e.g. Brown, 1957). However, these authors were unable to account for sightings made in the Arabian Sea during the austral summer. Reeves *et al.* (1991) presented a thorough review of historical and incidental records of humpback whales in the Northern Indian Ocean, and explored the hypothesis that some humpback whales may be resident (Whitehead, 1985; Winn *et al.*, 1981). Evidence arising from the catch of 238 humpback whales illegally taken off Oman and Pakistan in November and December 1966 suggests that Arabian Sea whales represent a separate stock, adhering to a Northern Hemisphere breeding cycle (Mikhalev, 1997; 2000).

High primary productivity associated with strong monsoon-driven upwelling in the Arabian Sea may create conditions suitable for feeding at latitudes more typically

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* *Environment Society of Oman, PO Box 3955, PC 112, Ruwi, Sultanate of Oman.*
+ *Sarawak Dolphin Project, Universiti of Malaysia Sarawak, Kota Samarahan 94300, Sarawak, Malaysia.*
^ *Wildlife Conservation Society Ocean Giants Program, 2300 Southern Blvd, Bronx, NY 10460-1099, USA.*
# *Oceanography Department, University of Cape Town, Rondebosch 7701, South Africa.*
~ *Center for Biodiversity and Conservation, American Museum of Natural History, Central Park West at 79th Street, New York, NY 10024, USA.*
** *Wildlife Conservation Society, Ocean Giants Program, 2300 Southern Blvd., Bronx, NY 10460-1099, USA.*
++ *School of Marine Science and Technology, Newcastle University, Newcastle upon Tyne, NE1 7RU, UK.*

associated with breeding (Baldwin, 2000; Mikhalev, 1997; Papastavrou and Van Waerebeek, 1997; Reeves *et al.*, 1991). Mikhalev (2000) found that over 50% of humpback whales caught and examined in the Arabian Sea ($n = 190$) had full stomachs, indicating that feeding occurred during the Austral summer, when Southern Hemisphere populations should be feeding in the Southern Ocean. In addition, biological data on reproductive females and calf lengths indicated a reproductive cycle in line with Northern Hemisphere populations (Mikhalev, 2000).

Although data collected prior to 2000 confirmed a population of humpback whales in the Arabian Sea, information on seasonal distribution, habitat use, population identity, abundance and status were limited. This paper reviews all available confirmed records of humpback whales in Oman including results of a series of small boat surveys and one shore-based survey carried out off the coast of Oman between February 2000 and October 2003. This review aims to investigate the seasonal distribution, habitat use, abundance and conservation status of humpback whales in Oman.

METHODS

Study areas and field survey methods

Small-boat surveys were conducted over a period of four and a half years in three main locations: the Gulf of Masirah; the Dhofar region (both on the Arabian Sea coast); and off Muscat in the Gulf of Oman (Fig. 1). Surveys were designed to target areas where published (Mikhalev, 2000) and unpublished records indicated potential humpback whale abundance, and the timing and location of surveys is detailed in Table 1. Survey timing was to some extent constrained by funding opportunities, personnel availability and logistic constraints, while rough seas and fog generated by the SW Monsoon limited effort along the Arabian Sea coast during the summer months (May–September). As a result, the Gulf of Masirah was typically surveyed during October and November, and the Dhofar region during February and March. Additionally, single-day surveys were conducted on an average of once a month in the Muscat region throughout the study period. While all available survey and photo-identification data from the 2000–03 surveys were used in the analyses below, the data from the 2004 Gulf of Masirah survey in this paper are limited to photo-identification data for use in mark-recapture analysis.

Tracks were designed to optimise coverage of nearshore and offshore (beyond the 200m isobath up to roughly 3,000m) waters within the determined survey region. However logistical considerations (range of the vessel, fuel supplies, safe anchorages, weather conditions, etc.) often limited the length and range of search tracks. Search speeds ranged from 12 to 15 knots.

The majority of surveys were conducted from a 6.5m rigid-hulled inflatable boat (RIB), powered by two outboard engines (70 or 85hp). Effort was logged to the minute, and all sightings were recorded using standardised data collection methods (e.g. Mattila *et al.*, 1994). Although the survey collected data on all species of cetacean encountered, priority was given to humpback whales. Types of data collected during each humpback whale sighting included (in order of priority) positional data, group composition, behaviour, photographic (tail flukes, right and left dorsal fins), skin samples and acoustic recordings.

Weather conditions were recorded on an hourly basis and search effort was suspended in Beaufort Sea states of 4 or higher. A minimum of two experienced observers positioned on the bow, on a 3m high A-frame, or on the deck of the boat scanned assigned arcs with the naked eye, in order to collectively cover 180 degrees forward of the beam. Surveys were conducted in closing mode, and search effort was suspended to approach and collect data on all cetaceans sighted. In January and February 2000, two observers conducted opportunistic searches from vessels involved in a multidisciplinary expedition off the Halaniyat Islands, while the survey conducted from 15–17 October 2000 used a 5.5m fibreglass fishing skiff powered by a 25hp engine to survey the northern portion of the Gulf of Masirah.

In an effort to address the paucity of sightings data from monsoon months and confirm or refute the presence of humpback whales during the Northern Hemisphere summer months, a four-day shore-based survey was conducted from cliff-tops near Duqm (in the southern portion of the Gulf of Masirah) in June 2001. Four observers worked in rotation with two observers searching the sea simultaneously, one with binoculars and one with the naked eye, for two-hour shifts. Sightings were recorded, but no data on movement or individual identification are available from this survey.

Tissue sampling and sex determination

Sloughed skin was collected opportunistically with a sieve from dive wells or following breaches (Amos *et al.*, 1992). From October 2001, biopsies were taken with a crossbow and hollow-tipped, barbed biopsy darts (Lambertsen *et al.*, 1994). Tissue samples were stored in salt saturated water with 20% dimethyl sulfoxide (DMSO) (Amos and Hoelzel, 1991) for genetic analysis.

Group composition and behaviour

Group types and behavioural classifications were based on a consensus of categories used in other studies (e.g. Baker and Herman, 1984; Brown and Corkeron, 1995; Clapham, 1993; Clapham *et al.*, 1992; Mattila *et al.*, 1989; Mattila *et al.*, 1994).

Acoustic watches

Acoustic watches were conducted from February 2001 onward with the primary aim of detecting humpback whale song. Search effort was suspended and a hydrophone (Offshore Acoustics, Vancouver) was deployed to a depth of 5–10m for a period of 15 minutes. Detected song was assigned to one of three perceived levels of intensity as a crude measure of the distance of the whale from the hydrophone: '1' being distant, '2' medium and '3' close range. Recordings were made using a Sony TCD-D100 digital audiotape (DAT) recorder. Efforts were then made to locate, photograph and biopsy the singing whale if it had not already been detected visually prior to the acoustic watch.

Photo-identification and matching

Every effort was made to photograph the ventral surface of the tail flukes (Katona and Whitehead, 1981) and the left and right sides of the dorsal fin of each humpback whale encountered. A variety of cameras was used, including both 35mm film and digital SLR cameras fitted with 70–300mm or 130–400mm zoom lenses.

Data analysis

Sighting classifications

All sighting data were entered into the Oman Cetacean Database (OMCD), an MS Access database, and were then classified into four effort categories.

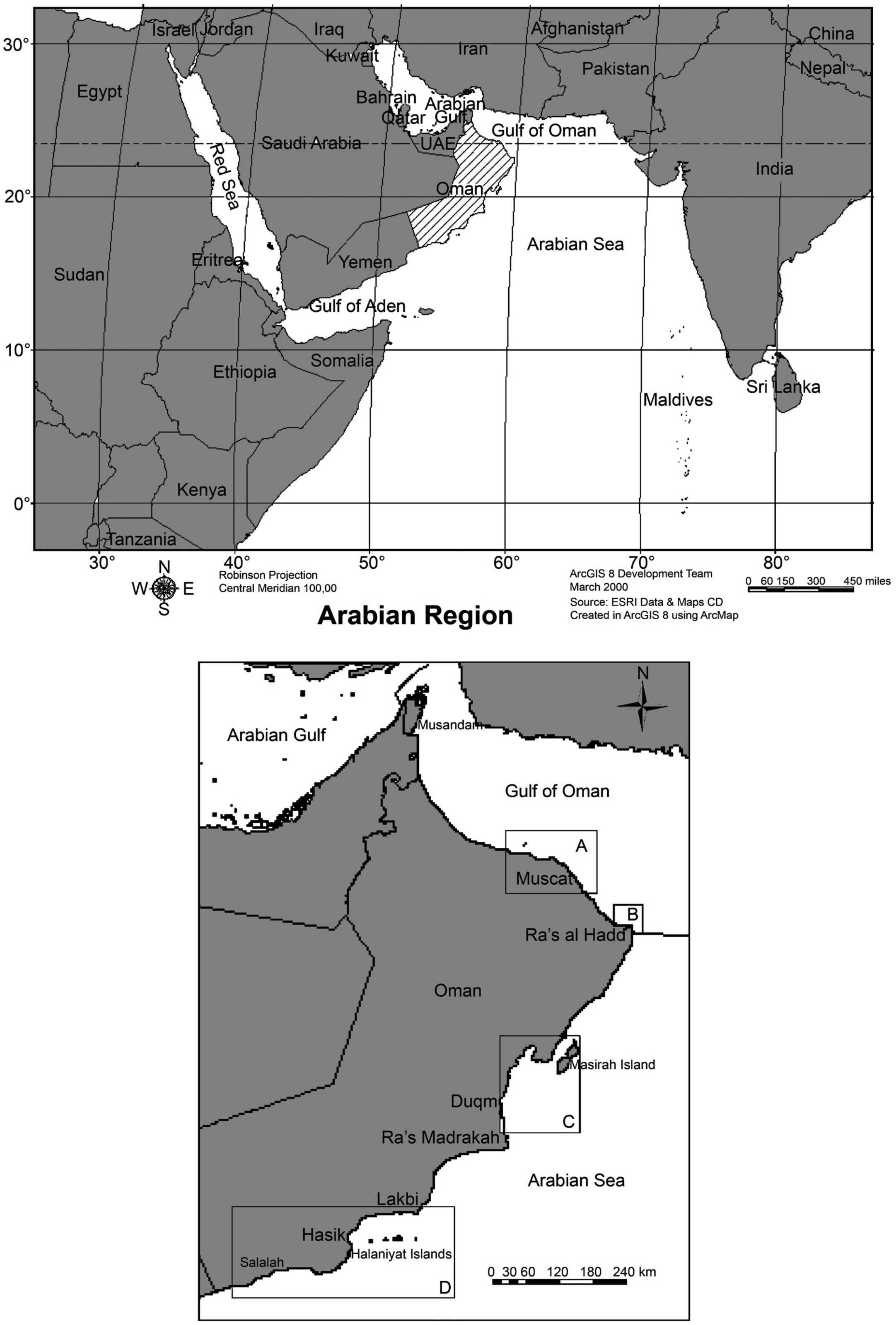

Fig. 1. Four main study areas in Oman. A: Muscat region, linear distance covered from 2001–2003 = 2,264km. B: R'as al Hadd (one survey only) = 200.8km. C: Gulf of Masirah = 2,555.24km. D: Dhofar region = 3,819.71km.

(a) Type 1 (*n* = 56): recorded during optimal survey effort (minimum of 2 observers, 12–15kt search speed).
(b) Type 2 (*n* = 3): recorded during sub-optimal survey effort (higher vessel speeds or fewer observers).
(c) Type 3: recorded while 'off effort' during surveys (*n* = 13), during acoustic watches (*n* = 6) or by authors outside of survey times with no associated effort (*n* = 7). Shore-based observations (*n* = 13) and seismic survey records (*n* = 47) are also included here (Baldwin, 1997). These have been treated as incidental sightings made by authors and no associated effort has been analysed.
(d) Type 4 (*n* = 25): Incidental or dedicated sighting records from reliable third parties (including Ballance and Pitman, 1998; Mikhalev, 1997; Reeves *et al.*, 1991; Salm

Table 1

Dates and locations of surveys and encounter rates for humpback whales sighted on effort during surveys.

Survey area	Survey dates	Effort hours[1]	Number of level 1 sightings	Number of whales	Sightings per hour	Number of whales per hour
Muscat[2]	15/03/01–15/07/03	104.21	0	0	0.00	0.00
Dhofar						
Halaniyat Islands	15–24/01/00 and 08–21/02/00	63.50	9	18	0.14	0.28
Dhofar	09–22/02/01	34.26	5	9	0.15	0.26
Halianiyat Bay	16–22/02/01	16.01	6	8	0.375	0.5
Dhofar	10/02/02–02/03/02	62.37	9	12	0.14	0.19
Halaniyat Bay	17/02/02–01/03/02	34.8	11	15	0.36	0.431
Hasik Bay	24–26/0602	4.32	0	0	0.00	0.00
Lakbe and Halaniyats	17–20/11/02	36.83	2	3	0.05	0.08
Dhofar	24/02/03–19/03/03	116.31	7	8	0.06	0.07
Halaniyat Bay	01–12/03/03	97.20	7	8	0.07	0.08
Dhofar (Hasik only)	15–17/0503	2.17	1	1	0.46	0.46
Dhofar[3]	04–29/03/04					
Dhofar total		*319.76*	*33*	*51*	*0.10*	*0.16*
Gulf of Masirah						
N. Gulf of Masirah	15–17/10/00	11.00	4	6	0.36	0.55
Gulf of Masirah	04–27/10/01	83.15	8	11	0.10	0.13
Gulf of Masirah	24/10/02–17/11/02	58.20	11	17	0.19	0.29
Gulf of Masirah[3]	04–29/11/04					
Masirah total		*152.35*	*23*	*34*	*0.15*	*0.22*
Shore-based observations						
Duqm	10–13/06/01	25.00	5	7	0.20	0.28

[1]Effort indicates time spent actively searching for whales and excludes time spent working with whales, in transit, or on breaks. [2]Monthly surveys. [3]Only photo-id data from these surveys are used in the analyses presented here for use in capture-recapture estimates.

et al., 1993), observations by M.D. Gallagher (1970–1998) and reports supported with photographs or video footage.

Only Type 1 sightings are used in analysis of relative abundance and encounter rates. However, Type 2–4 sightings are used to varying degrees in analysis of group composition, behaviour and seasonal distribution.

Sex determination

Both sloughed skin ($n = 12$) and biopsy samples ($n = 44$) were used for determination of sex, which was accomplished by PCR amplification and subsequent *Taq* I digestion of homologous regions on the X and Y chromosomes (ZFX/ZFY) (Palsbøll *et al.*, 1992). Sloughed skin was only definitively assigned to an individual if it was a singleton. Adult whales accompanied by a calf were considered females and singletons confirmed to be singing were considered male.

Photo-identification, matching and population estimates

Photographs (from 35mm print or slide film) were filtered for quality and the best representative photos of each feature (left dorsal, right dorsal or tail flukes) of each individual whale at each encounter were selected, scanned at high resolution (600 dpi), and cropped to best frame the identifying feature (dorsal fin or tail flukes). Raw digital images were labelled, filtered for quality and enhanced. The selected images were then linked to a database containing sighting history information.

All selected images were scored using one general quality ranking that included consideration of sharpness, contrast, angle and proportion of the identifying feature visible in the image. Scores ranged from 1 to 4.

1. Poor quality: ‘unmatchable’ under any circumstances, but with utility as a reference.
2. Fair quality: shows only a portion of the identifying feature (i.e. one half of the flukes), is out of focus, or compromised by glare. These images could be used to recognise distinctive individuals.
3. Good quality: in focus and shows all of the identifying features.
4. Excellent quality: shows all aspects of the identifying feature in great detail.

Scoring was based on photo quality and orientation only and was independent of the distinctiveness of individuals as described by Friday *et al.* (2000)**.**

Photo-identification data were used to: (1) compute estimates of abundance with capture-recapture methods; (2) investigate seasonal variation in movements; and (3) investigate the stock identity of whales from Oman by comparison with other populations in the Indian Ocean.

Matching was completed by comparing digital images on a computer screen and suspected matches were verified independently. All catalogue images were matched regardless of quality ranking but only those of quality 3 or higher were used in capture-recapture analysis. All but one of the individuals included in the sample were considered to be adults, with a low probability of changes occurring to their natural markings over time (Blackmer *et al.*, 2000; Carlson *et al.*, 1990). Matches made from poor quality images were included in the analysis of individual sighting histories and seasonal movements.

The Chapman’s-modified Petersen two sample estimator was used to compute capture recapture abundance estimates (Chapman, 1951) as illustrated in Seber (1982, p.60) with 95% log-normal confidence intervals. Three data pairings were chosen, all requiring some compromise between maximal sample size and minimisation of potential sources of bias.

1. Individuals photographed in the Gulf of Masirah in October 2001 as the first sample (n_1) and individuals photographed in the Gulf of Masirah in October–November 2002 as the second sample (n_2).
2. All individuals photographed in either the Gulf of Masirah or Dhofar between October 2000 and November

Table 2

Details of the total number of individuals and breakdown of photo quality for each feature of individuals held in the photo-ID catalogues for Oman, Zanzibar, Mayotte/Geyser (Comoros Archipelago) and Antongil Bay, Madagascar. LDF = left dorsal fin, RDF = right dorsal fin, TF = tail fluke. Photo quality rankings for all three catalogues followed the same criteria as adapted from Friday *et al.* (2000).

Research area	Total number of individuals	LDF' >1	LDF >2	RDF >1	RDF'> 2	TF >1	TF >2
Oman	54	38	24	40	24	43	32
Zanzibar	7	5	3	1	1	2	2
Mayotte/Geyser	185	104	39	101	42	44	26
Antongil Bay, Madagascar	1,104	736	380	753	382	601	357

2002 as the first sample (n_1) and all individuals photographed either the Gulf of Masirah or Dhofar between between March 2003 and November 2004 as the second sample (n_2).

(3) All individuals photographed in the Gulf of Masirah between October 2000 and November 2004 as the first sample (n_1) and all individuals photographed in Dhofar between January 2000 and March 2004 as the second sample (n_2).

Fifty-four individual whales photographed in Oman between 1999 and November May 2003 were matched against seven individuals photographed off Zanzibar in September 2002, 1,104 individuals from Antongil Bay, Madagascar (1996 through 2002), and 185 individuals from Mayotte/Geyser Reef, Comoros Archipelago (1999–2002) (see Table 2). The matching process included all available photos of tail flukes and dorsal fins, regardless of quality.

Photo quality ranking and fluke pigment assignations for the four compared populations were conducted by different researchers in each study area. However, clear definitions of quality scores and fluke types, shared across all catalogues, as well as authors' ability to review catalogues from different populations, should have kept any discrepancies to a minimum.

Individuals from all four regions for which tail fluke photographs of quality 3 or higher existed were assigned to pigmentation categories between 1 and 5, with 1 representing an all white fluke, and 5 representing an all black fluke (Carlson *et al.*, 1990). Comparison of frequencies of pigmentation categories between populations was conducted using the non-parametric χ^2 statistics. Sexing data was not available for the whales from the Zanzibar, Madagascar and Mayotte/Geyser catalogues at the time of this analysis, so comparisons were not stratified by sex.

Analyses of humpback whale caudal peduncle scars

Photographs of the peduncle region (right and left flanks, the leading edge of the flukes, dorsal and ventral aspects of the peduncle) were isolated and examined for evidence of scarring consistent with entanglement or encounters with fishing gear following Robbins and Mattila (2000). Caudal peduncle images were scored for quality on the same scale as that for individual identification. The selected photographs were then scored for the type of scarring present (scar code), and the 'probability of entanglement' status indicated by these scars (entanglement code) following Robbins and Mattila (2000).

RESULTS

Table 1 details the effort spent on each survey in each survey area between 2000 and 2004. On effort portions of surveys covered a total of 8,839km with search effort distributed somewhat unevenly between survey areas as follows: 2,264km in Muscat; 200.8km in Ras al Hadd; 2,555.24km in the Gulf of Masirah; and 3,819.71km in the Dhofar region (see also Fig. 2).

Seasonal distribution and relative abundance

Encounter rates of humpback whales per effort-hour (Table 1) varied between surveys, with some surveys (e.g. all Muscat surveys) yielding no on-effort humpback whale sightings, and other surveys yielding encounter rates as high as 0.55 whales per hour. However, the differences in encounter rates were not statistically significant ($\chi^2 = 1.49$, df 11, $p = 1.00$).

Relative abundance and depth and slope associations of humpback whales and other cetaceans encountered during surveys is discussed in greater detail elsewhere (Minton *et al.*, 2010; Corkeron *et al.*, 2011). Fig. 2 depicts humpback whale encounter rates per kilometre searched in each 0.1 × 0.1 decimal degree grid square (approximately 11 × 11km). Fig. 3 depicts all type 1–4 humpback whale sightings grouped by season.

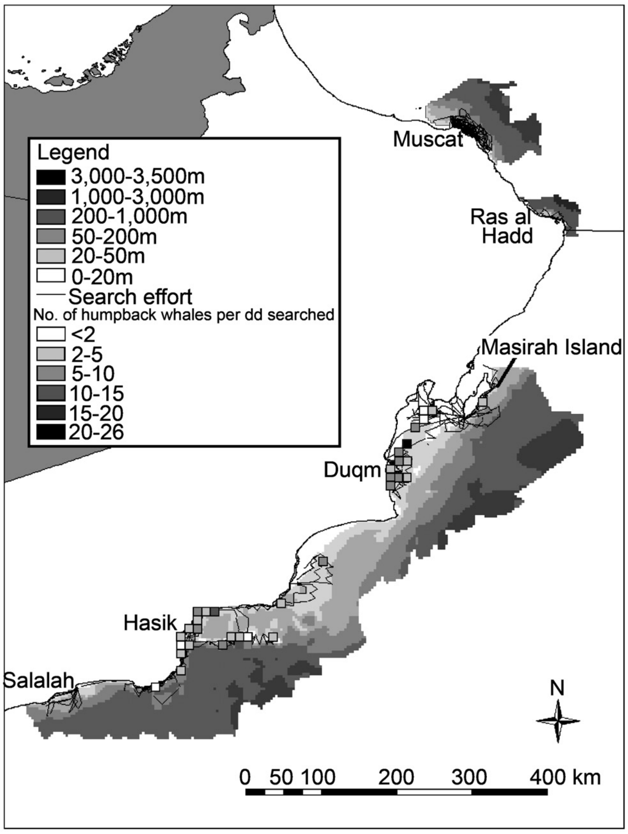

Fig. 2. Humpback whale encounter rates per kilometer searched in each 0.1 × 0.1 Decimal Degree grid square (approximately 11km × 11km). Darker shading indicates higher encounter rates relative to the distance searched.

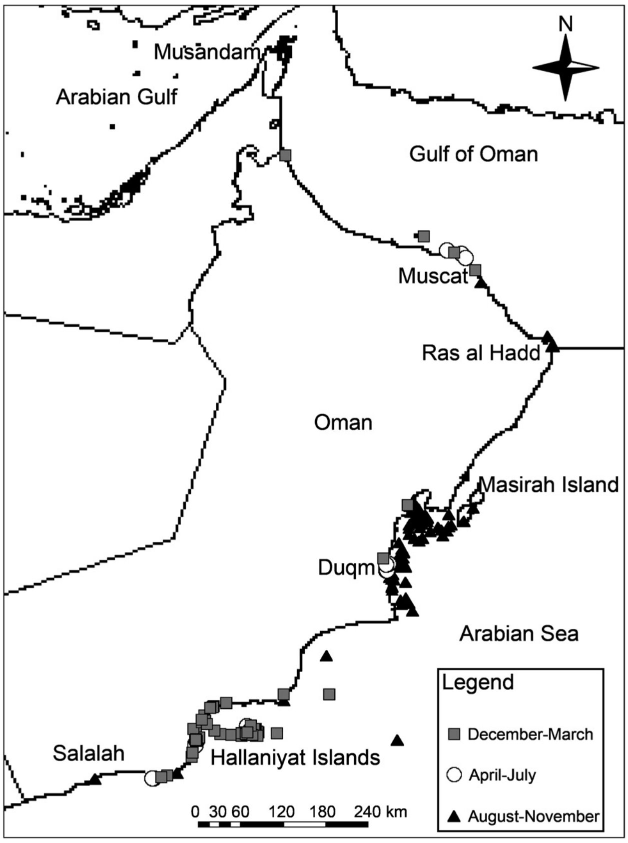

Fig. 3. Distribution of type 1–4 humpback whale sightings by season.

The sighting history of four whales (all males) photo-identified off Oman suggests that movements are seasonal (Fig. 4). With the exception of one single sighting (whale OM00-003, Fig. 4), all individuals were seen in the Dhofar region in February and in the Gulf of Masirah in October. While six of the males identified in Dhofar were also observed in the Gulf of Masirah, only one of the 19 known females observed in the Gulf of Masirah was also observed in Dhofar. Three additional females were re-sighted between years in the Gulf of Masirah.

Habitat use

The size and composition of groups sighted across surveys and regions is shown in Fig. 5. Type 1–3 sightings are included here because the sample size of Type 1 sightings is low ($n = 56$), and determination of group composition is not influenced by whether the groups were encountered on-effort.

Fifty percent of animals observed across surveys were singletons. G-tests using the observed group compositions from sightings in the Gulf of Masirah as the expected range and group compositions observed in Dhofar as the actual range show significant differences in the distribution of group composition categories between the two regions ($p < 0.01$). In Dhofar 62% ($n = 36$) of all sightings were singletons, of which 33% ($n = 12$) were confirmed singers. Pairs were the second most frequent group composition, comprising between 32% and 35% of all sightings. Trios were rare, occurring only in the Gulf of Masirah. Quartets and competitive groups were entirely absent across all surveys.

Sex was determined (either through genetic sampling, singing, or presence of calf) for 38 of 44 individually identified whales observed between October 2000 and November 2002 in the Gulf of Masirah and for 28 of 37 individually identified whales observed between 2000 and 2003 in Dhofar. Pairs or trios of whales in Masirah were more often of mixed sex, while in Dhofar, those pairs for which the sex of both individuals could be determined were most often male (Table 3).

Fig. 6 summarises the dominant behaviour categories observed during Type 1–3 encounters across surveys and per region. Behavioural categories were based on the most prominent behaviour of the groups encountered, excluding any behaviours that were judged to have been caused by interaction with the research vessel.

G-tests using the observed behaviours in the Gulf of Masirah as the expected range and behaviours observed in Dhofar as the actual range show significant differences in the distribution of behaviour categories between the two regions ($p < 0.01$). Singing was detected only in February and March in Dhofar, where it was the dominant behaviour (39%, $n = 44$). Confirmed instances of feeding at the surface span both the October/November and February/March observation periods, but were more common in the Gulf of Masirah in October/November. Singing was only detected in the Dhofar region (Table 4, Fig. 7).

Abundance

Table 5 depicts the results of the application of Chapman's modified Petersen model to three different pairings of data sets. All of the data pairings yield population estimates of less than 100 individuals with fairly narrow confidence intervals.

Stock identity

The comparison of the Oman catalogue with those from Zanzibar, Madagascar and Mayotte yielded no matches. Furthermore, there appeared to be notable differences in visible scaring and certain morphological characteristics between the populations. The Madagascar and Mayotte whales displayed a higher degree of barnacle scarring on the tail flukes, a higher rate of killer whale scarring, and a difference in the frequency of certain characteristic dorsal fin shapes (e.g. hooked dorsal fins are relatively common in Madagascar, but very rare in Oman).

Table 6 depicts the distribution of fluke pigmentation classes for the individuals sampled in the three different study areas. Sexing data was not available for the catalogues outside of Oman and is not presented here.

χ^2 tests detected significant differences between populations in the distribution of fluke pigmentation types. Two separate expected ranges were generated for Oman by multiplying the Antongil Bay ratios of fluke pigmentation by the total number of flukes in Oman (32), and then doing the same for Mayotte/Geyser. Observed frequencies in Oman varied significantly with respect to both Antongil Bay ($\chi^2 = 15.15$ df $= 4$, $p = 0.003$) and Mayotte/Geyser ($\chi^2 = 14.77$ df $= 4$, $p = 0.003$).

Entanglement histories and scarring

Twenty-three individual whales were included in the analysis of caudal peduncle photographs with a quality score of 2 (poor to fair) or higher. Of these 31% ($n = 7$) showed no scarring or scarring that was not characteristic of entanglement. In total, 70% of the animals had varying degrees of scarring on the peduncle region that could have been caused by encounters with fishing gear (linear wrapping scars or notches characteristic of net or rope lesions). However, only 39% ($n = 9$) were judged to have overall scarring patterns conclusive enough to be considered indicative of previous entanglement.

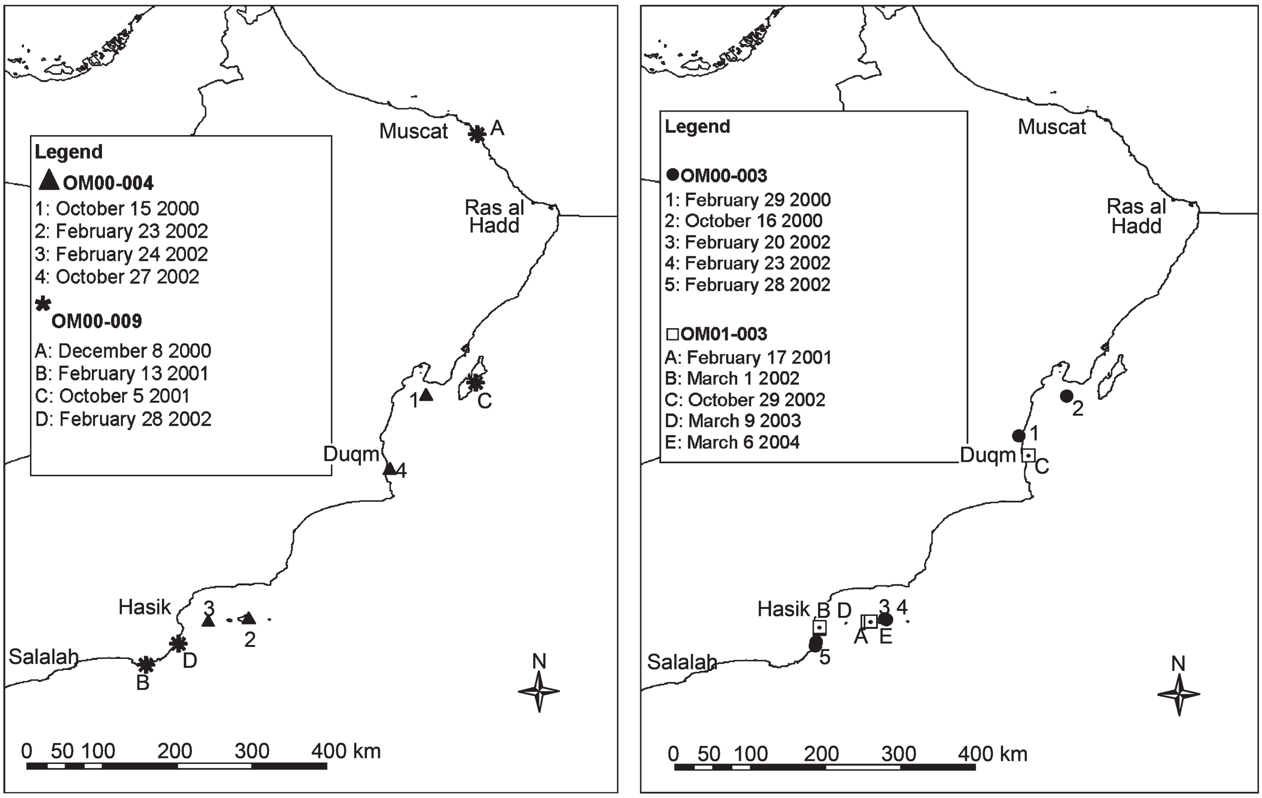

Fig. 4. Sighting histories and locations of 4 of the most frequently sighted individual humpback whales.

The same analysis was performed on a smaller sub-group of individuals who were assigned caudal peduncle photographic quality scores of 3 or higher. This sub-group comprised only 12 individuals. For this group, 42% of the animals (n = 5) showed random scarring that was not consistent with entanglement, while 58% (n = 7) had at least some scarring that could have been caused by entanglement. Of this smaller sub-group, 33% (n = 4) were considered to have overall scarring patterns likely to have been caused by previous entanglement.

DISCUSSION

Seasonal distribution, movements and relative abundance

The high proportion of re-sightings of previously photographed individuals across surveys provides some indication that the surveys targeted areas used regularly by at least some individuals within the Arabian Sea population. They provide a strong indication that a number of individual whales remain in Omani waters year-round, and that they frequent both the Gulf of Masirah and Dhofar. The relatively short duration of surveys, and the fact that surveys were designed to cover different portions of the survey areas on different days did not facilitate accurate analysis of occupancy rates, and may explain the relatively low rate of within survey re-sights (n = 8).

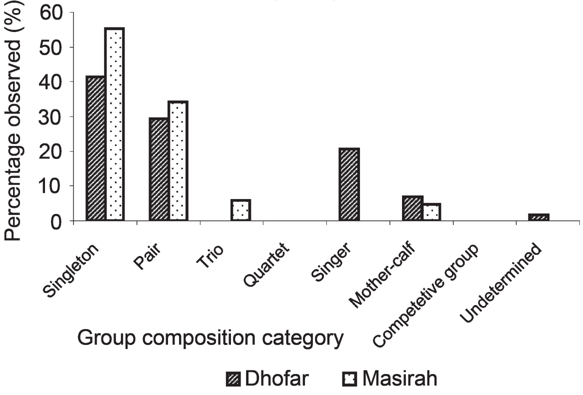

Fig. 5. Percentage breakdown of group composition categories assigned during type 1–3 humpback whale sightings made in the Gulf of Masirah (n = 85) and Dhofar (n = 58) regions.

Type 3 and 4 sightings (Fig. 4) and unpublished records in the OMCD suggest that there may be areas of seasonal abundance off the coast of Oman that have not yet been covered by our surveys. There is also a possibility that some whales rove the Arabian Sea on a seasonal basis or in response to shifts in productivity, utilising areas off the west coasts of Iran, Pakistan, India and Sri Lanka or the Gulf of Aden. Although a number of sources refer to sightings and

Table 3

Composition of groups in which individuals of known sex occurred.

	Male	Female	Mixed	Unknown
Gulf of Masirah				
Singleton	8	8	N/A	
Pair	0	2	2	3[1]
Trio	0	0	3	1[2]
Dhofar				
Singleton	14	0	N/A	
Pair	5	0	0	4[3]
Trio	0	0	0	0

[1] 2 pairs contained one male and one unknown, one pair contained a mother and calf of unknown sex; [2] one trio contained two females and one individual of unknown sex; [3] 2 pairs contained one male and one unknown individual, one pair contained one female and one individual of unknown sex.

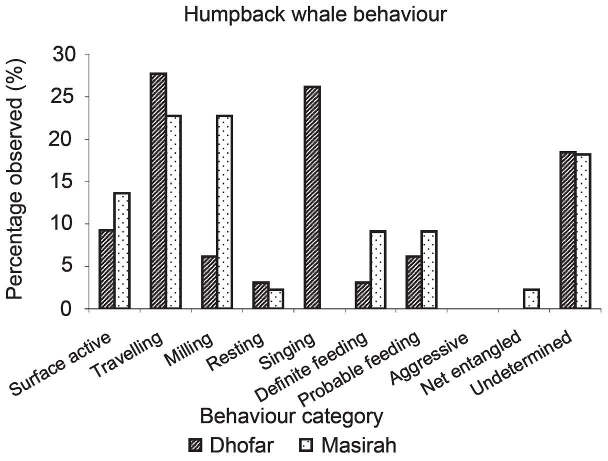

Fig. 6. Behaviour categories assigned (%) during type 1–3 sightings in the Gulf of Masirah (n = 44) and Dhofar (n = 65).

strandings of the species in this region (e.g. Ahmed and Rizvi, 1985; de Silva, 1987; Lal Mohan, 1992; Mathew, 1948; Mikhalev, 1997; Reeves *et al.*, 1991; Sathasivam, 2000; Slijper *et al.*, 1964; Whitehead, 1985), only a handful of dedicated cetacean surveys have been conducted anywhere in the Arabian Sea since the 1960s, and the majority (Alling *et al.*, 1982; Ballance and Pitman, 1998; Eyre, 1995) have focused effort in more offshore waters and have included no observations of humpback whales.

Habitat use

The high incidence of singers and detected song in the Kuria Muria Bay in February and March suggests that the area is used as a breeding ground (Payne and McVay, 1971; Tyack, 1981) and is consistent with a January–April breeding season predicted by Mikhalev (1997; 2000). The higher ratio of males to females observed in Dhofar is also similar to ratios reported from other breeding areas in the Southern Hemisphere, such as Antongil Bay, Madagascar (2.2–2.4:1), and Gabon (1.9–2.1:1) (Pomilla and Rosenbaum, 2006; Rosenbaum *et al.*, 2009).

Conversely, the conspicuous absence of competitive groups is inconsistent with observed abundances on Caribbean (Mattila *et al.*, 1989; Mattila *et al.*, 1994) or Hawaiian (Baker and Herman, 1984) breeding grounds. In Oman, observed group size never exceeded three individuals. On three occasions, interactions between pairs of adult males included surface active behaviour and fast swimming, but at no point were any of these activities conspicuously agonistic. This included a brief penis extrusion, a behaviour thought to be associated with male dominance contests (Pack *et al.*, 2002). A similar lack of competitive interactions is reported for humpback whales observed in New Caledonia (Garrigue *et al.*, 2001) and in other breeding grounds of the South Pacific where humpback whale densities are low (C.S. Baker, pers. comm.). Alternatively, competitive groups may be formed in areas not surveyed in this study.

The total lack of observations of mother-calf pairs since 2001 also contrasts with the high incidence of singing detected in February and March. The percentage of groups containing mother-calf pairs (7%) observed in the Dhofar region in February is much lower than on other breeding grounds, such as Samana Bay (Dominican Republic) where 15% of all sightings contained a calf (Mattila *et al.*, 1994), Antongil Bay, Madagascar, where 12% of groups observed were mother-calf pairs (Ersts and Rosenbaum, 2003; Rosenbaum *et al.*, 2002b), Mozambique, where 14% of all size-confirmed groups (n = 237) in September 2003 contained a calf (Findlay *et al.*, 2011), Mayotte and Geyser Atoll (Comoros Archipelago) where over 70% of sightings included mother-calf pairs (Ersts and Rosenbaum, 2002) and in Zanzibar in September 2002 where three of the five groups identified were mother-calf pairs. Following the lack of observations of mother-calf pairs in 2001 and 2002, the 2003 Dhofar survey was shifted to the first two weeks of March, as previous surveys might have been too early to cover peak calving periods. However, the 2003 survey yielded a lower encounter rate for humpback whales in general, with no calf sightings.

As with the competitive groups, it is possible that calving and nursing are taking place predominantly in areas (either in Oman or elsewhere) that were not covered in our surveys. One suspected nursery area is the Gulf of Masirah. Craig *et al.* (2003) and Smultea (1994) suggest that availability of protected, shallow waters may be the key variable limiting distribution of mother-calf pairs on breeding grounds. The Gulf of Masirah contains a much greater area of shallow,

Table 4

Surveys during which regular acoustic watches were held, number of acoustic watches held on each survey, and frequency with which song was detected on each survey.

Survey area	Survey dates	Number of acoustic watches	Number of incidences of song	% of acoustic watches with song
Muscat (monthly surveys)	15/03/01–15/07/03	25	0	0
Dhofar				
Dhofar	09–22/02/01	12	4	33
Dhofar	10/02/02–02/03/02	65	44	68
Hasik Bay	24–26/06/02	9	0	0
Halaniyat Bay	17–20/11/02	6	0	0
Dhofar	24/02/03–19/03/03	63	28	44
Dhofar (Hasik only)	15–17/05/03	1	0	0
Dhofar total		*156*	*76*	*49*
Gulf of Masirah				
Gulf of Masirah	04–27/10/01	6	0	0
Gulf of Masirah	24/10/02–20/11/02	16	0	0
Masirah total		*22*	*0*	*0*
Other areas				
Ra’s al Hadd	30/03/01–02/04/01	4	0	0

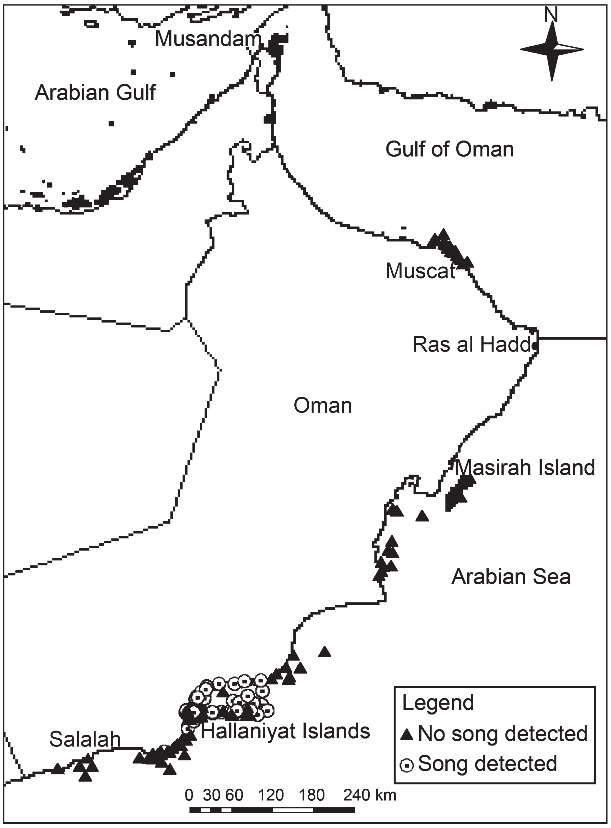

Fig. 7. Sites of acoustic watches throughout all survey areas in Oman (a), with triangles indicating no song detected and circles indicating detection of song. All song was detected during February and March surveys in the Dhofar region.

protected habitat than the Dhofar region (Fig 3). This area is also consistently characterised by high productivity (Brock and McClain, 1992; Brock *et al.*, 1998; Marine Science and Fisheries Center Oman, 2001). If productivity is linked to feeding opportunities for nursing females, it would seem reasonable to assume its attractiveness as a nursing area. One mother-calf pair (calf-size indicating several months old) was observed here in October 2001, but weather conditions and other logistic constraints have prevented the authors from surveying this area later in the breeding season (e.g. February–March), when more calves might be expected.

It seems inconsistent that cow-calf groups were observed around the Halaniyat Islands in February 2000, but not during equivalent periods in subsequent years. Mikhalev (2000) also noted a paucity of mother calf pairs in the Arabian Sea humpback whale population. Although 45% of the females examined in the Soviet catch were pregnant, only 3% of them were lactating, and only one mother-calf pair was observed during the hunt. Northern Hemisphere calves at this time of year could be approaching separation (Lockyer, 1981), but experienced observers would recognise these individuals as calves, as they are considerably smaller in length than the adults around them (7–9 m vs. 11–14m) (Clapham, 2000; Clapham *et al.*, 1999a). The Soviet catch data do not provide more explicit details of catches by region, so it is impossible to determine whether pregnant females were found in the Eastern Arabian Sea as opposed to the coasts of Oman.

The gender ratio in the Soviet catch neared parity (126:112), so the paucity of mother-calf pairs in recent observations cannot be explained by a bias in the Soviet catch toward females. There is a possibility that due to low population densities (Leaper *et al.*, 2006) or other fitness related factors, such as those affecting the North Atlantic right whale (IWC, 2001), birth rates are extremely low in the Arabian Sea population. Alternatively, birth rates may be resource dependent. Cerchio (2003) noted a pronounced decrease in reproduction of humpback whales in the Revelligigedo Islands in 1998, and a spike in reproduction in 2000 (as measured by percentage of mother-calf pairs observed), hypothesising that the dip was related to reduced prey availability during the El Niño event of 1997/98. The finding by Leaper *et al.* (2006) of a time-delayed relationship between sea surface temperature (SST) anomalies and southern right whale reproductive success lends further credibility to this theory. Brock and McClain (1992) reported that a weak 1982 southwest monsoon coincided with a 72% reduction in pigment concentration. This degree of variation could have significant impacts on prey availability for humpback whales. Visual inspection of remotely sensed chlorophyll-a data obtained for our survey periods indicated a high level of annual variation in Chlorphyll-a concentrations, but this could not be quantitatively analysed with respect to humpback whale distribution due to small sighting sample sizes in relation to the time-scale of the Chlorophyll-a data.

Feeding was observed in both Dhofar and the Gulf of Masirah. However observations of whales lunging at the surface with open mouths and/or extended throat pleats were rare, even in areas of conspicuously high productivity. This is surprising, particularly in light of Mikhalev's (1997) report that over 50% of humpback whales taken had full or half-full stomachs. It is probable that several instances of sub-surface feeding went undetected (e.g. Clapham, 1993).

Remotely sensed chlorophyll-a imagery shows consistently high levels of surface chlorophyll-a in the Gulf of Masirah (Brock and McClain, 1992; Brock *et al.*, 1998), while more recent studies detected a higher biomass of zooplankton in this region than any other of any part of Oman's coast (Marine Science and Fisheries Center Oman, 2001). In the Gulf of Masirah whales were often observed defecating and surfacing in large schools of shoaling fish after diving for long periods. The 1:1 ratio of males (19) to females (19) observed in the Gulf of Masirah is typical of a feeding ground (Clapham, 1993; Clapham *et al.*, 1995), and the higher percentage of milling whales in the Gulf of Masirah (23%) vs. Dhofar (6%), may be a reflection of

Table 5

Results of Chapman corrected Petersen population estimates and 95% confidence intervals for 3 data pairings, using tail fluke photographs of quality 3 or 4 only.

Data used for n(1)	Data used for n(2)	n(1)	n(2)	m(2)	*N*	CV	Lower 95% CL	Upper 95% CL
Gulf of Masirah 2001	Gulf of Masirah 2002	12	16	3	54	323	36	82
All individuals 2000–02	All individuals 2003–04	33	16	6	82	398	60	111
All Gulf of Masirah 2000–04	All Dhofar 2000–04	29	15	6	68	253	50	91

Table 6

Frequencies of five fluke pigmentation classes according to study region. Each individual was assigned tail fluke pigmentation categories between 1 and 5 (following Carlson *et al.* 1990 and Allen *et al.* 1994): 1 = all white; 2 = some black, but less than 25%; 3 = 25–75% black; 4 = some white but less than 25%; 5 = all black.

Study area	Fluke pigmentation class (fluke photo quality 3 or higher)											
	1		2		3		4		5		Total	Mean pigment
Oman	8	25.0%	11	34.4%	8	25.0%	8	12.5%	1	3.1%	32	2.34
Antongil Bay	169	47.3%	78	21.8%	43	12.0%	1	7.0%	42	11.8%	357	2.14
Mayotte/Geyser	12	46.2%	8	30.8%	4	15.4%	6	3.8%	1	3.8%	26	1.88

undetected feeding and/or a satiated, well-fed state (Lockyer, 1981).

It is highly probable that more active and regular feeding takes place outside of our survey periods, particularly between May and September, during peak upwelling associated with the seasonal southwest monsoon. Unfortunately, the monsoon also generates large swell and dense coastal fog, making both boat and shore-based observations difficult. Further research is required to better understand the availability and abundance of possible prey species in the region.

Mikhalev (1997) noted that humpback whales taken in the Eastern Arabian Sea had been feeding predominantly on Euphausiids of an unknown species, while humpbacks taken off the coast of Oman had been feeding exclusively on small shoaling fish (horse mackerels – Carangideae, mackerel, *Scomber sp.*, sardines, *Sardinella sp.*). It is also interesting to note that stomatopods (*Squilla* sp.) were found in the stomachs of several Bryde's whale specimens taken in the Soviet catch (Mikhalev, 2000). Stomatopods were also recovered from the stomach of a humpback calf found off the coast of South Africa (Findlay and Best, 1995) and, although no feeding was observed some humpbacks were sighted amid stomatopod swarms during the 2003 Dhofar survey.

Abundance

Mark-recapture abundance estimates were similar regardless of the method used to separate photographs into different data pairings. However, the application of Petersen estimates to this data set, which represents both a very small sample and a population about which very little is known, may violate at least two of the six key assumptions made in capture-recapture analysis (Seber, 1982). The first assumption that may be violated is that the population is closed. There are no data on recruitment or mortality for Oman humpback whales, and only limited data on the immigration or emigration into or from the survey area. It is possible that we have accessed only a sub-section of a larger Arabian Sea population with a range extending into neighbouring regions in Arabia, East Africa and the Indian sub-continent, and that the mark-capture estimates represent only the individuals in the Arabian population that utilise the study.

The second assumption that our study may violate, is that all animals in the population have an equal chance of being captured on the first occasion. Heterogeneity in capture probability is a recognised source of potential bias in most mark-recapture studies (see Hammond, 1990). Whales were more approachable and resultant photographs of higher quality during the Autumn Gulf of Masirah surveys, when 82% of sightings resulted in a tail fluke photograph of quality 2 or higher. Conversely during the February/March Dhofar surveys, only 44% of sightings yielded usable tail fluke photographs. This disparity is most likely linked to seasonal behavioural differences. In Dhofar, all but one of the identified whales were determined to be males (either genetically or behaviourally) and certain individuals appear to demonstrate a strong fidelity to specific sites. One individual has been observed (and confirmed to be singing) in the Hallaniyat Islands or Hasik in four successive years. Although six males identified in Dhofar were also observed in the Gulf of Masirah, only one of the 19 known females observed in the Gulf of Masirah has been observed in Dhofar.

High site fidelity of particular males in the Dhofar region may have biased the sample by violating random sampling assumptions. If the Dhofar region contains sites that are preferred by singing males, and surveys are biased toward these sites, our sampling of this region would have been non-random. On the other hand, this violation would not account for the high proportion of re-sights (and correlating low population estimate) obtained by using all Gulf of Masirah 'captures' as n_1 and all Dhofar 'captures' as $n_{2.}$

The three chosen data parings are subject to potential bias form these violated assumptions in the following manner. The first (whales photographed in the Gulf of Masirah in 2001 as n_1 and those photographed in the Gulf of Masriah in 2002 as n_2) may be the most robust, as it represents animals photographed in consecutive years, and a ratio of males to females nearing parity. However, sample sizes in this data pairing are very low. The second data paring (all animals photographed in 2001–02 as n_1 and all photographed in 2003–04 as n_2) is likely to have a negative bias, due to male heterogeneity (the higher likelihood that males would be sampled in Dhofar). The data pairing is also subject to a potential positive bias, as the combining of years violates the assumption of a closed population and introduces the possibility that new unmarked individuals entered the population between years. The third pairing (all individuals photographed in the Gulf of Masirah between October 2000 and November 2004 as n_1 and all individuals photographed in Dhofar between January 2000 and March 2004 as n_2) is also subject to both the negative bias of male heterogeneity and the positive bias of the time span/open population.

Despite the possible biases, the high proportion of resightings over this four year period suggests that a number of individuals remain in Omani waters year-round and that at least the Omani component of the Arabian Sea population is small, with numbers in the low hundreds or fewer. Genetic samples collected from Oman, revealed a low haplotype diversity, which could represent a small population or one that has gone through a recent bottleneck (perhaps even as recent as the depletion from Soviet whaling) (Rosenbaum *et al.*, 2009; Pomilla *et al.*, in prep).

Mikhalev (1997) reported 62 whales taken off the coast of Oman (30 from the Halaniyat Islands and 32 from near

Masirah Island), while a further 20 were observed but not taken. Mikhalev also reported 164 whales taken off the coasts of Pakistan and a further 12 off India, while 14 were observed but not taken off Pakistan. Scientists aboard the 1966 Soviet Fleet estimated that approximately 60% of the entire Arabian Sea population was taken, although they provide no detail on effort or the methods used to reach this assumption (Mikhalev, 1997).

Stock identity

The lack of matches found between the Oman, Madagascar, Comoros and Zanzibar catalogues, as well as the significant differences in frequency of fluke pigmentation categories between these populations, support the hypothesis that humpback whales in Oman comprise a separate stock from their Southern Indian Ocean counterparts.

Sexing data were not available for all whales included in photo matching or fluke pigmentation analyses. Previous studies have shown significant sex-related differences in fluke pigmentation. Analysis of whales in the Gulf of Maine and the Dominican Republic showed higher proportions of dark-fluked females and light-fluked males (Allen *et al.*, 1994). Bias toward one sex in a sampling region may also bias the results of fluke pigmentation analysis. It is possible that controlling for sex would yield either more or less significant differences between populations.

Evidence from Soviet catch data and seasonal behaviour and distribution, suggest that at least a significant portion of the humpback whales observed off the coast of Oman adhere to a breeding cycle asynchronous to that of their Southern Hemisphere counterparts. However this does not preclude the possibility that some individuals are engaged in local migrations or exchange across the equator.

While the lack of photographic matches between Oman and Zanzibar, Madagascar or Mayotte and the significant differences in distribution of fluke types both support the hypothesis of a discrete Northern Hemisphere/Arabian Sea population, the existence of several shared haplotypes between Oman and other southern Indian Ocean study areas (Rosenbaum *et al.*, 2009) indicates some genetic exchange may occur or could have occurred in the past.

A more recent and comprehensive genetic mtDNA analysis shows significant population differentiation between Oman and other populations in the western Indian Ocean, as well as the lowest comparative effective migration rates with other sampled populations (Rosenbaum *et al.*, 2009). In fact, the F_{st} values between Oman and other populations in the southwestern Indian Ocean (Breeding Stock C) and other sampled populations in that study are among the highest recorded for population differentiation values for any humpback worldwide (Rosenbaum *et al.*, 2009). These population level results provide unequivocal evidence for significant differentiation, unique population identity, and high restricted gene flow for the whales of Oman. Further analysis using nuclear markers and an expanded sample size is forthcoming (Pomilla *et al.*, in prep).

Although shared haplotypes may indicate recent or ongoing maternal gene flow between populations, shared maternal lineages do not necessarily establish a recent migratory connection as they can represent ancestral polymorphisms. Shared lineages occur between Southern and Northern Pacific populations of humpback whales in other ocean basins, such as the Eastern Pacific (Caballero *et al.*, 2001). However, exchange between the hemispheres, if it is ongoing, is thought to be limited to overlap of populations on low-latitude breeding grounds off the west coast of Central and South America (Caballero *et al.*, 2001). It is possible that a similar situation exists in the Indian Ocean. Individuals from Oman may come into contact with whales observed off the coast of East Africa (e.g. Kenya, Tanzania and Zanzibar), or the coasts of India, Sri Lanka and the Maldives. Although some anecdotal evidence exists for an ‘aseasonal’ distribution of whales in these regions (e.g. between the months of October and January) (Weru and Salm, pers. comm. cited in Rosenbaum (2002a)), the majority of reported sightings at these latitudes have been of mothers and calves in the months of August and September (Anderson, 2005; Weru, 2001; PB, unpublished data) indicative of a Southern Hemisphere breeding cycle.

Entanglement histories and scarring

Analysis of suitable caudal peduncle photographs for evidence of entanglement scarring indicated that between 30% and 40% of sampled whales had been entangled. This rate is lower than the 65% estimated for the Gulf of Maine (Robbins and Mattila, 2000), and lower than the 57% estimated, for North Atlantic right whales (Kraus, 1990). The Oman estimate is likely to be conservative, as some entanglements may have involved body parts other than the caudal pendunclе and some entanglement scarring may have healed or been masked by other types of scars over time. Although documented humpback whale mortalities from entanglement in Oman are low, when viewed in relation to the low population estimates for humpback whales off the coast of Oman, this entanglement rate may represent a significant threat, a concern shared with other small or isolated populations (Clapham *et al.*, 1999b; D’Agrosa *et al.*, 2000; Kraus, 1990).

Conclusions and recommendations

Presented with the evidence summarised in this paper, as well as the results of genetic analysis of samples from Oman (Pomilla and Rosenbaum, 2006), the IWC’s workshop on the Comprehensive Assessment of Southern Hemisphere humpback whales designated the Arabian Sea humpback whale population a separate breeding stock, Population X, isolated from other Indian Ocean stocks and resident in the Arabian Sea year round (IWC, 2011). Given the stock’s isolated status and low abundance estimate, the workshop ‘strongly recommended that further research be undertaken that will aid in protection of this stock’. Scarring analyses indicate that entanglement in fishing gear may present a significant threat to the population, and the rapid development of Oman’s economy and infrastructure, much of which is focused on coastal and marine areas, may have significant impacts on the identified feeding and breeding habitats of this population. The data presented here together with evidence of mounting developments and threats to coastal habitats in Oman also led to the designation of the Arabian Sea sub-population of humpback whales as Endangered in the IUCN Red List (Minton *et al.*, 2008). These potential threats require immediate emphasis to be placed on research, management and conservation efforts.

The workshop also recommended that studies be conducted in unsampled areas between Oman and other study areas in East Africa and Western Australia where humpback whales have been incidentally observed (e.g. Braulik *et al.*, 2010; Brown, 1957; Lal Mohan, 1992; Mikhalev, 1997; Reeves *et al.*, 1991; Sathasivam, 2000; Slijper *et al.*, 1964; Weru, 2001; Whitehead, 1985). It recommended further genetic sampling and analysis to more conclusively determine the degree of differentiation for humpback whales of Region X and the timing of its separation from other humpback whale populations. Finally, given the seasonal limitations in survey effort and an unresolved degree of movement and connectivity with other concentrations of humpback whales in the Indian Ocean, the Workshop also suggested that satellite telemetry studies be initiated. In 2011, the IWC Scientific Committee acknowledged that sufficient data exist on Arabian Sea humpback whales and possible anthropogenic threats to begin the process for the development of a Conservation Management Plan through which earlier recommendations for the study and conservation of the population may be most effectively achieved.

In addition to the conservation value of the recommended research, the study of non-migratory populations may shed light on the forces driving other populations to migrate (Clapham, 2000). Focal work on this population could elucidate other aspects of humpback whale behaviour and ecology. For instance there is still significant debate surrounding the function of humpback whale song. Other studies are generally conducted on densely populated breeding grounds where individual singers are difficult to isolate and monitor over time (Cherchio, 2003). Although whales in Oman are few, they are readily identifiable and show a high degree of site fidelity and are may be good candidates for behavioral work.

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Concerning demographic limitations on the population growth rate of West Australian (Breeding Stock D) humpback whales

A. BRANDÃO AND D.S. BUTTERWORTH

MARAM (Marine Resource Assessment and Management Group), Department of Mathematics and Applied Mathematics, University of Cape Town, Rondebosch 7701, South Africa
Contact e-mail: anabela.brandao@uct.ac.za

ABSTRACT

The upper bound of 0.126 on the maximum demographically possible annual growth rate for humpback whales that has standardly been imposed on recent applications of age-aggregated assessment models for this species in the IWC Scientific Committee, is based on an analysis that assumes steady age structure. It is conceivable that transient age-structure effects could admit greater population growth rates for short periods than suggested by such a bound. This possibility is addressed by developing an age-structured population model in which possible density dependent changes in pregnancy rate, age at first parturition and natural mortality are modelled explicitly, and allowance is made for the possibility of natural mortality increasing at older ages. The model is applied to the case of the west Australian humpback whale population (Breeding Stock D), for which breeding ground surveys over the 1982–1994 period provide a point estimate of 0.10 for the annual population growth rate. Results based upon the breeding population survey estimate of abundance of 10,032 in 1999 suggest that 0.12 is the maximum demographically feasible annual rate of increase for this stock over 1982–1994 if it is a closed population. This result is based on essentially the same parameter choices as led to the earlier $r = 0.126$ bound, i.e. that in the limit of low population size the age at first parturition approaches five years from above, the annual pregnancy rate 0.5 from below, and the annual natural mortality rate 0.01 from above. Transient effects do not appear able to reconcile the observed rate of increase with less extreme values of demographic parameters than led to the previously imposed upper bound of 0.126 on the maximum possible annual growth rate. Although use of extreme values reported for demographic parameters for Northern Hemisphere humpback whale populations, rather than those considered here, would reduce this suggested maximum rate of 0.12, the conclusion that transient effects have a very limited impact on observed population growth rates would be unlikely to change.

KEYWORDS: HUMPBACK WHALE; SOUTHERN HEMISPHERE; MODELLING; GROWTH; PREGNANCY RATE; PARTURITION

INTRODUCTION

Considerable debate has arisen over the extent to which the population growth rates suggested by time series of survey estimates of abundance for various South Hemisphere humpback whale populations are consistent with the bounds imposed by the species' demographics. More specifically, the upper bound on the maximum per capita annual growth rate, r, of 0.126 imposed on recent age aggregated model assessments of these populations in the IWC Scientific Committee has been questioned as perhaps too high (IWC, 2011).

The origin of this bound is calculations by Brandão *et al*. (1999), discussed further in Clapham *et al*. (2001), which relate population growth rates to biological parameter values. Essentially the higher the pregnancy rate (shorter the calving interval), the greater the annual survival rate and the lower the age at first parturition, then the higher the growth rate that the population can attain. The value of 0.126 selected as a bound corresponds to the following choices regarded as 'pushing the limits' for plausible values of biological parameters for humpback whales:

ρ	(annual pregnancy rate)	= 0.5;
S	(annual survival rate)	= 0.99;
a^{mat}	(age at first parturition)	= 5 yrs.

The questioning of the $r = 0.126$ bound in IWC (2011) arose primarily because at least some of these values were considered too extreme on the basis of estimates from various humpback whale populations. However, the calculations of Brandão *et al*. (1999) are based upon the assumption of a steady age structure. It is conceivable that over short periods of time (typically 1–2 decades), transient effects could lead to the attainment of higher population growth rates than indicated by the results of that paper. Expressed another way, such effects might allow high point estimates of population growth rate to be reconciled with less extreme values of demographic parameters.

The purpose of this paper is to investigate this possibility for the specific case of the west Australian humpback whale population (Breeding Stock D). Results from five breeding ground surveys of this population over the period 1982–94 (IWC, 1996) suggest an annual increase rate (the slope parameter from a log-linear regression against year) of 0.10 (95% CI: 0.03–0.18). This paper explicitly models possible density dependent changes in various biological parameters to determine to what extent this estimate is consistent with the feasible behaviour of a closed population of humpback whales.

DATA

The historic catch data used for these analyses are as agreed at a recent Southern Hemisphere humpback whale workshop (IWC, 2011). Two series are considered, the 'Core' and the 'Fringe' series (see Fig. 1), corresponding to different assumptions for the allocation of catches made in high latitude (south of 40°S) feeding areas among breeding stocks (Table 1). The 'Core' series makes the conservative assumption that only catches between 80° and 100°E come from Breeding Stock D, whereas the 'Fringe' series reflects the alternative extreme including all such catches between 50° and 130°E.

METHODS

The age-structured population model used for these computations is described in detail in the Appendix. For simplicity, sexes are not distinguished.

Table 1

Fixed parameters in the model for the reference case model and variants 2a-4d (see text).

Parameter	Value
a_r	4 yrs*
target year (y)	1999
target population size (N_y^T)	10,032
ρ_{max}	0.5

*The minimum legal length for humpback whale catches from 1950 to 1962 was 35ft, which compares with lengths at maturity of 39.5ft for females and 38ft for males (Chittleborough, 1965). Chittleborough also reports the immature fraction of the catch varying from 18-56% for females and 3-51% for males. This suggests a typical age-at-first capture (a_r) slightly less than the age-at-maturity. Given that this paper considers the age-at-first-parturition to range between 5 and 10 years, a choice of a_r=4 does not seem unreasonable.

The model is 'fit' to the data by adjusting the (initial) carrying capacity K so that the population's trajectory hits a target total (1+, i.e. survey is taken to count all animals of age 1 and above, so that only calves are excluded) population of 10,032 in the year 1999, as estimated from surveys of the breeding grounds (Paxton *et al.*, 2011).

The selectivity ogive for past catches is generally taken to be knife-edge at age $a_r = 4$ (see Table 1). However, for some of the models age structure effects lead to an inability to hit the target value in 1999 because of extinction. In such cases, the age-at-first capture (a_r) was reduced to two years to avoid this difficulty.

For a 'reference case' the maximum possible pregnancy rate for the population (ρ_{max}) is taken to be 0.5, corresponding to a minimum possible calving interval of two years. This applies in the limit of very low population size (so that values observed would be less than this). For an illustrative reference case (see Table 2), pregnancy rate is assumed to be the only (linearly) density dependent demographic parameter, decreasing to $\rho_{\text{min}} = 0.1$ when the population is at carrying capacity. Other biological parameters for this reference case are taken to be fixed (density independent); age at first parturition $a^{mat} = 5$ years and an annual natural mortality rate $M = 0.03\ \text{yr}^{-1}$.

Sensitivity to changes in these assumptions is then examined, first for single factors, and then for these factors in combination. Initially four factors are considered:

(A) Density dependence (linear) in the age at first parturition, first with $a^{mat}_{\text{max}} = 10$;
(B) Lower values for natural mortality;
(C) Nonlinear density dependence for ρ and a^{mat} reflected by the parameter μ (see Appendix equations A.14 and A.15); note that $\mu = 1$ reflects linear dependence, and $\mu > 1$ means that density dependent effects do not come into play as rapidly when the population grows from a low level, so that high growth rates can be sustained through to larger population sizes;
(D) Density dependence (linear) in natural mortality (Appendix equation A.16).

Not all combinations of parameter values are feasible. The condition of a steady population at carrying capacity K leads to restrictions on the value of natural mortality for the first year (M_0). Clearly M_0 cannot be negative. The computations reported below insist further that always $M_0 \geq M_1$ where M_1 is the natural mortality of age 1 humpback whales (which is identical to that of all older humpbacks for scenarios without

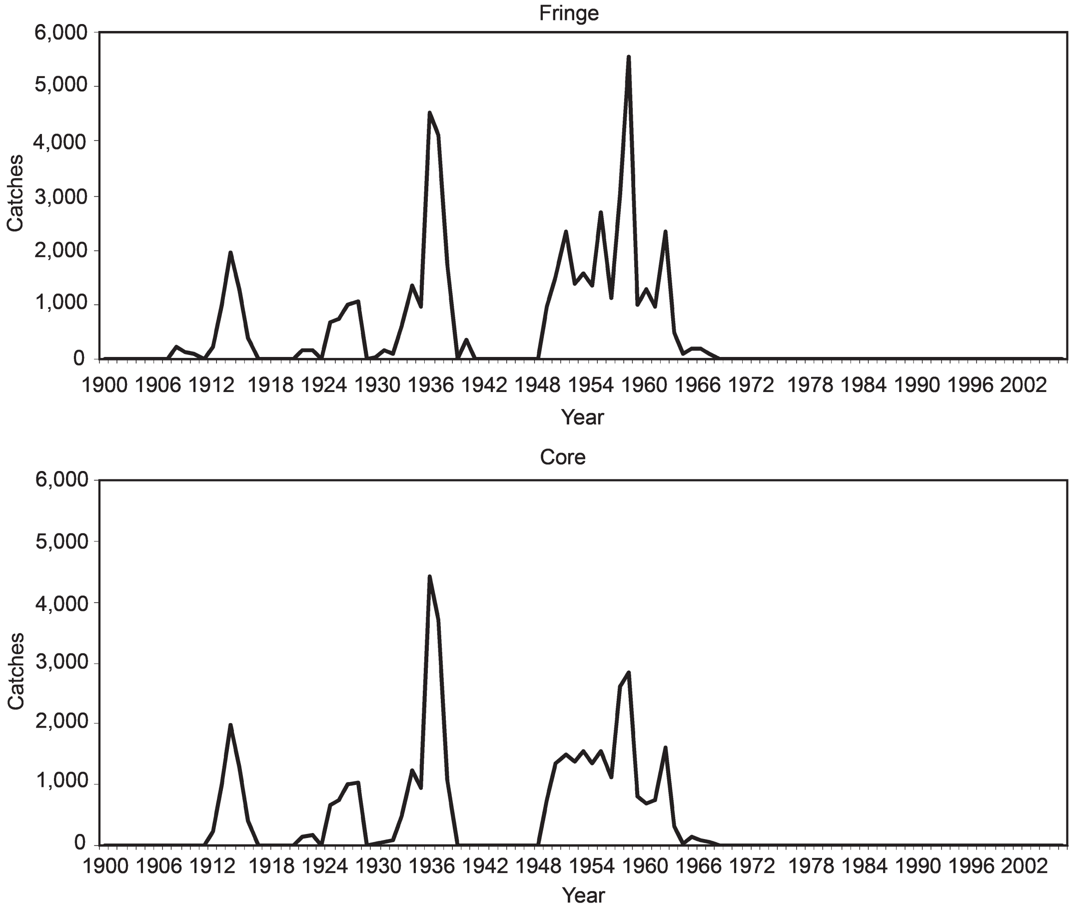

Fig. 1. Catch series for Breeding Stock D humpback whales for the Fringe (above) and Core (below) catch allocation hypotheses (IWC, 2011).

Table 2

Description of model variants and how they are referenced in the paper. The model indicated in brackets ( ) refers to the model of which the model under consideration is a variant; under description, what has been changed in the model under consideration is shown underlined. See the Appendix for detailed definitions of the symbols. The value calculated for natural mortality for the first year of life (M_0) (see equations A.11 and A.12) is also given, together with an asterisk (*) if it is limited by the constraint $M_0 > M_1$.

Model	Name	Description	M_0
1	Reference case	$a^{mat}_{\max} = 5$; $\rho_{min} = 0.1$; $\mu = 1$; $M^{min}_m = M^{\max}_m = 0.03$	0.348
2a (ref)	$a^{mat}_{\max} = 10$	$a^{mat}_{\max} = \underline{10}$; $\rho_{min} = 0.1$; $\mu = 1$; $M^{min}_m = M^{\max}_m = 0.03$	0.188
2b (ref)	$M_m = 0.02$	$a^{mat}_{\max} = 5$; $\rho_{min} = 0.1$; $\mu = 1$; $M^{min}_m = M^{\max}_m = \underline{0.02}$	0.688
2c (ref)	$\mu = 3$	$a^{mat}_{\max} = 5$; $\rho_{min} = 0.1$; $\mu = \underline{3}$; $M^{min}_m = M^{\max}_m = 0.03$	0.348
2d (ref)	M_m: 0.03 → 0.02	$a^{mat}_{\max} = 5$; $\rho_{min} = 0.1$; $\mu = 1$; $M^{min}_m = \underline{0.02}$; $M^{\max}_m = \underline{0.03}$ (i.e. M_m density dependent)	0.348
3a (ref)	All changes	$a^{mat}_{\max} = \underline{10}$; $\rho_{min} = 0.1$; $\mu = \underline{3}$; $M^{min}_m = \underline{0.02}$; $M^{\max}_m = \underline{0.03}$	0.188
3b (3a)	3a + max M_m decr.	$a^{mat}_{\max} = 10$; $\rho_{min} = 0.1$; $\mu = 3$; $M^{min}_m = 0.02$; $M^{\max}_m = \underline{0.034}$ (i.e. maximal M_m density dependence possible)	0.050
3c (3b)	3b + extreme values	$a^{mat}_{\max} = \underline{12}$; $\rho_{min} = 0.1$; $\mu = \underline{5}$; $M^{min}_m = \underline{0.01}$; $M^{\max}_m = \underline{0.032}$	0.051
4ai (ref)	Ref – *M* incr. with age	$a^{mat}_{\max} = 5$; $\rho_{min} = 0.1$; $\mu = 1$; $M^{min}_m = M^{\max}_m = 0.03$; $M_h - M_m = \underline{0.05}$; $a_2 = \underline{30}$; $a_3 = \underline{40}$	0.118
4aii (ref)	Ref – max *M* incr. with age	$a^{mat}_{\max} = 5$; $\rho_{min} = 0.1$; $\mu = 1$; $M^{min}_m = M^{\max}_m = 0.03$; $M_h - M_m = \underline{0.05}$; $a_2 = \underline{23}$; $a_3 = \underline{33}$	0.038
4bi (3a)	3a – *M* incr. with age	$a^{mat}_{\max} = 10$; $\rho_{min} = 0.1$; $\mu = 3$; $M^{min}_m = 0.02$; $M^{\max}_m = 0.03$; $M_h - M_m = \underline{0.02}$; $a_2 = \underline{30}$; $a_3 = \underline{40}$	0.039
4bii (3a)	3a – max *M* incr. with age	$a^{mat}_{\max} = 10$; $\rho_{min} = 0.1$; $\mu = 3$; $M^{min}_m = 0.02$; $M^{\max}_m = 0.03$; $M_h - M_m = 0.02$; $a_2 = \underline{29}$; $a_3 = \underline{39}$	0.032
4c (3b)	3b – *M* incr. with age	$a^{mat}_{\max} = 10$; $\rho_{min} = 0.1$; $\mu = 3$; $M^{min}_m = 0.02$; $M^{\max}_m = \underline{0.0302}$; $M_h - M_m = \underline{0.02}$; $a_2 = \underline{30}$; $a_3 = \underline{40}$	0.033
4d (3c)	3c – *M* incr. with age	$a^{mat}_{\max} = 12$; $\rho_{min} = 0.1$; $\mu = 5$; $M^{min}_m = 0.01$; $M^{\max}_m = \underline{0.028}$; $M_h - M_m = \underline{0.02}$; $a_2 = \underline{30}$; $a_3 = \underline{40}$	0.028*
5a (3c)	3c + preg = 0.6	$a^{mat}_{\max} = 12$; $\rho_{min} = 0.1$; $\mu = 5$; $M^{min}_m = 0.01$; $M^{\max}_m = 0.032$; $\gamma_{max} = \underline{0.6}$	0.051
6ai	Ref – 17,959 target	$a^{mat}_{\max} = 5$; $\rho_{min} = 0.1$; $\mu = 1$; $M^{min}_m = M^{\max}_m = 0.03$; $N^T_{1997} = \underline{17{,}959}$	0.348
6aii	Ref – 31,750 target	$a^{mat}_{\max} = 5$; $\rho_{min} = 0.1$; $\mu = 1$; $M^{min}_m = M^{\max}_m = 0.03$; $N^T_{2003} = \underline{31{,}750}$	0.348
6bi	3a – 17,959 target	$a^{mat}_{\max} = 10$; $\rho_{min} = 0.1$; $\mu = 3$; $M^{min}_m = 0.02$; $M^{\max}_m = 0.03$; $N^T_{1997} = \underline{17{,}959}$	0.188
6bii	3a – 31,750 target	$a^{mat}_{\max} = 10$; $\rho_{min} = 0.1$; $\mu = 3$; $M^{min}_m = 0.02$; $M^{\max}_m = 0.03$; $N^T_{2003} = \underline{31{,}750}$	0.188
7bi	6bi + $K^* = 1.5K$	$a^{mat}_{\max} = 10$; $\rho_{min} = 0.1$; $\mu = 3$; $M^{min}_m = 0.02$; $M^{\max}_m = 0.03$; $N^T_{1997} = 17{,}959$; $K^* = \underline{1.5K}$	0.188
7bii	6bii + $K^* = 2K$	$a^{mat}_{\max} = 10$; $\rho_{min} = 0.1$; $\mu = 3$; $M^{min}_m = 0.02$; $M^{\max}_m = 0.03$; $N^T_{2003} = 31{,}750$; $K^* = \underline{2K}$	0.188

age dependence in *M*) (see Appendix equations A.11 and A.12 and associated text).

The possibility that *M* increases at larger ages is implemented through equation A.13. Potentially this could introduce temporary high growth rates if the population for a time includes an over-representation of younger animals past the age at first parturition as it recovers from heavy depletion.

Other factors investigated are alternative target population levels and a change in carrying capacity. The alternative levels are: 31,750 for 2003 from JARPA surveys (Matsuoka *et al.*, 2011); and 17,959 for 1997 from the IDCR surveys (Branch, 2011).

An increase in *K* over the period 1930 to 1960 is considered as a manifestation of possible competitive release (as regards utilisation of krill) arising from the major reduction of blue and fin whales over that period as a result of harvesting.

RESULTS AND DISCUSSION

Table 2 lists the specifications of the reference case and other models implemented for Breeding Stock D, together with shortened names for each for ease of reference. It also lists the value of M_0 for each model, indicating cases where the $M_0 \geq M_1$ constraint has come into play.

Results are shown in Table 3 as annual rates of population growth for each model for three periods: the first five (1968–72) and first ten (1968–77) years after catching ceased (these are the periods where growth rates might be expected to be highest as the population is at its lowest level), and the 1982–1994 period over which breeding area surveys lead to an annual rate of increase estimate of 0.10.

Immediately evident from Table 3 is that there is very little difference between results for the Core and the Fringe catch allocation hypotheses. Hence the discussion that follows focuses on results for the Fringe case only.

For virtually all the models considered, the rate of population increase over the first ten years since catches ceased is greater than that over the first five years (the exceptions are for the higher JARPA and IDCR survey based target population sizes). The primary reason for this is likely the time lag until calves reach the age at which they can themselves reproduce and add to the population. In most cases increase rates over 1982–94 are less than those over the first ten years since catches ceased. In cases where this is not so (i.e. transient effects are sufficient to compensate for the opposite impact from density dependence), the differences are marginal. Further discussion focuses on the 1982–94 rates only, as this is the period for which an estimate is available from the survey series.

The reference case reflects an annual population increase rate of 0.070 over 1982–94. Density dependence in the age at first parturition (a^{mat} ranging from 5 to 10 years) and in the natural mortality *M* (ranging from 0.02 to 0.03 yr^{-1}) each separately increase this by about 0.01, as does nonlinearity in the density dependence (μ changed from 1, corresponding to linear dependence, to 3). The fact that lowering *M* from 0.03 to 0.02 in the absence of density dependence in *M* leads to a *drop* in the increase rate may seem surprising; it arises from the fact that balancing births and deaths at carrying capacity given a lower *M* value, requires an increase in M_0, which in turn reduces the rate at which the population can grow when reduced in abundance.

All of these changes together (model 3a) see the annual increase rate raised to 0.10 (which coincidentally happens to be the point estimate from the observations). If the extent to which *M* can change with density is maximised subject to the constraint that $M_0 > M$ (model 3b), the rate increases to 0.11. Finally if more extreme (but not impossible) ranges/values are used (a^{mat}: 5 to 12; $\mu = 5$; M : 0.01 to 0.032 – model 3c), a rate of 0.12 can be realised. Fig. 2 illustrates the population trajectories for a number of these cases.

Table 3

Annual rates of increase for the model variants considered. The periods considered are the first five (1968–72) and ten (1968–77) years after catches dropped to zero, and then the 1982–1994 period over which a relative abundance index is available for the breeding grounds which indicates an annual increase rate of 0.101 (95% CI: [0.028; 0.175]). 'Maximum' gives the maximum steady growth rate possible given the biological parameter values for the model in question. Models marked with an asterisk were fitted with age-at-first capture (a_r) of 2 rather than 4 years for reasons explained in the text. A double asterisk indicates that the change in the value of this parameter applies only to the Fringe catch allocations.

		Core			Fringe			
Model	Name	68–72	68–77	82–94	68–72	68–77	82–94	Maximum
1	Reference case	0.076	0.076	0.066	0.075	0.077	0.070	0.081
2a (ref)	$a^{mat}_{\max} = 10$	0.087	0.085	0.069	0.086	0.087	0.075	0.093
2b (ref)	$M_m = 0.02$	0.062	0.062	0.055	0.063	0.063	0.058	0.067
2c (ref)	$\mu = 3$	0.079	0.080	0.079	0.078	0.080	0.080	0.081
2d (ref)	M_m: 0.03 → 0.02	0.085	0.085	0.073	0.084	0.086	0.078	0.090
3a (ref)*	All changes	0.100	0.101	0.098	0.097	0.100	0.100	0.102
3b (3a)*	3a + max M_m decr.	0.110	0.112	0.108	0.105	0.111	0.110	0.113
3c (3b)*	3b + extreme values	0.118	0.120	0.118	0.111	0.119	0.119	0.122
4ai (ref)	Ref – M incr. with age	0.093	0.094	0.082	0.091	0.094	0.087	0.098
4aii (ref)**	Ref – max M incr. with age	0.099	0.100	0.088	0.098	0.101	0.092	0.104
4bi (3a)*	3a – M incr. with age	0.111	0.113	0.110	0.105	0.111	0.112	0.114
4bii (3a)*	3a – max M incr. with age	0.112	0.113	0.110	0.106	0.112	0.112	0.114
4c (3b)*	3b – M incr. with age	0.112	0.113	0.110	0.105	0.112	0.112	0.114
4d (3c)*	3c – M incr. with age	0.120	0.122	0.120	0.112	0.120	0.121	0.124
5a (3c)*	3c + preg = 0.6	0.129	0.135	0.134	0.115	0.132	0.135	0.138
6ai	Ref – 17,959 target				0.072	0.071	0.054	0.081
6aii	Ref – 31,750 target				0.056	0.052	0.024	0.081
6bi	3a – 17,959 target				0.099	0.100	0.085	0.102
6bii	3a – 31,750 target				0.037	0.025	0.001	0.102
7bi	6bi + $K^* = 1.5K$				0.099	0.101	0.095	0.102
7bii	6bii + $K^* = 2K$				0.100	0.101	0.090	0.102

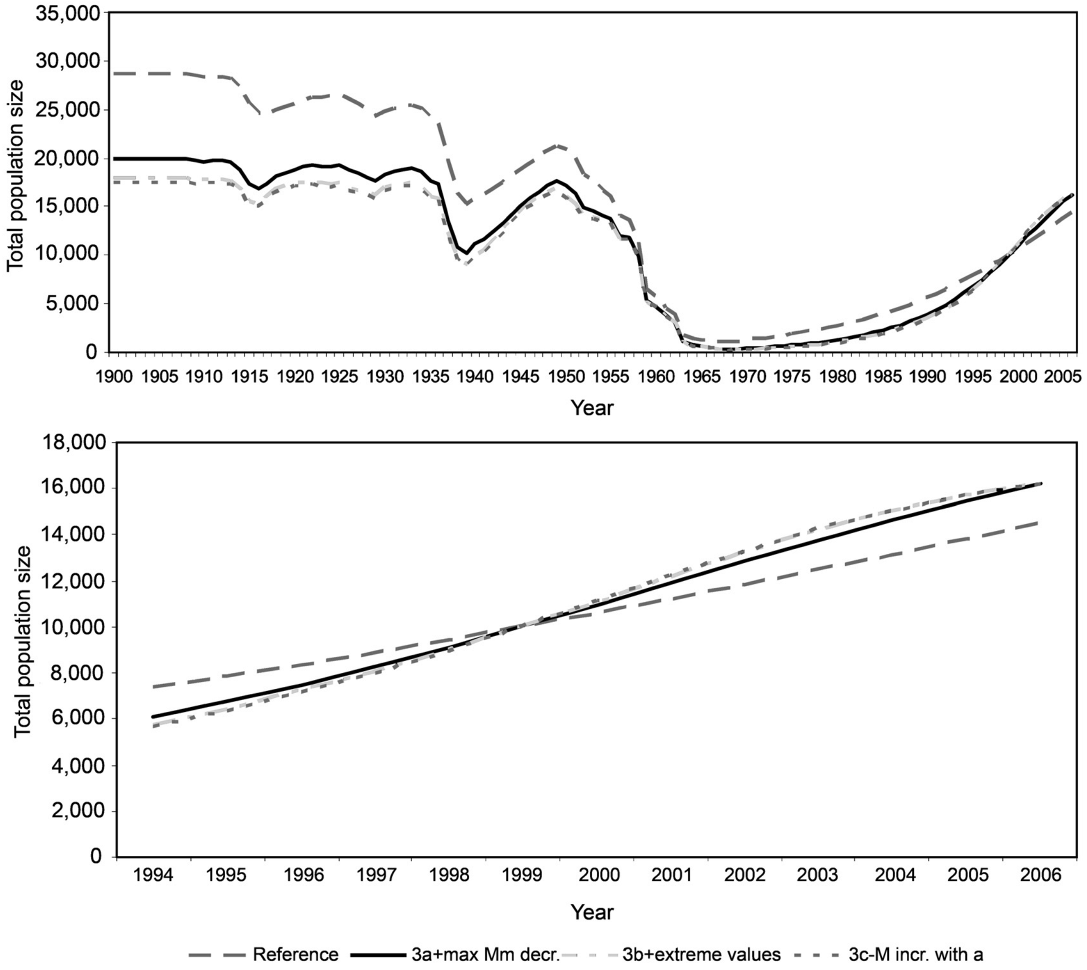

Fig. 2. Comparison of population trajectories for stock D humpback whales for the reference case model, and variants of this model in which all the parameters are changed. Trajectories are shown for the whole period since exploitation commenced (top) and for the 1994–2006 period only (bottom).

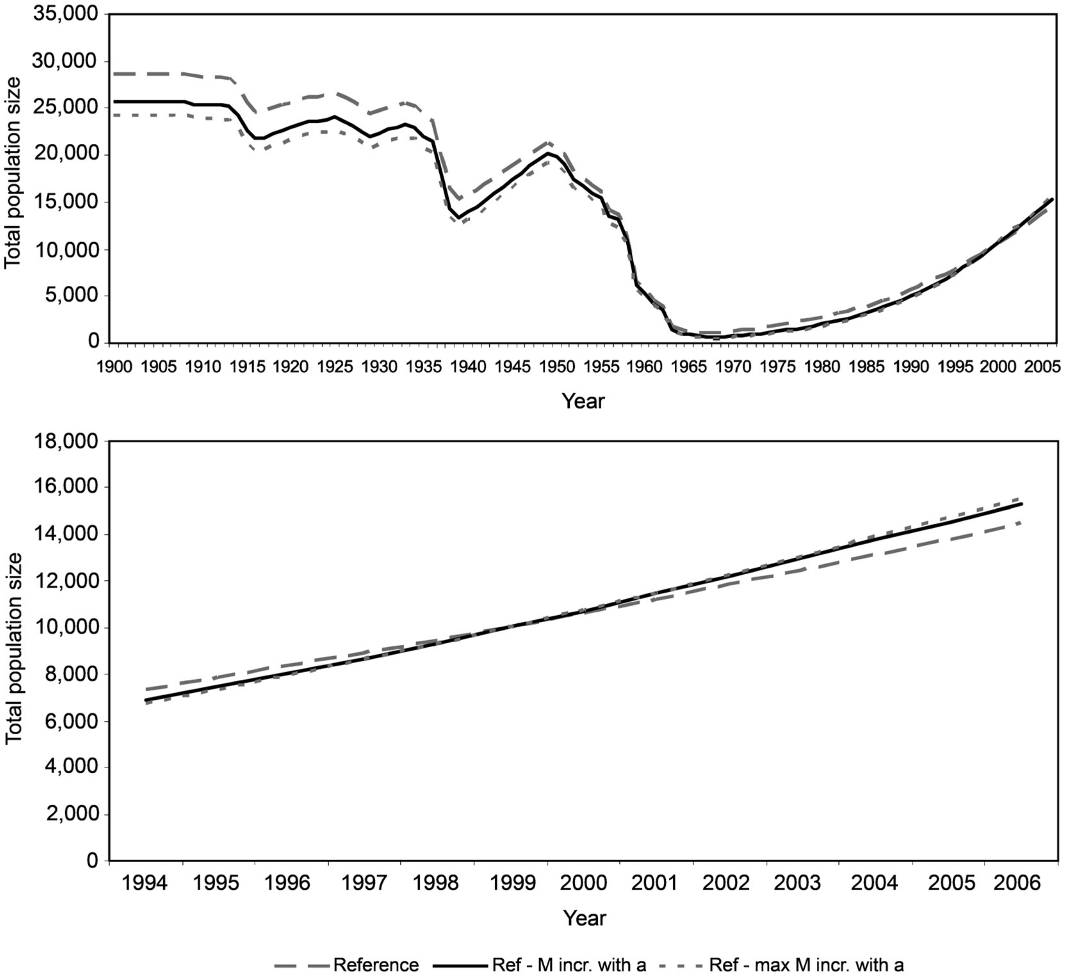

Fig. 3. Comparison of population trajectories for stock D humpback whales for the reference case model, and variants of this model which allow for various degrees of larger natural mortality at older ages. Trajectories are shown for the whole period since exploitation commenced (top) and for the 1994–2006 period only (bottom).

If higher natural mortality at larger ages is allowed (models 4ai and 4aii), the increase rate for the reference case becomes larger by about 0.02 (see Fig. 3). However, such higher mortality in combination with more extreme ranges for the other parameters (model 4d) can achieve only little extra increase in the growth rate. These increases are limited essentially because the $M_0 > M_1$ constraint comes into play (see Table 3), and precludes more extreme choices for the $M_m^{\max}$, a_2 and a_3 parameters.

Constraining the maximum pregnancy rate to 0.5 has an influential effect. Were annual compared to biennial calvings sufficiently frequent to increase the average maximum pregnancy rate from 0.5 to 0.6 (model 5a), the population annual increase rate could approach 14%.

In most instances with higher target levels for recent abundance (from JARPA or IDCR surveys – models 6), the population shows a relatively low rate of increase over 1982 to 1994, essentially because it is estimated to be close to carrying capacity by the start of that period. However the fact that the populations are never reduced to a very low level under some such scenarios (see Fig. 4) raises questions about their plausibility. This inconsistency can, however, be resolved if an increase in carrying capacity is postulated (model 7). An increase of K of 50% or 100% for target levels of, respectively, 17,959 in 1997 or 31,750 in 2003 sees annual increase rates back to near 0.10 (Fig. 4).

For all models considered the maximum steady growth rate possible given the biological parameters for the model in question is *greater* than the predicted rate of increase over 1982 to 1994. Thus these analyses provide no indication that the point estimate of the rate of increase observed can be reconciled with less extreme values of demographic parameters than led to the original $r = 0.126$ upper bound as a consequence of transient effects.

CONCLUSION

Unless the possibilities (in the limit of low population size) of an age at first parturition less than five years, or an average pregnancy rate above 0.5 can be entertained, it seems that 0.12 is about the maximum demographically feasible annual increase rate for a closed population of Breeding Stock D humpback whales over the 1982–94 period. Transient effects do not appear able to reconcile the observed rate of increase with less extreme values of demographic parameters than led to the previously imposed upper bound of 0.126 on the maximum possible annual growth rate[1].

[1] Subsequent to the original presentation of this paper, the IWC Scientific Committee (IWC, 2007) agreed that it was reasonable to revise down the upper bound on the maximum annual increase rate from the earlier 0.126 to 0.106, based on extreme values reported for Northern Hemisphere humpback whale populations for pregnancy rate, age at first parturition and natural mortality, though noting that the more extreme values still in the limit of very low population size could not be excluded. It is, however, unlikely that use of those Northern Hemisphere extreme values rather than those considered in this paper would change the conclusion that transient effects do not have an appreciable impact on the population growth rates observed.

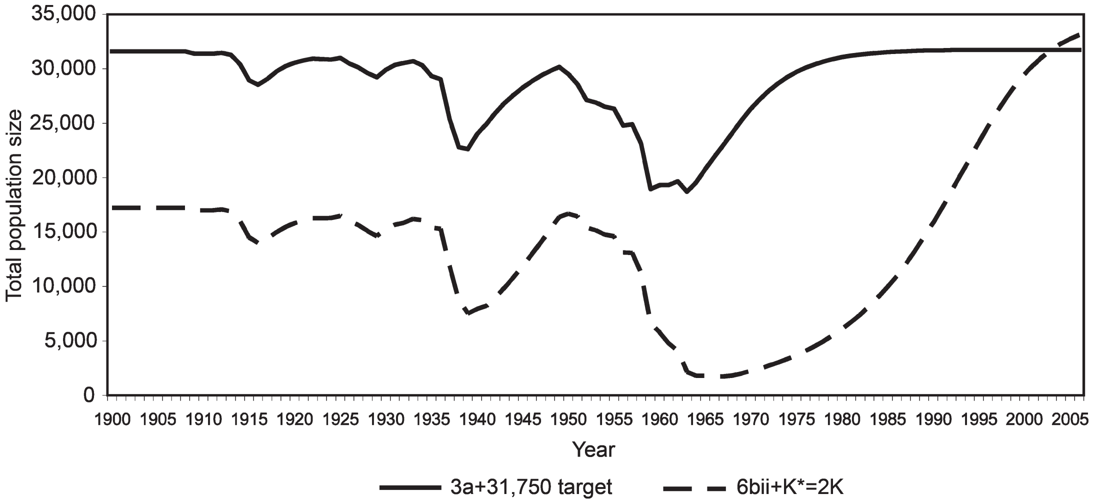

Fig. 4. Comparison of population trajectories for stock D humpback whales for the '3a' variant of the reference case model with a target population of 31,750 in 2003, and for this model with the inclusion of a 100% increase in carrying capacity from 1930 to 1960.

ACKNOWLEDGEMENTS

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Appendix

DETAILS OF THE AGE-STRUCTURED POPULATION MODEL

Population dynamics

$$N_{y+1,1} = 0.5\rho(N_y^T)e^{-M_0}N_y^m \qquad y \geq 0 \qquad \text{(A.1)}$$

$$N_{y+1,a+1} = (N_{y,a} - C_{y,a})e^{-M_a} \qquad 1 \leq a \leq 99 \qquad \text{(A.2)}$$

where:

$N_{y,a}$ is the number of humpback whales of age a in year y,

$C_{y,a}$ is the number of humpback whales of age a caught in year y,

M_a is the natural mortality rate at age a,

N_y^T is total population in year y (defined to be one year old and older humpback whales) given by:

$$N_y^T = \sum_{a=1}^{100} N_{y,a} \ ,$$

N_y^m is the mature population of humpback whales in year y given by:

$$N_y^m = \sum_{a=1}^{100} N_{y,a}\gamma_a \ ,$$

where:

γ_a is the fraction of humpback whales of age a that are mature, given by:

$$\gamma_a = \begin{cases} 0 & a < \mathrm{int}\left(a^{mat}\left(N_y^T\right)\right) \\ 1-\left(a^{mat}\left(N_y^T\right)-a\right) & a = \mathrm{int}\left(a^{mat}\left(N_y^T\right)\right) \\ 1 & a > \mathrm{int}\left(a^{mat}\left(N_y^T\right)\right) \end{cases} , \tag{A.3}$$

where:

a^{mat} (N_y^T) is the age at first parturition, as a function of the total population size, given by:

$$a^{mat}\left(N_y^T\right) = \left(a_{\max}^{mat} - a_{\min}^{mat}\right) N_y^T \big/ K_y + a_{\min}^{mat} \ , \tag{A.4}$$

where:

$a_{\max}^{mat}$ is the maximum age at first parturition,

$a_{\min}^{mat}$ is the minimum age at first parturition, and

K_y is the carrying capacity, which can change linearly over the years 1930 to 1960 from K to K^*:

$$K_y = \begin{cases} K & 1900 \le y < 1930 \\ K + \left(K^* - K\right)\dfrac{\left(y-1930\right)}{30} & 1930 \le y \le 1960 \\ K^* & 1960 < y \le 2006 \end{cases} , \tag{A.5}$$

$\rho(N_y^T)$ is the pregnancy rate, which depends on the total population size, and given by:

$$\rho\left(N_y^T\right) = \rho_{max} - \left(\rho_{max} - \rho_{min}\right) N_y^T \big/ K_y \ , \tag{A.6}$$

where:

ρ_{min} is the minimum pregnancy rate, and

ρ_{max} is the maximum pregnancy rate.

Note that it is assumed that all humpback whales reaching the age of 100 then immediately die. Given that the only instances of evidence of whales living beyond 100 is for bowheads, setting 100 as a maximum age seems reasonable.

The number of whales of age a caught in year y is given by:

$$C_{y,a} = \begin{cases} 0 & a < a_r \\ C_y \dfrac{N_{y,a}}{\sum_{a'=a_r}^{99} N_{y,a'}} & a \ge a_r \end{cases} \tag{A.7}$$

where:

a_r is the age at first capture, and

C_y is the catch in year y.

i.e. uniform selectivity for ages a_r and above is assumed.

The initial numbers at each age a are taken to follow an unexploited equilibrium distribution evaluated as follows:

$$N_{0,a} = \lambda N_a^* \text{ for } a = 1, \ldots, 100, \tag{A.8}$$

where:

$$\lambda = \frac{K}{\sum_{a=1}^{100} N_a^*} \ , \tag{A.9}$$

$$N_1^* = 1,\ N_2^* = N_1^* e^{-M_1},\ N_3^* = N_2^* e^{-M_2}, \text{ etc., and} \tag{A.10}$$

K is the (initial) carrying capacity.

Natural mortality

The natural mortality for the first year of life (M_0) is calculated by ensuring that the number of calves that reach age one each year balances the number of deaths (of humpback whales of age one and above) per year when the population is unexploited (i.e. when $N_0^T = K$). In this instance the number of such calves is proportional to (taking $a_{\max}^{mat}$ here to be integral):

$$0.5\rho_{min} e^{-M_0} \sum_{a=a_{\max}^{mat}}^{100} N_a^*, \tag{A.11}$$

and the number of deaths is in the same proportion to:

$$\sum_{a=1}^{99} N_a^* \left(1 - e^{-M_a}\right) + N_{100}^* \tag{A.12}$$

so that M_0 can be computed by equating A.11 to A.12.

The natural mortality for the first year of life (M_0) is constrained to be greater than the natural mortality of one year olds (M_1).

To allow for the possibility of increased natural mortality at older ages, the natural mortality at age is modelled to change smoothly by:

$$M_a = \begin{cases} M_m & 1 \le a < a_2 \\ M_m + \left(M_h - M_m\right)\dfrac{\left(a - a_2\right)}{\left(a_3 - a_2\right)} & a_2 \le a \le a_3 \\ M_h & a_3 < a \le 100 \end{cases}, \tag{A.13}$$

where:

M_m is the lowest value for natural mortality, and

M_h is the highest value for natural mortality with M_m increasing linearly to M_h over the age range a_2 to a_3.

When the value for M_h is set the same as that for M_m, natural mortality is independent of age.

Alternative forms of density dependence

Alternative formulations are considered to allow for density dependence in different forms in the calculation of age at first parturition ($a^{mat}(N_y^T)$), the pregnancy rate ($\rho(N_y^T)$) and the natural mortality M_a. Equation (A.4) is changed to:

$$a^{mat}\left(N_y^T\right) = \left(a_{\max}^{mat} - a_{\min}^{mat}\right)\left(N_y^T / K_y\right)^{\mu} + a_{\min}^{mat}, \tag{A.14}$$

equation (A.6) is changed to:

$$\rho\left(N_y^T\right) = \rho_{max} - \left(\rho_{max} - \rho_{min}\right)\left(N_y^T / K_y\right)^{\mu}, \text{ and} \tag{A.15}$$

the lowest value for natural mortality (M_m) in equation (A.13) is changed to:

$$M_m = M_m^{\min} + \left(M_m^{\max} - M_m^{\min}\right) N_y^T / K_y. \tag{A.16}$$

Fig. A.1 illustrates how different choices for μ affect the dependence of pregnancy rate on population abundance.

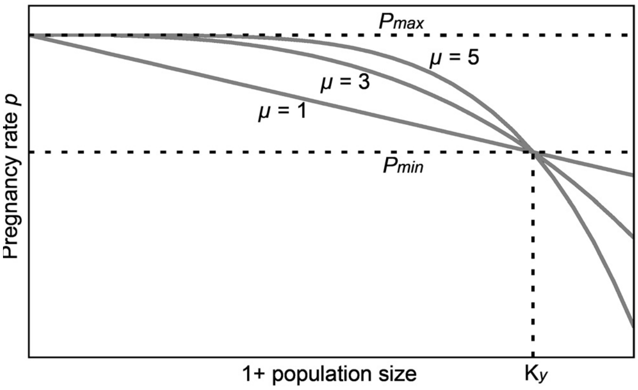

Fig. A.1. The variation of pregnancy rate with total population size in relation to the value of the μ parameter (see equation A.15).

Abundance estimates of Southern Hemisphere Breeding Stock 'D' humpback whales from aerial and land-based surveys off Shark Bay, Western Australia, 2008

Sharon L. Hedley*, John L. Bannister+ and Rebecca A. Dunlop#

Contact email: sharon@countingwhales.co.uk

ABSTRACT

Single platform aerial line transect and land-based surveys of Southern Hemisphere Breeding Stock 'D' humpback whales *Megaptera novaeangliae* were undertaken off Shark Bay, Western Australia to provide absolute abundance estimates of animals migrating northward along the western Australian coast. The aerial survey flew a total of 28 flights, of which 26 were completed successfully, from 24 June–19 August 2008. The land-based survey was undertaken from Cape Inscription, Dirk Hartog Island, Shark Bay, during the expected peak of the whales' northward migration, from 8–20 July. During the first week of the land-based survey, some double count effort was undertaken to provide information on the numbers of pods missed from the land station. The assumed period of northward migration was 2 June–7 September. Estimated abundance of northward-migrating whales during that time is 34,290 (95% CI: (27,340–53,350)), representing an annual rate of increase of 12.9% (CV = 0.20) since an estimate of 11,500 in 1999. This estimate is based on an estimate of relative abundance of surface-available whales of 10,840 (8,640–16,860), and an estimated $g(0)$ of 0.32. There were considerable practical difficulties encountered during the land-based survey which reduced the effectiveness of the dual-survey approach for estimating $g(0)$ for the aerial survey. Furthermore only about 15% of whales were estimated to be within the visual range of the land-based station. Alternative approaches for estimating $g(0)$ from these data are therefore also presented, resulting in considerably higher estimates of around 0.6–0.7, and yielding a conservative abundance estimate of 17,810 (14,210–27,720).

KEYWORDS: HUMPBACK WHALE; SOUTHERN HEMISPHERE; SURVEY-AERIAL; SURVEY-SHORE-BASED; MIGRATION; AUSTRALIA

INTRODUCTION

Following increasing reports of humpback whale (*Megaptera novaeangliae*) sightings in winter off the western Australian coast in the early-mid 1970s, aerial surveys of humpback whales during their northward migration were undertaken from Carnarvon, Western Australia (WA) in an area off Shark Bay where aerial spotter and other data from whaling operations were available for the last year of humpback whaling, 1963. Results of those surveys to 1988 (Bannister *et al.*, 1991) demonstrated that significantly more whales were seen in the area in the 1980s than in 1963. Further surveys, in 1991 and 1994, demonstrated an annual increase rate of 10.15 ± 4.6% to 1994 (see Bannister and Hedley, 2001). In comparison to the estimated population size of 568 at the end of 1963 (Bannister, 1964), the population size in 1994 was calculated to be some 4,000–5,000 animals (Bannister, 1995).

The 1994 survey results showed that to detect a significant difference in population in future years, at an annual increase of 10%, an interval of three years would be required between surveys, leading to a proposed further survey in 1997. Given funding constraints, that survey took place in 1999, its aim being to provide an estimate of absolute abundance. This aim was more ambitious than for its predecessors, from which only a relative index had been obtained. The survey was planned to cover as much of the northern migration period as possible, with flights every other day over a two month period, mid June–mid August. Given the prevailing generally poor weather conditions, only 18 of the 30 planned flights could be flown, of which only 15 were completed. Nevertheless allowing for animals missed while submerged, 1999 population size was estimated as 8,200–13,600 (Bannister and Hedley, 2001).

Given the disappointing coverage, a further survey was planned to take place as soon as possible over the same period and area, but to include an additional land-based component. That survey took place in 2005; the results are reported in Paxton *et al*. (2011). Unfortunately, although the 2005 survey had been designed with the aim of improving on earlier surveys (which were only able to apply ad hoc corrections to adjust for uncertain trackline detection), last-minute logistical changes to the land-based survey in 2005 reduced its effectiveness. In particular, the location of the land-based survey had to be moved northward to a location where, in the event, whales often exhibited 'milling' behaviour rather than directional swimming more typical of migrating animals, and to where the offshore distribution of whales extended far beyond the visual range of the land-based observers.

Given rather equivocal results from the 2005 survey, improvements to the design of the 2008 survey were planned as follows:

(1) The aerial survey component was expanded in area to extend offshore coverage (following some experimental work in 2007 to determine the most appropriate survey area).
(2) Aerial survey data were collected using a direct data acquisition system.
(3) The land-based component of the survey was expanded to include some double-platform independent observer

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* *Centre for Research into Ecological and Environmental Modelling, The Observatory, Buchanan Gardens, University of St Andrews, Fife, KY16 9LZ, UK.*
+*Western Australian Museum, Locked Bag 49, Welshpool DC, Western Australia 6986, Australia.*
Cetacean Ecology and Acoustics Laboratory School of Veterinary Science University of Queensland St Lucia, Qld 4072, Australia.

counts, and thus allow estimation of a correction factor for whales missed by the land-based observers.

(4) The location of the land-based platforms was at Cape Inscription, Dirk Hartog Island, Shark Bay. From previous surveys, it was expected that whales passing this location would be more identifiable as 'northward-migrating' and furthermore, that they would pass closer to the shore at this latitude.

This report details the analysis of data from the 2008 survey, the aerial component of which took place from 24 June–19 August, with the land-based component from 8–20 July.

FIELD METHODS AND DATA

Aerial survey

In 1999, most sightings were made within about 30km of the eastern edge of the survey area – an area of coastline delineated by the western coastlines of Bernier, Dorre and Dirk Hartog Islands (see Bannister and Hedley, 2001), although the transects had extended out to about 56km from those islands. In 2005, the sightings were spread more evenly (in relation to distance offshore) throughout the survey area (Paxton *et al.*, 2011). A small set of flights in 2007 over the same area but with two legs extending 92km offshore (to 112°E) suggested that humpback whales might be found out to 65km offshore (i.e. to about 112°25'E) but with only a very few further out. The 2008 flight path was therefore planned to cover an area reduced in latitudinal coverage from that surveyed previously, approximately 55km × 75km immediately west of Dorre and Dirk Hartog Islands on the western boundary of Shark Bay. The reduction in latitudinal effort allowed for two extended transect legs of about 70km length to be flown to provide information on the possible distribution of animals further offshore. These were located off the north of Dirk Hartog Island. In addition, on seven flights when the land-based survey was operating, short legs of about 20km were flown at the latitude of Cape Inscription. The survey area and a typical flight path are shown in Fig. 1. The approximate length of the two most northerly and two most southerly east-west transects was 45–50km. The survey area covered a region of approximately 6,570km^2.

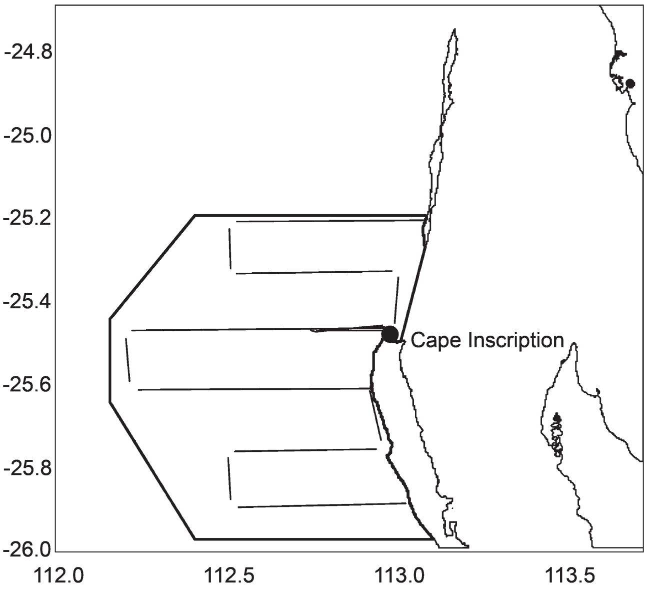

Fig. 1. Survey area for aerial survey, and typical flight path. (Flight 8 on 10 July shown).

As in 1999 and 2005, the 2008 survey flights were undertaken from a high-wing, twin-engine aircraft, mainly a Partenavia P68B (fitted with bubble windows), under charter from TropicAir Services Pty Ltd, flying out of Carnarvon, WA. On four flights, a Cessna 337 (with flat windows) was chartered from Norwest Air Work Pty Ltd, based in Exmouth, WA. On all flights, a GPS and on-board computer system were available to plot waypoints (as on previous surveys) and to log data (such as time, position and altitude); in addition, in 2008, Cyclopes software (Kniest, University of Newcastle, Australia) was employed to map the flight path. Separately for each side of the aircraft, the two observers recorded various weather covariates, including: Glare strength (a factor with four levels); Glare angle; Beaufort sea state; Wind strength (in knots); Wind direction; Percentage cloud cover; and Sightability, a subjective overall assessment of the sighting conditions (a factor with four levels). Observers used a clinometer (industry standard Suunto PM-5/360PC) and an angleboard to measure declination and horizontal angles to sightings. For each sighting, observers made every effort to record pod size and swimming direction. All sighting details were recorded on a Sony digital recorder for post-flight data entry. A total of four observers participated in the survey, with their levels of participation ranging from flying 24 of the 28 flights (85%) down to 7 (25%).

Of the 28 flights flown, 26 of were successfully completed and included in the analysis. The first three flights (on 24, 26 and 29 June) were flown in a northerly direction; the remainder were flown in a southerly direction. Because of glare, usually the latter is preferable for surveys in this location; historically (when transects were closer together) such a strategy has also been used in order to minimise the risk of double-counting animals (flying was in the opposite direction to the whales' migration path).

Table 1 details the date, total transect length and number of sightings for each flight. 'NM' sightings are those pods recorded with a northward swimming (migration) direction. NM+ sightings additionally include some pods of undetermined direction, randomly allocated to be travelling north in proportion to the sightings of known direction on a given day which were travelling northwards.

Land-based survey

Sighting survey

The land-based survey took place from Cape Inscription, on the northern end of Dirk Hartog Island – a rugged and exposed area with virtually no facilities at the site. The observation site was low, with the highest accessible point being just 25.5m above sea level.

Survey effort was scheduled for 9 hours each day from 8–20 July; 7 full days were completed together with three partial days (of 6, 7 and 2.5 hours respectively), with no effort possible on 11 and 20 July. During the first survey week (8–13 July), five hours of double-platform (independent observer) data were also collected on each day with suitable survey conditions (25 hours in total), with four observers assigned to each of the two teams ('Car' and 'Bush'). During the second week, reduced personnel resulted in it only being feasible to conduct single-platform survey; these observations were augmented by 'focal follows' (i.e. each surfacing of a detected pod recorded until out of visible range) without disruption to the sightings survey.

Whales were spotted by the observers and sightings were input directly into a notebook computer running Cyclopes (software specifically designed for the tracking of marine

Table 1

Summary of aerial surveys. Flights marked with an asterisk were aborted and their data excluded from the analysis. Numbers in parentheses are the numbers of pods/whales after left-truncation of perpendicular distances at 260m.

Flight	Aircraft	Date	Effort (km)	NM pods (after left-truncation)		NM whales (after left- truncation)		NM+ pods (after left-truncation)		NM+ whales (after left- truncation)	
1	Partnv	24/06/08	540	12	(12)	26	(26)	17	(17)	33	(33)
2	Partnv	26/06/08	410	3	(3)	3	(3)	6	(5)	8	(7)
3	Partnv	29/06/08	530	8	(5)	20	(13)	8	(5)	20	(13)
4	Partnv	02/07/08	570	43	(40)	71	(66)	57	(54)	92	(87)
5	Partnv	03/07/08	470	20	(19)	39	(37)	28	(27)	48	(46)
6	Partnv	08/07/08	540	29	(28)	55	(53)	35	(34)	67	(65)
7	Partnv	09/07/08	550	37	(35)	78	(72)	51	(49)	96	(90)
8	Partnv	10/07/08	510	53	(50)	83	(78)	67	(63)	100	(94)
9	Cessna	13/07/08	500	30	(30)	66	(66)	42	(41)	84	(82)
10	Cessna	14/07/08	570	46	(46)	68	(68)	54	(54)	77	(77)
11	Partnv	16/07/08	580	21	(20)	35	(33)	78	(76)	115	(112)
12	Cessna	17/07/08	580	15	(14)	32	(31)	32	(30)	55	(51)
13	Partnv	22/07/08	480	29	(25)	60	(49)	68	(62)	115	(101)
14	Partnv	23/07/08	480	37	(32)	70	(59)	56	(51)	95	(84)
15*	Partnv	24/07/08	190	7	(6)	9	(7)	11	(10)	13	(11)
16	Partnv	29/07/08	460	32	(30)	48	(44)	58	(56)	79	(75)
17	Partnv	02/08/08	490	15	(12)	25	(20)	37	(34)	52	(47)
18	Partnv	06/08/08	440	15	(15)	28	(28)	23	(23)	36	(36)
19	Partnv	08/08/08	460	7	(7)	13	(13)	14	(14)	23	(23)
20	Partnv	09/08/08	470	15	(13)	21	(19)	27	(24)	38	(35)
21	Partnv	10/08/08	470	23	(21)	43	(41)	28	(26)	48	(46)
22	Partnv	12/08/08	480	12	(12)	16	(16)	20	(19)	26	(25)
23	Partnv	13/08/08	480	17	(16)	28	(26)	26	(25)	38	(36)
24	Cessna	14/08/08	440	5	(5)	8	(8)	8	(8)	12	(12)
25	Partnv	15/08/08	400	12	(12)	21	(21)	23	(23)	35	(35)
26	Partnv	16/08/08	470	16	(16)	24	(24)	26	(26)	35	(35)
27*	Partnv	18/08/08	190	4	(4)	7	(7)	8	(8)	14	(14)
28	Partnv	19/08/08	470	8	(8)	11	(11)	12	(12)	15	(15)
Total			13,220	571	(536)	1,008	(939)	920	(876)	1,469	(1,387)

mammals). A theodolite, connected directly to the notebook computer, was also used to measure the positions of passing groups of whales in Cyclopes. One observer operated the theodolite, while another operated the computer. When a sighting was made, the theodolite operator pointed the theodolite at the surfacing pod and with the push of a button, vertical and horizontal bearings were transmitted to, and recorded directly in, Cyclopes. The position of the pod was calculated correcting for tides, curvature of the Earth and refraction, and was plotted on a map of the area. The computer operator added data on pod composition, behaviour and direction of travel, when these could be determined. Cyclopes was thus able to compute pod speed, course and distance from any reference point. For each pod sighted the following information was also recorded using Cyclopes: time (to the nearest second); unique pod identifier (A, B, C, etc.); species confirmation; calf presence; and cue, plus other relevant information such as whether or not the group went into or came from the Shark Bay area to the east of the islands. Whilst perpendicular distance offshore was rarely observed, it was calculable for pods with at least one fix either side of the 'abeam' line from the land-based platform.

The other two observers were 'spotters' who used naked eye or 7 × 50 binoculars to sight whales. The spotters were allocated adjacent sectors of the ocean to scan to spread sighting effort as much as possible. Each land-based team attempted to record the behaviour and all surfacings of every sighted group to increase chances of matching between the two land-based teams and the aerial survey. Inevitably however, this was not possible during periods of high densities of whales. Pods further offshore had an increased risk of being 'lost', only sighted once, or being confused with other pods at a similar bearing. Spotter observations were entered as 'additional observations'. The information above was entered for each 'additional observation' and the position was calculated from the bearing and reticule readings taken from the binoculars. Priority for theodolite fixes was given to new pods, after which, theodolite effort was spread as evenly as possible among the pods being tracked in the study site. Pods only sighted once or a small number of times in which group composition could not be accurately determined were counted as 1 animal (unless more than one animal had been spotted). For the double-platform data, an assessment of duplicate status was also recorded.

Weather conditions were recorded hourly and at the beginning and end of each day. Data recorded included sea state, swell height and direction, wind speed and direction, cloud cover (in oktas), glare (degrees of view obscured by glare) and other factors affecting visibility (e.g. smoke, haze, squalls).

Post data collection, all Cyclopes files were reviewed by the (primarily volunteer) researchers each evening and then, for consistency, by an experienced researcher (RAD), who has carried out the same type of work on previous land-based humpback whale surveys off the east coast of Australia.

In the event, a large proportion of the whales migrated past Cape Inscription at considerable distances from the shore, resulting not only in a high proportion of whales being missed, but also in difficulties obtaining theodolite fixes required for tracking of pods and accurate distance estimation. Beyond about 8km, whales were sighted 'on the horizon'; thus recorded distances >8km could not be considered reliable. The researchers recommended exclusion of all sightings beyond 12km as there was no accuracy in these measurements.

The matching process (undertaken by RAD) was severely hampered by the distance inaccuracies, but is assumed to

Table 2

Summary of land-based survey effort and humpback whale pod sightings. Sightings shown for NM and NM+ pods.

Date	Effort (hours)	Double platform effort (hours)	NM pods	NM pods with abeam distance recorded, truncated at 12km	NM pods truncated at 12km	NM+ pods	NM+ pods with abeam distance recorded, truncated at 12km	NM+ pods truncated at 12km
08/07/08	9	5	28	23	27	36	25	31
09/07/08	9	5	14	6	14	15	6	15
10/07/08	9	5	19	11	17	25	13	22
11/07/08	0	0	0	0	0	0	0	0
12/07/08	9	5	23	10	18	24	10	19
13/07/08	6	5	32	11	22	43	6	30
14/07/08	6	0	13	6	11	16	8	12
15/07/08	7	0	17	7	13	20	33	15
16/07/08	9	0	42	31	42	46	15	46
17/07/08	9	0	23	13	20	23	0	20
18/07/08	2.5	0	15	0	15	16	11	16
19/07/08	9	0	16	11	16	16	0	16
20/07/08	0	0	0	0	0	0	0	0
Total	84.5	25	242	129	215	280	127	242

have been completed without error in this analysis (i.e. no account is taken of incorrect duplicate identification). A summary of the land-based survey data is shown in Table 2. The number of NM and NM+ pods sighted is given, together with two further datasets: (1) the number of sightings after truncation at 12km offshore (and excluding pods for which no offshore distance was available; and (2) the number of sightings after truncation at 12km offshore (and including those pods with no offshore distance).

Focal follows

In addition to the survey data, a total of 22 focal follows were conducted during the land-based survey, primarily during the second week of the survey. During single platform survey, the focal follow team tracked randomly-selected pods of a range of sizes and composition (singletons, mother and calf groups and multiple adult groups) using a theodolite linked to Cyclopes; an additional observer (with binoculars) aided in keeping track of the group. The minimum time for a focal follow was 20 minutes (which encompassed at least three surface intervals and three deep dives). Surface intervals included shallow dives ('breathing dives') in which the animals disappear for a matter of seconds (usually no longer than 1 minute) before returning to the surface to breathe. These were differentiated from 'deep dives' in which the animals disappear for a number of minutes. For each surfacing of the followed pod, the length of surface interval, mean travel speed during the surface interval and number of blows/breaches and surface-active behaviours (all surface behaviours such as breaches, pectoral slaps, tail slaps and unidentified surface behaviours) per whale per minute of surface time were estimated. For each deep dive, the dive time and mean travel speed during the dive were also estimated. From these data, the mean dive time, surface interval, blow rate, breach rate, surface-active rate and speed of travel were calculated for each pod followed. Focally followed pods were limited to those considered to be travelling north.

ANALYSIS METHODS

Overview

The survey objective was to estimate the absolute abundance of northward-migrating humpback whales off Shark Bay. The aim of the aerial survey component was to estimate the number of whale pods seen on a given flight. This number would then require a correction so that it corresponded to the number of pods passing through the area during a given time, say, per day. Such a correction factor would depend on the whales' speed of travel during their northward migration. Without further adjustment, the number of pods per day would be an underestimate of the true number, since uncorrected estimates only estimate the number of whales at the surface and thus those that are available to be seen. In addition to this 'availability' bias, not all whales at the surface are detected, leading to so-called 'perception' bias (Marsh and Sinclair, 1989).

The aim of the land-based survey component was threefold: (1) to provide an estimate of absolute abundance of northward-migrating humpback whale pods during the two weeks of the aerial survey (and thus allow calibration of the corresponding aerial estimates); (2) using the focal follow data, to provide estimates of whale migration speed; and (3) to provide estimates of mean pod sizes (since it was expected that these would be underestimated from the aerial survey).

Combining the results from the two components, estimates of the absolute number of northward-migrating whales passing through the survey area for each day of the aerial survey may be obtained. Fitting a model to these estimates (to allow prediction of the number of whales passing through the area on non-survey days, including those at the very beginning and end of the expected period of northward migration), and integrating the fit throughout the migration period, yields an estimate of absolute abundance of northward migrating whales.

Modelling the aerial survey data to obtain relative density estimates

Note that in what immediately follows, 'density' refers to 'relative density', since no account for perception nor availability bias has been made (i.e. in this section, $g(0)$ is assumed to be equal to one).

For each flight, pod density is estimated using a spatial generalised additive model (GAM) similar to the 'count model' of Hedley and Buckland (2004). The response variable of the model is the number of pod sightings per 'segment' of the transect, where the segment length must be specified but should be selected such that sighting conditions (and geographic location) do not change appreciably within a segment. An offset variable is included in the model to account for differences in estimated probabilities of detection within each segment, and consequential potentially different effective search areas of the segments. The offset is estimated using multiple covariate distance sampling – single platform line transect estimation but with the ability to include covariates (such as sea state) in the scale parameter of the detection function (Marques and Buckland, 2003).

With a logarithmic link function, the general form of a GAM of this type may be written:

$$E[n_i] = \exp\left\{ \log(2l_i w \cdot \hat{p}_i) + \sum_k f_k(z_{ik}) \right\},$$

where E$[n_i]$ is the expected number of sighted pods in the i^{th} segment (assumed to follow a Tweedie distribution); l_i is the length of segment i; w is the perpendicular (right-) truncation distance; $\hat{p}_i$ is the estimated probability of detection of a pod in segment i; z_{ij}, $j = 1,\ldots k$ denotes the value of the j^{th} (spatial) covariate in the i^{th} segment; and the f_k are (smooth) functions. Extending this form, it is feasible for a function f_j to depend on more than one covariate (e.g. $f\,(lat_i, lon_i)$), and/or for the covariate to be temporal (e.g. Day).

Hedley and Buckland (2004) suggested that variance from a spatial model of this type may be estimated using an appropriate resampling scheme such as a non-parametric or parametric bootstrap. In practice, these bootstrapping techniques frequently give biased results when smoothing models. Wood (2006, p.246–7) proposed an alternative approach which can be much simpler to implement, and appears not to suffer from the bias often associated with the bootstrapping approaches. This approach uses a ‘prediction matrix’ to map the model parameters to the predictions of the linear predictor, in conjunction with simulation from the posterior distribution of the parameters. The analysis in this report uses Wood’s (2006) approach, conditioning on the estimated smoothing parameters.

The offset in the model above includes an estimate $\hat{p}_i$, of the probability of detection. We propagate the uncertainty by explicitly accounting for variability in $\hat{p}_i$ in the spatial model (Williams *et al.*, 2011).

Estimating mean pod size

Results from other studies have shown that aerial survey pod size estimates can be negatively biased, since the animals are in view only for a relatively short period of time. In contrast, some pods sighted from the land station could be tracked for over an hour, although such pods would tend to be those migrating closer inshore so may not necessarily be representative of all migrating pods.

In order to estimate mean pod size, we compared three methods: (a) the mean size of pods sighted from the land-based station within 12km; (b) the mean size of pods sighted within 0.7km of the trackline from the aerial survey; and (c) truncating at 0.7km as for method (b), a spatial model for estimated pod size was fitted to examine variation in pod size within the survey region. For method (a), 12km was selected as a truncation point beyond which recorded pod sizes were considered less reliable. For methods (b) and (c), 0.7km was selected as a truncation distance within which pod size did not affect detectability (i.e. to eliminate potential ‘size bias’ effects).

Estimating abundance from the land-based survey data

Within the visible range of the land-based observers (here, up to 12km offshore), the number of northward-migrating whales passing the land station per watch period (where a ‘watch’ is defined as a three hour period within a day, say) gives an estimate of their rate of passage. Using the double-platform data from the first survey week, logistic regression (Buckland *et al.*, 2001; 1993) may be used to estimate the proportion of whale pods missed. Three correction factors for pods missed are estimated, depending on the mode of survey operation at the time (i.e. ‘Car’ Platform only, ‘Bush’ Platform only, or Double Platform). It is assumed that the probability of detection of a pod from one platform is independent of whether it is detected from the other, and independent of whether other pods are detected by either platform. Detection probability may be modelled as a function of covariates. The counts from each watch are then adjusted according to the mode of survey operation. Summing, and standardizing for different hours of effort, daily estimates of pod abundance may be calculated. The estimates correspond to the survey region in view from the land-based station only.

RESULTS

Use of the aerial data

Prior to analysis, transect line lengths were calculated from the GPS positional data using *R* code adapted from Visual Basic Geofunc functions (J.L. Laake, National Marine Mammal Laboratory, USA). Corresponding formulae are given in Zwillinger (2002). Heading angles were corrected for aircraft drift angle, and perpendicular distances (x) to sightings were calculated using the following simple tangent formula (e.g. Pike *et al.*, 2008):

$$x = h(\tan(90 - \theta))\sin(\varphi),$$

where h is altitude; θ is declination angle to the sighting; and φ is drift-correcting heading angle.

During the aerial survey, the swimming direction of sighted pods was recorded where possible. Since the objective of the survey is to obtain estimates for the northward-migrating component of the population only, then the swimming direction is critical. Out of 855 pods with either a swimming direction recorded, or designated as ‘milling’, then 571 (67%) of these were recorded as travelling northwards (where NE and NW were classified as North). In total, 1,357 humpback (including ‘possible’ humpback) pods were recorded whilst on effort and 42% of these were recorded as travelling northwards. As in Paxton *et al.* (2011), humpbacks with no direction recorded (and not milling), were randomly allocated a swimming direction according to the relative proportions of directions observed on a given flight. This increased the sample size considerably to 920 northward-migrating whales (seen on effort). Hereafter, we analyse the data for whales recorded as travelling north (NM whales) separately from a dataset of NM whales augmented by sightings with unknown swimming direction, but randomly allocated to be travelling northwards (NM+ whales).

Detection function estimation: aerial data

Two aircraft were used on the aerial survey: the Partenavia, fitted with bubble windows, and the Cessna, with flat windows. Angles of declination taken from each aircraft suggested that strips of about 80m (40m either side of the trackline) and of about 260m were obscured from the view of observers immediately beneath the Partenavia and the Cessna respectively. Histograms of perpendicular distances suggested that some pods were being missed beyond this strip for the Partenavia, perhaps because it was uncomfortable for the observers to look down at such an angle. The problem was alleviated by extending the left-truncation distance to 260m for both aircraft; thus about 6% of the sightings were excluded from further analysis (see Table 1).

Initial exploratory analyses of the NM aerial line transect data were conducted in Distance v5.0 (Thomas *et al.*, 2010), and model selection for both NM and NM+ whales was based on these analyses. Potential factors or covariates included Cloud cover, Sightability, Side of Aircraft (Port/Starboard), Sea state, Wind speed, Observer, Pod size and Aircraft. The detection function was modelled as a function of perpendicular distance, and these variables were considered for inclusion via the scale parameter of this function (either a hazard-rate or a half-normal form). The perpendicular distance data were right-truncated at 3.0km for NM whales and 4.5km for NM+ whales. A stepwise forward selection procedure (starting with a model containing perpendicular distance only) based on Bayes' Information Criterion (BIC) was used for model selection.

For both NM and NM+ pods, the model selected by BIC alone would have included Pod size. However the fitted detection function from such a model was such that estimated probability of detection decreased as pod size increased, counter to expectation. For NM+ pods, the BIC also suggested a model including Sightability was better than a perpendicular-distance-only model. Similarly to pod size, however, probability of detection was estimated to be lower in 'Excellent' conditions than in 'Good' and 'Poor' conditions. The other covariates were not found to significantly improve upon a perpendicular-distance-only fit, and so in the absence of an explanation for the relationship between Detectability and Pod size, or between Detectability and Sightability, half-normal models of perpendicular distance only were fitted to both the NM and the NM+ data. Fitted detection functions are shown in Fig. 2. Estimated effective strip half-widths were 2.05km (± 0.088) and 2.46km (± 0.084) respectively.

Mean pod size estimation

Pods seen from the land-based survey ranged in size from 1–6 whales, with most groups sighted as singletons or pairs. During the Double Platform component of this survey, only about half of the pod sizes recorded was in agreement between the two platforms. Estimated mean pod size from the land-based survey varied from about 1.7 (±0.084) to 1.85 (±0.056), depending on the subset of data selected.

As for the land survey, most pods sighted from the air were of 1 or 2 whales; pod size ranged from 1–8. No spatial or temporal trend in pod size was detected from the aerial data, and there was no evidence of 'size bias'. In fact, as noted above, any effect of pod size on detectability appeared to be in the 'wrong' direction. Mean pod size from the aerial data was estimated as 1.80 (±0.043) for NM whales. The point estimate for NM+ whales was considerably lower at 1.64 (±0.032), but this is perhaps not surprising, since this dataset includes pods for which a swimming direction was not recorded, and presumably pod size would also be more difficult to ascertain for such pods also (and would tend to be under-estimated). Note therefore, that in this analysis for both NM and NM+ estimates, the mean pod size of 1.80 was considered most appropriate and used for all conversions from pod density to whale density.

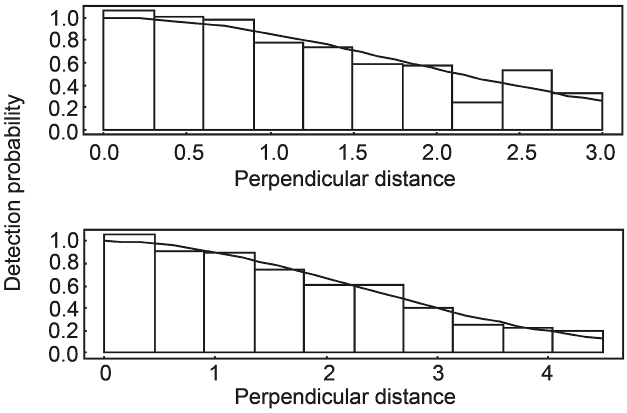

Fig. 2. Fitted detection functions (half-normal models) for aerial survey data. Perpendicular distances in km. NM pods: top panel. NM+pods: bottom panel.

Land-based survey

Sighting survey

Since sightings from the aerial survey extended far beyond the visible range of the land station, it was clear that an 'abundance' estimate from the land-based survey, even for the two weeks of its duration, would only represent a proportion of the migrating population. In this section, the estimate calculated corresponds to migrating animals passing within 12km of the shore. To use this estimate for calibration of the aerial estimates below requires abundance to be estimated for a corresponding region from the aerial survey (see 'Calibration of aerial survey').

To estimate the number of pods missed within 12km offshore during the land-survey, the double count data collected during the first week of that survey were fitted using logistic regression (Buckland *et al.*, 2001; 1993). In order to obtain a reasonable sample size, the model was fitted to NM+ data. Potential covariates were Team, Distance offshore, Sea State, Glare width, Wind speed, and Pod size, and interactions of the latter variables with team. The final model was selected by AIC using a backwards stepwise algorithm. The number of pods seen by at least one land platform was 74; this was reduced to 49 after truncation at 12km. Covariates selected for the untruncated data were team and the interaction term 'Team:Distance offshore'. When the data were truncated at 12km offshore, an additional interaction term 'Team:Pod size' was also selected. The number of pods seen on each watch period of the land survey was then adjusted according to the estimated correction factors (depending on which platform was operating) in Table 3. Since there was some daily variation in the number of hours of survey effort, the estimates were

Table 3

Estimated correction factors for numbers of pods missed from the land station.

Truncated at 12km			Untruncated		
Missed by both	Missed by Car	Missed by Bush	Missed by both	Missed by Car	Missed by Bush
1.032 (±0.026)	1.150 (±0.029)	1.297 (±0.033)	1.074 (±0.034)	1.262 (±0.039)	1.419 (±0.044)

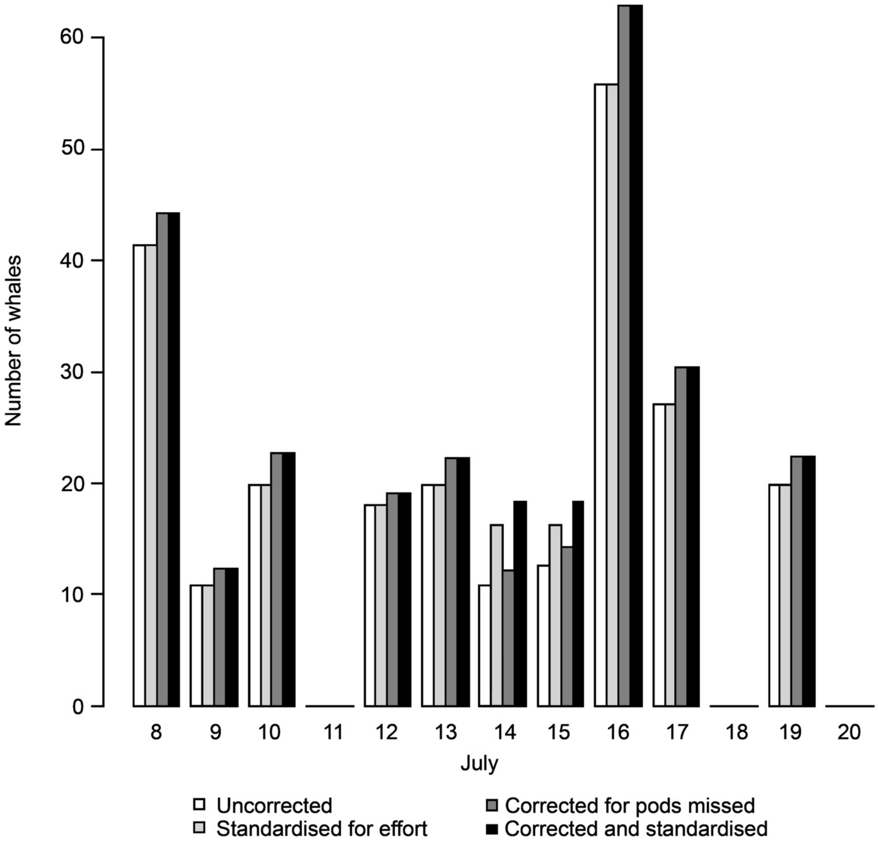

Fig. 3. Counts of number of whales passing the land station within 12km of the shore. 'Uncorrected' estimates are the raw counts; 'standardized for effort' adjusts the estimates to correspond to 9 hours of effort; 'corrected for pods missed' uses the correction factors in Table 3 (truncated at 12km) to adjust the counts.

also standardised by effort. Using a mean pod size estimate of 1.80, estimates for NM whales corrected and standardised to 9 hours per day are shown in Fig. 3. Data from 18th July, on which day there were 2.5 hours of effort, were excluded from the analysis. The total estimated number of pods was 154 (totalling 276 whales).

Focal follows

A total of 17 focal follows was carried out in week 2 (this small sample size was due to the amount of down time due to poor weather conditions). An additional 5 pods were focally followed in week 1, when the emphasis for two team effort was on obtaining double-platform count data. Pod compositions were 3 singletons, 11 pairs, 3 mother and calf groups, and one of each of a group of 3, 4, and 5 adults. The data are summarised in Table 4. As there was only a total of 22 focally followed pods, speed of travel, surfacing time and dive time were calculated averaging across all pod compositions. This assumption seemed quite reasonable for speed and dive time calculations; more variation across pod composition was evident in time spent at the surface (which includes time spent 'shallow diving', but for which it is considered that whales would still be visible from the air). The average speed of travel was calculated as 5.56km/h (±0.31); the mean proportion of time spent underwater was 0.43 and at the surface 0.57.

Spatio-temporal model of the aerial data

Transects covered on effort were divided into segments of length approximately equal to 10nm (18.5km), and the number of pods sighted in each segment was calculated. For each segment, an offset variable was computed as the logarithm of the effective area of the segment, where the effective area is given by twice the segment length multiplied by the estimated effective strip half-width from the detection function estimation described above. Potential spatial covariates were Latitude; Longitude and Bottom depth - sourced from a 1′ by 1′ grid from the US National Geophysical Data Center, NOAA Satellite and Information Service (*www.ngdc.noaa.gov/mgg/bathymetry*). In addition, Day or alternatively, Week (where Day 1 – and the first day of Week 1 – was defined to correspond to 2 June, the assumed start of the whales' northward migration period) were potential temporal covariates.

Model fitting and model selection were conducted in the mgcv package (Wood, 2008) available in R[1]. A number of forms for the smoothing components of the spatial models were considered, but none of these showed evidence for including Bottom depth in the model. Level of smoothing was determined by restricted maximum likelihood (REML); the final selected model was a tensor product smooth (Wood, 2006) of a two-dimensional thin-plate spline of Latitude and Longitude, and a thin-plate spline of 'Day'.

$$\log[E(\text{nsight}_i)] = \text{te}(\text{Latitude}_i, \text{Longitude}, \text{Day}) + \log(\text{estimated effective area}_i) + X$$

where $E(\text{nsight}_i)$ was assumed to follow a Tweedie distribution, with index parameter = 1.1; and te is a tensor

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[1] *R* Development Core Team. 2008. *R: a language and environment for statistical computing*. R Foundation for Statistical Computing, Vienna, Austria. ISBN: 3-900051-07-0 *http://www.R-project.org.*

Table 4

Summary of the raw focal follow data. Times are given as min:sec; rates are given per minute per whale.

Pod composition	Number of pods	Mean down time	Mean surface interval	Mean blow rate	Mean breach rate	Mean surface-active rate	Mean speed (km/h)
Singleton	3	03:23	09:04	3.11	0.189	0.313	3.96
Pair	11	04:31	04:52	2.14	0.062	0.122	5.74
Cow+calf	3	03:25	07:52	1.58	0.093	0.170	4.75
Multiple adult	5	04:02	08:47	1.95	0.036	0.117	6.63
Mean	-	04:06	06:45	2.11	0.073	0.147	5.56
SD	-	01:23	04:37	0.85	0.112	0.166	1.47

product of thin-plate spline smooths of Latitude and Longitude*,* and Day. The offset variable for the i^{th} observation, log(estimated effective area$_i$), was estimated using the effective strip widths estimated from the distance sampling analysis. X_i is a vector of first derivatives and was used to propagate variance, penalized according to the Hessian of the respective detection function fit (Williams *et al.*, 2011). Estimation of tail densities (before the first flight of the season and after the last) was improved by adding two zero counts to the data, one on 2 June and one on 7 September.

Integrating across the predicted density surfaces for each day within the assumed migration period gave snapshot estimates of abundance. To convert these estimates into daily estimates, the rate of passage through the survey area was estimated using an average speed of travel of travel of 5.56kmh^{-1}. The latitudinal width of the survey area was 86.7km, hence the snapshot estimates were multiplied by a correction factor equal to (5.56 × 24)/86.7 to convert them to daily estimates. (Estimated variance in speed of travel was not incorporated in the variance of the final abundance estimates.) Multiplying by the estimated mean pod size resulted in daily estimates of whale abundance, uncorrected for availability and detection bias (Fig. 4). Total relative abundance was 10,840 (8,640–16,860) for NM whales and 13,310 (11,010–18,840) for NM+ whales (Table 5).

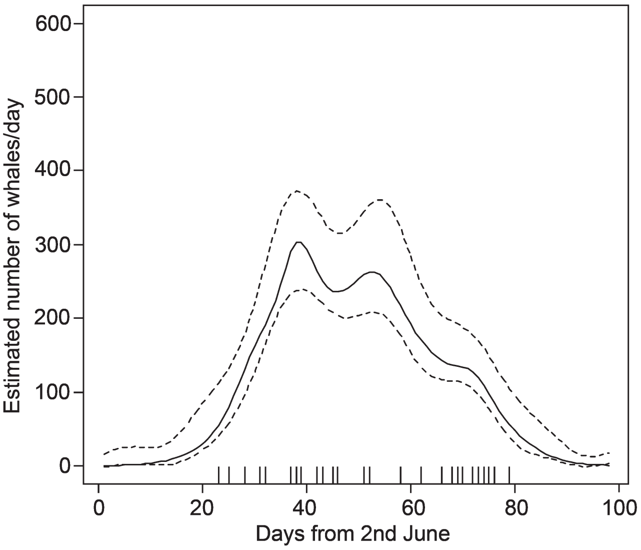

Fig. 4. Estimated whale abundance throughout the migration period from spatial modelling of aerial survey data. Dashed lines shows 95% percentile intervals obtained by simulating from the posterior distribution of the parameters of the fitted model. The intervals shown include variance in mean school size, but not in whales' migration speed. Rug plot (long ticks) along the x-axis shows days during this period on which flights were completed.

For illustrative purposes, a similar model with Week instead of Day was also fitted, yielding the plots shown in Fig. 5. These demonstrate how the distribution of whale pods varied during the course of the migration period. At the latitude of Cape Inscription, the estimated pod density as a function of distance offshore (averaged over flights during the two weeks of the land-based survey – i.e. weeks 7 and 8) is shown in Fig. 6. These plots indicate that density in week 7 increased gradually with distance offshore to a peak at around 30–35km offshore. During week 8, peak density was over a larger distance, at around 20–35km offshore. In both weeks, estimated density was very low beyond about 60km offshore. Within the region of the land-based station (lower panels of Fig. 6), the increase in density with distance offshore was slightly greater (and slightly more pronounced) during the second week.

Calibration of the aerial survey

From the land-based survey, we have two sets of estimates of pod abundance: $\hat{N}_{9L_1}$, $\hat{N}_{9L_2}$, ...$\hat{N}_{9L_{10}}$ for NM and for NM+ pods. (The subscript '9' denotes for the 9 hour period of a standard survey day; *L* denotes 'land-based survey' and these are for the 10 days for which there was at least 6 hours of survey effort.) Notwithstanding the difficulties in recording data from the land owing to the distances offshore at which many of the whales migrated, these estimates only correspond to the visible land-based survey region (here, assumed to be about 12km offshore).

From the aerial survey, we again have two sets of estimates of pod abundance, one set for NM pods and one for NM+ pods. These snapshot estimates are available not only for the days on which flights were flown, but by predicting from the spatio-temporal model above, also for any day within the assumed migration period. In order to use the land-based estimates for calibration of the aerial estimates, the calibration must correspond to the same survey region and over the same time period.

Since only about 15% of pods passed within the visible land-based survey region, the calibration approach adopted here is as follows:

(1) estimate 'snapshot' abundance for the seven 1′ by 1′ gridsquares at the latitude of Cape Inscription, for the corresponding ten days of the land-based survey;
(2) convert these to 9 hour estimates (using the estimate of speed of travel of 5.56km/h and a latitudinal width of 1.856km);
(3) fit a linear regression model (with no intercept) to estimate the slope of the regression of aerial estimates against land estimates; the slope is the calibration factor.

As would be expected, the calibration factor estimate varied substantially according to which subset of data was used for the calibration. We considered NM and NM+ pods

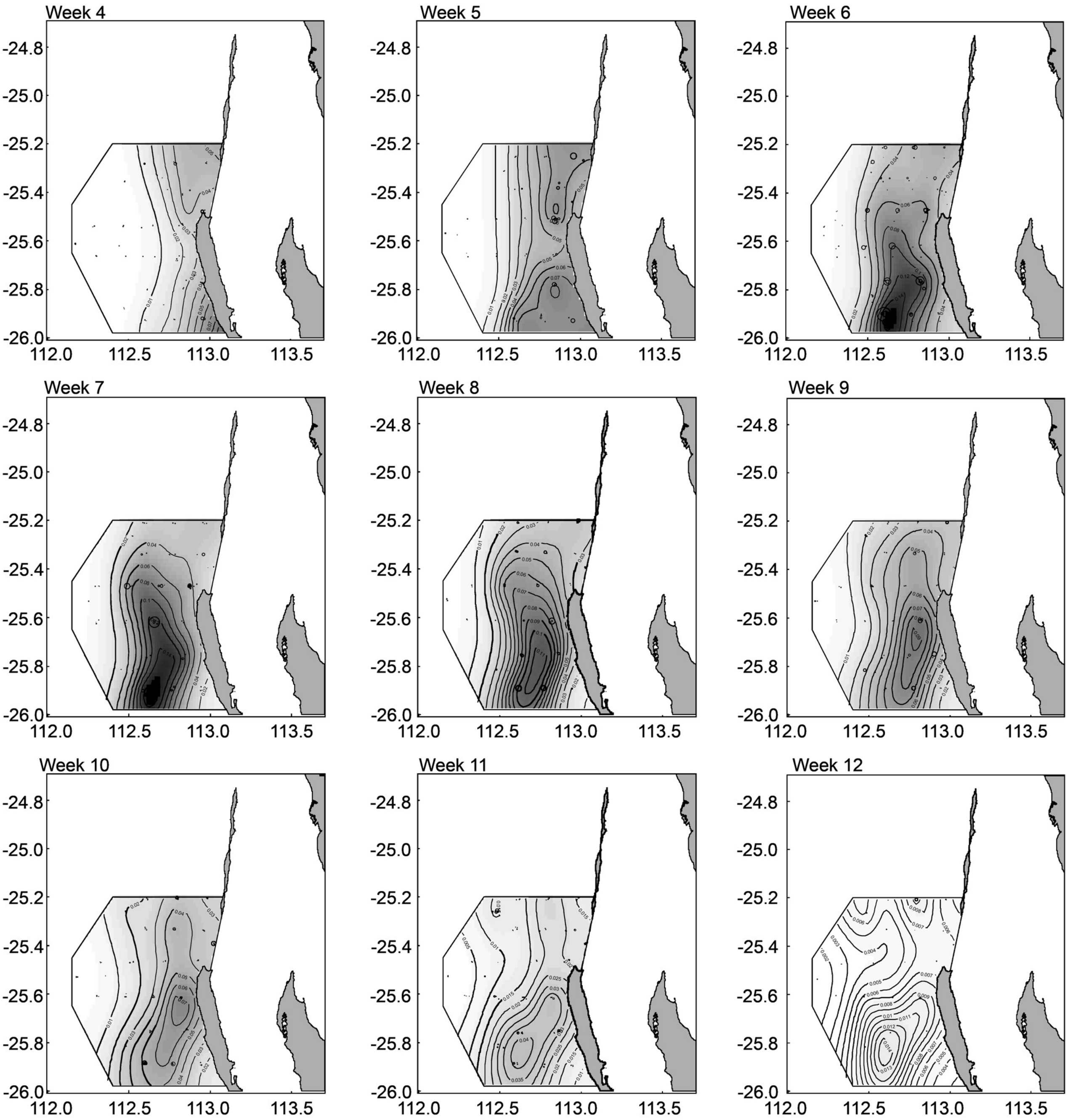

Fig. 5. Estimated spatial variation in NM pod density throughout the northward migration season, estimated from the aerial survey data. Weeks 1–3 and 13–14, all of which had relatively low densities, not presented here. Circles/dots represent 'data', i.e. weeks with at least one flight conducted (circles represent a segment with at least one sighting; dots represent no sightings in a segment). Week 2 corresponds to the w/c 9 June 2008. Week 12 corresponds to the w/c 18 August 2008.

separately, but took no account of possible differences in recording direction of travel between the two surveys. Because of the large number of land-based sightings that had no offshore distance recorded, a set of results was generated which included land-based sightings with offshore distances within 12km plus sightings with a missing offshore distance. This set of results gave an indication of the sensitivity of the results to the dataset used. The estimated total number of pods from the land-based survey increased by about 70–75%; the calibration factor went down by about 40–50%. The estimated calibration factors ($\hat{g}(0)$s) are shown in Table 5; applying these factors gives total whale abundance ranging from 17,810 (14,210–27,720) to 36,600 (30,520–52,250).

DISCUSSION

The estimates presented in Table 5 are very different, significantly so for the two rows of data which represent different subsets of the land-based data. The land survey was not particularly successful in providing a suitable 'calibration' for the aerial survey estimates, i.e. one that accounted for bias due to a lack of availability of diving pods and due to pods at the surface being missed. This is primarily due to the high proportion of animals that were beyond the range of the land-based observers, and so the overlap between the aerial survey – already for only a few days – was also spatially limited. Additionally, there may be some issues related to the different relative abilities of the aerial

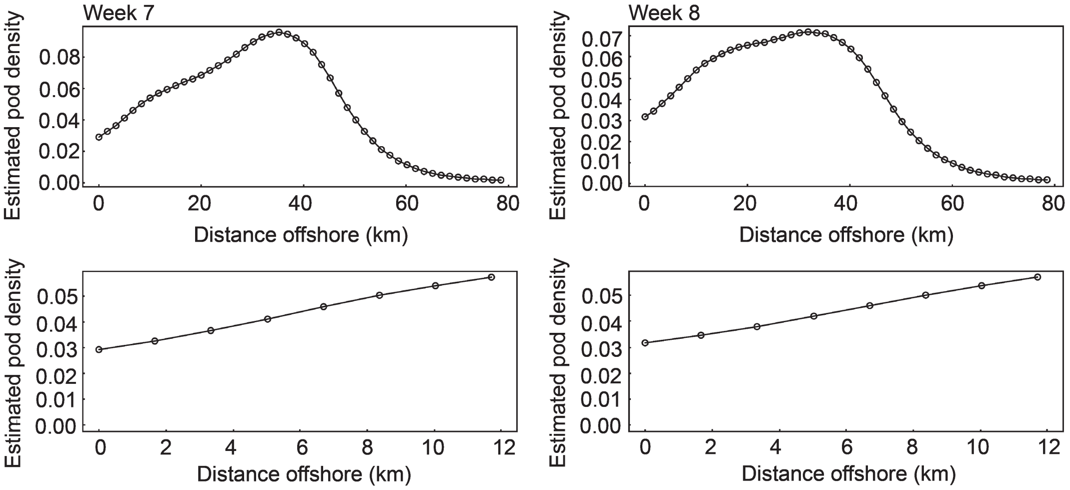

Fig. 6. Estimated pod density as a function of distance offshore (from Cape Inscription). Left panels for week 7 (w/c 8 July 2008); right panels for week 8 (w/c 15 July 2008). Upper panels show the estimated density from the shore to the western edge of the survey area; lower panels give this for the first 12km offshore only.

and land-based survey to identify the direction of a sighted pod. During the land-based survey, for pods sighted sufficiently closely for tracking purposes, recording direction was straightforward whereas for the aerial survey, determination of swimming direction was generally based on fewer cues over much shorter periods of time in view.

The primary objective of the 2008 survey was to obtain an estimate of absolute abundance of northward-migrating whales. Whilst we can be reasonably confident about the relative estimates presented in Table 5, there is wide variation in the absolute estimates as a result of substantially different estimates of $g(0)$. *A priori*, from previous analyses and studies elsewhere, estimates in the range 0.3–0.4 or so might have been expected, with such an estimate correcting for both availability and perception biases. It is therefore necessary to investigate further the reasons for the evidently much higher $\hat{g}(0)$ values reported here. The estimation method used by Paxton *et al.* (2011) estimated an 'availability curve' indicating the true (relative) density of pods with distance from shore. Within the region of the land-based observers, this showed a steady increase in density with distance offshore, up to a peak at around 10km. The detection function fitted to the distances offshore (using the land-based data) showed a very steady decrease in detectability with distance, based on a half-normal detection function. Differences between the two curves were used to correct the counts from the land-survey for pods missed from the land, and then $g(0)$ was estimated by comparing the aerial abundance in the region with the land-based abundance, over the two-week period of the land-survey in 2005. The correction factor applied to the land data for each day was about 1.5 (C.G.M. Paxton, pers. comm.) The data for the 2008 survey were markedly different from those obtained in 2005. Furthermore, they were very different even between the two weeks of the land survey duration (Fig. 7). The improvement to the design of the 2008 survey meant that the estimated number of pods missed from the land was able to be estimated from the double-platform effort during the first week of that survey, yielding correction factors by platform operation (see Table 3). The number of pods on which these calculations were based was 73 if the data were not truncated; it decreased to only 48 if the data were truncated at 12km. The estimates of Table 3 appear reasonably plausible compared with other studies of migrating populations, but if anything perhaps a little lower than might be expected, especially given the distances offshore at which the whales passed. If the estimates of Table 3 are in fact negatively biased, then the estimates of $g(0)$ would be lower (and abundance consequentially higher). Aside from the problems of the offshore distribution of the whales in 2008, the double-platform land-based approach to estimate the number of pods offshore would be preferable to the aerial-land calibration, since the data would be expected to be more reliable.

An alternative approach based directly on surface availability of pods (Barlow *et al.*, 1988) to estimate a $g(0)$ correction for availability bias was implemented in Bannister and Hedley (2001) in their analysis of the 1999 survey data:

$$P(\text{being visible}) = (s + t) / (s + d)$$

where s is the average time a whale stays at the surface; d is the average time spent below the surface (i.e. 'deep-diving'),

Table 5

Estimates of abundance for NM and NM+ whales. The large difference between rows depends on what portion of the land data are used in the calibration of the aerial survey estimates. 'Relative' estimates are uncorrected estimates from the aerial survey; 'absolute' estimates are those corrected by '$g(0)$' estimates from the land-aerial calibration. Numbers in parentheses are 95% percentile intervals; these do not include variance in $\hat{g}(0)$.

	NM whales			NM+ whales		
Land data, truncated at 12km	Relative	$\hat{g}(0)$	Absolute	Relative	$\hat{g}(0)$	Absolute
Missing distances excluded	10,840 (8,640-16,860)	0.61	17,810 (14,210-27,720)	13,310 (11,010-18,840)	0.59	23,060 (19,060-32,640)
Missing distances included		0.32	34,290 (27,340-53,350)		0.36	36,920 (30,520-52,250)

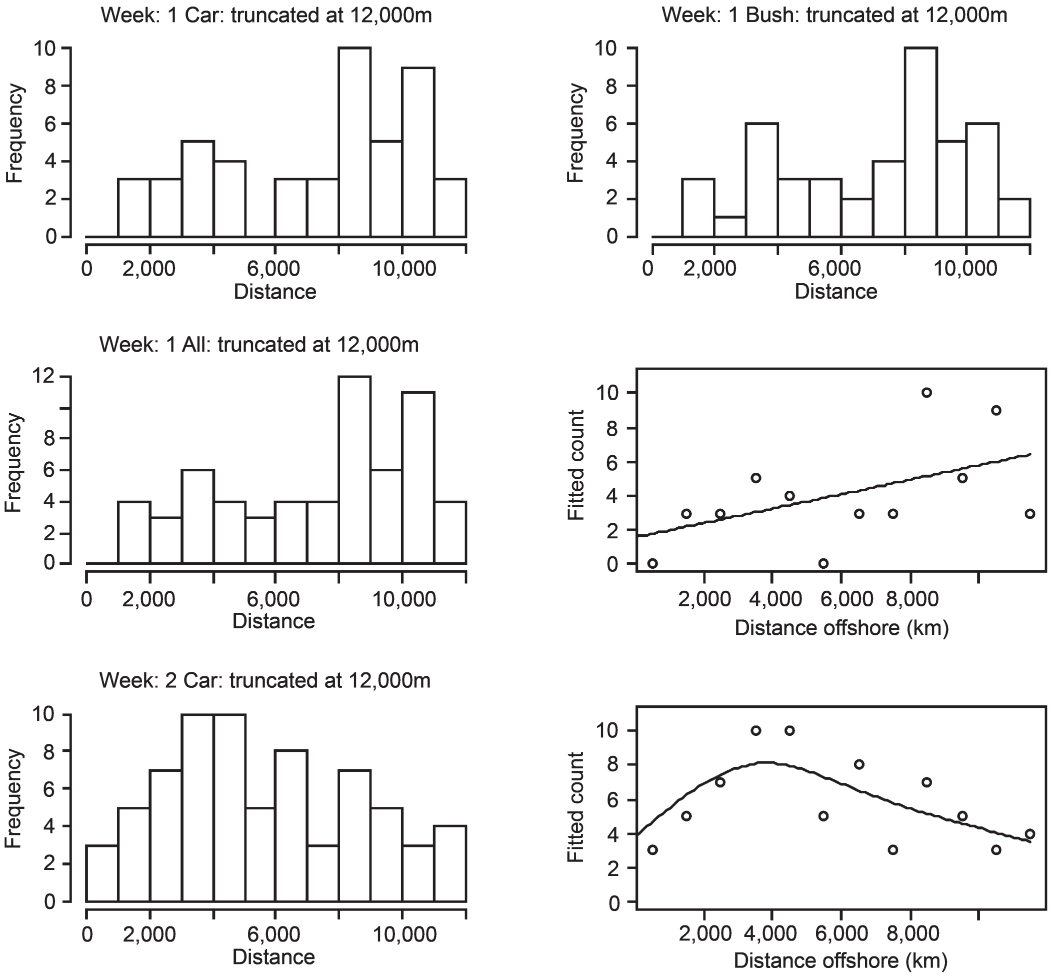

Fig. 7. Distribution of NM humpback whale pods with distance offshore, by platform and by week. Data have been truncated at 12km. (During the second week, only the 'Car' platform operated). Fitted curves are penalized regression splines with smoothing parameters selected by generalized cross validation (Wood, 2006; p130–133).

and *t* is the window of time during which an animal is within the visual range of an observer. A range of estimates for the values of *s* and *d* were made based mainly on observational data from experienced humpback whale scientists familiar with 'Australian' whales. A histogram of forward and aft distances was used to gain an idea of the time window, *t.* Ignoring the fact that two aircraft with rather different fields of view were employed on the 2008 survey, a similar histogram of distances to sighted pods is given in Fig. 8. This suggests that a maximum sighting 'window' can be estimated as about 8.5km, comprising animals seen ahead (generally up to 5.0km), abeam, and aft (up to 3.5km). These data suggest a rectangular sighting window of about 4.5km (estimated from a half-normal model). The focal follow data collected during the 2008 land-based survey were used to provide estimates of *s* and *d* of 405s and 246s (see Table 4). Average speed during the aerial survey was 132knots (244km/h). An estimate of *t* for a window of 4.5km is 66s, giving an estimate of $g(0)$ of 0.72 – again, much higher than from previous analyses. Estimates from this approach are fairly insensitive to quite large changes in window-width (for example values of $g(0)$ of 0.68 and 0.81 result from windows of 2.5km and 8.5km). The estimate of 0.72 is higher than those in the upper row of Table 5 (0.61 and 0.59) – i.e. those computed when sightings from the land-based survey with no offshore distance recorded were excluded. The former does not account for perception bias, however, so it would be expected to be higher than estimates from the combined survey approach which do.

The $g(0)$ estimates in the bottom half of Table 5 are some 40–50% lower than those in the upper half, but are more in line with our *a priori* expectation. These estimates are derived from land-based estimates which included sightings for which no offshore distance was recorded. This would most certainly mean that 'too many' pods were included in the land counts, especially since one of the main reasons for a missing offshore distance was difficulty in acquiring two theodolite fixes of the same pod. Even beyond 8km, whales were sighted on the horizon. Therefore at least some of the pods with missing distances would be expected to be within 12km offshore.

A second objective of the 2008 survey was to compare results with the 1999 and 2005 surveys. Previous analyses had estimated relative abundance of whales over a similar migration period to that assumed here as 3,441 for 1999 (Bannister and Hedley, 2001) and about 22,500 × 0.268 = 6,030 for 2005 (Paxton *et al.*, 2011; Table 2, results set 13) – an estimated increase rate of 9.8% per annum. The estimate of 10,840 presented here would represent an implausible rate of increase of 13.6% from the 1999 estimate; this rate is even more implausible were it based on only the 2005 estimate. Paxton *et al.* (2011) retrospectively applied a correction from their paper to the 1999 estimate to estimate absolute abundance of northward-migrating humpback whales as

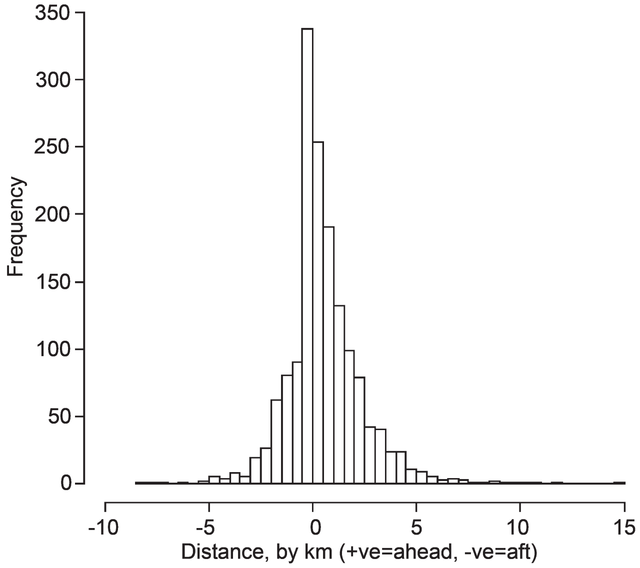

Fig. 8. Fore, abeam and aft distances from the aerial survey data.

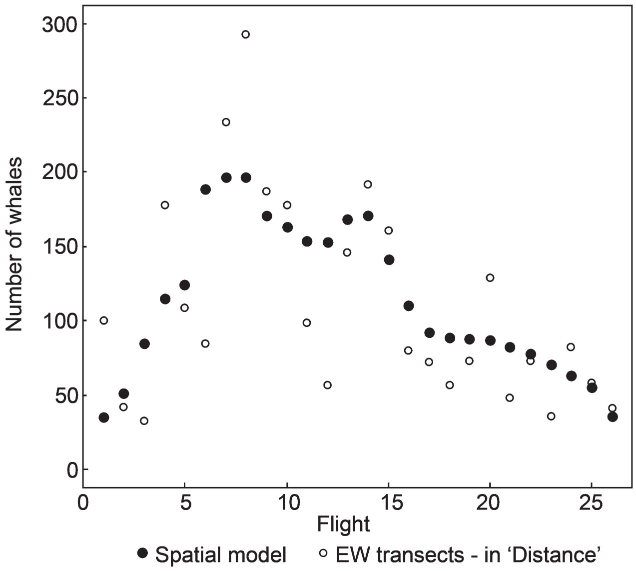

Fig. 9. Point estimates of abundance of humpback whales from each flight. Estimates from E–W transects are from a conventional line transect analysis in Distance; spatial model estimates are from the spatial model fitted in this report.

11,500 (95% CI 9,200–14,300) which fell within the range of 8,207–13,640 broadly estimated by Bannister and Hedley (2001) . This compares with 22,500 (10,000–72,200) from the 2005 survey. (Note: The estimate of 22,500 was not considered the 'best' estimate of abundance by Paxton *et al.* (2011) since they considered that extrapolation beyond the last flight of the aerial survey was unreliable due to a presumed 'second pulse' in the migration curve. It is used in the comparisons here as the estimate which best corresponds temporally to the 1999 and 2008 migration periods.) The corresponding estimates from the present analysis are 17,810 (14,210–27,720) or 34,290 (27,340–53,350). The latter represents an estimated rate of increase of about 12.9% (CV = 0.20) given an estimate of 11,500 in 1999, or about 15.1% (CV = 0.53) given an estimate of 22,500 in 2005. Given the conclusions of the Hobart Workshop on the Comprehensive Assessment of Southern Hemisphere Humpback Whales (IWC, 2011) that a rate of increase of 12.6% was biologically implausible, these estimated rates of increase are questionable. It is our belief, however, that the analysis in this paper is sufficiently robust that the point estimates of abundance obtained for the 2008 survey are reasonable. Clearly an infeasibly high rate of increase can result from initial abundance estimates being too low, as well as current estimates being too high.

Separate from the $g(0)$ estimation issue, is the question of the robustness of the estimates obtained from spatial modelling of the aerial survey data. Therefore, as a sensitivity test to the spatial modelling approach adopted for analysing these data, we compared the spatial modelling estimates (uncorrected for rate of passage and for $g(0)$) to those from a conventional line transect analysis in Distance (Thomas *et al.*, 2010). Data used in the spatial modelling included all on-effort data; only data from the main E–W transects were used in the design-based line transect analysis as was done previously (Bannister and Hedley, 2001; Paxton *et al.*, 2011; results sets 5 and 6). The results are shown in Fig. 9. It can be seen that the estimates from the spatial model are quite comparable to those from a standard line transect analysis, the main difference being that variation in encounter rate has been 'smoothed' out, as would be expected. Thus, there is no suggestion of anything untoward in the relative estimates presented in Table 5.

In conclusion, we propose that the best estimate for NM whales from the 2008 survey is 34,290 (27,340–53,350). The caveat to this that some of the land-based sightings from which the estimate of g(0) was derived would have been beyond the truncation distance of 12km offshore, so the analysis is not strictly consistent. However, a $\hat{g}(0)$ of 0.33 is perhaps rather more plausible than the alternative of 0.63 when those sightings were excluded. On the other hand, the higher $\hat{g}(0)$ is compatible with the estimate obtained by directly estimating surface availability (Barlow *et al.*, 1988). Since focal follow data were collected on this survey to estimate surfacing and diving times directly, there appears to be no obvious reason to discount these higher estimates, other than they are much higher than those obtained on previous aerial surveys. Therefore, we would also advocate a conservative estimate of 17,810 (14,210–27,720) for this population, until these issues have been resolved.

A similar argument applies for the estimates of NM+ whales (Table 5). When a proportion of unknown-direction pods are included in the analysis, the abundance estimates increase (by about 23% in the case of relative abundance) compared to the corresponding NM estimates. These estimates are presented here as a sensitivity to the main NM analysis, for which comparisons across the three surveys are currently more reliable.

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Group IV humpback whales: their status from aerial and land-based surveys off Western Australia, 2005

CHARLES G.M. PAXTON*, SHARON L. HEDLEY+ AND JOHN L. BANNISTER#

Contact e-mail: cgp2@st-andrews.ac.uk

ABSTRACT

Single platform aerial line transect and land-based surveys of Southern Hemisphere Group IV humpback whales were undertaken to provide absolute abundance estimates of animals migrating northward along the western Australian coast during June–August 2005. The aerial survey was designed to cover the whole period of northward migration but the resulting estimates from that survey alone could only, at best, provide relative abundance estimates as it was not possible to estimate $g(0)$, the detection probability along the trackline, from the data. Owing to logistical constraints, the land-based survey was only possible for a much shorter period (two weeks during the expected peak of the migration in mid-July). This paper proposes three methods that utilise these complementary data in different ways to attempt to obtain absolute abundance estimates. The aerial line transect data were used to estimate relative whale density (for each day), allowing absolute abundance from the land-based survey to be estimated for the short period of its duration. In turn, the land-based survey allowed estimation of $g(0)$ for the aerial survey. Absolute estimates of abundance for the aerial survey were obtained by combining the $g(0)$ estimate with the relative density estimates, summing over the appropriate number of days. The most reliable estimate of northward migrating whales passing the land station for the period of the land-based survey only was 4,700 (95% CI 2,700–14,000). The most reliable estimate for the number of whales passing through the aerial survey region for the duration of that survey (55 days from June through to August) was 10,300 (95% CI 6,700–24,500). This is a conservative estimate because the duration of the aerial survey was almost certainly shorter than the period of the migration. Extrapolation beyond the end of this survey was considered unreliable, but abundance from the estimated start of the migration to the end of the survey (87 days from mid-April to August) was estimated to be 12,800 (95% CI 7,500–44,600). The estimated number of whales depends crucially on the assumed migration and period of migration. Results for different migration parameters are also presented. The point estimates of abundance, whilst higher than those from a previous survey in 1999 (when adjusted for survey duration) are not significantly so. The peak of the whales' distribution was found at c.90m water depth.

KEYWORDS: HUMPBACK WHALE; MIGRATION; ABUNDANCE ESTIMATE; SOUTHERN HEMISPHERE; METHODOLOGY; LINE TRANSECT; SURVEY–COMBINED; MODELLING; TRENDS

INTRODUCTION

Between 1976 and 1994, a series of aerial surveys was flown at intervals off Shark Bay, Western Australia (WA), to provide information on possible increase in numbers in the Southern Hemisphere, Group IV, population of humpback whales (*Megaptera novaeangliae*). That population, summering mainly in the Antarctic between longitudes 90°E and 135°E, and wintering off the coast of western Australia, was severely depleted on two occasions in the twentieth century, 1934–39 and 1949–63 (Chittleborough, 1965). There were also some substantial but smaller catches from the population before 1934. By the end of 1963, when Australian humpback whaling ceased, the population was estimated to have been reduced to fewer than 600 animals (Bannister, 1964) from c. 7,800 in 1951 (estimates from mortality rates and catch per unit effort by Chittleborough, 1965); at that time it was believed that prior to 1934, the population size might have been as high as 10,200 (from sightings in Chittleborough, 1965).

Following increasing reports of humpback whale sightings in winter off the western Australian coast in the early-mid 1970s, aerial surveys of animals during their northward migration were undertaken from Carnarvon WA (24°52'S, 113°38'E) in an area off Shark Bay where aerial spotter and other data from whaling operations were available for 1963, the last year of humpback whaling.

Results of those surveys to 1988 (Bannister *et al.*, 1991) demonstrated that significantly more whales were seen in the area in the 1980s than in 1963. Further surveys, in 1991 and 1994, demonstrated an annual increase rate of 10.15±4.6% to 1994 (see Bannister and Hedley, 2001). In comparison to the estimated population size of 568 at the end of 1963 (Bannister, 1964), the population size in 1994 was calculated to be some 4,000–5,000 animals (Bannister, 1995).

The 1994 survey results showed that to detect a significant difference in population in future years, at an annual increase of 10%, an interval of at least three years would be required between surveys, leading to a proposed further survey in 1997. Given funding constraints, that survey took place in 1999.

The aim of the 1999 survey was to provide a direct estimate of absolute abundance. It thus differed from its predecessors where only a relative index was required. It was planned to cover as much of the northern migration period as possible, with flights every other day over a two month period, from mid June–mid August. Given the prevailing generally poor weather conditions, only 18 of the 30 planned flights could be flown, of which only 15 were completed. Nevertheless allowing for animals missed while submerged, 1999 population size was estimated as 8,200–13,600 (Bannister and Hedley, 2001). Given the disappointing coverage, a further survey was planned to take place as soon as possible over the same period and area, but to include an additional land-based component. Only northward-migrating whales were of interest in that their migration was the one

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* *Research Unit for Wildlife Population Assessment, Centre for Research into Environmental and Ecological Modelling, University of St Andrews, The Observatory, Buchanan Gardens, St Andrews, Fife, KY16 9LZ, UK.*

+ *The Schoolhouse, Denhead, St Andrews, Fife, KY16 8PA, UK.*

c/o The Western Australian Museum, Locked Bag 49, Welshpool DC, WA 6986, Australia.

most completely covered by the planned survey period. This paper details the analysis of data from that further survey, which took place in June–August 2005 with the aim of estimating the size of the northward migrating population of Group IV humpback whales.

METHODS

Overview

Estimating whale abundance from stocks such as the eastern Pacific gray whale (*Eschrichtius robustus*) and the east Australian humpback whale, which typically migrate close to the coastline, has been conventionally conducted using land-based (dual-platform) migration counts (Buckland *et al.*, 1993; Noad *et al.*, 2011). For logistical reasons, a similar land-based survey of the western Australian humpback whale stock has not been possible, but funding was obtained to investigate the feasibility of augmenting an aerial survey (to cover as much as possible of the migratory period) with a short land-based survey at the peak of the migratory period. Thus, in 2005, an aerial survey off Western Australia was planned to cover the period from 20 June–20 August (as in 1999), and to follow the same track design (see Bannister and Hedley, 2001), but to be augmented by a land-based component originally planned for three weeks to coincide with the expected peak of the whales' migration. Data from this component of the survey were intended to be used to 'calibrate' the relative density estimates from the aerial survey, so as to gain a better understanding of absolute density. In this paper, three different calibration methods are examined (all of which utilise data from the two components of the survey) and discuss the relative strengths and weaknesses of each method are discussed.

Method A uses the land-based data to estimate the passing rate of humpback whales past the point of the station, and hence to provide an estimate of abundance for the period of the land-based survey. The aerial survey data are used to estimate a relative density surface, which is used to estimate the true local distribution of whales close to the land-based station (since this distribution cannot be assumed to be uniform). The aerial data are also used to extrapolate westward, beyond the visual range of the land-based observers.

Method B directly compares the estimated relative densities from the aerial and land-based surveys (in the same area), to provide a simple calibration of the aerial survey.

Method C uses the aerial survey data to estimate a conventional line transect estimate of surfacing whales (using data from the designed east-westerly oriented transects only). A correction factor to account for whales being unavailable for detection because they were diving is then applied to obtain an estimate of whale density. Surfacing and diving rates were obtained for this correction factor from focal follows made from the land-based station. Method C was applied for comparison with earlier surveys for which no land-based data (but some surfacing and dive time behaviour) were available.

Field methods

As in the 1999 survey, all aerial survey work was undertaken from a high-wing, twin-engine *Partenavia* P68B aircraft, under charter from Tropicair Services Pty Ltd, flying out of Carnarvon. The survey was originally planned to cover the area surveyed in previous years, approximately 80 n.miles × 30 n.miles immediately west of Bernier, Dorre and Dirk Hartog Islands on the western boundary of Shark Bay, i.e. between 112°30'–113°10'E and 24°46'–26°09'S, with transect lines between seven and eight n.miles apart (Fig 1). The land-based station was originally intended to be located on the west coast of Dirk Hartog Island for three weeks, but logistical difficulties meant that an alternative site (at Quobba, 24°29'S, 113°25'E, shown as a large circle in Fig. 1) had to be used. As a result, survey effort was shifted correspondingly northwards, with four legs off the southern part of Dirk Hartog Island being transferred to cover the area north of Bernier Island/Carnarvon, to include the Quobba area. On two occasions, the flight path was extended to the west opposite Bernier Island, in an attempt to check on the distribution of migrating animals beyond the normal search area. A GPS and onboard computer system were available to plot waypoints and record sightings details. Two observers, one on each side of the aircraft used a clinometer (industry standard *Suunto* PM-5/360PC) and an angle board to measure declination and horizontal angles to sightings. The aerial survey took place between 22 June (day 173) and 15 August 2005 (day 227).

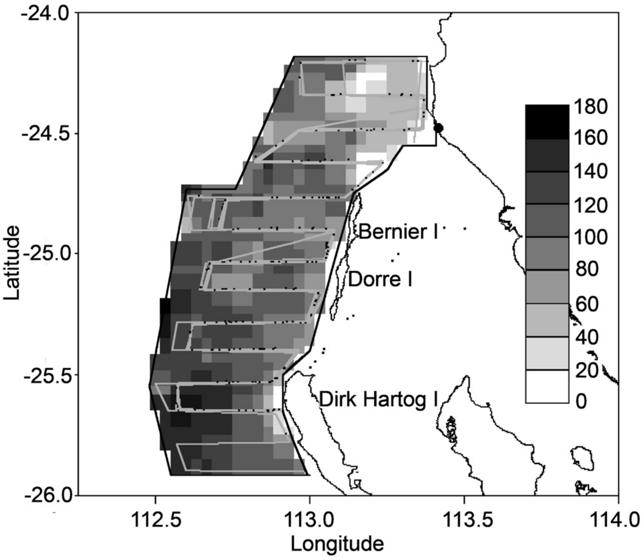

Fig. 1. Aerial tracklines over the entire survey period (grey lines), with locations of associated sightings (small black circles) of NM moving humpbacks at a 2km resolution. Land survey observation point is given by the larger circle situated on the coastline at about 24.5°S. Coloured area gives formal survey region with on effort sightings. Shading indicates depth in metres.

Additionally, owing to logistical constraints the land-based survey could only be conducted for a reduced period, namely the two week period from 9–22 July (days 190–203). The observation platform itself was located 1.22km inland. Surveying was carried out for up to 9 hours (8:00 to 17:00) each day with four observers on watch per hour, and was terminated if sea state reached 5 (wind speed 20–25 knots) or in the event of persistent rain. One observer continually scanned the south (190° to 260°) alternating between binoculars and the naked eye, a second did the same to the north (260° to 340°). The third observer operated a theodolite for bearings and declinations. The fourth observer operated the program 'Cyclopes' (see below; the program was developed by Eric Kniest, University of Newcastle, NSW), scanning the entire area when not recording data. A total of six observers was rotated on an hourly basis and none observed for longer than three hours without a break.

For accurate pod tracking, the theodolite was connected to a lap-top running 'Cyclopes'. Whales within a pod were located with the theodolite and the horizontal and vertical angles recorded. These were plotted on a map as icons linked to a data box, giving accurate distances and bearings of the pod from the observer station. The behaviour, pod composition, migration direction and other comments were filled in by the 'Cyclopes' operator. Pods were continually tracked as much as possible using the theodolite to eliminate the possibility of double counting pods. Other observer observations, not fixed by the theodolite, could be filled in as additional observations. Of special interest were the number of animals moving abeam, that is crossing an imaginary line of latitude extending from the land-based survey station, the speed of northern migration and dive time (the last two by reference to measurements made of a focal group of 26 pods). Weather was also recorded on an hourly basis, to include sea state, wind speed (knots) and direction, haze, cloud cover and visibility.

Further details of the survey design and methods are provided in Bannister *et al.* (2006).

Analysis methods

The methods described here were applied in an attempt to utilise the combined survey approach to correct for known biases. Conventional estimates from the aerial survey alone can only result in relative abundance estimates since $g(0)$ is typically less than one. Certain trackline detection (i.e. $g(0) = 1$) is an unrealistic assumption due to 'perception bias' (caused by a lack of detection of all whales at the surface) and 'availability bias' (whales are unavailable to be detected because they are submerged) as discussed *inter alia* by Marsh and Sinclair (1989). Conventional estimates from the land-based survey alone would likely suffer less from availability bias (since the fixed nature of and wide field of view from the land-observation point means that it is reasonable to assume that almost all whales passing the point would surface in view at least once) but a lack of conspicuousness of a surfacing whale or simply its distance from the observation point may preclude its detection, so perception bias (at least) should probably still be accounted for. However, because only single platform land-based data are available, we must assume that detectability is certain at some distance; the distance selected is zero perpendicular distance (i.e. at the shoreline). The combined operation allowed the three methods to be used to estimate the Group IV population and to correct for the above biases. All three methods utilised the results of the aerial survey so we began by using the aerial survey data to estimate a relative density surface (or 'spatial model') of whale pods in the survey region using the following modified version of the 'count model' (Hedley and Buckland, 2004; Hedley *et al.*, 1999), followed by the detailed descriptions of Methods A, B and C.

Aerial analysis

Transects covered during the aerial survey are divided into small 'segments', such that the sighting and geographic conditions do not change considerably within a segment. Unlike the single-stage count model noted above, a two-stage modelling approach is used for this survey, as implemented by Borchers *et al.* (1998). This approach may be considered when there is such a large proportion of segments with zero density that a single-stage analysis (with its associated distributional assumptions relating the variance to the mean) is clearly inappropriate. In the two-stage approach, the presence or absence of whale pods in a segment is first modelled using a logistic regression, and then the estimated number of whales in the non-zero segments is modelled separately, using quasi-likelihood estimation with variance proportional to the mean (see below for a discussion of the potential biases). Thus in the first stage the Bernoulli data were modelled as

$$E\left(\frac{p_i}{1-p_i}\right) = \exp\left(\theta_0 + \sum_k q_k(z_{ik})\right), \qquad i = 1,\ldots,T$$

where p_i is the probability that a whale is present in the i^{th} segment, θ_0 is the intercept parameter, the q_k are smooth functions of the k spatial covariates, z, and T is the total number of segments. The response variable for the non-zero data model is the estimated density of individuals based on the estimated number of individuals in each segment, $\hat{N}_i$, calculated using an estimator similar to the Horvitz-Thompson estimator (Horvitz and Thompson, 1952), as follows:

$$\hat{N}_i = \sum_{j=1}^{n_i} \frac{s_{ij}}{\int \hat{g}_{ij}(y,v)\,\pi(y)\,dy}, \qquad i = 1,\ldots,T$$

where, for each segment i containing at least one sighting, $\int \hat{g}_{ij}(y,v)\,\pi(y)\,dy$ is the estimated probability of detection (from a line transect analysis, see 'results') of the jth detected pod, n_i is the number of detected pods in the segment and s_{ij} is the size of the jth pod. By assumption, $\pi(y)$, the probability density function of perpendicular distances, is uniform.

Having obtained the estimated number of individuals in each segment, the estimated density, $\hat{D}_i$, is simply given by $\hat{N}_i/a_i$ where a_i is the area (twice the truncation width, w, multiplied by the length) of segment i. Non-zero pod density $\hat{D}_i$ (across segments with sightings only) was then modelled as a function of the k spatially referenced covariates, z, using a quasipoisson GAM with a log link function:

$$E(\hat{D}_i \mid \hat{D}_i > 0) = \exp\left(\beta_0 + \sum_k r_k(z_{ik})\right), \qquad i = 1,\ldots,T$$

where β_0 is the intercept parameter and the r_k are smooth functions of the k spatial covariates. For this method, only relative densities from the aerial survey data are required, so for estimation purposes, it can be assumed that $g(0)$ for the aerial survey is 1, and the procedure is valid so long as $g(0)$ does not vary spatially across the survey region. The area of interest in this case, however, is the region close to the land-based station; the spatial model provides an estimate (albeit a biased one) of the variation in true density in that region.

Sightings were allocated to these segments by reference to their time of observation. In addition to day (Dayofyear), the following spatially-referenced covariates were available for consideration for inclusion in the two-stage model: longitude (Lon); latitude (Lat); water depth (Depth)[1]; distance from eastern boundary of the survey (Disteastbound). Water depths were allocated to effort segments by finding the closest point in the bathymetry data to the midpoints of the effort segments using great circle distances. The bathymetry within the survey region is illustrated in Fig. 1. All covariates were considered for inclusion in the model as 1D smooths (thin plate regression splines) of the untransformed covariate values. In addition, 2D smooths (thin-plate splines, Wood, 2003) of Lat and Lon (suitably transformed) were considered for inclusion into the GAM. 2D and 3D smooths incorporating Dayofyear were also considered. Initially a maximum of six degrees of freedom (seven knots) was allowed in the selection of 1D smooths and up to 13 degrees of freedom (14 knots) were allowed in the case of 2D smooths, thus allowing moderate

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[1] Water depths were obtained from ETOPO2 2 minute resolution relief data available from NOAA (*http://www.ngdc.noaa.gov/mgg/global/seltopo.html*).

flexibility but reducing the likelihood of spurious fitting of unnecessarily complicated functions. In addition, the cost associated with fitting each degree of freedom was increased to 1.4 to minimise the risk of overfitting (Kim and Gu, 2004; Wood, 2006). Generalised cross validation (GCV) implemented in the mgcv package (Wood, 2001) in *R* was used for covariate selection, augmented with diagnostic plots, using the principles described in Wood (2001) to minimise the GCV with the extra criteria that a term must explain an additional 4% of the overall deviance or variance given other variables in the model and be associated with a significant probability of less than 5%. Owing to gaps in search effort along transects, effort could not always be split into segments of precisely 10km. Therefore, the area of each segment varied slightly around the mean of 100km^2 (= 10km × 2 × 5km) and so the models were weighted by segment area.

Method A: Adjusted land-based estimation

Sightings and catch data off WA suggest that northward-migrating whales are concentrated near the shore (Bannister and Hedley, 2001; Dawbin, 1966), with fewer animals seen further offshore. Thus, it is not reasonable to assume a uniform distribution of true abeam (or estimated-abeam) distances from the land-based station. In theory, however, distance sampling techniques can still be applied; the assumption that perpendicular distances are uniformly distributed needs to be modified to one that more closely represents the true distribution of whales from the shore. The program Distance (Thomas *et al.*, 2002) can then be used to fit a model to the abeam distances (with no monotonicity constraints). The resultant curve was a composite function, *f*(*x*), representing the variation in detectability with distance as well as variation in density. If it is then assumed that detectability is certain at zero distance, then this function can be rescaled to intercept the relative density curve (*d*(*x*)) at the shore. The composite, relative density and (unknown and inestimable) detection functions are related as follows:

$$f(x) = \frac{g(x)d(x)}{\int_0^w g(x)d(x)\,dx}$$

$$\therefore f(x) \propto d(x)g(x)$$

where *w* is the distance at which abeam distances are truncated. In fact, this is a slight simplification: in practice, the spatial model incorporates survey day as a factor, so that the estimated relative whale density can be estimated on a daily basis (to tally more directly with the daily land-based counts). The correction for absolute proportion of whales missed by the land station is estimated as

$$c_\kappa = \frac{\int_0^w g_\kappa(x)d_\kappa(x)\,dx}{\int_0^w d_\kappa(x)\,dx}$$

where the κ subscript denotes day. Note that the correction corresponds to the ratio of the areas under the two curves of Fig. 2. The corrected number of pods (P_κ) passing abeam per day within the visual region of the land-based observers (i.e. in a region truncated at *w* from the shore and excluding the land in this case) is then given by:

$$P_\kappa = c_\kappa \times r_\kappa \times 24$$

where r_κ is the number of pods per hour seen from the land-based station (within *w* of the shore) on day κ.

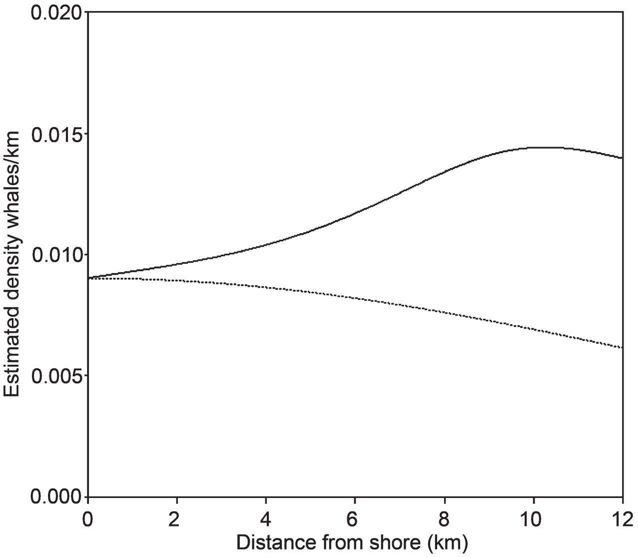

Fig. 2. The estimated availability function (estimated whale density; solid line) and land-based composite function (dashed line) for NM whales on day 190. The area under the solid line is proportional to the total number of pods at that latitude. The area under the dotted line is proportional to the total number of pods detected. The difference between these two areas represents the proportion of pods not seen and allows correction of the land-based estimates. Note: The predictor for the availability function (Depth) was smoothed to produce a smooth curve in the response.

This estimate was adjusted to account for whales passing beyond the visual range of the land-based observers (from the shore to 12km offshore) by considering the relative number of pods from the aerial survey within 12km of the shore to those in the region extending from the shore to the western edge of the survey region – see below).

Method B: Calibration of aerial survey

Allowing for the time taken for pods to pass through the survey area, daily estimates of relative abundance may be obtained from the predicted relative density surfaces (obtained as described in Method A). By reference to the days when the land-based survey and aerial survey overlapped, estimates of *g*(0) are obtained from the quotients of the daily land-based estimates of number of pods to those from the aerial survey (and thus a mean *g*(0) of the aerial survey could be crudely estimated), correcting for both availability and perception bias.

Method C: Availability at the surface from focal pod observations

An alternative distinct method of estimating *g*(0) is to construct an estimate from direct observations of diving pods made during the land-based survey. Bannister and Hedley (2001) estimated *g*(0) for aerial surveys of this population in 1999 using the following equation (from Barlow *et al.*, 1988):

$$P(\text{visible}) = \frac{s+t}{s+d}$$

where *s* = average time spent above the surface, *t* = window of time during which an animal is within the visual range of an observer and *d* is the average time below the surface. For the present analysis, we derived a modification of this estimator as:

$$P(\text{visible}) = \frac{s}{s+d} + \frac{t\left[1 - s/(s+d)\right]}{d_{\max}} \qquad \text{for } t > 0$$

where d_{max} is the maximum (observed) dive time. This assumes that if the whales are observed for a period of time greater than d_{max} then the animal will be observed if within the visual range of the observer. Using estimates of surfacing and diving times from focal studies on 26 pods conducted during the land-based survey, this estimator is used to provide estimates for the aerial survey which account for availability bias. Method C is applied in this paper to provide a comparison of results from other analyses (Bannister and Hedley, 2001) which also did not adjust for perception bias.

All three methods described above assume that the aerial survey covered the entire east-west width of the migration path. This may not be true (see below) in which case the resulting estimates represent an underestimate of the total number of whales.

Variance estimation

Variance was estimated using the non-parametric bootstrap (Efron and Tibshirani, 1993). Appropriate sampling units (assumed independent) are transect legs for the aerial survey and days for the land survey. This should ensure good bootstrap coverage for both surveys (samples are generated with replacement). Variance due to the migration speed of the whales was incorporated by sampling with replacement from the observed distribution of pod swimming speeds. Variance in surface availability for the $g(0)$ estimate derived from Method C is not readily incorporated – a weakness of the method.

RESULTS

Aerial data

Details of the aerial data are summarised in Table 1. Initially, all data available from north of 25.9°S outside the bay, i.e. to the west of the islands and up to 24.2°S (see Figs 11a and b, results sets 1–6;9–14, Table 2) were used in the analysis. The total usable aerial trackline length was 7,500km. There were 417 initially usable sightings of pods (mean size ± standard error, 1.81±0.04) within the entire aerial survey region; their locations are shown in Fig. 1. One aim of the survey was estimating the relative abundance of northward migrating (NM) humpback whales, and yet a 'northward migrating' whale is not easily identifiable in the field. Aerial observers recorded swimming direction; those recorded as swimming north (n = 178) formed the NM data subset. Whales of unknown swimming direction (n = 133) were randomly allocated a migration direction in proportion to the sightings of known direction on the same day. Those that were allocated a northerly swimming direction were added to the NM sightings and this formed a possible NM dataset (hereafter termed 'NM+'). The remaining sightings were either classified as swimming south (n = 96) or milling (n = 10). Examination of the distribution of perpendicular sighting distances suggested that some sightings close to the trackline were missed (Fig. 3), a feature of aerial surveys when, as for this survey, the aircraft is not fitted with bubble windows, so the data were left-truncated at 1km. The distance data also exhibited a long tail, with one sighting reported at over 25km which perhaps seems implausible. This sighting, along with others seen at over 6km from the trackline, were excluded from the analysis, resulting in a total of 303 sightings (of any swimming direction). Subsequent analysis was also performed on a data set from 25.9°S to 24.5°S (n = 224, see Figs 12a and b, results sets 7–8, Table 2). The former are here referred to as the 'main' data set (and grid) and the latter the 'southern' data set (and grid). Use of the southern data subset potentially reduced the chance of a milling pod to be misclassified as a NM pod.

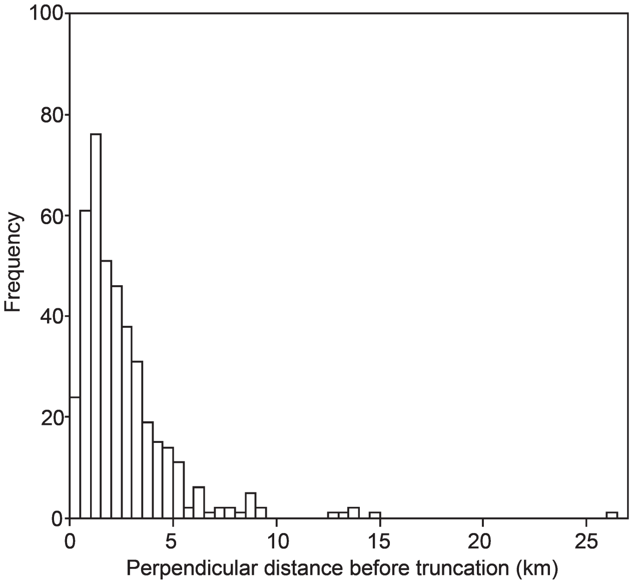

Fig. 3. Frequency distribution of horizontal perpendicular distances from the aerial survey of all on transect, in survey zone, sightings of humpback whales (n = 417).

Estimation of relative density from the aerial survey data (for Methods A, B and C)

First it was necessary to estimate the probability of detection of each pod sighted on the aerial survey. A multiple covariate distance sampling (MCDS) approach was adopted (Marques, 2001; Marques and Buckland, 2003) in which the effects of covariates (in addition to perpendicular distance) can be incorporated into the detection function via the scale parameter. Available covariates and factors were: Observer; Beaufort sea state; Cloud cover; Pod size; and Sightability.

A stepwise forward selection procedure (starting with a model containing perpendicular distance only) was used to decide which covariates to include in the model, as indicated by Akaike's Information Criterion (AIC). To determine the aerial detection function all available data in the survey region were considered regardless of recorded swimming direction.

Table 1

Sample sizes used in the survey. All available sightings were used in the detection function (n=303).

Data	Sightings (mean ± SE)	Pod sizes (mean ± SE)	Total number of segments	Segment area km^2 (mean ± SE)
Whole data set certain northern migrating whales (NM)	137	2.06 ± 0.08	749	100.70 ± 0.52
Whole probable northern migrating whales (NM+)	192	1.91± 0.06	749	100.70 ± 0.52
Southern data set certain northern migrating whales (NM)	116	2.07± 0.09	587	101.00 ± 0.59
Southern data set probable northern migrating whales (NM+)	155	1.94 ± 0.07	587	101.00 ± 0.59

Table 2

Estimates of abundance of western Australian humpback whales by various methods. All methods assumed a mean pod size of 2.051. Hourly migration was taken to be 5.35km/h. All aerial survey based models error estimates include a migration component unless otherwise stated. All aerial predictions based on a grid between –24.2° Lat and –25.9° Lat approximately apart from results sets 7–8.

Results set	Data set	Method	Detection/availability estimates and 95% confidence intervals	Date of time period [Days]	No. of days	Estimates and 95% confidence interval	Relevant figures
1	NM	A. Passing whales on land based survey. Relative abundance from aerial survey	Assumed land based $g(0) = 1$. Proportion of pods missed within the 12.5km truncation limit = 0.341. Proportion of aerial survey area at latitude covered by land based survey = 0.177.	9 Jul.–20 Jul.; 22 Jul. [190–201; 203]	12	5,500 (3,000–25,900)	Figs 7, 8 and 9
2	NM+	A. Passing whales on land based survey. Relative abundance from aerial survey	Assumed land based $g(0) = 1$. Proportion of pods missed within the 12.5km truncation limit = 0.342. Proportion of aerial line of latitude covered by land based survey = 0.211.	9 Jul.–20 Jul.; 22 Jul. [190–201; 203]	12	4,600 (2,700–14,000)	Figs 7, 8 and 9
3	NM	Aerial survey with $g(0)$ adjusted by reference to land based survey	Aerial $g(0) = 0.268$ (0.069–0.437)	27 Jun.–15 Aug. [173–227]	55	9,200 (5,700–34,000)	11a
4	NM+	Aerial survey with $g(0)$ adjusted by reference to land based survey	Aerial $g(0) = 0.310$ (0.125–0.492)	27 Jun.–15 Aug. [173–227]	55	10,300 (6,700–24,500)	11b
5	NM	Assumed uniform density from aerial survey (EW transects only) with $g(0)$ taken from focal pod observation	Aerial $g(0) = 0.279$	27 Jun.–15 Aug. [173–227]	55	7,200 (5,000–10,400)	
6	NM+	Assumed uniform density from aerial survey (EW transects only) with $g(0)$ taken from focal pod observations	Aerial $g(0) = 0.279$	27 Jun.–15 Aug. [173–227]	55	8,400 (6,100–11,400)	
7	NM	Aerial survey but predictions made across grid and from data to –24.5 Lat only	Aerial $g(0) = 0.279$	27 Jun.–15 Aug. [173–227]	55	10,000 (7,100–14,000)	12a
8	NM+	Aerial survey but predictions made across grid and from data to –24.5 Lat only	Aerial $g(0) = 0.279$	27 Jun.–15 Aug. [173–227]	55	12,700 (9,100–17,200)	12b
9	NM	Aerial survey with $g(0)$ adjusted by reference to land based survey	Aerial $g(0) = 0.268$ (0.073–0.437)	20 Apr.–15 Aug. [140–227]	88	9,400 (6,000–36,000)	
10	NM+	Aerial survey with $g(0)$ adjusted by reference to land based survey	Aerial $g(0) = 0.310$ (0.126–0.499)	20 Apr.–15 Aug. [140–227]	88	12,800 (7,500–44,600)	
11	NM	Aerial survey with $g(0)$ adjusted by reference to land based survey	Aerial $g(0) = 0.268$ (0.070–0.443)	11 Jun.–1 Sep. [162–242]	81	15,400 (8,500–56,500)	
12	NM+	Aerial survey with $g(0)$ adjusted by reference to land based survey	Aerial $g(0) = 0.310$ (0.100–0.500)	11 Jun.–1 Sep. [162–242]	81	15,500 (9,500–47,500)	
13	NM	Aerial survey with $g(0)$ adjusted by reference to land based survey	Aerial $g(0) = 0.268$ (0.081–0.439)	1 Jun.–8 Sep. [152–252]	101	22,500 (10,000–72,200)	
14	NM+	Aerial survey with $g(0)$ adjusted by reference to land based survey	Aerial $g(0) = 0.310$ (0.114– 0.496)	1 Jun.–8 Sep. [152–252]	101	19,400 (10,800–59,700)	

Further, to test whether detectability differed with recorded direction of movement, Direction was also considered as a factor in an analysis of a subset of the data where direction was known. All model selection was performed in Distance (v4.0, Thomas *et al.*, 2002), then the final selected model (a half-normal model with Observer fitted as a factor – see Fig. 4) was re-fitted using a set of unpublished customized functions in the statistical package *R v.2.2.1.* (Ihaku and Gentleman, 1996). This facilitated estimation of variance within *R* (see below). There was no evidence of detectability of whales varying with known direction of movement, nor was there evidence that pod size influenced detectability presumably owing to the lack of substantial variation in pod size. Therefore all sightings of whale pods within the truncation distance and survey area were considered to generate detection probabilities for subsequent analysis although only potentially northward migrating (NM+ or NM) pod sightings were used to estimate density. The same model was also fitted to the southern data set.

As described earlier, the number of sightings of NM pods was used to estimate a density surface for NM whales. Transects covered during the survey were divided into segments. Choice of segment length is a compromise between maximising the ratio of non-zero to zero segments, maintaining environmental resolution and giving some measure of spatial independence. We selected a segment length of 10km after some preliminary investigation of these aspects.

The final selected logistic model for presence-absence included two 1D smooths: Dayofyear (with 5 degrees of freedom) and Depth (with 5 degrees of freedom). Estimated probabilities of presence for each day are plotted against water depth in Fig. 5. The model explained about 8% of the deviance on the linear predictor scale in the case of NM whales and 5% in the case of NM+ whales. This was a binary model, so the explained deviances do not necessarily provide information about the agreement between the observations and the fitted probabilities (Collett, 1991; McCullagh and

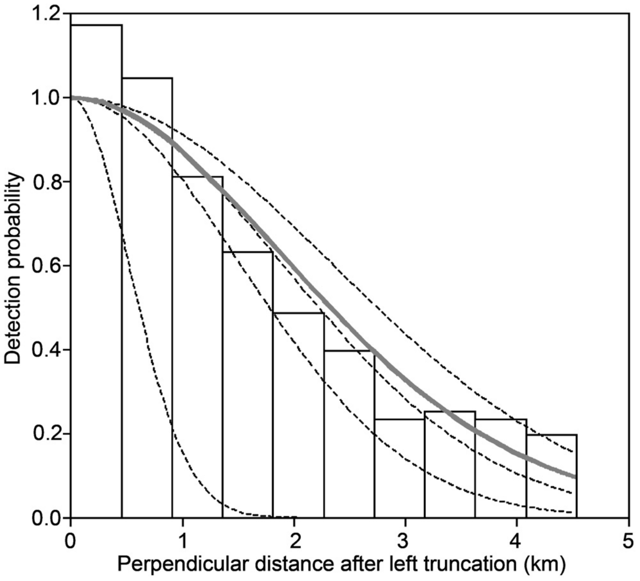

Fig. 4. Mean aerial detection function based on 303 humpback whale sightings between 1 and 6km apart. Dotted lines indicate the detection curves for individual observers. The solid line is the mean detection probability.

Nedler, 1989). For both datasets, extrapolation from the model suggested that there could be whales to the west of the survey area. The probability of humpback presence peaked at *ca* 90m water depth. The second stage of the density surface modelling used those segments of trackline in which sightings were made ($n = 112$, in the case of NM whales; $n = 156$ in the case of NM+ whales). In the case of the NM whales, the estimated along-trackline densities ($\hat{D}_i$) were between 0 and 0.165 whales/km^2 (mean: 0.008 whales/km^2). In the case of the NM+ whales, the estimated densities were between 0 and 0.182 whales/km^2 (mean: 0.010 whales/km^2). The estimated pod densities were not spatially correlated except possibly at very small distances (by inspection of a semi-variogram). Using a logarithmic link function and assuming that the variance of the observations was proportional to their mean, the best-fit model for NM whales included just one covariate – Depth (with 4 degrees of freedom) – and explained just 4% of the deviance. (Depth itself was non-significant both in the case of NM whales and NM+ whales, but according to other model selection criteria, such as GCV as outlined above, it was retained in the model.) Thus while water depth predicted pod presence it did not predict numbers of pods (although it was retained in the model for estimation).

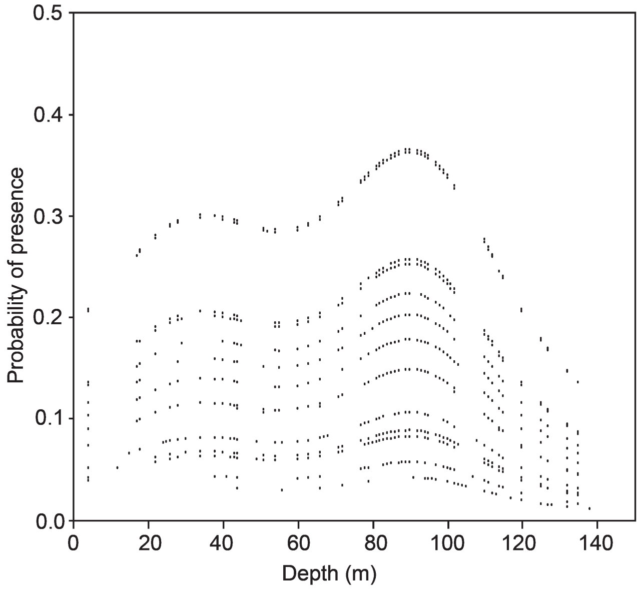

Fig. 5. Probability of presence of whale pods on different days (the separate curves) against depth.

Relative densities within the survey region were estimated for NM pods and for NM+ pods, based on the selected models for NM pods (Figs 11a and b), as products of the two predicted surfaces from the two-stage modelling. The region is bounded, therefore estimates should be considered as conservative because the survey does not appear to have covered the full longitudinal range of the whales' migration path. The corresponding estimated density surfaces within the smaller southern grid are shown in Figs 12a and b.

Prediction from the two-stage model throughout the survey region and across a range of days from day 100 (10 April) to day 230 (22 August) suggested that the peak day of the northern migration was day 191 (10 July). Extrapolation of the trend to the early part of the year suggested that there was negligible probability of the migration starting before April and that numbers only really started increasing in May. However such extrapolation assumes that the trend in pod numbers can be extended into the past and future. The model also predicted a second pulse in the northern migration from day 220 (12 August; see Fig. 6) for which there was only weak evidence from the data. We speculate that this is due to the poor temporal coverage achieved, resulting in little data to 'tie down' the tail of the migration period. An alternative approach would have been to assume a more traditional unimodal migration curve, and restrict the flexibility afforded to the GAMs accordingly.

Land-based survey analysis (Method A)

Having estimated the relative density surface within the survey region from the aerial survey data, it was assumed that this represented the shape of the true distribution of

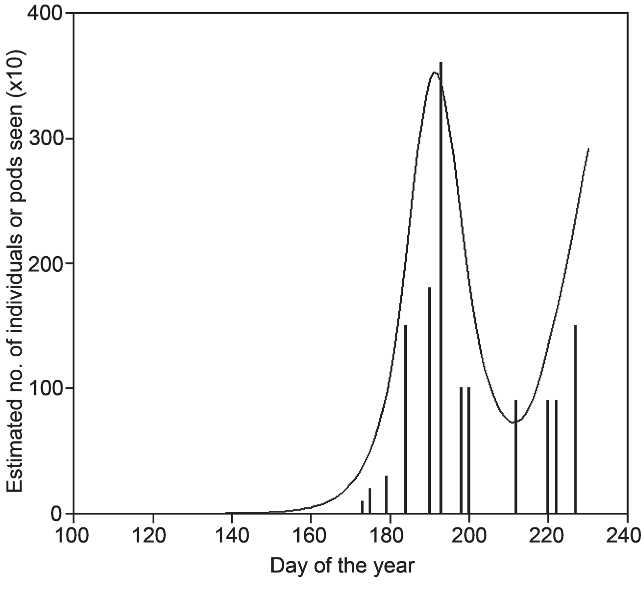

Fig. 6. Estimated number of available detected NM humpback individuals present assuming an instantaneous aerial survey of the shaded region in Fig. 2 from 10 April (day 100) to 22 August (day 230) (curve). Pod sightings per day (×10) are given as the bars. N.B. the (×10) is arbitrary to allow the data and the model predictions to be compared.

whales in the search region of the land-based observers. The land-based survey data were then used to estimate the 'composite' function of 'abeam' distance, x, from the shore; a function whose shape was determined by the decreasing detectability of pods with distance as well as varying underlying whale density. The land-based survey was undertaken from 9–22 July (days 190–203), but only one hour of effort was possible on day 202 (during which time no whales were seen); this day's effort was subsequently excluded from the analysis. Of 235 land-based sightings (mean pod size 1.62), 99 were classified as NM whales (mean pod size 1.79) of which 41 were actually seen abeam. Data were left-truncated at 1.22km (as the land station was located 1.22km inland) and right-truncated at 13.22km (to make estimation of the composite function more robust). The frequency distribution of distances to all 99 NM pods is given in Fig. 7; 93 of these were between 1.22 and 13.22km. The perpendicular distances were binned into 2km classes and the composite function of perpendicular distance from shore was fitted in *Distance,* allowing for the possibility of adjustment terms and with no monotonicity constraints. In addition, potential explanatory variables were Beaufort sea state (considered as continuous and as a factor), pod size and visibility (both continuous). The selected model was a simple function of perpendicular distance (Fig. 8). As detailed above, the hourly passing rates of NM pods (depicted in Fig. 9) were then adjusted to give estimates of the daily number of NM pods passing the observation point within 12km of the shore. The peaked distribution in time seen in the aerial survey data was not evident in these data, apart from a peak at day 199 (8 days after the aerial survey peak) presumably because of the limited time frame and paucity of sightings.

When this survey was planned, the land-based station was originally to be sited on the west coast of Dirk Hartog Island – a location where previous aerial surveys had indicated a relatively longitudinally-narrow migratory corridor (Bannister and Hedley, 2001), in which it was expected that the great majority of sightings would pass within the visual search region of the land-based observers. In the event, the land-based station had to be located at Quobba. However, even off Dirk Hartog Island further south (Fig. 1), the aerial survey data indicated that whales were distributed beyond the visual range of the land-based observers. Here, therefore, we use the ratio of estimated relative density curves at the latitude of the land station to estimate the total number of whales (to the western edge of the survey area, at 58.7km from the shore) passing the observation point during the period of the land-based survey as follows:

$$\frac{\int_0^{12} \hat{d}(x)\,dx}{\int_0^{58.7} \hat{d}(x)\,dx}.$$

The estimated NM mean pod size (2.05) from the aerial survey was then multiplied by the reciprocal of the above to obtain the estimated numbers of whales to the western edge of the survey area. Estimates were then summed over days

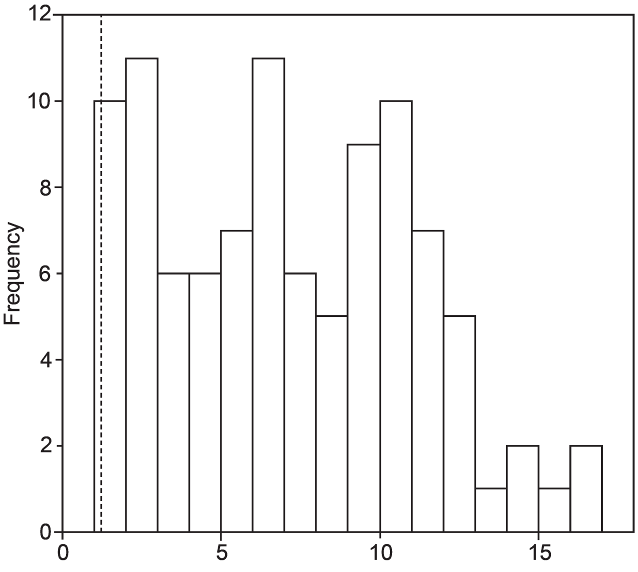

Fig. 7. Frequency distribution of horizontal distances to NM pods crossing either abeam of the land survey location or otherwise minimum distance to the shore ($n = 99$). Dashed line shows the shore line. Note: The lowest bar is artificially low as part of its bin region was in fact on shore.

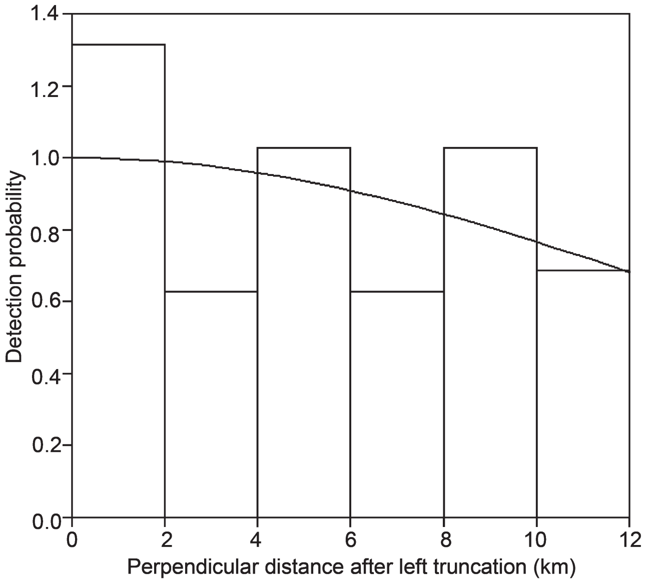

Fig. 8. Land-based abeam composite function for northward migrating whales ($n = 93$).

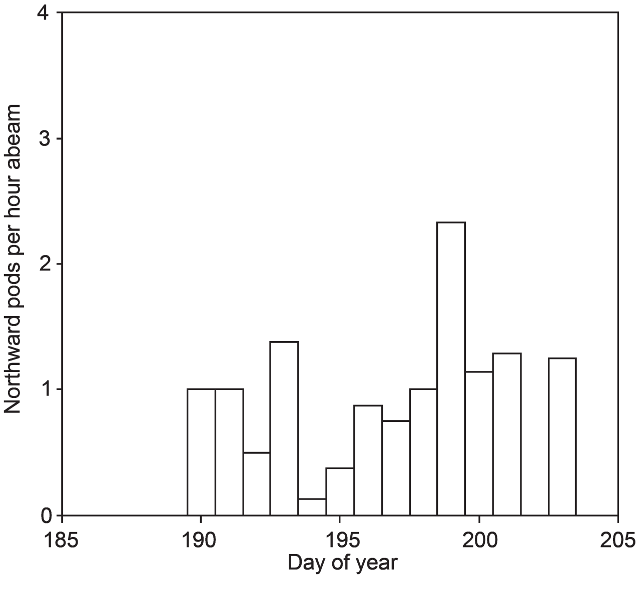

Fig. 9. Per hour passing rate for the land-based survey.

190–201 and day 203, to obtain an estimate of 5,500 NM whales (95% CI 3,000–25,900) during that period. The comparable estimate for NM+ whales was 4,600 NM (95% CI 2,700–14,000). Whilst the difference between these point estimates is not significant, it is somewhat counterintuitive (a consequence of the different GAMs in the two-stage density surface modelling). This suggests that alternative models for the density surfaces (perhaps using either zero-inflated models or the spatial models being developed by Bravington *et al*. (2008)) should be investigated in future.

Land-based behavioural analyses (for Methods B and C)
Estimated migration speeds (for Method B), diving and surfacing rates (for Method C), were derived by data from following 26 focal pods during the land-based survey. The mean observed migration speed was 5.35kmh^{-1} (SE = 0.58). The 26 focal pods were observed for an average of 31 minutes each and mean s and mean $(s + d)$ were calculated from the observed time submerged and the total time observed.

From the 26 individuals pods investigated, the maximum dive time recorded was 1,173 seconds. Assuming that, if for a given pod the basic instantaneous probability of being observed is $s/(s + d) = 0.1723$ and that it is definitely observed if watched for a period of time equal to the maximum dive length recorded (1,173 seconds), and if the function connecting those two points is treated as linear, then as a crude approximation:

$$P(visible) = 0.1723 + 0.0007t \quad \text{for } 0 < t \leq 1{,}173 \text{ seconds}$$

The window of time observed was calculated as per Bannister and Hedley (2001) from the frequency distribution of distances ahead, abeam and aft of the observers. The vast majority of sightings (99%) were between 2.6km aft and 7.4km forward (Fig. 10) implying a total window of opportunity of 10km. With the mean aircraft speed of 127.5 knots (= 236kmh^{-1}) then this distance would be travelled in 153 seconds implying, from equation (2), that the probability of observing a pod at the surface on the aerial survey is 0.279. This assumes that the observed maximum of 1,173 seconds is not substantially different from the maximum possible dive time during migration.

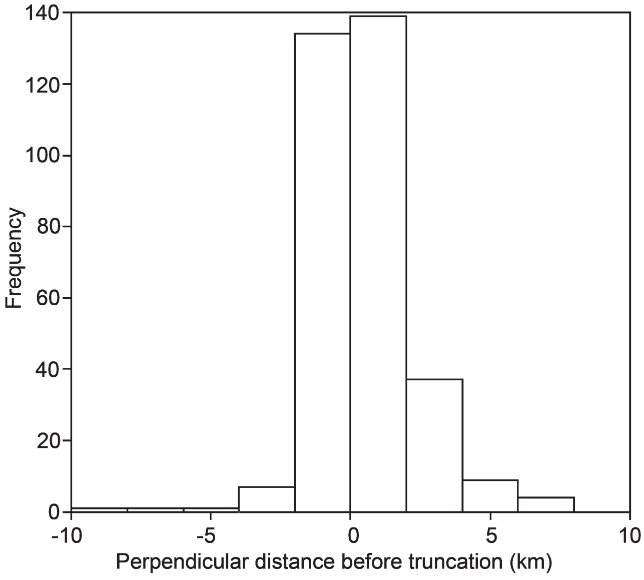

Fig. 10. Frequency of afore, abeam and aft horizontal distances to observed pods in the aerial survey.

Calibration of aerial survey (Method B)
For each relevant day, the predicted instantaneous number of detected pods was obtained as the product of the predictions of the logistic regression and the non-zero density regression as described above. These numbers were then modified by a correction factor that reflected the time taken for a pod to pass through the survey area (latitudinal range 1.735°, or 192.7km). For example, if the NM whales travelled at mean speed 5.35kmh^{-1} (the mean speed from the land based survey), then the correction was

$$(5.35 \times 24) / 192.7 = 0.665$$

Given the daily estimate of available whales from the aerial survey and the estimate of whales from the land-based survey, an estimate of $g(0)$ for the aerial survey is given by the quotient of the estimated number of pods from the aerial survey to the estimated number of pods from the land-based survey. For NM whales, was about 0.29, whilst for NM+ whales it rose to about 0.33. The higher in the latter case could be reflecting the 'detection' of unspecified-direction whales at the surface.

Abundance estimates
A wide selection of abundance estimates is presented in Table 1. Variants were:

(1) Aerial sightings dataset used: NM or NM+.
(2) Method: land; aerial with $\hat{g}(0)$ from land-aerial calibration; aerial with $\hat{g}(0)$ from observational data; aerial withassumed equal to 1; restricted aerial (E–W transects only and a uniform density model) with $\hat{g}(0)$ from observational data; aerial with $\hat{g}(0)$ from observational data but prediction only over a subset of the region.
(3) Period of days over which estimation is made: 190–201 and 203 (land method only); 173–227 (period of 2005 aerial survey); 162–242 (80 day migration period); 152–252 (100 day migration period); 140–227 (87 day period covering the start of the migration and the period of the 2005 aerial survey).

Summaries of the most important results from Table 2 are given below.

Results sets 1–2 (Method A. Land-based survey period: days 190–201, 203)
The total estimate of NM whales is 5,500 and for NM+ whales is 4,600. The land-based estimates assume that all whales in the survey area pass through the latitude of the land survey within a band at 24.48˚S of width 58.7km from 113.41°E to 112.85°E. These estimates are lower than all aerial estimates (except those which assumed $g(0) = 1$ – see below) but they are estimated over the shorter time frame of the land-based survey only.

Results sets 3–8 (Methods A and B. Aerial survey period: days 173–227)
Applying the $g(0)$ corrections derived from the land-based survey results in a total whale abundance of 9,200 NM whales for the duration of the aerial survey (results set 3). For NM+ whales the corresponding estimate is 10,300 (results set 4). Fig. 11 gives a density surface for (a) NM and (b) NM+ whales using the estimated mean migration speed from the focal pod study and the land-based survey-derived $g(0)$ estimates. Results sets 5 and 6 display the results of the analysis of the east-west transects only assuming a uniform density, as an equivalent to a conventional distance analysis.

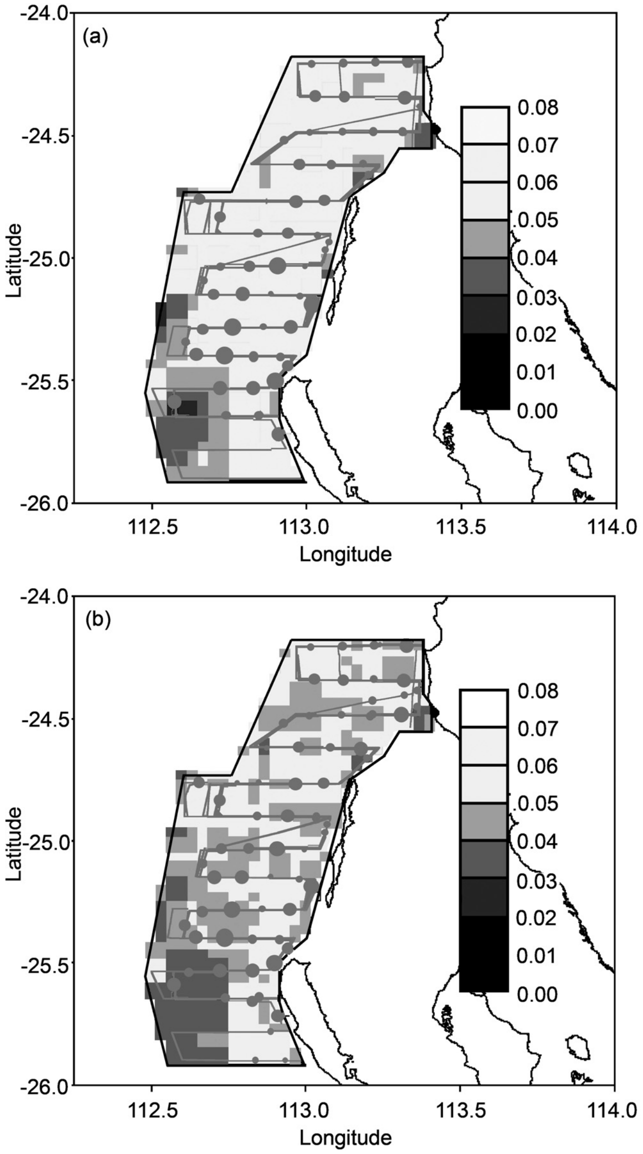

Fig. 11. Estimated densities for northward humpback whales (individuals per km^2) 2005 corrected for availability by reference to the land based survey (result sets 3 and 4) illustrated for the estimated peak of the migration at day 191. Grey lines are the transect lines and the area of the grey circles is proportional to the summed Horvitz-Thompson like estimate of the number of whales per segment. The black circle on the coast at 24.5° latitude is the location of the land based survey. Grey line shows boundary of survey region (a) NM whales, (b) NM+ northward whales.

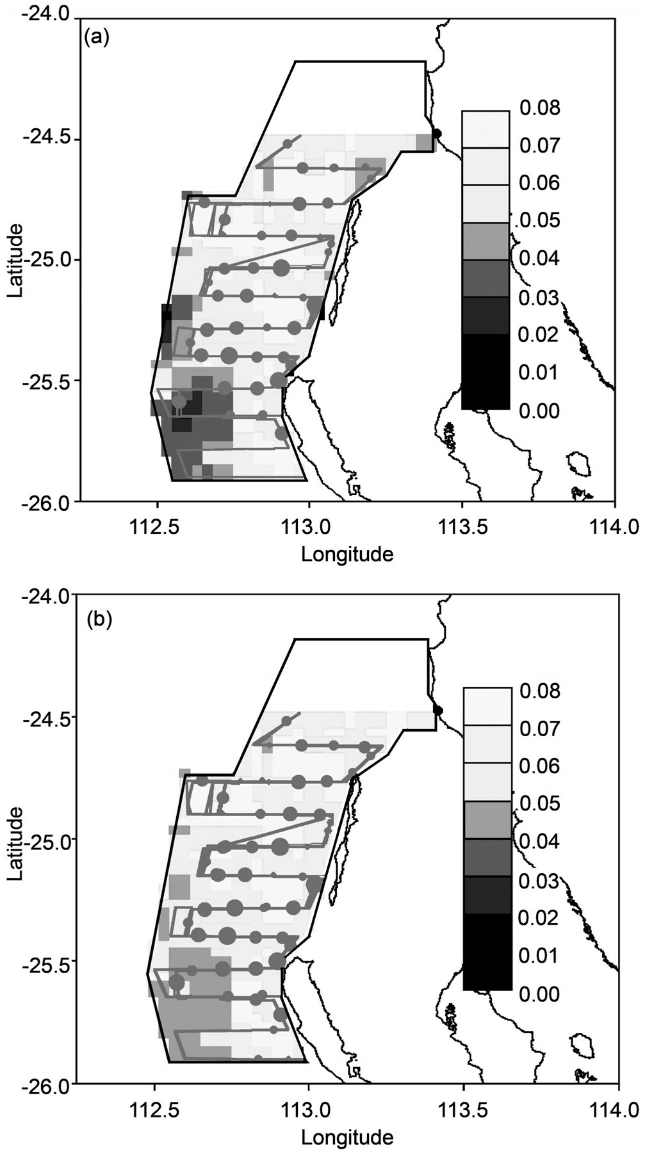

Fig. 12. Estimated densities for northward humpback whales (individuals per km^2) in 2005 assuming $g(0) = 0.279$, for the region south of 24.5°S. Result sets 7 and 8, illustrated for the estimated peak of the migration at day 191. Grey lines are the transect lines and the area of the grey circles is proportional to the number seen. The black circle on the coast at –24.5° latitude is the location of the land based survey. (a) NM whales, (b) NM+ whales.

The $g(0)$ estimate of 0.279 (from focal pod observations) fell within the range of that generated by the land-based survey. As a consequence the abundance estimates nested within the range of the estimates found in results sets 3 and 4. The analyses based on the southern data only and with g(0) again estimated from focal pod observations as 0.279 (results sets 7–8, Fig. 12) generated similar results to the other estimates presented for this survey period (except those which assumed $g(0) = 1$).

Results sets 9–11 (Estimated start of migration to end of aerial survey: days 140–227)

Fig. 6 suggests reasonable confidence in extrapolating beyond the range of the (aerial survey) data prior to its commencement, but the presence of the apparent second pulse at the end of the survey means that the results from any extrapolation after the end of the survey should be treated extremely cautiously. In this result set, therefore, abundance was calculated from the estimated start of the migration but only until the end of the aerial survey. Applying the $g(0)$ corrections derived from the land-based survey results in a total whale abundance of 9,400 NM individuals. For NM+ whales the corresponding estimate is 12,800.

DISCUSSION

This analysis represents a first attempt to apply a density surface to model distributional heterogeneity in a southern humpback population, although a similar method has been applied to North Atlantic humpback whales (Paxton *et al.*, 2007). There is a large amount of unexplained variance. Nonetheless all the available aerial data analyses suggest a population of about 10,000 individuals, albeit with substantial variance around that figure. However a major influence on the size of the estimate was its temporal range.

In the absence of a full scale land-based (independent observer) survey for the full period of the humpback whale migration, we have attempted to provide estimates of absolute abundance from a series of aerial surveys intended to cover the entire time period and a land-based survey that covered about 10–15% of the whole migration period. The aerial survey analysis provided 'snapshot' estimates of the relative density surfaces of a moving population of whales, a large proportion of which remain unavailable for detection to the aerial observers because they are diving whilst in the visual range of the observers. The initial analysis problem was thus twofold: to estimate the numbers that were below the surface and to convert snapshot estimates into estimates allowing for whale movement.

Surface availability

Two methods were used to assess the availability of animals at the surface in the aerial survey. Arguably the two methods are estimating different things. The estimate based on observed dive times is just for surface availability. The estimate based on the land survey is for surface availability plus under-detection on the trackline (in fact in this case at 1km from the trackline because of left-truncation). However under-detection on the trackline is possibly negligible given the similarity of the estimates. Using the land-based survey to estimate *g*(0) has the considerable advantage that its uncertainty can be readily included in the final estimate. Therefore, *c.*0.34 of northward migrating animals are detected at the surface on the trackline. The higher end of this range for *g*(0) is for analyses which incorporated some unknown-direction whales re-classified as northward whales, and as would be expected, this is higher than for analyses which used only whales with northward direction recorded on the survey (the lower end of the range).

Potential problems with the methods

The methods as implemented above could have a number of biases, as listed below.

(1) The two-stage zero-inflated modelling of pod densities could lead to an under-estimation of whale pod numbers as many zeros, if the pods are at low densities, are not true zeros but 'presences' with a low non-zero density. Further the choice of the quasipoisson distribution for the non-zero data was problematic. Finally the resolution of the model was crude to compare with the land based composite function.
(2) The consideration of NM-only data could lead to an underestimation of northward pod numbers if a disproportionate number of unknown direction pods are northward whales.
(3) The random allocation of probable northward status to unknown direction whales could lead to bias if the unknown whale pods did not represent a random selection of northward and southward whales.
(4) The trend in presence of pods with Depth as well as with Dayofyear suggests that only a subset of whales in space and time were enumerated, therefore there is a risk of underestimating abundance.
(5) The land-based calibration assumes that the distribution of whales relative to the shore is proportionately constant every day. In this analysis, no evidence was found of an interaction of Dayofyear with Depth (i.e. that distribution changed with depth but at a different rate each day). If this were to be the case then this would have to be incorporated into the density surface estimation. Further problems could arise if there was a systematic shift in response to transient environmental variables such as sea surface temperature.
(6) It is assumed all submerged whales crossing abeam at distance 0 are seen at some stage.
(7) In the estimates that are based on the calibration of the aerial surface with the land based survey, the swimming speeds are used twice introducing an element of circularity.

Comparison with the 1999 survey: are humpback whale numbers increasing?

Bannister and Hedley (2001) offered a variety of point estimates derived from the 1999 survey for two periods of 80 days and 100 days respectively (11 June–1 September and 1 June–8 September) during the migration season. Applying an approximate estimate of *g*(0) of 0.3 (from all analyses here) to their best unbiased surface individual estimates of 3,365 for 80 days and 3,441 for 100 days and crudely multiplying up their confidence intervals, gives new abundance estimates for 1999 of 11,200 (95% CI 9,000–13,900) and 11,500 (95% CI 9,200–14,300) respectively.

Using the generated estimates for whales from analysis set 4 (i.e. with estimates of *g*(0) from focal pod observations) but extended to cover the estimation range of the 1999 survey gave point estimates (and confidence intervals) for NM+ whales of 15,500 (9,500–47,500) for 80 days (results set 12, Table 1) and 19,400 (10,800–59,700) for 100 days (results set 14, Table 1). The variances are higher in the latter case because the new method includes uncertainty in *g*(0) even though presumably more variation in the density surface is explained. Despite the point estimates being higher for 2005 compared to the 1999 estimate using the same surface availability estimate, the estimates are not significantly different. For completeness, the corresponding estimates for NM whales only are also presented in Table 1 (results sets 11 and 13).

Environmental preferences

The apparent peak in the presence of pods at 90m reflects qualitative observations of humpback whale preferences for shallow water of the coast of Australia. Shallow water preferences in humpback whales have been quantified both in feeding (Paxton *et al.*, 2007) and nursing/breeding periods (Ernst and Rosenbaum, 2003) but less so during migration. Whether this depth preference is an active preference by whales or the outcome of some other mechanism remains to be elucidated.

Suggestions for future work

Further thought should be given to establishing the boundaries of the whale migration in space and time. Coverage of regions to the west of the current survey region could determine the western boundary of migration. Using a density surface could allow the boundaries to be readily determined even if surveying is patchy. The extrapolation of the temporal trend suggests that migration could continue from May; given the suggestion of a second pulse to the migration (Fig. 6), it is unclear what occurs after the survey period. Intensive overlap of land-based surveys and aerial surveys could enhance the estimation of *g*(0) especially if coupled with fine resolution environmental data (e.g. depth) which could allow reliable interpolation of the distribution of animals from the shore. A double platform analysis with two or more independent observers would provide an alternative method for estimating *g*(0) in both the aerial and land-based surveys. The most powerful advantage of an aerial survey is that it allows the distributional properties of the population to be mapped onto environmental features providing an insight into the biology of the animals.

Future work (perhaps using zero-inflated models) could better model the aerial density surface leading to more precise estimates of abundance.

The logistical changes to the land-based survey meant that its location was not ideal, as the whales were often seen milling. Whales passed by the land station far beyond the visual range of the observers, but in principle, that should not prove problematic for this combined analysis because the (relative) density of whales was also estimated from the aerial data. What the analysis did highlight, however, was the need for a reliable and informative model of the density distribution close to the land station. Another consideration for any land based survey is that the available sector for observation at distance 0 effectively encompasses the dive time of the whales. Failure to capture a wide enough window about the abeam line from shore will result in a bias if all north moving pods are not observed at distance 0.

Further investigation is required to investigate the possible 'reasons' for the somewhat peculiar shape of the migration curve (Fig. 6). Had more of the scheduled flights been able to have been completed, a unimodal curve might have been obtained, from which abundance estimates beyond the range of the data could more confidently be predicted. For this analysis, however, we prefer to adopt a cautious approach, preferring the abundance estimates from only the time covered by the aerial survey (or alternatively, those from the start of the migration to the end of the aerial survey), i.e. the estimates from results set 4 (or alternatively set 12) of 10,300 with 95%CI [6,700–24,500] (or 12,800 with 95% CI [7,500–44,600]) although the land-based survey results represent the best estimates for the days of that survey only.

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Long term trends in abundance of humpback whales in Hervey Bay, Australia

PAUL H. FORESTELL*, +, GREGORY D. KAUFMAN* AND MILANI CHALOUPKA#

Contact e-mail: paul.forestell@liu.edu

ABSTRACT

Seasonal abundance estimates of humpback whales resident during the austral winter in Hervey Bay, Queensland, Australia between 1987 and 2007 were obtained from a capture-mark-recapture study using photo-identification images of 3,155 individual whales. Hervey Bay is a major southbound stopover site for Breeding Stock E humpback whales returning to Antarctic waters from over-wintering in the vicinity of the Great Barrier Reef. Annual survival, recapture and abundance estimates were derived using a Cormack-Jolly-Seber modelling approach and a Horwitz-Thompson type abundance estimator. The best-fit model was a 2-ageclass Brownie-Robson type model that estimated apparent annual survival for the non-transient winter stopover ageclass at approximately 0.945 (95% confidence interval: 0.929–0.957). Apparent annual abundance of winter stopover humpback whales in Hervey Bay was estimated to have increased significantly over the past 21 years at *ca.* 13.4% per annum (95% CI 11.6–15.2). The most recent Hervey Bay winter stopover population (2007) was estimated to comprise *ca.* 6,246 post-yearlings (95% CI 5,011–7,482). This estimated rate of population increase is similar to estimates for other surveys along the east Australian coast but significantly higher than the intrinsic rate of increase (*rmax*) estimated recently for several recovering Southern Hemisphere humpback whale stocks based on the feeding ground sampling.

KEYWORDS: HUMPBACK WHALE; ABUNDANCE ESTIMATE; MARK-RECAPTURE; PHOTO-ID; AUSTRALIA; SOUTHERN HEMISPHERE; STATISTICS

INTRODUCTION

Humpback whales that migrate along the east coast of Australia are part of the Southern Hemisphere Breeding Stock E, which spend the austral summer in Antarctic Area V (130°E–170°W), and the austral winter breeding and calving in tropical waters in the vicinity of the Great Barrier Reef (Chittleborough, 1965; Dawbin, 1966; Kaufman *et al.*, 1990). Like stocks of humpback whales in other parts of the world, East Australia humpback whales were severely depleted by commercial whaling. By 1962, the entire Stock E was estimated to be between 200 and 500 animals (Allen, 1980; Chittleborough, 1965). The original ‘pre-exploitation’ population has traditionally been estimated at 10,000 (Chapman, 1974; Chittleborough, 1965), although doubt has been cast on the reliability of such estimates and subsequent population trend estimates by the revelation that the Soviets took some 40,000 unreported humpback whales in the Southern Hemisphere 1957–68 (Mikhalev, 2000). Nonetheless, since their protection from commercial whaling in 1963, there has been evidence that the number of humpback whales migrating along the east coast of Australia are increasing at a substantial annual rate, based on shore-based observations in Southern Queensland waters (Bryden *et al.*, 1990; Noad *et al.*, 2011; Paterson *et al.*, 2001), aerial surveys of the Great Barrier Reef Marine Park (Chaloupka and Osmond, 1998), and analysis of photo-identification data (Chaloupka *et al.*, 1999; Forestell *et al.*, 2003).

Despite favourable evidence of a general increase in the number of humpback whales observed along the east coast of Australia following cessation of commercial whaling, more detailed analyses of annual changes in estimated abundance remain important for assessing the extent to which those changes represent a real increase to the overall breeding stock size (or overall population of Southern Hemisphere humpback whales), and the extent to which observed changes represent seasonal increases associated with temporary movement of whales between breeding stocks (e.g. between Breeding Stock D and E; Chittleborough, 1965) or within the sub-groups of a given breeding stock (e.g. between east coast Australia and areas throughout Oceania; Garrigue *et al.*, 2000). As the number of potential impacts of human-generated activities and long term global cycles on marine mammal species becomes increasingly lengthy (Burns and Wandesford-Smith, 2002; Chaloupka *et al.*, 1999; Clapham *et al.*, 1999; Dawbin and Gill, 1991; Reeves and Reijnders, 2002; Stachowitsch *et al.*, 2005), the need to incorporate likely effects of those impacts on long term changes in abundance becomes increasingly apparent.

The east coast of Australia is an important area for studying humpback whales. It is relatively accessible along much of its length, and it lies along a major portion of the migratory route of Breeding Stock E humpback whales (Chaloupka and Osmond, 1998; Chittleborough, 1965; Dawbin, 1966). Shore-based and aerial observations near North Stradbroke Island indicate that most humpback whales migrating along the east coast of Australia move within 10km of shore (Bryden, 1985). During their southward migration towards the end of the austral winter, large numbers of humpback whales may be reliably observed in the protected waters of Hervey Bay, Queensland (approximately 25°S, 153°E), especially in Platypus Bay, along the northwestern shores of Fraser Island (Forestell *et al.*, 2003; Kaufman *et al.*, 1987). The data reported here are derived from a long term photo-identification-based capture-mark-recapture programme that commenced in Hervey Bay in 1987.

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* *Pacific Whale Foundation, Wailuku, Hawaii 97653, USA.*
+ *C.W. Post Campus of Long Island University, Brookville, NY 11548, USA.*
# *Ecological Modelling Services Pty Ltd, University of Queensland, St Lucia, Queensland 4067, Australia.*

MATERIALS AND METHODS

Study area and dataset

The study was conducted in the Hervey Bay Marine Park that comprises around 1,600km^2 in area (Chaloupka *et al.*, 1999). Hervey Bay is a large, shallow embayment on the east coast of Australia (25°00'S, 152°52'E) and is the major southbound stopover site for humpback whales returning to Antarctic waters from overwintering in the Great Barrier Reef (Chaloupka *et al.*, 1999). Boat-based observations were conducted on a daily basis during each field season, depending upon weather conditions, using a small (5–6m) inflatable vessel equipped with outboard motors. During each sampling day the survey team would opportunistically search for pods of humpback whales throughout the marine park area of the Bay. Radio communication with whalewatch boats in the area was also used on occasion to help locate pods. Photographs of the ventral surface of the tail flukes were obtained using 35mm film or digital cameras equipped with motor drives and 300mm lenses (Kaufman *et al.*, 1987). Date, time, location, sea state, wind speed, direction and degree of cloud cover, sea surface temperature, pod number, pod composition and image number and content of each photograph were recorded. Photographs were processed using previously described techniques (Forestell *et al.*, 2003; Kaufman *et al.*, 1993) and then used to create a photo-identification-based recapture history for each humpback whale encountered in the sampling area over the 21 year period from 1987 to 2007.

Statistical methods

The Cormack-Jolly-Seber (CJS) modelling approach (Lebreton *et al.*, 1992) was used to estimate recapture and survival probabilities from the 2,142 recapture histories. All models were fitted using MARK (White *et al.*, 2006) while model selection was based on the quasi-likelihood form of Akaike Information Criterion, which is corrected for sample size and possible overdispersion (QAICc; Anderson *et al.*, 1998). CJS model assumptions were evaluated using RELEASE and UCARE (Pradel *et al.*, 2005) while goodness-of-fit was assessed using a bootstrap approach implemented in MARK. The best-fit model was used to estimate recapture and survival probability estimates. Annual sampling effort measured as either boat-days or boat-hours was fairly constant in the study area over the 21 year period except for 2001 and 2003, when there was little or no sampling effort. Therefore, the recapture parameters for these two sampling occasions were fixed to zero in the model estimation. The best-fit model capture probabilities (and variance estimates) were then used to derive annual Horwitz-Thompson type abundance estimates ($N_i = (n_i/\rho_i)$) (McDonald and Amstrup, 2001) of the humpback whale population in the Hervey Bay sampling area between 1987 and 2007, where n_i is number of whales captured in the ith year, N_i is number of whales in the sampled population in the ith year and ρ_i is estimated recapture probability in the ith year. The appropriate variance formulae for this estimator are provided in detail by McDonald and Amstrup (2001). The expected population growth rate was derived using a generalised least squares regression of the CV^2-weighted annual abundance estimates with first order moving average (MA1) error structure, which was fitted using the *nlme* package in *R* (Pinheiro and Bates, 2000).

RESULTS

The dataset comprised the recapture histories for 3,155 individual post-yearling humpback whales sampled over the 21 year period from 1987 to 2007. The mark-resight summary statistics for the 3,155 resight profiles are shown in Table 1. Calves were not included in this study because they rarely expose the ventral surface of their flukes needed for photo-identification (Kaufman *et al.*, 1993) and there can be significant change in pigmentation patterning during the first year of postnatal development (Carlson *et al.*, 1990). Sex was not considered because few whales in the sample could be sexed reliably and also because younger males are more likely to be sexed than adult males due to frequent roll-over behaviour (Chaloupka *et al.*, 1999).

All CJS models fitted are summarised in Table 2. The reference or global model was the fully time-dependent model shown as model 3 in Table 2. Several other CJS models were also fitted to compare with the global model (models 2,4,5: Table 2). The adequacy of the global model was assessed using variants of TESTS 2 and 3 in RELEASE and UCARE (Pradel *et al.*, 2005), which indicated failure only of test component 3.SR ($\chi^2 = 120.37$, df = 17, $p<0.001$) but not Test 2.CT or Test 3.SM. Failure of test component 3.SR is considered to be a consequence of the transient behaviour of individuals that were just passing through the study area and were not seen again (Pradel *et al.*, 2005). Consequently, we also fitted a simple age-specific survival model to account for apparent transient behaviour by separating into two ageclasses: newly marked; and previously marked whales. Ageclass is used here for convenience to refer to two groups that are based on time-since-first-marking, which is a form of quasi ageing although age is not strictly known. The two ageclasses might reflect differences in site fidelity between neophyte migrants and experienced migrants on the southbound migration back to Antarctic feeding grounds. The best-fit model of all the five models fitted was the 2-ageclass-specific Brownie-Robson type model (model 1 in Table 2) and a simple bootstrap goodness-of-fit assessment suggested an adequate model fit overall ($p = 0.47$).

The estimated annual survival probability derived from model 1 (Table 2) for the newly marked ageclass or 'transients' in the Brownie-Robson model was 0.631 (95% CI 0.576–0.682). Estimated annual apparent survival probability for the previously marked ageclass in the Brownie-Robson model was 0.945 (95% CI 0.929–0.956). The transients might be younger (neophyte migrant) whales with lower survival probability or whales just rapidly moving through the study area and never seen again, which in the latter case would strongly confound survival and permanent emigration. The survival estimate for the previously marked (and perhaps older and experienced migrants) whales is significantly higher than the estimate for the newly marked whales and is presumably far less biased by any permanent emigration effect. The survival estimate for the previously marked humpback whales is also consistent with the expected annual survival probability of highly mobile, long-lived, later maturing marine species such as bowhead whales (Zeh *et al.*, 2002), right whales (Caswell *et al.*, 1999), sea turtles (Troeng and Chaloupka, 2007) and manatees (Langtimm *et al.*, 1998).

The estimated annual recapture probabilities derived from the best-fit model were time-dependent and ranged from 0.04–0.43 with a geometric mean *ca*. 0.13. These recapture estimates derived from model 1 (Table 2) were then used to derive the Horwitz-Thompson type estimates of humpback whale abundance in the sampling area that are shown in Fig. 1a. The expected annual population growth rate trend in these annual abundance estimates is shown in Fig. 1b and was estimated to be *ca*. 13.4% per annum (95% CI 11.6–

Table 1

Mark-resight summary statistics for humpbacks resident in the Hervey Bay Marine Park sampling area during the annual southward migration (1987 to 2007). Summary notation as follows: n_i = total number of humpbacks (marked + unmarked) sighted in *i*th period, m_i = number of marked humpbacks sighted in *i*th period, R_i = number of n_i released after *i*th period, r_i = number of R_i sighted in *i*th period and resighted in a subsequent period, z_i = number sighted before and after *i*th period but not in *i*th period, effort_i = total sampling effort in boat-days in *i*th period.

Period	Year	n_i	m_i	R_i	r_i	z_i	Effort_i
1	1987	30	0	30	19		27
2	1988	179	9	179	106	10	59
3	1989	159	42	159	86	74	30
4	1990	105	31	105	48	129	30
5	1991	129	36	129	63	141	31
6	1992	119	39	119	58	165	37
7	1993	212	68	212	100	155	48
8	1994	172	81	172	78	174	57
9	1995	89	43	89	32	209	16
10	1996	126	50	126	49	191	22
11	1997	161	44	161	55	196	30
12	1998	236	79	236	66	172	31
13	1999	189	60	189	46	178	35
14	2000	219	64	219	45	160	44
15	2001	0	0	0	0	205	0
16	2002	174	51	174	46	154	49
17	2003	0	0	0	0	200	0
18	2004	235	30	235	45	170	53
19	2005	453	97	453	66	118	59
20	2006	587	118	587	54	66	56
21	2007	643	120	643			62

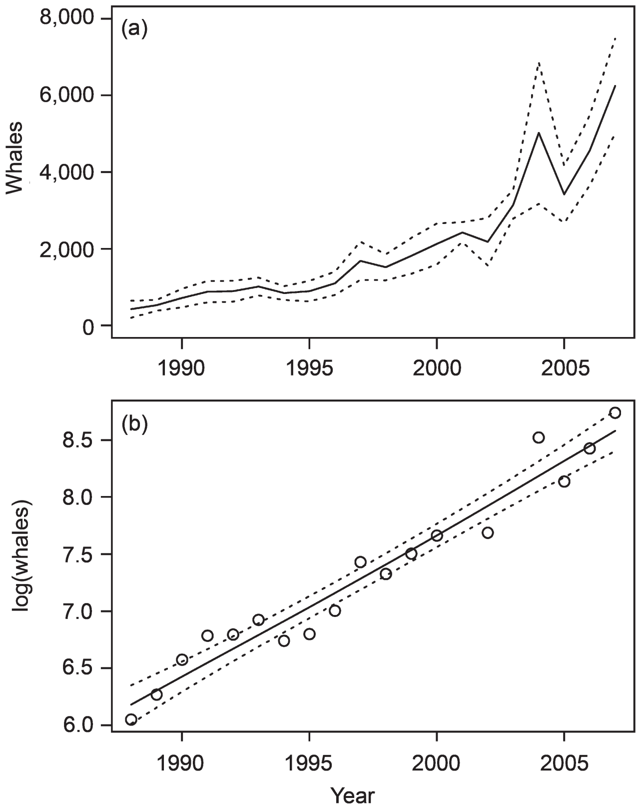

Fig. 1. Panel (a) shows Horwitz-Thompson annual abundance estimates (solid curve) and 95% confidence curves (dotted curves). Panel (b) shows on a log scale the Horwitz-Thompson annual abundance estimates (open dots) with the linear trend (solid curve) estimated by a linear regression model with MA(1) and 95% confidence bands (dotted lines) – model fitted using *nlme* package in *R*.

15.2). The highest winter stopover abundance estimate derived from this study to date was in 2007 (Fig. 1a) at *ca.* 6,246 post-yearling humpbacks (95% CI 5,011–7,482).

DISCUSSION

The Hervey Bay study area has shown a marked increase in the estimated number of humpback whales visiting there over the 21 years of this study. Fig. 1a demonstrates the increase was relatively minimal from 1987–95, moderate through to 2000, and remarkably high since then. This would explain the difference between the overall trend reported here up to 2005, and the earlier findings of Chaloupka *et al.* (1999), based on 10 years of Pacific Whale Foundation photo-identification data from Hervey Bay (1987–1996) and four years from the Whitsunday Islands, Queensland; and Forestell *et al.* (2003), based on a seven-year analysis of resights and exchange rates between Hervey Bay and the Whitsunday Islands. Those estimates suggested considerably lower overall rates of change in abundance, but they were based primarily on time periods prior to the onset of the rapid increases in more recent years demonstrated in the current findings. The overall increase in abundance estimates reported here is consistent with reports of increases in the number of humpback whales migrating along the east Australian coastline reported by others (Noad *et al.*, 2011; Paterson *et al.*, 2001), derived from shore-based counts of animals moving past North Stradbroke Island early in the season, during the northward phase of the annual migration.

Branch (2011) provides estimates of humpback whale abundance and rates of change based on three circumpolar surveys of Antarctic waters during the austral summer across the years 1978–2004. He reported a circumpolar annual rate of increase of 9.6% (95% CI 5.8–13.4), near the theoretical limit for humpback whales (Clapham *et al.*, 2006). Branch (2011) estimates annual rate of increase for Breeding Stock E at 14.4% (95% CI 9.6–19.2), similar to the Hervey Bay findings reported here. However, it is highly unlikely that the intrinsic rate of increase (*rmax*) for Breeding Stock E humpback whales could be so high (Clapham *et al.*, 2006). Branch (2011) notes that the small number of abundance estimates, high associated CVs, changes in survey design, and annual changes in humpback whale distribution severely limit the accuracy of the rate of change estimates for individual areas (stocks).

It is unlikely that the long term increase found for the Hervey Bay stopover population reflects the intrinsic rate of increase for Breeding Stock E humpback whales. The various estimated rates of increase of the population segment of the east Australian stock that migrates each year along the east Australia coast are all significantly higher than the

Table 2

Summary of model fits.

φ = survival probability, ρ = recapture probability, (.) = constant, (t) = time-dependent, $a2$ = Brownie-Robson 2-ageclass structure to account for apparent transience, QAICc = sample size and overdispersion corrected Akaike Information Criterion, Pars = number of model parameters. Overdispersion parameter used to adjust AICc c-hat = 1.19.

Model	Description	QAICc	ΔQAICc	Model likelihood	Pars	Deviance
1	$\varphi(a2)\,\rho(t)$	6,465.93	0.00	1.000	20	1,451.30
2	$\varphi(.)\,\rho(t)$	6,525.62	59.69	0.000	19	1,513.01
3	$\varphi(t)\,\rho(t)$	6,541.55	75.61	0.000	32	1,502.55
4	$\varphi(t)\,\rho(.)$	6,777.36	311.42	0.000	10	1,782.89
5	$\varphi(.)\,\rho(.)$	6,865.96	400.03	0.000	2	1,887.56

intrinsic rate of increase (*rmax*) estimated recently for various recovering Southern Hemisphere humpback whale stocks based on the feeding ground sampling (Johnston and Butterworth, 2006).

The humpback whales entering Hervey Bay were found to comprise two major ageclasses that demonstrate significantly different survival rates: those captured once and not seen again (transients); and those re-captured following initial sighting. The transient portion of the Hervey Bay animals could represent a range of possibilities that reflect important demographic differences in lower ageclass-specific mortality, or ageclass-specific dispersal behaviour. A measure of transient behaviour that reflects temporary shifts in distribution between breeding stocks or between areas within breeding stocks would be important for improving the accuracy of stock assessment and estimates of change in abundance, particularly in light of recent estimates of population abundance and rate of increase that do not consider the effect of transients over extended time periods (Noad *et al.*, 2008; Noad *et al.*, 2011; Paterson *et al.*, 2001; Paton *et al.*, 2006). More accurate measures require the use of multi-state models (Pradel *et al.*, 2005). While there have been limited efforts to undertake such an analysis (Forestell *et al.*, 2003; Paton *et al.*, 2006), there is a pressing need to complete a comprehensive comparison of all available photo-identification images for this stock of whales.

Finally, it should be noted that whatever evidence there may be that whales behave differently in the presence or absence of whalewatching boats in Hervey Bay (Corkeron, 1995), these differences appear not to have had a deleterious long term effect on the number of whales that visit the area annually.

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Absolute and relative abundance estimates of Australian east coast humpback whales (*Megaptera novaeangliae*)

Michael J. Noad*, Rebecca A. Dunlop*, David Paton+ and Douglas H. Cato#

ABSTRACT

The humpback whales that migrate along the east coast of Australia were hunted to near-extinction in the 1950s and early 1960s. Two independent series of land-based surveys conducted over the last 25 years during the whales' northward migration along the Australian coastline have demonstrated a rapid increase in the size of the population. In 2004 we conducted a survey of the migratory population as a continuation of these series of surveys. Two methods of data analysis were used in line with the previous surveys, both for calculation of absolute and relative abundance. We consider the best estimates for 2004 to be 7,090±660 (95% CI) whales with an annual rate of increase of 10.6±0.5% (95% CI) for 1987–2004. The rate of increase agrees with those previously obtained for this population and demonstrates the continuation of a strong post-exploitation recovery. While there are still some uncertainties concerning the absolute abundance estimate and structure of this population, the rate of annual increase should be independent of these and highly robust.

KEYWORDS: HUMPBACK WHALES; ABUNDANCE ESTIMATE; SURVEY-SHORE-BASED; TRENDS; MIGRATION

INTRODUCTION

Humpback whales undertake annual migrations between high-latitude summer feeding areas and low-latitude winter breeding areas (Chittleborough, 1965; Dawbin, 1966). Historically the western South Pacific was considered to contain one stock of humpbacks, the Group V population, that wintered around various low-latitude coastal and island areas and summered in the Southern Ocean between 130°E and 170°W (Area V). More recent work suggests, however, that the region contains several populations that inter-mingle to a variable but probably small extent (Garrigue *et al.*, 2000) and this metapopulation structure is partially reflected in the redesignation of Group V whales by the International Whaling Commission to Stocks E(i) (Australian east coast), E(ii)1 (those wintering around New Caledonia) and E(ii)2 (those wintering around Tonga) (Bannister, 2005). E(i), the Australian east coast population, is thought to be the largest of these.

Off the east coast of Australia the winter breeding area is probably dispersed inside the Great Barrier Reef (Paterson and Paterson, 1989; Simmons and Marsh, 1986) and the migration to and from these waters is along the eastern continental coastline. Off the southern coastline of Queensland the migratory corridor is narrow with most whales passing within 10km of some prominent headlands (Brown, 1996; Bryden, 1985) so the whales are available for land-based counts.

Prior to the 1950s, there was little exploitation of the east Australian humpback whale population. In 1952 industrial shore-based whaling commenced and, together with massive illegal pelagic whaling in the Southern Ocean (Mikhalev, 2000; Yablokov, 1994), took whales in such abundance that the population had collapsed by 1962. Chittleborough (1965) estimated the original Group V population to be ~10,000 whales but this has been recently revised by Jackson *et al.* (2006), in light of the only recently reported catches in the Southern Ocean, with median estimates ranging from 33,278 to 37,573. Estimates of the Group V population size in the early to mid-1960s include 104 (Bannister and Hedley, 2001) and 400 to 500 (Chittleborough, 1965). Paterson *et al.* (1994) estimated that the east Australian component of Group V was between 34 and 137. While the distribution of surviving whales was not known, the rapid recovery of east Australian whales and apparent lack of recovery of whales migrating past New Zealand suggests that most of these were of the east Australian population.

Post-whaling surveys of the east Australian population were initiated at Point Lookout, North Stradbroke Is., in 1978 and have continued most years since then (Fig. 1). At the latitude of Pt Lookout (27°30'S) in south-eastern Queensland, the northward migration peaks between mid-June and mid-July (Bryden *et al.*, 1990; Chittleborough, 1965; 1994). Surveys here have been conducted by two independent teams, the first headed by M. Bryden and then by M. Brown (Brown, 1996; 2003; Bryden, 1985; Bryden *et al.*, 1996; 1990; Bryden and Slade, 1988), hereafter known as the 'BB' (Bryden/Brown) surveys. The other series of surveys were by R. Paterson, P. Paterson and one of the current authors, DC (Paterson and Paterson, 1984; 1989; Paterson *et al.*, 1994; 2001; 2004), hereafter referred to as the 'PC' (Paterson/Cato) surveys. While both series of surveys were conducted at Pt Lookout, the BB surveys observed from a headland approximately 32m above sea level while the PC surveys were conducted from a 65m high hill approximately 300m inland from the headland. Despite some differences in survey site, survey design and data analysis, both series of surveys have been in broad agreement concerning the number of migratory whales and their rate of increase.

Recent estimates of annual rates of population increase for the Australian east coast (with 95% CI) are 12.3% (10.1–14.4%) (Bryden *et al.*, 1996) and 10.5% (10.0–11.1%) (Paterson *et al.*, 2004). These growth rates are among the

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* *School of Veterinary Science, University of Queensland, Gatton, Qld 4343, Australia.*
+ *Blue Planet Marine, PO Box 919 Jamison Centre, ACT 2614, Australia.*
# *Defence Science and Technology Organisation, Australian Technology Park, Eveleigh, NSW 1430* and *University of Sydney Institute of Marine Science, Australia.*

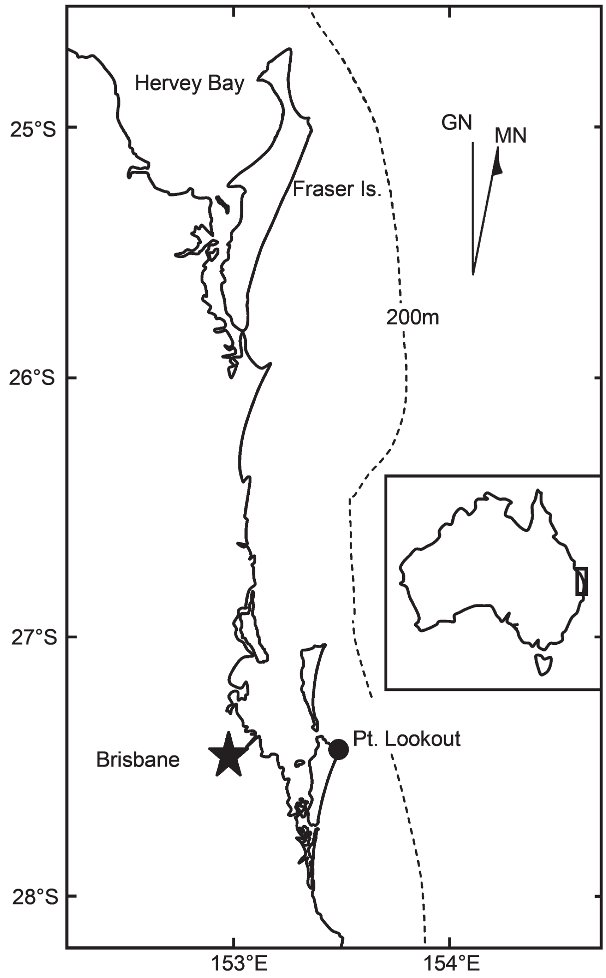

Fig. 1. Southeast Queensland showing the position of Pt Lookout on North Stradbroke Is. The edge of the continental shelf is indicated by the 200m isobath (dashed line).

highest recorded for any population (but similar to those of the Australian west coast population) and are close to the theoretical reproductive limit of around 12% for the species (Bannister and Hedley, 2001; Best, 1993; Brandão *et al.*, 1999). The rates of increase are also remarkably consistent over time.

In 2004 we conducted a land-based survey of the east Australian humpback population at Pt Lookout at the same site of previous BB surveys, and the results of this survey are presented here together with long term trends in abundance using the results of the previous surveys.

METHODOLOGY

2004 survey data collection

Field methodology for the 2004 survey was at the same site as, and closely followed, BB's structured surveys of 1996, 1999 and 2000 (Brown, 1996; Brown *et al.*, 2003; Bryden *et al.*, 1996). The survey was conducted from Pt Lookout (27°26'S, 153°28'E) on North Stradbroke Island, a large island off the coast of southern Queensland near Brisbane, over a 14 week period from 25 May to 27 August 2004 (Fig. 1). Aerial surveys have demonstrated that most humpback whales migrate within 10km of the Point, a distance within which it has been assumed that most whales should be observable under average conditions (Brown, 1996; Bryden, 1985).

Survey sites

As with the BB surveys, two survey sites were used to enable a blind double count of passing whales. The primary survey site was located at 'Norm's Seat' (27°26.067'S, 153°32.770'E). This location is approximately 32m above sea level. The second location, 'Whale Rock' (27°26.152'S, 153°32.758'E), used for the double counts, was located approximately 160m south of Norm's Seat, at a similar height above sea level. The two survey locations had a similar field of view extending from the east-south-east to the north. The two survey locations were visually and acoustically isolated from each other by vegetation and the topography of the headland.

Watch structure

At Norm's Seat observations were undertaken from 0700 to 1700 each day, except during inclement weather (heavy rain, sea state >mid 5). Each 10 hour day was divided into four shifts conducted by two teams or watches. The 'early' watch observed from 0700 to 1000 and from 1200 to 1400 and the 'late' watch ran from 1000 to 1200 and from 1400 to 1700.

At Whale Rock observations were carried out most days but usually by only one watch observing every second shift in line with either the 'early' or 'late' watches at Norm's Seat. Watches alternated daily between 'early' and 'late'. Occasionally there were insufficient observers for the three watches needed to run both the primary and double counts and the double counts were not conducted at these times.

Watches consisted of three to four observers and efforts were made to balance the experience and effort of the Norm's Seat and Whale Rock teams. Norm's Seat usually had four observers due to the use of a theodolite and notebook computer. One observer operated the theodolite, while another operated the computer, reducing both their search efforts compared with Whale Rock. At each location at least one observer was 'experienced' with a minimum of one month (approx 150 hours) survey time at Pt Lookout, or several seasons of prior field experience with humpback whales at other locations. During surveys, observers were allocated a section of the survey area, which was to be scanned at all times. Observers alternated between using binoculars (generally 7 x 50) and using the naked eye to scan their allocated section.

Data collected

The notebook computer at Norm's Seat ran Cyclopes software, developed specifically for the tracking of marine mammals (Eric Kniest, University of Newcastle, Australia). The theodolite operator points the theodolite at a surfacing group of whales and sends the vertical and horizontal angles directly to the computer. Cyclopes then calculates the position of the group correcting for tides, curvature of the earth and refraction and plots it on a map of the area. Cyclopes also accepts information on the group's composition, behaviour and direction of travel and will compute the group's speed, course and distance from any user-selected reference point (e.g. the survey site, another group, a boat). Surfacings not captured by the theodolite were also entered as distance and bearing estimates so that all observed surfacings of all groups were included in the Cyclopes file.

Double counts from Whale Rock were conducted using calibrated reticle and compass binocular sightings recorded manually. These data were entered into Cyclopes each evening for group matching with the Norm's Seat data.

Most whales were sighted several times allowing ample opportunity for positive identification based on characteristics of the blow and roll of the back, flukes or pectoral fins. Single sightings of a blow only were not counted as these were too easily confused with sea spray in windy conditions and are not sufficiently diagnostic of a humpback. Single sightings of a breach were counted.

For the purpose of the census, whales were only counted if they crossed a line extending seawards at 70° from true North between 0700 and 1700. Both numbers of groups and group size were recorded. South-bound groups, though recorded, were excluded from the analysis. Negligible initially, the number of south-bound groups exceeded that of north-bound groups after mid-August. Groups with no obvious direction of travel were assigned a direction based on the ratio of definite north and south-bound groups in that week.

Weather conditions were recorded every half hour and at the beginning and end of each day. Data recorded included sea state, swell height and direction, wind speed and direction, cloud cover, glare and any other factors affecting visibility (e.g. smoke, haze, rain).

Absolute abundance estimates for 2004 – general assumptions and approaches

In line with previous Pt Lookout surveys we assumed that all whales in the migratory stream passed within 10km of the Point and that all groups within 10km were available for sighting. It is assumed that group size was accurately assessed and that travel rate did not differ between day and night (Bryden, 1985).

Because of the long term rise and fall in numbers over the course of the migration (Fig. 2), data analyses need to separate this source of variance from that of the day to day variation in whale counts. The PC surveys (Paterson *et al.*, 1994; 2001; 2004) used stratified random sampling theory (Cochran, 1963) to calculate the population passing during the survey period while the BB surveys (Brown, 1996; Bryden *et al.*, 1996) used a more complex Hermite polynomial modelling approach. Both techniques are used here on the 2004 data.

Absolute abundance estimate I – the Hermite polynomial modelling approach

Bryden *et al.* (1996) and Brown (1996) used a method for calculating absolute abundance from a survey of migrating whales that was developed by Buckland *et al.* (1993a; 2004; 1993b) for use on migrating Californian gray whales (*Eschrichtius robustus*). The method fits a normal curve to the number of groups passing the survey point during each shift or watch each day. The curve is then adjusted slightly through the progressive addition of Hermite polynomial terms which adjust the curve for skewness and kurtosis seeking a better fit to the data. As each term is added, the resultant curve is tested for goodness-of-fit to the data. Akaike's Information Criterion (AIC) is also calculated for each model and compared with the previous model. The model using the least number of additional Hermite polynomial terms that gives a significant improvement in fit and reduction in AIC is taken to best represent the data. The resultant curve or model is then used to calculate the number of groups that passed (a) during the survey period and (b) before and after the survey period, i.e. an estimation of the tails of the migration. It is also used to calculate a standard error for the resultant number of groups based on the variance of the observed data around the modelled curve.

We used *GWNORM* software (S. Buckland, University of St Andrews, UK) for this analysis (Buckland, 1992; Buckland *et al.*, 1993a; 1993b). For each watch the following data are required: the time of the start and end of the watch (including the day from the presumed start of the migration) and the group count for that watch. As our watches were short compared to those of the gray whale surveys, we followed Bryden *et al.* (1996) and pooled them into morning and afternoon, i.e. 0700–1200 and 1200–1700. Watches that were truncated by more than 1h were excluded and the program was run in 'grouped' mode indicating that the data

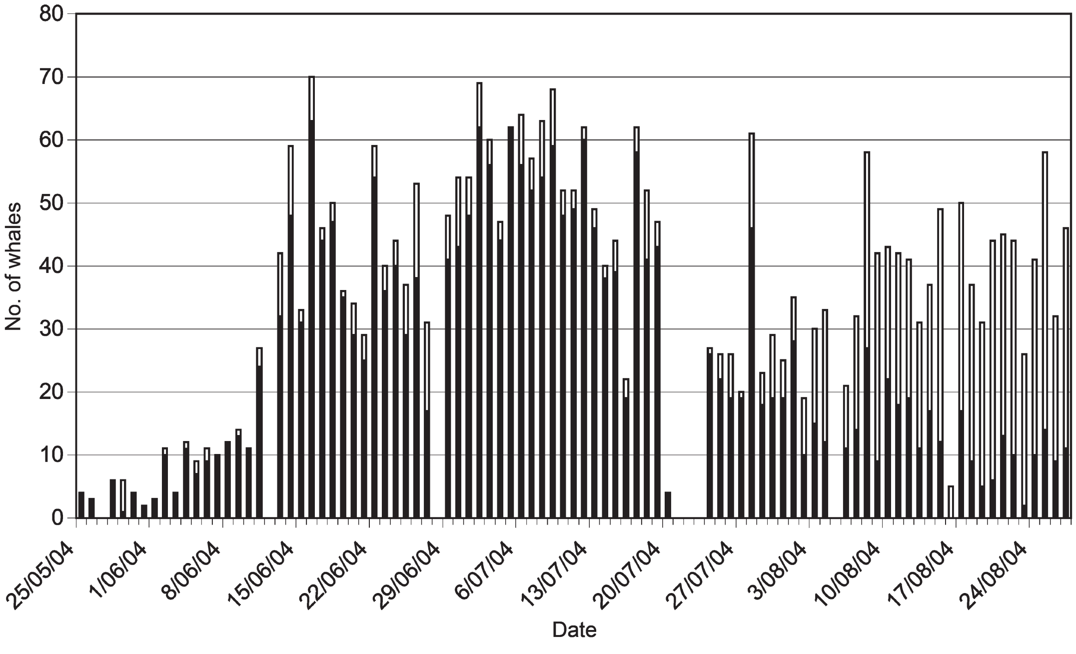

Fig. 2. Raw 2004 survey data. Confirmed northbound humpback whales passing Pt Lookout between 0700 and 1700 in solid black bars; whales southbound, unconfirmed or passing outside of survey hours shown in white bars. There were similar numbers of northbound and southbound whales in the first half of August after which southbound whales predominated. Except for 27 May when no whales were seen, gaps are days without survey (*n* = 6). Counts include Norm's Seat data only.

were grouped within the watch periods indicated. The output of the program gives a number of results for the normal model and for models using from one to four additional Hermite polynomial terms. For each model, the results include (with SE for each): (a) a correction factor for groups passing during the survey period (to account for unmonitored periods), (b) estimated number of groups passing during the survey period, (c) estimated numbers of groups passing before and after the survey period and (d) an estimated total number of groups passing during the migration.

The total population is calculated as:

$$N_{BB} = msf_t f_m \quad (1)$$

where N_{BB} is the total population of whales, m is the number of groups counted, s is the mean group size, f_t is the correction factor for groups passing during non-survey time (which may or may not include the tails of the migration before and after the survey period) and f_m is a correction factor for groups available for counting during survey time but missed (modified from Bryden *et al.*, 1996). The standard error of N_{BB} is then calculated as:

$$Se(N_{BB}) = N_{BB}.\sqrt{\{CV(m)\}^2 + \{CV(s)\}^2 + \{CV(f_t)\}^2 + \{CV(f_m)\}^2} \quad (2)$$

Ninety-five percent confidence intervals are then calculated based on a log-normal distribution (Buckland *et al.*, 1993a).

Calculation of f_t – the Hermite polynomial model
Although *GWNORM*'s output includes a correction factor, it is only for groups missed during the survey period. The BB surveys have, however, used the model to calculate several types of f_t depending on whether one includes the tails outside the survey period, the limits of the dates on these tails and other constraints that might be placed on the model. The various correction factors (all termed f_t) used by the BB surveys for groups missed therefore include:

(a) During the period of the survey only, where there are no assumptions about the start and end of the migration and the polynomial is fitted only to the data without constraint.
(b) During the nominated migration period with the curve fitted to the data without constraint. The pre- and post-survey estimates of passing groups are made based on the area under the curve outside the survey period but within the nominated migratory start and end dates (the values of which only matter if the model does not reach 0 within these dates). For our analysis we chose the 15 May and 30 September as the reasonable limits of the northward migration.
(c) During the nominated migration but for a curve recalculated so that it is constrained by zero counts added at the nominated start and end of migration taken (in the BB surveys) as 15 May (day 0) and 23 August (day 100) and with data after day 99 truncated. In other words counts before 16 May and after 22 August were assumed to be zero.

To be clear, we have renamed these $f_{t(s)}$ for 'survey', $f_{t(m)}$ for 'migration' and $f_{t(c)}$ for 'constrained', respectively. Depending on whether or not the input data include the zero constraints mentioned in (c), *GWNORM* will produce $f_{t(s)}$ and $f_{t(c)}$ as part of its output. The correction factor $f_{t(m)}$ has to be derived by dividing the estimate for groups passing during the migration (which includes groups passing before and after the survey) by the number of groups observed. Alternatively *GWNORM*'s estimate of total groups passing during the migratory period (with its associated SE) can be used to replace terms mf_t in equation 1.

Correction for groups available but missed (f_m)
A correction factor f_m for groups available for counting but missed is calculated using the double count data. The first step is to attempt to match groups seen from Norm's Seat with those from Whale Rock. Matching was performed daily using the Cyclopes files and checked again post-fieldwork. Most of the time group matches were obvious from similar group tracks at similar times. During busy or confused periods, however, sightings were considered individually to prevent incorrect assumptions concerning group identity. A match required at least two sightings matched in time and space from the two survey sites. Matching of individual sightings depended on estimated bearing and distance, time and group size. Some flexibility was necessary to account for differences in data capture techniques, differences in survey site positions and recording error. Times had to match to within 30sec and group size could vary by one. Distance estimates had to agree to within 500m for groups within 2km of shore, to within 1km for groups 2–5km from shore, and to within 2km for groups 5–10km from shore. Bearings had to agree to within 10° for groups more than 1km from shore and to within 20° for groups less than 1km from shore. We assumed that the sightings from each survey site were independent of each other and that matches were made without error.

These matched data were then analysed using mark-recapture techniques. The BB surveys used a logistic regression model summarised by Buckland *et al.* (1993a; 1993b) which incorporates co-variates to allow for heterogeneity in mark-recapture experiments. An alternative approach is to use the simple Petersen estimate (Seber, 1982) which calculates P, the size of a population as:

$$P = \frac{MC}{R} \quad (3)$$

where M is the number of animals 'marked' during the first capture episode, C is the number of animals 'captured' during a second capture episode and R is the number of those caught in the second episode that had been marked in the first. Both were used by Bryden *et al.* (1996) who calculated $f_m s$ of 1.111 and 1.104 using the logistic regression and Petersen methods, respectively. They concluded that the effects of heterogeneity were small. We therefore elected to use the simpler Petersen estimate.

When applied to our survey, M can be taken as the number of groups observed from Norm's Seat, C is the number observed from Whale Rock, and R is the number observed by both. The correction factor to be applied to M will therefore be given by C/R. In theory M and C are reversible depending on which survey point is considered to be the marker and which the capturer and so M/R is also a valid correction factor for groups seen from Whale Rock. However, Norm's Seat was our primary survey site and generated the data used for the population estimates while Whale Rock was only a part-time survey. Therefore, for the purposes of this study, C/R was the appropriate correction factor for the count data. In any case C/R and M/R were not significantly different.

To calculate C/R with a standard error, C/R was calculated by grouping consecutive days of data until R was approximately 40 in each group. These measures were averaged and a standard error calculated. C/R daily or weekly was not calculated, as early measures of daily or weekly C/R (using far fewer groups), had a much higher variance than estimates using more groups, causing an overestimate of the standard error. There was no significant difference between the mean C/R for early in the season and the peak of the migration.

Mean group size (s)

Mean group size *s* was calculated using the initial size of the group as assessed at Norm's Seat. Subsequent splits into small groups or joins with other groups to create larger groups were ignored. As with the count of groups, only groups passing a line seaward between 0700 and 1700 and heading north were included.

As with previous Pt Lookout surveys, we assumed that the group sizes recorded were correct. Bryden *et al.* (1990) found no difference between group sizes observed from the land and air at Pt Lookout and Findlay and Best (1996) found no significant difference between group size as estimated by land-based observers of humpbacks off South Africa and confirmed by boat, providing the group had been sighted at least twice.

The standard error of the number of passing groups (m)

This is given by Buckland *et al.* (1993b) by first calculating a dispersion parameter estimate (the appropriate Hermite polynomial model's χ^2 goodness-of-fit statistic divided by its degrees of freedom), then taking the square root of this multiplied by the original number of groups seen.

Absolute abundance estimate II – the stratified random sampling approach

A detailed explanation of the stratified random sampling approach, as applied to the Pt Lookout humpback surveys, can be found in Paterson *et al.* (1994). Sampling was carried out every day, weather permitting, during the survey period and was well distributed over the full 14 weeks of the migration (Fig. 2). One full 10h day of observations is taken to represent one sample unit. On this basis the sampling is considered to be a reasonable approximation to random sampling of the stream of humpback whales passing Pt Lookout. Days with less than 10h of observations (truncated by rain or wind) were normalised to a 10h day based on the sighting rate of the surveyed part of that day. This method does not estimate the contribution from whales passing outside the survey period, so requires the survey period to extend over as much of the migration as possible to obtain an estimate of the population. Previous PC surveys extended to the end of October rather than the end of August as in this survey.

The sample was split into seven strata each comprising two weeks of observations, the first stratum being the fortnight starting 25 May and the seventh being the slightly truncated fortnight starting 17 August. The number of humpback whales seen per 10h in an equivalent 10h observation period is considered to be a sample unit. Over the total period of 95 days (which includes all strata), there were 228 10h periods. The sample can then be considered to be the selection of those 10h periods when observations were actually made. This gives a total of 89 sample units.

From Cochran's equation (5.14), the estimate of the total population from which the sample was drawn, with 95% confidence interval, is

$$N\bar{y}_{st} \pm tNs(\bar{y}_{st}) \tag{4}$$

Here $N = 228$ is the number of equivalent 10h units in the total period of 95 days over which the observations were made and

$$\bar{y}_{st} = \sum_{h=1}^{7} N_h \bar{y}_h / N \tag{5}$$

is the weighted mean (Cochran's equation 5.1) where $\bar{y}_{st}$ is the sample mean and N_h the total number of units in stratum *h*. Also, from Cochran's equation (5.11),

$$s^2(\bar{y}_{st}) = \sum_{h=1}^{7} N_h(N_h - n_h)s_h^2 / (N^2 n_h) \tag{6}$$

is the estimate of the variance of $\bar{y}_{st}$, where s_h^2 is the sample variance of stratum *h*, n_h is the number of samples in stratum *h* and *t* is Student's *t* for the effective number of degrees of freedom given by Cochran's equation (5.15).

Correction for groups available but missed

Although the PC estimates did not use a correction factor for groups available but missed, we included this to improve the accuracy of the estimate. This was identical to f_m as calculated above.

Population estimate

The final population estimate is given by

$$N_p = N\bar{y}_{st} \cdot f_m \tag{7}$$

The standard error for N_P was calculated by combining the standard errors of its contributing factors in a manner similar to that used in equation 2. Ninety-five percent confidence intervals were then calculated based on a log-normal distribution.

Rate of population increase I – relative abundance estimate method

The BB surveys use a measure of 'relative abundance' to calculate the annual rate of increase. In the early surveys (pre-1991) data were sparse and zero counts at the presumed start and end of migration had to be added to constrain the Hermite polynomial model and prevent it predicting unrealistically large tails (Buckland *et al.*, 1993b). The dates chosen, based on data at the time, were 15 May and 23 August (days 0 and 100, assumed to be the start and end of migration, respectively). Although subsequent surveys with increased whale numbers have shown that the migration extends as a long tail until around the end of September, the addition of 0 values at these dates and truncation of data collected after 23 August was continued to maintain continuity and enable the calculation of a comparable 'relative abundance' measure. Doing this fundamentally alters the shape of the Hermite polynomial model and results in a new constrained correction factor for groups missed $f_{t(c)}$ (described above). The other feature of the calculation of the BB 'relative abundance' measure was the omission of f_m (as no double counts were performed in earlier surveys). Using this methodology, the relative population size P_{RA} is given by:

$$P_{RA} = msf_{t(c)} \tag{8}$$

The rate of increase was calculated from the simple logarithmic regression of the relative abundance estimates produced against year. Later surveys produced a range of estimates for various time spans (Brown, 1996; Bryden *et al.*, 1996).

Rate of population increase II – the rate of whales passing method

The difficulties and limitations of estimating the rate of increase of this stock have been discussed by Paterson and Paterson (1989) and Paterson *et al.* (1994). The PC surveys use a procedure in which the index chosen for the calculation of relative abundance is the number of humpback whales observed per 10h averaged over the four, eight and ten consecutive weeks with the highest counts across the survey period. This is effectively the four, eight and ten weeks around the peak of the northward migration. Fixed dates were not used as the peak of the migration shifts by up to two weeks from year to year (Chittleborough, 1965; Paterson *et al.*, 2004). Data are available for the 19 years from 1984 to 2002 except 1993, 1995, 1997 and 2000 (Paterson *et al.*, 1994; 2001; 2004). In all years a rate of increase based on the four weeks around the peak was possible, however the survey period was not of sufficient length to allow eight and ten week comparisons for all years surveyed, so there are fewer data points for these indices.

This technique requires the assumption that the proportion of the stock passing in the period chosen at the peak of the northern migration is constant from year to year. This assumption was tested by Paterson *et al.* (2001) using the data of 1987, 1992 and 1999 when the observation period covered almost the full migration and was shown to be reasonable as the proportion of the population estimated to be passing during these periods varied by no more than 2% between years.

RESULTS

Data collected

The 2004 survey was conducted from 25 May to 27 August (95 days). Surveys were cancelled completely on six days and were truncated on a further 13 days, seven of these by less than two hours. Excluding southbound groups, single blows and other unconfirmed sightings, and groups not passing between 0700 and 1700, 1,250 groups containing 2,239 whales were observed passing the Pt Lookout during the survey (Fig. 2).

Mean group size (s)

The mean group size *s* of northbound groups was 1.80 (SE 0.023). The largest group seen contained nine whales (Fig. 3).

Correction for groups available but missed (f_m)

Double count data were used from 43 days (26 May–9 July) to calculate the correction factor for groups available but missed by the primary survey site, Norm's Seat. On the watches when both Norm's Seat and Whale Rock surveys were operating Norm's Seat observed 451 groups (*M*) and Whale Rock observed 464 groups (*C*). Of these 423 groups were observed from both survey points (*R*). The correction factor for groups available but missed by Norm's Seat is 1.10 (SE 0.021).

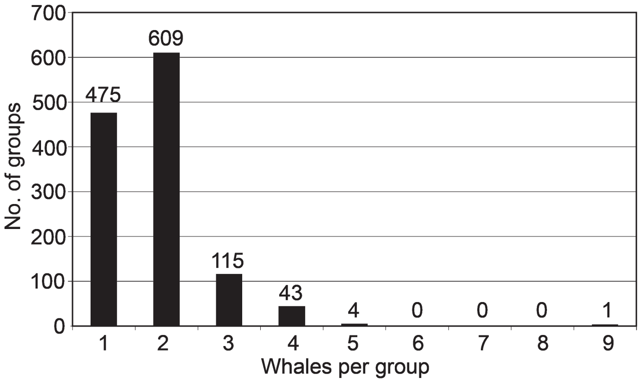

Fig. 3. Numbers of groups seen by size. The number of groups is also displayed above each bar

Absolute abundance estimate I – the Hermite polynomial modelling approach

Of the 1,250 confirmed, northbound groups sighted, 1,212 were seen during complete (or nearly complete) pooled morning and afternoon shifts and were input into *GWNORM*. The model was run for 'grouped' data with migration start and end dates as 15 May and 30 September, respectively. This produced five models corresponding to a normal model plus four Hermite polynomial models with from one to four additional polynomial terms. The one-term (or 'third-order') polynomial model was significantly better than the normal model at explaining the underlying trend in the number of passing groups (AIC = 747.6 and 796.8, respectively), but

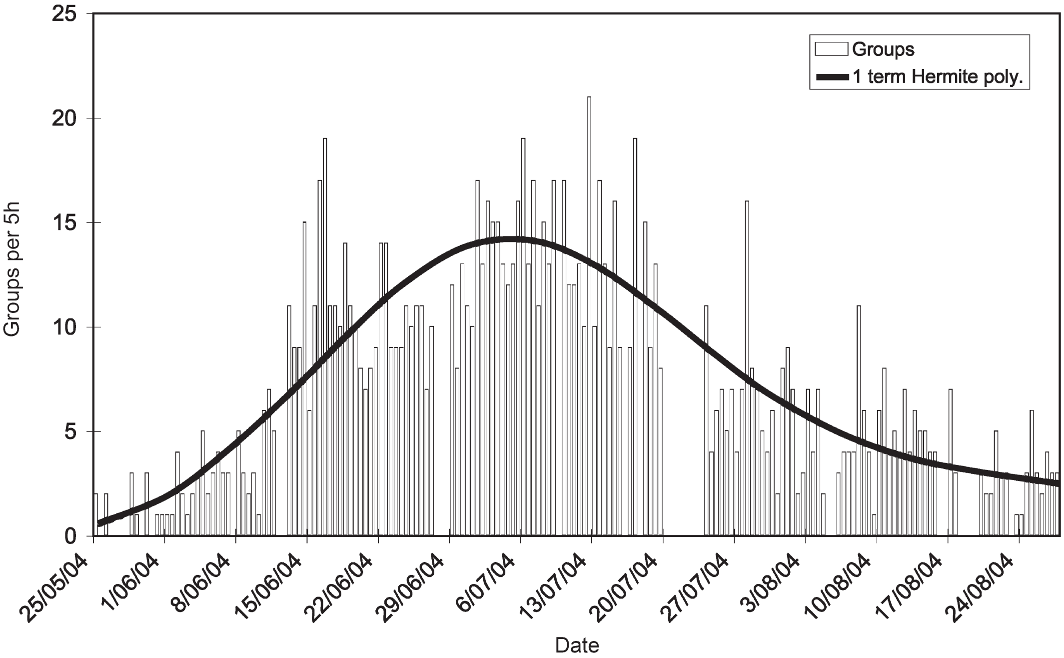

Fig. 4. The one-term Hermite polynomial model produced by *GWNORM* superimposed on the morning and afternoon group counts used as input.

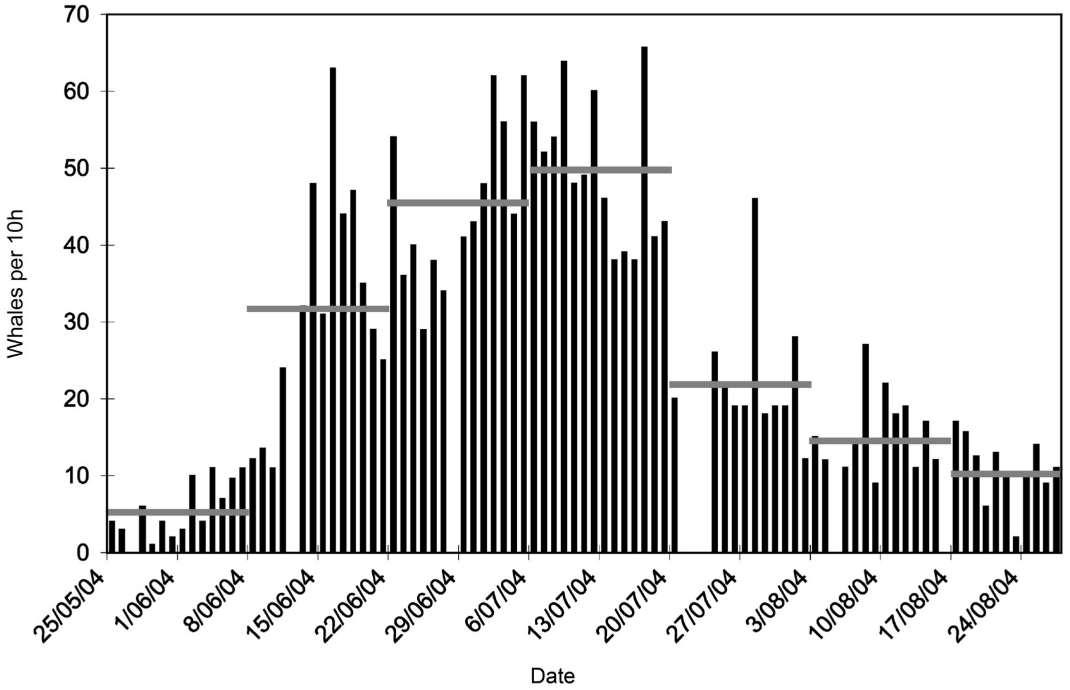

Fig. 5. Confirmed, northbound whales passing per 10h together with strata means (horizontal bars). Except for 27 May and 16 August when no confirmed, northbound whales were seen, gaps are days without survey ($n = 6$). Counts include Norm's Seat data only.

there was no significant improvement using the two-term model (AIC = 747.5). Results for the one-term model are given in Table 1 and the model is shown in Fig. 4.

From this the estimated population passing within the survey period (25 May–27 August) is 6,699 (CV = 3.9%; 95% CI = 6,209–7,226). The estimated population size passing during the entire estimated migratory period (15 May–30 September) was 7,090 (CV = 4.8%; 95% CI = 6,459–7,782).

Absolute abundance estimate II – the stratified random sampling approach

Using stratified random sampling theory, the resulting estimate of the passing population during the survey period (uncorrected for groups available but missed or those passing outside the period of the survey) is 5,965 (CV = 2.6%; 95% CI = 5,668–6,278) (Fig. 5). If f_m is applied to this result to correct for groups available but missed, the population estimate is 6,555 (CV = 3.0%; 95% CI = 6,177–6,956).

Rate of population increase I – relative abundance estimate method

Between the start of the survey and 22 August (inclusive) 1,186 groups were seen passing Pt Lookout. Zero values were added to day 0 (15 May) and day 100 (23 August) and the model run again. The resultant $f_{t(c)}$ was 2.82. This produced a relative abundance estimate P_{RA} of 6,011 whales (SE 200) (Table 2).

Logarithmic regression of P_{RA} from 1981–2004 yields an annual rate of increase of 12.17 ± 1.52% (95% CI) (Fig. 6). As methodology, particularly survey effort, changed considerably in 1991, excluding years prior to 1991 may produce a more realistic estimate: 10.91 ± 2.67% (95% CI) for 1991–2004. Yet another, and probably superior, estimate

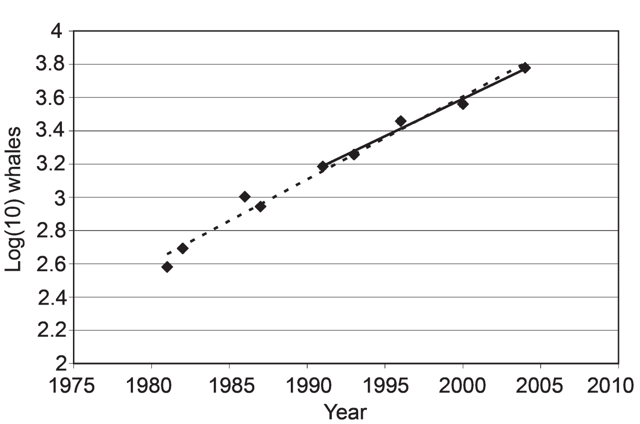

Fig. 6. Linear regression of $\log_{10}$ of relative abundance population estimates from Table 2 against year for all years 1981–2004 (dashed grey line) and for 1991–2004 (solid black line). A constant annual rate of increase will appear as a straight line. Correlation coefficient r is >0.99 for both.

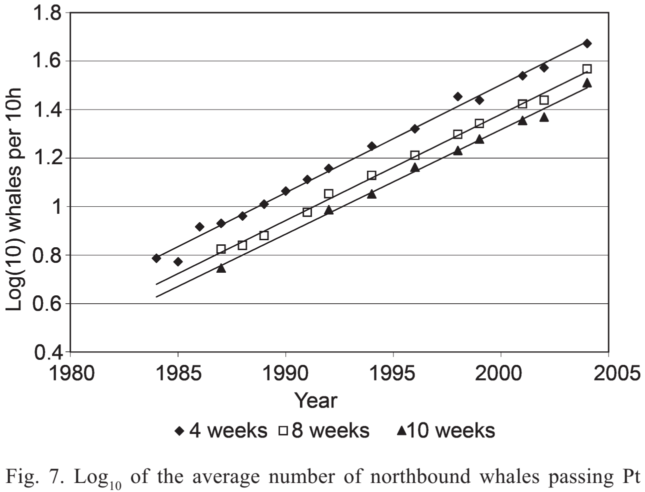

Fig. 7. Log_{10} of the average number of northbound whales passing Pt Lookout per 10h over the four, eight and ten weeks around the peak of migration. All data except for 2004 from Paterson *et al.* (1994, 2001, 2004). Correlation coefficient r is >0.99 for all three data sets.

Table 1

Results of unconstrained Hermite polynomial model. The migratory period was taken as 15 May to 30 September. The skewness of the 1-term polynomial model used produced small pre-survey and large post-survey estimates compared with the normal model. Results in italics were not produced directly by *GWNORM*, but were calculated separately.

Parameter	Value (SE)
No. of groups seen during complete survey shifts (*m*)	1,212 (*37*)
Multiplier to estimate number of groups passing during survey period ($f_{t(s)}$) (25 May–27 August)	2.800 (0.0051)
Estimated number of groups passing during survey period	3,394 (104)
Estimated number of groups passing before survey	4 (3)
Estimated number of groups passing after survey	194 (100)
Estimated total number of groups passing during migration	3,592 (149)
Multiplier to estimate groups passing during the migration ($f_{t(m)}$)	*2.964* (*0.0823*)

Table 2

Relative abundance estimates 1981–2004. Data 1981–2000 from Brown *et al.* (2003).

Year	1981	1982	1986	1987	1991	1993	1996	2000	2004
Groups observed passing 15 May–23 Aug. (*m*)	40	58	107	131	346	345	395	566	1,186
Mean group size (*s*)	1.55	1.67	1.83	1.70	1.64	1.80	1.53	1.61	1.80
$f_{t(c)}$	6.16	5.09	5.15	3.94	2.70	2.91	4.76	3.99	2.82
P_{RA}	381	493	1,008	879	1,533	1,807	2,872	3,634	6,011

would be possible using the survey period absolute abundance estimates for these years as the survey period was similar for all years and variability in estimation of the pre- and post-survey tails would not be included. The $f_{t(s)}$ for the 2000 survey has not yet been published, however.

Rate of population increase II – rate of whales passing method

Fig. 7 is a plot of the logarithm of the number of humpback whales per 10 hour averaged over the four, eight and ten weeks at the peak during the northern migration for each year from 1984 to 2004. Annual rates of increase are shown in Table 3.

Summary of humpback whale survey results

Table 4 presents a summary of the results using the two different methodologies.

DISCUSSION

The results of the 2004 survey support the results of the BB and PC series of surveys conducted previously at Pt Lookout. Despite differences in survey site height and outlook, number and experience of observers, numbers of days surveyed per migration, number of years surveyed and analysis of data, the similarity in relative and absolute abundance estimates of these survey series is remarkable and underlines the robustness of the results previously obtained. The current survey's results again support these results by demonstrating a continuing strong growth in the east Australian humpback population at close to their theoretically maximal rate.

Table 3

Apparent rates of population increase for the east Australian humpback whale population including data from Paterson *et al.* (1994, 2001, 2004).

	Four weeks	Eight weeks	Ten weeks
No. of data points	16	12	9
Annual rate of increase	10.80%	10.62%	10.44%
95% confidence interval	± 0.54%	± 0.48%	± 0.72%
Correlation coefficient (*r*)	0.997	0.998	0.997

For absolute abundance we consider the best estimate to be 7,090 (CV = 4.8%; 95% CI = 6,459, 7,782) as the Hermite polynomial method allows for the tails of the migration to be included. Its slightly larger confidence interval compared with the results of the stratified random sampling theory approach is probably a consequence of modelling a curve to the data rather than allowing the data to shape the strata means more freely. The best estimate of rate of change is 10.6% ± 0.5% (95% CI) using the PC methodology with the eight-weeks-around-the-peak-of-migration index. This gives the smallest CI, combining a large number of data points with slightly less fluctuation around the regression line than the four week data, probably due to its greater spread over the migration. While the BB relative abundance estimate approach has merit and delivers a similar central value estimate, fewer data points have resulted in a much larger CI.

The population remains much lower than estimated pre-exploitation levels with Jackson *et al.* (2006) estimating a median recovery level of around 21% of pre-exploitation levels. Another issue though is whether the pre-exploitation levels can be expected to provide a reasonable expectation of post-recovery carrying capacity. With the removal of huge numbers of predators from the Southern Ocean in the 20th Century, it would be unrealistic to expect no change to the ecosystem. How this might affect a new status quo for whale populations is unknown and only continued monitoring of population levels will allow us to measure this.

While the population trend is strong and robust, the absolute abundance estimates can still be improved upon. Brown *et al.* (1995) biopsied whales during the northward and southward migration in 1992 and found that the sex ratio was skewed with 2.4 males to every female (180 whales sampled). They suggest that not all females migrate along the east Australian coast every year, instead remaining in the southern feeding areas. Dawbin (1997), in an analysis of thousands of humpback whales caught at 11 whaling stations between latitudes of 1° and 41° in the Southern Hemisphere, noted that an average of 1.4 males were caught for every female but considered that the imbalance was probably due to temporal segregation and sampling bias. Dawbin (1997) also showed that the number of immature females migrating was approximately the same as the number of males, so does

Table 4

Summary of results. No result is given for the population estimate over the entire migration for the PC methodology as this does not estimate the contribution outside the survey period. Only the best estimates of the rate of increase are included: that with the smallest 95% confidence interval (PC results) and that which included previous surveys with a standardised methodology (BB results).

Parameter	BB methodology	PC methodology
2004 population estimate over the surveyed period (95% CI)	6,699 (6,209–7,226)	6,555 (6,177– 6,956)
2004 population estimate over the full migration (95% CI)	7,090 (6,459–7,782)	–
Best estimate of rate of population increase (95% CI)	10.91% (± 2.67%) (years 1991–2004)	10.62% (± 0.48%) (years 1987–2004)

not support the Brown *et al*. (1995) hypothesis that it might be immature females that do not migrate. This also seems unlikley as the non-migration of immature females would produce a sex ratio of around 1.7:1 males to females, not the 2.4:1 sex bias reported, and it is not clear why immature females should not migrate while immature males do. Some mature females may not migrate, but with the high reproductive rate requiring an average calving interval of two years, this also seems unlikely as females would, theoretically at least, need to migrate each year to alternately calve and mate. Therefore while there may be more males than females migrating, the ratio is likely to be less than 2.4:1. Further, carefully designed studies need to be directed towards determining the sex bias in the migratory population. If not all females migrate, this would lead to a downward bias in our population assessments.

The other main possible cause of underestimation of absolute abundance (but not relative abundance) is the underlying assumption that most whales pass within 10km of land and that all whales within that range are counted. This is akin to a strip sampling approach that is likely not to be accurate. The difficulty with developing a more robust line transect approach, however, is that the distribution of the whales is not random with a higher density of whales passing through the inshore area. Thus shore-based observations will not provide a robust detection function and future aerial surveys, providing an unbiased measure of distribution, will be required to address this issue.

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Abundance of East coast Australian humpback whales (*Megaptera novaeangliae*) in 2005 estimated using multi-point sampling and capture-recapture analysis

David A. Paton[1,2,3,*], Lyndon Brooks[1,4], Daniel Burns[1,2,4], Trish Franklin[1,2,4,5], Wally Franklin[1,2,4,5], Peter Harrison[1,2,4] and Peter Baverstock[1,4]

Contact e-mail: dave@blueplanetmarine.com

ABSTRACT

The humpback whales (*Megaptera novaeangliae*) that migrate along the east coast of Australia were hunted to near extinction during the last century. This remnant population is part of Breeding Stock E. Previous abundance estimates for the east Australian portion of Breeding Stock E have been based mainly on land-based counts. Here we present a capture-recapture abundance estimate for this population using photo-identification data. These data were collected at three locations on the migration route (Byron Bay – northern migration, Hervey Bay and Ballina – southern migration) in order to estimate the population of humpback whales that migrated along the east coast of Australia in 2005. The capture-recapture data were analysed using a variety of closed population models with a model-averaged estimate of 7,041 (95% CI 4,075–10,008) whales.

KEYWORDS: HUMPBACK WHALE; ABUNDANCE ESTIMATE; PHOTO-ID; CAPTURE-RECAPTURE

INTRODUCTION

Humpback whales (*Megaptera novaeangliae*) in the Southern Hemisphere undertake an annual migration during the austral winter months from their Antarctic feeding areas in higher latitudes to their tropical breeding areas (Chittleborough, 1965; Paterson, 1991). There is temporal segregation of different classes of whales on this migration, with lactating females and yearlings the first to leave the feeding grounds, followed by immature whales of both sexes, mature males and resting females, and lastly pregnant females migrating to the breeding grounds (Dawbin, 1966; 1997). On the return journey to the Antarctic feeding grounds, newly pregnant females are the first to leave tropical waters, followed by immature whales, mature males and resting females, and lastly mothers with calves (Dawbin, 1966; 1997). Chittleborough (1965) concluded that the population of humpback whales that migrate along the east coast of Australia comprises part of the Area V population (130º0’E to 170º0’W). This population was previously known as Group V. Recent studies suggest that the region contains several populations that intermingle to a variable but probably small degree (Garrigue *et al.*, 2000; Garrigue *et al.*, 2011). Group V humpback whales have now been divided into three sub-stocks known as Breeding Stock E(i), those wintering off the Australian east coast, E(ii), those wintering around New Caledonia, and E(iii), those wintering around Tonga (Bannister, 2005; Olavarria *et al.*, 2006). Breeding Stock E(i), the Australian east coast population, is thought to be the largest of these.

Last century, the Area V humpback whale population was subjected to both land and vessel-based hunting from a number of locations throughout its migratory range, including the east Australian coastline and Antarctica. Prior to the 1950s there was little exploitation of this east Australian population. At this time the population size of the entire Group V population was estimated to be between 10,000 and 26,000 whales (Bannister and Hedley, 2001; Chittleborough, 1965). However, these figures are potentially an underestimate of the pre-exploitation population for Group V. The total number of 20th Century and post World War II humpback whale catches in Area V and their purported breeding area (E) was 64,252 (Clapham and Zerbini, 2006) and 38,146 respectively (Clapham *et al.*, 2005). Therefore, it can be assumed that the pre-exploitation population was likely to have been larger for Group V, potentially in the range of 30,000 to 40,000 humpback whales (Jackson *et al.*, 2006).

Massive illegal pelagic whaling in the Southern Ocean, coupled with industrial shore-based whaling, resulted in a major population collapse by 1962 (Chittleborough, 1965; Clapham *et al.*, 2005). Estimates of the remaining population varied from 104 for all of Group V (Bannister and Hedley, 2001) to 500 for the east Australian and New Zealand populations (Chittleborough, 1965), which represents less than 5% of the original estimated population.

Since 1963, the east Australian population of humpback whales has shown signs of partial recovery (Brown *et al.*, 2003; Noad *et al.*, 2011; Paterson *et al.*, 2001). The apparent lack of recovery of the humpback whale population migrating past New Zealand (Constantine *et al.*, 2006; Gibbs and Childerhouse, 2004), and low numbers recorded in some regions of the South Pacific (Garrigue *et al.*, 2002; Garrigue *et al.*, 2000), suggest that most of the humpback whales

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[1] *Southern Cross University, PO Box 157 Lismore, NSW 2480, Australia.*
[2] *South Pacific Whale Research Consortium, Cook Islands Whale Research, Box 3069 Avarua, Rarotonga, Cook Islands, South Pacific.*
[3] *Blue Planet Marine, PO Box 919 Jamison Centre, 2614 ACT, Australia.*
[4] *Southern Cross University Whale Research Centre, PO Box 157 Lismore, NSW 2480, Australia.*
[5] *The Oceania Project, PO Box 646, Byron Bay, NSW 2481 Australia.*
* Current address for correspondence: *PO Box 919, Jamison Centre, Canberra, 2614 ACT, Australia.*

remaining in Area V at the termination of whaling probably form the east Australian population. The most recent abundance estimate for the east coast Australian population of humpback whales utilised land-based counts at Stradbroke Island, Queensland, with an estimate for the 2004 season of 7,090±660 (95% CI) (Noad *et al.*, 2011). However, all methods of estimating abundance have inherent assumptions and biases. Therefore, a more robust population estimate can be obtained by using a number of techniques.

The technique of identifying individual humpback whales by photographing the underside of their tail flukes is widely accepted (Hammond *et al.*, (eds) 1990; Katona *et al.*, 1979), and has been used extensively for capture-recapture analyses to estimate population parameters and abundance (Buckland, 1990; Calambokidis and Barlow, 2004; Calambokidis *et al.*, 1990; Hammond, 1986; Smith *et al.*, 1999; Urbán *et al.*, 1999).

This study represents a capture-recapture population estimate for the portion of the humpback whale Breeding Stock E, which migrated along the east coast of Australia during 2005, using multipoint sampling and fluke identification photographs. To date, most of the estimates of the abundance of the eastern Australian humpback whale migration have been based on simple counts and distance sampling methods. This population estimate is based on an analysis of an ongoing dataset of photo-identification data collected by the authors. We have used the 2005 photo-identification data to establish a point of reference for future photo-identification studies and to provide a point comparison of estimates obtained independently by distance sampling and capture-recapture methods.

METHODS

Study areas and survey effort

Three sampling sites were used on the humpback whale migratory corridor on the east coast of the Australian mainland: Byron Bay in northern New South Wales (NSW); Hervey Bay in Queensland (Qld); and Ballina in northern NSW. All three sites are the locations for long-term independent studies by four of the authors (DP, DB, TF, WF) on the biology, behaviour and population characteristics of eastern Australian humpback whales.

Vessel based photo-identification surveys were undertaken as whales migrated past each of the study sites within one migratory season during the 2005 austral winter and spring months (June–November 2005). Field surveys at each of the study sites were timed to include the major part of the migration on either side of the peak past that location (Dawbin, 1997; Paterson, 1991). Due to the timing of the migration and the locations of the three study sites on the migration corridor, surveys commenced first at Byron Bay during the northern migration, followed by surveys in Hervey Bay and Ballina on the southern migration. There was limited temporal overlap (six days) between sampling during the northern migration at Byron Bay and the commencement of sampling in Hervey Bay during the southern migration. Surveys at Hervey Bay and Ballina were undertaken mostly concurrently during the southern migration. Geographical location, survey effort and equipment used are summarised in Table 1.

The study sites of Byron Bay and Ballina are on the migratory corridor at, or close to, the most easterly point of the Australian mainland, where the vast majority of humpback whales migrate within 10km of the coast (Bryden, 1985). The width of the humpback whale migration corridor was re-assessed in 1991 (Brown, 1997) and 2007 (Noad and Dunlop, 2007), and found to be consistent with the results of Bryden (1985). Humpbacks travel past Ballina and around the eastern point of Australia at Byron Bay, in both a northerly and southerly direction, en-route between the Antarctic feeding grounds and the Great Barrier Reef breeding grounds (Paterson, 1991). At Byron Bay and Ballina, the research vessel was assisted in finding pods of whales by a team of land-based observers using the ‘Cyclopes’ (theodolite/computer) whale tracking system (Kniest and Paton, 2001).

The third study site is located in Hervey Bay, a sheltered, shallow bay formed between the Queensland coast and Fraser Island, 60 n.miles below the southern end of the Great Barrier Reef. During the southern migration, many humpback whales travel into and out of the eastern side of Hervey Bay from the north. The distance between Hervey Bay and the Byron Bay and Ballina study area is approximately 550km (Fig. 1).

A standard sampling protocol for photo-identification was adopted for each sampling site. Photography of ventral fluke surfaces was obtained during a maximum of ten terminal dives and/or a maximum of 45 minutes with each pod (Smith *et al.*, 1999). Photographs of the ventral fluke surface of calves were not included in this study. All images were cropped to a common 3 × 2 pixel ratio as high quality .jpeg digital files.

Photo-identification analysis

The principal photographers examined all images for each of their respective study sites and selected the best single photograph for each individual whale. Composites of multiple images of a single fluke were constructed if these

Table 1

Summary of locations, survey effort and equipment utilised.

	Byron Bay	Hervey Bay	Ballina
Migration direction	North	South	South
Latitude/longitude	28°37’ S, 153°38’ E	25°00’ S, 153°00’ E	28°52’ S, 153°37’ E
General geography	Open ocean off most easterly point of Australian mainland	Shallow, sheltered bay close to western shore of Fraser Island	Open ocean off Ballina and Lennox Head
Dates of survey	04/06/05 to 12/08/05	07/08/05 to 14/10/05	17/08/05 to 04/11/05
Survey period	69	68	79
Number of survey days	50	60	39
Daily effort (Av. hours per day)	7hrs 56mins	7hrs 20mins	6hrs 32mins
Research vessel	5.4-metre centre console powerboat	12-metre power catamaran	5.8-metre centre console powerboat
Photographic equipment	Canon EOS 20D, 100–400mm lens F3.5–5.6 L IS	Canon EOS 20D, 100–300mm lens F3.5–5.6	Nikon D100, 70–200mm lens F2.8 VR, and 1.4X converter
Supported by land-based spotters	Yes	No	Yes
Principal photographer	DP	TF	DB

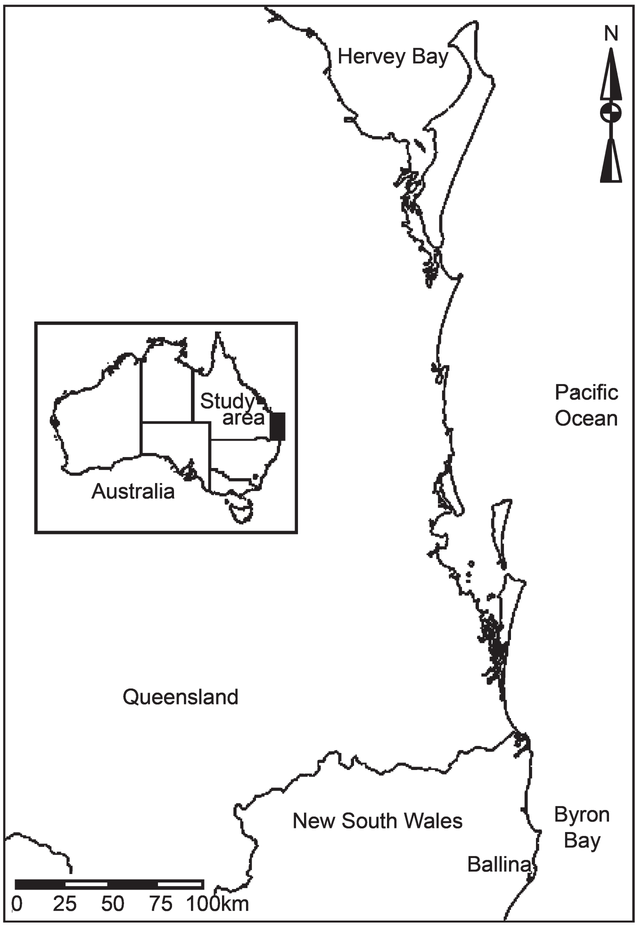

Fig.1. Study area.

provided sufficient information to accurately identify the whale (see Fig. 2). All images for each study site were assessed for within-season resights to eliminate duplicates.

In order to produce the final dataset for analysis, the principal photographers then collectively reviewed the fluke catalogue for each sampling site using a protocol developed in the northern hemisphere for grading humpback whale fluke identification photograph quality (Calambokidis *et al.*, 2001). This included scoring all flukes according to five different characteristics of photo quality: (1) exposure/contrast/lighting; (2) fluke angle; (3) photographer/lateral angle; (4) focus/sharpness; and (5) proportion of fluke visible. Each photograph was given a score from 1 to 5 (highest quality to lowest) for each characteristic, and all flukes with at least one score of 4 or lower (5) were excluded from the dataset.

Prior to matching, each of the principal photographers stratified their catalogue according to one of two independently-evolved fluke matching systems: the Byron Bay and Ballina fluke catalogues were stratified using a system developed by one of the authors (DB), while the Hervey Bay catalogue was stratified using a system developed by another author (TF). The stratified matching systems used in this analysis are based on individual fluke characteristics including percentage black, characteristics of the centre and characteristics of the trailing edge of the fluke for each identification photograph. These systems were used to reduce the number of comparisons required in the matching process.

Pair matching using digital images was conducted by two independent matchers for each site as follows: DB matched Ballina against the Byron Bay and Hervey Bay Catalogues; DP matched Byron Bay against the Ballina and Hervey Bay Catalogues; and TF matched Hervey Bay against the Byron Bay and Ballina Catalogues. All matched flukes, including matches found by only one of the two matchers, were collectively reviewed and reconciled.

Fig.2. Example of a composite image used in the analysis.

Statistical models

Our approach to estimation assumed that the population was closed to immigration, emigration, births and deaths during the sampling period and that images of the same individuals were reliably matched (i.e. no tag loss). After assessing the credibility of the closure assumption and the likelihood of tag loss, we considered a number of different assumptions about the sources of variation in capture and recapture probabilities that might be incorporated in models; whether capture probabilities varied by occasion (temporal variation), differed on any occasion between previously captured and newly captured individuals (behavioural response) or varied among individuals (heterogeneity). The program CAPTURE (Otis *et al.*, 1978; Rexstad and Burnham, 1992) was employed to provide an initial indication of the most likely sources of variation. Finally, the program MARK (Version 5.0: *www.phidot.org/software/mark/*) was employed to fit and compare a set of credible models.

Population closure

The data were collected within one migratory cycle (within a 6 month period). It is assumed that whales migrating north past Byron Bay during the northern migration of 2005 returned south to the feeding grounds along the east coast of Australia during the southern migration and were potentially available for capture at Hervey Bay and/or Ballina. This assumption is supported by a study of genetic diversity (Olavarria *et al.*, 2006), an analysis of interchange rates between eastern Australia and Oceania based on photo-identification (Garrigue *et al.*, 2011) and within-season returns of Discovery marks in the region (Dawbin, 1964). Deaths, immigration and emigration were assumed to have had negligible effects on the estimate. Calves were not included in this analysis, thereby eliminating the effects of births or calf mortality. Therefore, for the purposes of this analysis, the population was considered to be closed.

Tag loss

Effective tag loss resulting in an overestimate of the population size may have occurred in this study if flukes changed markings between sampling occasions, and might have occurred if poor quality, difficult-to-match photographs had been included. Significant changes in natural fluke markings are likely to have been minimal during the short survey period. The use of a widely accepted protocol, based on photo quality (Calambokidis *et al.*, 2001), minimises the potential for tag loss due to poor image quality.

A further source of effective tag loss may be human error in failing to match fluke photographs. By using two independently evolved stratification systems and having two independent matchers each separately conduct the match for each site, before reconciling the results, the probability of missing a match is considered to be low.

Time-specific capture probabilities

Survey effort varied among the sites (Table 1) with approximately 397, 440 and 255 survey hours at Byron Bay, Hervey Bay and Ballina respectively. Environmental conditions, vessel speeds and survey protocols also varied slightly. It is highly likely therefore that capture probabilities were variable among the sites and lower at Ballina than at the other two sites in particular.

Behavioural response

Whilst there is no reason to expect that whales either sought or avoided the survey vessels following capture, there is reason to consider it possible that apparent behavioural response was present in the data due to non-random mixing between samples. Dawbin (1997) reported that the migration is structured in a temporal sequence led by lactating females and yearlings, immature whales of both sexes, mature males and resting females, and lastly pregnant females migrating to the breeding grounds. This sequence is largely the same during the migration south, with newly pregnant females the first to leave the breeding grounds, followed by immature whales, mature males and resting females, and lastly mothers with calves (Dawbin, 1966; 1997). Although the surveys were timed to spread across a sizeable part and centred on the expected peak of the migration past each of the sites, it is possible that such classes of whales were not present in the same proportions during the survey periods at the three sites. Under these circumstances, the whales captured at a site may be more or less prevalent with probabilities of recapture at subsequent sites that differ from the probabilities of first capture at those sites, inducing apparent behavioural response.

Heterogeneity of capture probabilities

The probability of capture of a whale is conditional on the time it is available for capture at a site, its response to vessels and its fluking behaviour. The typical time spent in the presence of vessels and the typical frequency and duration of fluking activity may vary among such classes of whales as immature whales, mature resting females, mature males and mothers with calves (Rice *et al.*, 1987). Following the previous example, mothers with calves may be more or less likely to fluke up than other whales and indeed may typically spend a shorter or longer period in Hervey Bay. Therefore, heterogeneity of capture probabilities is possible.

Tests of assumptions and goodness of fit

The seven tests from program CAPTURE (Otis *et al.*, 1978; Rexstad and Burnham, 1992) were run to gain insight into a likely appropriate model structure. However, given the potential complexity of the data-generating process and a high probability of time-specific capture probabilities, it's notable that CAPTURE provides no tests for the pertinent comparisons of M_t vs M_{th} or M_t vs M_{tb}.

The full likelihood-based closed capture models available in the program MARK (Version 5.0: *www.phidot.org/software/mark/*) provide a means of fitting a number of models of the forms M_t and M_{tb} (Otis *et al.*, 1978). These models were compared by means of the minimum AICc criterion (Williams *et al.*, 2002), and estimates from a set of selected models were averaged following the procedure of Buckland *et al.* (1997). Modelling was restricted to these models except for the non-likelihood based M_{th} model of Chao *et al.* (1992) which was employed to provide an informal comparison of its estimate to those from the M_t and M_{tb} models referred to above.

RESULTS

A total of 1,085 fluke photographs were assessed for inclusion in the analysis (Byron Bay 406, Hervey Bay 391, Ballina 288). Following collective evaluation of each image against the photograph quality protocols, 222 fluke photographs were excluded from the dataset based on photographic quality. The final dataset comprised a total of 863 fluke photographs (Byron Bay 343, Hervey Bay 321, Ballina 199). Of these, 829 whales were determined to be unique individuals, with a total of 34 (4.1%) whales being captured at two different survey sites during the study period. No whales were sampled at all three survey sites within the study period. The matches and frequencies of capture histories are reported in Table 2.

Tests of the assumptions

The goodness of fit tests from program CAPTURE (Otis *et al.*, 1978; Rexstad and Burnham, 1992) indicated probable behavioural response (test 2: M_0 vs. M_b), probable time-specific variation in capture probabilities (test 3: M_0 vs. M_t), probable heterogeneity in capture probabilities (test 4: M_h vs. not M_h), probable behavioural response (test 5: M_b vs. not M_b), and probable behavioural response in the presence of heterogeneity (test 7: M_h vs. M_{bh}). The expected values were too small to test for heterogeneity (test 1: M_0 vs. M_h) or time-specific variation (test 6: M_t vs. not M_t). CAPTURE suggested that the appropriate model was probably M_{tb} but encountered a computational problem in trying to fit the model and did not produce a reliable estimate (offering 28581).

Among the set of eight full and reduced M_t and M_{tb} likelihood based models (Otis *et al.*, 1978) that might notionally be fitted, it was not possible to simultaneously estimate the six parameters of the most general of these models with different capture probabilities at each site and recapture probabilities different both to each other and any capture probability. This is because at least one constraint relating the capture and recapture probabilities is required for identification. Among the remaining seven models of this type, a model that proposed equal capture probabilities in

Table 2

Frequencies of capture histories.

Byron Bay	Hervey Bay	Ballina	Frequency
1	0	0	319
0	1	0	297
0	0	1	179
1	1	0	14
1	0	1	10
0	1	1	10
1	1	1	0

Table 3

Results from six full and reduced M_t and M_{tb} models.

Model[1]	AICc	ΔAICc	AICc wt.	Likelihood	Params.	Deviance	Nhat	SE	L95%CI	U95%CI
112123	–7417.436	0.000	0.340	1.000	3	10.462	7,024	1,139	5,163	9,685
123234[2]	–7416.195	1.241	0.183	0.538	4	9.697	7,021	1,138	5,160	9,680
112324	–7416.033	1.403	0.169	0.496	4	9.859	6,303	1,298	4,290	9,486
112134	–7415.775	1.662	0.148	0.436	4	10.118	7,843	2,007	4,876	12,985
123435	–7414.554	2.883	0.081	0.237	5	9.330	6,447	1,346	4,365	9,754
123245	–7414.528	2.908	0.079	0.234	5	9.356	7,834	2,005	4,871	12,971

[1]The models are numbered according to their parameters: capture probabilities in Byron Bay, Hervey Bay and Ballina, recapture probabilities in Hervey Bay and Ballina, and the estimated population size. Where a subsequent parameter is specified as equal to a previous one, the previous parameter number is used. For example, model 112123 indicates the same capture probabilities in Byron Bay (1) as in Hervey Bay (1) but a different capture probability off Ballina (2); that the recapture probability in Hervey Bay is the same as the capture probability in Hervey Bay (= Byron Bay) (1), and that the recapture probability off Ballina (2) is the same as the capture probability off Ballina (2). The population estimate parameter takes the next value (3). [2]Darroch M_t.

Byron Bay and Hervey Bay and that the two recapture probabilities differed both from each other and from any capture probability also lacked the required constraint and produced an unrealistically low estimate of population size (3,059). Pertinent results from the remaining six models are reported in ascending order of AICc in Table 3.

Among a small set of models that assumed equal capture probabilities, the best fitting (111234) had an AICc that was 5.59 larger than the worst fitting of the M_t and M_{tb} models in Table 3 (123245) indicating, as expected, a high probability of time-specific variation in capture probabilities.

For comparison with the estimates provided by this set of models, the M_{th} model (Chao *et al.*, 1992) from program CAPTURE provided an estimate of 7,014 (95% CI 5,163–9,685) with equal probabilities of capture off Byron Bay and in Hervey Bay.

Model selection

The deviances of these models were very similar and the minimum AICc criterion accordingly ordered the models largely in terms of parsimony, i.e. it favoured models with fewer parameters. Although *c*-hat could not be estimated, an experiment in which its value was assumed to be 2 resulted in the more parsimonious models being even more strongly favoured in terms of relative AICc values.

Population estimate

The range of population estimates (6,303–7,843) among the models reported in Table 3 was not wide relative to the width of the confidence intervals. Consequently, the considerable uncertainty encountered in selecting among the models on the basis of AICc was not as serious a limitation on obtaining a reasonable estimate as it might otherwise have been. However, if only one of these models were to be chosen for interpretation it would be the simplest, with a likelihood nearly twice the size of that of the next most likely model; i.e. the 3-parameter model (112123) which assumed equal capture probabilities at Byron Bay and in Hervey Bay, and recapture probabilities equal to capture probabilities (no behavioural response). Further in favour of this model, if overdispersion were present in the data, as would be reflected in a higher *c*-hat, its likelihood would have been even greater relative to the other models. This model provided an estimate of 7,024 (95% CI 5,163–9,685) whales, which lies approximately in the middle of the range of the several estimates. Nonetheless, while apparent behavioural response cannot be excluded theoretically, and the four models in the set that do assume some form of apparent behavioural response cannot be reliably distinguished among nor from the simpler models by the AICc criterion, it may be appropriate to use the very similar model-averaged estimate of 7,041 (95% CI 4,075–10,007) whales.

None of the models considered so far has treated animal level heterogeneity of capture probabilities. As a point of reference, the M_{th} model of Chao *et al.* (1992) provided an estimated population size of 7,014 (95% CI 5,133–9,718) whales.

DISCUSSION

This collaborative study represents a multi-point sampling capture-recapture abundance estimate using photo-identification for humpback whales migrating along the east coast of Australia during 2005. It was known from previous research that the migration has a temporal sequence of different classes of whales. It was considered particularly important on this account that the surveys at each site were timed to include the major part of the migration on either side of the peak past that location in order to repeatedly sample from the entire population rather than from a somewhat different subset at each site. It was expected that apparent behavioural response would be manifested in the models to the extent that we were unsuccessful in this and that the whales sampled at one site were present in greater or lesser proportion at another. There was some evidence of this in as far as the models displaying a behavioural response structure could not be reliably distinguished from those that did not by the AICc criterion. Nonetheless, the simplest model with equal capture probabilities at Byron and Hervey Bay and no behavioural response had twice the likelihood of any behavioural response model. While this situation may have created a dilemma had these models produced markedly different population estimates, the similarity of the estimate from this model and the model averaged estimate which included the behavioural response models is reassuring.

Another recent abundance estimate for this population was based on land-based counts from Stradbroke Island, with an estimate for the 2004 season of 7090±660 (95% CI) and an annual increase of 10.6± 0.5% (95% CI) (Noad *et al.*, 2007). Extrapolating this figure to 2005 would produce an estimate of 7,842 (95% CI 7,112–8,572). Here we have estimated of the number of whales that migrated along the east coast in 2005 and provide a single best estimate of 7,024 (95% CI 5,163–9,685) whales and a model averaged estimate of 7,041 (95% CI 4,075–10,007) whales.

Further considerations

Data collection over a series of seasons would enable a more accurate, reliable and informative analysis through the use of a robust design model (e.g. Kendall and Nichols, 1995; Kendall *et al.*, 1997; 1995).

This analysis only considers humpback whales that undertook migration along the east coast of Australia during 2005. However, Brown *et al*. (1995) suggested that a percentage of females may not undertake the migration annually. This hypothesis could be tested by undertaking inter-year capture-recapture studies.

Chaloupka *et al*. (1999) suggest that only a portion of the whales migrating along the east coast of Australia enter Hervey Bay and therefore would not be available for sampling in Hervey Bay. This factor will not bias this analysis assuming that these whales were available for capture at Byron Bay and Ballina. Aerial surveys off the coast of Byron Bay and Ballina would also help to establish the width of the current migration corridor, and determine whether it is possible that some whales are not available for capture at any of the three sites because they migrate further offshore at Byron Bay and Ballina and do not enter Hervey Bay.

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Population growth of Australian East coast humpback whales, observed from Cape Byron, 1998 to 2004

DAVID A. PATON*,+,# AND ERIC KNIEST+,^

Contact email: dave@blueplanetmarine.com

ABSTRACT

Humpback whales (*Megaptera novaeangliae*) that migrate past the east coast of Australia comprise part of Group V (E(i) breeding stock). From 1995 to 2004 an annual 16 day survey was conducted from Cape Byron (28°37'S, 153°38'E), the most easterly point on the Australian mainland, monitoring the peak of the humpback whale northern migration. The annual rate of increase between 1998 and 2004 of humpback whales observed off Cape Byron is 11.0% (95% CI 2.3–20.5%). This rate of increase is consistent with that recorded from other studies of the humpback whale population off the east coast of Australia. The large confidence intervals associated with this estimate are due to considerable inter-annual variation in counts. The most likely explanation for this being the short survey period, which may not have always coincided with the peak of migration, and in some years a large proportion of whales passed Cape Byron at a greater distance out to sea, making sightability more difficult.

KEYWORDS: HUMPBACK WHALE; SURVEY-SHORE-BASED; TRENDS; GROWTH; MIGRATION; SOUTHERN HEMISPHERE; PACIFIC OCEAN

INTRODUCTION

Humpback whales (*Megaptera novaeangliae*) migrate north from Antarctica, along the east and west coasts of Australia during the Austral winter, to breed and give birth in the warm waters of northern Australia. The humpback whales that pass the east coast of Australia are thought to comprise part of the group that feeds in Antarctic Area V (130°E to 170°W). This group is therefore identified as 'Group V whales'. Recent studies suggest that there is sub-stock structure on the tropical breeding grounds and that these sub-stocks intermingle to at least a small degree (Garrigue *et al.*, 2000). Group V humpback whales on their tropical breeding grounds have been divided into three sub-stocks known as: Breeding Stock E(i), those wintering off the Australian east coast; E(ii), those wintering around New Caledonia; and E(iii), those wintering around Tonga (Bannister, 2005; Olavarria *et al.*, 2006). Breeding Stock E(i), the Australian east coast population, is the largest.

Historically, the Group V population was hunted from both land- and vessel-based operations throughout its migratory range, including the East Australian coastline and the Antarctic. Land-based whaling was conducted from several locations on the east coast of Australia, commencing in 1952. These locations included Twofold Bay, Jervis Bay, Byron Bay and Tangalooma on Moreton Island. Other locations where whaling activities occurred in the South Pacific include Norfolk Island, Cook Strait in New Zealand and Tonga. Small numbers of whales were also taken in Fiji and Vanuatu. Considerable illegal hunting of humpback whales was undertaken in Antarctic waters from 1959 to 1961 by the Soviet Union (Clapham *et al.*, 2005; Paterson *et al.*, 2001).

Prior to the 1950s there was little exploitation of the E(i) sub-stock. At this time the population size of the entire Group V population was estimated to be between 10,000 and 26,000 whales (Bannister and Hedley, 2001; Chittleborough, 1965). These figures are potentially an underestimate of the pre-exploitation population for Group V as the total number of 20th century humpback whale catches in Area V and in breeding area (E) was 102,398 whales (Clapham *et al.*, 2005; Clapham and Zerbini, 2006). Given the large number of whales killed and recent population modelling, it is now thought that the pre-exploitation population of the Group V whales was considerably larger than previously thought, potentially in the range of 30,000 to 40,000 humpback whales (Jackson *et al.*, 2006).

The industrial shore-based whaling and large scale illegal pelagic whaling in the Southern Ocean resulted in a population collapse by 1962 (Chittleborough, 1965). Estimates for the remaining population vary in size from 104 for all of Group V (Bannister and Hedley, 2001) to 500 for the east Australian and New Zealand populations (Chapman, 1974; Chittleborough, 1965). These estimates are less than 5% of the pre-exploitation size. In the 45 years since 1963, the east Australian population of humpback whales is one of a number of populations that has shown strong recovery (Brown *et al.*, 2003; Paterson *et al.*, 2001). The apparent lack of recovery of whales migrating past New Zealand (Childerhouse and Gibbs, 2006; Gibbs and Childerhouse, 2000), and low numbers recorded in some regions of the South Pacific (Garrigue *et al.*, 2002; Gibbs *et al.*, 2003), indicate that the strong increases seen in East Australia have not been seen across other parts of the South Pacific.

Shore-based observation stations have been utilised to monitor trends in a number of populations of cetaceans (Bryden *et al.*, 1996; Buckland and Breiwick, 2002; Paterson *et al.*, 2004). Long term studies have been conducted on humpback whales in Cape Vidal, Natal (Findlay and Best, 1996b) and North Stradbroke Island, Australia (Brown, 1996; Bryden *et al.*, 1996; Noad *et al.*, 2011; Paterson *et al.*, 2004). Humpback whales migrate along the continental

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* *Blue Planet Marine, PO Box 919 Jamison Centre, 2614 ACT, Australia.*

+ *South Pacific Whale Research Consortium, c/o Cook Islands Whale Research (CCRC) Box 3069, Avarua, Rarotonga, Cook Islands.*

Southern Cross University, PO Box 157, Lismore, NSW, Australia.

^ *University of Newcastle, School of Engineering, University Drive, Callaghan, NSW 2308 Australia.*

inshore waters along the east coast of Australia. Bryden (1985) demonstrated that the migratory corridor between Cape Byron and Cape Moreton, was particularly narrow, with 96% of humpback whales passing within 10km of headlands within this region. The width of the humpback whale migration corridor was reassessed in 1991 (Brown, 1996) and 2007 (Noad and Dunlop, 2007) and found to be consistent with the results of Bryden (1985).

The demonstrated effectiveness of using shore-based observations to monitor cetacean population trends combined with the fact that humpback whales are known to migrate close to the coast off northern New South Wales, make Cape Byron an ideal location for a long term assessment of the recovery of the E(i) Breeding Stock. This paper reports on land-based counts collected between 1998 and 2004 and the observed increase in humpback whales observed off Cape Byron during this period.

MATERIALS AND METHODS

Cape Byron is located at the most easterly point on the Australian mainland (28°38'S, 153°38'E). Early surveys were conducted from a location (28°38'19"S, 153°38'10"E) *ca*. 200m from the most easterly point on Cape Byron. This location has an altitude of 83m and unobstructed visibility from the south-southeast to the north-northeast (190º–346º). The Cape Byron Whale Research Project (CBWRP) operated at this location from 1995 until 1998. For the 1999 survey the CBWRP relocated to a location on the upper balcony of the Cape Byron Lighthouse. This location (28°38'19"S, 153°38'11"E) is 173m from the original land-based survey location and is 33m higher (total height is 116m above sea level). The new survey location has a slightly better outlook (south-southeast to the north-northwest) and has access to a reliable power supply for operating a computer. It also provides shelter during inclement weather and improved accuracy for distance determination because of the increased altitude.

The timing for the CBWRP was based upon historical whaling data collected at the Byron Bay station, which operated between 1954 and 1962 (Chittleborough, 1965). During this period 1,146 whales (primarily humpback whales) were taken near Byron Bay (Chittleborough, 1965). The survey period was chosen to coincide with the peak of the catches at the whaling station during the northern migration as it is assumed that this peak catch related to the peak in numbers of the northern migration. Observations were carried out from the land station during a 16-day period annually (i.e. last week of June and first week of July). Observations were carried out between the hours of 07:00 and 16:30 daily, weather permitting. Observations were suspended when rain made it impossible to undertake surveys; when wind strength reached a point making it impracticable to operate (25–30 knots) or lightning activity made it unsafe to be in the lighthouse. Two shifts operated each day with a 15 minute overlap, the first from 07:00 to 12:00 and the second from 11:45 to 16:30.

A software package named 'Cyclopes' was developed by staff and students from the University of Newcastle, Australia specifically for the CBWRP to improve and allow more reliable tracking of marine mammals and vessels. This real time tracking system uses an electronic theodolite interfaced to a laptop computer. The theodolite is used to acquire the location of the pod by measuring the horizontal and vertical angles to the pod, which are sent directly to the computer. Cyclopes then calculates the position of the pod correcting for tides, earth curvature and refraction. The program determines which pod was observed and plots its position on a map shown on the computer screen. Cyclopes also has the capability to record information regarding the pod's make up, activity, speed, course, distance, direction and time of observation (Kniest and Paton, 2001).

The project operated with a mean of six observers (range 2–8). Due to operational requirements, during lighthouse tours (about half an hour a couple of times a week), the survey team was reduced to two experienced observers for this short period. Survey effort was consistent over the period of the study (1998–2004). Normal survey operations included at least two observers scanning the ocean to the south and east of the Cape, and at least one scanning to the north of the Cape. For over 90% of the observation period, an experienced observer was present to confirm sightings of pods, species and composition. An observer was deemed to be experienced if they had already been involved with the project for two years, or if they had several seasons of prior field experience working with humpback whales. A research vessel worked in conjunction with the land station to undertake fluke photo-identification, confirmation of pod size, collection of behavioural data and to collect genetic samples.

Observers used both the naked eye and binoculars (7×50 Tasco compass binoculars and 10×50 Nikon binoculars) to detect whales. Once pods were sighted, a theodolite operator (who was in addition to the dedicated observers) using a Leica TC1105 (or similar) theodolite would take fixes on the location of the pod and track movement of the pod while within the field of view of the land station. When additional personnel were available a person was dedicated to operating Cyclopes and assisting the research vessel to locate pods. At all times at least one observer was scanning for new pods.

Records of effort and weather were kept during all observation periods. Weather information including wind speed and direction, cloud cover, sea state (Beaufort), swell, visibility (estimated in km) and any other factors such as smoke haze, were recorded using Cyclopes' weather recording function. In addition Cape Byron headland has a meteorological station with detailed weather information available for the site from the Australian Bureau of Meteorology.

When pods were first observed and an experienced observer confirmed the species, the observers would estimate pod composition and continually track each pod as it approached the Cape from the south. The pod composition would be adjusted (and confirmed by an experienced observer) when necessary. Careful notes were taken when pods split or joined, or there was a sudden change in behaviour. Pod composition was confirmed by the research vessel when the vessel intercepted the pod. The research vessel, under normal operating protocols, operated north of the Cape so as not to potentially disturb the movements of whales prior to passing the Cape.

Observers would monitor a pod's activity and direct the theodolite operator to the surfacing of pods. Where possible one event out of each surfacing cycle would be fixed using Cyclopes to monitor the movement pattern of the pod. Once a number of sightings of the pod were recorded, the program was able to predict the direction and speed of travel and any changes in course or speed. These data were plotted in real time on the computer screen showing the trackline of pods passing the land station. The program was extremely useful in eliminating duplicate counts of the same pod especially when pods were located close together or when a pod was lost for a period of time.

ANALYSIS

To determine the number of whales (and pods) migrating past the Cape during the survey period, all sighting data were converted to a standard 10hr day, consistent with the methodology used in other migratory humpback whale surveys (Brown, 1996; Bryden *et al.*, 1996; Findlay and Best, 1996b; Paterson *et al.*, 2004). The standard survey period was 9.5hr, therefore sighting rate was scaled pro-rate to a 10hr survey period. Due to the expansive field of view from the land station (over 180°), only pods that had crossed a line due east of the Cape during the survey period were included in the analysis. The time each pod passed the line extending east of the cape was calculated by projecting from the pod's closest observed position along a line representing its mean course and speed. These pods were included in the analysis if they were determined to have passed east of the Cape during the survey period. Only humpback whales observed travelling in a northerly direction were included in the analysis.

To avoid double counts or missing whales when pods split into separate groups or when other whales would join a previously tracked pod, the number of whales was only counted in the initial pod. After an affiliation or disaffiliation of a pod occurred, the new pods formed would be assigned new names. During analysis these pods would have the number of whales in the pod set to zero (although the pod composition is still noted). For example if pod 'D' (size = 1) joined pod 'H' (size = 2), the new pod formed would be called 'H/D' with composition noted as 3 but the pod size is assumed to be zero for the sake of determining whale counts; and the new pod is not included in the count as an extra pod.

Determining which days should be excluded from the analysis due to adverse weather can be subjective. For the purposes of this analysis, the following protocol was used for the exclusion of days: (1) days with a mean sea state greater than Beaufort 3 and/or mean visibility less than 15km for extended periods; and (2) days on which fewer than five hours of survey were conducted.

Each day's count was converted to a standard 10hr count for that day, given by:

$$C_i = 10/\mathrm{h}_\mathrm{i} \times N_i$$

Where:

i is the i^{th} day of the survey

h_i is number of hours of survey for the i^{th} day (5hr < h_i < 10hr)

N_i is the number of whales that passed the survey point during the h_i hours.

The mean 10hr count (R_y) for each year was calculated from all the daily 10hr counts (C_i, where $i = 1$ to D_y, and D_y = the number of days surveyed for year y). A simple linear regression was fitted to the natural log of the mean 10hr count for each year (R_y) over the survey period to determine the growth rate (percentage increase per year).

A growth model has also been fitted by generalised least squares. Full details of the growth model are shown in Appendix 1.

RESULTS

Between 1998 and 2004 a total of 105 days (897hr, 45min) of land-based surveys were conducted from Cape Byron. During this period a total of 1,768 pods, comprising 3,340 humpback whales (including 19 neonate calves) were observed travelling north past the Cape. Nineteen pods of humpback whales (i.e. 1% of all pods seen), were observed to have a direction of travel other than in the general north direction (i.e. east, southeast or southwest). These pods were typically observed to be moving in a direction to interact with other pods of humpback whales. No pods were observed with a clear southerly migration direction during the survey. It is therefore assumed that, during the survey period all pods of humpback whales observed off Cape Byron have a clear northerly migration direction and therefore all pods were included in this analysis.

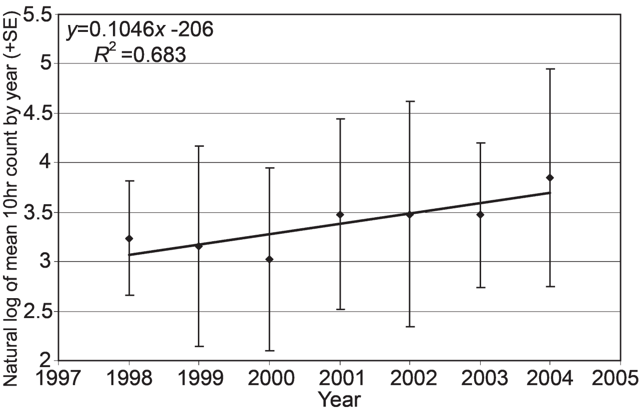

Fig. 1. Natural log of the mean 10hr count by year with standard errors show. A simple linear regression has been fitted.

Most years of the CBWRP survey suffered from days with poor weather conditions and therefore not all days were surveyed. Other days were surveyed with below average conditions (such as rough seas) and have been eliminated from the analyses. Both 1999 and 2000 had a higher proportion of bad weather days than other years. Four days were lost due to rain in 1999 and another four days were removed because of rough seas or poor visibility.

Fig. 1 indicates the increase in the mean number of whales observed per 10hr for the seven years of the survey. Based on the fitting of a simple linear regression to the log of the mean 10hr counts for the 16-day survey period, the annual growth rate for the humpback population was estimated to be 11% (95% CI 2.3–20.5, see Appendix 1).

The seven-year survey had large variations in the mean distance offshore of pods as shown in Fig. 2. In 1998 and 2004, whales passed significantly closer to the Cape Byron survey station than other years except 2002 ($p<0.05$ ANOVA, post hoc Bonferroni Test). The overall mean number of humpback whales in each pod was 1.9±0.16 with slightly higher values in 1998 and 2004. The mean pod speed is reasonably consistent over years (Table 1). There was an increase in the number of newborn calves observed over the survey. The number of newborn calves observed annually, is approximately 0.5 to 1% of the total number of whales observed. Most pods had a composition of one (38%), two (43%) or three (12%) animals, while the rest of pods had between four to eight (7%) animals.

DISCUSSION

The annual rate of increase between 1998 and 2004 for humpback whales observed off Cape Byron is calculated to be 11.0% (95% CI 2.3–20.5). This annual rate of increase is consistent with results recorded at Point Lookout, North Stradbroke Island (134km north of Cape Byron) by two

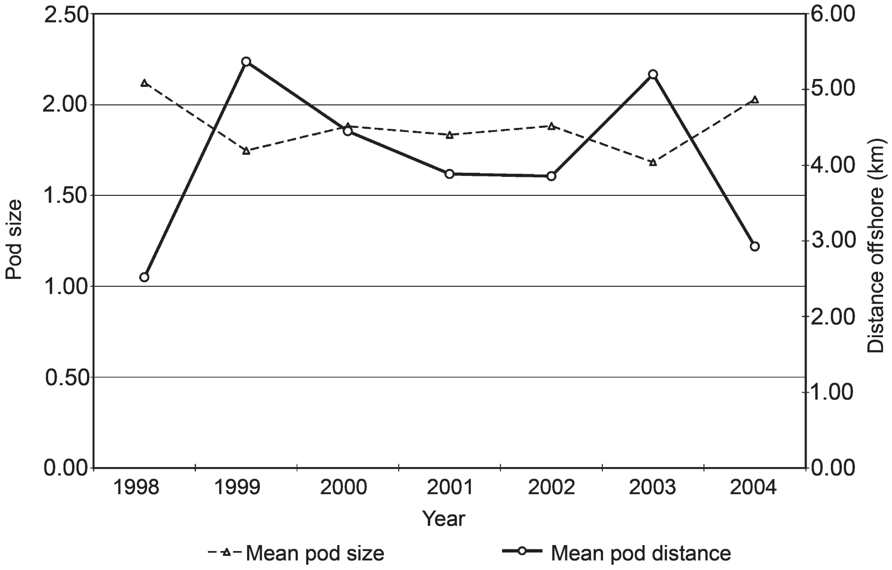

Fig. 2. Graph of the mean pod distance off shore and pod composition from 1998–2004.

independent land-based surveys. Surveys conducted by Paterson (Paterson *et al.*, 2004) estimate a growth rate of 10.5% per annum for the humpback whale population from 1984 to 2002. Other surveys conducted by Bryden *et al.* (1996) and Brown (1996) reported slightly higher annual rates of population recovery of about 12.3%. Brown *et al.* (2003) reassessed the Bryden/Brown data using more appropriate models and re-estimated the population increase (1981–2000) to be between 8.52% and 10.08%. However, Noad, continuing the Bryden/Brown surveys, reported a 10.6% (95% CI 10.1–11.1%) for the period 1987–2004 (Noad *et al.*, 2011) and an increase of 10.9% (95% CI 10.5–11.4%) for the period 1984–2007 (Noad *et al.*, 2008). While these population growth rates lie near or above the theoretical reproductive maximum of the species (Bannister and Hedley, 2001; Best, 1993; Brandao *et al.*, 1999; IWC, 2008), which on the whole, are based on life history estimates for Northern Hemisphere humpback whale stocks where estimates for population growth rates are lower than determined for the southern hemisphere, (IWC, 2008), they are remarkably consistent over time with a very tight correlation between log-transformed, normalised whale counts and year (Noad *et al.*, 2011).

While this survey provides a useful estimate of population growth rate for the E(i) breeding stock, there are several important considerations and some potential sources of bias that may influence the CBWRP estimate. There are several explanations for the observed variation in the number of whales counted per 10hr period over the survey period:

(1) there are large inter-annual variations in the number of humpback whales migrating up the east Australian coast;
(2) some of the surveys were influenced by bad weather or poor visibility conditions;
(3) the short (16 day) survey missed some of the peak migration period in some years; and
(4) large variations in the average pod distance out to sea may lead to differences in their sightability.

A degree of inter-annual variation is expected when monitoring a natural system. Forestell *et al.* (2003) suggested that El Niño-Southern Oscillation (ENSO) events may have a significant impact on fluctuations in whale numbers on the east coast of Australia. They suggested that humpback whales might migrate to other foraging areas in the high-latitude feeding grounds as a result of ENSO-related effects on food stocks. The whales might then migrate from there to different low latitude breeding grounds leading to variation in the number of whales observed between years. However, the long term survey conducted by Paterson from North Stradbroke Island shows little variation in the overall humpback whale population count over the years (Noad *et al.*, 2011; Paterson *et al.*, 1994; 2001; 2004); there is no indication of large fluctuations in the migrating population from year to year. Clapham and Zerbini (2006) have also suggested that the rapid growth rate of the E(i) breeding stock may be a result of immigration from other populations. While these theories are plausible, the South Pacific Whale Research Consortium recently tested this hypothesis by undertaking an assessment of fluke identification

Table 1

Yearly summary of data collected from CBWRP, 1998-2004. The average pod distance is the estimated distance from the coastline to the pod. The average pod speed is given in km/h, and distances are in kilometres.

Year	Raw count	10hr count ± SE	Average pod size	Average distance	Average speed	No. of calves	Max. pod size	Max. distance
1998	375	25.47 (±1.79)	2.12	2.52	6.49	0	5 (4 pods)	8.5
1999	229	23.38 (±2.75)	1.75	5.37	6.11	1	7 (1 pod)	13.6
2000	302	20.52 (±2.52)	1.88	4.45	5.88	0	5 (4 pods)	15.2
2001	522	32.33 (±2.62)	1.83	3.88	6.16	3	5 (1 pod)	18.4
2002	563	32.36 (±3.13)	1.88	3.85	5.70	3	8 (1 pod)	15.3
2003	505	32.12 (±2.09)	1.68	5.20	5.39	5	5 (2 pods)	16.6
2004	814	47.02 (±3.01)	2.03	2.93	6.20	7	8 (1 pod)	15.8

photographs collected throughout Oceania (Breeding Stocks E(ii), E(iii) and F) and eastern Australia (Breeding Stock E(i)). This analysis, coupled with the recovery of Discovery marks from this region, indicates a very low level of interchange between eastern Australia and the Oceania region, which does not support this theory (Garrigue *et al.*, 2011a; Garrigue *et al.*, 2011b; Paton and Clapham, 2006).

Brown *et al.* (1995) report a bias in the sex ratio of humpback whales sampled off the east coast of Australia. They suggest that not all animals migrate every year as there is little reason for females who are not calving or mating to make the long migration. This may mean that, depending on environmental conditions, there may be inter-annual variation in the proportion of females undertaking migration, which in turn may lead to variation in survey counts. This issue remains unresolved with respect to eastern Australian humpback whales but has the potential to influence survey results between years.

Environmental conditions during surveys can have a significant impact on the sightability of whales. Some of the years appear to have been influenced by poorer than average weather conditions. In particular, 1999 and 2000 were badly affected by rain and poor weather and a large number of survey days were lost. Throughout the survey the average for the 10hr survey period was estimated only for those days with reasonable conditions. This should lead to an unbiased average from a smaller sample size but perhaps with a higher variance. Standardising effort between surveys in his manner should minimise any effect of environmental conditions on differences in whale counts between years.

The population growth estimate from this study is based on a maximum survey period of 16 days in any one year and represents an incomplete survey of the total migration period. While the assumption is that the weeks surveyed are representative of the full migration period, the accuracy of this assumption remains unknown. The survey was undertaken at the same time each year and studies of the timing of the migration have provided good evidence that migratory patterns are reasonably consistent between years, but the peak in migration may vary by up to a couple of weeks (Dawbin, 1966; Paterson *et al.*, 2001). It is therefore likely that the two-week survey period did not always capture the entire peak of the humpback migration each year. To investigate this, data from Cape Byron can be compared with data collected at North Stradbroke (134km north of Cape Byron), which are collected over a much longer period. It takes almost one day for the humpback whales to travel from Cape Byron to Stradbroke at an average speed of 6.0km hr^{-1}.

A comparison of 10hr counts averaged on a weekly basis for the equivalent two weeks (e.g. accounting for the one day travel time difference between the two sites) at Cape Byron and North Stradbroke Island can be seen in Fig. 3. While there are fluctuations between the two sets of data, the Byron count is generally less than the Stradbroke count for most years except for 2001 and 2004 where the data are very similar. Fig. 2 shows that the average pod distance is also much lower than most other years (except 1998). Because of the large variations in the Stradbroke weekly counts it is difficult to determine if the Cape Byron survey was conducted at the height of the peak migration period; it appears the peak migration often spans about a four-week period usually starting one week before the Byron survey starts.

The distance at which the humpback whales pass the Cape varies considerably within and between years. All years of the Cape Byron survey except 1998 had observations of pods more than 10km offshore and most years had observations of pods that were 15km or more offshore. The estimated average percentage of pods that travelled more than 10km offshore was 3.0% (range 0–16%); and the average for pods passing more than 5km out was 35.0% (range 13.4– 53.0%). A preliminary vessel-based survey across the continental shelf off Cape Bryon conducted in 1996 (CBWRP, unpublished data) indicated that approximately 90% of humpback whales passing Cape Byron did so within 10km of the shoreline; the remainder travelling up to 23kms offshore. Had the CBWRP survey been conducted in 1998 or 2004 one would expect similar results to those of the present study; while quite different results would have most likely been obtained had the CBWRP study been completed in 1994 or 2003. Findlay and Best (Findlay and Best, 1996a)

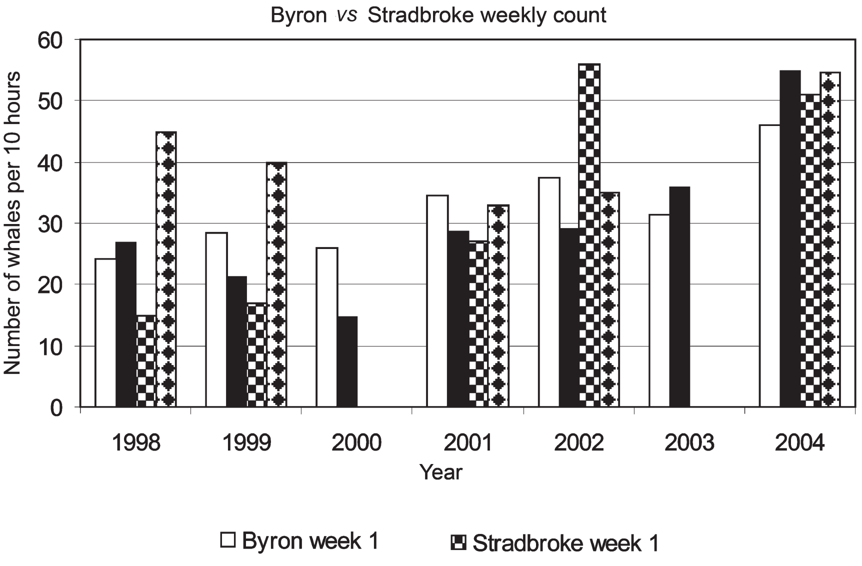

Fig. 3. Byron and North Stradbroke Island weekly 10 hours counts. The 1998 to 2002 Stradbroke Figures are from Paterson's surveys (Paterson *et al.*, 2001; 2004) and the 2004 Stradbroke Figures are from Noad *et al*. (2011).

found that between 40%–50% of whales travelling from 6–10km offshore can be missed during counts. About 37% of whales were measured further than 6km from the shoreline in 1999, 2000 and 2003. This implies there could be an error of about 18% in the counts for these years. Only ~10% of whales were observed more than 6km from the shoreline in 1999 and 2004.

Two factors affect precision of the rate of growth calculated from the Cape Byron surveys: (1) precision of R_y; and (2) number of survey years. Power calculations based on what is known about the migration patterns of this population could be conducted to determine whether annual surveys should be continued or whether a longer survey each second or third year would result in a greater improvement in precision per additional survey.

The 2004 count may be viewed as an outlier as it appears to be inflated compared to other years. However, it may in fact be a more reliable count than most years due to good weather conditions and the average pod distance offshore being less than other years. In addition, 2004 was the last year of the survey period and therefore will have the highest count for this study due to the population growth rate and this will further exaggerate this perceived bias. Some of the other years of the survey (2000 and 2003) have low counts of whales, which may have been a result of the greater average pod distance offshore and prevailing weather conditions. This may explain the difference between the growth rate calculated from the present study (11%, $R^2 = 0.683$) and the plausible IWC (2008) maximum biological increase of around 10.3%. A weighted least squares model can be used to improve the estimated growth rate of the humpback population by partly removing this bias. The weight (or variance) for each year's 10hr count (R_y) could be based on the standard error for each day's count (C_i) for that year. However the standard error generally increased with the increasing numbers of whales that passed each year, therefore the standard error for each year is divided by the average 10hr count for that year to determine the normalised weight. The weighted least squares linear regression produced a growth rate of 10.1% with a slightly improved solution ($R^2 = 0.713$).

The data collected by the CBWRP may be better suited for detailed studies of humpback behaviour patterns. The data may also be useful in studying the cause and effect of variables that influence observing conditions. A number of different relationships between pod behaviour and distribution patterns along with other factors that influence viewing conditions can be further studied.

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Appendix 1

GROWTH IN 10HR SIGHTING RATES IN BYRON BAY 1998–2004

The data analysed were:

Year	Rate	ln(rate)
1	25.471	3.238
2	23.375	3.152
3	20.518	3.021
4	32.331	3.476
5	32.357	3.477
6	32.118	3.469
7	47.020	3.851

A growth model was fitted by generalised least squares (REML)[1] according to the function:

$$\ln(rate)_{time} = \beta_0 + \beta_1 * time + \varepsilon_{time}.$$

In terms of rate:

$$rate_{time} = e^{\beta_0} * e^{\beta_1 * time} * e^{\varepsilon_{time}}.$$

The parameter estimates on the log scale with 95% confidence intervals were:

$$\beta_0 = [2.598 < 2.965 < 3.332];$$
$$\beta_1 = [0.022 < 0.105 < 0.187]$$

The growth parameter on the rate scale with 95% confidence interval was (by back-transformation):

$$e^{\beta_1} = [1.02 < 1.11 < 1.21];$$

i.e. the estimated growth rate with 95% confidence interval was 2.3% < 11.0% < 20.5%.

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[1] Using function GLS in package *nlme* (Pinheiro and Bates, 2000) in program *R* (*R Development Core Team*, 2006).

This cannot be correctly stated as mean ± 95%CI because the interval was not symmetric about the estimate.

RSQ for the model was 0.683.

A plot of the autocorrelation function (ACF) on the residuals indicated little serial correlation structure and a second model which fitted an AR1 structure was found not to be a significantly better fit than the original model by the likelihood ratio test ($p = 0.994$). The estimate of the AR1 parameter with 95% confidence interval was:

$$phi(AR1) = [-0.864 < 0.006 < 0.868].$$

The estimated growth rate with 95% confidence interval from the AR1 model was

$$2.3\% < 11.0\% < 20.5\%.$$

First assessment of interchange of humpback whales between Oceania and the East coast of Australia

CLAIRE GARRIGUE[1], TRISH FRANKLIN[2,7], ROCHELLE CONSTANTINE[3], KIRSTY RUSSELL[3], DANIEL BURNS[3], MICHAEL POOLE[4], DAVE PATON[2,5], NAN HAUSER[6], MARC OREMUS[3], SIMON CHILDERHOUSE[7], DAVE MATTILA[8], NADINE GIBBS[9], WALLY FRANKLIN[2,13], JOOKE ROBBINS[10], PHIL CLAPHAM[11] AND C. SCOTT BAKER[3,12]

Contact e-mail: op.cetaces@lagoon.nc

ABSTRACT

The interchange of individual humpback whales between the wintering grounds of Oceania (South Pacific) and the east coast of Australia were documented by individual identification photographs collected from 1999 to 2004. Interchange was assessed using regional catalogues of fluke photographs, totalling 672 individuals from Oceania (represented by New Zealand, New Caledonia, Vanuatu, Fiji, Samoa, Tonga, Niue, Cook Island, French Polynesia and American Samoa) and 1,242 individuals from Hervey Bay and Byron Bay representing the southbound and the northbound migration along the east coast of Australia (EA). Overall, there were seven documented movements between EA and Oceania. Four instances of movement of four individuals were documented between EA and the closest breeding grounds of New Caledonia. A further three movements were recorded between EA and a small catalogue ($n = 13$) from the New Zealand migratory corridor. In contrast, during this same period, 20 cases of interchange were documented among nine breeding grounds: French Polynesia, Cook Islands, Niue, American Samoa, Samoa, Tonga, Fiji, Vanuatu and New Caledonia. The low level of interchange between Oceania and the east coast of Australia has important implications for understanding the stock structure and abundance of humpback whales in the South Pacific.

KEYWORDS: HUMPBACK WHALE; PHOTO-ID; MOVEMENTS; SITE FIDELITY; PACIFIC OCEAN; BREEDING GROUNDS

INTRODUCTION

Little is known of the movement of humpback whales (*Megaptera novaeangliae*) between the east coast of Australia (EA) and the winter breeding grounds of Oceania. The first information on movements of humpback whales in the South Pacific came from the Discovery marking and recovery programme between the 1950s and 1960s (Dawbin, 1959; 1964; Paton and Clapham, 2006). The results (Chittleborough, 1959; Dawbin, 1964) mainly highlighted the migration of humpback whales between Antarctic Area V (130°E to 170°W) and Australia and New Zealand, but also showed limited exchange between New Zealand and Australia (three marks recovered), Norfolk Island (one mark) and Fiji (two marks) and between Australia and Fiji (one mark). Dawbin (1966) concluded that the population of humpback whales passing along the east coast of Australia was part of the population of Area V known as 'Group V'.

Dawbin (1959) also reported the presence of whales in several island groups of Oceania as part of the Discovery marking programme used to track the journeys of humpback whales. However, some inherent problems with the programme included the limited marking of whales in Oceania, the fact that this technique relied on whales being killed to recover Discovery marks, and the lack of whaling activity in Oceania during this period (apart from some limited whaling in Tonga). These problems are likely to have contributed to the lack of any recorded movement between or within the islands of Oceania from the Discovery programme. It was not until photo-identification studies were started in the 1990s (Abernethy *et al.*, 1992; Garrigue *et al.*, 2001; Gibbs and Childerhouse, 2004; Hauser *et al.*, 2000; Poole, 2002) that whale movements were able to be investigated within the region. Recent studies suggest that the South Pacific region contains several populations that intermingle to a variable, but probably small, degree (Constantine *et al.*, 2007; Garrigue *et al.*, 2002; 2000). Group V humpback whales have recently been divided into three sub-stocks known as Breeding Stock E(i), those wintering off the Australian east coast; E(ii), those wintering around New Caledonia and E(iii), those wintering around Tonga (Garrigue *et al.*, 2006; IWC, 1998; Olavarria *et al.*, 2007). The Australian east coast population, E(i), is thought to be the largest of these sub-stocks (Noad *et al.*, 2008).

The regular comparison of flukes of humpback whales assembled in regional catalogues highlighted movements within Oceania (Garrigue *et al.*, 2002; 2011) and allowed the estimation of rates of interchange to be made between the

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[1] *Opération Cétacés, BP 12827, 98802 Nouméa, New Caledonia.*
[2] *Southern Cross University Whale Research Centre, Southern Cross University, PO Box 157, Lismore, NSW 2480, Australia.*
[3] *School of Biological Sciences, University of Auckland, Private Bag 92019, Auckland, New Zealand.*
[4] *Marine Mammal Research, BP698 98728, Maharepa, Moorea, French Polynesia.*
[5] *Blue Planet Marine, PO Box 5535, Kingston, ACT 2604, Australia.*
[6] *Cook Islands Whale Research, Takuvaine Valley, PO Box 3069, Avarua, Rarotonga, The Cook Islands.*
[7] *University of Otago, PO Box 56, Dunedin, New Zealand.*
[8] *Hawaiian Islands Humpback Whale National Marine Sanctuary, Honolulu, Hawaii 96812, USA.*
[9] *Department of Conservation, PO Box 5086, Wellington, New Zealand.*
[10] *Provincetown Center for Coastal Studies, 5 Holway Avenue, Provincetown 02657, USA.*
[11] *Alaska Fisheries Science Center, National Marine Mammal Laboratory, 7600 Sand Point Way NE, Seattle, WA 98115, USA.*
[12] *Marine Mammal Institute, Oregon State University, 2030 SE Marine Science Dr, Newport, OR 97365, USA.*
[13] *The Oceania Project, PO Box 646, Byron Bay, NSW 2481, Australia.*

island groups. There has been opportunistic documentation of movement between Oceania and the migratory corridors of New Zealand and Australia (Garrigue *et al.*, 2000) but the rate of exchange has only been calculated for New Zealand (Garrigue *et al.*, 2002).

To assess the population size of humpback whales in the South Pacific, information is needed on the rate of exchange between the east coast of Australia and Oceania. Therefore, this project aimed to quantify and compare rates of interchange between Oceania and EA in order to better estimate abundance and describe stock structure of the humpback whale populations inhabiting the western and central parts of the South Pacific.

The results of comparisons between catalogues representing EA and nine regions of Oceania are reported here. More detailed analyses and comparisons utilising genetic tagging and differentiation techniques are being undertaken to better understand this interchange (e.g. differences in interchange between sexes, ages and directions of movements). Overall, it will provide a better understanding of the population structure of humpback whales in the South Pacific and allow for an improved and more robust estimate of abundance for humpback whales there.

MATERIALS AND METHODS

Catalogues

Dedicated humpback whale surveys have been conducted in the Oceania region since 1991 (South Pacific Whale Research Consortium, 2001; 2002; 2003; 2004; 2005). Photo-identification, acoustic and genetic data collection is connected to general information about group size, composition and behaviour. Only the fluke identification catalogues currently held by members and affiliates of the South Pacific Whale Research Consortium (SPWRC) working in Oceania and EA were considered in this study. Photo-identification of individual whales was conducted within each study site by each primary investigator. Following Katona *et al.* (1979), regional catalogues were compiled of all individual humpback whales identified from photographs of the unique markings on the ventral surface of their tail flukes. Original photographs were collected during the study period on both film and/or digitally. In the former case photographs were scanned at the highest possible level of resolution for digital storage and exchange. For the purpose of this study, a synoptic period was defined encompassing all the years from 1999 to 2004 and is hereafter referred to as the synoptic years.

The review presented in Garrigue *et al.* (2011) led to a fully reconciled catalogue for Oceania (the Oceania Catalogue). For the purposes of this exercise it is composed of whales' flukes from New Caledonia, Tonga (comprising Vava'u, Eua, Ha'apai, Niuatoputapu), Cook Islands, French Polynesia, Vanuatu, Fiji, Niue, Samoa, American Samoa and New Zealand.

The EA catalogue is composed of regional fluke catalogues of Hervey Bay and Byron Bay representing the southbound and northbound migrations of humpback whales respectively on the east coast Australian migratory corridor (Franklin and Franklin 1992–2006[14]; Paton *et al.*, 2011). These two reconciled regional catalogues from EA were compared, leading to a single fully reconciled catalogue (EA catalogue) composed of unique individual humpback whales (Paton *et al.*, 2011). The selected photographs were then compiled into two electronic catalogues (EA and Oceania) with attached information for each region.

Quality control and matching process

As is typical for humpback photo-identification research (Friday *et al.*, 2000), all photographs used in the EA – Oceania comparison were reviewed following a set of quality control standards in order to minimise bias in the dataset that will be used in the future to generate an abundance estimate for the Oceania population. All images were reviewed according to a standard set of quality control criteria that were originally developed for the SPLASH program in the North Pacific. This is a scoring system based on objective quality measures of the images that are irrespective of distinctiveness of the fluke (Calambokidis *et al.*, 2001). It consists of five quality criteria to score photos from one to five in each category, agreed combinations of criteria are then used to accept or reject photos. All the images were graded from the highest quality (1) to the lowest quality (5). These five criteria categories were (i) proportion of the fluke visible, (ii) fluke angle, (iii) the lateral angle of the photographer, (iv) exposure quality and (v) contrast quality as described in Calambokidis *et al.* (2001). An image that received one or more four or five scores in any of the five categories was considered to be of insufficient quality for a representative comparison of resight rates between sites, and was therefore removed from the data set. To minimise errors in the dataset by inaccurate scoring of the images, an independent reviewer familiar with SPLASH protocol scored a subset of the dataset to determine consistency between the North and South Pacific projects.

Matching was undertaken using electronic images of similar size and resolution. The matching method used was a rational rather than exhaustive pair-wise comparison, as a full pair-wise comparison of EA to Oceania would have required over 860,000 matches. This meant that flukes in the Oceania catalogue were ranked (ordered) in a continuum from all white to all dark colouration. As in SPLASH, a single fluke photograph from EA was compared to all fluke photographs from Oceania starting at the relevant section of the catalogue, i.e. a dark fluke image was matched to all other dark fluke images but not to the all white fluke images. Once the reviewer was satisfied that no further match was possible, a new fluke was then matched to the appropriate part of the catalogue. A record was kept for each EA photograph of which sections of the Oceania catalogue it had been matched to and this was used to measure matching effort and allowed checks of the matching process to be made.

The Oceania catalogue was sorted into three approximately equal-sized groups to allow more efficient matching. Group one was composed of Cook Islands and French Polynesia, group two encompassed Tonga (only Vava'u) and group three comprised all the rest of the Oceania catalogue (New Caledonia, Niue, Fiji, Samoa, American Samoa, Vanuatu, Tonga (except Vava'u) and New Zealand). Once the catalogues were fully reconciled, all matches were confirmed by another person familiar with fluke matching.

RESULTS

Quality control and matching

The original datasets submitted for quality control screening contained 995 photographs for Oceania and 1,844 photographs

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[14] Franklin, T. and Franklin, W. 1992–2006. A long-term study of the ecology and behaviour of humpback whales (*Megaptera novaeangliae*) in Hervey Bay by The Oceania Project: annual field reports. Queensland Environment Protection Agency (QEPA), Maryborough, Queensland. [Available from the author].

Table 1
Summary of all photographs of unique individuals submitted for quality control by study site, East Australia and Oceania, between 1999 and 2004.

Region	No. of photos submitted	No. of photos rejected	% of rejection	No. of photos accepted
Byron Bay	598	183	31	415
Hervey Bay	1,246	375	30	871
Unreconciled East Australia catalogue	**1,844**	**558**	**30**	**1,286**
Reconciled East Australia catalogue				**1,242**
French Polynesia	230	107	47	159
Cook Islands	90	64	71	36
Niue	2	0	0	2
American Samoa	39	8	21	31
Samoa	2	1	50	1
Tonga	422	140	33	282
Fiji	2	0	0	2
Vanuatu	6	0	0	6
New Caledonia	185	25	14	160
New Zealand (NZ)	17	4	24	13
Unreconciled Oceania catalogue	**995**	**349**	**35**	**692**
Reconciled Oceania catalogue				**672**

for EA. Overall, 32% ($n = 907$) of the photographs had one or more four or five scores from the quality control criteria and thus, were excluded from the final dataset (30% for EA and 35% for Oceania, Table 1). The rejection rate of the regional catalogues ranged from 0 to 71%.

Table 1 presents the number of individual whales photo-identified in each regional study site and gives the final sizes of the two unreconciled catalogues after quality control had been undertaken. Following reconciliation, the two quality controlled catalogues for EA and Oceania contained 1,242 and 672 individually identified humpback whales respectively (Table 1) and these were then reconciled with each other to quantify the rate of interchange.

A rational pair-wise comparison of the two catalogues resulted in a total of 710,558 comparisons being made, 19% less than would have been done using a pair-wise comparison. Approximately three-quarters of the flukes in the EA catalogue (76%) were compared to 86% of the Oceania catalogue. To test the accuracy of the matches a double blind test was conducted on a subset of the catalogues, including part of Byron Bay and part of New Caledonia (NC). An inexperienced matcher found the same results as the experienced matcher for the same images (two matches between BB and NC).

Interchange

The comparison of the EA and Oceania catalogues resulted in seven matches between these two regions; four from the Oceania breeding grounds and three from the New Zealand migratory corridor (Fig. 1, Table 2). All four individuals from EA resighted in the breeding grounds of Oceania were first observed in New Caledonia (Table 3). Two of these were resighted in Hervey Bay, EA during the southern migration and the other two were resighted in Byron Bay, EA on the northern migration. All four whales were identified as males using molecular markers (Garrigue *et al.*, 2004; Gilson *et al.*, 1998). Three of the four resighted whales were observed in more than one year in New Caledonia with one observed in three different years, two sighted in two years and one identified on a single occasion. These whales were

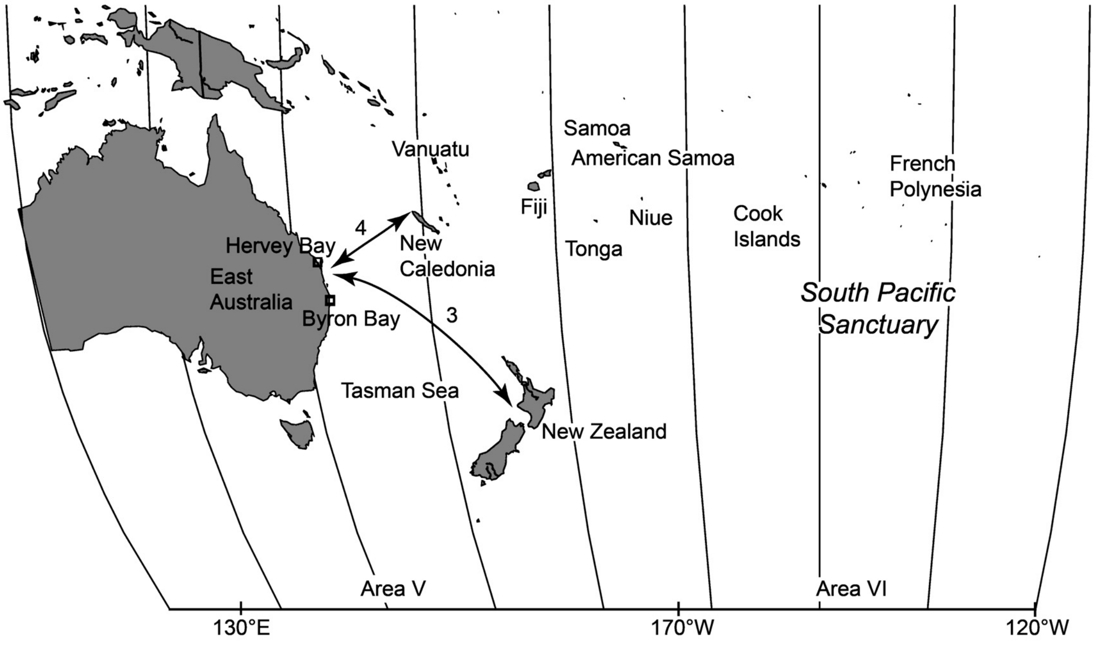

Fig. 1. Map of the study area showing the interchange of whales between east Australia and Oceania.

Table 2

Movement by individual whales between East Australia and Oceania.

Study sites	BB	HB	NZ	NC	VT	FI	SA	TG	NI	CI	FP	AS
Byron Bay (BB)		44	0	2	0	0	0	0	0	0	0	0
Hervey Bay (HB)			3	2	0	0	0	0	0	0	0	0
East Australia total			3*	4	0	1**	0	0	0	0	0	0

*Discovery marking documented interchanges of three individuals between EA and NZ.
**Discovery marking documented interchange of one individual between Fiji and EA.

encountered in different types of social groups (single, pod of two and a reproductive pod) (Table 3). Interestingly two of these whales were first identified as young animals but not calves (this was assumed based on their apparent size). One of them was encountered with a female and was hypothesised to be a yearling as the microsatellite analysis identified them as a potential mother and calf pair (Garrigue *et al.*, 2004).

Of the three whales matched between the EA catalogue and the New Zealand migratory corridor, two were observed only once at each site and the third whale was observed three times in Hervey Bay, EA (Table 3). Interestingly these three whales were sighted in Cook Strait, New Zealand during the northbound migration in 2004 and sighted in Hervey Bay during the southbound migration (Table 3). Two resights occurred in the same year (2004) with intersight intervals of 87 and 92 days. Both were sexed as male, one by molecular analysis and the other by field observation supported by photo-identification of the genital area (TF).

DISCUSSION

Quality control and matching

It is important in large-scale matching projects to consider the most efficient and unbiased design for quality control and the structure of the comparison. The use of a system that allows evaluation of the quality of the photograph, rather than the distinctiveness of the marks on the flukes reduces bias towards distinctive whales (Friday *et al.*, 2000) and improves accuracy for population estimation (Hammond, 1990). The use of the SPLASH scoring system (Calambokidis *et al.*, 2001) showed the efficacy of quality control even though the South Pacific whales are predominantly white (86% *ca.* 10–20% in the North Pacific) and the North Pacific whales are predominantly black. The difference in colouration meant that we relied on patterns on the underside of the flukes as well as marks on the trailing edge, whereas matching of the North Pacific whales relied more on marks on the trailing edge.

The rational pair-wise comparison saved approximately 20% of the matching time in this project, compared to a full comparison. Given that it would be extremely unlikely that a predominantly black fluke photograph would match a fluke that is predominantly white, we considered that the rational pair-wise method was a more efficient, yet still accurate, method.

Interchange and isolation

The results presented here represent the first systematic comparison of individual movement across the migratory corridors and wintering grounds of humpback whales thought to feed in Areas V and VI (130°E–110°W) of the Antarctic. The three matches documented between EA and New Zealand suggests an even stronger connection between these two corridors than previously thought based on Discovery marking and recovery (Table 3). However, the catalogue for the New Zealand corridor remains small (reflecting the low level of recovery of this stock (Childerhouse and Gibbs, 2006)), and the relatively high rate could reflect an episodic, rather than ongoing, exchange.

Only four individuals were resighted between EA and New Caledonia, the closest breeding ground in Oceania. All four whales were male but the interchange is unlikely to be sex-biased as few whales resighted outside of the synoptic period were female (Garrigue *et al.*, 2000; CG, DP and TF, unpublished data). These movements are not age-biased as both young, independent whales and adult whales were resighted. The movements also do not appear to be related to a specific social grouping as the resighted whales were recorded in a mixture of group types including single whales, members of pair, an escort of a mother and calf pair and individuals involved in competitive group.

With only four individuals resighted between EA and the breeding grounds of Oceania the level of interchange was

Table 3

Direction of movement of individual humpback whales between the study sites of East Australia and Oceania with information on sex, age class and social group composition.

First region	Direction	Second region	Sex	Age	Social group composition
New Caledonia	**East**	**Hervey Bay**			
1995, 1999		2000, 2001	Male	Young, then adult	Single, pod of 6, pod of 2
2000, 2005		2002	Male	Adult	Pod of 2, pod of 3, reproductive pod
New Caledonia	**East**	**Byron Bay**			
1999, 2000, 2001		2002	Male	Yearling, adult	Yearling + mother, single, pod of 2, reproductive pod
2001		2002	Male	Adult	Pod of 2, reproductive pod
Hervey Bay		**New Zealand**			
1997, 1999, 2002		2004	Unknown	Adult	Single, pod of 2, pod of 5
New Zealand		**Hervey Bay**			
2004		2004	Male	Adult	Pod of 3, pod of 2
2004		2004	Male	Adult	Mother, calf and escort, pod of 2

surprisingly small, given the relatively large catalogues used in this comparison spanning a six-year period; this provides strong evidence for subdivision within Breeding Stock E (formerly Group V). By comparison, the rate of interchange within the different regions of Oceania for the same period is five times higher, highlighting the low rate of interchange between Oceania and EA on both the northern and southern migrations. The 20 resightings of whales among breeding grounds of Oceania indicate a limited, but not insignificant, interchange across this vast region (Garrigue *et al.*, 2011).

It is worth noting that all the interchanges between EA and Oceania were found with the nearest of the Oceania breeding grounds in New Caledonia. This area exhibited roughly the same rate of exchange between the other Oceania grounds for the same period (with five matches all located in the south-western part of the Pacific including Vanuatu and Tonga) (Garrigue *et al.*, 2011). With this level of interchange between New Caledonia and the rest of Oceania it is surprising that there were no matches between EA and any of the other regions within Oceania during the six-year synoptic period. It must be noted that other matches between EA and Oceania have been found outside the synoptic period, e.g., Tonga and Ballina, EA (DB, unpublished data). Nevertheless, this study included a large number of photo-identified individuals from several major breeding grounds and two important migratory corridors (EA and New Zealand) therefore, the results of this study are likely to be representative of the primary patterns of movement between EA and Oceania. Future work will focus on planning for an expansion of the synoptic period to investigate matches over a longer time frame.

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Movement of individual humpback whales between wintering grounds of Oceania (South Pacific), 1999 to 2004

Claire Garrigue[1], Rochelle Constantine[2], Michael Poole[3], Nan Hauser[4], Phil Clapham[5], Michael Donoghue[6], Kirsty Russell[2], Dave Paton[7,8], Dave K. Mattila[9], Jooke Robbins[10] and C. Scott Baker[2,11]

Contact e-mail: op.cetaces@lagoon.nc

ABSTRACT

The movement of individual humpback whales between regional breeding grounds of Oceania (South Pacific) was documented by individual identification photographs collected from 1999 to 2004. Photographs were collected with comparable effort across the six years in four primary island breeding grounds: New Caledonia, Tonga (Vava'u) the Cook Islands and French Polynesia (Mo'orea and Rurutu); with smaller effort in adjacent regions: Vanuatu, Fiji, Samoa, Niue and American Samoa. Interchange among wintering grounds was assessed first with all usable photographs included in each regional catalogue, representing 1,080 regional sightings (including within-region and between-region resightings) of 949 individual whales from Oceania. From this, 28 cases of movement between (mostly adjacent) regions were documented. Previously undocumented interchange was found between regions of central Oceania and the western South Pacific. No individual was sighted in more than two regions during this six-year period. The documented movement between regions was one-directional, except for one individual sighted first in French Polynesia, then in American Samoa and then back in French Polynesia (each in different years). Only one whale was resighted in more than one region during the same winter season. No directional trend was apparent and movement between regions did not seem to be sex specific. A systematic quality control review of all catalogues was then implemented to calculate standardised indices of within-region return and between-region interchange, resulting in a quality controlled catalogue of 776 regional sightings of 659 individuals. The standardised indices confirmed that the probability of between-region interchange was low, relative to within-region return, supporting the assumption of multiple management units or stocks in Oceania. The relative isolation of breeding regions and the movement of individuals across the longitudinal borders of Antarctic management Areas V and VI has important implications for the allocation of historical catches from the Antarctic and therefore, for assessing current levels of recovery for breeding stocks.

KEYWORDS: HUMPBACK WHALE; PHOTO-ID; MOVEMENTS; SITE FIDELITY; SOUTH PACIFIC; SOUTHERN HEMISPHERE

INTRODUCTION

Preliminary comparisons of humpback whales in the South Pacific through photographic catalogues and genetic analyses demonstrate fidelity to local wintering grounds, as well as a low level of migratory interchange among wintering grounds of Oceania, South Pacific (Garrigue *et al.*, 2002; Olavarria *et al.*, 2007; Baker *et al.*, 2006b). In this paper the previously published information on individual movement between wintering grounds of Oceania is extended using photo-identification (photo-id) records collected during six winter seasons (1999–2004) in four primary and five secondary regions. All useable photographs were compared to document movement or interchange between regions. A thorough quality control review of all photographs was then implemented to calculate standardised indices of within and between region return. The fully reconciled (i.e. exhaustively compared) and quality controlled catalogue provided new insight into the migratory fidelity and interchange of individuals among breeding stocks E and F, as recognised by the IWC (Garrigue *et al.*, 2006; IWC, 1998; Olavarria *et al.*, 2007).

MATERIAL AND METHODS

Dedicated surveys of humpback whales in Oceania were conducted during the austral winters of 1999 to 2004, referred to as 'the synoptic years' in the four primary regions described below: New Caledonia, Tonga, the Cook Islands and French Polynesia (Fig. 1). Although photo-id records are available from previous years for most regions, comparisons described in this paper were restricted to these synoptic survey years. Surveys were conducted in only one or two seasons during the synoptic years in other adjacent regions: Vanuatu; Fiji; Samoa; Niue; and American Samoa, where surveys began in 2003 (Fig. 1).

Primary study sites

New Caledonia

The Exclusive Economic Zone (EEZ) waters of New Caledonia encompass over 1,450,000 km² between 18° and 23°S and between 158° and 172°E. Some whaling is known to have occurred in the Loyalty Islands of this region, although most of the effort was concentrated in the Chesterfield area (Townsend, 1935). Humpback whale

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*[1] *Opération Cétacés, BP 12827, 98802 Nouméa, New Caledonia.*
[2] *School of Biological Sciences, University of Auckland, Private Bag 92019, Auckland, New Zealand.*
[3] *Marine Mammal Research, BP698 98728, Maharepa, Moorea, French Polynesia.*
[4] *Cook Islands Whale Research, Takuvaine Valley, PO Box 3069, Avarua, Rarotonga, The Cook Islands.*
[5] *Alaska Fisheries Science Center, National Marine Mammal Laboratory, 7600 Sand Point Way NE, Seattle, WA 98115, USA.*
[6] *Department of Conservation, PO Box 5086, Wellington, New Zealand.*
[7] *Southern Cross University Whale Research Centre, Southern Cross University, PO Box 157, Lismore, NSW 2480, Australia.*
[8] *Blue Planet Marine, PO Box 5535, Kingston, ACT 2604, Australia.*
[9] *Hawaiian Islands Humpback Whale National Marine Sanctuary, Honolulu, Hawaii 96812, USA.*
[10] *Provincetown Center for Coastal Studies, 5 Holway Avenue, Provincetown 02657, USA.*
[11] *Marine Mammal Institute, Oregon State University, 2030 SE Marine Science Dr, Newport, OR 97365, USA.*

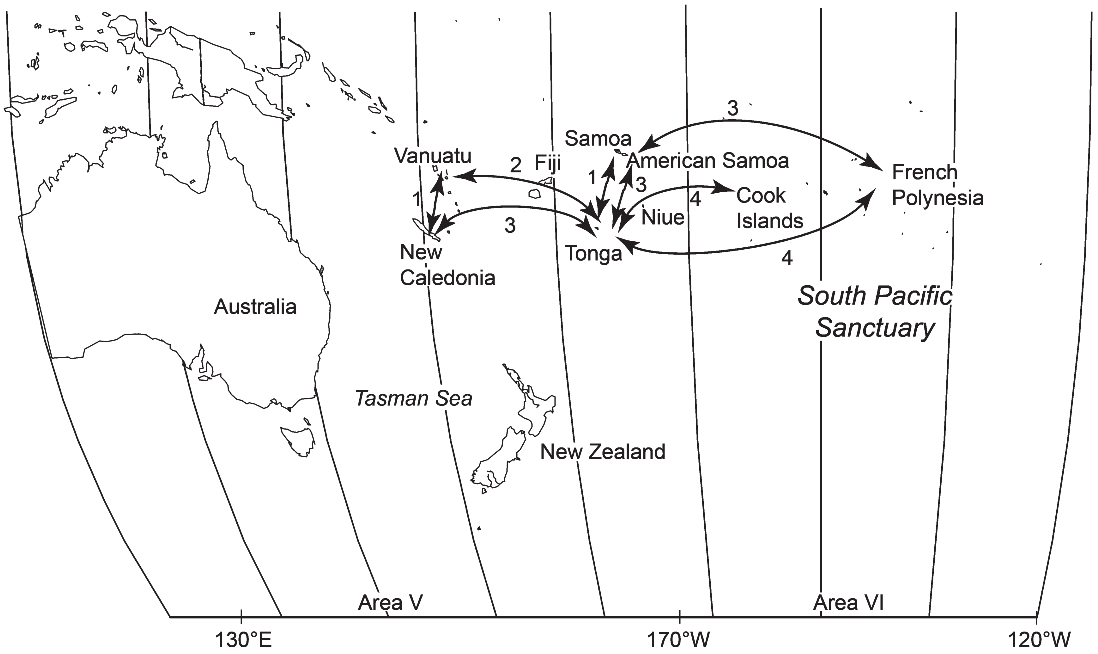

Fig. 1. Location of primary and secondary study regions for photo-identification of humpback whales in Oceania (South Pacific).

photo-id surveys were conducted opportunistically beginning in 1991 (Garrigue and Gill, 1994) and systematically for two to three months each austral winter from 1995 onwards (Garrigue *et al.*, 2001). The present study site covers approximately 1,000km^2 and is located in the southern lagoon off the main island, which is thought to be the primary area of humpback whale density.

Tonga

The Tongan archipelago is a series of volcanic islands and coral atolls extending 800km from Ata in the south to Niuafo'ou in the north with an EEZ of approximately 700,000km^2. The primary areas of humpback whale density are thought to be the three major island groups; Tongatapu in the south; the Ha'apai group in the middle; and the Vava'u group in the north. Vessel-based surveys and the collection of individual identification photographs were initiated in 1991 (Abernethy *et al.*, 1992) and continued in most years prior to the synoptic period of 1999–2004. Each of the three main island groups has been surveyed in at least one year but most of the field effort from 1999 to 2004 was concentrated around Vava'u. The majority of fieldwork has been conducted in August and early September, although work in some years included late July and early October.

Cook Islands

The Cook Islands are a group of islands and atolls scattered over approximately 2,000,000km^2 of the southwestern South Pacific. Surveys for humpback whales in the southern Cook Islands began with an exploratory three week project in 1998 and continued with a four-month field effort each winter from 1999 until 2004 (Hauser *et al.*, 2000). To date the survey has been focused on three locations: (1) Palmerston Atoll, a small atoll lying at 18°04'S, 163°10'W on the north western margin of the Southern Cook group; (2) Aitutaki, an island located at 18°55'S, 159°47'W, roughly 300km east of Palmerston; and (3) Rarotonga, an island located at 21°14'S, 159°48'W, roughly 430km southeast of Palmerston. Other brief surveys included the islands of Atiu and Mangaia.

French Polynesia

French Polynesia comprises five archipelagos (the Marquesas, the Tuamotu atolls, the Gambiers, the Society Islands and the Australs) in the central South Pacific Ocean. Sightings of humpback whales in French Polynesia's waters have been noted since 1988 (Poole and Darling, 1999). The primary study area for fieldwork has encompassed the nearshore waters of the high island of Mo'orea in the Society Islands, lying at 17°30'S and 149°50'W, 18km northwest of Tahiti. Observational surveys of humpback whales in the nearshore waters of Mo'orea began in 1991. Additional shore- and boat-based observations of humpback whales began in 1999 at Rurutu in the Austral Islands. From 1999 to 2004 most of the field effort was concentrated around Mo'orea and Rurutu (Poole, 2002).

Individual identification and matching process

Humpback whales were individually identified in each region from photographs of the unique markings on the ventral surface of their tail flukes, i.e. photo-id (Katona *et al.*, 1979). All photographs considered 'usable' (e.g. potentially matchable) by the regional coordinators were first matched within regions, leading to 'reconciled' regional catalogues of all annual sightings within regions and between years.

These regional catalogues of unique individuals for the nine regions were then matched by exhaustive pair-wise comparisons during annual meetings of the South Pacific Whale Research Consortium (SPWRC). The number of between-region (within- and between-year) resightings were recorded. All between-region resightings were confirmed by three independent matchers. This initial comparison resulted in a fully reconciled, non-quality controlled catalogue, including all within-region (between-year) resightings and all between region (within- and between-year) resightings. Although it was assumed that usable photographs of marginal quality would be more difficult to match, no evidence of false matches (e.g. mismatches, Perry *et al.*, 1990) was found in the subsequent quality control review of all catalogues (see below).

The results of this initial non-quality controlled comparison were reported to the IWC workshop on the Comprehensive Assessment of Southern Hemisphere humpback whales held in Hobart in April 2006 (SPWRC *et al.*, 2006). Subsequent to this workshop, members of the SPWRC agreed to review all photographs following a set of quality control standards in order to minimise bias (i.e. missed matches, defined as a match that is not recognised because of poor quality photographs) in calculating return and interchange rates, as well as for subsequent estimates of abundance.

Quality control review

All images of the fully reconciled, non-quality controlled catalogue of Oceania were reviewed according to a standard set of quality control criteria originally developed for the SPLASH programme in the North Pacific (Calambokidis *et al.*, 2008). This is a scoring system based on objective quality measures of the images, irrespective of distinctiveness of the fluke. It consists of five quality criteria, each of which is scored from the highest (1) to the lowest (5) quality. These five categories were: (i) proportion of the fluke visible; (ii) fluke angle; (iii) the lateral angle of the photographer; (iv) exposure quality; and (v) contrast quality, as described in Calambokidis *et al.* (2001). An image that received a score of four or five in any of the five quality categories was judged to be of insufficient quality for a standardised comparison of within-region return rates and between-region resight rates. As recommended by Friday (1997) and Friday *et al.* (2000), the quality control review of all catalogues was undertaken by a single researcher familiar with cetacean photo-id (RC) in order to ensure consistency. Exhaustive matching of all regional catalogues using the quality control scores resulted in a single 'quality controlled, fully reconciled' catalogue for Oceania.

Return and interchange indices

The within-region return index and the between-region interchange index were calculated to evaluate the relative magnitude of migratory interchange (Garrigue *et al.*, 2002) following Baker *et al.* (1986) and Calambokidis *et al.* (2001).

The return index of within-region annual resightings was calculated as:

$$Rij = Mi,j / (Ai \times Bi) \times 1{,}000$$

where

Ai = number of whales marked in all the years before 2004;

Bi = number of whales identified in 2004; and

Mi,j = number of whales marked in any previous years and resighted in 2004.

An interchange index of between-region resights was calculated as:

$$Rij = Mi,j / (A1 \times B2) \times 1{,}000$$

where

A1 = number of whales identified in region A;

B2 = number of whales identified in region B; and

Mi,j = number of whales identified in both regions.

The indices were considered to be zero when there were no whales were sighted within or between regions (i.e. when Mi,j = 0).

Indices were calculated for the synoptic period 1999–2004 using all photographs contained in the fully reconciled, quality controlled catalogue of Oceania.

RESULTS

Between-region resightings

The fully reconciled, non-quality controlled catalogue of Oceania represented 1,080 regional sightings (including within-region, between-year resightings) of 949 individually identified humpback whales in Oceania. This comparison provided 28 matches documenting movements between regions (Tables 1 and 2), of which 22 involved movement from or to Tonga, a central Oceania region represented by the largest catalogue. Of the 28 total, 9 corresponded to individuals observed in one of the four primary regions (mostly Tonga) and resighted in one of the secondary study regions (Vanuatu 3, Samoa 1, American Samoa 6, Niue 1). The other matches (*n* = 17) were between Tonga and New Caledonia, the Cook Islands or French Polynesia. One individual was resighted during the same year in two regions (ID: TGVA9989-CIMn081999, Tonga and the Cook Islands). The majority of observed movements were uni-directional with one exception: an individual was sighted in French Polynesia, then in American Samoa and then back in French Polynesia (FP0003/AS012; Table 2). No individual was sighted in more than two regions during the six years of synoptic surveys.

Quality control review

Following the quality control review of the regional catalogues, 34% of the submitted photographs were judged to be of insufficient quality for standardised comparisons and were excluded from calculation of resighting rates (Table 3). The number of individual whales photographically identified

Table 1

Movement by individual whales between regions before quality control (below diagonal) and after quality control (above diagonal, in italics).

Regions	NC	VT	FI	SA	TG	NI	CI	FP	AS
New Caledonia (NC)		*1*	*0*	*0*	*3*	*0*	*0*	*0*	*0*
Vanuatu (VT)	1		*0*	*0*	*2*	*0*	*0*	*0*	*0*
Fiji (FI)	0	0		*0*	*0*	*0*	*0*	*0*	*0*
Samoa (SA)	0	0	0		*1*	*0*	*0*	*0*	*0*
Tonga (TG)	4	2	0	1		*0*	*4*	*4*	*2*
Niue (NI)	0	0	0	0	0		*0*	*0*	*0*
Cook Island (CI)	0	0	0	0	7	1		*0*	*0*
French Polynesia (FP)	0	0	0	0	6	0	0		*3*
American Samoa (AS)	0	0	0	0	2	0	1	3	

Table 2

Summary of movement of individual humpback whales between the regions of Oceania based on all usable (non-quality controlled) fluke ID photographs (underline indicates photographs that did not pass quality control ranking). Direction: East (E), West (W) or Northeast (NE).

ID	First/third region/year	Direction	Second region/year	Sex
	New Caledonia		**Vanuatu**	
HNC102/VT001	2001	E	2003	Female
	New Caledonia		**Tonga**	
HNC209/TGVA0363	2001	E	2003	Male
HNC193/TGVA0248	2000	E	2002	Male
	Tonga		**New Caledonia**	
TGVA9946/HNC217	1999	W	2001	Male
TGVA9977/HNC239	1999	W	2001	Male
	Tonga		**Vanuatu**	
TGVA0208/VT004	2002	W	2003	Unknown
TGHA0003/VT002	2000	W	2003	Male
	Tonga		**American Samoa**	
TGVA9984/AS062	1999	NE	2004	Unknown
TGVA9905/AS049	1999	NE	2004	Unknown
	Tonga		**Samoa**	
TGVA0410/SA01-002	2001	NE	2004	Unknown
	Tonga		**Cook Islands**	
TGVA0082/CIMn082802	2000	E	2002	Female
TGVA9952/CIMn83103	1999/2001	E	2003	Unknown
TGVA9920/CIMn092102	1999	E	2002	Unknown
	Cook Islands		**Tonga**	
CIMn081999/TGVA9989	1999	W	1999	Male
CIMn080700/TGVA0226	2000	W	2002	Male
CIMn082200/TGVA0146	2000	W	2001	Female
CIMn100900/TGVA0413	2000	W	2004	Unknown
	Cook Islands		**Niue**	
CIMn080700/Niue0102	2000	W	2001	Unknown
	Cook Islands		**American Samoa**	
CIMn081903/AS036	2003	E	2004	Unknown
	Tonga		**French Polynesia**	
TGVA0064/FP0452	2000	E	2004	Unknown
TGVA9938/FP0453	1999	E	2004	Unknown
TGVA9968/FP0464	1999	E	2004	Unknown
TGVA0170/FP0463	2001	E	2004	Unknown
TGVA0057/FP0337	2000	E	2003/2004	Unknown
	French Polynesia		**American Samoa**	
FP0201/AS005	2002	W	2003	Unknown
FP0003/AS012	2000/2004	W/E	2003	Unknown
FP0316/AS059	2003	W	2004	Unknown
	French Polynesia		**Tonga**	
FP200212/TGVA0402	2002	W	2004	Unknown

in each region after the quality control, and the number of individual whales resighted within region are presented in Table 3 (South Pacific Whale Research Consortium, 2001; 2002; 2003; 2004; 2005). The comparison of the fully reconciled, quality controlled catalogue of Oceania represented 776 regional sightings of 659 individual humpback whales in Oceania (Table 3). Of the 28 cases of between region movement documented in the non-quality controlled catalogue, 8 involved a photograph judged to be of unacceptable quality for calculating the standardised resighting indices (Table 1, upper diagonal). In each case, only one of the two photos was rejected from these matches (5 for Tonga, 2 for Cook Islands and 1 for American Samoa). Despite the lower quality of these photographs, there was no uncertainty in matches to the higher quality photographs and, thus, no uncertainty in the documentation of these individual movements.

Within-region resightings and resighting indices

In the quality-controlled catalogue of 776 regional sightings, 78 resightings were found between years within three of the primary regions. Between 1999 and 2004 a total of 33 individuals were resighted in New Caledonia representing 21% of the individually identified humpback whales during the same period (Table 3). In Tonga a total of 25 (9%) individual whales were resighted within the region. In French Polynesia, a total of 20 (13%) individual whales were resighted within the region (Table 3). All but one individual were resighted only once in Tonga and French Polynesia. More than one-third of the resighted individuals were observed more than once in New Caledonia with 11 individuals sighted three times and one sighted in four occasions. No individual was resighted between years in the Cook Islands (Table 3). These results lead to high within-region return indices for all primary regions except for Cook Islands (Table 4). No individual was resighted within the secondary regions in which sampling took place for more than one year (e.g. Samoa and American Samoa, Table 3).

Comparisons of the within- and between-region resight indices confirmed the previous reports of fidelity to individual breeding grounds (Table 4; Garrigue *et al.*, 2001).

Table 3

Summary of individual identification photographs of humpback whales by regions of Oceania between 1999 and 2004, with the number of sightings by region and number of individual whales resighted within regions.

Regions	Years of sampling effort	Number of usable ID photos	Number of ID photos after quality control	Number of annual sightings	Number of individual whales resighted between years, within regions
New Caledonia (NC)	1999–2004	185	160	206	33
Vanuatu (VT)	2003	6	6	6	–
Fiji (FI)	2002–03	2	2	2	0
Samoa (SA)	2001, 2003	2	1	1	0
Tonga (TG)	1999–2004	422	282	312	25
Niue (NI)	2000–01	2	2	2	0
Cook Island (CI)	1999–2004	90	36	36	0
French Polynesia (FP)	1999–2004	230	159	180	20
American Samoa (AS)	2003–04	39	31	31	0
Unreconciled, non-quality controlled catalogue of Oceania	1999–2004	949	–	776	–
Unreconciled, quality controlled catalogue of Oceania	1999–2004	–	679	776	78
Total individuals in reconciled, quality controlled catalogue	1999–2004	–	659	–	–

Only the interchange between Tonga and the Cook Islands showed a resight index of the same order of magnitude as the return index calculated for Tonga, suggesting a close migratory connection. This connection was recently highlighted using satellite telemetry (Hauser *et al.*, 2010).

DISCUSSION

The first information on movements of individual humpback whales in the South Pacific came from Discovery marking (Dawbin, 1959; 1964). However, given the pattern of marking and recovery, no exchanges between the islands of Oceania were revealed by this method. The first, and only previous records have come from photo-id studies initiated in the early 1990s (Abernethy *et al.*, 1992; Garrigue *et al.*, 2001; Hauser *et al.*, 2000; Poole, 2002). The present study confirms that the majority of inter-annual resightings of humpback whales in Oceania occurred within regions (80% of the matches for the quality-controlled catalogue). This is an order of magnitude greater that the between-region interchange, with the exception of Tonga and the Cook Islands (Table 4) confirming both site fidelity and limited demographic exchange between breeding grounds (Garrigue *et al.*, 2002). The rate of resightings varied within the four primary regions presumably due to local abundance. The highest percentage of within-region resightings was measured in New Caledonia (21%) and the lowest in the Cook Islands, where none were observed in the course of this six-year study. No within-region resighting was reported from the secondary study regions where numbers appear low and sample sizes were small. Although surveying of all regions of known historical abundance (e.g. Fiji and Samoa) has been attempted, it is also probable that humpback whales inhabit other regions of Oceania where sampling has not yet been conducted.

Table 4

Within-region return index (in italics) and between-region interchange index of humpback whales calculated from quality control catalogues for the four primary breeding grounds of Oceania.

Regions	NC	TG	CI	FP
New Caledonia (NC)	*4.28*	0.07	0.00	0.00
Tonga (TG)		*0.94*	0.39	0.09
Cook Islands (CI)			*0.00*	0.00
French Polynesia (FP)				*3.42*

The between-region resightings reported here contributed to previously reported observations of connections (see Introduction) and revealed several new connections, especially in central Polynesia. Tonga showed interchange with Samoa, American Samoa, the Cook Islands and French Polynesia. Similarly, French Polynesia showed interchange with American Samoa. In the western South Pacific exchange was documented between Vanuatu and both New Caledonia and Tonga. No individual whale was sighted in more than two regions and all observed movement was limited to adjacent regions. Most of the whales resighted between regions have been identified only once in each region, suggesting that these movements are transient or exploratory (Madon, 2010) rather than permanent dispersal events (see below).

Most (70%) of the between-region resightings were in the central South Pacific and involved Tonga, the Cook Islands, French Polynesia, American Samoa and Samoa. The others (30%) were observed in the western South Pacific and involved New Caledonia, Vanuatu and Tonga. No movements were documented between the central and western South Pacific during the six years of this study. However, photo-id records outside of the synoptic years and recent genotyping comparisons (South Pacific Whale Research Consortium, 2008) revealed the movement of one whale from New Caledonia (1998) to Tonga (2001) and then on to French Polynesia (2004) and one whale from New Caledonia (2000) to the Cook Islands (2007). Thus, it is clear that, although infrequent, there is movement on an ocean-wide scale over years. No directional trends were found in the movements. Half of the documented movement was in a westerly direction and half in an easterly direction. Sex information was available for eight of the whales that moved between regions; six males and two females. Even though the sample size is small, this suggests that movement is not sex-specific (although it might be sexed biased).

Overall, the level of movement of individuals between adjacent sites within Oceania, and the apparent transient nature of this interchange, is consistent with the significant levels of differentiation observed in mtDNA from these regions (Olavarria *et al.*, 2007). Assuming Wright's Island model of gene flow and a generation time of 18 years, Olavarria *et al.* (2007) used the estimated F_{ST} from mtDNA haplotypes to calculate an exchange rate of about one female per year among the breeding grounds of Oceania. These low levels of maternal gene flow and the relatively low rates of between-region interchange (relative to within-region return) from the photo-id comparisons, suggest that populations of humpback whales wintering near or in New Caledonia, Tonga and French Polynesia are independent from each other (and from breeding grounds to the east and west), on a demographic time scale, and should be recognised as individual breeding stocks. This does not seem to be the case for the Cook Islands, which shows less evidence of isolation from neighbouring regions. Consequently, a comprehensive assessment of South Pacific stocks should, ideally, attempt to consider each of these primary breeding grounds independently in regards to current abundance, past catches and rates of increase. However, we recognise that such a fine-scale assessment might not be possible in the near term, given regional samples sizes available for estimating abundance and the uncertainty of allocating historical Antarctic catches. Other approaches should be explored, including aggregating regional catalogues for estimating abundance (Baker *et al.*, 2006) and Bayesian modelling of catch allocation to two stocks, eastern Australia and Oceania (Jackson *et al.*, 2008). In the longer term, a greater sampling effort for photo-identification and individual genotying (Steel *et al.*, 2008) is needed to better estimate abundance and interchange between breeding grounds and describing connections between Oceania and Antarctic feeding areas.

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Entanglement of humpback whales in artisanal fishing gear in Ecuador

FERNANDO FÉLIX[1], MERCEDES MUÑOZ[1], JÉSSICA FALCONÍ[2], NATALIA BOTERO[3] AND BEN HAASE[1]

Contact e-mail: fefelix90@hotmail.com

ABSTRACT

Southeastern Pacific humpback whales (Breeding Stock G) congregate along the northwest coast of South America during the austral winter (July–October). Information collected from stranded animals for more than a decade in Ecuador and Colombia indicates that entanglement in fishing gear is a major threat for this population during the breeding season. Twelve new cases are reported here of live individual whales entangled in artisanal gillnets on the central coast of Ecuador from 2004 to 2007. The varying severity of the entanglement and the behaviour of the animals involved indicated that they had differing chances of survival. The findings confirm that the problem persists, although the impact on the population is unknown. The necessity of taking conservation measures to reduce the current level of entanglement is reiterated. Creation and training of rescue teams seems an appropriate alternative in the short-term, but in the long-term it will be necessary to design and implement actions with a wider regional scope, since the problem extends also to at least other two neighbouring countries.

KEYWORDS: INCIDENTAL CATCHES; GILLNETS; HUMPBACK WHALE; BREEDING GROUNDS; SOUTH AMERICA; SOUTHERN HEMISPHERE

INTRODUCTION

Cetacean bycatch in fishing gear is a conservation issue of increasing concern (Northridge, 1985; Perrin *et al.*, 1994; Read *et al.*, 2006; Reeves *et al.*, 2003). Interactions with fisheries occur mainly with artisanal and industrial fishing gillnets and both small and large cetaceans are involved. Global bycatch of cetaceans is estimated to be in the hundreds of thousands, although in most regions information is still fragmentary (Read *et al.*, 2006). Due to its coastal distribution, the humpback whale (*Megaptera novaeangliae*) is one of the most threatened large cetacean species. A few attempts to assess the impact of bycatch on humpback whales have been made at feeding grounds (e.g. Baird, 2003; Johnson *et al.*, 2005; Lien, 1994; Robbins and Mattila, 2001), but much less is known from the breeding grounds in tropical areas where the problem could have different characteristics.

Bycatch has been identified as the major anthropogenic threat for southeastern Pacific humpback whales (Breeding Stock G) during the breeding season in Ecuadorian and Colombian waters (Alava *et al.*, 2005; Capella *et al.*, 2001; Felix and Haase, 2005; Félix *et al.*, 1997; Flórez-Gonzáles *et al.*, 2007). Most cases of bycatch in Ecuador occur in artisanal multifilament gillnets of 10–15cm wide mesh and to a lesser extent in industrial gear (Félix *et al.*, 1997). Álava *et al*. (2005) estimated that around a third (29%) of the humpback whales stranded on the coast of Ecuador during the period 1991–2004 had gillnets around their bodies or deep cuts in their appendages and tailstock. A case of a humpback whale calf that died when it became entangled in an artisanal gillnet in the north of Peru was reported in a Peruvian newspaper[1].

Assessing the impact of fisheries in eastern tropical Pacific countries has been considered as a priority activity in several conservation strategies and action plans such as the International Union for the Conservation of Nature (IUCN) Action Plan for cetaceans 2000–10 (Reeves *et al.*, 2003), the Conservation of Migratory Species (CMS) Workshop on Aquatic Mammals in South America (Hucke-Gaete *et al.*, 2004) and the regional strategy for the conservation of the humpback whales in the Southeast Pacific (Flórez-Gonzáles *et al.*, 2007). The case of Ecuador is of particular concern because the country has the largest artisanal fishing fleet of all the Southeast Pacific countries (CPPS, 2003). By the end of the 1990s, the artisanal fleet in Ecuador numbered approximately 15,500 boats and 56,000 fishermen; this is around 5% of the economically active population inhabiting the Ecuadorian coast (Martínez and Viteri, 2005; Solís-Coello and Mendívez, 1999).

In this paper new cases of humpback whales entangled in artisanal gillnets found off Ecuador are presented. In contrast to previously reports which focused on strandings, these new cases involve live whales. This represents a first attempt to understand the magnitude of a problem that is not restricted to Ecuador, but potentially covers the entire breeding area of this population.

METHODS

Humpback whales were recorded during the breeding season (late June–early October) aboard whalewatching boats used as research platform off Salinas, Ecuador (2°10’S, 81°00’W) (Fig. 1). These data are part of the information collected within the framework of a long-term study of this species (see Félix and Haase, 2005; 2001). As standard, whales were photographed with a Canon Rebel Digital camera (6.3 megapixels) equipped with a 70–300mm zoom lens for

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[1] A note with a photograph of the dead specimen on the beach was published in the newspaper ‘El Comercio’, 26 July 2007.

[1] *Museo de Ballenas, Av. Enríquez, Gallo Entre Calles 47 y 50, Salinas, Ecuador.*
[2] *Fundación Ecuatoriana para el Estudio de Mamíferos Marinos, Salinas, Ecuador.*
[3] *Fundación Macuáticos Colombia, Calle 27 # 79–167, Medellin, Colombia.*

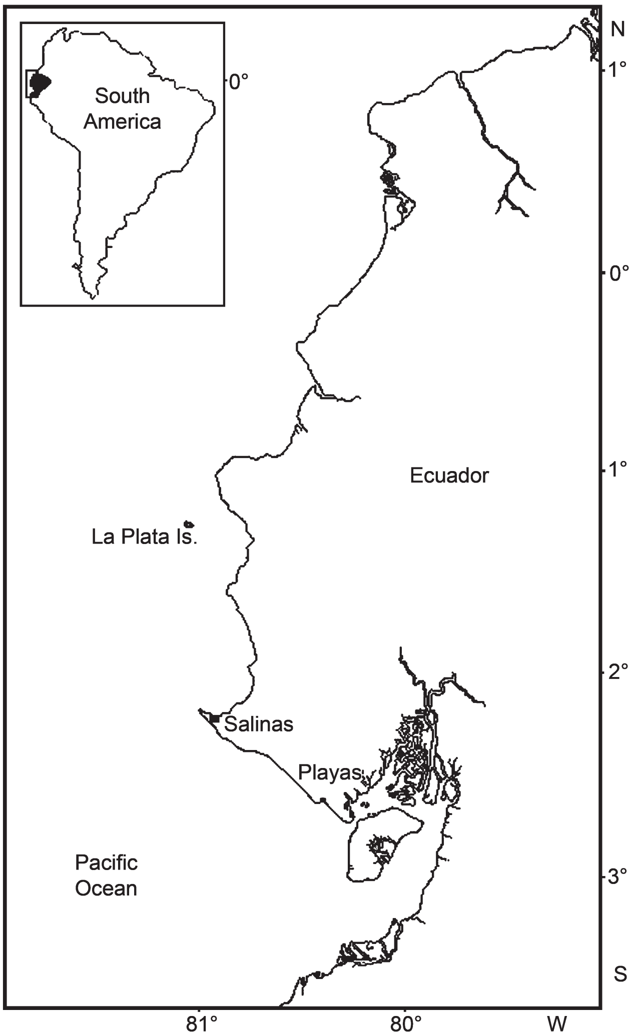

Fig. 1. The study site on the coast of Ecuador.

individual identification (dorsal fin and/or flukes). A summary of research effort can be found in Table 1.

During the seasons 2004–07, several whales were seen towing gear or ropes and these are referred to as 'entangled animals'. Some cases involved exhausted and slowly swimming animals with the flippers and tail compromised. Some less severe cases passed unnoticed in the field but were found during subsequent analysis of the photographs.

RESULTS

Case recorded in 2004

A whale observed breaching on 29 August 2004 was subsequently found to have a rope extending from head to tail along its left side (Fig. 2). The whale was escorting a mother with calf and during the sighting period breached six times. The rope was visible in three photographs taken at 12:36, 12:47 and 12:53, which indicate that the rope was tightly fastened to the body. This case of entanglement went unnoticed in the field, despite the group being followed for 48 minutes. Photographs of the whale's back and right side do not show signs of either rope or net.

Table 1

Research efforts in the period 2004–07.

	2004	2005	2006	2007	Total
Number of trips	77	74	135	104	390
Observation time (hr)	68.3	59.1	123.1	92.9	249.9
Net navigation time (hr)	136.3	94.8	301.4	167.4	533.4
Total navigation time (hr)	204.6	153.9	424.5	260.3	783.3
Total distance surveyed (km)		2,031	2,899	3,019	7,949

Fig. 2. Breaching whale with a rope hanging from the left side of the body.

Cases recorded in 2005

Three entangled whales were recorded during the 2005 season on 26 June, 10 August and 11 August (Fig. 3). All three cases involved adult animals. Since only the back of the whales was visible during the encounters, it was not possible to determine the extent of entanglement in each case or whether the whales had a chance to rid themselves of the fishing gear. The whale found in June was a severe case with a net around the anterior part of the body including the head. A long strip of net with yellow floaters showed the whale was towing several meters of gear, suggesting that the tail could be also compromised. The individual found on August 10 was a female who had previously been seen with a newborn calf for a short time; there was a net along the side of the body and no calf was present on August 10. The case on August 11 appeared more serious. The photographs show that the net was wrapped around the central part of the back and the dorsal fin; most likely the tail and possibly the flippers were also compromised.

The whale found in June moved slowly and stayed around the same area. It was evident during the observation period

Fig. 3. Whales recorded entangled off Salinas during the 2005 season. The order of the photographs is according to the date of the sighting.

that the net impacted on and slowed down its movements. In contrast, the other two whales moved apparently without problems. In the first and second cases (26 June and 10 August) the whales were a few hundred meters from shore off the Salinas tip, but the third whale (11 August) was located 2–3km north of this point.

Cases recorded in 2006

Three entangled whales were recorded in 2006 on 7 July, 23 July and 26 August (Fig. 4). The first case was an adult animal with net and ropes around the tail. This animal was photographed from a long distance and the net was not noticed during the sighting. The second whale was single and immature, found close to shore. That whale swam fast and made quite regular dives (5’07”, 5’02” and 4’50”), coming up for five to ten breaths. At close range it was seen that both the tail and at least the left flipper were seriously entangled in green mesh gillnet, ropes and floaters.

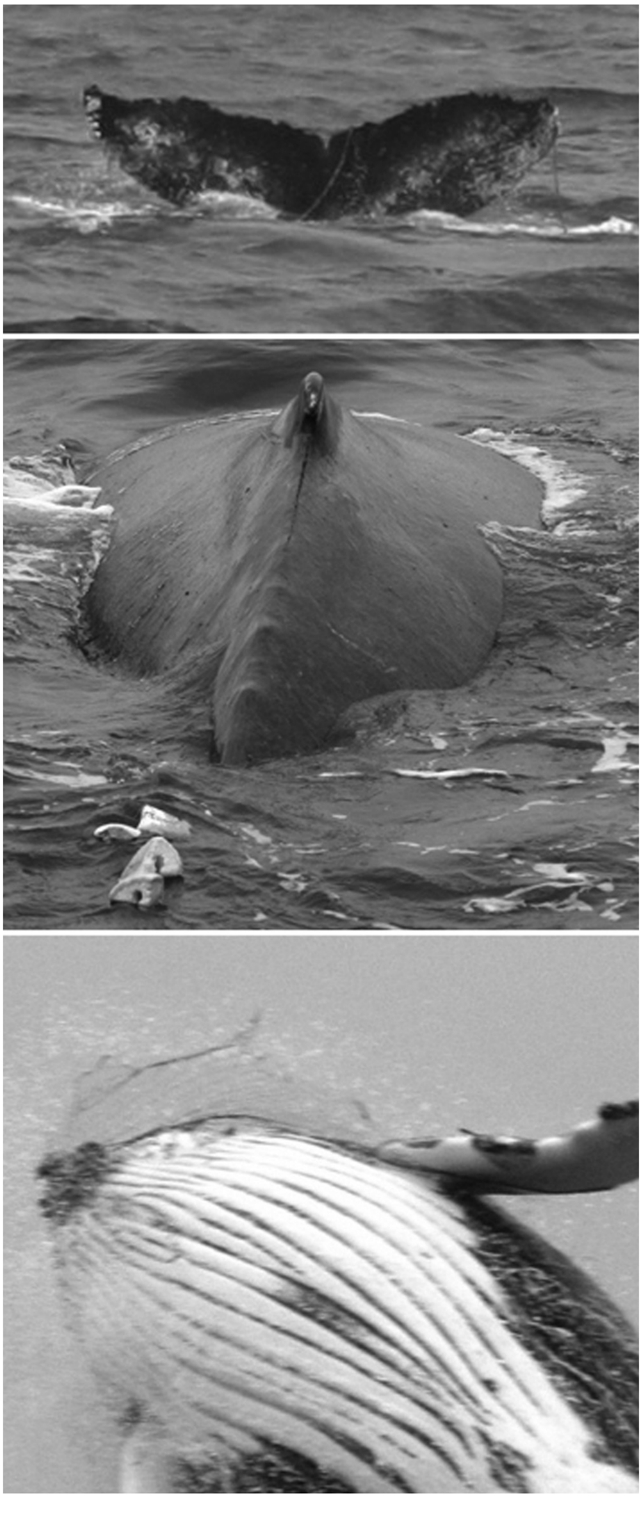

Fig. 4. Whales recorded entangled off Salinas during the 2006 season. The order of the photographs is according to the date of the sighting.

The third case in 2006 was similar to that of 2004. A breaching whale was seen with remains or parts of gillnets and ropes hanging from the left side of the head. The net was tied to the left flipper and the chin knobs, but the tail and right flipper were apparently free. The whale was a solitary sub-adult that moved around slowly and close to shore. During the observation period (36 min) the animal was active and executed three breaches, two tail slashes and on two occasions raised its head out of the water. The net was not noticed in the field but was detected on three frames during the photographic analysis.

Another entangled whale was recorded on 25 October 2006 at Playas, located at about 80km southeast of Salinas (02°35’S, 80°23’W). Since this last case was not recorded during a whalewatching trip it was not taken into account when estimating the entanglement rate. The whale, a 14–15m adult animal, was seen from the shore from the early morning until 14:00, when a rescue attempt was made (Fig. 5). This was a serious case of entanglement, with most of the whale’s back and tail wrapped in a 15cm–wide green gillnet. The whale looked exhausted, stayed almost motionless at the surface and breathed once every four to five minutes. The whale moved up and down along the beach with the tide. A small piece of gillnet of 10m long was cut away, but the rescue was interrupted due to poor visibility and inappropriate equipment. The whale was not seen again.

Cases recorded in 2007

Four cases were recorded in 2007 (14, 27 and 29 July, and 20 August) (Fig. 6). The first case involved a solitary whale with a net around the peduncle. The rear central border looked red due to a fresh wound. After two or three low blows, the whale started long dives (up to 8 min), appearing again a few dozens of meters away. It was noted that the whale made extra effort to get enough impulse from the tail before starting the long dive.

In the second case, remains of net and ropes were seen embedded in the blubber around the peduncle and flukes of the whale. The growth of barnacles on the gear indicated that the whale had been towing it for long time. This case may have occurred during the previous season. The whale swam and dove ‘normally’ and it was seen together with two other whales.

In the third case, a whale was seen with a net around the right side of its head, although other parts of the body, such

Fig. 5. A severe case of an entangled whale with a net around most of the body.

Fig. 6. Whales recorded entangled off Salinas during the 2007 season. The order of the photographs is according to the date of the sighting.

as the right flipper, may also have been compromised. This whale was accompanied by another whale, swimming together but doing short forward breaches and frequently raising its head out the water.

The final case involved a whale completely wrapped in net. A fresh wound to the tip of the dorsal fin indicated that the entanglement had occurred only a short time before.

Overview

In summary, six cases were considered severe, i.e. the whale was totally or partially wrapped in the net and/or the tail was compromised. Five cases were less severe, with just the remains of nets and ropes visible and a high probability that the whale could rid itself of them. In one case the gear was probably towed for months or even a year. In less severe cases, animals seemed to swim normally and were able to breach. More severe cases were found close to shore (five out of six cases), which may be a natural defensive reaction to the entanglement. This exposes the whales to other coastal gear and makes them also more likely to strand. Some completely entangled whales remained close to the surface. Some breathed frequently with a low blow, but others performed longer dives and breathed once when surfacing.

Photographs of the dorsal fin and/or flukes of the entangled whales indicated that all of them were different individuals and therefore there was no risk of duplication. In all cases when the net was clearly visible (n = 9, 75%), including the case when a piece of net was retrieved from a whale, the net was of the same type as used by Ecuadorian artisanal fishermen to catch large pelagic fish (a green 10–15cm width multifilament mesh).

DISCUSSION

The information obtained near Salinas during the period 2004–07 confirms previous reports which warned about the high bycatch rate of humpback whales in the Ecuadorian artisanal fishery (Table 2). Besides the twelve cases reported here, the authors knew of at least three other cases that occurred in other parts of the country involving stranded whales with gillnets around their bodies. Furthermore, sailors and naturalist guides reported to the authors additional cases of entangled whales off Salinas (not considered here) every year since whalewatching started in 2001 in this port. It is believed that the entanglement of humpback whales in artisanal gillnets in Ecuador and also in Colombia has had an upward trend in the last decade (Alava *et al.*, 2005; Capella *et al.*, 2001).

As gillnets are not fixed, it is not possible to confirm whether all cases occurred off Salinas or even in Ecuador. Most probably, entangled whales were recorded in Salinas due the concentration of research effort in the area. As no detailed data on artisanal fishing areas are available, it is difficult to assess the circumstances involved in the entanglements. It is not possible to establish the direct impact on the population since no data on survival are available. Many entangled whales presumably die of exhaustion or eventually of starvation if the entanglement lasts long enough to prevent them from migrating (e.g. the case recorded at the end of October 2006). Others may become easy prey to killer whales or sharks (see Mazzuca *et al.*, 1998). Photographs of the whales presented here show different chances of survival. Serious cases included single animals with gear compromising the tailstock and flukes, moving with limited or low speed and probably unable to free themselves. In less serious cases, only ropes or small portions of the nets were attached to the body. As four of the eleven cases (36%) remained undetected during field observations and were only noticed upon examination of photographs, the number of entanglements reported here must be considered a minimum. Several studies elsewhere indicate that true entanglement rate may be much higher than the number of cases recorded (Johnson *et al.*, 2005; Knowlton and Kraus, 2001; Robbins and Mattila, 2001). In particular, studies based on photographs of scars on the peduncle indicate that up to 65% of the humpback whales in the Gulf of Maine showed signs of previous entanglement (Robbins and Mattila, 2004) and up to 71% in Northern Southeastern Alaska (Neilson *et al.*, 2007).

Since all cases in which the fishing gear was identified involved pelagic surface gillnets, it may be concluded that such nets represent the greatest risk for humpback whales during the breeding season off Ecuador. This must be related to the behaviour of the whales in tropical waters, where humpbacks spend more time in the upper water column rather than performing deeper dives such as those when foraging (Johnson *et al.*, 2005; Robbins and Mattila, 2004). However, as humpback whales are susceptible to entanglement or entrapment in a variety of passive fishing gears (e.g. Johnson *et al.*, 2005; Lien, 1994) it cannot be ruled out that for the other three cases, when the gear were

Table 2

Number of sightings, whales and entanglement rate estimated per year (period 2004–07).

	2004	2005	2006	2007	Overall
Number of sightings	147	148	300	221	816
Number of non-entangled whales	322	346	710	551	1,929
Number of entangled whales	1	3	3	4	11
Entanglement rate	0.0031	0.0086	0.0042	0.0072	0.0057

not identified, remains of longlines or even industrial gear could have been involved. From previously reported cases of entanglement in Ecuador (including strandings) only one case was attributed to industrial gear (Alava *et al.*, 2005; Félix *et al.*, 1997). Considering that the Ecuadorian industrial fisheries are focused on small pelagic fish and tuna and that humpback whales do not feed during the breeding season, direct interaction with industrial purse seiners seems unlikely.

The data indicate that both adult and immature animals, probably of both sexes, are victims of entanglement. In the case of females accompanied by a calf (e.g. case number 2, 2005), the impact on the population would be even bigger, since calves would subsequently starve to death. Although not found off Salinas, calves occasionally do become entangled; at least two cases have been reported in Ecuador (Alava *et al.*, 2005; Scheidat *et al.*, 2000) and seven in Colombia (Capella *et al.*, 2001). Calves of the year were identified as the more affected class from entanglements in Hawaiian waters, a major breeding area of the North Pacific humpback whales (Mazzuca *et al.*, 1998).

CONCLUSION

As both fishing effort and the humpback whale population are probably increasing, it is expected that the number of entangled whales will continue to increase in the future unless counter-measures are taken. Several management actions have been proposed, including research, education programmes for artisanal fishermen, closed seasons, changes of fishing gear and ongoing disentanglement schemes (Alava *et al.*, 2005; Felix and Haase, 2005; Félix *et al.*, 1997; Félix and Samaniego, 1994). Some of these could be implemented on a temporary basis during the humpback whale breeding season or for specific areas with higher densities of whales. It is recommended that any proposal and/or decision must be agreed with relevant stakeholders including fishing authorities, artisanal fishermen associations and NGOs. Fishing and port authorities must be taken into account in the creation of rescue teams to free entangled whales. Despite the development of successful disentanglement programmes for large whales elsewhere, it has been recommended that efforts in the Ecuador area should be concentrated on trying to understand the factors involved in the entanglement rather than rescuing affected animals (Johnson *et al.*, 2005; Robbins and Mattila, 2001).

Major efforts are required to address bycatch in Ecuador and throughout the region, and the use of appropriate statistical procedures are required in order to establish the real magnitude of bycatch of humpbacks in the area. However, there is already enough information available to decision makers to start taking precautionary measures. Considering that the Southeastern Pacific humpback whale is a long-distance migrating species that occurs or disperses during the breeding season along the coast of at least five countries (Flórez-Gonzáles *et al.*, 2007; Rasmussen *et al.*, 2007), it is highly recommended that the problem be addressed in a practical regional context.

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The 2005 Galápagos humpback whale expedition: a first attempt to assess and characterise the population in the Archipelago

FERNANDO FÉLIX[1], DANIEL M. PALACIOS[2,3], SANDIE K. SALAZAR[4], SUSANA CABALLERO[5], BEN HAASE[1] AND JÉSSICA FALCONÍ[6]

Contact e-mail: fefelix90@hotmail.com

ABSTRACT

It has been known for some time that humpback whales (*Megaptera novaeangliae*) occur in waters of the Galápagos Islands, an oceanic archipelago located 1,000km west of Ecuador, South America (1°S, 91°W), but their presence there has been poorly documented. Although presumed, no linkage has been established between Galápagos and southeast Pacific humpback whales (Breeding Stock G), the nearest breeding stock. An expedition to Galápagos was carried out between 31 August and 10 September 2005 to document the presence of humpback whales, their distribution, and their relationship to other stocks in the Pacific. Surveys covered 722km of the central and southern parts of the archipelago. Only one adult with a newborn calf was found at Santa Fé Island (0°47'S, 90°05.1'W), yielding an encounter rate of 0.27 whales per 100km of survey. A hydrophone with a response frequency range of 0.25–25kHz was dropped 25 times, but no whale sounds were heard. A skin sample was obtained by darting of the adult at Santa Fé, and was used for genetic analysis of the mtDNA control region. The haplotype of the Galápagos specimen has been found in a few individuals sampled previously off Colombia, Ecuador and the Antarctic Peninsula, thus establishing at least some degree of relatedness with Breeding Stock G. The observations, combined with a compilation of historical and recent sighting information in the archipelago, support the idea that Galápagos is a breeding area for the species. Further studies are needed to establish the level of discreteness, size and other basic aspects of the Galápagos humpback whale population.

KEYWORDS: SOUTH AMERICA; GALÁPAGOS ISLANDS; BREEDING GROUNDS; HUMPBACK WHALE; SURVEY-VESSEL; OPPORTUNISTIC SIGHTINGS; GENETICS

INTRODUCTION

The importance of the Galápagos Islands for large cetaceans has been known for a long time, particularly for sperm whales (*Physeter macrocephalus*; Townsend, 1935; Whitehead and Hope, 1991). However, in the past few decades, a number of scientific expeditions have highlighted the importance of the archipelago's waters for several other cetacean species, including both baleen and toothed whales (Alava, 2002; Clarke, 1962; Clarke *et al.*, 2002; Leveque, 1963; Loesch, 1966; Lyrholm *et al.*, 1992; Palacios, 1999; Palacios, 2003; Palacios *et al.*, 2000; Whitehead, 1986). Despite the existence of confirmed observations of humpback whales (*Megaptera novaeangliae*) in Galápagos, mostly made by naturalist guides (Day, 1994; Jackson, 1993; MacFarland, 1977; Merlen, 1995), the low number of records suggests that the species is not common in the waters of the archipelago. This could be due not only to a potentially small population using the archipelago, but to a comparatively low search effort by the above-mentioned expeditions in the nearshore areas where humpback whales are expected to occur.

The nearest humpback whale population to Galápagos is the southeast Pacific stock (also referred to as Breeding Stock G; see IWC, 1998), which is distributed along the coast of western South America. A number of studies based on photo-identification (Acevedo *et al.*, 2007; Flórez-González *et al.*, 1998; Stevick *et al.*, 2004) and genetics (Caballero *et al.*, 2001; Félix *et al.*, 2007; Olavarria *et al.*, 2007), have identified the breeding areas for Breeding Stock G off northwestern South America, and the corresponding feeding areas off the Antarctic Peninsula and the Magellan Strait. However, so far no link has been established between Galápagos and South American humpback whales.

The 'Galápagos Humpback Whale Expedition' was conducted during the austral winter of 2005. The expedition aimed to establish the identity and status of the humpback whales that occur in Galápagos in order to create a knowledge baseline for management purposes. The study was made in the context of a long-term investigation of the southeast Pacific humpback whale stock that the Ecuadorian Foundation for the Study of Marine Mammals (Fundación Ecuatoriana para el Estudio de Mamíferos Marinos, FEMM) has been conducting along the coast of Ecuador since 1991 (Félix and Haase, 2005; Félix and Haase, 2001). The most relevant findings from this expedition are presented here and a molecular comparison is made with continental whales in a first attempt to establish the identity of Galápagos humpback whales. A compilation of historical and recent humpback whale records in Galápagos are also presented to provide a clearer picture of the distribution and temporal occurrence of the species within the archipelago. This effort is highly relevant to one of the key aspects highlighted in a regional conservation strategy recently designed for the southeast Pacific humpback whale population (Flórez-Gonzáles *et al.*, 2007), which calls for the generation of basic information from less-studied areas within the breeding grounds that could be considered critical for the species.

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[1] *Museo de Ballenas, Av. Enríquez, Gallo entre calles 47 y 50, Salinas, Ecuador.*
[2] *Joint Institute for Marine and Atmospheric Research, University of Hawai'i at Manoa, 1000 Pope Road, MSB 312, Honolulu, HI 96822, USA.*
[3] *NOAA, NMFS, SWFSC, Environmental Research Division, 1352 Lighthouse Avenue, Pacific Grove, CA 93950-2097, USA.*
[4] *Galapagos Academy Institute of Arts and Sciences (GAIAS)-USFQ, Puerto Baquerizo Moreno, San Cristóbal, Galápagos.*
[5] *Laboratorio de Ecología Molecular de Vertebrados Acuáticos, Departamento de Ciencias Biológicas, Universidad Los Andes, Carrera 1 No. 18A–10, Bogotá, Colombia*
[6] *Fundación Ecuatoriana para el Estudio de Mamíferos Marinos (FEMM). Salinas, Ecuador.*

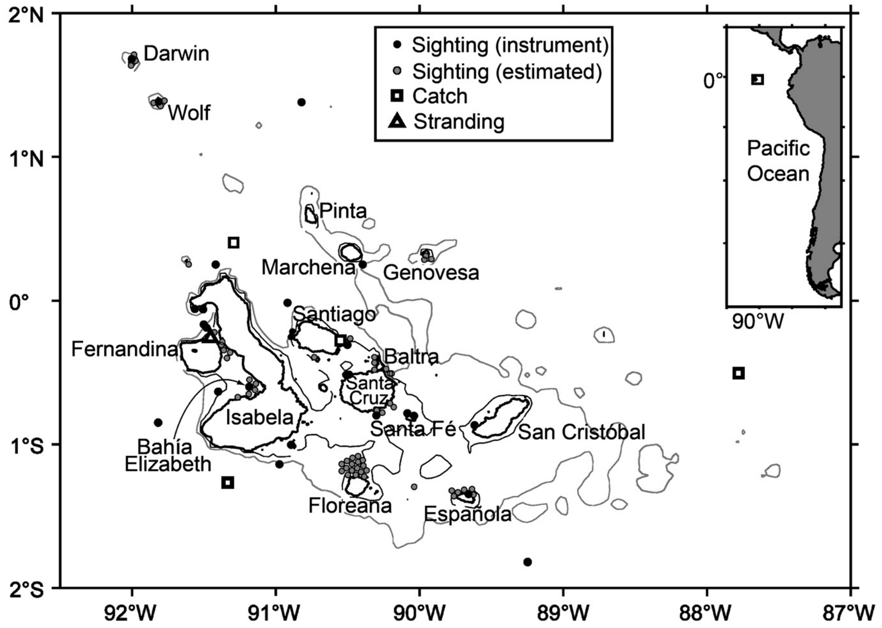

Fig. 1. Distribution of 89 historical and recent humpback whale records in the Galápagos Islands (see Appendix 1 for sources). Bathymetric contours for the 200m (thin black line) and 1,000m (thin grey line) isobaths are shown. Inset shows the location of the study area in relation to western South America.

MATERIAL AND METHODS

Study area

The Galápagos archipelago is formed by a group of 13 large islands (>10km^2), six smaller islands, and over 100 islets and rocks (Jackson, 1993; Snell *et al.*, 1996). It is located 1,000km west of the coast of Ecuador, South America (1°S, 91°W) (Fig. 1). The islands are surrounded by narrow shelves and abrupt slopes, with some shallow areas in the central part of the archipelago. In the outer areas, depth increases rapidly to 3,000m or more, particularly in the western and southern regions. A marine protected area extending 40 n.miles (74.1km) from the baseline surrounding the entire archipelago and covering an area of about 138,000km^2, was established in 1998 as the 'Galápagos Marine Resources Reserve' (Heylings *et al.*, 2002). The highly productive waters of the archipelago, especially on the western side (Palacios, 2002; Palacios *et al.*, 2006), create favourable conditions for a high abundance and diversity of marine mammals (Palacios and Salazar, 2002; Palacios, 2003).

Historical and recent records

In preparation for the expedition previous records of humpback whales from three sources were compiled as follows.

(1) Townsend Whaling Charts (Townsend, 1935). Capture locations within Galápagos waters were extracted from monthly maps containing 2,883 humpback whale catch records from North American ('Yankee') pelagic whale vessel logbooks dating from 1761 to 1920. Each record in the charts corresponds to the location of a whaling ship on a day when one or more whales were taken, and does not necessarily reflect the number of whales caught. These data are available in digital format from the Wildlife Conservation Society (*http://www.wcs.org/sw-high_tech_tools/landscapeecology/townsend_charts*).

(2) Sighting locations collected in Galápagos waters by scientific observers aboard tuna fishing vessels (Archer *et al.*, 2002; Buckland *et al.*, 1992) and research vessels (Hill *et al.*, 1991; Kinzey *et al.*, 1999) under programmes conducted by the Southwest Fisheries Science Center (SWFSC) of the US NOAA/National Marine Fisheries Service. Sightings collected by a team from Dalhousie University, Canada while conducting sperm whale research in Galápagos (Smith and Whitehead, 1999; Whitehead, 1986) were also included.

(3) Weekly reports by licensed naturalist guides to the Galápagos National Park (GNP) and from a 'Sightings Logbooks Program' created under an inter-institutional agreement between the GNP and the Charles Darwin Foundation (CDF). The objective of this programme is to establish a uniform reporting standard and to improve the quality of information reported by the different users of the Galápagos Marine Resources Reserve. Sightings logbooks are distributed among users, to be completed whenever cetacean sightings are recorded. Tour vessels operating in the Reserve must follow established routes to visitor sites and carry aboard naturalist guides trained in marine mammal identification. About 40 vessels currently participate in the programme. The programme was officially implemented in 2001, but it contains records starting from 1995. The reports are quality-controlled for errors and are entered into a database maintained by the CDF (Salazar and Hernandez, 2000). For mapping purposes, the geographic coordinates for records for which only the approximate locality was reported were georeferenced using the GIS software *ArcView* 3.2 with the animal movement extension. Throughout the text, these positions are referred to as 'estimated' to differentiate them from exact positions obtained directly in the field, which are referred to as 'instrument'.

Surveys

Between 31 August and 10 September 2005, ten surveys were conducted in the central part of the archipelago aboard four different vessels: three small boats (6–8m in length) with outboard engines, and the 12m sailboat '*Bronzewing*', which was used as a live-aboard platform for seven days. Daily trips lasted 5–12h depending on weather conditions and on finding a safe place to overnight. Surveys were carried out over the shelf of several islands in areas where the presence of humpback whales had previously been reported. Trips plans were made and updated on a daily basis, based on the progress made during the day. For this purpose, the navigation Chart IOA 21 (INOCAR, Ecuador) and a GPS Garmin 60™ were used. In the case of the small boats, observations were made from the cabin's rooftop, about 2–2.5m above the waterline. Boats moved at an average speed of 12kt (22.2km h^{-1}). On the sailboat, which was powered by a small inboard diesel engine, observers were located on the main deck, both at the bow and amidships, at an average height of 1.5m above the waterline. The sailboat's speed ranged between 5 and 7kt (9.3–13km h^{-1}).

Sea state conditions were fairly constant during the study period, ranging between 2 and 3 on the Beaufort scale. When conditions worsened, sighting effort was stopped (this occurred twice). During the observation periods, information on group size and composition, position, heading, speed and general behaviour was obtained. Photographs were taken with a digital camera equipped with a 70–300mm zoom lens.

A hydrophone model C10 (Cetacean Research Technology) with a response frequency range of 0.25–25kHz and a digital voice recorder *Archos G-Mini* 120 were used for listening and recording whale songs. The hydrophone was used on an irregular basis, in some cases every 60min of survey, especially on the small boats. Aboard the sailboat, the hydrophone was used sporadically at the beginning and end of the daily surveys.

Molecular analysis

A skin sample was obtained from a humpback whale at Santa Fé Island with a Barnett crossbow equipped with a 60cm-long arrow and modified tips (see Lambertsen, 1987). The biopsy was preserved in a solution of dimethylsulfoxide saturated in sodium chloride. Approximately a 520bp fragment of the mitochondrial DNA control region was amplified via the Polymerase Chain Reaction (PCR) using standard reaction conditions (Palumbi, 1996; Saiki *et al.*, 1988). For the PCR, the primer combination t-Pro-whale (5'-TCACCCAAAGCTGRARTTCTA-3') and Dlp8 (5'CCATCGWGATGTCTTATTTAAGRGGAA-3') was used (Baker *et al.*, 1998; Olavarria *et al.*, 2007). The PCR profile used was as follows: an initial denaturation at 95°C for 2min; 36 cycles of 94°C for 30s, 55°C for 1min, 72°C for 1.30min; and a final extension at 72°C for 5min. Free nucleotides and primers were removed from the PCR products using shrimp alkaline phosphatase and exonuclease I (ExoI, USB) and directly sequenced in both directions using the standard protocols of *Big Dye* terminator sequencing chemistry on an ABI 3100 automated capillary sequencer (Perkin Elmer).

A 480bp fragment was analysed for haplotype determination. The sequence was manually edited and aligned using *Sequencher* 4.1 software (Gene Codes Corporation). The control region haplotype was defined using MacClade (Maddison and Maddison, 2000) and compared with haplotypes previously defined for other humpback whale populations in the South Pacific (Caballero *et al.*, 2001; Félix *et al.*, 2007; Olavarría *et al.*, 2006; Olavarria *et al.*, 2007). Haplotype nomenclature follows Olavarría *et al.* (2007).

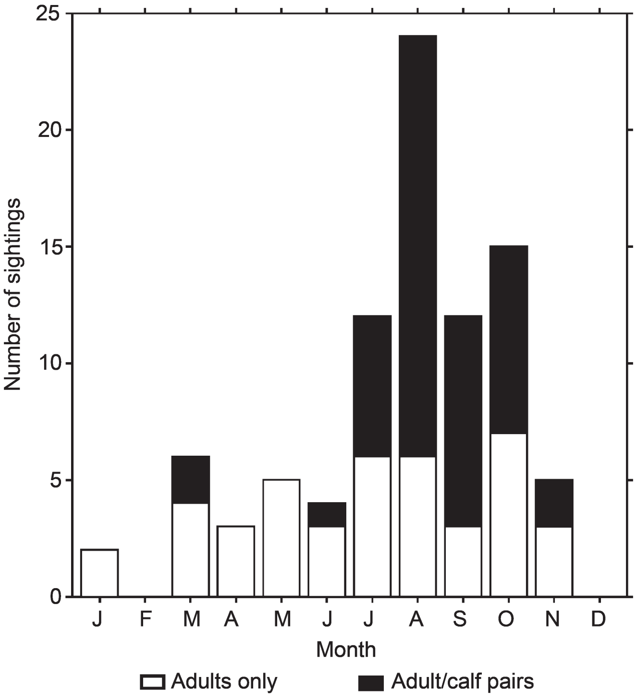

Fig. 2. Frequency distribution per month of historical and recent humpback whale records in the Galápagos Islands for groups containing adults only and adult/calf pairs.

RESULTS

Historical and recent records

A total of 89 humpback whale records were obtained, including four captures, one stranding and 84 sightings (Fig. 1, Appendix 1). Most of the records were concentrated around the islands of the central (Santiago, Santa Cruz, Floreana) and western (Isabela) side of the archipelago, although whales were also seen over the shelf of all main islands except for Pinta.

The frequency distribution of sightings per month (including sightings involving adult-calf pairs) is shown in Fig. 2. Humpback whales were recorded over ten different months, with a clear peak between July and October, and with fewer records in May, June and November. In addition, 11 sightings (12.5%) were made between January and April, including two female-calf pairs.

Visual and acoustic survey effort

The surveyed areas covered waters around the following islands: west and north of San Cristóbal; east and north of

Table 1

Details of the surveyed areas during the 'Galápagos Humpback Whale Expedition', 31 August-10 September 2005.

Date	Survey	Duration (hr)	Distance (km)
31/08/05	West and NW sides of San Cristóbal	7.90	100.50
01/09/05	San Cristóbal-Santa Fé-Santa Cruz	6.16	74.50
03/09/05	Santa Cruz-Santa Fé	5.21	38.60
04/09/05	Santa Fé-Floreana	9.25	72.50
05/09/05	Floreana - southeast of Isabela	11.83	91.39
06/09/05	SE of Isabela-Rábida	11.48	72.28
07/09/05	Rábida-Baltra	10.13	58.61
08/09/05	Baltra - north of Santa Cruz	6.21	37.63
09/09/05	West of Santa Cruz-Puerto Ayora	7.71	93.99
10/09/05	Santa Cruz-San Cristóbal	5.40	82.36
Total		81.33	722.36

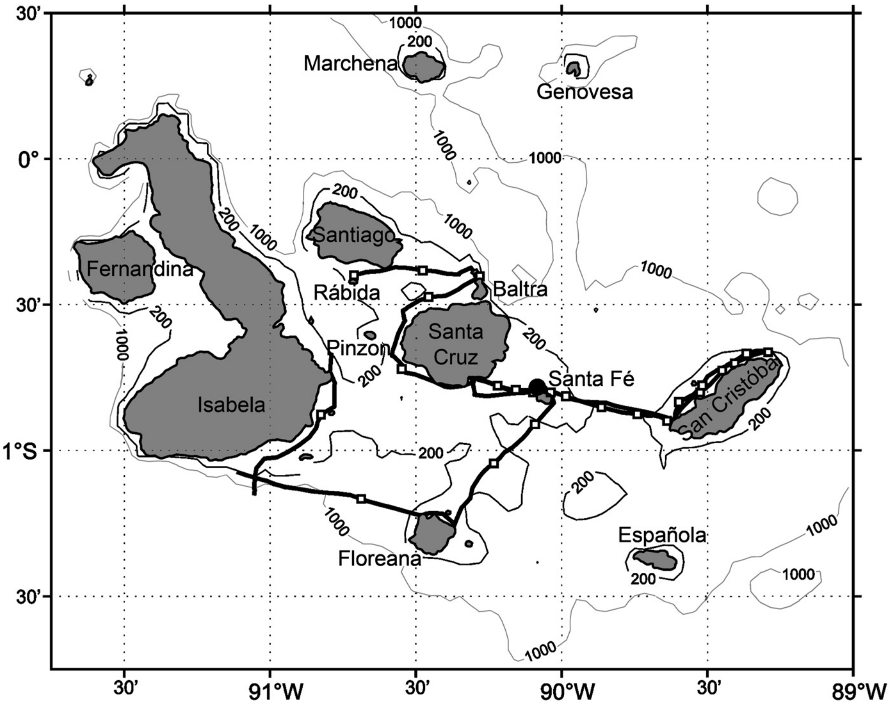

Fig. 3. Survey tracks (bold black line) during the 'Galápagos Humpback Whale Expedition', 31 August–10 September 2005. Hollow squares denote the 25 acoustic stations. The black solid circle near the centre of the map indicates the location of the adult/calf pair sighting. The 200m and 1000m isobaths are shown.

Santa Fé; north of Floreana; southeast of Isabela; north, west and south of Santa Cruz; southeast of Santiago; and the waters between them (Fig. 3). The total distance covered was 722.36km and the total navigation time was 81.33hr (Table 1). The hydrophone was dropped for 5min (±1min) at 25 different sites (Fig. 3), but no sounds were heard during the entire expedition.

Encounter rate

The only humpback whale observation made during the expedition was near Santa Fé Island (0°47.6'S, 90°05.1'W) (Fig. 3). The group was made up of an adult with a small calf, probably a couple of weeks old judging by its very small size and the light grey colour of its skin (Fig. 4). The pair was found over a shallow area of less than 20m in depth, northwest of the island. According to the navigation chart IOA 21, Santa Fé Island has a shelf of 100m in depth extending some 10km on its southeast side, but in the northwest part, where the pair was found, the shelf only extends out to about 3km. However, the sighting was made over a shallow flat area marked on the navigation chart as 13m depth and with an area of about 3–4km^2. Photographs of the dorsal fins were taken since none of the animals showed their flukes. The encounter rate for humpback whales during this expedition was of 0.276 whales per 100km of survey.

Fig. 4. Humpback whale adult-calf pair encountered at Santa Fé Island. Notice the calf's very small size compared to that of the adult and the lighter colour of its skin.

Control region haplotype

The Galápagos haplotype was identified as SP61, which has previously been found in one individual from mainland Ecuador (Félix *et al.*, 2007), one from Colombia (Olavarria *et al.*, 2007) and two from the Antarctic Peninsula (Olavarría *et al.*, 2006).

DISCUSSION

Relative abundance and habitat use

While the GNP-CDF database was useful in establishing that humpback whales may be found in nearshore waters throughout the archipelago, further interpretation is complicated due to three sources of bias in this data set: (1) recording does not follow a systematic effort, making it impossible to obtain estimates of relative abundance; (2) the same animal(s) could be reported by more than one observer at sites visited by multiple vessels in a short time period; and (3) the reports came from lots of observers with different levels of experience in identifying whale species, increasing the possibility of misidentification.

The 2005 'Galápagos Humpback Whale Expedition' was the first attempt to quantify the presence of this species in the archipelago. Nevertheless, during the study period, it was not possible to survey all the sites where humpback whales have been reported previously (Fig. 1), particularly the highly productive areas between Isabela and Fernandina Islands. The survey was limited to the central, southern and southeastern parts of the archipelago, over the shelf of several islands and the deep-water zone between them. Since extensive areas of the archipelago remained unsurveyed, the findings should not be considered representative of the entire archipelago.

There was a large difference in whale density in the surveyed areas in Galápagos compared to the breeding areas off mainland Ecuador, where the encounter rate was 59 times higher during the same season (Felix *et al.*, 2004). It should be recognised, however, that survey conditions were not the same between these two areas, since sea state conditions are slightly better and faster boats are used at the mainland sites. Despite these differences, the data presented herein support the notion that Galápagos contains a low density of humpback whales, as previous reports have suggested (Day, 1994; Merlen, 1995). It is possible that humpback whales were never abundant in Galápagos, considering that 19th century American whalers concentrated their effort on humpback whales in the continental waters of Panamá, Colombia and Ecuador, while the Galápagos Islands were considered a major whaling area for sperm whales (Townsend, 1935).

A low humpback whale density seems to be characteristic of oceanic archipelagos in the South Pacific. For instance, Gannier (2004) reported encounter rates between 0.35 and 1.54 whales per 100km of survey in French Polynesia, which is between 1.3 and 5.7 times higher than for the Galápagos Islands. Although Gannier primarily used a similar 12m sailboat, both studies also used data obtained from other types of vessels. Therefore, caution should be exercised with this interpretation, as the data are probably not fully comparable. It is also known that humpback whales show a clustered distribution around archipelagos, with sites of high concentration of animals and extended zones of low densities. In Hawai'i, for example, there is high density in a shallow area known as the Penguin Bank and also in the Four Island area off Maui (Herman and Antinoja, 1977; Salden, 1988). In the Caribbean, 85% of the entire North Atlantic population concentrates for breeding at Silver and Navidad Banks off the northern Dominican Republic (Winn *et al.*, 1975), although whales can be found as far south as the Lesser Antilles (Swartz *et al.*, 2003). While it is not implausible that such a type of distribution may occur in Galápagos, it seems unlikely that local high whale concentrations have passed unnoticed in an area with such a high level of tourism activities.

A determining factor for the low encounter rate may have been the low observation height onboard the vessels. However, the lack of song detection is supportive of a low whale density at the time of the survey. An alternative explanation to the low encounter rate and to the lack of singers could be that reports of humpback whales in Galápagos correspond to transient animals and/or unusual visitors from other sites in the southeast Pacific. However, the sighting, together with previous records of adult-calf pairs in Galápagos (MacFarland, 1977; Merlen, 1995; see also Appendix 1) provide strong support to the idea that the archipelago's waters are used for more than merely transiting and are probably a calving area for humpback whales.

The predominantly coastal distribution of humpback whales in Galápagos (Fig. 1) is consistent with the habitat preferences reported for the species at the breeding grounds along mainland Ecuador (Felix and Haase, 2005), as well as at other calving areas worldwide (Ersts and Rosenbaum, 2003; Johnston *et al.*, 2007; Smultea, 1994; Vang, 2002). This distribution pattern has local conservation implications because adult-calf pairs could be particularly sensitive to the intense maritime traffic generated by tourism (see Salden, 1988), the main economic activity in Galápagos. Therefore, the overlap between vessel routes and areas of humpback whale presence and the impact of maritime traffic on whale behaviour are aspects that need to be assessed.

Population identity

Historical and recent records of humpback whales in Galápagos indicated that the species occurred primarily during the austral winter months (Fig. 2, Appendix 1), as is expected for a Southern Hemisphere population during its breeding period in the tropics. The few records from May, June and November could reflect normal variations in the timing of migration, as has been recorded along mainland Ecuador (Félix and Haase, 2001).

However, 12.5% of the sightings occurred between January and April, leading to the possiblity that at least some of the whales sighted in the early part of the year may belong to a Northern Hemisphere stock. It has been demonstrated that the breeding areas for Northeast Pacific and southeast Pacific humpback whales overlap in waters off Panamá and Costa Rica (Acevedo-Gutiérrez and Smultea, 1995; Rasmussen *et al.*, 2007), and possibly as far south as southern Colombia, where two haplotypes from a North Hemisphere stock have been found (Caballero *et al.*, 2001). Another possibility is that these whales did not migrate and remained during the entire year around Galápagos. The high local productivity, especially in the western part of the archipelago (Palacios, 2002; Palacios *et al.*, 2006), could provide food for non-migrating animals, as has been proposed in other tropical areas with intense upwelling (Papastavrou and Van Waerebeek, 1997). One of these areas is the coast of Perú, a few hundred kilometers southeast of Galápagos, where humpback whales have been reported throughout the entire year (Ramírez, 1988).

The molecular biology study showed a relationship between Galápagos humpback whales and Breeding Stock G, since the same haplotype has been found in Colombia, Ecuador and the Antarctic Peninsula. However, the Galápagos haplotype was not among the most common ones found in Breeding Stock G, as it has only been found four times in about 400 samples from the southeast Pacific and the Antarctic Peninsula (Félix *et al.*, 2007; Olavarria *et al.*, 2007). Genetic (Félix *et al.*, 2007; Olavarría *et al.*, 2006), and photo-identification (Acevedo *et al.*, 2007) studies indicated that Breeding Stock G shows some degree of heterogeneity in its distribution, with at least two well-defined subunits.

The possibility that Galápagos humpback whales could be part of a discrete subunit with a low degree of exchange with the continental population cannot be excluded. Genetic differentiation between continental and insular populations has been found in Northeast Pacific humpback whales breeding at the Revillagigedo Archipelago, relative to whales breeding along central mainland Mexico, only 700km apart (Urban *et al.*, 2000). Further sampling and analysis are needed to establish the degree of discreteness, genetic variability and the main lineages in Galápagos, among other key population parameters.

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Appendix 1

Table with 89 historical and recent records of humpback whales in the Galápagos Islands, including date, geographic coordinates, group composition, nearest island, specific locality and sources. Position denotes whether the geographic coordinates were obtained in the field with an instrument or estimated subsequently using GIS software based on the nearest locality reported (i.e. georeferenced). Note that the records from the Townsend Whaling Charts correspond to the location of a whaling ship on a day when one or more whales were taken, and that they only reported the month but not the year.

Date	Lat/Long	Adults	Calves	Total	Island	Locality	Position	Source
June	0°24.3’N; 91°17.6’W					Offshore capture N of Isabela	Estimated	Townsend (1935)
July	0°30.3’S; 87°46.9’W					Offshore capture ENE of San Cristóbal	Estimated	Townsend (1935)
July	1°15.6’S; 91°20.4’W				Isabela	Capture S of Isabela	Estimated	Townsend (1935)
August	0°16.6’S; 90°33.0’W				Bartolomé	Capture	Estimated	Townsend (1935)
16/07/1979	0°38.0’S; 91°24.0’W	1		1	Isabela	Bahía Elizabeth	Instrument	SWFSC tuna vessel
23/09/1990	1°49.1’S; 89°14.8’W	1		1		Offshore sighting SE of Floreana	Instrument	SWFSC research vessel
24/04/1995	0°15.1’N; 90°23.6’W	1		1	Marchena		Instrument	Dalhousie University
1998	1°21.6’S; 89°45.6’W	1	1	2	Española	Punta Suárez	Estimated	GNP-CDF database
07/11/1998	1°00.2’S; 90°53.6’W	1	1	2	Isabela	Tortuga Is.	Instrument	SWFSC research vessel
24/05/1999	0°12.9’S; 90°53.0’W	2		2	Santiago	Puerto Egas	Estimated	GNP-CDF database
24/05/1999	0°23.7’S; 90°43.9’W	1		1	Rábida	Rábida	Estimated	GNP-CDF database
07/1999	1°12.8’S; 90°26.6’W	2	1	3	Floreana	Bahía Post Office	Estimated	GNP-CDF database
07/1999	1°09.9’S; 90°26.0’W	1	1	2	Floreana	Bahía Post Office	Estimated	GNP-CDF database
08/1999	1°11.5’S; 90°24.3’W	1	1	2	Floreana	Bahía Post Office	Estimated	GNP-CDF database
02/08/1999	1°08.9’S; 90°23.4’W	2		2	Floreana	Bahía Post Office	Estimated	GNP-CDF database
03/10/1999	1°10.9’S; 90°28.3’W	1	1	2	Floreana	Bahía Post Office	Estimated	GNP-CDF database
21/10/1999	0°17.4’N; 89°55.0’W	2		2	Genovesa	Back side of cliff	Estimated	GNP-CDF database
11/11/1999	1°07.3’S; 90°25.6’W	2		2	Floreana	Bahía Post Office	Estimated	GNP-CDF database
02/04/2000	0°15.5’S; 91°27.2’W	1		1	Fernandina	Stranding at Punta Espinoza	Estimated	GNP-CDF database
06/08/2000	0°42.9’S; 90°12.3’W	1	1	2	Santa Cruz	Garrapatero	Estimated	GNP-CDF database
13/10/2000	0°24.0’S; 91°20.4’W	1		1	Isabela	Canal Bolívar	Estimated	GNP-CDF database
22/07/2001	0°48.0’S; 90°18.0’W	1	1	2	Santa Cruz	Outside Bahía Academia	Instrument	GNP-CDF database
26/07/2001	0°28.9’S; 90°18.8’W	1		1	Baltra	Canal de Itabaca	Estimated	GNP-CDF database
28/07/2001	1°22.5’N; 91°51.0’W	1	1	2	Wolf		Estimated	GNP-CDF database
08/2001	1°40.1’N; 91°58.5’W	1	1	2	Darwin		Estimated	GNP-CDF database
04/08/2001	1°21.2’N; 91°48.0’W	1	1	2	Wolf	Bahía de Anciate	Estimated	GNP-CDF database
04/08/2001	0°30.5’S; 90°11.6’W	1		1	Santa Cruz	Baltra-Rocas Gordon	Estimated	GNP-CDF database
07/08/2001	0°31.0’S; 90°30.5’W	1	1	2	Santa Cruz	In front of Cerro Dragón	Instrument	GNP-CDF database
11/08/2001	1°23.5’N; 91°46.4’W	1	1	2	Wolf		Estimated	GNP-CDF database
12/08/2001	1°22.8’N; 90°49.2’W	1		1		Offshore sighting N of Pinta	Instrument	GNP-CDF database
16/08/2001	0°17.1’S; 91°22.3’W	1	1	2	Isabela	Caleta Tagus	Estimated	GNP-CDF database
31/08/2001	0°48.2’S; 90°02.3’W	1	1	2	Santa Fé	Bahía Santa Fé	Instrument	GNP-CDF database
09/2001	0°28.5’S; 90°13.9’W	1		1	Santa Cruz	Canal Itabaca-Islas Plazas	Estimated	GNP-CDF database
15/09/2001	0°15.1’N; 91°36.3’W	1	1	2	Isabela	Roca Redonda	Estimated	GNP-CDF database
18/09/2001	0°52.0’S; 89°37.0’W	1	1	2	San Cristóbal	Outside Puerto Baquerizo Moreno	Instrument	GNP-CDF database
22/09/2001	0°15.5’S; 90°31.8’W	1		1	Bartolomé		Estimated	GNP-CDF database
10/2001	1°13.5’S; 90°23.0’W	1		1	Floreana		Estimated	GNP-CDF database
01/10/2001	1°42.7’N; 91°59.1’W	1		1	Darwin	Arco de Darwin	Estimated	GNP-CDF database
02/10/2001	0°11.3’S; 91°28.8’W	1		1	Isabela	Bahía Banks	Instrument	GNP-CDF database
12/10/2001	1°38.1’N; 92°00.4’W	1		1	Darwin	Arco de Darwin	Estimated	GNP-CDF database
22/10/2001	1°08.3’S; 90°28.3’W	1	1	2	Floreana	Punta Cormorant	Estimated	GNP-CDF database
22/10/2001	0°45.8’S; 90°17.8’W	1	1	2	Santa Cruz	Bahia Academia	Estimated	GNP-CDF database
30/10/2001	1°12.8’S; 90°29.9’W	1	1	2	Floreana	Corona del Diablo	Estimated	GNP-CDF database

Cont.

Date	Lat/Long	Adults	Calves	Total	Island	Locality	Position	Source
17/03/2002	1°10.9’S; 90°22.1’W	1		1	Floreana	4.8 mi from Floreana	Estimated	GNP-CDF database
20/03/2002	0°20.7’S; 91°21.7’W	1		1	Fernandina	Canal Bolívar	Estimated	GNP-CDF database
10/04/2002	0°46.8’S; 90°15.6’W	1		1	Santa Cruz	Bahía Academy	Estimated	GNP-CDF database
22/04/2002	0°03.5’S; 91°33.8’W	1		1	Isabela	Bahía Banks	Instrument	GNP-CDF database
25/05/2002	0°01.0’S; 90°55.1’W	1		1	Santiago	NW of Santiago	Instrument	GNP-CDF database
18/06/2002	0°51.0’S; 91°49.0’W	1		1	Isabela	Offshore sighting	Instrument	GNP-CDF database
12/08/2002	1°40.9’N; 92°00.1’W	1	1	2	Isabela	Canal Bolívar	Instrument	GNP-CDF database
08/09/2002	1°09.9’S; 90°30.5’W	1	1	2	Floreana	Bahía Post Office	Estimated	GNP-CDF database
11/09/2002	1°07.0’S; 90°30.2’W	1	1	2	Floreana	La Lobería	Estimated	GNP-CDF database
30/09/2002	0°10.0’S; 91°30.0’W	1	1	2	Floreana		Instrument	GNP-CDF database
08/10/2002	0°18.5’S; 90°30.1’W	2		2	Bartolomé		Instrument	GNP-CDF database
25/10/2002	0°18.7’N; 89°57.3’W	1	1	2	Genovesa	Inside Bahía Darwin	Estimated	GNP-CDF database
03/11/2002	1°23.1’N; 91°48.8’W	1		1	Fernandina		Instrument	GNP-CDF database
13/03/2003	0°13.2’S; 91°25.6’W	1	1	2	Fernandina	Punta Espinosa	Estimated	GNP-CDF database
07/05/2003	0°36.0’S; 91°11.0’W	1		1	Isabela	Bahía Elizabeth-Bahía Urbina	Instrument	GNP-CDF database
21/06/2003	0°44.5’S; 90°10.7’W	1		1	Santa Cruz	Garrapatero	Estimated	GNP-CDF database
24/06/2003	0°03.7’S; 91°30.3’W	1	1	2	Isabela	Bahía Banks	Instrument	GNP-CDF database
26/07/2003	0°30.9’S; 90°29.4’W	1	1	1	Santa Cruz	Tortuga Bay	Instrument	GNP-CDF database
26/07/2003	1°08.3’S; 90°58.5’W	1		2	Isabela	Cuatro Hermanos	Instrument	GNP-CDF database
29/07/2003	0°23.7’S; 90°18.8’W	1	1	2	Seymour N.		Estimated	GNP-CDF database
12/08/2003	0°15.1’N; 91°25.1’W	1	1	2	Isabela	Punta Vicente Roca	Instrument	GNP-CDF database
18/08/2003	0°40.3’S; 91°15.8’W	1	1	2	Isabela	Caleta Derek	Estimated	GNP-CDF database
24/08/2003	1°20.0’S; 89°44.0’W	1	1	2	Española	Punta Suárez	Estimated	GNP-CDF database
03/09/2003	1°05.7’S; 90°27.9’W	1	1	2	Floreana	Corona del Diablo	Estimated	GNP-CDF database
03/11/2003	1°11.2’S; 90°32.5’W	1	1	2	Floreana	Bahía Post Office	Estimated	GNP-CDF database
19/05/2004	0°34.7’S; 91°08.3’W	2		2	Isabela	Bahía Elizabeth, N of Marielas Is.	Estimated	GNP-CDF database
30/07/2004	1°19.0’S; 89°41.4’W	1		1	Española	Manzanillo	Estimated	GNP-CDF database
01/08/2004	0°37.3’S; 91°08.6’W	1	1	2	Isabela	Bahía Elizabeth	Estimated	GNP-CDF database
01/08/2004	0°25.9’S; 90°18.8’W	1	1	2	Baltra	In front of Baltra	Estimated	GNP-CDF database
14/08/2004	1°19.3’S; 89°46.6’W	1	1	2	Española	Punta Suárez	Estimated	GNP-CDF database
25/08/2004	0°21.7’S; 91°19.1’W	2		2	Isabela	Canal Bolívar	Estimated	GNP-CDF database
28/08/2004	1°21.0’S; 89°34.7’W	1	1	2	Española	Bahía Gardner	Estimated	GNP-CDF database
31/08/2004	1°08.3’S; 90°32.5’W	1		1	Floreana	Punta Cormorant	Estimated	GNP-CDF database
10/10/2004	0°39.0’S; 91°11.2’W	1	1	2	Isabela	Bahía Elizabeth	Estimated	GNP-CDF database
24/10/2004	0°33.1’S; 91°10.9’W	1	1	2	Isabela	Bahía Elizabeth	Estimated	GNP-CDF database
13/08/2005	1°20.8’S; 89°39.5’W	1	1	2	Española	Bahia Gardner	Instrument	GNP-CDF database
19/08/2005	1°18.7’S; 89°38.1’W	1	1	2	Española	Bahia Gardner	Estimated	GNP-CDF database
01/09/2005	0°47.0’S; 90°05.0’W	1	1	2	Santa Fé NW	Bahía Gardner	Instrument	This study
03/09/2005	1°06.6’S; 90°23.7’W	1	1	2	Santiago	N side	Estimated	GNP-CDF database
26/09/2005	0°15.2’S; 90°53.7’W	2	1	3	Floreana	Puerto Egas	Estimated	GNP-CDF database
10/10/2005	1°05.0’S; 90°25.6’W	1	1	2	Floreana	Corona del Diablo	Estimated	GNP-CDF database
14/11/2005	0°15.8’S; 90°28.9’W	2		2	Bartolomé	Corona del Diablo	Estimated	GNP-CDF database
12/01/2006	1°17.7’S; 90°02.2’W	4		4	Española	Punta Suárez-Puerto Velasco Ibarra	Estimated	GNP-CDF database
17/01/2006	0°18.4’S; 91°22.6’W	1		1	Isabela	Canal Bolivar	Estimated	GNP-CDF database
05/03/2007	0°30.5’S; 90°12.3’W	1		1	Santa Cruz	Punta Carrión-Plazas	Estimated	GNP-CDF database
10/03/2007	0°17.0’N; 89°58.0’W	1	1	2	Genovesa	Off the bay	Estimated	GNP-CDF database

Abundance and survival estimates of the southeastern Pacific humpback whale stock from 1991–2006 photo-identification surveys in Ecuador

FERNANDO FÉLIX[1], CRISTINA CASTRO[2], JEFFREY L. LAAKE[3], BEN HAASE[1] AND MEIKE SCHEIDAT[4]

Contact e-mail: fefelix90@hotmail.com

ABSTRACT

Southeastern Pacific humpback whales (Breeding Stock G) breed along the northwestern coast of South America and farther north up to Costa Rica. Photo-identification surveys conducted aboard whalewatching vessels during the migration/breeding season from June to September between 1991 and 2006 off the coast of Ecuador (2°S, 81°W) have produced a database of 1,511 individual whales. Comparisons of photographs produced 190 between-year re-sightings of 155 individual whales. Closed and open capture-recapture models were used to estimate abundance and survival. The best estimate of abundance in 2006 with the Chapman modified-Petersen was 6,504 (95% CI: 4,270–9,907; CV = 0.21). Abundance estimates from open population models were considerably lower due to heterogeneity in capture probability which produced a 'transient' effect. Our best estimate of true survival was 0.919 (95% CI: 0.850–0.958). Heterogeneity most likely occurred from inter-annual variation in sampling and unknown structure and variation in the migration timing and corridor. A more extensive collaborative effort including other wintering areas further north as well as integrating breeding-feeding data will help to reduce heterogeneity and increase precision in abundance and survival estimates.

KEY WORDS: HUMPBACK WHALE; ABUNDANCE ESTIMATE; SURVIVORSHIP; MARK-RECAPTURE; PHOTO-ID; SOUTH AMERICA.

INTRODUCTION

Humpback whales (*Megaptera novaeangliae*) migrate in the southeast Pacific between their feeding grounds located around the Antarctic peninsula (Stevick *et al.*, 2004) and south of Chile (Gibbons *et al.*, 2003) and their breeding grounds located along the coasts of Ecuador, Colombia, Panama and south of Costa Rica (Clarke, 1962; Félix and Haase, 2001a; Flórez-González, 1991; Rasmussen *et al.*, 2007; Scheidat *et al.*, 2000). This southern stock, also known as west South American or Breeding Stock G (IWC, 2006), was extensively exploited during the 20th Century in Antarctic waters and along the coasts of Chile and Peru until the mid-1960s (Clarke, 1980; Ramírez, 1988). Although for a long time the southeastern Pacific stock has been considered distinct from the other six southern Hemisphere stocks, its discreteness was only recently confirmed through molecular biology studies (Caballero *et al.*, 2001; Olavarria *et al.*, 2007) and photo-identification (Stevick *et al.*, 2004). By the mid-1960s, it was thought that only a few hundred individuals remained in each southern humpback whale stock (Chapman, 1974). The current status and the level of recovery of the Southeast Pacific humpback whale stock are still poorly known.

The first attempts to estimate the size of the southeastern humpback whale stock at the breeding grounds were made during the mid-1980s around Gorgona Island, Colombia, using mark-recapture models (e.g. Capella *et al.*, 1998; Flórez-González, 1991; Ojeda and Hurtado, 1992) and the coast of Ecuador using direct counts (Haase, 1990). As whalewatching activities developed by the mid-1990s, studies on humpback whales increased on the coast of Ecuador using tourist vessels as platforms of opportunity for research. This allowed several research groups to develop long-term photo-identification programs. New population estimates, albeit with wide confidence intervals, were obtained on the central coast of Ecuador using mark recapture models during the mid-1990s (Félix and Haase, 2001b; Scheidat *et al.*, 2000) and early 2000s (Castro *et al.*, 2004; 2003; 2005). These latter estimates indicated that the population contained around 3,000 whales in 2003. Recent mark-recapture estimates of Breeding Stock G using photo-identification data from both breeding and feeding grounds (Stevick *et al.*, 2006) and from line transect data collected during the International Whaling Commission IDCR/SOWER circumpolar surveys (Branch, 2011) showed similar estimates (3,851 CV = 0.02 and 3,337 CV = 0.21, whales respectively) by the mid-1990s. Photo-identification and genetic studies have demonstrated that a biased sex ratio occurs at breeding grounds, with males outnumbering females in a proportion of 1.67–1.95:1 (Olavarria *et al.*, 2007; Palsbøll *et al.*, 1997; Smith *et al.*, 1999), which would explain the difference found between breeding and feeding grounds sampling approaches.

New abundance and survival estimates are presented here for the southeastern Pacific humpback whale stock using mark-recapture models for both closed and open populations. The database pools the data from two research teams and includes 16 years of fieldwork conducted off Ecuador. It is at least three times larger than those previously used in breeding-breeding estimates for this stock and as a result, the level of uncertainty was reduced considerably.

The study area

The study area includes two sites on the central coast of Ecuador. The northern site comprises *ca*. 700km^2 between La Plata Island and two fishing villages, Puerto López and Puerto Cayo (1°26'S, 80°50'W). The latter two sites are located

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[1] *Museo de Ballenas, Av. Enríquez, Gallo entre Calles 47 y 50, Salinas, Ecuador.*

[2] *Pacific Whale Foundation, PO Box 17-21-872, Quito, Ecuador.*

[3] *National Marine Mammal Laboratory, AFSC, NMFS, 7600 Sand Point Way NE, Seattle, WA 98115, USA.*

[4] *Forschungs und Technologiezentrum Westkueste, Universität Kiel, 25761 Buesum, Germany.*

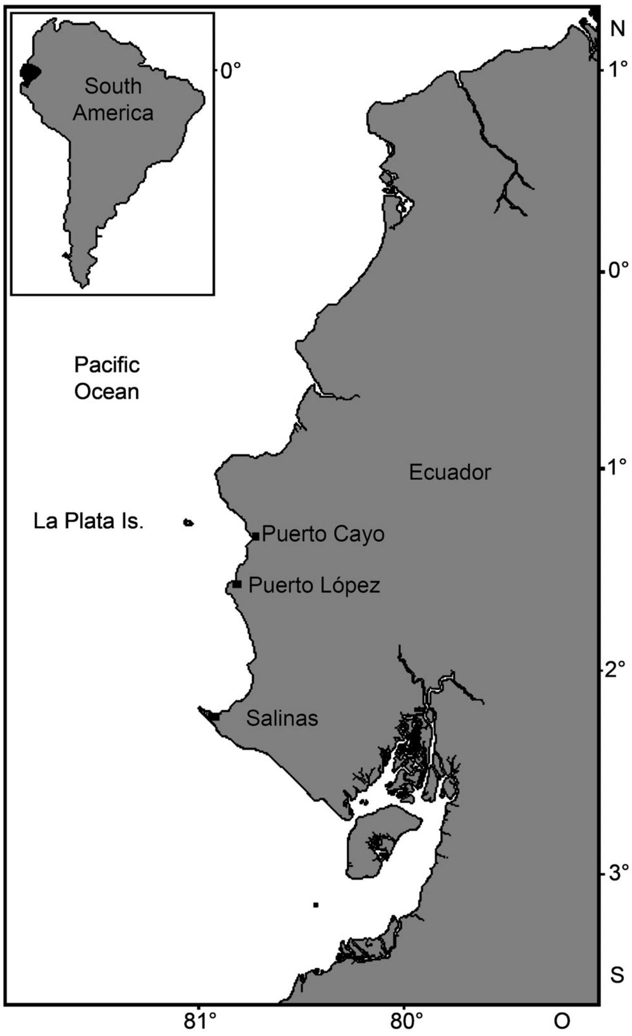

Fig. 1. The coast of Ecuador and the study sites.

22km apart whereas La Plata Island is located approximately 40km offshore. The second study site is Salinas, located 80km south of the former site (2°10'S, 81°05'W) on the westernmost tip of the Santa Elena peninsula. The surveyed area in Salinas comprises around 150km^2 over a narrow platform around the peninsula (Fig. 1).

MATERIAL AND METHODS

Survey effort

Photographs of the ventral side of whales' flukes (see Katona *et al.*, 1979) were obtained for individual identification during the breeding season (June–October) between 1991 and 2006 onboard whalewatching vessels. For this purpose, both film and digital cameras equipped 70–300mm zoom lenses were used.

Vessels departed from three different ports: Puerto Lopez, Puerto Cayo and Salinas. In the first years, whalewatching trips were not conducted on a regular basis but were opportunistic, taking place when tourists were more numerous, especially on weekends. As the whalewatching industry became more established and more boats were available, trips were more regular and so the field season extended from a few days in the first years of the study to 69 days of fieldwork in 2006 off Salinas (Table 1). In Puerto López the sampling period has been continuous since 1991 and in Salinas since 2002. Puerto Cayo was sampled in only two field seasons (1996–1997), but for the same number of days as in Puerto López. In general, effort was more uniform after 2004 in both Puerto López and Salinas. Most of the effort within the season was concentrated in July and August (29% and 41% of the effort, respectively), then in September (22%); only 7.62% of the trips were in the remaining three months sampled (May, June and October) (Table 2).

In Puerto López, trips lasted between 8 and 10 hours, including a 3-hour stop at La Plata Island and then a return to port in the evening. From 2002 a land station on top of a cliff was used for whale tracking and trips were conducted around La Plata during the 3-hour period that passengers visited the island. Researchers on the boat were guided to the whales by an observer from the coastal station. In Puerto Cayo, trips lasted 2–3 hours and were carried out mainly over a shallow platform west of the port. In Salinas, trips lasted between 2 and 3 hours and occasionally longer. In this port up to two trips were conducted per day during the peak of the tourist season. Additional information on the trip methodology and complementary data taken during the trips are available (e.g. Castro and González, 2002; Félix and Haase, 2001a; 2001b; 2005; Scheidat *et al.*, 2000).

Analysis of photographs

Photographs used in this study are part of the catalogues maintained by the Ecuadorian Foundation for the Study of Marine Mammals (FEMM) and Pacific Whale Foundation-Ecuador (PWF), which contain multiple photographs of 1,839 different individuals.

The digitised catalogues were exchanged and analysed separately by the research teams of both institutions. Besides identifying common individuals, each group separated the photographs considered unsuitable for comparison due to poor quality (i.e. blurred, inappropriate angle) based on their expertise. However, no specific criteria for photographic quality or individual distinctiveness were used to evaluate photographs. Neither calves nor whales identified only by one lobe of the tail were included in the analysis. Photographs of 1,511 different adult individuals remained for the analysis (82% of the total animals originally considered) covering 16 years. The comparison of photographs produced 190 between-year re-sightings of 155 individuals: 129 individuals were re-sighted once, 23 individuals twice, 2 individuals three times, 1 individual four times and 1 individual five times.

Mark-recapture models

Whales were considered to be 'captured' for the year (sampling occasion) if they were identified in a photograph from one or more trips that extended anywhere during the breeding season of each year. The 16 years of data were used to construct a capture-history for each of the 1,511 unique whales. The capture-history data were evaluated with models for closed and open populations and then the results were compared.

Closed population

Closed population models assume that the population is closed demographically and geographically (i.e. N is constant), that all animals are equally catchable for specified subsets as defined by the model (e.g. during a sampling year), that marks are permanent and all marks are reported (Hammond, 1986; Seber, 1982). We used the Chapman (1951) modified-Petersen estimator for two occasions using consecutive field seasons 1996 and 1997 and from 2001 to 2006.

Table 1

Annual effort and number of sightings made in each site (period 1991–2006).

Site	1991	1992	1993	1994	1995	1996	1997	1998	1999	2000	2001	2002	2003	2004	2005	2006	Total
Puerto López																	
Days	7	4	2	7	15	29	22	44	47	38	50	61	65	75	84		550
Trips	7	4	2	7	16	28	24	52	47	38	67	82	89	144	129		736
Sightings	17	8			43	64	50	134	129	96	141	135	189	252	223		1,481
Observation time (hours)	9.5	12.8	0.9	9.9	22.7	27.6	21.6	45	32	31	70	85	95	110.4	110		683.4
Puerto Cayo																	
Days						19	12										31
Trips						21	24										45
Sightings						41	50										91
Observation time (hours)						27.1	22										49.1
Salinas																	
Days												30	28	65	60	68	251
Trips												35	47	87	74	96	339
Sightings												78	109	163	148	213	711
Observation time (hours)												34.4	48	76.5	59.1	82.35	300.4

Open population

The POPAN formulation (Schwarz and Árnason, 1996) for the Jolly-Seber model was used in Program MARK (White and Burnham, 1999) to examine a series of proposed models for estimation of abundance and survival. Jolly-Seber models are used to represent open populations which allow gains from immigration and births, and losses from mortality and permanent emigration. The latter are confounded in the apparent survival parameters φ which can be constant, time-dependent or represented by any other appropriate structure. Capture-probability parameters, p, can also be constant, time-dependent or modelled with a covariate that is known for all members of the population. The abundance parameter N is a super-population size which is the total number of animals that were in the population at some point during the study. Entry (immigration/birth) into the population in the POPAN formulation is represented by parameters *pent* which are probabilities that sum to 1. The parameter *pent*(0) is the proportion of N that was in the population just prior to the beginning of the study. MARK provides estimates and standard errors of the size of the population at each sampling occasion (year) throughout the study.

As with models for closed populations, abundance estimators from open population models can underestimate abundance if there is any unmodelled heterogeneity in capture probability. In addition, apparent survival will be lower than true survival if there is any 'permanent' emigration during the course of the study. Any transient animals that appear only once and then leave the study area will also reduce apparent survival and will lower the abundance estimate. Both of these influences were potentially important issues in modelling the capture-recapture data collected in this study. The sampled whales included some that might remain in or near the study area during the breeding season ('local') and others that would only migrate through the area to breed farther north. Whales that migrate through the area might travel through the sampled area in one year and be photographed but they might take a different course from that point on and would appear to be transient. Whales migrating to the north could easily pass through the 100km stretch of sampled coast in 1 to 2 days. Unless sampling occurred every day of the week many migrating whales would have 0 probability of being captured; whereas, whales that remained would have a much higher probability of being photographed. Undoubtedly, this was more important prior to 2004 when sampling occurred

Table 2

Effort deployed by month as number of days of fieldwork by the two research teams (FEMM and PWF) during the period 1991–2006.

	May		June		July		August		September		October	
Year	FEMM	PWF	FEMM	PWF	FEMM	PWF	FEMM	PWF	FEMM	PWF	FEMM	PWF
1991					4		2		1			
1992					1		2		1			
1993							1		1			
1994			2		2		2		1			
1995					3		4		8			
1996	1		4		7		10		7			
1997			2		7		10	18	3	7		
1998				1		16		22		5		
1999				13		14		15		5		
2000				1	5	11	2	13	1	5		
2001				2		5		28		15		
2002			3		9	13	9	29	8	19	1	
2003			1		11	17	10	27	4	21	2	
2004			4	3	21	25	24	29	14	18	2	
2005			4	8	25	29	27	29	3	16	1	2
2006			2		14		29		19		4	
Total	**1**		**22**	**28**	**109**	**130**	**132**	**210**	**71**	**111**	**10**	**2**

primarily on weekends. To address these issues, at least partially, we considered models in which transient behaviour was accommodated by fitting a separate survival for the interval following the first sighting of a whale. We also used within-year resightings of whales to assign whales to 'local' versus 'migrant' groups. Whales were initially assumed to be migrants and were only assigned to the local group once they were resighted on more than one day within a year separated by at least 3 days and not more than 50 days, if only seen twice. Those values were chosen to accommodate a migrating whale being seen close together in time as it migrated through and others that might be seen migrating north and then south (> 50 days). 'Local' whales were allowed to have a different and presumably higher capture probability for any year after their assignment to the local group.

We fitted and compared 36 POPAN models using the R (*R* Development Core Team, 2008) package RMark v1.7.7 (http://www.phidot.org/software/mark/rmark/; Laake and Rexstad, 2008) which constructs the model and runs MARK to fit the models. The 36 models were constructed from all combinations of the sub-models: 3 models for *p* (constant, time, time + local), 3 models for φ (constant, time, transient) and 4 models for *pent* (constant, time, time bins, and Time-linear trend). The 'time' model contains a parameter for each of the 16 years whereas the 'Time' model contains an intercept and slope and assumes a linear trend over time. The time bins for *pent* were constructed to create a simpler reduced model with constant probability of entry (except *pent*(0)) for 1991–2002 and a time-varying rate for years 2003 to 2006. These times were chosen to reflect the expanded effort throughout the week that began in 2003. Models weights were calculated using Akaike Information Criterion (AICc) (Burnham and Anderson, 2002) and estimates of abundance were averaged across the models with ΔAICc < 6. Chi-square tests 2 and 3 for the recapture-data were computed from RELEASE as a guide for goodness of fit test of a general model with full time-dependent effects.

RESULTS

Closed population model

Estimates were constructed using the 1996–1997 samples and consecutive years between 2001 and 2006 (Table 3). Capture probability in the other years was too low to provide reliable results. The most precise estimates were obtained using the 2004–2006 data when sampling effort was quite extensive; however, those estimates were dramatically larger than the estimates prior to 2004 and the implied increase was not biologically plausible (see Clapham *et al.*, 2001).

Open population model

The goodness-of-fit test of the fully time-dependent model did not suggest any important lack of fit ($\chi^2 = 42.0$, df = 37, p = 0.26). Of the 36 fitted POPAN models, the top four models represented 99.99% of the weight of evidence (Table 4). All of the top models contained a transient effect in φ, time dependence in *p*, and *pent* constant over the specified time bins or linear over time (Time). Otherwise, they only differed because the top two models also contained the effect of 'local' whales having higher recapture probability.

Estimated annual 'apparent survival' was 0.446 (95% CI: 0.320–0.579) in the year after a whale was first seen; whereas, annual survival for subsequent years was 0.919 (95% CI: 0.850–0.958). The low 'apparent survival' in the first year reflects transient behaviour in which the whales permanently emigrate from the population or more likely do not migrate through the area that was sampled in subsequent years and had very low subsequent recapture probability.

The transient effect in survival influences the estimates of abundance which are decreased because the model predicts the current abundance excluding those that have 'left' the population. The super-population size was estimated to be 5,494 (95% CI: 3,784–8,491, CV = 0.21) but the population size in 2006 was only estimated to be 3,333 (Table 5) or roughly two-thirds of the abundance estimate from the closed model. The difference is reflected in the estimated capture probabilities which are much higher in the POPAN models than the closed models for 2004–2006 (Fig. 2). The open models assume that the whales left (lower apparent survival) and has higher capture probabilities for the remaining whales; whereas, the closed model assumes the abundance is fixed and has lower capture probabilities. We re-fitted the best POPAN model but fixed $\varphi = 0.919$ (assumed true survival) based on the assumption that the transients have the same true survival as the non-transients. The model does not fit the data as well but doing so provides an estimated abundance in 2006 of 5,456 which is much more consistent with the closed model result because it is estimating the size of the entire population.

DISCUSSION

The collaborative effort of two different research groups working in Ecuador (FEMM and PWF) has provided a more reliable estimation of the abundance of southeastern Pacific humpback whale stock (Breeding Stock G) on the breeding grounds. Based on closed models, the abundance estimate in 2006 was about 6,500 whales and 5,500 whales with open models if we assume constant true estimated survival of 0.919 for all whales. Our estimates are higher than previous estimates conducted at breeding grounds (e.g. Capella *et al.*,

Table 3

Estimates obtained with the Chapman-modified Petersen estimator ([n_1 + 1][n_2 + 1]/[m +1])for consecutive years with sufficient sampling. For each two-year period the number seen in each year are n_1 and n_2, the number of whales re-sighted is *m*, population estimate is *N* with its 95% log-normal confidence interval (CI) and coefficient of variation (CV).

Period	n_1	n_2	*m*	*N*	CI 95%	CV
1996–97	84	62	5	892	460–1,726	0.35
2001–02	47	147	3	1,775	802–3,929	0.42
2002–03	147	187	8	3,091	1,741–5,486	0.30
2003–04	187	369	26	2,575	1,855–3,574	0.17
2004–05	369	407	27	5,390	3,855–7,538	0.17
2005–06	407	286	17	6,504	4,270–9,907	0.22

Table 4

Model selection results for the best 4 of the fitted POPAN models and the POPAN equivalents for models B, A, and D in program JOLLY in the bottom 3 rows, respectively.

Phi	*p*	Pent	No. par	AICc	Δ AICc	Weight
transient	time+local	time	22	1,628.32	0.00	0.59
transient	time+local	time bins	24	1,629.68	1.44	0.29
transient	time	time	21	1,632.23	4.00	0.08
transient	time	time bins	23	1,633.54	5.30	0.04
constant	time	time	32	1,669.24	41.01	0.00
time	time	time	45	1,691.37	63.14	0.00
constant	constant	constant	4	2,573.07	944.84	0.00

Table 5

Model averaged estimates, 95% log-normal confidence intervals and coefficient of variation (CV) for humpback whale abundance from open population models.

Year	N	95% CI	CV
1991	1,260	268–5,929	0.93
1992	1,218	294–5,053	0.83
1993	1,182	325–4,301	0.74
1994	1,156	364–3,677	0.65
1995	1,138	410–3,158	0.56
1996	1,129	465–2,742	0.48
1997	1,122	525–2,396	0.40
1998	1,134	597–2,156	0.34
1999	1,179	686–2,026	0.28
2000	1,249	788–1,982	0.24
2001	1,359	904–2,044	0.21
2002	1,509	1,017–2,240	0.20
2003	1,697	1,102–2,613	0.22
2004	2,098	1,486–2,962	0.18
2005	2,798	2,043–3,833	0.16
2006	3,333	2,326–4,775	0.18

1998; Castro *et al.*, 2004; Félix and Haase, 2001a) but concordant with others obtained by Stevick *et al.* (2006) with a feeding-breeding approach and the one obtained during IDCR/SOWER circumpolar surveys (Branch, 2011). Furthermore, our estimate is slightly lower but within the interval of the IDCR/SOWER estimate projected to 2006 of 6,973 whales (CI 95% 4,845–8,626) (IWC, 2006).

However, even with the increased effort and collaboration there are still some uncertainties about the results from both the closed and open models. The Petersen estimator is robust to failure of closure as long as there are losses (consistent across all individuals) or gains (Kendall, 1999; Seber, 1982) but not both, except under some circumstances (Kendall, 1999). For our study, there are likely to be both gains and losses from births and deaths and from temporary emigration if some whales, primarily females, do not always return to the breeding grounds each year. Also, it is quite likely that there is unmodelled heterogeneity (variation) in capture probabilities. Possible sources of heterogeneity in capture probability at breeding grounds have been addressed elsewhere including individual variation in behaviour, habitat use and migration timing (e.g. Hammond, 1986; Palsbøll *et al.*, 1997; Smith *et al.*, 1999; Stevick *et al.*, 2003) as well as the sex ratio in the sample (Olavarria *et al.*, 2007; Palsbøll *et al.*, 1997; Smith *et al.*, 1999). Such topics have not yet been fully addressed in this population, but a major source of heterogeneity in this study was related to the uneven distribution of sampling on the breeding grounds (Table 2) and the heterogeneity introduced from some whales simply migrating by or through the sampling area off Ecuador and breeding near Colombia and Panama and others that remained in or around Ecuador for breeding. Typically, heterogeneity causes negative bias (Kendall, 1999) because there is a positive correlation in capture probabilities across occasions if some whales have higher/lower capture probabilities that remain consistent across occasions. However, it is also possible to introduce a positive bias in abundance if there is a negative correlation in capture probabilities between occasions. An example would be a shift in the timing of sampling within the years if whales are fairly regimented in their migration timing. For example, if there was high effort during the tails of the migration (June, September) in year 1 and low effort in year 2, then capture probability for whales that regularly passed Ecuador during June or September would be negatively correlated. A similar negative correlation occurs with temporary emigration.

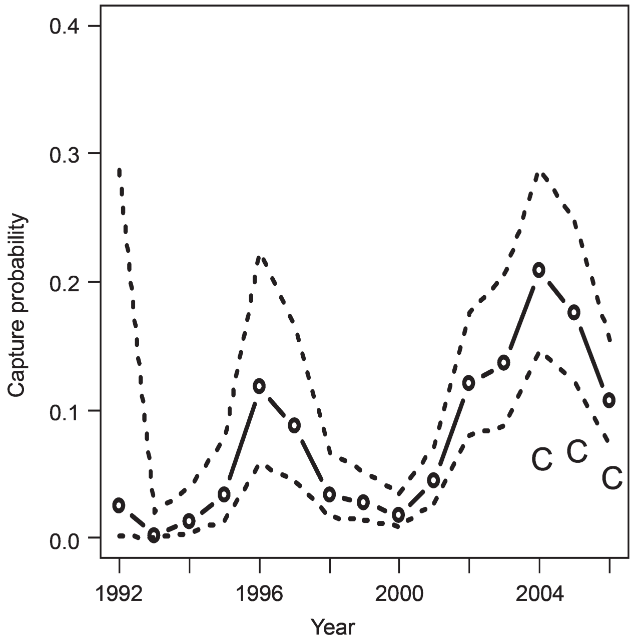

Fig. 2. Model averaged capture probability estimates from POPAN models with 95% confidence intervals (dashed lines) and closed model capture probability estimates (‘C’) for 2004–2006.

Ideally, these data would be modelled as an open population because the population is subject to both gains and losses and this allows simultaneous modelling of all 16 years of the data with presumably an increase in precision. Also, it provides the added benefit of yielding an estimate of annual survival. Even though the open model is more biologically realistic, the realities of the sampling situation and whale migration pose some formidable problems. Heterogeneity in capture probabilities affects open models as well. Our modelling showed that whales seen on multiple days within a year were more likely to be seen in the following years. The use of this covariate for ‘local’ whales improved the model fit but surely did not completely eliminate capture heterogeneity because it could only be used to remove heterogeneity after the whale was identified as ‘local’ by sighting it multiple days within the year and certainly there are some ‘local’ whales that were not seen on multiple occasions.

While unmodelled heterogeneity primarily introduces bias in abundance estimators it can also affects survival estimates. A positive bias in p due to heterogeneity will introduce a negative bias in φ because the parameters enter the models as products and thus are negatively correlated. In addition, φ is apparent survival which incorporates permanent emigration. Permanent emigration and some forms of heterogeneity can be confounded in the model. These are issues here because whales are being sampled in one portion of the migratory corridor. Consider a whale that typically breeds to the north of Ecuador and typically migrates to the west of the study area. Now assume that in one year it migrates through the study area and is seen but in all future years it continues its normal pattern. This appears to the model as permanent emigration but it should really be viewed as capture heterogeneity which is termed a ‘behavioural’ effect (trap shy). Once ‘caught’ the whale is less likely to be caught. This is an analogy to standard small mammal capture-recapture concepts and we are not saying that the whale modified its behaviour from being photographed. However, an unknown structure in both the migration timing and corridor can introduce numerous sources of heterogeneity. This heterogeneity is being captured in the 'transient' effect in which estimated 'apparent survival' for the year after first 'capture' is only 0.446 which means about one-half of the whales are never seen again but most are alive. The whales have effectively emigrated from the study area 'population'. The estimated survival rate in subsequent years of 0.919 is a better representation of true survival but it may also be biased low by remaining heterogeneity because it is lower than the survival reported for other humpback whale populations such as those in the Northeastern Pacific (Survival = 0.96) (Calambokidis and Barlow, 2004; Mizroch *et al.*, 2004) and the North Atlantic (Survival = 0.95 and 0.96) (Barlow and Clapham, 1997; Clapham *et al.*, 2003).

CONCLUSION

For management purposes, it is necessary to define whether the new estimates presented in this study are representative of the entire Southeast Pacific population (Breeding Stock G) or just a part of it. The available information suggests a complex migrating pattern and different habitat use by humpback whales in the breeding area that needs to be better understood for appropriate modelling. Despite the improvement in the estimates obtained, the current estimates likely represent only part of the population inhabiting the entire Southeast Pacific. Therefore, major efforts are still required to reduce the current level of uncertainty. One of the challenges in future assessments of this population at breeding grounds is obtaining a representative sample of a population distributed over 1,500km along the coast of South and Central America, from the north of Peru to Panama/Costa Rica and perhaps even further north (Flórez-González *et al.*, 1998; Rasmussen *et al.*, 2007). The easier alternative is to increase the photo-identification sample by bringing together catalogues of institutions working with this population in other countries (e.g. Colombia, Panama and Costa Rica). In addition, it would be useful to carry out an analysis using samples from breeding and feeding grounds. Such an approach has been demonstrated to be more consistent than those using only within-breeding or within-feeding grounds data (e.g. Smith *et al.*, 1999; Stevick *et al.*, 2006). A larger sample size would also help to improve our knowledge of other population parameters such as survival and birth rates, population growth rates and movements, all of which are still poorly known for this population.

It has been demonstrated here that whalewatching vessels are a valuable research platform for mark-recapture studies due to the near-coastal distribution of humpback whales. Although research activities are rather limited aboard whalewatching boats, they represented a unique and inexpensive opportunity for data collection. One advantage of using whalewatching boats was that (once the operations were well established in the country) there was the opportunity to work during the entire season with similar effort, thus improving data quality and reducing bias due to whale migration behaviour. On the other hand, the preference of whalewatching boats to approach more visible groups or groups with breaching individuals, as well as repeated surveying over the same coastal areas, likely violates the assumption of random sampling as required by mark-recapture models. The extent of such biases is difficult to assess in a study like this because the information came from three different sites and was taken onboard of different boats and therefore boat operations, geographic conditions and habitat use by the whales could not be the same in every studied site as we had originally assumed.

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A Bayesian approach to assess the status of Southern Hemipshere humpback whales (*Megaptera novaeangliae*) with an application to Breeding Stock G

SUSAN J. JOHNSTON*, ALEXANDRE N. ZERBINI+ AND DOUG S. BUTTERWORTH*

Contact e-mail: Susan.Holloway@uct.ac.za

ABSTRACT

The Bayesian stock assessment methodology presently being applied in the Comprehensive Assessment of the Southern Hemisphere humpback whales, which uses a sex- and age-aggregated population model, is detailed. This methodology is applied to Breeding Stock G, which winters off the west coast of South America. This application takes into account the recently updated historic catch series, as well as the most recent estimates of absolute abundance and population trend information.

KEYWORDS: HUMPBACK WHALE; BAYESIAN ASSESSMENT; SOUTHERN HEMISPHERE; MODELLING

INTRODUCTION

Humpback whales (*Megaptera novaeangliae*) were heavily exploited by commercial whaling in the Southern Hemisphere (Tønnessen and Johnsen, 1982). It is estimated that nearly 200,000 whales were captured in both wintering and feeding grounds (Findlay, 2000). Currently, seven Southern Hemisphere humpback whale breeding stocks are recognised by the International Whaling Commission (IWC, 1998; 2011). Breeding Stock G corresponds to whales wintering off the eastern coast of Central and South America, between Peru and Costa Rica (Acevedo-Gutiérrez and Smultea, 1995; Félix and Haase, 2001; Flórez-González *et al.*, 1998; Rasmussen *et al.*, 2007; Scheidat *et al.*, 2000). Whales from this population migrate to two likely discrete feeding grounds in the Magellan Strait, Chile (Acevedo *et al.*, 2007), and near the Antarctic Peninsula (Rasmussen *et al.*, 2007; Stevick *et al.*, 2004; Stone *et al.*, 1990).

The history of exploitation of Breeding Stock G is poorly known before the beginning of modern whaling (post-1900). During this period, whales were taken only in wintering grounds and migratory routes off Panama, Colombia, Ecuador, Peru, Chile and near the Archipelagos of Galapagos and Juan Fernandez (Townsend, 1935). The total pre-1900 catch is unknown, but estimated to be at least 4,000 whales in the 1800s (Smith *et al.*, 2006). Modern whaling catches in the wintering grounds totaled nearly 2,300 whales (Allison, 2006). Most catches were taken from land bases on the coast of Chile, but about 330 whales were taken by a factory ship that followed migrating whales to Peru, Ecuador and Colombia (Findlay, 2000). These catches were of relatively small scale (an annual average of 37 whales from 1908–68 and no more than 270 catches in a single year). Whaling in the feeding grounds was of greater magnitude, with nearly 15,000 whales taken between 1905 and 1961 (Findlay, 2000). The peak of catches occurred between 1905 and 1915, when over 11,000 whales were captured (Allison, 2006).

During the Comprehensive Assessment of Southern Hemisphere humpback whales, it has been customary to use a sex- and age-aggregated dynamic production model, with a surplus production function of the Pella-Tomlinson form, to assess population status. The reason more complex population models have not been employed is the relatively coarse nature of much of the available data, and in particular the methods used to allocate catches on the feeding grounds in the far south to stocks which breed in lower latitudes (fig. 1 in IWC, 2011). Earlier applications of this approach estimated the two parameters of the population model (the intrinsic growth rate r and pre-exploitation abundance K) by having the population trajectory hit a recent survey estimate of absolute abundance, and also replicate the trend shown by some time series of population estimates (for example from coastal surveys) or alternatively fixing r at a value estimated for another breeding stock. Examples of this approach may be found in Findlay *et al.* (2000), Findlay and Johnston (2001) and Johnston *et al*. (2001).

The approach was subsequently refined and cast in a Bayesian framework to provide improved indications of the precision of the estimates obtained (Zerbini, 2004, in an application to Breeding Stock A). This refinement has since been applied to assessments of other breeding stocks, making allowance also in some cases for the use of abundance estimates from surveys of the feeding grounds, and also mixing of breeding stocks on these grounds (Johnston and Butterworth, 2005a; 2005b; Johnston and Butterworth, 2006).

This paper documents this Bayesian methodology, as recently adapted and agreed (IWC, 2011), and then applies it to Breeding Stock G.

Due to the difficulty in allocating past catches to breeding stocks, applications of this assessment methodology generally considers sensitivity of results to three different options for this allocation of catches south of 40°S (allocation of catches north of 40°S being straightforward by comparison). The 'core' and the 'fringe' options can be

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* *Marine Resource Assessment and Management Group, Department of Mathematics and Applied Mathematics, University of Cape Town, Rondebosch, 7701, South Africa.*

+ *Washington Cooperative Fish and Wildlife Research Unit, School of Aquatic and Fishery Sciences, University of Washington, Box 355020, Seattle, WA 98195-5020, USA.*

considered as two extremes, the former reflects the smallest longitudinal range (and hence lowest catches) considered certain to correspond to the breeding stock under consideration, while the latter covers the greatest range considered plausible. The 'overlap' option defines longitudinal ranges for the stock under consideration and the two on either side. Eighty percent of the catch from the central of these three ranges and 10% of the catches from the ranges on either side, are assumed to reflect removals from the stock being assessed.

DATA AND METHODS

The data related to Breeding Stock G

Historic catch data

The historic catch records for Southern Hemisphere humpback whales, which have recently (May 2006) been updated by Cherry Allison (IWC Secretariat) can be conveniently separated into catches taken north of 40°S and those taken south of that latitude. The updated catch records for whales caught north of 40°S are reported in Table 1a. Catches south of 40°S are reported in Table 1b for the 'core', 'fringe' and 'overlap' models as recently re-defined (IWC, 2011). The fringe catch series, together with the differences in the core and overlap catches compared to the fringe model catches are shown in Fig. 1. Table 1b also reports catches taken off the Falkland Islands which are used in a sensitivity test.

The longitudinal boundaries that correspond to the hypotheses above for apportionment of the catch are as follows for Breeding Stock G:

Core: 50°W–100°W
Fringe: 50°W–100°W + 50% of catches from 100°W–120°W

The overlap series consists of 80% of the catch from the range of 60°W–110°W associated with the original naïve catch allocation model (as described in IWC, 1998) for Breeding Stock G, and 10% from each of the ranges associated with the naïve catch allocation models for Breeding Stocks A and F (the two stocks to the east and west of Breeding Stock G) which are taken to be 20°W–60°W and 110°W–170°W respectively (see fig. 8 of IWC, 2011).

Absolute abundance data

The estimates of recent absolute stock abundance for Breeding Stock G which are considered here are reported in Table 2a, along with their associated estimated CVs. The estimate of 6,504 provided by Felix *et al.* (2011) for 2006, which relates to the breeding area, was selected by the recent humpback workshop (IWC, 2011) as being the most reliable, and is used here for the Reference Case (RC). This estimate is based on the Petersen estimator. A test of sensitivity to using the Felix *et al.* (2011) Jolly-Seber abundance estimate of 5,456 for 2006 is also conducted. The other two abundance estimates are for the feeding areas – these being the most recent IDCR/SOWER estimate of 3,310 whales (in 1996) provided by Branch (2011) from the third circumpolar set of IDCR/SOWER surveys, and 6,991 whales (in 2000) provided by Hedley *et al.* (2001) from a joint CCAMLR-IWC survey that year. These estimates are used under the assumption that each is unbiased and representative of the complete population.

Trend information

Abundance estimates which can be used to provide information on trends for Breeding Stock G are available from IDCR/SOWER sightings surveys in the feeding grounds, as reported by Branch (2011). Those of Branch's estimates which have been corrected to represent comparable areas for the three circumpolar sets of surveys are used. These are listed in Table 2b.

Table 1a

Catches taken north of 40°S for Southern Hemisphere humpback whales for BS G (C. Allison, pers. comm.). There are no catches after 1973.

Year	Catch	Year	Catch
1900	0	1937	28
1901	0	1938	6
1902	0	1939	7
1903	0	1940	0
1904	0	1941	0
1905	0	1942	0
1906	0	1943	0
1907	0	1944	0
1908	16	1945	0
1909	44	1946	15
1910	62	1947	19
1911	92	1948	5
1912	86	1949	6
1913	45	1950	5
1914	195	1951	26
1915	30	1952	27
1916	15	1953	29
1917	15	1954	106
1918	23	1955	7
1919	24	1956	10
1920	21	1957	5
1921	21	1958	0
1922	19	1959	3
1923	16	1960	2
1924	34	1961	3
1925	248	1962	4
1926	277	1963	1
1927	40	1964	35
1928	36	1965	143
1929	26	1966	58
1930	33	1967	0
1931	53	1968	3
1932	21	1969	1
1933	11	1970	0
1934	13	1971	0
1935	31	1972	0
1936	18	1973	0

The population dynamics model and Bayesian estimation framework

The population dynamics model described here is an aggregated (over both sex and age) model. The basic population dynamics equation is:

$$N_{y+1} = N_y + rN_y\left(1-\left(N_y/K\right)^{\mu}\right) - C_y \tag{1}$$

where

N_y is the total population size at the start of year y, and is set equal to K in years prior to the onset of exploitation;

K is the pre-exploitation population size;

r is the intrinsic or maximum growth rate (i.e. the maximum per capita rate the population can achieve when its size is very low);

μ is set at 2.39, which fixes the MSY level, MSYL = $0.6K$, as conventionally assumed by the IWC Scientific Committee; and

C_y is the total catch (in terms of number of animals) in year y.

Table 1b

Catches taken south of 40°S for Southern Hemisphere humpback whales for Breeding Stock G. Catches have been apportioned from feeding area catches advised by C. Allison (pers. comm.). These catches correspond to either the core, fringe or overlap catch allocation hypotheses (IWC, 2011). Catches off the Falkland Islands used in sensitivity 8 are also given. There are no catches after 1973.

Year	Core	Fringe	Overlap	Falklands	Year	Core	Fringe	Overlap	Falklands
1900	0	0	0	0	1937	0	0	24	0
1901	0	0	0	0	1938	0	0	0	0
1902	0	0	0	0	1939	0	0	0	0
1903	1	1	1	0	1940	0	0	4	0
1904	0	0	18	0	1941	0	0	1	0
1905	23	23	47	0	1942	0	0	0	0
1906	498	498	422	0	1943	0	0	0	0
1907	366	366	419	0	1944	0	0	6	0
1908	1,246	1,246	1,182	9	1945	0	0	24	0
1909	1,481	1,481	1,524	94	1946	0	0	3	0
1910	2,527	2,527	2,668	70	1947	0	0	2	0
1911	2,039	2,039	2,204	17	1948	0	0	3	0
1912	976	976	1,035	8	1949	0	0	7	0
1913	1,038	1,038	895	7	1950	271	271	317	0
1914	656	656	609	12	1951	0	0	6	0
1915	219	219	337	0	1952	0	0	4	0
1916	21	21	55	0	1953	0	0	27	0
1917	69	69	61	0	1954	0	0	37	0
1918	81	81	72	0	1955	14	14	53	0
1919	181	181	153	0	1956	600	666	551	3
1920	149	149	129	0	1957	59	90	73	0
1921	0	0	1	0	1958	52	52	1	52
1922	189	189	188	0	1959	201	282	218	0
1923	96	96	90	0	1960	88	88	348	6
1924	102	102	108	0	1961	1,167	1,265	1,201	1
1925	163	163	156	0	1962	278	321	269	32
1926	88	88	82	0	1963	0	0	0	0
1927	3	3	2	2	1964	0	0	0	0
1928	16	16	14	0	1965	0	0	53	0
1929	0	0	5	0	1966	0	0	24	0
1930	1	1	12	0	1967	0	0	11	0
1931	0	0	2	0	1968	0	0	0	0
1932	0	0	2	0	1969	0	0	0	0
1933	0	0	13	0	1970	0	0	0	0
1934	0	0	6	0	1971	0	3	0	0
1935	0	0	5	0	1972	0	0	0	0
1936	0	0	11	0	1973	0	0	0	0

The following prior distributions for r and an estimate of absolute abundance are considered:

(i) If the assessment model is fit to data with information on trend (from the IDCR/SOWER surveys) then $r \sim U[0, 0.106]$. If no such trend data are used in the model fit, then $r \sim$ posterior derived from an assessment of Breeding Stock A (Zerbini *et al.*, 2011). The upper boundary of 0.106 corresponds to the maximum growth rate given a range of life history parameters observed for several humpback whale populations (Clapham *et al.*, 2006).

(ii) $\ln N_Y^{X,obs} \sim U[\ln \hat{N}_Y^{X,obs} - 4CV_Y, \ln \hat{N}_Y^{X,obs} + 4CV_Y]$

where $N_Y^{X,obs}$ refers to the absolute abundance estimate for a humpback breeding stock X in year Y.

Note that the prior distribution from which target absolute abundance estimates ($N_Y^{X,obs}$) are drawn at random is uniform on a natural logarithmic scale, corresponding to the conventional approach in the IWC Scientific Committee to make distributional assumptions for abundance estimates transformed in this way. The upper and lower bounds are set by adding and subtracting four times the CV of the survey estimate.

For each of n_1 replicates, values of $N_Y^{X,obs}$ and r are drawn from their prior distributions. A bisection method is used to calculate K such that the model value of N_Y^X is identical to the randomly drawn value $N_Y^{X,obs}$.

For each of the n_1 replicates, using the generated r and calculated K values, a negative log likelihood is then computed by comparing the population model output to observed data – these including the recent absolute abundance estimate, preferably from the breeding grounds (see Table 2a). The components of the negative log likelihood are calculated as follows for Breeding Stock G.

For the absolute abundance estimate, the negative log-likelihood component is:

$$-\ln L = \frac{1}{2CV_Y^2}\left(\ln \hat{N}_Y^{X,obs} - \ln N_Y^X\right)^2 \qquad (2)$$

where

$\hat{N}_Y^{X,obs}$ and CV_Y are the survey estimate of population size at the start of year Y for breeding stock X and the associated survey-sampling based coefficient of variation, and

N_Y^X is the model value for population size at the start of year Y for this breeding stock.

It is assumed that the abundance estimates used to provide trend information are log-normally distributed about their model values:

$$I_y^X = q^X N_y^X e^{\varepsilon_y} \qquad (3)$$

where

I_y^X is the survey-based abundance index for year y,

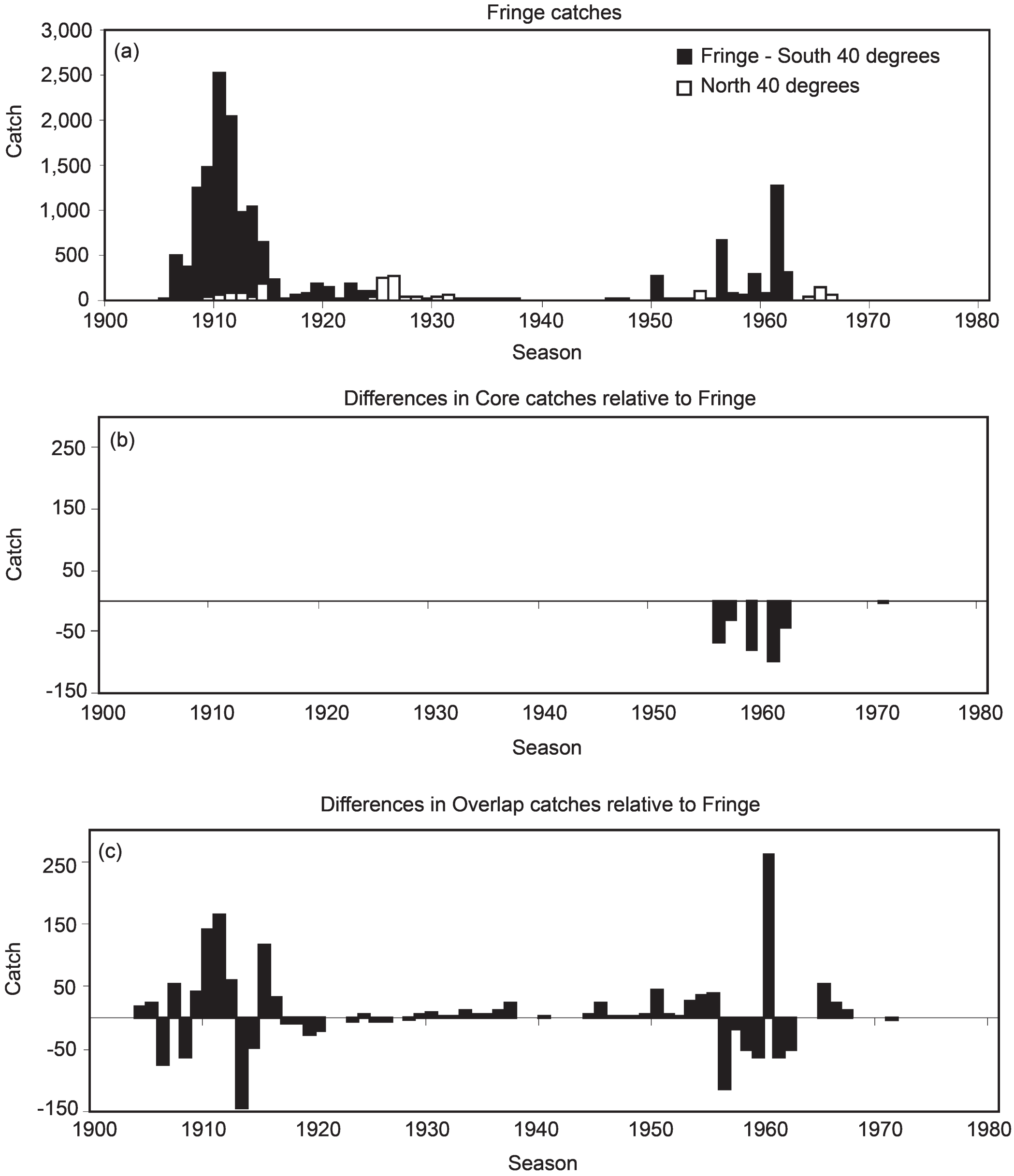

Fig. 1. The fringe catch series together including the catches North of 40° is shown in (a), with the differences in the core and overlap catches compared to the fringe model catches shown in (b) and (c) respectively.

q^X is the constant of proportionality between that index and the absolute abundance of breeding stock X,

N_y^X is the model value for population size at the start of year y for breeding stock X, and

ε_y is from $N(0,\sigma_X^2)$.

The contribution of these data to the negative of the log-likelihood function is then given by:

$$-\ln L = n^X \ln \sigma_X + \frac{1}{2\sigma_X^2}\sum_y \left(\ln I_y^X - \ln q^X - \ln N_y^X\right)^2 \tag{4}$$

with the total negative log-likelihood thus being:

$$-\ln L = n^X \ln \sigma_X + \frac{1}{2\sigma_X^2}\sum_y \left(\ln I_y^X - \ln q^X - \ln N_y^X\right)^2 + \frac{1}{2CV_Y^2}\left(\ln \hat{N}_Y^{X,obs} - \ln N_Y^X\right)^2 \tag{5}$$

The Bayesian approach applied also requires integration over priors for σ_X, the standard deviation of the residuals about the data used for trend information, and the constant of proportionality q^X. Taking these priors to be respectively

Table 2a

Recent absolute abundance estimate considered for assessments of Breeding Stock G.

Year	Abundance estimate	Area	Source
2006	6,504 (CV=0.21)	Breeding	Felix *et al.* (2011): Petersen[#]
2006	5,456 (CV=0.21)[@]	Breeding	Felix *et al.* (2011): Jolly-Seber[#]
1996	3,310 (CV=0.21)	Feeding	Branch (2011)*
2000	6,991 (CV=0.32)	Feeding	Hedley *et al.* (2001)[+]

[@]As no CV was provided for the Jolly-Seber estimate, the same CV is assumed as for the Petersen estimate. [#]Survey areas covered the wintering grounds off the coast of Ecuador, varying slightly amongst years but ranging approximately 01°26'S, 80°50'W to 02°10'S, 81°05'W. *Survey area south of 60° and between 110° W-50°W. [+]Survey area around the Antarctic Peninsular of approximately between 60°S-65°S and between 70°W-50°W.

Table 2b

Abundance estimates for Breeding Stock G from the IDCR-SOWER sighting surveys for comparable areas (Branch, 2011) that are used to provide information on population trend.

Year	Abundance estimate
1982	1,452 (CV=0.65)
1989	2,817 (CV=0.38)
1996	3,310 (CV=0.21)

proportional to σ_X^{-3} and uniform in log-space allows the integration over these parameters to be performed analytically, with the resultant negative logarithm of the marginal likelihood of the same form as equation (5) with σ_X and q^X each substituted by their maximum likelihood estimates for the values of *r* and under consideration [see proof in Geromont and Butterworth (1995) from a generalisation of the results of Walters and Ludwig (1994)]:

$$\hat{\sigma}_X = \sqrt{1/n\sum_y\left(\ln I_y^X - \ln q^X - \ln \hat{N}_y^X\right)^2} \tag{6}$$

where

n is the number of data points in the abundance series, and

q^X is the constant of proportionality for the index of abundance which is substituted by its maximum likelihood estimate:

$$\ln \hat{q}^X = 1/n\sum_y\left(\ln I_y^X - \ln N_y^X\right) \tag{7}$$

The negative log likelihood is then converted into a likelihood value (*L*). The integration of the prior distributions of the parameters and the likelihood function then follows the Sampling-Importance-Resampling (SIR) algorithm presented by Rubin (1988) as described in Zerbini (2004). For a vector of parameter values θ_i, the likelihood of the data associated with this vector of parameters (*L*) as described above is calculated and stored. This process is repeated until an initial sample of n_1 $\theta_i s$ is generated. This sample is then re-sampled with replacement n_2 times with probability equal to weight w_j, where:

$$w_j = \frac{L\,(\theta_j\,/\,data)}{\sum_{k=1}^{n_1} L\,(\theta_k\,/\,data)} \tag{8}$$

The resample is thus a random sample of size n_2 from the joint posterior distribution of the parameters (Rubin, 1988).

The value of n_1 (the original number of replicates) used is 500,000 and of n_2 (number of re-samples) is 5,000. Convergence is checked by examining results for different random number seeds, and ensuring that no sample contributes more than 0.001% of the total weight.

$N_{\min}$ *constraint*

It has been suggested (Jackson *et al.*, 2006) that genetic constraints be used in the assessment of humpback whale populations, given the observed genetic diversity. This idea had previously been discussed by Baker and Clapham (2004), who advocated that demographic and genetic approaches should be integrated to better describe whale population dynamics. In the application of this assessment methodology to Breeding Stock G, this approach has been used to determine how low the minimum population size of the humpback whales from Breeding Stock G could have been, given their observed genetic diversity. Baker and Clapham (2004) suggested that the number of extant haplotypes sampled in a population which has undergone a recent bottleneck provides an absolute minimum bound on the number of mature females in the population at the time of the bottleneck. Jackson *et al.* (2006) suggested a correction factor of four to scale the number of sampled haplotypes (minimum number of mature females) to the total (1+) population size when the population was at its minimum. The rationale behind this correction factor is that the number of haplotypes must be multiplied by two to account for the male population (assuming an even sex ratio) and also by a further two to correct the minimum effective population size to a lower estimate of total population size [as described by Nunney (1993) and used in Roman and Palumbi (2003)]. Jackson *et al.* (2006) point out that this correction factor is normally too small, but nevertheless remains useful to provide a minimum population number.

In the application to Breeding Stock G, the minimum population size () of 108 whales (in any year) is set as such a constraint. This is four times the total number of mtDNA haplotypes (27) observed for this breeding stock (Rosenbaum *et al.*, 2006).

The methodology as currently agreed and applied in the Scientific Committee then excludes any population trajectory which violates this constraint (see also comments in the final section of this paper). Generally this has the effect of excluding some of the trajectories with higher *r* values.

Reference case and sensitivity tests

The Reference Case (RC) assessment uses inputs and makes assumptions as follows:

(a) The fringe catch allocation hypothesis is assumed for the historic catch.
(b) The Felix *et al.* (2011) Petersen estimate of 6,504 in 2006 (from the breeding grounds) is used as the absolute abundance estimate.
(c) The trend information from IDCR/SOWER surveys as reported in Branch (2011) is used.
(d) The prior for *r* is *r* ~ U[0, 0.106].

The following sensitivities are explored:

Sensitivity 1: The most recent abundance estimate from the IDCR/SOWER information (3,310 in 1996, Branch, 2011) is used in place of the Felix *et al.* (2011) Petersen estimate for the recent absolute abundance estimate (though note that the Branch estimate corresponds to a slightly different longitudinal range to that which the fringe catch allocation prescription applies).

Sensitivity 2: The abundance estimate from Hedley *et al.* (2001) is used in place of the Felix *et al.* (2011) Petersen estimate for the recent absolute abundance estimate.

Sensitivity 3: The Petersen estimate for abundance is replaced by the open population estimate of 5,456 for 2006 provided by Felix *et al.* (2011). This estimate is based on a Jolly-Seber analysis with a survival rate adjusted to be the same for transient and non-transient animals.

Sensitivity 4: The model fits to the RC breeding ground abundance estimate as well as to the two abundance estimates from the feeding grounds in Table 2a. This involves adding further terms to equation (2).

Sensitivity 5: The model fits to the Felix *et al*. (2011) Petersen estimate only, and replaces data with trend information by an informative r prior taken from the r posterior for Breeding Stock A (as estimated by Zerbini *et al.*, 2011).

Sensitivity 6: The core catch allocation hypothesis replaces the fringe hypothesis.

Sensitivity 7: The overlap catch allocation hypothesis replaces the fringe hypothesis.

Sensitivity 8: The catches made off the Falkland Islands (reported in Table 1b) are included in the total catch history.

Note that the purpose of many of these sensitivities is to provide a broad indication of how dependent key outputs are to certain inputs. Thus, for example, sensitivities 1 and 2 are intended to provide only some sense of the possible range for recent abundance, rather that to suggest that these abundance estimates from the feeding grounds correspond exactly to the breeding stock being modelled.

Projections

In this study, the population is projected into the future (to 2040) assuming that no future catches are taken.

RESULTS AND DISCUSSION

Table 3 reports results for the RC and eight sensitivity tests. Posterior medians with the 5th and 95th percentiles (in parentheses) are reported. These results show that for Breeding Stock G there is very little sensitivity of results to the alternate historic catch series used (sensitivity tests 6–8). There is far greater sensitivity to the estimates of current abundance selected, with the Felix *et al.* (2011) Petersen estimate producing results which show Breeding Stock G to be currently around $0.56K$, while the use of the IDCR/SOWER current abundance estimate for the feeding grounds (sensitivity 1) produces results which are less optimistic, with a current abundance estimate of $0.49K$. The use of the Hedley *et al.* (2001) estimate (sensitivity 2) from the feeding grounds produces a more optimistic result however, with a current abundance estimate of $0.78K$. When all three recent estimates of abundance are fit instead of only one (sensitivity 4), precision is improved with the width of the 90% PI on current depletion reduced by about one third. Excluding the trend data, and using a prior for r from the posterior from Breeding Stock A (sensitivity 5) produces similar results to those for the RC. For all nine models explored here, the lowest population size $N_{\min}$ does not drop below the bound deduced from genetics data of 108 for any of the trajectories simulated.

Table 3

Breeding Stock G model parameter estimates. Posterior medians with the 5th and 95th percentiles (in parentheses) are reported. An $N_{\min}$ constraint >108 is imposed for all models. Headers in *italics* reflect choices differing from those for the Reference Case.

	Reference Case	**Sensitivity 1**	**Sensitivity 2**
r prior	**$r\sim$ U[0, 0.106]**	**$r\sim$ U[0, 0.106]**	**$r\sim$ U[0, 0.106]**
Historic catch	**Fringe**	**Fringe**	**Fringe**
Recent abundance	**Felix *et al.* (2011): Petersen**	*IDCR/SOWER*	*Hedley et al. (2001)*
Trend information	**IDCR/SOWER**	**IDCR/SOWER**	**IDCR/SOWER**
r	0.063 [0.023; 0.093]	0.062 [0.024; 0.092]	0.068 [0.029; 0.099
K	11,584 [10,590; 14,878]	11,617 [10,610; 14,363]	11,382 [10,424; 14,123]
N_{min}	731 [238; 2959]	608 [266; 1758]	760 [414; 2843]
N_{2006}	6,579 [4,698; 9,817]	5,736 [3,757; 8,135]	9,004 [5,699; 10,798]
N_{min}/K	0.063 [0.022; 0.198]	0.052 [0.028; 0.125]	0.067 [0.040; 0.200]
N_{2006}/K	0.561 [0.376; 0.833]	0.493 [0.281; 0.723]	0.783 [0.450; 0.987]
N_{2020}/K	0.885 [0.575; 0.988]	0.829 [0.422; 0.979]	0.972 [0.692; 1.000]
N_{2040}/K	0.994 [0.818; 1.000]	0.990 [0.660; 1.000]	0.999 [0.913; 1.000]
	Sensitivity 3	**Sensitivity 4**	**Sensitivity 5**
r prior	**$r\sim$ U[0, 0.106]**	**$r\sim$ U[0, 0.106]**	*$r\sim$ post (A)*
Historic catch	**Fringe**	**Fringe**	**Fringe**
Recent abundance	*Felix et al. (2011): Jolly-Seber*	*RC + Sen 1 + Sen2*	**Felix *et al.* (2011): Petersen**
Trend information	**IDCR/SOWER**	**IDCR/SOWER**	None
r	0.062 [0.023; 0.090]	0.065 [0.036; 0.093]	0.066 [0.025; 0.089]
K	11,619 [10,655; 14,813]	11,500 [10,594; 13,162]	11,480 [10,695; 14,457]
N_{min}	586 [204; 2334]	647 [283; 1615]	655 [244; 3150]
N_{2006}	5,504 [3,885; 7,970]	6,557 [5,210; 8,162]	6,539 [4,634; 9,361]
N_{min}/K	0.051 [0.019; 0.163]	0.056 [0.026; 0.123]	0.057 [0.023; 0.211]
N_{2006}/K	0.468 [0.317; 0.695]	0.568 [0.419; 0.742]	0.557 [0.375; 0.813]
N_{2020}/K	0.820 [0.496; 0.961]	0.893 [0.660; 0.981]	0.891 [0.570; 0.984]
N_{2040}/K	0.989 [0.734; 1.000]	0.995 [0.991; 1.000]	0.996 [0.784; 1.000]
	Sensitivity 6	**Sensitivity 7**	**Sensitivity 8**
r prior	**$r\sim$ U[0, 0.106]**	**$r\sim$U[0, 0.106]**	**$r\sim$U[0, 0.106]**
Historic catch	*Core*	*Overlap*	*Fringe+Falklands*
Recent abundance	**Felix *et al.* (2011): Petersen**	**Felix *et al.* (2011): Petersen**	**Felix *et al.* (2011): Petersen**
Trend information	**IDCR/SOWER**	**IDCR/SOWER**	**IDCR/SOWER**
r	0.063 [0.024; 0.092]	0.062 [0.025; 0.092]	0.063 [0.027; 0.092]
K	11,569 [10,601; 14,589]	11,887 [10,866; 14,956]	11,785 [10,804; 14,475]
N_{min}	719 [242; 2922]	749 [252; 2831]	720 [246; 2662]
N_{2006}	6,573 [4,630; 9,694]	6,620 [4,678; 9,742]	6,634 [4,723; 9,579]
N_{min}/K	0.062 [0.023; 0.197]	0.062 [0.023; 0.189]	0.061 [0.023; 0.185]
N_{2006}/K	0.561 [0.376; 0.824]	0.550 [0.370; 0.808]	0.554 [0.378; 0.810]
N_{2020}/K	0.887 [0.585; 0.986]	0.877 [0.575; 0.985]	0.881 [0.593; 0.985]
N_{2040}/K	0.994 [0.820; 1.000]	0.994 [0.820; 1.000]	0.994 [0.832; 1.000]

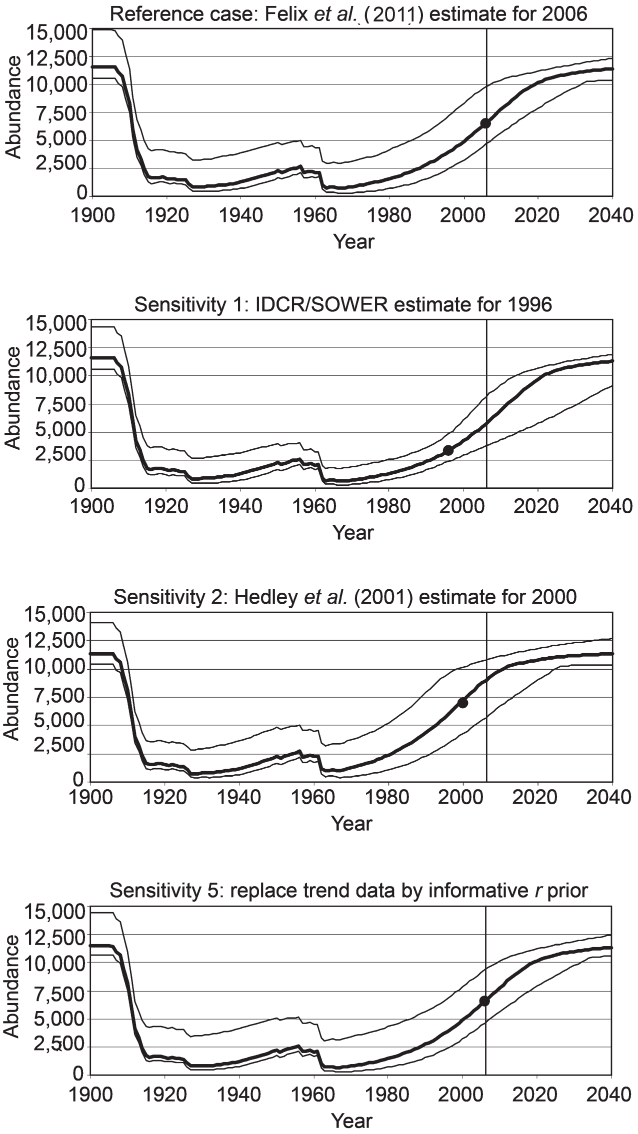

Fig. 2. Estimated population trends for Breeding Stock G, with projected trajectories which assume a continued zero catch. The posterior medians with 90% probability interval envelopes are illustrated. The vertical lines at 2006 separate assessments from projections. The scenarios shown are the Reference Case and Sensitivities 1, 2 and 5 (which explore fitting to the IDCR/SOWER recent estimate as the recent abundance data and to the Hedley *et al.*(2001)) estimate from the feeding grounds, and then omitting the IDCR/SOWER trend data by using an informative prior for the intrinsic growth rate parameter r obtained from the assessment of Breeding Stock A (Zerbini *et al.*, 2011). The single dots show the recent abundance estimate fitted by each model which replaces the Felix *et al.* (2011) Petersen estimate of recent abundance by those from the IDCR/SOWER surveys or from Hedley *et al.* (2001) for the feeding grounds for sensitivities 1–2.

Fig. 2 shows the population abundance trends for the RC and for sensitivities 1, 2 and 5. These plots also show projected trajectories which assume a continued zero catch. The posterior medians together with the 90% PI envelopes are illustrated. Fig. 3 shows the RC model fit to the abundance data provided by the IDCR/SOWER sightings estimates to inform on trend. It is evident that the model is able to fit adequately to both the Felix *et al.* (2011) recent Petersen abundance estimate (Fig. 2), as well as to the abundance data series from the feeding grounds provided by the IDCR/SOWER survey sightings (Fig. 3).

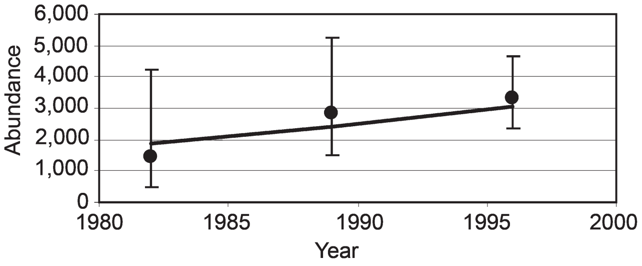

Fig. 3. The RC model fit to the abundance data used to provide trend information, as obtained from the IDCR/SOWER sightings surveys. The dots show the abundance estimates from the surveys, together with their 90% confidence intervals, and the curve shows the model posterior medians. Note that the model estimates reflect the population abundance estimates adjusted by the estimated constant of proportionality q.

Assuming future zero catches, the RC estimates the breeding stock (in median terms) to reach 0.89*K* by 2020 and 0.97*K* by 2030. Slightly less optimistic projection estimates are obtained for sensitivity 1 (fitting to the IDCR/SOWER recent abundance estimate) for which the stock is estimated to reach 0.83*K* by 2020 and 0.95*K* by 2030, and more optimistic estimates for sensitivity 2 (fitting to the Hedley *et al.*, 2001 estimate) which reflects near full recovery (0.97*K*) by 2020.

POSSIBLE FURTHER DEVELOPMENTS

This paper has documented the Bayesian methodology currently agreed for use in the Scientific Committee for Southern Hemisphere humpback stock status evaluation, and applied that to data for Breeding Stock G. There are some ways in which the method could be technically improved and/or further sensitivities explored, some specific to the Breeding Stock G case:

(a) when using feeding ground estimates of abundance, evaluate abundance for longitudinal ranges which correspond to the basis used to develop the historical catch series for higher latitudes;
(b) take account of the CVs for the abundance estimates in Table 2b used to provide information on trend, rather than assume these to be the same (the σ_X parameter);
(c) integrate over a prior distribution for the μ parameter (or equivalently MSYL) rather than fix this at a single value;
(d) apply alternative Bayesian population model approaches (note that the approach applied here corresponds to the 'Backwards' variant of the various approaches that have been applied in assessment of the Bering-Chukchi-Beaufort bowhead whale population – see for example Punt and Butterworth (1999); and
(e) change to a population model which disaggregates by sex and age.

A number of these would require considerably extra work, e.g. the further survey abundance estimates required under (a), or the incorporation of additional variance and more complex integration over q^X and σ_X needed for (b). Thus given the relatively coarse nature of the abundance and trend information available, and that it seems unlikely that these factors listed would greatly impact results, such additional analyses do not seem an immediate priority, and reflect a level of sophistication perhaps more appropriate to the stage when the population model is refined to incorporate age- and sex-structure as suggested in (e). A higher priority is further information on trend, as the data available do not update the prior used for r appreciably (see Fig. 4).

In the longer term a multi-stock procedure will be need, in particular so that proper account is taken of the co-

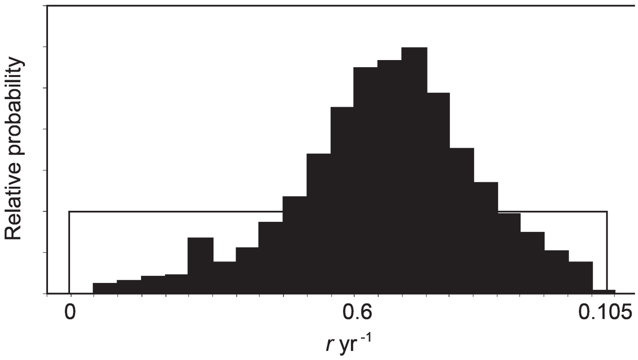

Fig. 4. Comparison of the uniform prior distribution (horizontal line) used for the intrinsic growth rate parameter *r* and the associated posterior (histogram) for the RC model for Breeding Stock G.

variances that arise for the different catch allocation hypotheses because catches taken to come from one breeding stock need then to be precluded from coming also from neighbouring breeding stock.

In the application here, the $N_{\min}$ constraint played no role. However in instances where it does so, greater care needs to be exercised as this constraint effectively modifies the independent prior distributions for *r* and absolute abundance by introducing covariance, and raises Borel's paradox difficulties (Brandon *et al.*, 2007).

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Keyword index

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