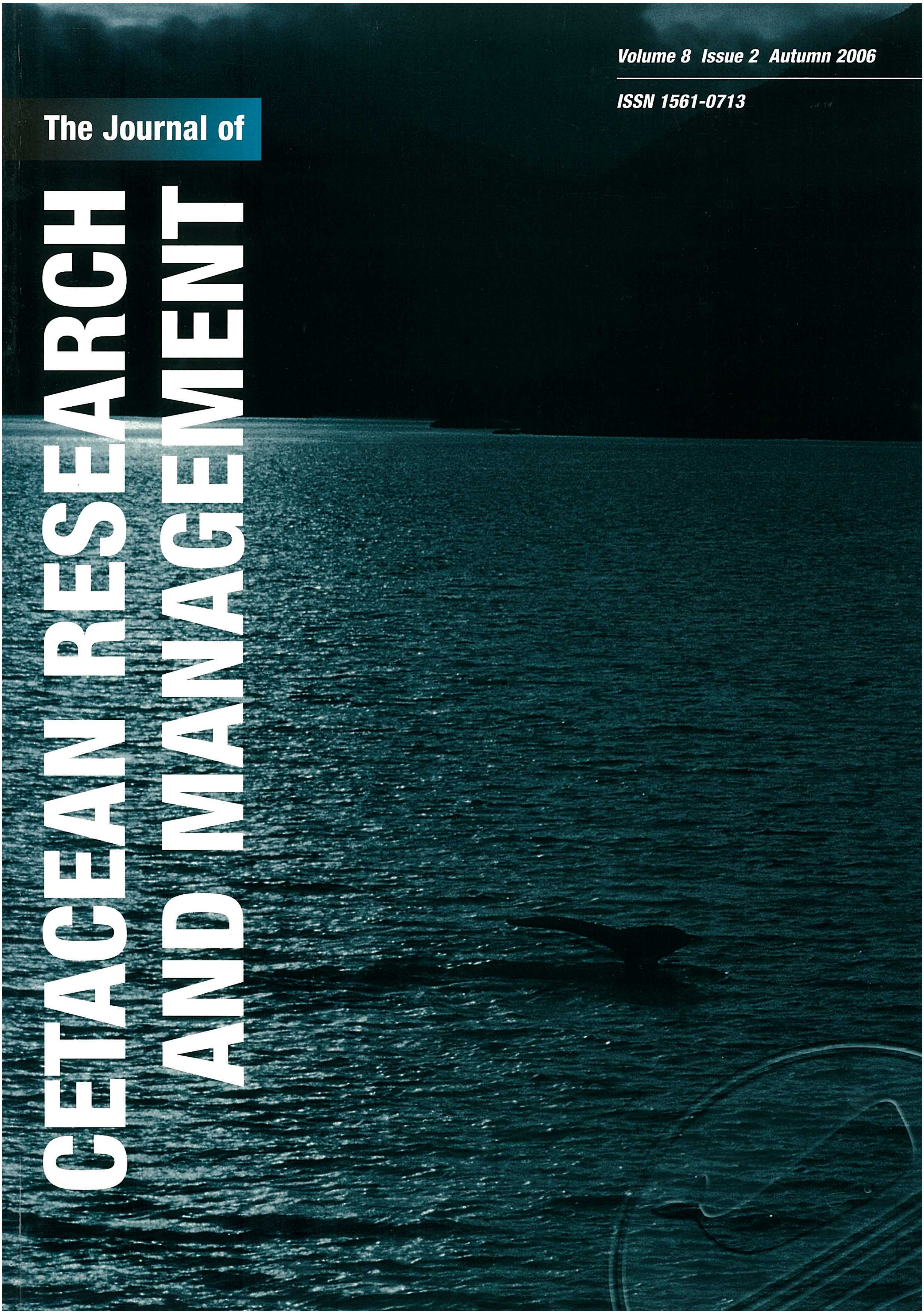

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Contents

Editorial

This summary of the work of the Scientific Committee at the recent annual meeting follows the 2006 meeting of the International Whaling Commission held in St Kitts and Nevis. Details of the Commission meeting will be published in the next *Annual Report of the International Whaling Commission*. The full report of the Scientific Committee will be published in spring 2007 as *J. Cetacean Res. Manage*. 9 (Suppl.).

REVISED MANAGEMENT PROCEDURE

After the adoption of the moratorium on commercial whaling in 1982, the Committee spent over eight years developing the Revised Management Procedure (RMP) for baleen whales. In brief, the RMP is a generic management procedure designed to estimate safe catch limits for commercial whaling of baleen whales. This was adopted some time ago by the Commission, at the 1992 meeting. However, the Commission has stated that it will not set catch limits for commercial whaling for any stocks until it has agreed and adopted a complete Revised Management Scheme (RMS) which will include a number of non-scientific matters, including inspection and enforcement. The RMS has been the subject of a considerable amount of discussion within the Commission. The Commission had received a proposal by the Chair of the Commission for an RMS package of measures that he believed was a fair and balanced approach to move to the rapid completion of the RMS. However, this was not accepted as a package by the Commission, and despite further work, the Commission agreed that it was at an impasse at the 2006 meeting in St Kitts and Nevis.

Process for revision of the *CLA*

The *CLA* (*Catch Limit Algorithm)* is used to determine safe removal limits under the RMP and was agreed in 1992. As a result of a request by Norway, the Committee reviewed the process agreed in 1992 and clarified some issues. The result of the review was to:

(1) agree that comparison of any proposed revision will be for a 100 year time period;
(2) agree an appropriate range of maximum sustainable yield rates for trials after a review at the 2007 meeting;
(3) agree requirements for an appropriate set of trials including additional trials to model environmental degradation;
(4) agree requirements for an appropriate set of performance statistics.

Implementation Simulation Trials

Implementation Simulation Trials are trials that are carried out before using the RMP to calculate a catch limit and involve investigating the full range of plausible hypotheses related to a specific species and geographic area, particularly with respect to issues of stock structure.

The process of developing *Implementation Simulation Trials* is not the same as identifying the 'best' assessment for the species/region, but involves considering a set of alternative models to examine a broad range of uncertainties with a view to excluding variants of the RMP that show performance that is not sufficiently robust across the trials. Account needs to be taken of the plausibility of the various trial scenarios when evaluating RMP variants.

In the light of difficulties experienced in recent years, particularly with respect to the North Pacific region (common minke whales and Bryde's whales), the Committee has spent some time discussing the general question of how best to ensure that the process of carrying out *Implementations* (or *Implementation Reviews*) is efficient and prompt, whilst taking into account the available information. To achieve this it agreed that they should be conducted at discrete intervals, using the data available at one point in time. This year, the Committee reviewed the process from *'pre-Implementation Assessment'* to initial *Implementation* and *Implementation Reviews* based on the experience gained thus far, and particularly with respect to the difficulties faced during the *Implementation* process for western North Pacific common minke whales. As a result, the Committee developed detailed the requirements and guidelines for the *Implementation* process as well as updating its document detailing requirements and guidelines for conducting surveys and analysing data within the Revised Management Procedure. These were published in *J. Cetacean Res. Manage*. 7 (Suppl.).

North Pacific Bryde's whales

The Committee had made relatively slow progress up to 2005 on completing the *Implementation* for western North Pacific Bryde's whales *inter alia* due to its heavy workload. While noting that it was in the *pre-Implementation Assessment* stage, the Committee noted the considerable work already undertaken and agreed that it should be possible to move faster towards *Implementation* than would be the case for new situations. The Committee held an intersessional Workshop in March 2005 and at the 2005 annual meeting it was agreed that the *pre-Implementation* stage had been completed and that the *Implementation* process would now begin, following the new guidelines referred to above. The first intersessional Workshop under the new guidelines took place in Shimizu, Japan in October 2005 and further progress was made at the 2006 Annual Meeting. The second intersessional workshop will be held in December 2006 and the *Implementation* should be completed at the 2007 Annual Meeting in Anchorage, USA.

North Atlantic fin whales

The Committee reviewed the available information in order to determine whether there was sufficient information to warrant the initiation of a *pre-Implementation Assessment* for North Atlantic fin whales. It agreed that there was and the Commission agreed with its recommendation that the Committee initiate the *pre-Implementation Assessment*. The first stage of this was reviewed at the 2006 annual meeting and it is hoped to complete the *pre-Implementation* stage at the 2007 annual meeting. To progress this work, a co-operative intersessional Workshop was held in March 2006 with the NAMMCO scientific committee on general scientific issues of common interest, particularly with respect to stock structure, abundance and catch history. The results of that workshop were discussed and endorsed at the 2006 Annual Meeting and it was agreed that the *pre-Implementation Assessment* was complete. For practical reasons, it was agreed that the *Implementation* would begin after the 2007 Annual Meeting.

Bycatches of large whales

The RMP estimates a limit for the number of non-natural removals, not simply a catch limit for commercial whaling. It is therefore important to estimate the numbers of whales removed from the population by indirect means including bycatches in fishing gear and ship strikes, for example.

The Scientific Committee began to consider this issue in some detail three years ago. It agreed that priority should be given to those areas where the RMP is likely to be implemented – such as the northwestern Pacific and the northeastern Atlantic. Four steps are required: (1) identification of the relevant fisheries; (2) description and categorisation of those fisheries to allow a sampling scheme to be devised; (3) identification of a suitable sampling strategy or strategies; and (4) design and implementation of the sampling scheme to enable estimation of the total bycatch.

The Committee has reviewed general methods for estimating bycatches. These fall under two headings: (1) those based on fisheries data and observer programmes; and (2) those based on genetic data. The former have been used successfully for several small cetacean populations. The Committee agreed that independent observer schemes are generally the most reliable means of estimating bycatch rates in a statistically rigorous manner, but that they may not always be practical and will require careful design.

Genetic approaches potentially represent a new way of estimating bycatches. The Committee has agreed that although genetic methods based on market samples may not be the primary approach to estimating bycatch, they could provide useful supplementary data that could not be obtained in another way. The use of market samples to provide absolute estimates should not be ruled out. However, further developments in sampling design with input from experts with detailed knowledge of market sampling issues are needed. A Workshop on that subject was held immediately prior to the 2005 meeting, in Ulsan, Korea. The objectives of the Workshop were:

(1) to review available methods that have been used to provide estimates of large cetacean bycatches via market samples, including a consideration of their associated confidence intervals in the context of the RMP;

(2) to provide advice as to whether market-sampling-based methods can be used to reliably estimate bycatch for use in addressing the Commissions objectives regarding total removals over time and, if so, the requirements for such methods.

The Committee agreed that market sampling provided potentially useful methods to supplement bycatch reporting schemes and agreed to a proposal for a follow-up workshop to investigate this further. It also agreed that any such bycatch estimates obtained from market surveys would be improved considerably if carried out in conjunction with the use of data from DNA registers on whales entering the market. Whilst recognising the political sensitivity of market-related issues in an IWC context, the Committee respectfully requested relevant governments to consider a collaborative effort to investigate these methods as a potentially valuable source of information for management and use in the RMP. At the 2006 Annual Meeting it was noted that considerable progress had been made and a list of further work requirements was agreed as a pre-requisite to holding a second workshop; this will probably occur after the 2007 Annual Meeting.

Other sources of anthropogenic mortality: vessel strikes

The Committee reviewed the report of a workshop on large whale ship strikes in the Mediterranean held by ACCOBAMS and the Pelagos Sanctuary and endorsed its recommendations on work related to estimating the number of whales struck and possible mitigation measures. It also agreed on the need to establish an international database of vessel strikes and established a working group to take this forward. It also recommended further work on histopathological techniques to determine if whales have been struck by vessels. It also made a number of recommendations related to improved reporting of ship strikes.

REGIONAL WORKSHOPS TO ADDRESS CETACEAN BYCATCH ISSUES

Outside the context of the RMP, the IWC Scientific Committee and others have identified the incidental capture of cetaceans in fishing gear as one of the most important threats to the conservation and management of their populations and it is known to be a significant threat to survival in certain cases (e.g. the North Atlantic right whale, and the vaquita). In order to address the full management implications, reliable information is needed on bycatch numbers, stock identity and movements, the abundance of the affected population(s), and the population dynamics of the cetaceans.

In some areas, considerable advances have been made in the assessment and mitigation of cetacean by-catch since the pioneering IWC La Jolla Workshop held in 1990. In other areas, however, little progress has been made and, as a result, a growing number of cetacean species (both large and small) face critical conservation problems as a result of fisheries bycatch. Rather than holding another large generic workshop, it was agreed that given the case- and area-specific nature of the problem, a series of broad-based regional workshops would be more effective, focusing on regions where bycatch problems have been given priority by the Scientific Committee and are not already being addressed.

The general objectives of such workshops will be to develop a short- and long-term approach to the successful management and mitigation of the cetacean bycatch problems in the region, building upon work already undertaken by the Committee. The Committee agreed a mechanism whereby this process can be facilitated. It also recommended collaboration with other organisations with an interest in this matter (e.g. the Convention on Migratory Species, the Committee on Fisheries of the UN Food and Agriculture Organisation, IUCN and relevant international and regional fishery organisations). Work to set up the first such workshop is continuing.

DEVELOPMENT OF AN ABORIGINAL WHALING MANAGEMENT PROCEDURE

With the completion of the RMP, the Commission asked the Scientific Committee to begin the process of developing a new procedure for the management of aboriginal subsistence whaling. Such a procedure must take into account the different management objectives for such whaling when compared to commercial whaling. This is an iterative and ongoing effort. The Commission will establish an Aboriginal Whaling Scheme that comprises the scientific and logistical (e.g. inspection/observation) aspects of the management of all aboriginal fisheries. Within this, the scientific component might comprise some general aspects common to all fisheries (e.g. guidelines and requirements for surveys and for data c.f. the RMP) and an overall AWMP within which there will be common components and case-specific components.

At the 2002 meeting, the Committee completed its work with respect to the Bering-Chukchi-Beaufort Seas stock of bowhead whales. It agreed a *Strike Limit Algorithm (SLA)* for bowhead whales and the scientific aspects of a Scheme; this was adopted by the Commission. It noted that should the Commission decide, it would be possible to apply the *Bowhead SLA* at that meeting. After considerable work and two intersessional workshops, the Committee made a formal recommendation to the Commission for a *Strike Limit Algorithm* for gray whales in 2004. It believed that this *SLA* met the objectives of the Commission set out in 1994 and represented the best scientific advice that the Committee could offer the Commission with respect to the management of the Eastern North Pacific stock of gray whales. This was adopted by the Commission.

The situation for the Greenlandic fisheries for fin and minke whales is less promising. A considerable amount of research, especially concerning stock identity, is required and to this end, the Committee has developed a research programme in cooperation with Greenlandic scientists (see below). High priority is being accorded to this work.

ASSESSMENT OF STOCKS SUBJECT TO ABORIGINAL SUBSISTENCE WHALING

Aboriginal subsistence whaling is permitted for Denmark (Greenland, fin and minke whales), the Russian Federation (Siberia, gray and bowhead whales), St Vincent and The Grenadines (Bequia, humpback whales) and the USA (Alaska, bowhead and gray whales). It is the responsibility of the Committee to provide scientific advice on safe catch limits for such stocks and until the AWMP is completed then the Committee provides advice on a more *ad hoc* basis, carrying out major reviews according to the needs of the Commission in terms of establishing catch limits and the availability of data. It also carries out brief annual reviews of each stock.

The present catch limits have been set up to the 2007 season and so at the 2007 meeting, the Committee has to provide management advice for all of the stocks considered. The Commission sets catch limits based on the scientific advice and a ‘need’ statement from the countries involved.

Eastern gray whales

In 2002, the primary assessment carried out was for the eastern gray whale population (Issue 1 of volume 4 of the *Journal of Cetacean Research and Management* was devoted to gray whale papers). New information on abundance, distribution, catches and ecology was presented. The population is believed to be close to carrying capacity. The Committee agreed that an annual take of up to 463 whales was acceptable; based on the submitted need statement, the Commission set a total for the 2003-07 seasons of 620 with a maximum of 140 in any one year. The Committee confirmed this advice this year using the *Gray Whale SLA*.

Bering-Chukchi-Beaufort Seas stock of bowhead whales

In addition to the work on the *Bowhead SLA*, the Committee has also been examining the status of the Bering-Chukchi-Beaufort Seas stock of bowhead whales. The most recent abundance estimate (for 2001) is 10,500 (95%CI 8,200-13,500) giving a rate of increase between 1978 and 2002 of 3.2% (95%CI 1.4%, 5.1%). The Committee undertook an in-depth assessment at the 2004 meeting. At that meeting, the discussions of uncertainty over stock structure issues made it clear that these must form a major component of the *Implementation Review* to be completed in 2007. However, given the continued evidence of an increase in abundance estimates, the spatio-temporal distribution and opportunistic nature of the hunt and the low numbers of whales struck annually in St. Lawrence Island and Chukotka, the Committee agreed that the *Bowhead SLA* remains the most appropriate tool for providing management advice for this harvest, at least until the 2007 *Implementation Review* is completed. This indicated that no change was required to the already agreed limit for the 2003-2007 (total landed whales not more than 280, with no more than 67 strikes in any one year).

The *Implementation Review* process began in 2006 and in particular is examining the robustness of the *Bowhead SLA* to plausible stock hypotheses via simulation trials. Discussions at the 2006 Annual Meeting focussed on progress being made in stock structure studies and preparation for the 2007 assessment. A timeline for this work was agreed and the second intersessional workshop will take place in January 2007 with a Third Workshop in March 2007.

Minke and fin whales off West Greenland

In 2002, despite a lack of scientific advice, the Commission established the same catch limits for the 2003-07 period as previously in force i.e. West Greenland minke whales – an annual limit of up to 175 strikes; East Greenland minke whales – an annual catch of up to 12 animals; West Greenland fin whales – an annual catch of up to 19 whales. The Committee had been unable to provide scientific advice on safe catch limits at that time and had stressed that its inability to provide any advice on safe catch limits was a matter of great concern.

In 2005, the Committee had received abundance estimates from a new photographic aerial survey technique and new assessments from Greenlandic scientists. The Committee had identified a number of problems with these but was still concerned that taken at face value, the preliminary (and not accepted) estimate of abundance for common minke whales suggests that about a 90% decline has occurred since the previous survey in 1993 although there are several indications that such a decline has probably not occurred. Nonetheless, the Committee urged that considerable caution be exercised in setting catch limits for this fishery because it has no scientific basis for providing advice on safe catch limits. It also made a number of strong recommendations for future scientific work.

Similarly, in 2005, the Committee was not in a position to accept the estimate for fin whales, and also urged that considerable caution be exercised in setting catch limits for this fishery and as interim *ad hoc* advice, the Committee advised that a take of 4-10 animals (approximately 1% of the lower 5th percentile and of the mean of the estimate of abundance) annually was unlikely to harm the stock in the short-term, particularly since this does not take into account the possibility that the fin whale stock extends beyond West Greenland. This advice would be re-evaluated in the light of the intersessional work recommended.

This year, the Committee was extremely pleased to receive and accept new abundance estimates for the common minke whale (3,500, 95%CI 1,500-7,700) and fin whale (1,700 95%CI 840-3,500) off West Greenland, based on a traditional aerial survey.

As a result it stressed that it was in a considerably stronger position than it was last year. For the common minke whale, in addition to the new abundance estimate, progress has been made on incorporating the sex ratio data into an assessment and in examining whether the genetic data can be used to obtain a lower bound for the abundance of the total population. It also noted that further progress will be made on these issues during the intersessional period, although it could not guarantee that this work would necessarily result in an acceptable assessment in 2007. The Committee therefore agreed that the Commission should exercise caution when setting catch limits for this stock.

For the fin whale, in addition to the new abundance estimate, which it recognises is an underestimate, considerable progress has been made on developing an assessment method although some have some concerns as to whether the data available are sufficiently informative to use it for providing management advice. It again therefore agreed that it was not in a position to give satisfactory management advice.

Humpback whales off St Vincent and the Grenadines

In 2002, after considerable debate in the Commission, a catch of up to 20 whales for the period 2003-07 was agreed. The Committee has received positive confirmation that eastern Caribbean humpback whales are part of the West Indies breeding population (abundance in 1992/93 – 11,570, 95%CI 10,100-13,200) and agreed that the catch limit set by the Commission would not harm the stock.

HISTORIC ABUNDANCE ESTIMATION, GENETIC METHODS

In 2004, in the light of a genetic modelling paper published in 2003 (Roman, J. and Palumbi, S.R. 2003. Whales before whaling in the North Atlantic. *Science* 301:508-10), the Committee had considered the general methodological issue of estimating carrying capacity and/or pre-exploitation population size in the context of the Committee's assessment work. As a result of its discussions, the Committee agreed that such genetic methods have the potential to be one of a suite of tools that can be used to examine pre-exploitation abundance but that there are a number of limitations and uncertainties that must be considered when examining such data in a present-day management context. The Committee had agreed that the estimates of historic abundance provided in the Roman and Palumbi paper for the initial pre-whaling population sizes of humpback, fin and common minke whales in the North Atlantic have considerably more uncertainty than reported, and can not be considered reliable estimates of immediate pre-whaling population size. Particularly important in this regard is the mismatch between the time-period to which genetic estimates apply (i.e. the time period is difficult to determine and extremely wide) and the population sizes of whales immediately prior to exploitation. It also agreed that the paper provides no information to suggest that changes are required in either the RMP or AWMP approaches to management.

The Committee had identified further work necessary to assess whether genetically-based estimates of 'initial' abundance can provide useful information for the management of cetaceans; little progress has been made in this regard and at the 2006 meeting the Committee agreed that it should not consider this issue further until additional publications describing methodological and analytical progress are available.

STOCK IDENTITY

Of general concern to the assessment of any cetaceans is the question of stock identity. Examination of this concept in the context of management plays an important role in much of the Committee's work, whether in the context of the RMP, AWMP or general conservation and management. In recognition of this, the Committee has established a Working Group to review theoretical and practical aspects of the stock concept in a management context. The Committee has noted that it is important, in any application of stock structure methods, to examine the sensitivity of conclusions to different *a priori* decisions about the definition of initial units, and as to which population structure hypotheses to examine.

A specialist Workshop to examine the use of simulation testing to assess the performance of methods to identify population structure was held in January 2003. The Workshop developed a suitable simulation framework to allow evaluation of genetic methods used in inferring population structure both in general terms (the issue is of great relevance to conservation and management outside the IWC) and from a specifically IWC viewpoint (particularly in an RMP/AWMP context).

This is a complex project that must proceed in an iterative fashion. Great progress was made on the most challenging module, i.e. the development and validation of a program to simulate realistic genetic datasets and the Committee reviewed the results of an intersessional workshop to build on this and begin the testing of some existing methods held at the University of Potsdam in March 2006. The primary achievements of the Workshop are summarised below.

(1) Considerable progress was made in the detailed computing work needed to:
    (a) identify and fix problems in the linking of the coalescent (SIMCOAL) and individual based model (RMETASIM) required for simulating datasets;
    (b) complete the control program that generates genetic samples from the datasets developed by RMETASIM, passes the samples to the boundary setting methods, runs the management algorithms, and collates the performance statistics.
(2) The technical specifications for the initial TOSSM trials (demographic structure, genetic structure, initialising the population matrix, harvesting and catch control, sampling and trials) were completed.
(3) An initial set of methods to be tested within the framework was identified, along with issues related to automation for boundary-setting, and the people who would 'champion' each method.
(4) Preliminary results were available from two population structure methods, showing example boundary-setting algorithms in use through a complete run of TOSSM.

The Committee endorsed the report of the Workshop and the plans to take this work forward during the intersessional period.

COMPREHENSIVE ASSESSMENT OF WHALE STOCKS

The 'Comprehensive Assessment' of whale stocks

The 'Comprehensive Assessment' can be considered as an in-depth evaluation of the status of all whale stocks in the light of management objectives and procedures; this would include the examination of current stock size, recent population trends, carrying capacity and productivity. Clearly, it is not possible to 'comprehensively assess' all whale stocks simultaneously, and the Committee has been working in an iterative manner towards this, initially concentrating on stocks that have recently or are presently being subject to either commercial or aboriginal subsistence whaling. Some of these stocks have already been discussed in the sections on the RMP and AWMP.

Antarctic minke whales

The Committee has carried out annual surveys in the Antarctic (south of 60°S) since the late 1970s. The last agreed estimates for each of the six management Areas for minke whales were for the period 1982/83 to 1989/90. At the 2000 meeting, the Committee agreed that whilst these represented the best estimates for the years surveyed, they were no longer appropriate as estimates of current abundance. An initial analysis of available recent data had suggested that current estimates might be appreciably lower than the previous estimates.

Subsequently, considerable time has been spent considering Antarctic minke whales with a view to obtaining final estimates of abundance and considering any trend in these. This has included a review of data collection methods and analytical methodology. After considering many of the factors affecting abundance estimates, there is still evidence of a decline in the abundance estimates, although it is not clear how this reflects any actual change in minke abundance. Three hypotheses that might explain these results have been identified:

(1) a real change in minke abundance;
(2) changes in the proportion of the population present in the survey region at the time of the survey;
(3) changes in the survey process over time that compromise the comparability of estimates across years.

A considerable amount of work has been undertaken and further work is ongoing. The final part of the Third Circumpolar Survey undertaken as part of the IWC's SOWER research programme has been completed and preliminary work suggests that the estimated abundance may be down to about 40% of the estimates from the Second Circumpolar Survey. Experimental work to examine possible causes has been undertaken on the 2004/05 and 2005/06 cruises. Further work will be undertaken on the 2006/07 cruise. Work to finalise an assessment of Antarctic minke whale is continuing in a number of ways and will again be a priority item for discussion at the 2007 meeting.

Southern Hemisphere blue whales

The Committee is beginning the process of reviewing the status of Southern Hemisphere blue whales. An important part of this work is to try to develop methods to identify pygmy blue whales from 'true' blue whales at sea and progress is being made on this. Work on genetic and acoustic differentiation techniques is continuing and there is considerable progress with morphological methods. The Committee has agreed that (1) on average, the Antarctic blue whale population is increasing at a mean rate of 7.3% per annum (1.4–11.6%); (2) had an estimated circumpolar population size of 1,700 (860–2,900) in 1996; and (3) that this population is still severely depleted with the 1996 population estimate estimated to be at 0.7% (0.3–1.3%) of the estimated pre-exploitation level.

The Committee reviewed progress towards undertaking an in-depth assessment at its 2006 meeting and has developed a workplan for next year.

Southern Hemisphere humpback whales

Considerable progress has been made in recent years in working towards an assessment of humpback whales. Attention has focussed both on data from historic whaling operations and on newly acquired photo-identification, biopsy and sightings data. Considerable progress has been made towards completing an assessment for three Breeding Stocks (A: off eastern South America, D: off western Australia and G: off western South America), particularly as a result of an intersessional workshop held in Hobart, Australia in April 2006. At the Annual Meeting, the Committee reviewed and endorsed the report of the Workshop and its recommendations. It also reviewed the results of assessment modelling. The Committee agreed that of the three stocks assessed, the most reliable results were those for Breeding Stock A. This is because there was trend information from surveys on the breeding grounds and less uncertainty about catch allocation from the feeding grounds. It agreed that there has been an increase in abundance in recent decades but that the stock remains well below initial unexploited levels. For Breeding Stock G, the only trend information available was for the feeding grounds and there was also uncertainty about possible stock structure within this stock. For Breeding Stock D, although there is breeding ground trend information and an absolute estimate of abundance, catch allocation is less certain and perhaps influenced by mixing with Breeding Stock E.

North Pacific common minke whales

After the completion of the *Implementation* of North Pacific common minke whales in 2003, it was agreed that preparations should begin for an in-depth assessment of common minke whales in the North Pacific, with special emphasis on the J-stock.

This year, the Committee was pleased with the substantial intersessional progress made including receiving results from three cruises and a successful collaboration between Japanese and Korean scientist for genetic analysis. With respect to stock structure, there is now sufficient information available to begin specifying some plausible hypotheses for stock structure but recommends biopsy sampling for some areas where data are sparse. This will require co-operation amongst range states.

Similarly in terms of distribution and abundance, the Committee requested co-operative work by all range states to fill in information gaps. This will be facilitated by a workshop of range state scientists being held in Korea in late 2006.

North Atlantic right whales

The Committee has paid particular attention to the status of the North Atlantic right whale in the western North Atlantic in recent year and is extremely concerned about this population, which, whilst probably the only potentially viable population of this species, is in serious danger (*ca* 300 animals). By any management criteria applied by the

IWC in terms of either commercial whaling or aboriginal subsistence whaling, there should be no direct anthropogenic removals from this stock.

The Committee has on several occasions noted that individuals are continuing to die or become seriously injured as a result of becoming entangled in fishing gear or being struck by ships. It repeated that it is a matter of absolute urgency that every effort be made to reduce anthropogenic mortality in this population to zero. This is perhaps the only way in which its chances of survival can be directly improved. There is no need to wait for further research before implementing any currently available management actions that can reduce anthropogenic mortalities.

The Committee reviewed progress on a number of research and management recommendations concerning this stock.

Western North Pacific gray whales

This is one of the most endangered populations of great whales in the world. It numbers less than 100 animals and there are a number of proposed oil and gas-related projects in and near its only known feeding ground. The population is very small (about 120), and suffers from a low number of reproductive females (about 23), low calf survival, male-biased sex ratio, dependence upon a restricted feeding area and apparent nutritional stress (as reflected in a large number of skinny whales in some years – about 15% in 2006). Other major potential concerns include behavioural reactions to noise (notably in light of increasing industrial activity in the area) and the threat of an oil spill off Sakhalin which could cover all or part of the Piltun area and thus potentially exclude animals from this feeding ground. Again, this year, the Committee stressed the urgency of reducing anthropogenic mortality to zero – particularly in the light of three fatal entanglements in fishing gear in 2005.

Last year, the Committee welcomed and supported the report and recommendations of the independent scientific review panel (ISRP) that had included five members of the IWC Scientific Committee (Brownell, Cooke, Donovan, Moore and Reeves). It commended SEIC (the Sakhalin Energy Investment Corporation) for requesting this review and IUCN for facilitating the process. Despite some difficulties, it believes that this process represented an important step forward for western gray whale conservation.

The Committee strongly supported efforts to build upon this in the future and to develop a framework for collaborative research, monitoring and mitigation efforts between oil companies, independent experts, national programmes and authorities and the IWC and other intergovernmental organisations. It particularly urged that other companies in the area co-operate with this process. It was therefore pleased to hear this year that plans for a long-term group were proceeding (see *http://www.iucn.org/themes/marine/sakhalin/*). The Committee made a number of research recommendations, particularly with respect to telemetry work.

The Committee has also concurred with need identified by the ISRP for a comprehensive strategy to save western gray whales. In addition to time spent in the Sakhalin region, gray whales spend approximately half their time in other waters in eastern Asia (Japan, the Republic of Korea, the Democratic People's Republic of Korea and China) and there is a need for mitigation measures for the many potential threats to the western gray whale throughout its range. The IWC has agreed to play an active and facilitating role in the process.

EFFECTS OF ENVIRONMENTAL CHANGE ON CETACEANS

There is an increasing awareness that whales should not be considered in isolation but as part of the marine environment; detrimental changes to their habitat may pose a serious threat to whale stocks. The Committee has examined this issue in the context of the RMP and agreed that the RMP adequately addresses such concerns. However, it has also emphasised that the species most vulnerable to environmental threats might well be those reduced to levels at which the RMP, even if applied, would result in zero catches. Over a period of several years, the Committee has developed two multi-national, multi-disciplinary research proposals. One of these, POLLUTION 2000+, has two aims: to determine whether predictive and quantitative relationships exist between biomarkers (of exposure to and/or effect of PCBs) and PCB levels in certain tissues; and to validate/calibrate sampling and analytical techniques. The other, SOWER 2000, is to examine the influence of temporal and spatial variability in the physical and biological Antarctic environment on the distribution, abundance and migration of whales.

At the 2006 meeting, a pre-meeting was held on the potential for seismic surveys to impact cetaceans. This included members of the Scientific Committee as well as industry representatives, geophysical contractors, members of national regulatory agencies and individuals representing funding bodies.

The issues addressed are complex and it was agreed that any approach to addressing the potential impacts of seismic surveys on cetaceans needs to be scientifically-based and risk-averse. Overall, the scientific presentations and discussions considerably advanced the Committee's ability to:

(1) evaluate the potential impacts from seismic surveys on cetaceans;
(2) help interpret observed scientific results in the context of effects on critical life functions and on animals at the population level;
(3) provide a current synthesis of studies addressing issues related to seismic surveys and cetaceans;
(4) advance the dialogue, communication and exchange of ideas and information between the IWC Scientific Committee, the wider scientific community and members of industry in order to address this issue effectively;
(5) identify areas where additional research, review and discussion are needed (especially related to measuring and translating scientific results into assessments biological significance, as well as to improving existing and developing new mitigation and monitoring approaches);
(6) highlight areas where risk to cetaceans may be reduced by greater consideration to these issues in the planning stages of seismic surveys; and
(7) to serve as a resource for member nations that issue permits authorising seismic surveys within their EEZ.

The Committee made a large number of recommendations for further work on this important issue, stressing the need for co-operation amongst stakeholders including governments. Particularly important were recommendations on monitoring and mitigation measures, and advice to member governments. Governments were recommended to implement appropriate monitoring programmes, develop and/or evaluate nationally relevant mitigation procedures and identify and facilitate research and monitoring and mitigation measures that address the recommendations detailed in the Committee's report. The Committee also recommended the earliest possible establishment of long-term monitoring programmes for vulnerable species, and that seismic surveys be designed to use only the amount of acoustic output required for the desired geological objectives.

The Committee also considered the final report of the two sub-projects comprising Phase 1 of the POLLUTION 2000+. The objectives of the bottlenose dolphin sub-project were (1) to select and examine a number of biomarkers of exposure to and/or effect of PCBs and determine whether a predictive and quantifiable relationship with PCB levels in certain tissues exists and (2) to examine the relationships between concentrations of variables obtained by biopsy sampling with those of concentrations in other tissues that can only be obtained from fresh carcases. For the first time an individual based model was constructed that simulated the accumulation of PCBs in the population and allowed modification of first year calf survival based on maternal blubber PCB levels. The objective of the harbour porpoise sub-project was to determine changes in concentrations of selected variables with post-mortem times. This makes it possible to use incidentally caught animals in pollutant studies. The Committee commended the scientific output of Phase I and agreed that it had certainly contributed to the Commission's request to give priority to research on the effects of environmental changes on cetaceans. The Committee concurred with a recommendation from the POLLUTION 2000+ Steering Group that before any decision is taken on implementing Phase II, an interdisciplinary workshop should be held to identify the needs for a Phase II and, if appropriate, design an outline research proposal for continuation of the programme.

Ecosystem modelling

The question of ecosystem modelling in the context of cetacean conservation is an important one and has been addressed by the Scientific Committee on a number of occasions before. This year the Committee has agreed to work collaboratively with both CCAMLR and FAO initiatives. The Committee agreed on the following with respect to the applicability of ecosystem models for the use of the Committee in providing advice to the Commission:

(1) spatial modelling is a valuable tool to explore possible effects of anthropogenic stressors;
(2) there is a great need for the proper incorporation of uncertainty in ecosystem models;
(3) there is a critical lack of data, in particular at the lower trophic levels, to evaluate the reliability of models;
(4) some models can be useful to generate hypothesis regarding trophic dynamics; and finally
(5) that there is a need for an increased collaboration between scientists designing field studies and those developing analytical models.

Other habitat related matters

The Committee also discussed further collaboration in Southern Ocean research with organisations such as CCAMLR and SO-GLOBEC and other issues related to sea ice. It also agreed to hold a special symposium on infectious and non-infectious diseases in marine mammals prior to the next annual meeting

SMALL CETACEANS

Despite disagreement within the Commission over the management responsibilities of the IWC with respect to small cetaceans, it has been agreed that the Scientific Committee can study and provide advice on them. As part of this programme, the Committee has reviewed the biology and status of a number of species and carried out major reviews of significant directed and incidental catches of small cetaceans.

In 2001, the Government of Japan had indicated that it would no longer co-operate with the Committee on small cetacean related matters. In 2002, the Committee referred to the great value of the information provided by the Government of Japan on the status of small cetaceans in previous years and respectfully requested that the Government of Japan reconsider its position on this matter and resume the valuable contribution of Japanese scientists to its work on small cetaceans. Unfortunately, this has still not yet happened.

This year, the primary topic was small cetaceans in the Caribbean and western tropical Atlantic. In general, although work is being carried out in several areas, considerable additional work is needed to understand the distribution, stock structure, abundance and status of species in the region. Few abundance estimates exist and stock structure remains unknown in most cases. This requires local and international collaboration, co-operation, training and assistance.

Directed takes in this area include subsistence removal for food and live capture for dolphinaria both within the region and globally. There was little new information on the subsistence takes and the extent of current directed hunts is unclear. There is evidence of incidental catches of several species in many fisheries but little information on levels. The situation with respect to live captures and dolphinaria is somewhat unclear. Boat traffic, and habitat degradation, including chemical pollution are also potential threats to cetaceans in the region. A collaborative effort is required to assess the impact of removals and other threats, and to document the status of populations in the region.

The Committee also reviewed progress on previous recommendations, in particular on the baiji of the Yangtze River, the world's most endangered cetacean. It welcomed news of some international collaboration. It noted that there are apparently plans to capture baijis and put them in a semi-natural oxbow reserve. While noting its previous discussions on the relative merits of this approach, it agreed that should any baijis be found and captures attempted, scientists with relevant expertise must be able to contribute directly to the process.

The vaquita is also critically endangered. The Committee welcomed new initiatives to estimate current abundance and to study habitat requirements, but emphasised that highest priority must be the urgent investment of more resources for bycatch mitigation. In this regard, the Committee emphasised that pingers are not an appropriate measure for the vaquita.

The harbour porpoise is exposed to high bycatches throughout most of its range. The Committee therefore welcomed new results on abundance in the North Sea and adjacent waters from the SCANS II project, and plans for further studies in the North Atlantic (e.g. as part of the trans-NASS programme). It noted information from NAMMCO that there are probably substantial levels of bycatch in Icelandic and Norwegian fisheries and endorsed the view of the NAMMCO Scientific Committee that better estimates are needed to assess the sustainability of these bycatches as well as directed catches in Greenland.

The Committee has also previously expressed concern at the degradation of important habitats for the humpback dolphins. It expressed serious concern over plans for industrial development in Sanniang Bay, Southern China where there is a small resident population in an as yet pristine area. Given information on captures of humpback dolphins in Guinea, the Committee recommended that appropriate surveys be implemented to obtain further information on distribution and abundance.

The Committee reviewed progress on other recommendations, *inter alia* on white whales and narwhals, small cetaceans in the Black Sea, and Dall's porpoise, and reiterated its previous concerns and recommendations. It also endorsed plans for a major survey in the ACCOBAMS region (which includes the Black Sea). In 2004, it had recommended surveys to be undertaken on the abundance of franciscana, and was pleased to receive new information from the southern coast of Brazil.

Finally, the Committee repeated previous requests for all Governments to submit relevant information on direct and incidental catches of small cetaceans in their national progress reports and for improved information on stock identity and abundance.

SCIENTIFIC ASPECTS OF WHALEWATCHING

The major topic this year concerned quantitative methods for assessing the impacts of whalewatching on cetaceans. The results of three studies, two carried out in Australia, suggested that cumulative effects could jeopardise the viability of populations already at risk or small closed or resident populations. Long-term studies are essential to assess whether changes at the individual and/or population level are caused by the whalewatching activities. It is also essential to obtain baseline data from prospective whalewatching areas.

The Committee reviewed a number of careful and well designed studies (in New Zealand, Australia, Canada and Croatia) that provided compelling evidence that the fitness of individual odontocetes repeatedly exposed to whalewatching vessel traffic can be compromised and that this can lead to population level effects. The Committee recommended that similar studies be carried out, wherever possible. The Committee also strongly encouraged the development of similar studies on large whales, in particular, research to determine sustainable levels of whalewatching.

The Committee stressed the need for appropriate study design and analytical methods to enable discrimination between natural ecological variability and anthropogenic impacts when examining short-term behavioural changes. The Committee recommended that a dedicated workshop to develop a world-wide research design be held.

The Committee also reviewed: data sources from platform of opportunity of potential value to the Committee; reports from a number of intersessional working groups; potential impacts of 'swim with' programmes; progress on developing a compendium of whalewatching guidelines and regulations from around the world; and risk to cetaceans from colliding with whalewatching vessels.

REVIEW AND COMMENT ON SCIENTIFIC PERMITS ISSUED FOR SCIENTIFIC RESEARCH

All proposed scientific permits have to be submitted for review by the Scientific Committee following guidelines issued by the Commission. However, in accordance with the Convention the ultimate responsibility for issuing them lies with the member nation.

Three continuing permits were discussed this year.

JARPA II was a new proposal last year. Its stated objectives of the new long-term research programme proposal are: (1) monitoring of the Antarctic ecosystem; (2) modelling competition among whale species and developing future management objectives; (3) elucidation of temporal and spatial changes in stock structure; and (4) improving the management procedure for the Antarctic minke whale stocks.

The proposed catches for the full programme were: 850 (with 10% allowance) Antarctic minke whales, 50 humpback whales (not to begin for two years) and 50 fin whales (10 in the first two years). There was considerable disagreement over the value of this research both within the Scientific Committee and the Commission. As in previous years, there was severe disagreement within the Committee regarding advice that should be provided on a number of issues, including: the relevance of the proposed research to management, appropriate sample sizes and applicability of alternate (non-lethal) research methods.

JARPN II is a long-term research programme primarily aimed at feeding ecology in the context of contributing to the 'conservation and sustainable use of marine living resources in the western North Pacific, especially within Japan's EEZ'. The programme involves the taking of 150 minke whales, 50 Bryde's whales, 50 sei whales and 10 sperm whales in the western North Pacific.

A proposed permit by Iceland, primarily for feeding ecology studies for 100 common minke whales, 100 fin whales and 50 sei whales in each of two years was presented two years ago; the government had only given a permit for 25 common minke whales from Iceland in 2004. Again, as in the past, different views on the value of this research were expressed in the Scientific Committee.

The Committee continued preparations for a full review of the JARPA programme (an 18 year programme that finished in 2004). Now that the complete set of results is available, the review workshop will be held in December 2006.

In the absence of any new Special Permit proposals to review, the Committee focused on a discussion on how to improve our procedures for review of such proposals. The Committee agreed that there is a need to improve the review process we currently use and a proposal for a new method will be the starting point for discussions next year. In the meantime, the Committee agreed on a *pro forma* to be used by the proponents of special permit proposals when submitting such proposals to the Scientific Committee.

WHALE SANCTUARIES

In 2004, when reviewing the Southern Ocean Sanctuary (SOS), the Committee endorsed a number of recommendations that were to be implemented generically to the review of sanctuary proposals.

(1) The purpose(s) of IWC Sanctuaries should be better articulated through a set of refined overall objectives (e.g., preserving species biodiversity; promoting recovery of depleted stocks; increasing whaling yield).

In particular, the relationships between the RMP and the Sanctuary programme should be articulated.

(2) Appropriate performance measures both for Sanctuaries in general, and the SOS in particular, should be developed. These performance measures should link the refined objectives of the SOS with monitoring programmes in the field.

(3) Systematic inventory and research programmes should be established or further developed so as to build the required information base for a Sanctuary management plan and subsequent monitoring programmes.

(4) A Sanctuary management plan should clearly outline the broad strategies and specific actions needed to achieve Sanctuary objectives.

(5) A monitoring strategy that measures progress toward achieving the Sanctuary objectives should be developed and subsequently implemented. A key component of this monitoring strategy would be the development of tangible indicators to monitor progress.

(6) Review criteria that reflect the goals and objectives of the Sanctuary (as described above) should be established.

(7) The Sanctuary management plan should be refined periodically to account for ecological, oceanographic and possible other changes in an adaptive fashion.

In previous years, the Committee has received requests to review proposals for a South Atlantic Sanctuary and a South Pacific Sanctuary. There has been disagreement within the Committee over whether such Sanctuaries were justified scientifically. This year no proposals were received for review.

Faecal sampling using detection dogs to study reproduction and health in North Atlantic right whales (*Eubalaena glacialis*)

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ABSTRACT

Conservation and management of many cetaceans is hindered by the difficulty of acquiring samples from free-swimming individuals to obtain essential data on health, diet, reproduction and physiological impacts of environmental and anthropogenic stressors. This is particularly true for large whales, which are logistically difficult to live-capture for sampling. In North Atlantic right whales (*Eubalaena glacialis*), a significant decline in reproduction and health in the 1990s led to the application of faecal-based analyses to study stress and reproductive endocrinology, marine biotoxin exposure and prevalence of disease-causing protozoa. However, this approach was limited by low sample acquisition rates with opportunistic faecal (scat) collection methods. The work presented here evaluates the relative sampling efficiency of scent detection dogs trained to locate North Atlantic right whale scat versus opportunistic scat collection during photo-identification surveys. Three years of sample collection using both detection dogs and opportunistic methods are summarised. Faecal sample collection rates using detection dogs were over four times higher than opportunistic methods. The use of detection dogs for scat collection from free-swimming right whales has for the first time provided adequate numbers of samples for statistical analyses. The endocrine, disease, genetic and biotoxin studies currently being performed on these samples markedly improve the ability to address fundamental questions vital to effective conservation and management of highly endangered right whales.

KEY WORDS: SAMPLING STRATEGY; NORTH ATLANTIC RIGHT WHALE; HORMONES; REPRODUCTION; GENETICS; DISEASE

INTRODUCTION

Effective conservation and management of many cetaceans has been hindered by insufficient non-lethal methods to acquire data on feeding ecology, reproductive parameters, individual and population health and the physiological impacts of environmental and anthropogenic stressors (e.g. marine biotoxins, contaminants, global climate change). This has been particularly problematic for large whales, which are elusive and extremely difficult to live-capture for sampling of blood or tissues. While remote biopsy darting provides samples for genetic, contaminant and fatty acid analyses, the data that can be obtained from skin and blubber cores are limited.

A significant decline in reproduction and health in the western North Atlantic right whale population (*Eubalaena glacialis*) in the late 1990s raised concern among managers and researchers (Kraus *et al.*, 2001; Pettis *et al.*, 2004; Hamilton and Marx, 2005). In response, the International Whaling Commission (IWC) Workshops on the Comprehensive Assessment of Right Whales, and Status and Trends of Western North Atlantic Right Whales (IWC, 2001a; b) gave priority recommendations to develop methods for assessing health, stress and reproductive failure. Subsequently, a suite of faecal-based studies were validated and applied to northern right whales to assess the reproductive status of individual whales, and to study factors potentially affecting health and fecundity.

Measurement of faecal metabolites of steroid hormones has now been used to determine reproductive status of free-swimming right whales (Rolland *et al.*, 2005). That study showed that concentrations of reproductive hormone metabolites were reliable predictors of gender, pregnancy and lactation in females and sexual maturity in males. Current extensions to this work involve identifying individuals by creating genetic profiles using right whale DNA isolated from their faeces (R. Gillett, unpublished data) and measuring metabolites of adrenal hormones to assess relative stress levels (Hunt *et al.*, 2006). Faecal parasitology studies have shown that right whales have the highest prevalence of infection with potentially pathogenic protozoa (*Giardia* spp. and *Cryptosporidium* spp.) of any marine mammal yet examined (Hughes-Hanks *et al.*, 2005). In that study, over 70% of the faecal samples collected from right whales were *Giardia* spp. positive and 24% were positive for *Cryptosporidium* spp. Finally, faecal measurements of the paralytic shellfish poisoning (PSP) toxins produced by the ‘red tide’ organism *Alexandrium* showed that sampled right whales were being exposed to this potent neurotoxin by feeding. In some cases, toxin levels reached 0.5μg saxitoxin equivalents g^{-1} faeces, near the levels at which human advisories for shellfish are issued, although the biological effects on right whales remain unknown (Doucette *et al.*, 2006). All of these studies were derived from multiple assays of the same faecal (scat) samples where the individual whale can frequently be identified either photographically (by comparison with the North Atlantic Right Whale Catalogue; Hamilton and Martin, 1999) or genetically (by comparing scat DNA profiles to biopsy DNA profiles of known whales). Preliminary results show that at least 14 whales have been sampled more than once within a field season and/or in multiple years (R. Rolland, unpublished data). These studies represent the foundation of an individual-based profile of health and reproductive status, that when integrated with the Right Whale Catalogue, provide insights into population-based models of reproduction, health, mortality and trends.

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Despite the wealth of data available from these analyses, this approach has been restricted by the difficulty of opportunistically locating scat at sea, limiting the number of available samples. This led to evaluating the use of domestic dogs (*Canis familiaris*) professionally trained to detect wildlife scat (Wasser *et al.*, 2004) to increase sample collections from right whales. In terrestrial studies, detection dogs significantly increased scat collection rates from kit foxes (*Vulpes macrotis mutica*; Smith, D.A. *et al.*, 2003), grizzly (*Ursus arctos*) and black bears (*U. americanus*; Wasser *et al.*, 2004). In those studies, dogs located scat from targeted wildlife with 100% accuracy (based on genetic species confirmation), and increased sampling rates four-fold, compared to experienced human observers. This paper describes the use of detection dogs to locate faecal samples from right whales over three years. Faecal sampling efficiency of surveys with dogs is compared to opportunistic methods and species identity is confirmed genetically for a subset of samples.

METHODS

Study area and survey methods

This work was conducted during August and September, 2003-05 in the waters around Lubec, Maine (training) and in the Bay of Fundy, Canada (surveys), where right whales congregate seasonally to feed (Murison and Gaskin, 1989). Faecal sample collection surveys using detection dogs were conducted aboard a 6.4m boat with a global positioning system (GPS) chart plotter. The chart plotter was used to mark the location of tracklines and positions where dogs detected scent from right whale scat, and helped orient the boat relative to wind and tide direction to locate samples. The crew included one dog and three to four people (dog handler, driver, photographer/data recorder). In addition, opportunistic faecal sample collections occurred aboard a 9.0m vessel with a crew of six to eight people conducting standardised right whale photo-identification surveys.

Surveys used two detection dogs alternately in 2003 and 2004, and a single dog in 2005. Given the demands of working on a boat, dogs that had good physical stability, persistence in locating samples and a calm disposition were selected. Scat detection dog training follows techniques used for narcotic, search and rescue and bomb detection dogs (Wasser *et al.*, 2004). When the dog detects the targeted scent there is a characteristic change in behaviour (recognised by tense body posture and ear position), motivated by the expectation of a reward. Scent from right whale scat was added to these dogs' repertoires through initial exposure using a scent box (Wasser *et al.*, 2004), followed first by searches on land, then from the bow of a boat. Previously collected scat samples from male and female right whales of varied ages were used for training. Initial training occurred over a period of nine days, and 'refresher' work for both handlers and dogs occurred annually for one or two days prior to the start of each field season.

All surveys using dogs were conducted with a Beaufort sea state ≤3 and wind speeds ≤10 knots. Boat transects were conducted perpendicular to the wind direction at a speed of five to seven knots, downwind from aggregations of right whales or areas where right whales had been previously sighted. The dogs were positioned on the bow for the duration of the trial. On land, the dog leads the handler directly to the sample by following the scent cone along an increasing odour gradient. On the water, since the dog could not lead the handler, the helmsman steered according to the direction indicated by the dog (as interpreted by the handler) until the sample was located (Fig. 1). If the dog lost the scent during the approach, perpendicular transects were resumed until the dog's behaviour indicated that the vessel was back in the scent cone from the sample (Fig. 2). When faecal samples were successfully collected, the dog was rewarded immediately by playing with a tennis ball on a string.

Fig. 1. The dog handler signalling to the helmsman the direction to steer as indicated by the detection dog during a search for a right whale scat sample.

Sample collection

Floating pieces of clumped right whale scat were collected using a 300μm nylon dipnet (Sea-Gear Corp., Melbourne, Florida, USA; Rolland *et al.*, 2005). Scat samples were identified in the field by size, shape, brown-orange colour, characteristic odour and presence of fine baleen hairs. Salt water was drained off the faeces, samples were stored in polypropylene jars and placed on ice until frozen at −20°C for subsequent analyses. The date, time and position of collection were recorded for each sample. When defecation was witnessed, the whale was photographed for subsequent photo-identification analysis (Kraus *et al.*, 1986).

Comparison of sample collection methods

The sampling efficiency of the detection dog surveys was calculated by dividing the number of faecal samples collected per day by the total time that the dog was working. Hours of dog survey effort were defined as the total time the dog was working 'on watch' during transects. These results were compared with opportunistic faecal sample collections made during right whale photo-identification surveys. Opportunistic collections occurred when whales were observed defecating at the surface or observers detected scat by odour. Hours of opportunistic effort were defined as the time observers were 'on watch' between the first and last whale photographed that day. Samples collected per hour of survey effort were calculated over three years (2003-05). Comparisons between opportunistic surveys and detection dog surveys were only made on days when both vessels were working to control for variability in weather conditions and whale density.

Data analysis was performed using *SPSS* 13.0 (SPSS Inc., Chicago, Illinois, USA). The data were not normally distributed, thus non-parametric tests were used. Differences

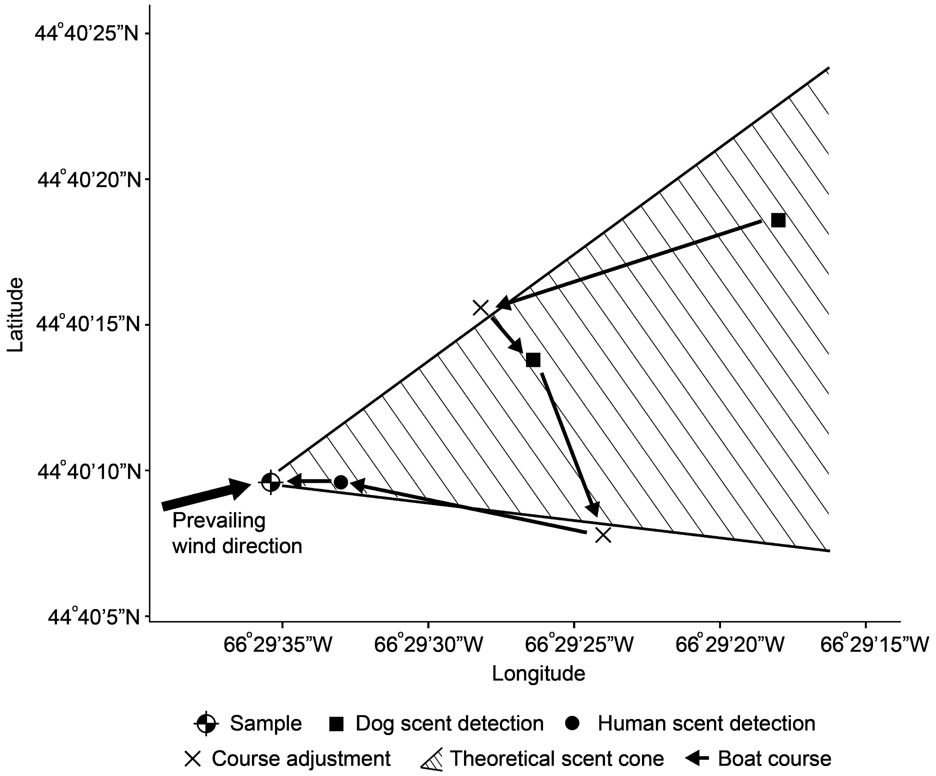

Fig. 2. An example of the search pattern the research vessel followed (→) to locate a right whale scat sample with a detection dog. As the vessel enters the scent cone coming from the sample (striped area), the dog detects the odour (■) as indicated by a change in the dog's ear set and body position, prompting the boat driver to steer into the wind. The dog loses the odour when the vessel leaves the scent cone (X). The vessel then resumes a transect perpendicular to the wind until the dog has another detection, turning into the wind again to find the sample. The human crew smelled the sample just before it was collected (●). The distance from the first scent detection by the dog to the final position of sample collection was ~0.5km.

were considered significant if $p<0.05$. The number of samples collected per day and the sampling efficiency using detection dogs were compared to results from opportunistic collection methods using a Mann-Whitney U test. Differences in sampling efficiency between years were analysed for each method separately using the Kruskal-Wallis test. The detection distance for each sample located by the dogs was estimated by calculating the distance between the GPS positions of the first observed change of behaviour (indicating scent acquisition) and the location of sample collection. These are estimates of distance because tidal motion may have moved the scat (closer or farther depending on the stage) relative to the location of the dog's first detection.

Genetic analyses

Species identity was determined genetically for 54 samples collected in 2003 by extraction and amplification of mitochondrial control region DNA. DNA was extracted in duplicate from frozen, lyophilised faecal samples using a modified Qiagen DNeasy extraction protocol (Qiagen, Valencia, CA). Nucleic Acid Purification Grade Lysis Buffer (1X, 1.6ml; ABI) was added to ~70-90mg of the each sample, then samples were vortexed (1min) and incubated (65°C, 1hr). Following incubation, 25μl Proteinase K (>600mAU ml^{-1}; Qiagen) and 600μL AL buffer (Qiagen) were added. Tubes were inverted and incubated for an additional hour. Ethanol was added (100%, 600μl), the tubes were mixed, and the contents were run through a silica spin column. Samples were washed and eluted following steps four through seven of the Qiagen DNeasy protocol, incubated (65°C, 10min) to evaporate any residual ethanol and frozen at −20°C.

The mitochondrial control region was amplified using the polymerase chain reaction (PCR) with the primers UP098 and LP282 (Malik *et al.*, 2000; Rastogi *et al.*, 2004). Amplification consisted of a 25μl reaction (0.3mg bovine serum albumin, 1X PCR Buffer, 0.2μM of dNTP mix, 2μM magnesium chloride, 0.3μM each primer, 0.1U *Taq* DNA polymerase and ~1.5ng template DNA) with the following cycling conditions: 94°C for 5min; 50 cycles of 94°C for 30s, 52°C for 60s, 72°C for 60s; 60°C for 45min. Extraction and PCR negative controls were included to test for contamination.

RESULTS

Results from the detection dog and photo-identification surveys were compared for 19 days (2003-05) on which both detection dog and opportunistic survey vessels were working. Detection dog surveys located significantly more samples (n=97) compared to the opportunistic method (n=30; Mann-Whitney U test, Z=-3.418, $p<0.001$). Detection dogs located many scat samples in areas where the human crew did not observe whales in close proximity. The mass of faeces collected varied from approximately 20g to 0.5kg or more. Mean sampling efficiency of the detection dog surveys from 2003-05 was 1.1 samples hr^{-1} (range: 0.80 to 1.43 samples hr^{-1}), significantly greater than 0.25 samples hr^{-1} (range: 0.15 to 0.32 samples hr^{-1}) for opportunistic surveys (Table 1; Mann-Whitney U=5.000, Z=-5.129, p<0.001). Although the sampling efficiency of both methods appeared to be higher in 2005 (Table 1), there were no significant differences between years for either method, indicating consistency in the survey methodologies.

Table 1

Comparison of yearly and overall faecal sample collection rates from right whales (2003-05) using opportunistic methods or detection dogs trained to locate samples. Sampling efficiency using detection dogs was significantly higher than opportunistic sample collection during photo-identification surveys (p<0.001). There is no significant difference in sample collection rates between years for either method.

	Samples collected per hour	
Year(s)	Opportunistic	Detection dogs
2003	0.15	1.07
2004	0.28	0.80
2005	0.32	1.43
Overall 2003-05	0.25	1.10

Estimated detection distances for the dogs ranged 22m to 1.93km (just over one nautical mile). In 2003, the only year that this was measured, humans detected seven samples (by smell) at 56-359m, while the dogs detected the same samples at 150-563m. All faecal samples found by the dogs and humans in 2003 have been confirmed to be from right whales by mitochondrial DNA analyses, and the remainder are currently undergoing analysis.

Statistical comparisons only included a subset of samples collected on days when both research vessels were working in the Bay of Fundy. Another 72 faecal samples were obtained between 2003-05 on other survey days, in other habitats or by other vessels in the Bay of Fundy (total samples from 2003-05 = 199). Prior to using detection dogs (1999-2002), an additional 86 samples were collected opportunistically, bringing the total samples for all faecal-based studies to 285. All samples were collected for reproductive and stress hormone analyses. In many cases sufficient faecal material was collected to allow for sub-dividing of samples for multiple assays, so that 128 of these samples are also being examined for marine biotoxins, and 111 for parasites. Additionally, all samples will eventually be characterised genetically using mitochondrial and nuclear markers to confirm the species of origin and determine individual whale identity.

DISCUSSION

These results demonstrate that scat detection dogs can work from boats to dramatically increase faecal sampling rates from free-swimming right whales. Sampling efficiency of detection dogs was over four times higher than opportunistic collection methods over a three-year period. In addition, dogs detected samples from as far as one nautical mile away, greatly increasing the area that can be sampled. The success of this method depended upon the involvement of a professional dog trainer, an experienced handler and dogs and a boat driver with intimate knowledge of the local tide and wind patterns. It also involved use of a dedicated vessel for detection dog surveys, because of methodological conflicts between visually-based photo-identification surveys and detection dog survey protocols. Nevertheless, using dogs to collect large numbers of scat samples from right whales has significantly increased sample sizes, enhancing the utility of the diversity of faecal analyses in quantitatively assessing this population's status.

These assays and faecal collection methods are potentially useful in multiple species, and can address a wide array of questions. Faeces have been collected opportunistically from bottlenose dolphins (*Tursiops truncatus*) for genetic studies (Parsons *et al.*, 2003), sperm whales (*Physeter macrocephalus*) for feeding ecology research (Smith and Whitehead, 2000), blue whales (*Balaenoptera musculus*) and humpback whales (*Megaptera novaeangliae*) to study marine biotoxin exposure (Lefebvre *et al.*, 2002) and North Atlantic right whales for environmental toxicology (Weisbrod *et al.*, 2000). Faecal analyses provide estimates of exposure to synthetic chemicals and biotoxins, both issues of concern to cetaceans worldwide because of increasing human impacts on the marine environment.

In addition to the assays described here, DNA markers from prey species in scat are being used in cetaceans to identify dietary components and diversity to understand marine food webs with more accuracy than previous work relying on analysis of hard parts of prey in faeces or stomach contents (e.g. Jarman *et al.*, 2002). Recent advances in extraction and amplification of host nuclear and mitochondrial DNA from scat samples permits PCR-based studies using genetic markers to determine species, sex and individual identity (Wasser *et al.*, 2004). Although faecal DNA tends to be more degraded than that obtained by biopsy, in this study 100% of the faecal samples analysed yielded sufficient DNA for species determination.

Many cetaceans are at-risk or poorly studied, and researchers require physiological and biomedical data to assess population health and reproductive status. Such information is not easily obtained using conventional methods. Enhanced sampling of cetacean scat by using detection dogs, coupled with endocrine, toxicological and molecular analyses, opens a new window into the physiology, health and genetic status of free-swimming whales that can contribute greatly to their conservation and management.

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Assessing the Bering-Chukchi-Beaufort Seas stock of bowhead whales using abundance data together with data on length or age

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ABSTRACT

The 1998 assessment of the Bering-Chukchi-Beaufort (B-C-B) Seas stock of bowhead whales (*Balaena mysticetus*) was conducted using a Bayesian estimation framework. That assessment ignored information on the length-frequency and age-composition of the harvests and the detailed length-frequency information from photogrammetry studies. The modelling framework used to assess the B-C-B Seas bowhead whales is therefore extended to make use of these data. The results indicate that selectivity is not uniform, as assumed in previous assessments, but rather domed-shaped, with young animals most vulnerable to harvest. The length-frequency, proportion, age-composition and abundance data are inconsistent to some extent. Fitting the model to the age-composition data leads to the most pessimistic estimates of stock status and productivity. The results of projections based on these assessments in which strike limits are set using the *Bowhead Strike Limit Algorithm* (*SLA*) suggest that none of the data sets are such that the scenarios considered when testing the *Bowhead SLA* should now be considered implausible.

KEYWORDS: BOWHEAD WHALE; ARCTIC; ABORIGINAL WHALING; AGE DATA; LENGTH DATA; MODELLING; ABUNDANCE ESTIMATE

INTRODUCTION

The 1998 assessment of the Bering-Chukchi-Beaufort (B-C-B) Seas stock of bowhead whales (*Balaena mysticetus*) was based on fitting the age- and sex-structured population dynamics model, Baleen II (de la Mare, 1989; Punt, 1999b), to data on population counts and the proportion of calves and mature animals in the population in 1988/89 (IWC, 1999). This assessment was based on Bayesian techniques, using the 'backwards' (Butterworth and Punt, 1995; Punt and Butterworth, 1999) and 'full pooling' (Poole and Raftery, 1998) methods.

The Scientific Committee (SC) of the International Whaling Commission (IWC) has recommended a *Strike Limit Algorithm* (*SLA*) for the B-C-B Seas stock of bowhead whales (IWC, 2003a). This implies that it is no longer necessary to conduct regular traditional stock assessments to provide management advice for setting catch limits. However, it is nevertheless worthwhile to continue to conduct assessments to evaluate whether the scenarios on which the *Bowhead SLA* was based remain plausible given the implications of recent data and analyses.

In this context, there are several potential sources of information that have not been included explicitly in recent assessments of the B-C-B Seas bowhead whales. In particular: (1) the information on length-at-age (George *et al.*, 1999; J. Zeh, pers. comm.); (2) the length-frequency of the early harvests (e.g. Bockstoce and Botkin, 1983; Bockstoce and Burns, 1993); (3) the length-frequency of the recent harvests (e.g. Braham, 1995; Punt *et al.*, 2003; Suydam and George, 2004; George, pers. comm.); (4) the length-frequency of the population in recent years (e.g. Angliss *et al.*, 1995; Koski *et al.*, 2006); and (5) the estimates of abundance from photogrammetry (e.g. da Silva *et al.*, 2000; Schweder, 2003) were not included in the likelihood function used when estimating model parameters during the 1998 assessment.

Some of these data have been examined before. For example, George *et al.* (1999) speculated that the 'gap' in the age-frequency distribution (roughly between ages 70 and 135) may be due to the large removals during the period of commercial whaling (approximately 1848–1910). Additionally, Bockstoce and Burns (1993) noted that 'the largest whales were taken in the earliest years of the fishery, although paradoxically, one or two very big whales were taken in the last years', and Schweder and Ianelli (2000) noted that the formulation of the Baleen II model applied for the 1998 assessment is unable to mimic the age-frequency data adequately. Schweder (2003) noted that the estimate of abundance based on the photo-identification data is consistent with the estimates of abundance from visual and acoustic methods. The analyses of this paper do not use the photo-identification estimate of abundance as it is only a single datum. Likewise, the early length-frequency information is ignored because lengths[1] are available for only 333 of the 3,198 animals in the database constructed by Bockstoce and Botkin (1983).

Schweder and Ianelli (2000), in common with all assessments of the B-C-B bowhead stock in recent years, assumed that the harvest is taken randomly from the animals aged one and older. In contrast, Punt *et al.* (2003) showed that the length-frequency of the catch varies by village and that the fraction of the catch taken by each village has changed over time.

Age- and length-composition data are used in conventional fisheries stock assessments for two main reasons: (a) to estimate the strength of recent cohorts; and (b) to determine the selectivity pattern of the harvest[2]. The sample sizes for the B-C-B Seas bowhead whales are much too small to expect that it will be possible to estimate even patterns in historical recruitment adequately. However, the length-frequency information can potentially inform assumptions regarding the selectivity pattern of the harvest. This paper therefore develops a variant of the Baleen II model that can include age- and length-composition data as well as proportion and abundance data in a single modelling framework and in which the selectivity pattern of the harvest need not be uniform above some pre-specified age. The

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[1] Actually the number of barrels of oil produced.

[2] Selectivity in this context is the combined effect of hunter behaviour and the availability of whales of different sizes/ages to the hunters.

estimation is based on the ‘backwards’ approach to Bayesian analysis which was used for the 1998 assessment of the B-C-B Seas bowhead whales and on which the trials used to evaluate alternative *SLAs* for this stock were conditioned (e.g. IWC, 2003a).

METHODS

Basic formulation

Each data source is included separately in the assessment using a length-based Synthesis approach (Smith and Punt, 1998; Methot, 2000). The population dynamics model underlying the analyses is identical to the standard Baleen II model, except that account is taken of length-specific selectivity. The probability of harvesting an animal of age *a* and sex *s* during year *y*, $p^s_{y,a}$, depends on the relative frequency of animals of age *a* and sex *s* in the population and the selectivity on animals of age *a* and sex *s*, i.e.:

$$p^s_{y,a} = \frac{S^s_a N^s_{y,a}}{\sum_{a'} S^s_{a'} N^s_{y,a'}} \qquad (1)$$

where

$N^s_{y,a}$ is the number of animals of age *a* and sex *s* at the start of year *y*,

S^s_a is selectivity as a function of age and sex (S^s_0 is set equal to zero for all of the analyses of this paper to reflect the fact that calves are not harvested):

$$S^s_a = \frac{\sum_L S_L X^s_{a,L}}{\max_{a'} \sum_{L'} S_{L'} X^s_{a',L'}} \qquad (2)$$

S_L is selectivity as a function of length,

$X^s_{a,L}$ is the proportion of animals of sex *s* and age *a* in length-class *L* i.e.:

$$X^s_{a,L} = \int_{\bar{L}-\Delta L}^{\bar{L}+\Delta L} \frac{1}{\sqrt{2\pi}\sigma^s \ell} \exp\left(-\frac{(\ell n \ell - \ell n \ell^s_a)^2}{2(\sigma^s)^2} \right) d\ell \qquad (3)$$

$\bar{L}$ is the average of the upper and lower limits of size-class *L*,

ΔL is half the width of a length-class (taken here to be 25cm),

ℓ^s_a is the length of a bowhead of age *a* and sex *s* and

σ^s is (approximately) the coefficient of variation of length-at-age for animals of sex *s*.

Data to estimate selectivity-at-length are only available for recent years, so selectivity is assumed to be uniform for the period 1848–1914.

Length-at-age for animals aged 1 and older is based on the Schnute (1981) formulation i.e.:

$$\ell^s_a = \left((\ell^s_1)^{\beta^s} + ((\ell^s_{40})^{\beta^s} - (\ell^s_1)^{\beta^s}) \frac{1-\exp[-\kappa^s(a-1)]}{1-\exp[-\kappa^s 39]} \right)^{1/\beta^s} e^{\varepsilon}$$

$$\varepsilon \sim N(0;(\sigma^s)^2) \qquad (4)$$

where

κ^s is a growth rate parameter for animals of sex *s*,

β^s is a shape parameter for animals of sex *s* and

σ^s determines the extent of variation about the mean length-at-age for animals of sex *s*.

The estimable parameters of this growth model are the lengths at ages 1 and 40 (ages chosen to encompass the bulk of the ages represented in the length-at-age data set), κ, β and σ. The mean length of a calf is set to 4.54m, the mean length of calves in the data set analysed by Koski *et al.* (2006). This assumption is, however, inconsequential for the analyses of this paper because the population dynamics model is fitted to data for animals aged 1 and older only.

The values for the parameters of Eq. (4) are determined by maximising the following likelihood function:

$$L = \prod_s \prod_a \prod_i \frac{1}{\sqrt{2\pi}\sigma^s \tilde{L}^{s,i}_a} e^{-\frac{(\ell n \tilde{L}^{s,i}_a - \ell n \ell^s_a)^2}{2(\sigma^s)^2}} \qquad (5)$$

where

$\tilde{L}^{s,i}_a$ is the observed length of the *i*th animal of age *a* and sex *s* in the data set on length-at-age.

The measurements of the lengths of animals in the catch (and hence in the data set on which the growth model is based) exceed the actual lengths of these animals owing to the impact of stretching. Therefore, when fitting the growth model (and for all other uses of the catch length data), the lengths are multiplied by 0.918 (George *et al.*, 2004a).

Likelihood function

As noted above, there are several potential sources of data that could be used in an assessment of the B-C-B Seas stock of bowhead whales. The data used in the analyses of this paper are: (a) the annual catches (Table 1); (b) the estimates of abundance from visual and acoustic surveys at Point Barrow, Alaska (Table 2); (c) the information on the fraction of calves and mature animals in the population in 1988-89[3]; (d) the length-frequency from the surveys during 1985-1994; and (e) the age-composition of the catches during 1973-92.

The indices of abundance are based on data collected from visual and acoustic surveys at Point Barrow, Alaska (see George *et al.*, 2003; 2004b for a brief summary of the history and methods of the studies). Estimates of the number of animals passing within the 4km visual range from the observation ‘perch’ from which whales are counted are combined with estimates of the proportion of whales which passed within this range using a model in which the proportion within visual range is treated as a random effect (Zeh and Punt, 2005). The contribution of the abundance data to the negative of the logarithm of the likelihood function (ignoring constants independent of the model parameters) is:

$$-\ell n L_1 = 0.5 \sum_{y_1} \sum_{y_2} (\ell n \hat{N}_{y_1} - \ell n N^{obs}_{y_1})^T \Sigma^{-1}_{y_1,y_2} (\ell n \hat{N}_{y_2} - \ell n N^{obs}_{y_2}) \qquad (6)$$

where

N^{obs}_y is the N_4/P_4 estimate for year *y*,

$\hat{N}_y$ is the model estimate of 1+ abundance for year *y*[4] and

Σ is the variance-covariance matrix for the logarithms of the estimates of abundance.

[3] The data used actually relate to the period 1985-94, but are fitted to the model predictions for 1988-89. This is appropriate given the slow dynamics of the B-C-B Seas bowhead stock.

[4] The estimates of N_4/P_4 actually include some, but not all, calves. Sensitivity tests (not shown here) indicate that the results of assessments are not sensitive to whether the N_4/P_4 estimates are treated as indices of 0+ or 1+ abundance.

Table 1

B-C-B Seas bowhead whale kill, 1848-2004. Values in parenthesis are the catches used in the 1998 assessment where these catches differ from those used in the present assessment.

Year	Total kill	Year	Total kill	Year	Total kill	Year	Total kill
1848	18	1888	160	1928	30	1968	27
1849	573	1889	127	1929	30	1969	32
1850	2,067	1890	136	1930	17	1970	48
1851	898	1891	284	1931	32	1971	25
1852	2,709	1892	346	1932	27	1972	44
1853	807	1893	180	1933	21	1973	51
1854	166	1894	234	1934	21	1974	42
1855	2	1895	117	1935	15	1975	32
1856	0	1896	118	1936	24	1976	74
1857	78	1897	130	1937	53	1977	72
1858	461	1898	309	1938	36	1978	15
1859	372	1899	234	1939	18	1979	20
1860	221	1900	148	1940	20	1980	32
1861	306	1901	55	1941	38	1981	26
1862	157	1902	162	1942	26	1982	14
1863	303	1903	116	1943	14	1983	16
1864	434	1904	86	1944	8	1984	16
1865	590	1905	105	1945	23	1985	14
1866	554	1906	69	1946	20	1986	22
1867	599	1907	96	1947	21	1987	29
1868	516	1908	123	1948	8	1988	28
1869	382	1909	61	1949	11	1989	25
1870	637	1910	37	1950	23	1990	41
1871	138	1911	48	1951	23	1991	47
1872	200	1912	39	1952	11	1992	46
1873	147	1913	23	1953	41	1993	51
1874	95	1914	61	1954	9	1994	39 (38)
1875	200	1915	23	1955	36	1995	56 (57)
1876	76	1916	23	1956	11	1996	42 (45)
1877	270	1917	35	1957	5	1997	62
1878	80	1918	27	1958	5	1998	51
1879	266	1919	33	1959	2	1999	47
1880	480	1920	33	1960	33	2000	42
1881	435	1921	9	1961	17	2001	65
1882	242	1922	39	1962	20	2002	45
1883	42	1923	12	1963	15	2003	37
1884	160	1924	41	1964	24	2004	43
1885	377	1925	53	1965	14		
1886	168	1926	35	1966	24		
1887	240	1927	14	1967	12		

The summations in Eq. (6) are restricted to the years for which estimates of N_4/P_4 are available (Table 2).

The age-composition of the catches for 1973-1992 (Table 3) is assumed to be multivariate normally distributed about the model predictions (Schweder and Ianelli, 2000). Schweder and Ianelli (2000) constructed the age-compositions in Table 3 by first modelling the relationship between length and age based on data for 42 bowhead whales reported in George *et al.* (1999) and then allocating the observed lengths in the catch from 1973-92 (Braham, 1995) to ages using this relationship. The uncertainty associated with the age-compositions was determined by bootstrapping the construction of the age-at-length data. There are, however, some concerns with the basis for the age-composition information provided by Schweder and Ianelli (2000) as detailed below.

(1) Schweder and Ianelli (2000) ignored sex when constructing their age-compositions because George *et al.* (1999) did not identify a statistically significant difference between male and female growth. However, the sample size available to George *et al.* (1999) to estimate growth (42 animals) was small in comparison to the age-length data set on which the analyses of this paper was based. This larger sample size supports different growth curves for males and females. One consequence of ignoring sex when creating the age-composition data was that the fraction of very old (100+) animals was over-estimated (all animals aged to be 100+ were males; the two oldest females were 38 and 69 respectively);

(2) Schweder and Ianelli (2000) mis-interpreted the meaning of animals in George *et al.* (1999) that had negative standard errors.

The age-compositions reported by Schweder and Ianelli (2000) have not been updated for this paper because a primary reason for conducting the analyses reported herein, was to determine the reasons for the inability of the Baleen II model to mimic these data.

Studies attempting to document the length structure of B-C-B Seas bowhead stock using photographic survey methods were conducted near Point Barrow, primarily by scientists from the National Marine Mammal Laboratory, but also by other researchers (Withrow and Angliss, 1992; 1994; Angliss *et al.*, 1995). The surveys were conducted from about mid-April to early June in 1985, 1986 and 1989-92. Less extensive spring surveys were conducted in 1989 and during 1994. A variety of papers have documented the

Table 3

Age-composition data (fraction of the catch in each of six age-groups). Source: Schweder and Ianelli (2000).

Age-range	Estimate	SE	Correlation matrix					
0-20	0.667	0.029	1	-0.55	-0.56	-0.88	-0.83	-0.30
21-40	0.110	0.018	-0.55	1	0.64	0.44	0.06	-0.54
41-60	0.073	0.008	-0.56	0.64	1	0.71	0.25	-0.49
61-80	0.053	0.006	-0.88	0.44	0.71	1	0.76	0.11
81-100	0.035	0.005	-0.83	0.06	0.25	0.76	1	0.62
100+	0.063	0.019	-0.30	-0.54	-0.49	0.11	0.62	1

Table 2

Estimates, CVs (actually standard errors of the logarithms) and the correlation matrix for the indices of abundance for the B-C-B Seas stock of bowhead whales. Source: Zeh and Punt (2005).

Year	Estimate	CV	Correlation matrix										
1978	4,765	0.305	1.000										
1980	3,885	0.343	0.118	1.000									
1981	4,467	0.273	0.056	0.050	1.000								
1982	7,395	0.281	0.094	0.084	0.035	1.000							
1983	6,573	0.345	0.117	0.104	0.049	0.084	1.000						
1985	5,762	0.253	0.070	0.062	0.020	0.078	0.062	1.000					
1986	8,917	0.215	0.072	0.064	0.017	0.092	0.064	0.113	1.000				
1987	5,298	0.327	0.124	0.110	0.052	0.088	0.110	0.065	0.067	1.000			
1988	6,928	0.120	0.028	0.025	0.013	0.017	0.024	0.009	0.007	0.026	1.000		
1993	8,167	0.071	0.001	0.001	0.001	0.000	0.001	-0.001	-0.002	0.001	0.000	1.000	
2001	10,545	0.128	0.008	0.007	0.005	0.001	0.007	-0.004	-0.008	0.008	0.003	0.000	1.000

methods employed (e.g. Koski *et al.*, 2006), but briefly the surveys were conducted from fixed-wing aircraft with search effort focused along open water areas, especially near the land-fast ice edge. A variety of ways exist for analysing the data from these surveys. Two of these are considered in this paper: (a) the approach of Angliss *et al.* (1995); and (b) the 'base case' analysis of Koski *et al.* (2006)[5]. The length-frequency data can be included in the assessment either as the actual length-frequency (Fig. 1) or as the proportion of calves and mature animals (Table 4). The 1998 assessment was based on the second of these alternatives only.

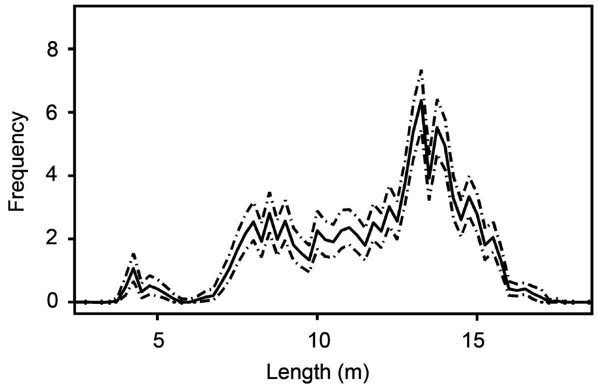

Fig. 1. The photogrammetry-based length-frequency distribution. The lengths are grouped in 25cm length bins. The solid lines denote the estimates on which the analyses of this paper are based and the dashed lines are bootstrap 95% confidence intervals.

Table 4

Proportion of calves and mature animals.

Scenario	P_c	σ_{p_c}	P_m	σ_{p_m}
Koski *et al.* (2006)	0.0339	0.0040	0.3975	0.0100
1998 assessment (IWC, 1998)	0.052	0.0164	0.411	0.0286

The contribution of the fraction of the population that consists of calves and mature animals ('the proportion data') to the negative of the logarithm of the likelihood function is based on the assumptions that these fractions are normally-distributed (Koski *et al.* (2006) data) or *t*-distributed (Angliss *et al.*, 1995 data) i.e.:

$$-\ell n L_2 = \frac{1}{2\sigma_{p_c}^2}(p_c - p_c^{obs})^2 + \frac{1}{2\sigma_{p_m}^2}(p_m - p_m^{obs})^2 \tag{7a}$$

$$-\ell n L_2 = \frac{6}{2}\ell n(1 + \frac{1}{5}\{\frac{p_c - p_c^{obs}}{\sigma_{p_c}}\}^2) + \frac{6}{2}\ell n(1 + \frac{1}{5}\{\frac{p_m - p_m^{obs}}{\sigma_{p_m}}\}^2) \tag{7b}$$

where

p_c^{obs}	is the observed fraction of the population that consisted of calves in 1988/89[3],
σ_{p_c}	is the standard deviation of p_c^{obs},
p_c	is the model-estimate of the fraction of the population that consisted of calves in 1988/89,
p_m^{obs}	is the observed fraction of the population that consisted of mature animals in 1988/89[3],
σ_{p_m}	is the standard deviation of p_m^{obs} and
p_m	is the model-estimate of the fraction of the population that consisted of mature animals in 1988/89.

The survey length-frequency data are assumed to be multinomially distributed about the model predictions i.e.:

$$-\ell n L_3 = -\omega \sum_L \rho_L \ell n(\hat{\rho}_L / \rho_L) \tag{8}$$

where

ω	is the effective sample size,
ρ_L	is the observed fraction of the length-frequency distribution that is in (25cm) length-class L (Fig. 1) and
$\hat{\rho}_L$	is the model-estimate of the fraction of the length-frequency distribution that is in length-class L i.e.:

$$\hat{\rho}_L = \frac{\sum_{y=1985}^{1994} \sum_s \sum_{a>1} X_{a,L}^s N_{y,a}^s}{\sum_{y'=1985}^{1994} \sum_{s'} \sum_{a'>1} N_{y',a'}^{s'}} \tag{9}$$

The base-case value for ω is taken to be 2,000 which corresponds roughly to the effective sample size of the proportion-at-length data in Koski *et al.* (2006).

Parameters and priors

The parameters of the population dynamics model are: (a) the total (1+) pre-exploitation size of the resource, K_{1+}; (b) $MSYR_{1+}$; (c) $MSYL_{1+}$; (d) the age-at-sexual-maturity, a_m; (e) the survival rate of adults in the absence of exploitation, $s_{adult} = \exp(-M_{adult})$; (f) the survival rate of juveniles in the absence of exploitation, $s_{juv} = \exp(-M_{juv})$; and (g) the greatest age at which juvenile natural mortality applies, a_T. Rather than placing a prior on s_{juv}, a prior is instead placed on the pregnancy rate in the limit of zero population size, f_{max} and the system of equations that relate f_{max}, $MSYR_{1+}$, $MSYL_{1+}$, s_{juv}, and s_{adult} is solved for s_{juv} and the parameters of the density-dependence function (see Punt (1999b) for details). If the value for s_{juv} is larger than that for s_{adult}, the set of parameters is ignored (implemented by assigning the parameter vector a likelihood of zero).

A prior is not placed on K_{1+}. Instead, a prior is placed on the 1993 1+ population size and the value for K_{1+} calculated so that if the population is projected from unexploited equilibrium in 1848 to 1993, the 1993 1+ population size equals the generated value for N_{1993}^{1+}. This 'backwards' approach to parameterising the Baleen II model formed the basis for the 1998 assessment of the B-C-B bowhead stock.

In principle, selectivity-at-length could be estimated as part of the model-fitting process. However, this would make the calculations prohibitively time consuming given the approach used to sample parameter vectors from the posterior distribution (the Sample-Importance-Resample, SIR, algorithm). Instead, selectivity-at-length is pre-specified using the length-frequency of recent harvests and the length-frequency of the surveys conducted at Point Barrow. Specifically, the length-specific selectivity pattern on which the analyses are based is determined by taking the ratio of the numbers caught (in 1m length-classes) to the

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[5] Koski *et al.* (2006) provide several length-frequency distributions based on varying the assumptions of their analysis method. Results (not shown here) indicate that the outcomes from the assessment are not notably sensitive to changing these assumptions.

numbers observed during the surveys (also in 1m length-classes) i.e.:

$$S_L = \frac{C_L / V_L}{\max\limits_{L'}(C_{L'} / V_{L'})} \tag{10}$$

where

C_L is the total catch of animals in 1m length-class L during 1984-95 (the years that encompass those on which the length-frequency distributions are based) (Fig. 2) and

V_L is the fraction of the numbers observed during the surveys in 1m length-class L, based on the surveys conducted during 1985-94 (see Fig. 1).

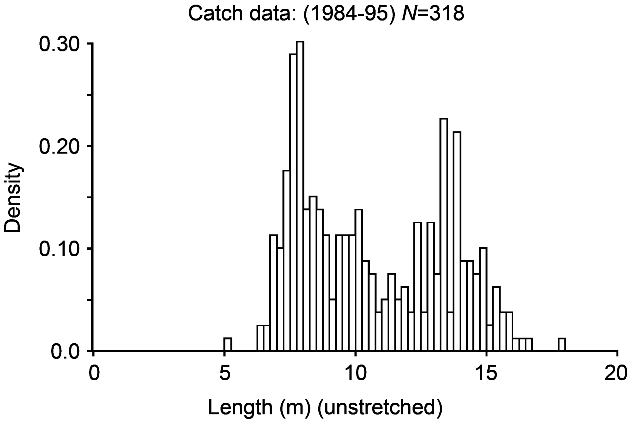

Fig. 2. The catch length-frequency distribution used when defining selectivity-at-length.

Table 5

The prior distributions (IWC, 1998).

Parameter	Prior distribution
$MSYL_{1+}$	U[0.4, 0.8][a]
$MSYR_{1+}$	U[0.01, 0.7][b]
a_T	DU[1, 9][c]
a_m	N(20,3^2), truncated at 13.5 and 26.5[d]
S_{adult}	N(1.059, 0.0378^2) truncated at 0.995 with no constraint on the maximum age[e]
S_{juv}	Constrained by the population dynamics equation to be less than S_{adult}
$f_{\max}$	$1/f_{\max} \sim$ U[2.5, 4][f]
N^{1+}_{1993}	N(7,800, 1,300^2)[g]

[a] Selected to encompass the range of values commonly assumed when conducting assessments of cetacean populations.

[b] Based on reported estimates of the current rate of increase (ROI) for cetacean populations (IWC, 1994); the upper limit is somewhat lower than the upper confidence limit for ROI, while the lower limit is consistent with the range of values used to develop the Aboriginal Whaling Management Procedure.

[c] Selected by the Scientific Committee (SC) of the IWC (IWC, 1995) although there is little information on the value of this paper (Givens *et al.*, 1995).

[d] Based on a best estimate of 20 years and lower confidence intervals for the age-at-maturity of 14 years (IWC, 1995).

[e] See main text for details.

[f] Selected by the SC of the IWC (IWC, 1995).

[g] Selected by the SC of the IWC (IWC, 1995) based on the prior distribution assumed for the Bayes empirical Bayes estimate of abundance (Raftery and Zeh, 1991).

Table 5 lists the priors on which the analyses of this paper are based. These priors are the same as those used for the 1998 assessment, except that the prior placed on the survival rate of adults is set to a truncated normal distribution that mimics the posterior distribution for adult survival rate obtained by Zeh *et al.* (2002). Assuming a maximum survival rate of 0.995 (corresponding to an average age of 200) leads to the prior for adult survival of $N(1.059, 0.0378^2)$ bounded between 0 and 0.995. The 1998 assessment included a case in which there was a maximum lifespan of 100 years (IWC, 1999; Punt, 1999a). However, this case is considered implausible given that the age-composition data include animals aged to be 100+ (Table 3).

Scenarios

Table 6 lists the scenarios considered in this paper. None of the analyses that involve fitting to the survey length-frequency data also involve fitting to the proportion data because the proportion data are based on the survey length-frequency data (see Koski *et al.*, 2006). Similarly, analyses that use the age-composition data ignore the length-frequency data and the proportion data.

RESULTS AND DISCUSSION

Growth curve estimation

The estimates of the values for the parameters of the growth model are listed in Table 7. The results in Table 7 are based on the full (10-parameter, 5 parameters per sex) model. The decision to base the growth curves on which the assessment is based on the full model was supported by application of likelihood ratio tests in which various sub-models were compared; all of the sub-models provided fits that were significantly poorer than the full model at the 5% significance level. Fig. 3 shows the fit of the growth model to the data on length-at-age and Fig. 4 shows the length-at-age distributions obtained using Eq. (4) and the estimates of the parameters of the growth model in Table 7. As expected, the 95% confidence intervals for the data encompass the bulk of the data and the solid lines mimic the central tendency of the data well.

Length-specific selectivity

Selectivity-at-length (Fig. 5) is defined using 1m length-classes even though the population dynamics model uses 25cm size-classes. This is because the sample sizes for some of the 25cm size-classes are very small (see Figs 1 and 2), which would have resulted in highly variable (and hence unrealistic) estimates of selectivity-at-length. The survey and catch length-frequencies are pooled into minus- and plus-groups at 8m and 16m respectively. This reduces the impact of growth during the first years of life and also avoids fitting the model to very small proportions.

Selectivity-at-length is greatest for the smallest (and hence youngest) animals and is relatively constant for animals from 12m. Selectivity-at-length (and hence selectivity-at-age) is markedly different from the ‘uniform from age one’ assumption that underlies past stock assessments of this stock, and most other stocks, of baleen whales, and as well as the operating model used to evaluate *SLAs* for the B-C-B Seas bowhead whales.

Assessment results

Comparison of models that account for and ignore length-specific selectivity

Alternative models for the B-C-B bowhead whales have, in the past, been compared using Bayes factors (Brandon and Wade, 2006). This approach is used to compare models based on the two selectivity patterns. According to the guide to interpreting Bayes factors developed by Kass and Raftery (1995), there is ‘positive’ support (Bayes Factor >3 but <20) for the analysis in which selectivity is based on Fig. 5 when

Table 6

The data-scenarios considered in the analyses of this paper.

Abbreviation	Abundance data	Koski *et al.* (2006) proportions	1998 proportions	Survey length data	Catch-at-age data
With Koski *et al.* (2006) proportions	Yes	Yes	No	No	No
With 1998 proportions	Yes	No	Yes	No	No
With length data	Yes	No	No	Yes	No
With age data	Yes	No	No	No	Yes

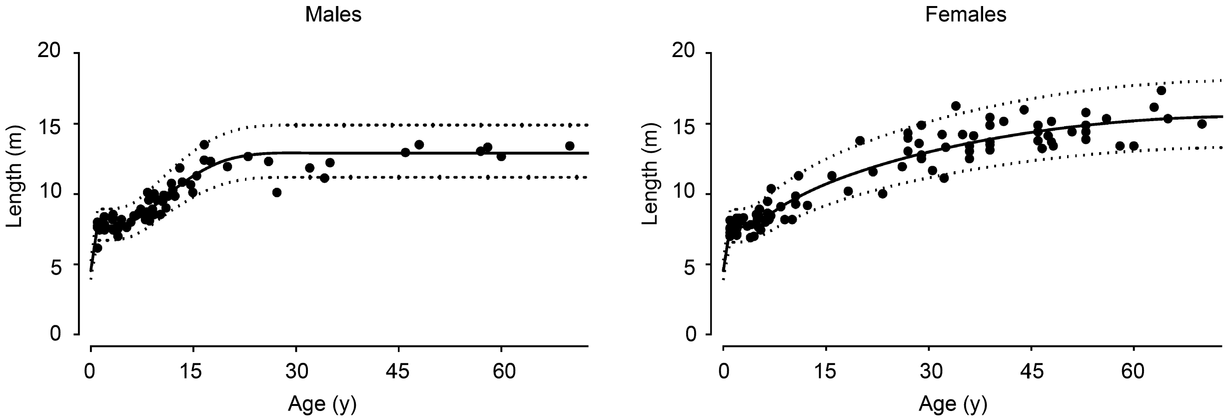

Fig. 3. Fits of the growth model to the data on length-at-age. The solid line is the maximum likelihood estimate and the dotted lines indicate the 95% confidence intervals for an individual data point (i.e. the combined impact of the uncertainty associated with the mean length-at-age and the individual variation about the mean length-at-age). Data points for ages 75 and older are omitted from this figure for improved clarity.

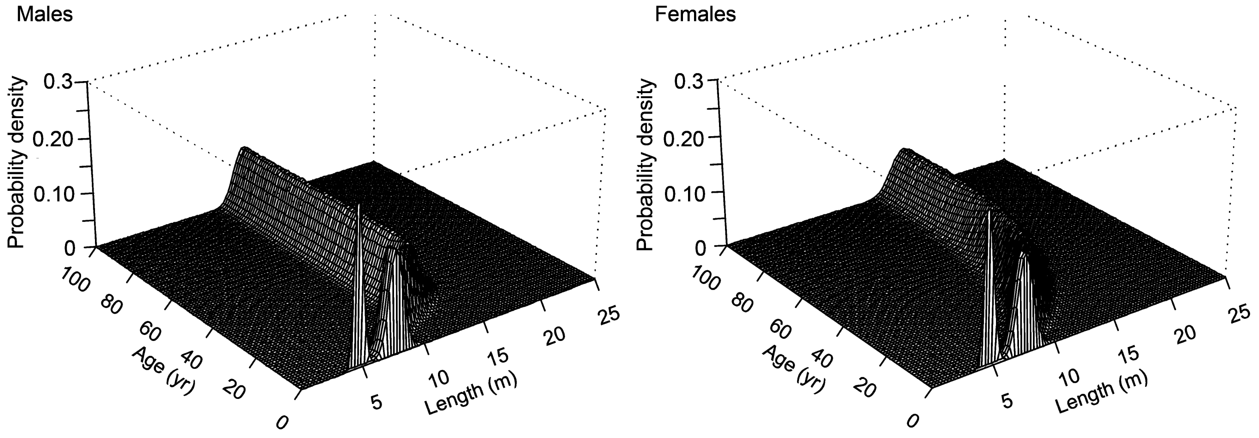

Fig. 4. The point estimates of the length-at-age distributions.

Table 7

Values for the parameters of the growth equation.

Parameter	Males	Females
l_1(m)	7.73	7.64
l_{40} (m)	12.91	13.98
κ (yr^{-1})	1.021e-8	9.608e-8
β	9.131	15.892
σ	0.0734	0.0781

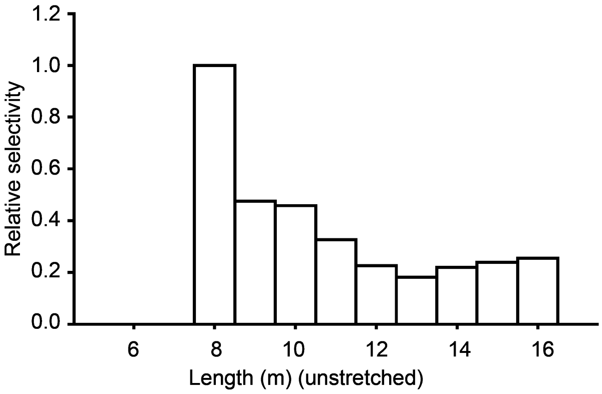

Fig. 5. Selectivity-at-length for the B-C-B stock of bowhead whales.

the model is fitted the length-frequency data and 'very strong' support for this analysis when the model is fitted to the age-composition data (Bayes factor >150; see Fig. 6). Thus, it seems as if a key reason for the earlier inability to mimic the catch age-composition data (Schweder and Ianelli, 2000) was due to the assumption of uniform selectivity harvesting when this is not actually the case. The data provide little ability to discriminate between the two selection patterns (uniform selectivity and the selectivity based on Fig. 5) when the model is fitted to the proportion data (Bayes factor < 3). The latter result is not surprising because this is a case in which the model is fitted to data aggregated over age and length. As a result, there is not much information on the pattern of abundance within fairly large groups of ages. The remaining analyses of this paper are based on the model in which the selectivity pattern is given by Fig. 5 (henceforth referred to as the 'base-model').

Results for base-model

Table 8 lists the results (posterior medians, means and 95% probability intervals) for the base-model in terms of the values for the following seven quantities of management interest.

K_{1+} – the pre-exploitation size of the 1+ component of the population.

P^{1+}_{2004} / K_{1+} – the ratio (expressed as percentage) of the size of the 1+ component of the population at the start of 2004 to K_{1+}.

P^{f}_{2004} / K^{f} – the ratio (expressed as percentage) of the size of the mature female component of the population at the start of 2004 to the corresponding pre-exploitation size.

$P^{1+}_{2004} / MSYL_{1+}$ – the ratio (expressed as percentage) of the size of the 1+ component of the population at the start of 2004 to *MSYL*.

$MSYR_{1+}$ – *MSYR* for uniform selectivity harvesting of the 1+ component of the population, expressed as a percentage.

RY (2004) – the replacement yield for 2004 (the catch during 2004 so that the population size at the start of 2005 equals that at the start of 2004).

Slope – the annual rate of increase of the 1+ population from 1978 to 1993, expressed as a percentage[6].

Fig. 7 provides diagnostic statistics (the fits to the age-composition data, the length frequency data, the abundance indices, and the proportion data) for the analyses that fit to: (a) the Koski *et al.* (2006) proportion data; (b) the length frequency data; and (c) the age-composition data.

The results of the assessment are quite sensitive to the choice of data set. Specifically, the productivity of the resource (expressed in terms of $MSYR_{1+}$ and the '*slope*' statistic) is lower when the model is fitted to the length or age data (posterior medians for $MSYR_{1+}$ ~ 1.3-2.0% compared to 2.7-2.9% when the model is fitted to the proportion data).

The model mimics the trend in the abundance data best when it is not fit to the length or age data, suggesting that there is conflict between these data sources. In contrast, the abundance and proportion data are totally consistent (Fig. 7a). The model does not mimic the age-composition data adequately unless it is fitted to these data (Figs 7a and 7b, upper left panels). Specifically, the model predicts that a much larger fraction of the catch should be animals aged 0-20 years (Fig. 7a) and 20-40 years (Fig. 7b) than is actually the case and that a much lower fraction of the catch should be animals aged 100+. Similarly, only the analysis that fits to the length frequency data mimics these data well; the fit to the length data for the case in which the model is fit to the proportion data is particularly poor as it severely underpredicts the abundance of animals 12m and longer (Fig. 7a).

The B-C-B Seas stock of bowhead whales is assessed to be above or approaching *MSYL* at present (Table 8). However, the exact status of the stock remains uncertain because, for example, the ratio of current to pre-exploitation population size is higher (markedly so in terms of the 1+ component of the population) if the length and age data are

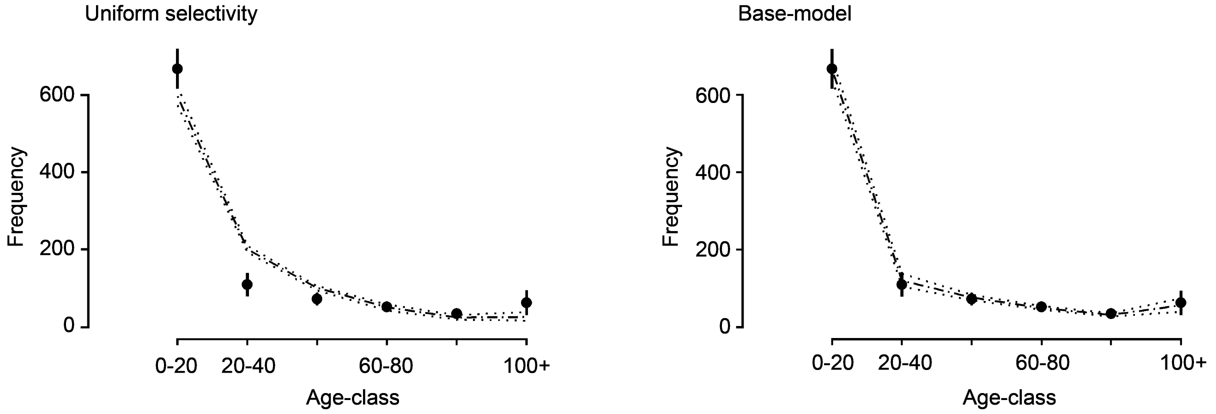

Fig. 6. Posterior distributions (medians and 90% probability intervals) for the catch age-compositions based on models fitted to the age-composition data. Results are shown for the analysis in which selectivity is uniform and for the base-model.

Table 8

Estimates of seven management-related quantities for the B-C-B Seas stock of bowhead whales. The point estimates given are posterior medians, followed by posterior means in round parenthesis. Posterior 90% probability intervals are given in square parenthesis. The analyses in this table are based on the base-model.

	K_{1+}	*RY* (2004)	P^{1+}_{2004} / K_{1+}	P^{f}_{2004} / K^{f}	$P^{1+}_{2004} / MSYL_{1+}$	$MSYR_{1+}$	*Slope*
With Koski *et al.* (2006) proportions	11,261 (11,411)	143 (135)	86.6 (85.3)	53.5 (54.4)	127.0 (125.7)	2.90 (2.91)	2.60 (2.59)
	[9,943 13,432]	[76 171]	[69.0 96.8]	[43.8 68.7]	[110.1 136.0]	[1.96 3.83]	[1.80 3.31]
With length data	14,067 (14,101)	134 (133)	66.1 (66.1)	48.8 (48.9)	123.6 (123.6)	1.96 (1.95)	1.60 (1.58)
	[13,219 15,119]	[124 141]	[58.3 74.4]	[42.3 55.9]	[112.1 135.2]	[1.66 2.23]	[1.36 1.76]
With age data	15,662 (15,658)	138 (140)	57.5 (58.0)	40.0 (40.2)	81.9 (82.2)	1.31 (1.34)	1.23 (1.25)
	[14,138 17,118]	[109 182]	[49.7 68.2]	[35.5 45.7]	[68.0 97.0]	[1.04 1.73]	[0.94 1.66]
With 1998 proportions	11,710 (11,941)	162 (157)	85.2 (83.3)	52.7 (53.4)	117.3 (114.9)	2.70 (2.70)	2.60 (2.60)
	[10,174 14,491]	[85 212]	[63.5 96.7]	[42.5 67.0]	[91.0 131.0]	[1.65 3.76]	[1.59 3.60]

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[6] The slope statistic is based on the years 1978-93 for comparability with the assessment conducted in 1998.

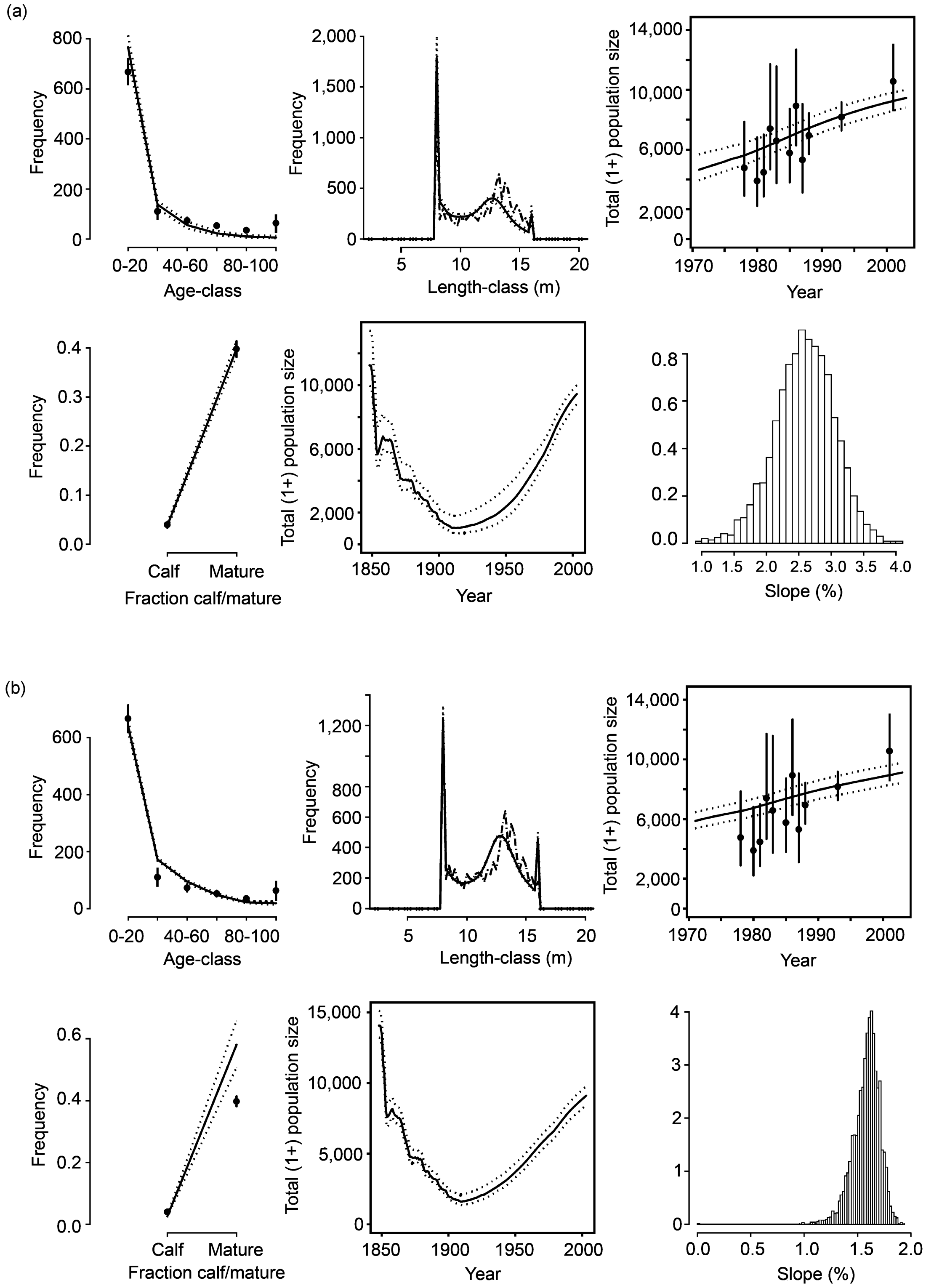

Fig. 7. Diagnostic statistics (fits to the age-composition, length frequency, abundance, and proportion data), the posterior distribution for the time-trajectory of 1+ population size, and the posterior distribution for the 'slope' statistic. Results are shown for analyses that fit to: (a) the Koski *et al.* (2006) proportion data; (b) the length frequency data; and (c) the age-composition data. The solid lines are posterior medians and the dotted lines indicate posterior 90% intervals. The dashed line in the upper centre panel indicates the observed length-frequency distribution.

ignored when conducting the assessment. The ratio of current population size to $MSYL_{1+}$ is more robust than the ratio of current to unexploited population size, except for the case in which the assessment is based on the age-composition data (Table 8).

Sensitivity to weights

The results of an assessment often depend on the weight assigned to the various data sources when these data sources are contradictory. Fig. 8 explores the sensitivity of the posterior distribution for $MSYR_{1+}$ to reducing the effective sample size assumed for the length-frequency data and to changing the emphasis placed on mimicking the age-composition data (implemented by multiplying the standard deviations in Table 3 by various constants).

A marked reduction in the median of the posterior distribution for $MSYR_{1+}$ occurs even if a relatively small (~100) effective sample size is assigned to the length frequency data (Fig. 8; left panel); increasing this effective sample size beyond 100 leads to narrower probability

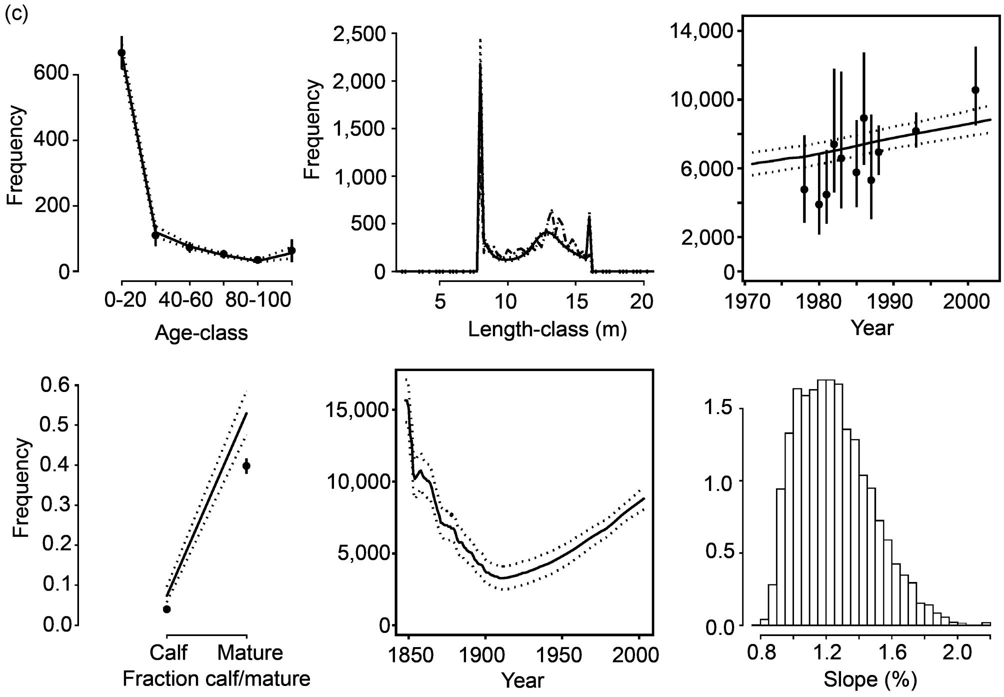

Fig. 7 *continued.* Diagnostic statistics (fits to the age-composition, length frequency, abundance, and proportion data), the posterior distribution for the time-trajectory of 1+ population size, and the posterior distribution for the 'slope' statistic. Results are shown for analyses that fit to: (a) the Koski *et al.* (2006) proportion data; (b) the length frequency data; and (c) the age-composition data. The solid lines are posterior medians and the dotted lines indicate posterior 90% intervals. The dashed line in the upper centre panel indicates the observed length-frequency distribution.

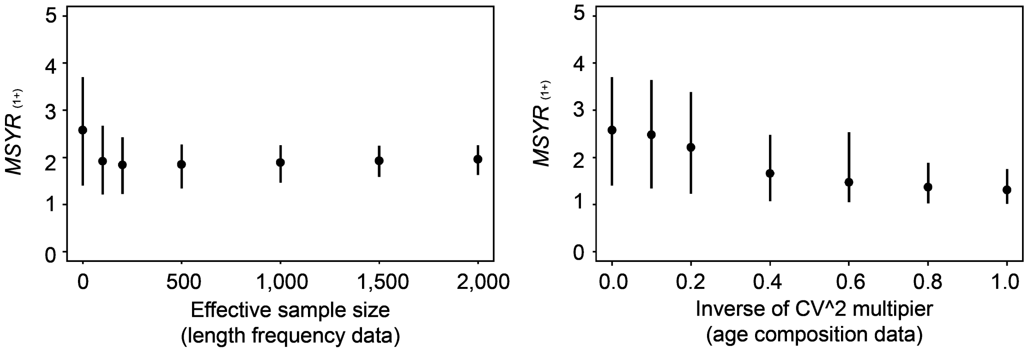

Fig. 8. Posterior distributions (medians and 95% probability intervals) for $MSYR_{1+}$ for different assumed effective sample sizes for the length-frequency data and for different levels of emphasis on the age-composition data.

intervals, as would be expected. In contrast to the case for the length frequency data, there is no obvious CV multiplier at which the median of the posterior for $MSYR_{1+}$ changes markedly (Fig. 8; right panel). In contrast, the median for $MSYR_{1+}$ continues to decline almost continuously with increasing emphasis on the age-composition data.

Management implications

From a management viewpoint, none of the lower 5th percentiles of the posterior distributions for the 2004 replacement yield are less than the current strike limit of 68 (Table 8). However, a more appropriate way to determine the management implications of the results of this paper is to evaluate the performance of the *Bowhead SLA* (IWC, 2003a) when the operating model is parameterised in terms of the results outlined above. Table 9 therefore presents the values for five of the mandatory performance measures selected by IWC (2003a) for simulation trials in which the final need level is set to 134 and in which it is set to 201 for a variety of specifications related to the assumed form of selectivity and the data used when conditioning the trials.

The conservation-related performance measures (D1 – Final depletion, and D10 – Relative increase) are higher when selectivity is not uniform (presumably because less of the catch is taken from the mature age-classes; Fig. 5). However, the differences are not particularly marked, except possibly for the lower 5th percentiles of the final depletion distribution. There is almost no impact from the choice of selectivity pattern on need satisfaction. The results are again more sensitive to the choice of data used when conditioning than to the form of the selectivity pattern. As expected, final depletion and need satisfaction are lowest when the operating model is conditioned using the age data because these data imply the lowest productivity (Table 8). However, the results for even this case are not poorer than when the *Bowhead SLA* is used to manage a population for which $MSYR_{1+}$=1% (see IWC, 2003b for full details).

General discussion

This paper shows that it is possible to 'integrate' more sources of data into the assessment of the B-C-B Seas bowhead stock than has been done to date. This process of

Table 9

Performance measures for the *Bowhead SLA* for trials in which the biological parameters are based on the results of the assessments of the population. Results are shown for final need levels of 134 and 201.

	Final depletion; 1+ population (D1)			Relative increase; 1+ population (D10)			Average need satisfaction (N9-20 years)			Average need satisfaction (N9-100 years)			Mean downstep (N12)		
Scenario	5%	Med	95%	5%	Med	95%	5%	Med	95%	5%	Med	95%	5%	Med	95%
Final need = 134															
Uniform selectivity															
With Koski *et al.* (2006) proportions	0.816	0.930	0.972	1.010	1.100	1.280	1.00	1.00	1.00	0.85	0.98	1.00	0.000	0.004	0.020
Base-model															
With Koski *et al.* (2006) proportions	0.842	0.937	0.969	1.020	1.110	1.260	1.00	1.00	1.00	0.86	0.99	1.00	0.000	0.003	0.021
With length data	0.724	0.786	0.844	1.110	1.190	1.320	1.00	1.00	1.00	0.87	0.99	1.00	0.000	0.003	0.019
With age data	0.659	0.854	0.940	1.300	1.490	1.660	0.99	1.00	1.00	0.89	1.00	1.00	0.000	0.000	0.018
With 1998 proportions	0.871	0.950	0.978	1.010	1.140	1.410	1.00	1.00	1.00	0.86	0.99	1.00	0.000	0.002	0.018
Final need = 201															
Uniform selectivity															
With Koski *et al.* (2006) proportions	0.776	0.921	0.970	1.000	1.090	1.240	0.96	1.00	1.00	0.73	0.88	0.95	0.004	0.010	0.033
Base-model															
With Koski *et al.* (2006) proportions	0.822	0.931	0.967	1.020	1.100	1.210	0.96	1.00	1.00	0.73	0.88	0.95	0.003	0.010	0.035
With length data	0.667	0.755	0.829	1.040	1.140	1.300	0.95	1.00	1.00	0.73	0.88	0.94	0.004	0.011	0.029
With age data	0.639	0.813	0.919	1.240	1.430	1.580	0.94	1.00	1.00	0.72	0.91	0.96	0.002	0.007	0.030
With 1998 proportions	0.834	0.941	0.977	1.010	1.130	1.370	0.96	1.00	1.00	0.73	0.90	0.96	0.003	0.009	0.030

integration allows an examination to be conducted to determine whether some of the available data sources are contradictory (i.e. imply different impressions of stock status and productivity). The results of this paper highlight that there is some inconsistency among the proportion data, the length frequency data, the age-composition data and the abundance estimates. The age-composition data are least compatible with the other data, and suggest the least amount of recovery and the lowest levels of productivity of the B-C-B Seas bowhead stock. However, the quantitative results for the case in which the model is fitted to the age-composition data should be interpreted with caution owing to the problems in how the age-compositions were constructed by Schweder and Ianelli (2000). Nevertheless, all of the analyses considered in this paper confirm that the B-C-B Seas bowhead stock has been recovering steadily over the last few decades (Fig. 7), even though the present analyses suggest that the certainty associated with the rate of increase in the past may have been over-estimated.

The assumption underlying past assessments that selectivity is uniform above age one appears to be violated for this stock (Fig. 5). Rather, it appears that hunters take smaller (younger) animals rather than larger (older) animals. Whether this pattern is due to preference or differences in the availability of different age-classes cannot be assessed conclusively with the available information, but subsistence hunters have expressed a preference for smaller animals that are easier to manoeuvre to shore and they were encouraged to take smaller animals by the IWC for several years (e.g. Donovan, 1982; IWC, 1995). However, with respect to the estimated status of the population, the consequences of differences in selectivity among age-classes are minor compared to the choice of which sources of data are to be included in the assessment.

A number of factors could not be accounted for in the analyses of this paper. Specifically, no account of the uncertainty associated with estimating selectivity-at-length was taken because no attempt was made to treat selectivity-at-length as estimable. In principle, selectivity-at-length could be treated as parameters of the model and included when calculating the posterior distributions. Unfortunately, the number of selectivity parameters is quite large (see Fig. 5) and attempting to allow for their uncertainty using the SIR algorithm to sample from the posterior distribution would lead to prohibitively long computation times. In principle, uncertainty regarding the selectivity parameters could be accounted for if a different approach was used to sample from the posterior distributions (e.g. by using an MCMC algorithm).

Selectivity is assumed to be uniform prior to 1914. In contrast, Bockstoce and Burns (1993) noted that ‘the largest whales were taken in the earliest years of the fishery, although paradoxically, one or two very big whales were taken in the last years’. Although the sample sizes for length frequency for the early harvests are low, it may be possible in future to develop a selectivity pattern for those harvests which is more realistic than the current assumption of uniform selectivity harvesting. This might help to fit the length-frequency data for the largest animals although the management implications of historical selectivity differing from uniform above age one are likely to be fairly minor.

Finally, although the results of the assessment suggest that selectivity is not uniform and that the various data sources are inconsistent to some extent, the results of the projections (Table 9) provide no evidence that the scenarios considered during the testing of the *Bowhead SLA* are insufficient to cover the plausible range.

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Winter abundance of bowhead whales, *Balaena mysticetus*, in the Hudson Strait, March 1981

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ABSTRACT

Satellite tracking studies of bowhead whales (*Balaena mysticetus*) in West Greenland and the eastern Canadian Arctic have documented that Hudson Strait is an important wintering ground for animals summering in the Baffin Bay-Davis Strait area and the Hudson Bay-Foxe Basin area. In light of this new information, data were re-examined on abundance of bowhead whales at this wintering ground derived from a systematic strip census survey conducted in March 1981. Three strata in Hudson Strait were covered by equally spaced north-south transect lines. Most sightings were in the western stratum, with one and none in the central and eastern strata, respectively. Abundance estimates were corrected for whales at the surface missed by observers using data from a similar survey in the Beaufort Sea. Corrections for whales submerged when the survey aircraft passed were developed using new data from time-depth recorders deployed on seven bowhead whales in Disko Bay, West Greenland, in April-May 2002-05. The fully corrected abundance estimate for the Hudson Strait in March 1981 was 1,349 (95% CI 402-4,529) whales. Similar surveys were conducted along West Greenland in March 1981 and 1982; the combined estimate was 1,549 (95% CI 589-4,072). Other unsurveyed areas in Baffin Bay may contribute an additional 8% to this combined estimate. The projected population size for both areas was 3,633 (95% CI 1,382-9,550) in 2004, assuming a population growth rate of 3.4% per year (George *et al.*, 2004), which may not be appropriate for this population. However, increased sighting rates and traditional knowledge reports confirm that the population is growing. The use of availability and detection biases together with the restricted seasonal distribution of whales in March makes this the most complete estimate of this population in the 1980s to date.

KEYWORDS: BOWHEAD WHALE; ARCTIC; ABUNDANCE ESTIMATE; HUDSON STRAIT; BAFFIN BAY; SURVEY-AERIAL; BEAUFORT SEA; DISTRIBUTION

INTRODUCTION

The International Whaling Commission has recognised two management stocks of bowhead whales (*Balaena mysticetus*) in the eastern Canadian Arctic and West Greenland (IWC, 1978; 1992): the Baffin Bay-Davis Strait (BB-DS) stock, believed to summer along the east coast of Baffin Island and in the fjords and channels of the Canadian High Arctic; and the Hudson Bay-Foxe Basin (HB-FB) stock, believed to summer in northern Hudson Bay and Foxe Basin and winter in the Hudson Strait. Recent results from studies of bowhead whales equipped with satellite transmitters suggest that both putative stocks overwinter in the Hudson Strait (Heide-Jørgensen *et al.*, 2006). Furthermore, satellite tracking of bowhead whales in Foxe Basin also indicates a shared summering area in the Prince Regent Inlet with whales from Baffin Bay (Dueck *et al.*, 2006). These two new pieces of evidence cast doubt over the current concept of two separate populations of bowhead whales.

Animals in the BB-DS area were severely reduced by commercial whaling between the early 1700s and the early 1900s from an estimated unexploited abundance of no less than 12,000 (Ross, 1993; Woodby and Botkin, 1993); after the cessation of whaling in 1915, their abundance was unknown (Ross, 1993). A population estimate from the mid 1980s suggested that the BB-DS animals numbered at least 350 (Zeh *et al.*, 1993) and therefore were still severely below the pre-whaling size. Local knowledge (NWMB, 2000) suggests that bowhead whale numbers have been increasing in recent years.

The majority of the available information on the winter distribution of bowhead whales in the Hudson Bay-Baffin Bay region has been obtained from whaling records drafted in the late 1800s and early 1900s, i.e. towards the end of the exploitation period (Ross, 1993). Based on these records, bowhead whales were noted to winter in two areas: (1) along the coast of West Greenland north to Disko Island; and (2) in Hudson Strait (Eschricht and Reinhardt, 1861; Brown, 1868; Low, 1906). Aerial surveys conducted over the past 20 years along the coast of West Greenland in March have detected a consistent, but low number of bowhead whales during winter (Born and Heide-Jørgensen, 1983; Reeves and Heide-Jørgensen, 1996; Heide-Jørgensen and Acquarone, 2002). Estimated bowhead whale abundance (corrected for submergence) in West Greenland in 1998 was 246 whales (95% CI 62-978, Heide-Jørgensen and Acquarone, 2002). A few bowhead whales were sighted in winter along the pack ice edge in Davis Strait but these were probably whales *en route* to West Greenland. Many bowhead whales were caught on the 'sou'west fishing grounds' along the edge of the pack ice off Cumberland Sound as early as March (Brown, 1868; Kumlien, 1879; Lubbock, 1937), but lack of catches in mid-winter suggest that those whales may have been early migrants from wintering areas in Hudson Strait (Anderson, 1934).

During the whaling era, the HB-FB population was also reduced from an unknown initial population of at least 580 animals (Mitchell, 1977, as modified by Woodby and Botkin, 1993). In 1995, the HB-FB population was estimated to be about 345 animals (DFO, 1999) based on surveys conducted by Cosens *et al.* (1997) and Cosens and

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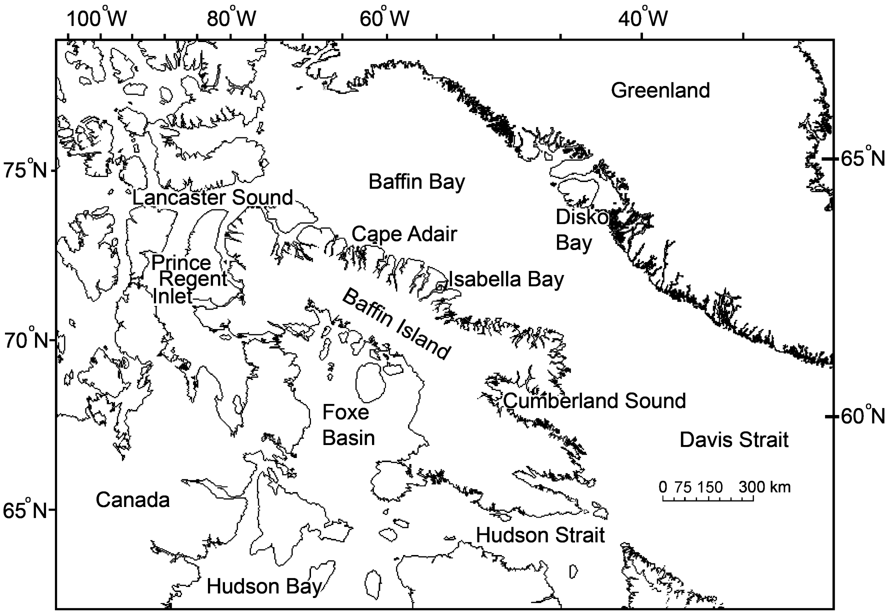

Fig. 1. Map of area and localities mentioned in text.

Innes (2000). This was probably a considerable underestimate since the estimate did not include a correction for animals below the water surface at the time of the survey.

Estimates of the winter abundance of bowhead whales in Hudson Strait in 1981 are presented in this paper. Although the survey was carried out some 25 years ago, it is the only survey undertaken in this area at this time of the year, recently recognised to be an important wintering ground for bowhead whales for animals from both the HB-FB and BB-DS areas (Heide-Jørgensen *et al.*, 2006). Consequently abundance estimates from 1981 are relevant to management decisions and population projections.

MATERIALS AND METHODS

Survey procedures

Systematic aerial surveys of wintering bowhead whales were conducted in Hudson Strait from 14-30 March 1981 (Fig. 1). The surveys were conducted in a deHavilland Twin Otter at a target altitude of 150m. Survey speed averaged 259km h^{-1}. Three observers were present and recorded sightings of bowhead whales. Sightings within 100-800m on either side of the aircraft were considered 'on transect' and those >800 or 0-100m from the centre line were considered 'off transect' and were not included in the density estimation. The inner and outer transect boundaries were marked on the wing struts and windows with tape. Bowhead sightings were circled to confirm species identification and group size. Sightings and effort within 100m of the centre line were excluded because visibility was seriously impaired in the Twin Otter with standard flat windows (see Thomas *et al.*, 2002). The Twin Otter was equipped with a VLF navigation system that determined aircraft position and a radar altimeter that assisted in maintaining the target altitude.

North-South transect lines were evenly distributed at 1° longitude (approx. 26km apart) from eastern Hudson Bay through Hudson Strait to the northern Labrador Sea (Fig. 2). The total study area was ~216,613km^2. Hudson Strait was divided into three strata of similar size; western, central and eastern. The survey area and transect lengths were estimated using a geographic information system and whale densities were extrapolated to the area of the strata.

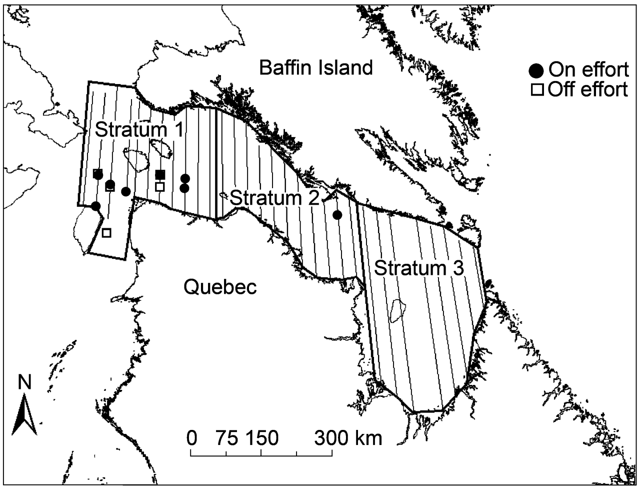

Fig. 2. Survey effort, location of bowhead sightings and stratification of the survey conducted in March 1981.

Correcting for perception and availability bias

Visual observers miss animals at the surface because of the difficulty of detecting whales among ice floes, simultaneous surfacing of several animals, sun glare impeding visibility or observer fatigue (Marsh and Sinclair, 1989). No survey specific correction factors for this perception bias were available from the original survey. Instead values were obtained from a recent double observer experiment on bowhead whales in the Beaufort Sea using a similar aircraft including one or sometimes both of the primary observers from the original survey (Thomas *et al.*, 2002).

The proportion of time that whales were at the surface and visible to observers was estimated using data on bowhead whale surface times from time-depth-recorders deployed on seven whales in May 2002 and 2003 and April 2005 in Disko Bay, West Greenland. The instruments were MK9 time-depth recorders (Wildlife Computers, Redmond, Washington, USA) mounted on a float tethered to the whale. The float had an additional two instruments used for tag recovery: a satellite transmitter for coarse positioning and a VHF transmitter for fine-scale positioning. The floats were attached to the whales with a harpoon head pushed under the

Table 1

Summary statistics for aerial surveys conducted during March 1981 in Hudson Strait. Strip width was 1,400m and numbers in parentheses are coefficients of variation (*CV*). Corrected density and abundance of whales includes correction factors for availability and perception bias (see text).

Stratum	Study area (km^2)	No. of transect lines	Survey effort (km)	No. of sightings on/off	Mean group size	Density of whales (no. km^2)	Corrected density of whales (no. km^2)	Corrected abundance of whales
1. Western Hudson Strait	72,688	11	2,346	8/7	1.25 (0.13)	0.003 (0.47)	0.02 (0.56)	1,236 (0.56)
2. Central Hudson Strait	55,713	11	1,960	1/0	1	0.0004 (0.99)	0.002 (1.03)	113 (1.03)
3. Ungava Bay and eastern Hudson Strait	88,211	8	2,531	0/0	0	0	0	0
Total	216,613	30	6,837	9/7				1,349 (0.60)

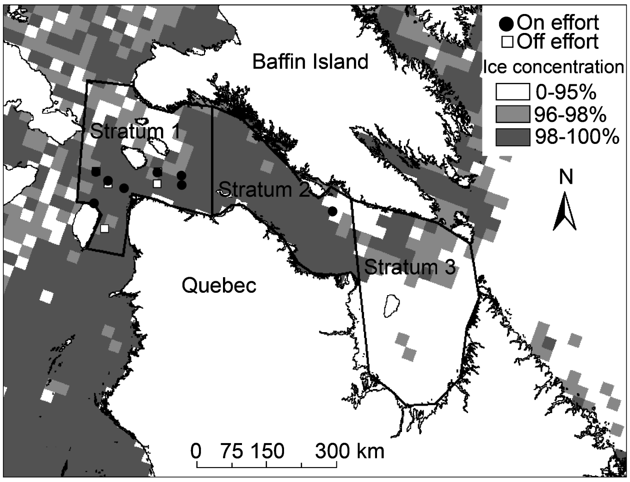

Fig. 3. Sightings of bowhead whales made on and off effort 14-30 March 1981 and SSMR/SSMI sea ice concentrations in 25 sq km pixels from 14 March 1981.

skin with an 8m long fibreglass pole. The float was released from the whale within 24h with a corrosive magnesium bolt. Processing of dive data included zero-offset correction using *Instrument Helper* (Wildlife Computers).

Sea ice concentration data for March 1981 were obtained from passive microwave telemetry (the Nimbus-7 Scanning Multichannel Microwave Radiometer) from the National Snow and Ice Data Center (NSIDC). Sea ice concentration (1% resolution) was derived using the bootstrap algorithm following the procedure of Comiso (1995), where daily sea ice concentrations were mapped to a polar stereographic projection (true at 70°N) at a 25km resolution. Sea ice data obtained from the NSIDC were converted from raw binary to ASCII format using a program written in Compaq Visual Fortran 90 and imported into a geographic information system (*ESRI ArcINFO 8.3*) as raster grids.

All estimates are presented with CV calculated as a standard error in proportion to the mean and 95% confidence intervals were constructed assuming a log-normal distribution of whale densities (see Burnham *et al.*, 1987).

RESULTS

During the course of 6,837 linear km of survey, 16 separate sightings of 29 bowhead whales were obtained (Table 1; Fig. 2). Seven of these sightings were off transect (either outside the width of the census strip or during off-effort periods). The average group size of all sightings was 1.8 (range 1–7; SD 1.5). All sightings of bowhead whales were in >95% ice concentration even though areas with a larger fraction of open water were available (Fig. 3).

Despite evenly distributed survey effort across all three strata, all but one (in central Hudson Strait) sighting occurred in western Hudson Strait; no bowhead whales were observed in eastern Hudson Strait or Ungava Bay. The uncorrected density of bowhead whales in western and central Hudson Strait was 0.003 and 0.0004 bowhead whales km^{-2}, respectively (Table 1).

Since the speed of the survey platform was relatively rapid (approx. 40ms^{-1}) relative to the dive cycle of bowhead whales (most dives last more than 1min), it was assumed that no repeat sightings of the same whale were made. It was also assumed that the area searched by the observers represented a snapshot of the availability of whales. Thomas *et al.* (2002) estimated that the perception bias for a single set of visual observers flying a bowhead whale survey in a Twin Otter in the Beaufort Sea was 0.59 (CV=0.27). This value was applied to this study and used to correct for sightings missed by the observers.

Dive data collected from seven bowhead whales instrumented with time-depth recorders were used to calculate the fraction of time whales spent at the surface and estimate an availability bias across a range of depths (1-5m). The seven individuals spent, on average, 30.4% of their time (SD=1.0%) at =2m, probably the deepest depth at which bowhead whales are seen during surveys. This fraction varied widely with the selection of 'surface depth' mainly due to large differences in whale diving behaviour (Laidre, unpublished data). However for the case of surface time calculations, the selection of 2m provided an estimate with relatively low variability (Table 2).

The perception and availability biases were combined to derive an estimate of an overall correction factor useful for correcting the abundance estimate for animals missed within the survey strip. The combined values for the perception bias ($\hat{p}$=0.59, CV=0.27) and the availability bias (*a*=0.30,

Table 2

Surface times from 7 whales instrumented with time-depth recorders in Disko Bay, West Greenland, May 2002 and 2003 and April 2005. Proportion of time at the surface is indicated for 5 different depths (1-5m) where bowhead whales could be seen from the air.

Whale ID	Date tagged	Sample size (hr, min)	1m	2m	3m	4m	5m
02-01	5/5/02	2, 20	0.232	0.250	0.259	0.269	0.283
02-02	5/8/02	10, 12	0.193	0.371	0.523	0.653	0.718
02-03	5/12/02	12, 48	0.274	0.371	0.523	0.653	0.718
03-01	5/17/03	7, 50	0.383	0.470	0.501	0.520	0.530
03-02	5/18/03	8, 46	0.220	0.234	0.241	0.243	0.264
05-01	4/22/05	53, 5	0.171	0.201	0.228	0.242	0.257
05-02	4/23/05	20, 31	0.208	0.228	0.238	0.243	0.246
Mean			0.240	0.304	0.359	0.403	0.431
(SD)			(0.071)	(0.101)	(0.147)	(0.197)	(0.219)

CV=0.13) resulted in an estimate of the overall correction factor of 0.18 with CV=0.30. Abundance estimates for bowhead whales corrected for both perception and availability bias were thus 1,236 (CV=0.56) in western Hudson Strait, 113 (CV=1.03) in central Hudson Strait, and 0 in eastern Hudson Strait (Table 1). This resulted in a total abundance of 1,349 (CV=0.60, 95% CI 402-4,529) whales for the entire survey region in March 1981.

DISCUSSION

The presence of a substantial number of bowhead whales in northeast Hudson Bay and western Hudson Strait in March, together with recent satellite tracking results documenting that whales arrive in Hudson Strait in November (Heide-Jørgensen *et al.*, 2006), indicate this is an important wintering area used by bowhead whales. The whales found in this area are probably the same whales that summer in Hudson Bay, Foxe Basin, Lancaster Sound and adjacent fjords and along the east coast of Baffin Island. Satellite tracking studies have documented the movement of animals into this area from all of these summer localities (Heide-Jørgensen *et al.*, 2006; Dueck *et al.*, 2006).

Coincident with the 6,837km survey reported here about 20,650km of surveys in other potential bowhead whale wintering habitat were conducted in northern Hudson Bay (including Roes Welcome Sound), off the Labrador coast, off SE Baffin Island, and over the pack-ice and open-water areas in southern Baffin Bay and northern Davis Strait during March and early April (see Koski and Davis (1994) for survey coverage in these areas). Only seven bowhead whales (including off effort sightings) were seen outside of the Hudson Strait and four of those were off West Greenland, in the area identified by Reeves and Heide-Jørgensen (1996) as a bowhead whale wintering area. Thus, 33 of 36 bowheads (92%, including off effort sightings) recorded during the late winter surveys in 1981 were either in Hudson Strait or off West Greenland, providing even further support that these two areas are the major wintering grounds.

The abundance estimate of 1,349 (CV=0.60) whales for Hudson Strait thus represents a major proportion of the population size in 1981. The average abundance estimate of bowhead whales wintering off West Greenland in 1981 and 1982 reported by Reeves and Heide-Jørgensen (1996) was 36 (95% CI 24-54), and if this estimate is corrected for the same availability and detectability biases as in Hudson Strait the resulting abundance in West Greenland would be 200 whales (95% CI 100-401). If these estimates are combined (West Greenland and Hudson Strait) then 1,549 bowhead whales (95% CI 589-4,072) were present in the northwestern Atlantic in 1982. This combined estimate does not incorporate the abundance contributed by the 8% additional bowhead whales sighted outside of these two localities or whales present in areas not covered during surveys such as the North Water polynya. Richard *et al.* (1998) surveyed the North Water polynya in March 1991 and sighted two bowhead whales, but surveys by Finley and Renaud (1980) in the same area in 1978 and 1979 did not find any, suggesting that although bowhead whales occur in the area it may not support a high abundance.

The most recent estimate of the summer abundance of bowhead whales in BB-DS (based on data collected in the late 1970s and mid-1980s) suggested that the BB-DS population was at least 350 animals (Zeh *et al.*, 1993). This estimate was obtained from a mark-recapture study of photographically identified whales in Isabella Bay in 1986-87, a late summer concentration area on the east coast of Baffin Island, plus an estimate of the number of bowheads that migrated past Cape Adair during late September to early October 1978 and 1979 (Davis and Koski, 1980). Zeh *et al.* (1993) noted that the Isabella Bay estimate included only ‘marked whales’ and was therefore a minimum estimate; however most whales seen in Isabella Bay are large well-marked animals so this negative bias may be small. In addition, it is highly likely that some bowhead whales migrated south after shore-based observations at Cape Adair ended because whales were observed on the last survey days in both 1978 and 1979. Satellite tracking results show that some bowhead whales do not enter Isabella Bay, and instead migrate past Cape Adair in late October (the period after the Davis and Koski (1980) surveys were completed), confirming as Zeh *et al.* (1993) noted, that their abundance estimate is negatively biased.

The HB-FB summer abundance of bowhead whales was estimated to be about 345 whales in 1995 based on aerial surveys partially covering the summer range (Cosens *et al.*, 1997; Cosens and Innes, 2000). However, large areas of potential summer distribution of bowhead whales were not surveyed and no complete estimate of summer abundance could be calculated. In addition, the HB-FB estimate did not include correction factors for availability bias at the time of the survey. When the negative biases associated with the mid-1980s BB–DS estimate and mid-1990s HB-FB estimate are considered, the combined estimates may not be significantly different from the estimate obtained from this study. However, the estimate presented here accounts for potential biases more completely than other presently available estimates.

Potential biases in this study result from lack of site-specific data on perception and availability bias. There is also a lack of data on the population growth rate if population projections are used to estimate current abundance. Bowhead whales missed by observers were corrected based on data from a summer survey in the Beaufort Sea using some of the same observers, the same type of aircraft and the same flying altitude. It is uncertain as to what extent this correction factor is applicable to the 1981 Hudson Strait survey; however, they are the best available data. It should be noted that a survey for white whales (*Delphinapterus leucas*) in West Greenland estimated a perception bias of the same magnitude (Heide-Jørgensen and Acquarone, 2002).

The corrections for availability bias for whales submerged below 2m were derived from time-depth-recorders deployed in April-May in West Greenland. It can be argued that this correction factor might differ for bowhead whales in Hudson Strait in March. However, the fraction of time near the surface (~30%) is similar to that reported for bowhead whales based on satellite-linked time depth recorders from other areas (Heide-Jørgensen *et al.*, 2003) and that reported for white whales and narwhals (*Monodon monoceros*; Heide-Jørgensen *et al.*, 2001; Heide-Jørgensen and Acquarone, 2002; Laidre *et al.*, 2002), although it is lower than for bowhead whales on their summer feeding grounds (Thomas *et al.*, 2002).

Bowhead whales observed during this survey were found in the heaviest pack ice in Hudson Strait and are apparently capable of wintering in dense ice conditions in other areas as well, including Hudson Bay and Baffin Bay (cf. Heide-Jørgensen and Laidre, 2004). The occurrence of bowhead whales in such severe pack ice in Hudson Strait may also explain why 19th century whalers did not realise this was a major concentration area for bowhead whales.

Local and traditional knowledge suggests that the bowhead whale population around Baffin Island and in West Greenland is increasing (NWMB, 2000; Heide-Jørgensen, unpubl. data). Beginning with the 1981-82 combined estimate, adding 8% for whales outside the surveyed area and assuming the central population growth rate of 3.4% per year until 2004 (George *et al.*, 2004) results in a projected population size of 3,633 (95% CI 1,382-9,550) whales present in Hudson Strait and West Greenland in 2004. The use of the growth rate from the Bering-Chukchi-Beaufort Seas Stock may be too high, as it probably represents the maximum potential growth rate of the population. However, several other depleted populations of large cetaceans have demonstrated clear recoveries with growth rates in the same magnitude after a period of protection (Best *et al.*, 2001; Stevick *et al*., 2003).

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Reconciling data on the trends and abundance of North Atlantic humpback whales within a population modelling framework

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ABSTRACT

Populations of humpback whales (*Megaptera novaeangliae*) in the North Atlantic appear to have been increasing at least during the last few decades, following the cessation of substantial hunting almost 100 years ago. Several sources of data are available for these populations (survey and mark-recapture estimates of absolute and relative abundance, estimated catches, and estimates of the proportion of the animals on two feeding grounds that are from the West Indies breeding ground). These data were analysed using an age- and sex-structured population dynamics model that is spatially-explicit to the extent that abundance is tracked on five feeding and two breeding grounds. Several alternative hypotheses, including depensation and changes over time in carrying capacity, were captured within the model framework. Two scenarios form the focus of the analyses, based on alternative interpretations of the size of the breeding population off the Cape Verde Islands. The results of these analyses confirm the increase in the number of humpback whales in the North Atlantic, although it is not possible to determine the extent of such increases. Whether both the West Indies and Cape Verde Islands breeding stocks have increased depends on whether the estimate of abundance for the Cape Verde Islands population of approximately 100 animals is valid. Although many of the data sources can be reconciled given the model applied, some conflicts remain; resolution of these conflicts will require collection of additional data.

KEYWORDS: HUMPBACK WHALES; MODELLING; ATLANTIC OCEAN

INTRODUCTION

In the North Atlantic, the humpback whale (*Megaptera novaeangliae*) ranges from tropical waters north to the Arctic pack ice (e.g. Winn and Reichley, 1985). During winter, the majority of animals congregate in low latitude areas to mate and calve. The principal breeding/calving areas documented in recent times lie on offshore banks and off insular coasts on the Atlantic margins of the West Indies (Winn *et al.*, 1975; Whitehead, 1982; Smith *et al.*, 1999). Historically, humpback whales wintered further south along the Antillean arc through the Windward Islands (Winn *et al.*, 1975; Mitchell and Reeves, 1983; Reeves *et al.*, 2001) and around the Cape Verde Islands (CVI) in the eastern North Atlantic (Braham, 1984; Reeves *et al.*, 2002); they currently occur in low numbers in these regions. In spring, North Atlantic humpback whales migrate to several high-latitude feeding grounds, which they occupy during the summer and autumn (Smith *et al.*, 1999). Feeding grounds are located in the Gulf of Maine, off the eastern Canadian maritime provinces (Canada), along West Greenland, around Iceland (including Jan Mayen), and to the north of Norway (Fig. 1). However, 19th century whaling logbooks and some recent sighting surveys include summer sightings of humpback whales in the mid North Atlantic to the west of and on the Mid-Atlantic ridge, well away from present day known feeding grounds (Reeves *et al.*, 2004)

Humpback whales were apparently reduced to low levels throughout the North Atlantic by intensive hunting during the late 19th and early 20th centuries (Braham, 1984; Mitchell and Reeves, 1983; Winn and Reichley, 1985). Aboriginal subsistence whaling for a small number of humpback whales continued in West Greenland until 1985, the allowance was removed by the International Whaling Commission (IWC) because of uncertainties regarding regional abundance and stock structure (IWC, 1986). On Bequia (an island part of St Vincent and The Grenadines) in the Windward Islands, a small aboriginal subsistence fishery continues today (IWC, 1994). The humpback whale is listed as 'endangered' by the Convention on International Trade in Endangered Flora and Fauna and as either 'endangered' or 'vulnerable' by various governments and international conservation organisations (Klinowska, 1991).

The reduction in catches led to an increase in population size at least in the western North Atlantic. Capture-recapture data provide the longest time-series of estimates of abundance for this component of the humpback whale population. These data suggest a rate of increase of 0.031 (SE=0.005) per annum over the 14-year period 1979-92 (Stevick *et al.*, 2003b). These estimates are, however, not the only data that relate to the abundance and population dynamics of humpback whales in the North Atlantic; data on relative and absolute abundance are also available for several of the feeding grounds (e.g. Larson and Hammond, 2004) and estimates of the proportion of the animals off Iceland and Norway that breed in the West Indies based on analyses of genetics data are also available (IWC, 2002; 2003).

Assessments of several whale stocks that have been the subject of intensive hunting have been conducted under the auspices of the Scientific Committee of the IWC. In general, these assessments have been based on a limited number of data sources (usually just catches and estimates of absolute abundance from surveys) and simple age-aggregated (e.g. humpback whales in the Southern Hemisphere – Johnston *et al.*, 2001; Johnston and Butterworth, 2002) or age-structured population dynamics models (e.g. bowhead whales in the Bering, Chukchi, and Beaufort Seas – Givens *et al.*, 1995; gray whales off the west coast of North America – Punt *et al.*, 2004). In contrast, there are several data sources for humpback whales in the North Atlantic and considerable uncertainty exists regarding some of the historical catches, the number of breeding grounds (at least two associated with the West Indies and CVI; IWC, 2002), and several feeding

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grounds. Furthermore, some of the data sources (e.g. the estimate of abundance for Iceland, the proportion of animals off Iceland that are not from the West Indies breeding stock, and the estimate of the size of population off the CVI) appear to be in conflict.

This paper attempts to reconcile the various data sources for North Atlantic humpback whales by developing a population dynamics model that is capable of representing several stocks simultaneously and that can include various hypotheses regarding the factors determining the population dynamics of these whales. The values for the parameters of this model are estimated either directly from sampled data or indirectly by fitting it to the available data sources to provide estimates of the pre-exploitation size of the population and how population size has changed over time, regionally and across the entire North Atlantic. The uncertainty associated with these estimates is examined by varying the assumptions of the model and by applying a bootstrap technique to estimate variance.

METHODS

Breeding and feeding grounds

The analyses of this paper assume that there are two breeding grounds (nominally ‘West Indies’ and ‘CVI’) and that each breeding ground consists of animals from five feeding grounds (Fig. 1); the possible mid-Atlantic ridge feeding ground (IWC, 2002) is ignored in this paper. Animals from more than one breeding ground may be found on the same feeding ground. The model considers the dynamics of each feeding ground – breeding ground combination (referred to here as a ‘stock’) separately although density-dependence is assumed to be a function of the total number of animals on a feeding ground. Some of these combinations may, of course, have no animals. Animals from the West Indies breeding ground are found on all five feeding grounds while animals from the CVI breeding ground have only been identified so far on the Norway and Iceland feeding grounds. There are therefore seven non-zero ‘stocks’ in the analyses of this paper.

Data available for assessment purposes

Catch data

Humpback whales have been taken in the North Atlantic since the 1600s in several fisheries operating throughout the area. Reeves and Smith (2002) describe the available information on historical catches for each of 27 fisheries or sub-fisheries. While some of these fisheries were directed toward humpback whales, most targeted a wide range of baleen and toothed whales. Humpback whales were often not the first choice in these fisheries, but became increasingly targeted as the abundance of the more lucrative species declined and as catching technology improved.

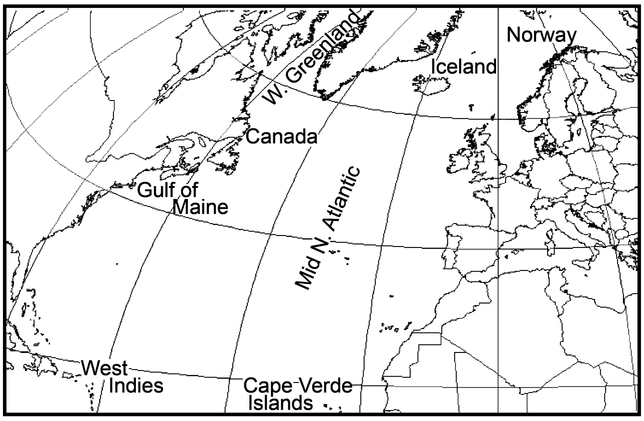


Fig. 1. Approximate location of five known present day feeding grounds (Gulf of Maine, Canada, W. Greenland, Iceland, and Norway), one possible feeding ground (Mid-N. Atlantic) and two breeding grounds (West Indies and CVI) used by humpback whales in the North Atlantic Ocean.

Descriptions of humpback whale fishing operations have been published in a wide range of sources, and approximate locations and periods of operations for each fishery are generally known. Information on catches and landings ranges from: (1) detailed statistics for each animal reported to the Bureau of International Whaling Statistics in the 20th century; (2) to summary descriptions of commercial products shipped in various national and fishermen’s reporting records; (3) to tabulations of landings from individual voyages in the 19th century; and (4) to irregular summaries and lists prepared for various reasons for earlier periods. These data were assembled by Smith and Reeves (2003b) into catches by feeding and breeding ground, separately for calves, non-calf females and non-calf males (Fig. 2).

The catches in Fig. 2 are known to be uncertain, so the sensitivity of the results from the model to this uncertainty is explored by considering scenarios regarding upper bounds for the historical catches. These scenarios are based on the sources of uncertainty identified by Smith and Reeves (2002; 2003a; b). None of the scenarios adjust the post-1880 catches because there is no evidence of deliberate misreporting or under-reporting for that period in the North Atlantic; however some of the catches in the early years (1880-1920) were unspecified to species and therefore the humpback whale component had to be estimated by proration.

Scenario A. This scenario considers the uncertainty introduced when it was necessary to interpolate annual landings between years because of incomplete data series. This involved replacing the baseline estimates of such catches by the highest levels reported for the surrounding years (see fig. 2 of Smith and Reeves, 2002), as this placed a reasonable upper bound on these catches.

Scenario B. This scenario considers the uncertainty associated with the estimated landings for the American non-mechanised pelagic fishery. These landings were based on reported whale oil returns (in barrels), assuming an average number of barrels from each whale, or were based on the average number of humpback whales landed per voyage. The catches by this fishery were set to upper bounds by increasing the annual landings estimates by twice the standard error of the estimates for the West Indies and the CVI sub-fisheries for the years 1865-86 (see table 4 of Smith and Reeves, 2003a).

Scenario C. This scenario considers the uncertainty associated with accounting for the numbers struck but lost. The loss factor for mechanised whaling was estimated to be 1.02 from detailed daily data from two North Pacific shore stations (Smith and Reeves, 2002). Here, a somewhat higher rate (1.06) based on fewer data from a North Atlantic land station is considered. For the American non-mechanised pelagic fishery, Smith and Reeves (2003a; b) followed Mitchell and Reeves (1983) by using a struck but lost correction factor of 1.85, or a proportion of struck animals landed of 0.54. Mitchell and Reeves (1983) developed this correction factor based on the inferred degree of injury. The catches shown in Fig. 2 are based on the assumption that all struck animals were in fact killed. Under this assumption, the voyage-specific proportions of struck animals that were

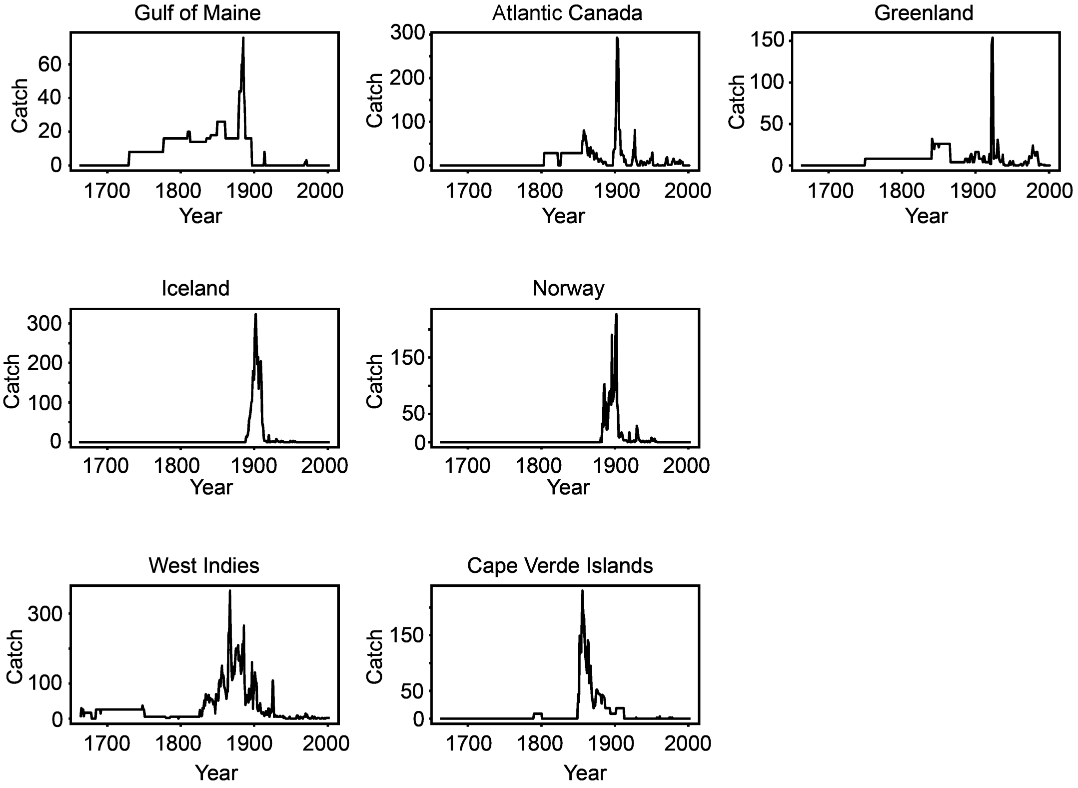


Fig. 2. The baseline catch series (aggregated over sex) by feeding and breeding ground.

landed ranged from 0.17 to 0.67 (mean 0.49, 95% CI 0.42-0.56). Scenario C is based on the next to smallest observed proportion landed (0.33), noting that the smallest observed proportion is 2.4 standard errors below the mean. This rate implies a proportion that is 62% of that originally used, with the corresponding correction factor now 3.0 (= 1/0.33). The factor of 1.5 for the remaining non-mechanised and transitional fisheries, which was based primarily on anecdotal information, was arbitrarily adjusted downwards by 62% as well.

Scenario D. This scenario accounts for the catches for the years prior to 1850 being based on substantially poorer data than those for the later years. It involves arbitrarily doubling the removals for the years prior to 1850.

Scenario E. This scenario combines the effects of scenarios A-D.

The removals for scenarios A-D were 11% to 46% higher than the baseline removals, and those for the multiple-factor scenario (E), 135% higher (Table 1). Scenarios C and E were used to explore the sensitivity of the model results to uncertainties regarding the estimates of the historical catches.

Table 1

Total removals of North Atlantic humpback whales as estimated by Smith and Reeves (2003a) and as calculated for sensitivity purposes under five scenarios.

		Increase over baseline	
Scenario	Total estimated removals (000s)	Number (000s)	%
Baseline	29		
A	33	4	11
B	33	4	11
C	43	14	46
D	37	8	25
E	69	40	135

Abundance indices and proportion data

Information on absolute and relative abundance is available from surveys and mark-recapture studies. Tables 2 and 3 list, respectively, the estimates of absolute and relative abundance used when estimating the values for the parameters of the model for the baseline analyses. The estimate for the CVI (99 animals; Table 2) was based on data collected during an ongoing study (Jann *et al.*, 2003). Preliminary photographic mark and recapture data for 2003 and 2004 collected around the two easternmost islands in the group (Sal and Boavista) were used to obtain this estimate. The estimate of 99 is the largest of several abundance estimates that could be derived from the available data. It was based on seven animals resighted from 18 and 41 animals sampled during the two years (Beatrice Jann and Frederick Wenzel, pers. comm.). The representativeness of this estimate for the entire breeding ground is unknown, and further studies are underway to evaluate this.

Published abundance estimates which were presented as ranges rather than point estimates with associated estimates of precision (e.g. Whitehead, 1982) or which did not include sufficient information to calculate coefficients of variation (e.g. Balcomb and Nichols, 1982; Winn *et al.*, 1975) are not included in Table 2. Furthermore, the abundance estimates for Newfoundland/Labrador obtained by Hay (1982) and for the Grand Banks obtained by Whitehead and Glass (1985) are not included in Table 2 because they are estimates for a subsection of a feeding area in the model.

Estimates of the proportion of animals off Iceland and Norway from the West Indies breeding stock (0.60, SE=0.050 and 0.13, SE=0.057, respectively) are available from genetics studies (IWC, 2002).

Estimates of the rate of increase for humpback whales in the Gulf of Maine feeding ground are available based on demographic models (e.g. Barlow and Clapham, 1997; Clapham *et al.*, 2003). These estimates were not used, however, because some of the quantities used in their

Table 2

The estimates of absolute abundance for North Atlantic humpback whales used in the baseline analyses of this paper.

Breeding ground		Feeding ground	
Year	Estimate (CV)	Year	Estimate (CV)
West Indies[1]		**Gulf of Maine**[2]	
1979	7,260 (0.16)	1992	652 (0.29)
1979	6,918 (0.15)	1999	902 (0.41)
1980	9,439 (0.22)	**West Greenland**[3]	
1980	8,119 (0.20)	1988	357 (0.16)
1981	7,234 (0.18)	1989	355 (0.12)
1981	9,695 (0.19)	1990	566 (0.42)
1982	8,864 (0.15)	1991	376 (0.19)
1982	7,064 (0.10)	1992	348 (0.12)
1983	7,603 (0.12)	**Iceland**[4]	
1983	7,309 (0.13)	1995	7,900 (0.22)
1984	9,200 (0.18)	**Norway**[5]	
1984	9,948 (0.29)	1995	1,210 (0.255)
1985	10,310 (0.31)		
1985	8,100 (0.36)		
1986	11,185 (0.39)		
1986	9,083 (0.36)		
1987	10,297 (0.32)		
1987	11,144 (0.25)		
1988	12,582 (0.25)		
1992	10,752 (0.07)		
Cape Verde Islands[6]			
2001	99 (0.23)		

[1]Stevick *et al.* (2003b); [2]Clapham *et al.* (2003); [3]Larson and Hammond (2004); [4]Pike *et al.* (2002); [5]Øien (2003); [6]calculated based on unpublished mark-recapture data from 2003 and 2004 courtesy of Beatrice Jann and Frederick Wenzel, with assistance of Philip Hammond and Peter Stevick.

Table 3

The estimates of relative abundance for North Atlantic humpback whales on their feeding grounds used in the baseline analyses of this paper.

Year	Estimate (CV)	Year	Estimate
Gulf of Maine[1]		**Iceland**[3]	
1978	122	1970	0.11
1979	171	1971	0.37
1980	188	1972	0.25
1981	211	1973	0.31
1982	238	1974	0.64
1983	281	1976	0.16
1984	380	1977	0.59
1985	448	1978	0.63
Canada/Newfoundland[1]		1979	0.66
1978	3,222	1980	0.54
1979	2,423	1981	0.88
1982	1,903	1982	1.01
West Greenland[1]		1983	0.33
1981	183	1984	1.20
1982	239	1985	0.87
Norway[2]		1986	1.34
1988	1,126	1987	1.93
1989	698	1988	1.83

[1]Katona and Beard (1990); [2]Øien (2003); [3]Sigurjónsson and Gunnlaugsson (1990).

calculation such as age-specific survival rates and the fraction mature at age were also used when fitting the population dynamics model.

Model formulation

The population dynamics model (Appendix A) is density-dependent, age- and sex-structured, and allows for multiple feeding and breeding grounds. Apart from the ability to deal with spatial structure, this model also generalises the model used conventionally as the basis for assessments of baleen whale populations by the IWC Scientific Committee (BALEEN II; de la Mare, 1989; Punt, 1999) by allowing:

(a) density-dependence (which is assumed to impact fecundity/infant survival, and to be functionally related to the size of the 1+ component of the population) to be governed by either a Pella-Tomlinson or a Ricker-like function (Equations A.2a and A.2b);
(b) depensation to occur at low population size if density-dependence is governed by a Ricker-like function (Equation A.2b);
(c) carrying capacity to vary over time (the scenarios considered in this paper assume a linear change in carrying capacity which started in 1910); and
(d) the values for the resilience parameter and for the extent of change in carrying capacity to depend on feeding ground or be independent of feeding ground.

Another difference between the population dynamics model in Appendix A and the BALEEN II model is that the population is not divided into 'recruited' and 'unrecruited' components. However, given the assumption of uniform selectivity on animals aged one and older on which this paper is based, this difference has no impact on the results because the two treatments of recruitment are identical.

Several other variants of the population dynamics model were examined on an exploratory basis (e.g. allowing a time-lag in the density-dependence term, allowing density-dependence to depend on stock or breeding ground rather than on feeding ground, allowing for density-dependent movement between feeding and breeding grounds, and allowing for 'inertial dynamics' (Witting, 2003)). The results of these variants either showed little difference from those presented, or suggested that the factor considered led to much poorer fits, so results for these exploratory analyses are not presented here.

Parameter estimation

The parameters of the population dynamics model can be divided into those whose values are estimable directly from data and those whose values are determined by maximising the likelihood function (see Appendix B for the contributions of the various data sources to the negative of the logarithm of the likelihood function and Table 4 for a full list of the parameters of the population dynamics model).

Table 4

The estimable parameters of the population dynamics model for the model variant which estimates the greatest number of parameters. The number of parameters is based on seven stocks.

Symbol	Description	No. parameters
$K_{1664}^{j,1+}$	Carrying capacity of stock *j* in 1664	7
$K_{2001}^{j,1+} / K_{1910}^{j,1+}$	Change in carrying capacity for stock *j* from 1910-2001*	5
A^j	Resilience parameter for stock *j**	5
β	Extent of depensation	1
Total		18

*Same for all stocks in each feeding ground.

Table 5 lists the values for the parameters that are determined from information not included in the likelihood function. Two sets of estimates for the proportion of females by age that have reached parturition are listed in Table 5. Both sets of estimates are based on the ratio of known-age (and frequently observed) females in the Gulf of Maine feeding ground that are known to have given birth prior to the age concerned. One set of estimates is based on a period

(1979-92) when the humpback population in the Gulf of Maine was increasing rapidly while the other data set is based on a longer period (1979-2004). Most of the analyses of this paper are based on the larger data set, but sensitivity is explored using the smaller data set. This is because the estimates based on the longer period may reflect the consequences of the Gulf of Maine component of the population starting to approach its (current) carrying capacity.

Table 5

Values for model parameters that are fixed based on auxiliary information.

Age	Survival, S_a[1]	Fraction 'mature', M_a[2]	
		1979-92 (n=19)	1979-2004 (n=53)
0	0.875	0	0
1	0.96	0	0
2	0.96	0	0
3	0.96	0	0
4	0.96	0	0
5	0.96	0.29	0.14
6	0.96	0.67	0.29
7	0.96	0.88	0.45
8	0.96	1	0.52
9	0.96	1	0.70
10	0.96	1	0.71
11	0.96	1	0.71
12	0.96	1	0.83
13+	0.96	1	1

[1]Barlow and Clapham (1997); [2]Jooke Robbins (Center for Coastal Studies, Provincetown, MA 02657, pers. comm.).

Alternative models, model selection and variance estimation

A large number of alternative models could be developed given the model structure (e.g. should carrying capacity change over time? if so how? and how should the change be expressed spatially?) and data set choices (e.g. should all of the data be used or only subsets?).

No attempt was made to conduct an exhaustive evaluation of all combinations of model structure and data set choice. Instead, two key data-related scenarios were constructed based on hypotheses concerning stock structure and each of these scenarios was analysed using 18 alternative models (see Table 6). These two scenarios arise from the conflict between the data on the proportion of the animals at the Iceland and Norway feeding grounds that breed in the West Indies and the estimates of absolute abundance for Iceland, Norway and the CVI. These data can (potentially) be reconciled by: (a) ignoring the CVI estimate of abundance when fitting the model (abbreviation 'No CVI Est'); and (b) ignoring the information on the proportion of animals at the Iceland and Norway feeding grounds that are from the West Indies breeding stock (abbreviation 'No Proportions').

The first data scenario captures the possibility that either there are breeding grounds in the North Atlantic additional to those in the West Indies and the CVI, or that the estimate of abundance for the CVI is severely negatively biased. The second data scenario captures the possibility that the proportion data are biased and/or imprecise because of spatially or seasonally unrepresentative sampling. For example, there are no genetic samples for the CVI breeding ground so the genetic make-up of this breeding ground had to be inferred from samples taken off Norway.

Model selection was conducted separately for the two data scenarios. This involved first fitting each model and checking the results for biological realism and then using $\mathrm{AIC_c}$ (Burnham and Anderson, 2002) to select among the remaining models. $\mathrm{AIC_c}$ is more appropriate than AIC in this case owing to the low ratio of parameters to data points for some of the models. Note, however, that use of $\mathrm{AIC_c}$ is not truly valid because of the inclusion of a penalty on the extent of inter-feeding ground variability in the value of the resilience parameter (see Equation B.3).

A parametric bootstrap approach was used to quantify the uncertainty associated with the estimates of the model parameters. Each of the 500 bootstrap replicate data sets involved adding noise to the actual survey and proportion data based on either the pre-specified coefficients of variation (absolute abundance estimates), pre-specified standard deviations (proportion data), or estimated residual standard deviations (relative abundance indices). It was not possible to determine that all of the bootstrap replicates converged to the true minimum of the negative log-likelihood function. As each bootstrap replicate was started from the point estimates of the parameters corresponding to minimum of the negative log-likelihood based on the fit to the actual data, any convergence to a local minimum will tend to lead to the bootstrap procedure underestimating the actual extent of uncertainty.

RESULTS

Selection of the baseline model

Table 6 compares the 18 models for the two data-related scenarios using $\mathrm{AIC_c}$. The model with the lowest $\mathrm{AIC_c}$ for the 'No CVI Est' scenario is the one in which density-dependence is governed by the Ricker-like function, K varies among stocks, the resilience parameter is the same for all stocks, there is no depensation, and carrying capacity changed after 1910 (but to the same extent for all stocks). This model achieved an $\mathrm{AIC_c}$ that was only slightly smaller than that for the model with the same specifications except that carrying capacity was independent of time. The fits of these two models differ by 3.7 log-likelihood units, but the penalty imposed by $\mathrm{AIC_c}$ on the ratio of the number of parameters to data points makes this difference less consequential than would AIC. The model with the lowest $\mathrm{AIC_c}$ for the 'No Proportions' scenario is that in which density-dependence is governed by the Ricker-like function, K varies among stocks, the resilience parameter is the same for all stocks, there is no depensation, and carrying capacity is time-invariant.

The models with the lowest $\mathrm{AIC_c}$ values differ from those corresponding to the lowest negative log-likelihoods (see the models indicated by asterisks in Table 6) because the improvement in fit gained by adding additional parameters is not warranted given the large number of parameters involved. These models consequently have a very large $\mathrm{AIC_c}$.

Figs 3 and 4 show the fits of the two models with the lowest $\mathrm{AIC_c}$ values to the absolute and relative abundance indices. The vertical bars in Figs 3 and 4 are 95% confidence intervals for the data (the estimated residual standard deviations are used to compute the confidence intervals for the relative abundance indices).

The model is consistent with the estimates of absolute abundance for both data scenarios, although the results for the 'No CVI Est' scenario mimic the observed trend in abundance in the Gulf of Maine and in the West Indies better than those for 'No Proportions' scenario. However, the model-predicted rate of increase for the West Indies breeding ground over 1979-92 for the 'No CVI Est' scenario is only 1.2% per annum rather than the 3.1% per annum implied by the raw data, even though carrying capacity is estimated to have increased by almost 200% since 1910.

Table 6

Comparison among models based on AIC$_c$. The models with the lowest AIC$_c$ for each data scenario are indicated using bold-underline typeface, and the models with the lowest negative log-likelihoods are indicated by asterisks. The column '# pars' lists the number of parameters (those of the population dynamics model as well as the qs and σs for the relative abundance indices).

				No CVI Est		No Proportions	
Density-dependence function	Area-specific A	Depensation	# pars	AIC$_c$	ΔAIC$_c$	AIC$_c$	ΔAIC$_c$
Constant carrying capacity							
Pella-Tomlinson	-	-	16	50.94	3.29	68.61	12.96
Pella-Tomlinson	Yes	-	20	77.48	29.83	96.56	40.91
Ricker-like	-	-	16	47.85	0.21	**55.65**	**0.00**
Ricker-like	Yes	-	20	74.22	26.57	84.18	28.53
Ricker-like	Yes	Yes	21	84.34	36.69	96.26	40.61
Ricker-like	-	Yes	17	52.95	5.30	60.92	5.27
Changing carrying capacity – area specific							
Pella-Tomlinson	-	-	21	67.34	19.69	78.43	22.78
Pella-Tomlinson	Yes	-	25	149.94*	102.29	187.15*	131.50
Ricker-like	-	-	21	67.60	19.95	93.23	37.57
Ricker-like	Yes	-	25	150.25	102.60	201.96	146.31
Ricker-like	Yes	Yes	26	196.69	149.05	274.46	218.81
Ricker-like	-	Yes	22	80.50	32.85	108.75	53.10
Changing carrying capacity – same change over all feeding grounds							
Pella-Tomlinson	-	-	17	55.92	8.27	67.09	11.44
Pella-Tomlinson	Yes	-	21	86.73	39.09	103.25	47.60
Ricker-like	-	-	17	**47.65**	**0.00**	59.48	3.83
Ricker-like	Yes	-	21	77.62	29.97	93.14	37.49
Ricker-like	Yes	Yes	22	81.45	33.81	108.62	52.96
Ricker-like	-	Yes	18	53.60	5.96	66.09	10.44

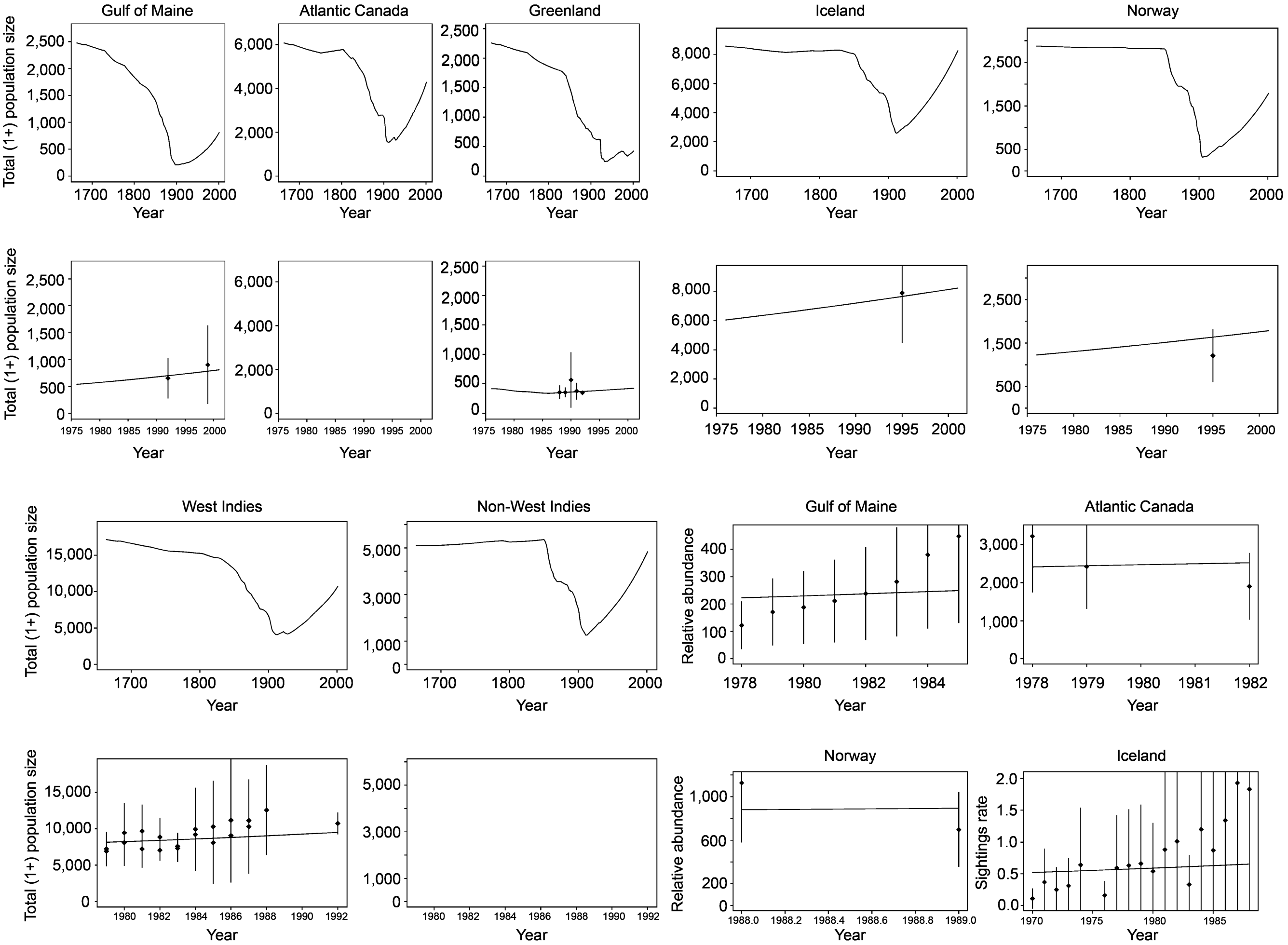


Fig. 3. Summary of the fit of the model with the lowest AIC$_c$ to the 'No CVI Est' data-related scenario.

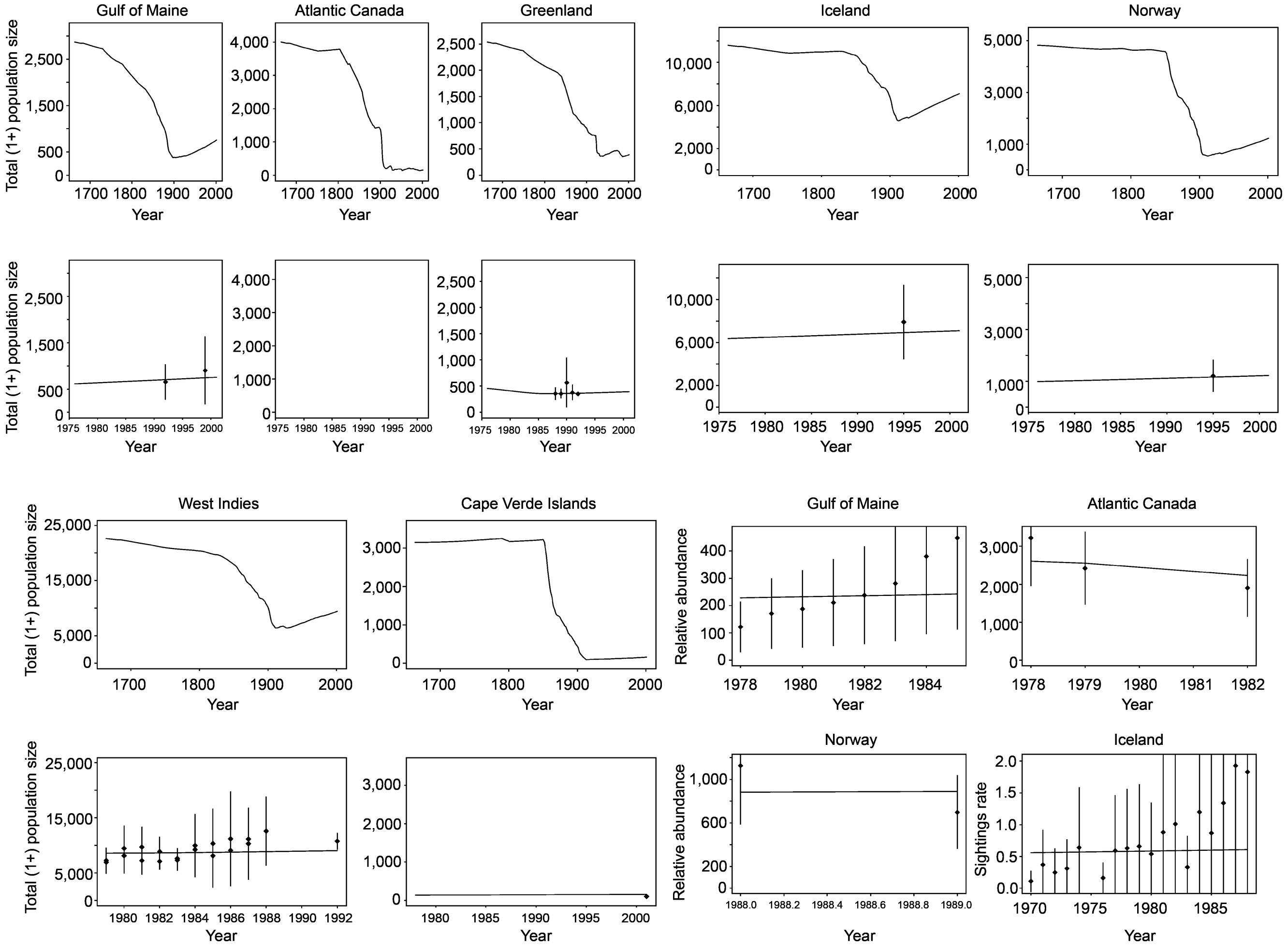


Fig. 4. Summary of the fit of the model with the lowest AIC_c to the ‘No Proportions’ data-related scenario.

Although better fits are possible with larger amounts of change in carrying capacity or by starting the change in carrying capacity more recently, these options were not pursued because the amount of change required in the first case appears biologically unrealistic and because in the latter case there is no information to support such differences. In any case, better fits occur when allowance is made for the carrying capacity for the Norway feeding ground to decline rather than increase over time. The reason for the inability to mimic the trend in the West Indies is primarily that, had the population been as productive as implied by the change over time in the estimates of abundance, it would have recovered to its carrying capacity many years ago.

Neither of the models in Figs 3 and 4 is capable of mimicking the relative abundance indices for the Gulf of Maine and Iceland. It is not really possible to comment on the fit to the relative abundance indices for Atlantic Canada and Norway given the low number of data points involved. The relative abundance indices for the Gulf of Maine are inconsistent with the absolute abundance estimates for the same area and, given that the coefficients of variation for the absolute abundance indices are pre-specified based on the extent of sampling error (Table 2) while the residual standard deviations for the relative abundance indices are estimated when fitting the model, the model chooses to mimic the estimates of absolute abundance.

Neither model is able to mimic the Icelandic relative abundance index based on sightings on whaling grounds to the west of Iceland. It is perhaps noteworthy that the rate at which this index increases from 1970-88 (11.4%) is consistent with a trend in relative abundance from aerial surveys during 1986-2001 of 11.6% (Gunnlaugsson and Víkingsson, 2002).

The results for the two data-related scenarios differ markedly in terms of predicted abundance and trend. This is most evident for Atlantic Canada (for which there are no estimates of absolute abundance that could be included formally in the analyses) and the CVI. The current abundance for the latter area is close to 5,000 for the ‘No CVI Est’ scenario and only 100 for the ‘No Proportions’ scenario. This is perhaps not unexpected given that the ‘No Proportions’ scenario includes an estimate of absolute abundance of 99 for the CVI breeding ground. One consequence of the lower estimated abundance for the CVI is that almost all of the animals on the Norwegian and Icelandic feeding grounds must be West Indies animals. Given the constraint on the total abundance of the West Indies breeding population implied by the estimates of abundance for the West Indies, it follows that the population off Atlantic Canada must be fairly small.

The low estimates of abundance for Atlantic Canada in recent years from the ‘No Proportions’ scenario (Fig. 4) seem unrealistic given past survey effort in the area (Hay, 1982; Whitehead, 1982; Katona and Beard, 1990; Smith *et al.*, 1999; EC YoNAH, 2001; IWC, 2002). Estimates for sub-regions of Atlantic Canada range from a minimum of 738 (95% CI=235-1242) for eastern Newfoundland and southeastern Labrador from a line-transect survey in 1980 (Hay, 1982) to 3,236 (SE=484) for Newfoundland from a mark-recapture analysis for 1979 (Katona and Beard, 1990). The YoNAH project attempted to provide an overall

Table 7

Results of the sensitivity tests based on modifying some of the assumptions of the model/data set choices.

	West Indies			Non-West Indies			
	N^{1+}_{1664}	N^{1+}_{2001}	K^{1+}_{2001}	N^{1+}_{1664}	N^{1+}_{2001}	K^{1+}_{2001}	$-\ell nL$
'No CVI Est' scenario							
Baseline	17,151	10,711	51,298	5,091	4,831	15,227	3.55
Alt Iceland ests	18,134	10,413	54,402	5,990	7,226	17,971	4.21
Alt West Indies ests	17,919	12,707	52,933	5,211	4,826	15,392	3.72
Alt cat-C	24,347	11,059	72,919	6,539	4,802	19,585	2.70
Alt cat-E	39,601	11,023	117,061	7,760	4,717	22,939	3.00
Alt rates	17,188	10,745	51,359	5,083	4,841	15,187	3.54
No rel abund	17,658	10,582	52,603	5,255	4,748	15,653	9.32
Alt Baseline	17,965	9,627		5,519	4,306		6.21
Alt Iceland ests	19,643	9,355		6,886	6,215		7.45
Alt West Indies ests	18,872	11,384		5,656	4,406		6.58
Alt cat-C	24,772	10,030		6,794	4,366		4.95
Alt cat-E	39,034	10,383		7,737	4,365		4.53
Alt rates	18,155	9,636		5,557	4,296		6.18
No rel abund	17,802	9,632		5,532	4,511		11.29
'No Proportions' scenario							
Baseline	22,647	9,444		3,152	160		9.36
Alt Iceland ests	21,185	9,645		3,067	173		12.17
Alt West Indies ests	25,199	11,100		3,203	147		9.06
Alt cat-C	37,036	9,136		5,521	217		14.56
Alt cat-E	56,082	9,251		7,485	225		14.54
Alt rates	20,133	9,746		2,985	186		9.72
No rel abund	23,766	9,360		3,178	149		14.14

estimate for Atlantic Canada, but found that sampling was highly variable spatially, not all areas of known concentration were sampled, and sampling intensity in sub-regions was variable relative to known prior densities. Stratifying the data into three regions within which effort was more consistent resulted in an estimate of 2,509 (CV=0.077), but the method of estimation ignored movement of individuals among strata. This estimate is also thought to suffer from significant negative bias due to spatial heterogeneity in sampling (EC YoNAH, 2001; IWC, 2002). Therefore, although the two data scenarios are examined further to capture uncertainty, the weight of qualitative evidence supports the 'No CVI Est' scenario.

Bootstrap quantification of uncertainty

Figs 5 and 6 show bootstrap median and 90% confidence intervals for 1+ population size by breeding ground (Fig. 5) and feeding ground (Fig. 6) for the two data-related scenarios. The model for each data-related scenario is that with the lowest AIC_c in Table 6. The estimates of 1+ population size for the West Indies breeding ground are precise in recent years, as are the estimates of population size for the CVI (non-West Indies) breeding ground for the 'No proportions' data scenario. This is perhaps not very surprising given that estimates of absolute abundance are available for these years. The estimates of population size are least precise for the Atlantic Canada feeding ground because there are no estimates of absolute abundance for this feeding ground, and its abundance is determined essentially by the difference between the number of whales estimated to be on the Gulf of Maine, West Greenland, Iceland and Norway feeding grounds and the total abundance of both breeding stocks.

Figs 7 and 8 show bootstrap median and 90% confidence intervals for 1+ population size for the four feeding grounds for which absolute abundance estimates are available and for the West Indies breeding ground since 1970, along with the data points used to estimate the values for the model parameters. The results in Figs 7 and 8 confirm that the models are broadly comparable with the data used for fitting purposes. The results are, however, suggestive of an inability of the 'No Proportions' scenario to mimic the estimate of abundance for Iceland.

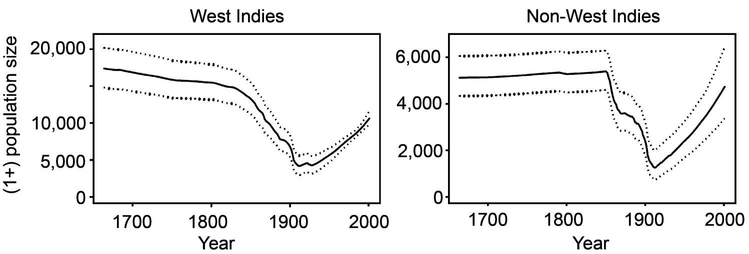
Sensitivity analyses

Table 7 lists the point estimates of population size by breeding stock in 1664 and 2001 for the models with the lowest AIC_c values (the baseline models) and for an alternate baseline model (time invariant carrying capacity) for the 'No CVI Est' data scenario ('Alt Baseline' in Table 7). An 'alternative baseline' model is considered in Table 7 because the baseline model does not provide a fit that is markedly better than this model. This table also lists the current (2001) carrying capacity for the baseline model for the data-related scenario in which the estimate of abundance for the CVI is ignored. Table 7 lists these quantities for a number of sensitivity tests.

(A) Alternative estimates of abundance for the Iceland feeding ground. The estimate of abundance for the Iceland feeding ground used in the baseline analyses (7,900) was selected by the Scientific Committee of the IWC. Alternative estimates of the abundance for the Iceland feeding ground exist (1995 – 22,305 (CV=0.59); 2001 – 14,259 (CV=0.50); Burt *et al.*, 2003) based on the NASS 95 and NASS 2001 surveys. This sensitivity test (abbreviation 'Alt Iceland ests') involves replacing the 7,900 estimate by these two estimates.

(B) Increased estimates of abundance for the West Indies. Stevick *et al.* (2003a) found that migration timing is influenced by feeding ground origin with animals from Greenland, Iceland, and Norway having later mean sighting dates in the West Indies. This raises the

(a) 'No CVI Est'



(b) 'No Proportions'

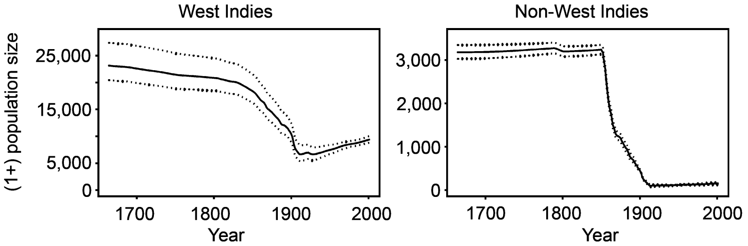
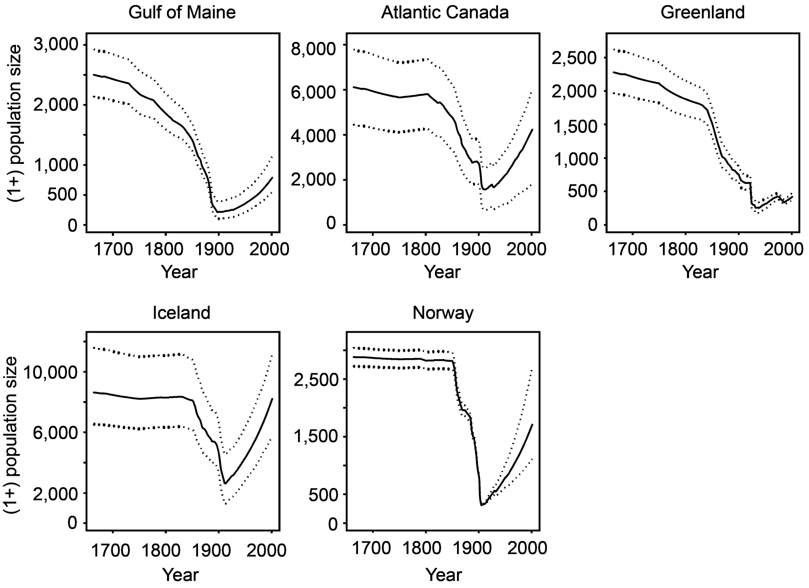


Fig. 5. Bootstrap median and 90% confidence intervals for the total (1+) population size by breeding ground.

(a) 'No CVI Est'



(b) 'No Proportions'

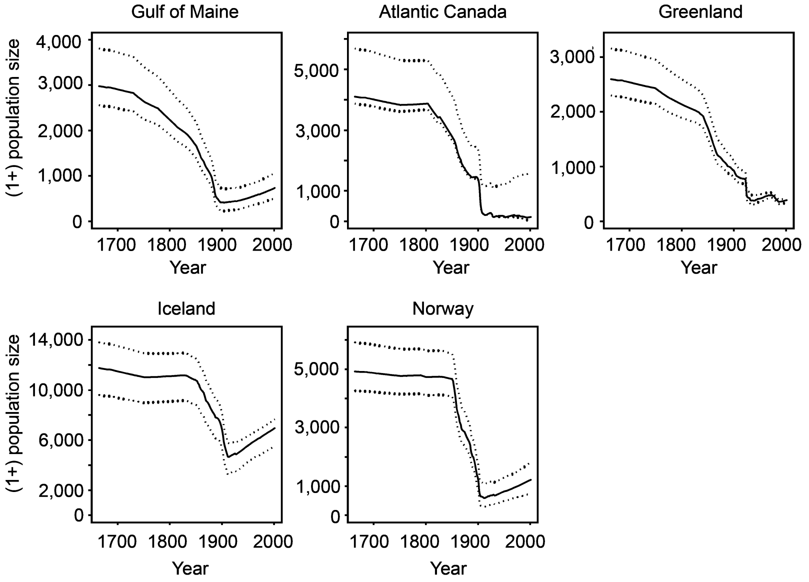


Fig. 6. Bootstrap median and 90% confidence intervals for the total (1+) population size by feeding ground.

possibility that animals from Iceland and Norway have a lower probability of capture in the West Indies because of a later arrival date and a zero probability of capture on the feeding grounds since these areas were not included in Stevick *et al.*'s (2003b) West Indies estimates. This possible heterogeneity in sampling probability would cause a negative bias in the West Indies abundance estimates. This sensitivity test (abbreviation 'Alt West Indies ests') involves increasing the estimates of abundance for the West Indies by 20%.

(C) Alternative catch series. These sensitivity tests (abbreviations 'Alt cat-C' and 'Alt cat-E') involve replacing the baseline catch series (Fig. 2) by catch series C and E.

(D) Alternative reproductive rates. This sensitivity test (abbreviation 'Alt rates') involves replacing the values for the age-specific proportion of females that have reached parturition by those based on the data collected during 1979-92 (Table 5).

(E) Ignoring the relative abundance data. This sensitivity test (abbreviation 'No rel abund') involves dropping all of the relative abundance indices from the analysis and using only the absolute abundance and proportion data. The rationale for considering this sensitivity test is that the indices for the Gulf of Maine and those for Iceland are clearly in conflict with the remaining data.

Sensitivity is not explored to survival rates for animals age one and older because the estimate of 0.96 derived for the Gulf of Maine is virtually identical to that obtained by Larsen and Hammond (2004) for West Greenland (0.957, SE=0.028).

For the 'No CVI Est' scenario, replacing the abundance estimate of 7,900 for the Iceland feeding ground by the two alternative estimates (sensitivity test 'Alt Iceland ests' in Table 7) has relatively little impact on estimates of the size of the West Indies breeding stock, but does lead to an increase in the number of animals in the Iceland feeding ground, which in turn leads to an increase in the size of the non-West Indies breeding stock. It also leads to a reduction in the number of animals estimated to occur off Atlantic Canada (current abundance of 388 compared to 4,278 for the baseline analysis). In contrast to the situation for the 'No CVI Est' scenario, replacing the estimate of abundance for the Iceland feeding ground barely impacts the results for 'No Proportions' scenario'; the fit to the data simply deteriorates.

Increasing the abundance estimates for the West Indies by 20% (sensitivity test 'Alt West Indies ests' in Table 7) leads, as expected, to larger estimates of the pre-exploitation size and (particularly) the current size of the population. However, only for the 'No Proportions' scenario is the fit of the model to the data improved if the estimates of abundance are negatively biased by 20%.

The impact of increasing the historical catches (sensitivity tests 'Alt cat-C and Alt cat-E' in Table 7) is, as expected, an increase to the pre-exploitation population size. Interestingly, the fit to the data (as quantified by the value of the negative log-likelihood) for the 'No CVI Est' scenario improves slightly when the historical catches are larger. Replacing the maturity at age estimates and dropping the relative abundance indices has only a small impact on the results.

The two baseline models imply similar pre-whaling abundances, 17,151 versus 22,647 for the West Indies population, and 5,091 and 3,152 for the Non-West Indies population. However, carrying capacity is estimated to have increased by a factor of roughly three for the baseline model that allows for time-dependent carrying capacity. The estimated present depletion from pre-whaling abundance differs between the West Indies and Non-West Indies populations. In addition, the depletion of the Non-West Indies population is very sensitive to the data scenario, being 0.05 for the 'No Proportions' scenario, but 0.95 and 0.78 for the baseline and alternate baseline models for the 'No CVI Est' scenario. For this scenario, the depletion relative to the current estimates of carrying capacity for the baseline model is 0.21 and 0.32 for the two populations, respectively. The pre-whaling abundances for the two populations together range from 22,000 to 26,000 animals for the two baseline models.

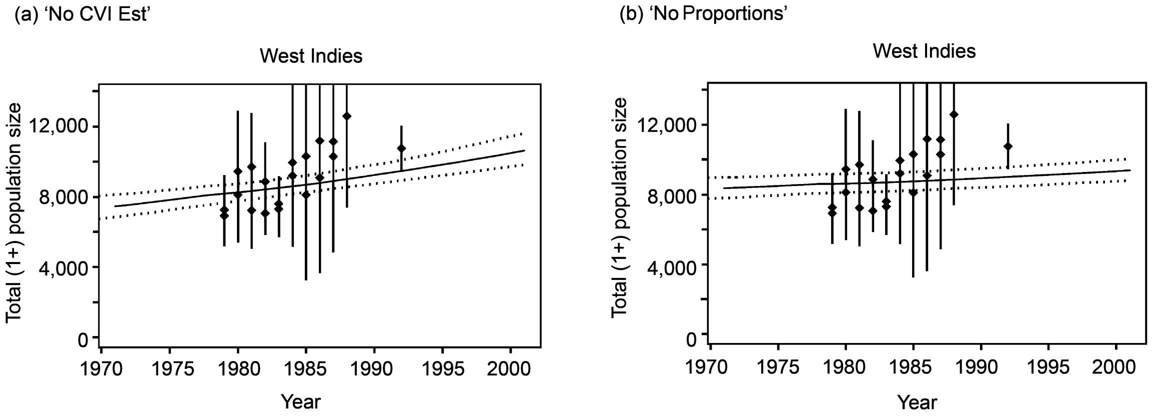
DISCUSSION

The results of the analyses of this paper confirm the increase in the number of humpback whales in the North Atlantic. Whether both the West Indies and CVI breeding stocks have increased depends on whether the estimate of abundance for the CVI of approximately 100 is a valid estimate of the current size of this stock. The West Indies breeding stock is estimated to be approaching, but still well below its historical and current carrying capacities and continued increases in abundance of this stock are likely.

The analyses in this paper are based on a model that is spatially-explicit in that it considers seven 'stocks', two breeding grounds and five feeding grounds. Most of the recent assessments of marine mammal populations (e.g. Givens *et al.*, 1995; Johnston and Butterworth, 2002; Punt *et al.*, 2004) are based on the assumption that the population being assessed is a single homogeneous unit. Johnston *et al.* (2001) account for stock mixing by allocating catches by proration in areas where multiple stocks are found and then conducting assessments for each stock separately using a single-stock assessment technique. This approach will, however, be biased if the abundance of the stocks concerned is not changing at the same rate over time. Spatially-explicit models are the basis for the operating models used to evaluate the performance of variants of the IWC's Revised Management Procedure for the North Atlantic, Southern Hemisphere and North Pacific minke whales (IWC, 1993; 2004), although only in the last case has a population dynamics model been formally fitted to the available data.

A more complex model was necessary to reconcile the data for humpback whales in the North Atlantic because of this species' complex spatial and population structure. It is not clear whether the need for a complicated spatially-structured model reflects the uniqueness of the spatial and population structure of North Atlantic humpback whales or whether there is, as yet, insufficient information for other marine mammal species to determine that similarly complicated models are needed for these species as well. It is possible that models such as those considered in this paper will become the norm for assessments of marine mammal species once there is improved information on movement patterns.

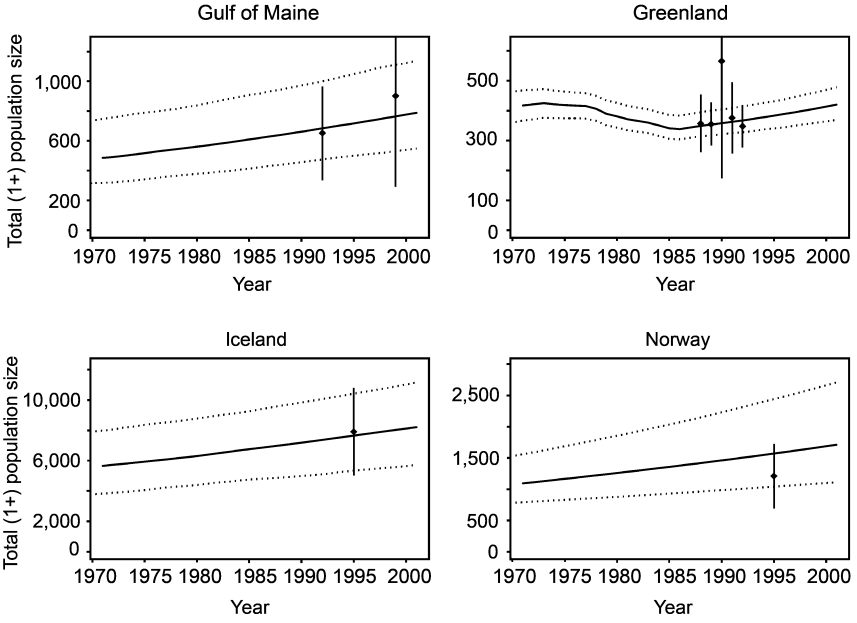
Most of the data sources for North Atlantic humpback whales are broadly consistent once allowance is made for feeding ground differences in such factors as carrying capacity changes since 1910 (Figs 3 and 4). However, some of the data sources are in conflict, as reflected by the selection of two baseline models. Thus, depending on the model, either there are substantially more humpback whales


(a) 'No CVI Est'

(b) 'No Proportions'

Fig. 7. Bootstrap median and 90% confidence intervals for the total (1+) population size for the West Indies breeding ground (1970-2001) and the data points used when fitting the model.

(a) 'No CVI Est'



(b) 'No Proportions'

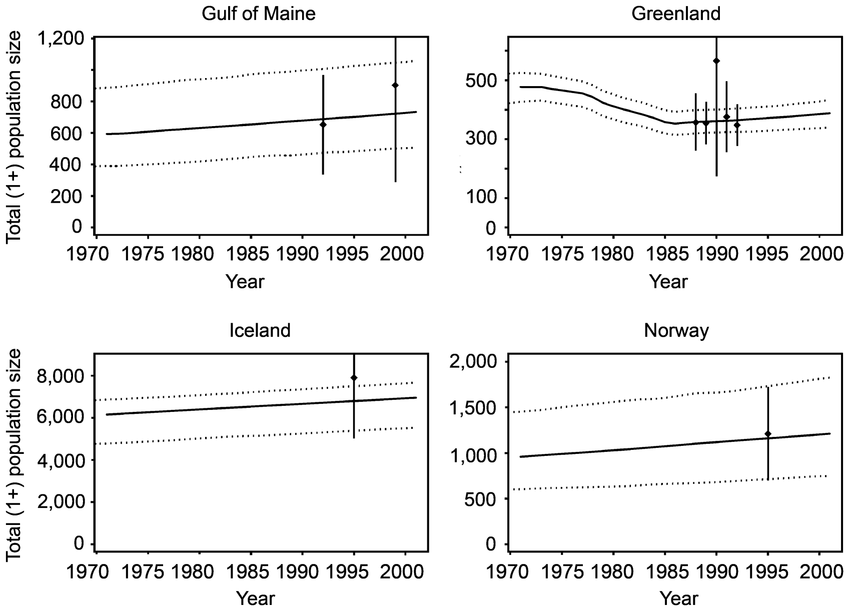


Fig. 8. Bootstrap median and 90% confidence intervals for the total (1+) population size by feeding ground (1970-2001) and the data points used when fitting the model.

using the CVI breeding area or other non-West Indies areas, or more animals that use the eastern North Atlantic feeding grounds also use the West Indies breeding ground than is suggested by the available data. Additional genetics and photographic samples from both the CVI and the eastern North Atlantic would help resolve this uncertainty.

The large differences in the estimated depletion of the CVI population between the two baseline models is related to the time-dependent carrying capacity allowed in the model. The large estimated increase in carrying capacity over the last century implies a much lower degree of depletion for the CVI population from its pre-whaling abundance. The possible causes of such implied ecosystem changes are not clear, although there has been substantial depletion of several whale and fish species in portions of the North Atlantic over the last century. As expected, the pre-whaling abundance estimates for both populations together for the several models considered were below the 'notional upper limit' (present abundance plus total catches; Holt, 2004). For all models considered, including those that explored the upper bounds on estimated catches, total pre-whaling abundance (Table 7) was substantially below the estimate of average abundance over evolutionary time scales of approximately 240,000 reported by Roman and Palumbi (2003) and criticised in IWC (2005, pp.32-4).

Even the best fitting models, however, fail to closely fit some of the data. For example, although the trend in abundance for the West Indies breeding ground is at least partially mimicked, the trend in the relative abundance for the Iceland feeding ground cannot be replicated. One possible explanation for these apparent inconsistencies is that there are more than two populations of humpback whales in the North Atlantic. For example, there may be a third stock of humpback whales in the North Atlantic, perhaps one that migrates between Iceland and Norway, a possibility suggested by winter observations of full term foetuses in northern Norway by Ingebrigtsen (1929) and by winter acoustic observations by Clark (IWC, 2002, p.232). Such a population would be consistent with observations of humpback whales in Icelandic waters throughout the winter (Gisli Víkingsson, pers. comm.). In such a case, the proportion of non-West Indies breeding animals in the Iceland and Norway feeding grounds data used when fitting the model would relate to the CVI breeding population and this putative third stock. From a modelling context, it would then be possible to include the proportion data and the CVI abundance simultaneously in the model. Preliminary explorations of such a model were encouraging, but the fits obtained were not as good as for the two stock model. This is because, although the three-stock model resolves the inconsistency between the estimates for the CVI and the proportion data, it cannot resolve problems such as the inability to mimic the trend in the estimates of abundance for the West Indies breeding ground. Further information on population structure in the eastern North Atlantic may help resolve this uncertainty.

Alternatively, it is possible that the abundance indices from Iceland pertain to only part of the whales using the Iceland feeding area. For instance, the Icelandic index was derived from fishing vessels operating to the west of Iceland, while recent abundance surveys have identified dense and variable aggregations to the north and east. Thus, long term shifts in distribution may have been occurring, perhaps related to fluctuating abundance of prey (Holst *et al.*, 2002). Further examination of the geographic distribution of both the historic catch data and the fisheries sighting data may shed light on this.

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Appendix A : The Population Dynamics Model

Basic dynamics

The dynamics of 'stock' *j* are governed by the equation:

$$N_{y+1,a}^{j,s} = \begin{cases} N_{y+1,0}^{j,s} & \text{if } a = 0 \\ N_{y,0}^{j,s}(1-\sum_k P_j^k F_y^{F,k,0}) & \\ \quad (1-\sum_k Q_j^k F_y^{B,k,0})S_0^j & \text{if } a = 1 \\ N_{y,a-1}^{j,s}(1-\sum_k P_j^k F_y^{F,k,s,1+}) & \\ \quad (1-\sum_k Q_j^k F_y^{B,k,s,1+})S_{a-1}^j & \text{if } 2 \le a < x \\ (N_{y,x-1}^{j,s}+N_{y,x}^{j,s})(1-\sum_k P_j^k F_y^{F,k,s,1+}) & \\ \quad (1-\sum_k Q_j^k F_y^{B,k,s,1+})S_x^j & \text{if } a = x \end{cases} \tag{A.1}$$

where

$N_{y,a}^{j,s}$	is the number of animals of sex *s* and age *a* in 'stock' *j* at the start of year *y*,
S_a^j	is the survival rate (from natural causes) for animals of age *a* in 'stock' *j*,
$F_y^{F,k,0}$	is the exploitation rate on calves on feeding ground *k* during year *y*,
$F_y^{B,k,0}$	is the exploitation rate on calves on breeding ground *k* during year *y*,
$F_y^{F,k,s,1+}$	is the exploitation rate on fully-selected animals of sex *s* on feeding ground *k* during year *y*,
$F_y^{B,k,s,1+}$	is the exploitation rate on fully-selected animals of sex *s* on breeding ground *k* during year *y*,
P_j^k	is the proportion of animals from 'stock' *j* that is found on feeding ground *k*,
Q_j^k	is the proportion of animals from 'stock' *j* that is found on breeding ground *k*, and
x	is the oldest considered (treated as a plus-group).

The oldest age, *x*, is taken to be the 14+ age class because fecundity, the probability of being recruited and the survival rate from natural causes is independent of age for ages greater than thirteen (see Table 5).

Births

The equation that determines the number of calves of sex *s* born to 'stock' *j* at the start of year *y* depends on the number of animals of 'stock' *j* that have reached the age-at-first-parturition, the number of animals aged 1 and older on each feeding ground, the form of the stock-recruitment relation (Ricker or Pella-Tomlinson), and whether there is depensation:

$$N_{y,0}^{j,s} = \delta f_0^j \tilde{N}_y^j \begin{cases} \sum_k P_j^k\{1+A^k[1-(\bar{N}_y^k/\bar{K}_y^k)^z]\} & \text{(A.2a)} \\ \sum_k \begin{matrix} P_j^k \exp(\ell n A^k[1-\beta\bar{N}_y^k/\bar{K}_y^k]\times \\ [1-\bar{N}_y^k/\bar{K}_y^k]) \end{matrix} & \text{(A.2b)} \end{cases}$$

where

$\tilde{N}_y^j$	is the number of mature females in 'stock' *j* at the start of year *y*:

$$\tilde{N}_y^j = \sum_a M_a N_{y,a}^{j,f} \tag{A.3}$$

M_a	is the fraction of females of age *a* that are 'mature' (i.e., have reached the age-at-first-parturition),
f_0^j	is the birth rate at pre-exploitation equilibrium for 'stock' *j*,
$N_y^{j,1+}$	is the number of 1+ animals in 'stock' *j* at the start of year *y*:

$$N_y^{j,1+} = \sum_s \sum_{a \ge 1} N_{y,a}^{j,s} \tag{A.4}$$

$K_y^{j,1+}$	is the carrying capacity of 'stock' *j* during year *y* (in terms of the number of 1+ animals),
$\bar{N}_y^k$	is the number of 1+ animals on feeding ground *k* at the start of year *y*:

$$\bar{N}_y^k = \sum_j P_j^k N_y^{j,1+} \tag{A.5}$$

$\bar{K}_y^j$	is the carrying capacity of feeding ground *k* during year *y* (in terms of the number of 1+ animals),
A^j	is the 'resilience' parameter for 'stock' *j*,
δ	is the sex ratio at birth (assumed to be 50:50 – Smith *et al.*, 1999),
β	is the parameter that determines the extent of depensation, and
z	is the 'degree of compensation' parameter (assumed to be 2.39 for the analyses of this paper).

Catches and exploitation rates

Catches are available for calves and non-calves (by sex) and separately for the feeding and breeding grounds. The exploitation rates during year *y* for 'stock' *j* are determined using the equations:

$$F_y^{F,k,0} = \frac{C_y^{F,k,0}}{\sum_j P_j^k \sum_s N_{y,0}^{j,s}}$$
$$F_y^{B,k,0} = \frac{C_y^{B,k,0}}{\sum_j Q_j^k \sum_s N_{y,0}^{j,s}(1-\sum_l P_j^l F_y^{F,l,0})} \tag{A.6a}$$

$$F_y^{F,k,s,1+} = \frac{C_y^{F,k,s,1+}}{\sum_j P_j^k \sum_{a\ge 1} N_{y,a}^{j,s}}$$
$$F_y^{B,k,s,1+} = \frac{C_y^{B,k,s,1+}}{\sum_j Q_j^k \sum_{a\ge 1} N_{y,a}^{j,s}(1-\sum_l P_j^l F_y^{F,l,s,1+})} \tag{A.6b}$$

where

$C_y^{F,j,0}$	is the catch of calves during year *y* on feeding ground *j*,
$C_y^{B,j,0}$	is the catch of calves during year *y* on breeding ground *j*,
$C_y^{F,j,s,1+}$	is the catch of non-calves of sex *s* during year *y* on feeding ground *j*, and
$C_y^{B,j,s,1+}$	is the catch of non-calves of sex *s* during year *y* on breeding ground *j*.

Initial conditions

The initial conditions (1664) correspond to a population at its pre-exploitation equilibrium size.

Appendix B : The Likelihood Function

Three sources of data (estimates of absolute abundance, relative abundance indices, and estimates of the proportion of the animals on a given feeding ground that are from the West Indies breeding ground) are available to determine the values for the 'free' parameters of the model.

Absolute abundance estimates

The contribution of the data for each of the absolute abundance indices to the negative of the logarithm of the likelihood function (ignoring constants) is given by:

$$-\ell nL = \sum_y \left\{ \ell n\sigma_y^{S,j} + \frac{(\ell n S_y^j - \ell n\hat{S}_y^j)^2}{2(\sigma_y^{S,j})^2} \right\} \qquad \text{(B.1)}$$

where

S_y^j	is the (observed) estimate of (1+) abundance for year *y* and area (a breeding or feeding ground, depending on the index concerned) *j*,
$\hat{S}_y^j$	is the model-estimate of the number of 1+ animals in area *j* at the start of year *y*, and
$\sigma_y^{S,j}$	is the observed standard deviation of S_y^j.

Relative abundance estimates

The contribution of the data for each of the relative abundance indices to the negative of the logarithm of likelihood function is given by:

$$-\ell nL = \sum_y \left\{ \ell n\sigma^S + \frac{(\ell n S_y^j - \ell n[q^S \hat{S}_y^j])^2}{2(\sigma^S)^2} \right\} \qquad \text{(B.2)}$$

where

S_y^j	is the relative abundance index for year *y* and area *j*,
$\hat{S}_y^j$	is the model-estimate of the number of 1+ animals in area *j* at the start of year *y*,
q^S	is the coefficient that relates the abundance indices to 1+ abundance, and
σ^S	is the standard deviation of S_y^j.

The values for q^S and σ^S are treated as estimable parameters when fitting the model.

Estimates of the fraction of West Indies animals

The estimate of the fraction of West Indies animals on feeding ground *j* is assumed to be normally distributed about the corresponding model prediction.

Penalty on the resilience parameters

If the resilience parameter is assumed to depend on feeding ground, the following term is added to the objective function minimised to find the values for the model parameters to constrain the extent to which resilience can differ among 'stocks'/feeding grounds:

$$\frac{1}{2CV_A^2} \sum_j \left(\ell nA^j - \ell n\bar{A} \right)^2 \qquad \text{(B.3)}$$

where

CV_A	is the inter-feeding ground coefficient of variation for the resilience parameter (assumed to be 0.2 for the calculations of this paper), and
$\ell n\bar{A}$	is the average of the ℓnA^j s.

Baleen whales in the Scotia Sea during January and February 2003

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ABSTRACT

Different species of baleen whales display distinct spatial distribution patterns in the Scotia Sea during the austral summer. Passive acoustic and visual surveys for baleen whales were conducted aboard the RRS *James Clark Ross* in the Scotia Sea and around South Georgia in January and February 2003. Identified calls from four species were recorded during the acoustic survey including southern right (*Eubalaena australis*), blue (*Balaenoptera musculus*), fin (*B. physalus*) and humpback whales (*Megaptera novaeangliae*). These acoustic data included up calls made by southern right whales, downswept D and tonal calls by blue whales, two possible types of fin whale downswept calls and humpback whale moans and grunts. Visual detections included southern right, fin, humpback and Antarctic minke whales (*B. bonaerensis* sp.). Most acoustic and visual detections occurred either around South Georgia (southern right and humpback whales) or south of the southern boundary of the Antarctic Circumpolar Current (ACC) and along the outer edge of the ice pack (southern right, blue, humpback and Antarctic minke whales). Fin whales were the exception, being the only species acoustically and visually detected primarily in the central Scotia Sea, along the southern ACC front. In addition to identifiable calls from these species, two types of probable baleen whale calls were detected: 50Hz upswept and pulsing calls. It is proposed that minke whales may produce the pulsing calls, based on their similarities with minke whale calls recorded in the North Atlantic Ocean. There was an overlap between locations of fin whale sightings and recordings and locations of 50Hz upswept calls in the central Scotia Sea, but these calls were most similar to calls attributed to blue whales in other parts of Antarctica. More study is required to determine if baleen whales produce these two call types, and if so, which species. The efficiency of acoustics and visual surveys varied by species, with blue whales being easier to detect using acoustics, Antarctic minke whales being best detected during visual surveys and other species falling in between these two extremes.

KEYWORDS: BALEEN WHALES; SURVEY-ACOUSTIC; SURVEY-VESSEL; ANTARCTIC; SOUTHERN RIGHT WHALE; BLUE WHALE; FIN WHALE; HUMPBACK WHALE; ANTARCTIC MINKE WHALE; OCEANOGRAPHY

INTRODUCTION

South Georgia was one of the prime commercial whaling grounds in the early 20th century and during this time most stocks of baleen whales were depleted from the area (Moore *et al.*, 1999). According to International Whaling Commission (IWC) records, the total numbers of baleen whales taken from Area II (which encompasses the area from 0 to 60°W south of 40°S, including South Georgia and the Scotia Sea; see Fig. 1a) since 1931 were 518 southern right (*Eubalaena australis*), 32,810 blue (*Balaenoptera musculus*), 149,678 fin (*B. physalus*) and 1,305 humpback whales (*Megaptera novaeangliae*). These data, however, do not include Soviet catches since World War II, which were often falsely reported until the 1990s, slightly overestimating blue and fin whale and grossly underestimating humpback whale catches (Yablokov, 1994). While there are no current population estimates for Area II, the total whale sightings during four summer-season IWC cruises in Area II in the 1980s and 1990s (Branch and Butterworth, 2001a) were 14 southern right, 18 blue, 31 fin, 38 humpback and 1,621 Antarctic minke whales (*B. bonaerensis* sp.).

The focus of the JR82 cruise aboard the RRS *James Clark Ross* was to study the large scale distribution and transport of Antarctic krill (*Euphausia superba*), as well as ecosystem dynamics of the Scotia Sea (Anon., 2003). The study area links two well studied and krill-rich regions of the Southern Ocean, the Antarctic Peninsula and South Georgia, that have been the focus of ecosystem research since the Discovery expeditions of the 1930s (e.g. Mackintosh, 1936). In the Scotia Sea, the Antarctic current system loops north, steered away from the winter pack ice zone by the bathymetry and the Antarctic Peninsula land mass projection (Orsi *et al.*, 1995). This region features both high rates of primary productivity and high densities of krill in spring and summer (El-Sayed and Weber, 1982; Priddle *et al.*, 1988; Hewitt *et al.*, 2004; Holm-Hansen *et al.*, 2004). In addition to the work in the Scotia Sea, the cruise included a fine-scale sampling section near South Georgia, in the Western Core Box (WCB), part of the British Antarctic Survey's (BAS) long-term fine-scale ecological monitoring program (Reid *et al.*, 2000).

The goal of the marine mammal acoustic monitoring programme during JR82 was to conduct an along-track passive acoustic survey for cetaceans using opportunistic deployments of sonobuoys. These recordings can provide insight into the acoustic repertoire as well as the spatial distribution of various species of cetaceans. The acoustic survey was focused on southern right, blue, fin, humpback and minke whales, since calls from these species have not previously been reported in this area. In other locations, each species produces distinctive low-frequency (<1kHz) calls, which are the only calls that have been analysed in this study. During daylight hours there was concurrent visual survey for cetaceans conducted by a team of two experienced IWC observers.

The majority of previous cetacean visual surveys in the Scotia Sea have been conducted under the auspices of the IWC in collaboration with German, US and UK polar and multidisciplinary research programmes, e.g. as part of Commission for the Convention on Antarctic Marine Living Resources (CCAMLR) and Southern Ocean Global Ocean Ecosystem Dynamics (SO-GLOBEC) studies (Kasamatsu *et al.*, 1988; 1996; Pankow and Kock, 2000; Reid *et al.*, 2000; Secchi *et al.*, 2001; Reilly *et al.*, 2004). Generally, blue and

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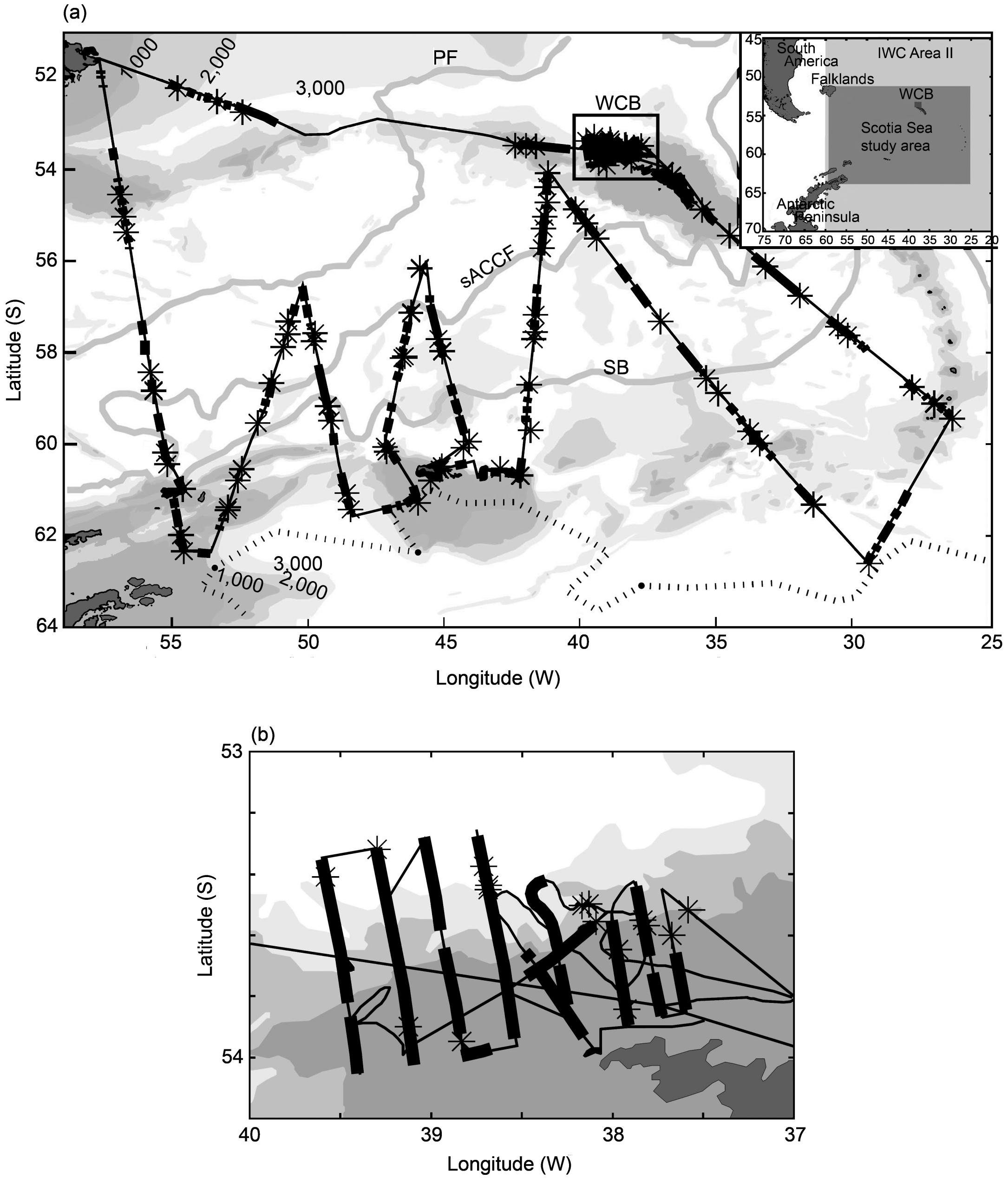

Fig. 1. Cruise track across (a) the Scotia Sea and (b) the Western Core Box (WCB), with locations of sonobuoy deployments (stars) and tracks of visual survey effort (thick line segments). Bathymetry is shaded in 1,000m isobath increments and land is the darkest shading. Thick grey lines represent major fronts in the area, after Orsi *et al.* (1995): PF = polar front; sACCf = southern Antarctic Circumpolar Current front; SB = southern boundary of the ACC. The broken black line is the inferred ice edge (15% cover) on 1 February 2003 from the NSIDC satellite image. Inset image shows a larger area including nearby continents and indicating locations of surveys, as well as IWC Area II.

Antarctic minke whales are known to occur further south than fin whales, which are not commonly associated with sea ice; humpback whales can occur over a range of latitudes and southern right whales occur near island groups (Kellogg, 1929; Kasamatsu *et al.*, 1988; 1996; Moore *et al.*, 1999). Whaling records also indicate that blue, fin and humpback whales associate with the southern boundary of the Antarctic Circumpolar Current (ACC; Tynan, 1998). All of these species have been sighted previously in the Scotia Sea. Fin whale sightings occurred further to the north of humpback whales in the vicinity of Elephant Island in December 1996 (Pankow and Kock, 2000). Minke whale sightings were common east of the Antarctic Peninsula, while humpback whale sightings were common around South Shetlands and South Georgia in surveys conducted from 1997 to 2000 (Secchi *et al.*, 2001; Reilly *et al.*, 2004).

Call characteristics

Calls of some baleen whale species have been studied extensively (reviewed in Richardson *et al.*, 1995). Calls from southern right whales off Argentina have been described by many authors (e.g. Cummings *et al.*, 1971; 1972; Payne and Payne, 1971; Clark, 1982; 1983). The most commonly described southern right whale call is the up call, sweeping in frequency from 50 to 200Hz and lasting 0.5-1.5s. This call has been associated with swimming animals and appears to be a contact call (Clark, 1983). Blue whales make low frequency (below 100Hz), long duration (10-20s), repetitive calls that vary between regions (Kibblewhite *et al.*, 1967; Edds, 1982; Alling *et al.*, 1991; Stafford *et al.*, 1998; McDonald *et al.*, 2006) and they also produce a shorter and less stereotyped call (D call) whose general characteristics are consistent between regions (Thompson *et* *al.*, 1996; Thode *et al.*, 2000; McDonald *et al.*, 2001; Mellinger and Clark, 2003; Rankin *et al.*, 2005). There are no blue whale recordings from the South Atlantic Ocean, but blue whale calls have been recorded south of 60°S in the region between 0-30°W and at 38°W in the Weddell Sea (Ljungblad *et al.*, 1998; Clark and Fowler, 2001). These calls consist of three segments: a 28Hz tone that lasts approximately 8s, immediately followed by a short (1s) downsweep to 19Hz and a slightly downswept tonal from 19 to 18Hz, lasting about 8s. The same type of call has been reported at other locations around Antarctica (Matsuoka *et al.*, 2000; Širović *et al.*, 2004; Rankin *et al.*, 2005), although all three components may not always be present. Rankin *et al.* (2005) suggested the '28Hz tonal' is the identifying feature. Fin whales produce regular, short (1s duration) downsweeps ranging in frequency from approximately 40 to 15Hz, the exact frequency range and repetition rate dependant on the geographic location (Thompson *et al.*, 1992). These calls occur throughout the Northern Hemisphere (Watkins, 1981; Edds, 1988; McDonald *et al.*, 1995), but the only report from the Southern Hemisphere is from the Western Antarctic Peninsula (Širović *et al.*, 2004). Stafford *et al.* (1999) recorded pulse series similar to calls produced by fin whales south of the equator in the eastern tropical Pacific, however fin whale sightings are rare in this area (Wade and Gerrodette, 1993). There have also been reports of higher frequency (75-40Hz) calls produced by fin whales from the North Atlantic (Watkins, 1981).

Humpback whales are acoustically among the best studied baleen whale species (e.g. Payne and McVay, 1971; Winn and Winn, 1978; McSweeny *et al.*, 1989; Clapham and Mattila, 1990; Helweg *et al.*, 1998; Cerchio *et al.*, 2001). Even though songs from low-latitude breeding grounds have been the focus of most research, there is evidence of singing from high-latitude feeding grounds (Mattila *et al.*, 1987; McSweeny *et al.*, 1989; Clark and Clapham, 2004). In the Southern Hemisphere, recent acoustic work on humpback whales has included Atlantic, Indian and Pacific waters (Helweg *et al.*, 1998; Noad *et al.*, 2000; Cato *et al.*, 2001; Razafindrakoto *et al.*, 2001; Darling and Sousa-lima, 2005). Leaper *et al.* (2000) reported 'moan' type calls from humpback whales off South Georgia, but otherwise humpback whale calls in the Antarctic are under-sampled. Antarctic minke whales in the Ross Sea produce very short downsweeps (~0.3s) that have variable starting and ending frequencies, generally between 130 and 60Hz (Schevill and Watkins, 1972; Leatherwood *et al.*, 1981). Other minke whale recordings from the Southern Hemisphere are not of the Antarctic minke, but of the dwarf minke whale (*B. acutorostrata*) from lower latitudes and generally include more complex and higher frequency calls (Gedamke *et al.*, 2001). No calls from any of these species have been reported previously from the Scotia Sea since past acoustic surveys in the area focused on frequencies higher than 300Hz and did not focus on baleen whales (Leaper and Scheidat, 1998; Leaper *et al.*, 2000). Although knowledge of baleen whale calling in this area is scant, whaling data indicate that it was once a very productive whaling ground and that it was historically abundant in baleen whales (Kellogg, 1929; Mackintosh, 1966; Horwood, 1986).

METHODS

The JR82 cruise departed Stanley, Falkland Islands, on 7 January 2003. Eight long transects across the Scotia Sea from north of the southern Antarctic Circumpolar Current front (sACCf) to approximately 63°S were completed during the first part of the cruise along 4,300 miles of transect (Anon., 2003). During the second stage of the cruise, four pairs of 80km transects were conducted in the WCB (Fig. 1b). Data collected during the cruise included: conductivity-temperature-depth profiles, expendable bathythermograph profiles, acoustic Doppler current profiler data, nutrient analyses, phytoplankton biomass, primary production, krill abundance and growth. Sonobuoys were deployed when marine mammals were visually detected, prior to arrival to oceanographic stations, as well as occasionally throughout the cruise. The visual survey was conducted during daylight hours when weather conditions were favourable. The JR82 cruise ended on 23 February 2003 in Stanley, Falkland Islands.

Acoustic survey

Two types of sonobuoys were used during this cruise due to their differences in direction-finding capabilities and frequency response characteristics. Omnidirectional sonobuoys (AN/SSQ-57B) have a broadband frequency response of 10-20,000Hz, but it is not possible to determine the direction of the sound source using individual omnidirectional sonobuoys. DIFAR (directional frequency analysis and recording; AN/SSQ-53D) sonobuoys, in contrast, have directional detection capabilities within individual sonobuoys and a frequency response of 10-2,400Hz. Sound bearing relative to the sonobuoy can be determined from direction sensors and an internal compass located within the sensor package of the DIFAR sonobuoys (McDonald, 2004). Sonobuoy specifications require the bearing error to be less than 10°. Using these bearings, acoustic data can be correlated to visual observations of marine mammals.

Custom electronics and software were used to record and analyse the sonobuoy data. The antenna used for the reception of the sonobuoy radio signal during the cruise was a 160MHz omnidirectional *Cushcraft Ringo Ranger* ARX-2B. The maximum range for the radio transmission during the cruise was approximately 8 n.miles, but was variable dependant on weather conditions. A software controlled *ICOM* IC-PCR1000 scanner radio receiver, modified to provide improved low frequency response, for reception of sonobuoy signal (frequency response from 10-1,000Hz ±1dB) was used. Data were recorded continuously on digital audiotapes while receiving the signal using a *Sony* PCM-M1 digital audio recorder (frequency response from 20-22,000Hz ±1.0dB at 48kHz sample rate) and reviewed in real-time using the *SpectraPlus* software package. When DIFAR sonobuoys were deployed, bearings to interesting sounds were calculated in real-time using Greeneridge Sciences DIFAR demultiplexing software and beam forming code developed by M. McDonald. Upon each deployment the following were recorded: time, latitude, longitude and depth at deployment; sonobuoy type, channel, time and depth settings; speed of the ship; and the reason for deployment. After deployment, the sonobuoys transmitted their radio signal to the underway ship for a maximum of 8h before scuttling and sinking.

During the post-processing analyses, recordings of interest were reviewed using *SpectraPlus* with 32,768-point Fast Fourier Transform (FFT), 90% overlap and a Hanning window. Periods that were not monitored in real-time during the cruise were reviewed. Frequency and temporal characteristics were measured for calls with a good signal-to-noise ratio (SNR) using the above spectral parameters. For southern right whale up calls, both types of fin whale calls, blue whale D calls and 50Hz upswept calls, the starting and ending frequency and the duration of the calls were measured. The middle point of the tonal frequency was measured for blue whale calls along with the duration of the call and it was also noted if the downswept part of the call was present. Intercall interval was measured for blue whale 28Hz tonal, fin whale low and high frequency and 50Hz upswept calls. For pulsing calls, the energy band over which pulsing occurred was measured and the pulse duration and rate were calculated. The averages and standard deviations for all call characteristics were reported. Due to the variability in the duration of blue whale D calls, the duration range was also reported and the locations at which different call types occurred were plotted. *Ishmael* software (Mellinger, 2001) was used for verification of bearing calculations, as well as the calculation of bearings to additional calls. All reported bearings are in true degrees. Data were decimated before making spectrograms of representative calls.

The noise levels from the RRS *James Clark Ross* were generally low and decreased as the ship moved away from the sonobuoy. The noise did not affect the quality of recordings, except when using the bow thrusters at stations. As most of the cruise took place in ice-free waters, there was no ice breaking noise to decrease the SNR. The data from periods when the noise of the ship was too loud to distinguish possible calls were not used for analyses.

Comparison with visual survey

Acoustic data were compared to the visual sightings data (the two data sets, however, were not collected independently). Two experienced observers conducted the visual survey during all daylight hours according to a standard line transect methodology for cetaceans (Buckland *et al.*, 2001). Each observer's search area included a 90° arc from the trackline to abeam of the ship and extending all the way to the horizon. Search was conducted in passing mode with *Fujinon* 7×50 binoculars from the bridge roof (eye height 18.3m). *Nikon* 10×50 binoculars were available for species identification and group size estimation. Sightings data were entered into a laptop computer running the *WinCruz* software program, recording casual-effort and off-effort sightings separately. Sightings data reported here were collected while observers were on full-effort, unless otherwise stated. For fin and southern right whales the sightings of 'like fin' and 'like right whale' were pooled together with the confirmed sightings of their respective species. For minke whales, sightings of the following categories were pooled: 'minke (ordinary)'; 'like minke'; 'like ordinary minke'; 'undetermined minke'.

Acoustic and visual data were compared to oceanographic and sea ice data. The positions of mean locations of three main oceanographic fronts (Polar Front, PF; sACCf; and the southern boundary of the ACC, SB) were obtained from Orsi *et al.* (1995). The location of the ice edge (defined as 15% or less sea ice cover) on 1 February 2003 was determined from the National Snow and Ice Data Centre (NSIDC) daily sea ice concentration satellite image with 25km resolution (Comiso *et al.*, 1991). Locations of these features were plotted on the same maps as the locations of visual and acoustic whale detections for qualitative comparison.

RESULTS

A total of 107 sonobuoys (80 omnidirectional and 27 DIFAR) were deployed during the JR82 cruise and there were 167 hours total of acoustic effort (Figs 1a and 1b). Of the deployed sonobuoys, four DIFARs and 12 omnidirectionals failed (15% failure rate for each type). Baleen whale calls detected during the cruise included: southern right whale up calls (Fig. 2a); blue whale 28Hz tonal and D calls (Figs 2b and c); low and high frequency fin whale calls (Figs 2d and 2e); and humpback whale calls (Fig. 2f). Two types of calls were acoustically detected that cannot be attributed to a particular species, but, since we propose they are likely to come from baleen whales, their characteristics are described and locations of occurrence are also shown. These calls were referred to as 50Hz upswept and pulsing calls (Figs 2g and 2h). Calls from sperm whales, as well as some other unidentified odontocetes were recorded during the cruise, but were not analysed for this paper. The visual survey resulted in 220 hours of survey effort and a total of 217 sightings of groups or individuals. Baleen whales sighted were: southern right, fin, sei (*B. borealis*), humpback and minke whales.

Southern right whales

Southern right whales were detected visually and acoustically at three locations: in the vicinity of the South Orkneys; in the vicinity of South Georgia; and in the southeastern Scotia Sea (Fig. 3a). There was a total of 20 sightings of 33 southern right whales while the only call type recognised as a southern right whale call was the up call (Fig. 2a). Southern right whales were detected twice visually and acoustically during the same time, but during every southern right whale occurrence other species of whales were sighted in the vicinity as well. During one such visual encounter, on 13 February 2003, a deployment of a directional sonobuoy made it possible to calculate bearings to calling whales. They were compared to locations of the two groups of southern right whales detected by the visual observers (who were off-effort at the time) and it was found that the bearing of one group of three calls at 165±8° corresponded to the bearing of one of the two visually detected groups, which were observed at 176° and 260°. A group of 14 sei whales was detected by the observers during the same time period at 235°.

A total of 31 up calls from three different days of recordings were measured to determine their temporal and frequency characteristics. The average starting frequency of the calls was 92±11Hz, the ending frequency was 173±11Hz and the average duration was 0.7±0.1s. The average sweep rate of the up calls was 125±24Hz s^{-1}.

Blue whales

Most blue whale acoustic detections occurred along the southern edges of the survey area in the Scotia Sea, with two detections in the northern area closer to South Georgia (Fig. 3b). There were no blue whale sightings throughout the cruise, so it was not possible to relate any of these acoustic detections to visual ones. Two different call types detected during the JR82 cruise were from blue whales, the 28Hz tonal call and the D call. Blue whale 28Hz tonal calls were detected on seven sonobuoys and temporal and frequency characteristics were analysed from 29 calls. Generally, only the flat, 27.7±0.1Hz tonal component was visible, lasting an average of 8±1s (Fig. 2b) and the average intercall interval was 65s. The downswept part ('28Hz downsweep' in Rankin *et al.*, 2005) was visible in 14 analysed calls. D calls occurred on five sonobuoys and four of these also had 28Hz tonal detections (Fig. 3b). Fifty D calls from four sonobuoys were analysed. These calls varied in duration from 1.0-3.7s (with average 2.1±0.8s) and their frequency changed from 80±8Hz to 38±7Hz (Fig. 2c). The average sweep rate was

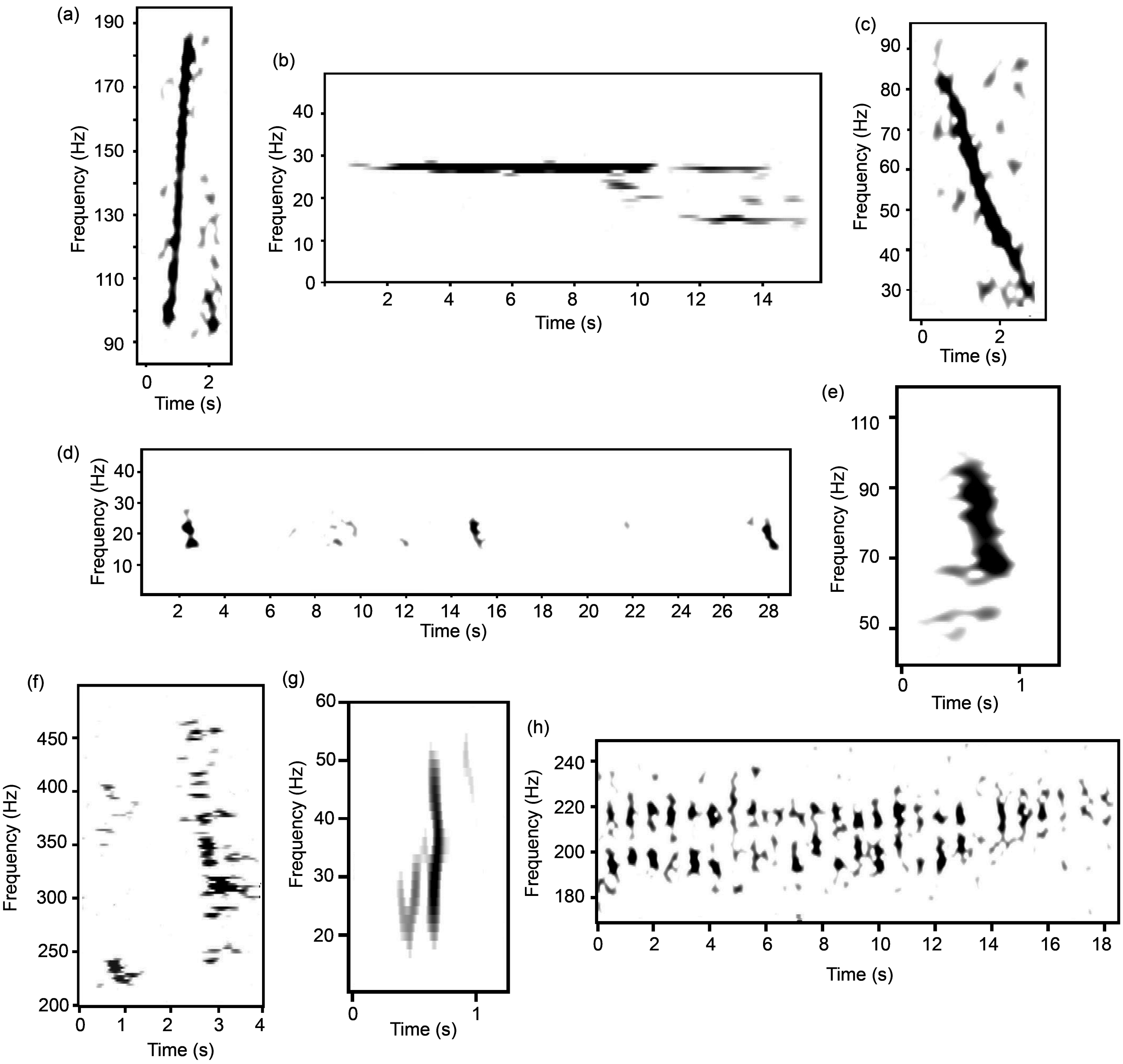

Fig. 2. Spectrograms of calls recorded during JR82 cruise: (a) southern right whale up call (600-point FFT, 99% overlap, Hanning window); (b) blue whale 28Hz tonal call (parts of the downsweep and the second tonal are also visible; 2,400-point FFT, 95% overlap, Hanning window); (c) blue whale D call (1,200-point FFT, 99% overlap, Hanning window); (d) fin whale low frequency call (900-point FFT, 95% overlap, Hanning window); (e) fin whale high frequency call (300-point FFT, 99% overlap, Hanning window); (f) sample of humpback whale calls (600-point FFT, 95% overlap, Hanning window); (g) unidentified 50Hz upswept call (100-point FFT, 99% overlap, Hanning window); (h) unidentified pulsed calls (600-point FFT, 99% overlap, Hanning window).

23±10 Hz s^{-1}. Five out of 50 analysed D calls started with a short upsweep in frequency and one started with a flat tone before the main, downswept part. The flat tone was at the same frequency as the beginning of the downsweep and the upsweeps were variable in their duration and frequency range. These calls did not have regular intercall intervals.

Blue whale calls were detected on two occasions on directional sonobuoys, on 26 and 30 January 2003. Bearings to both 28Hz tonal and D calls were calculated on 26 January. Bearings to seven 28Hz tonals were calculated around 19:30 GMT, while the ship was on the 110° heading, and were found to belong to at least two different animals with bearings 10±18° (calculated from 3 calls) and 335±10° (from 4 calls). There were no D calls at this time. Bearings to four 28Hz tonal calls around 21:00 GMT were found to be 319±7°, while bearings to four D calls during that period were 313±5°. The ship's bearing during this time was 90°. On 30 January it was possible to determine the bearings to four 28Hz tonal calls over a one-hour period and they changed between 147° and 128°. The ship's bearing during this period was steady at around 270°.

Fin whales

In general, sightings of fin whales occurred in the central Scotia Sea and correspond well to areas where two types of fin whale calls were detected on 10 sonobuoys (Fig. 3c). Low frequency fin whale calls were detected on eight of these sonobuoys, all of them deployed in the central Scotia Sea. A total of 49 low frequency fin whale calls were measured to determine their frequency characteristics. The calls were repetitive downsweeps in frequency from 31±2Hz to 15±1Hz (Fig. 2d). Downsweeps lasted on average 0.7±0.1s and had a sweep rate of 25±4Hz s^{-1} and intercall intervals of 13.0±0.9s. On five occasions fin whale sightings were made within an hour of call recordings and once other identified species of cetaceans (pilot whales,

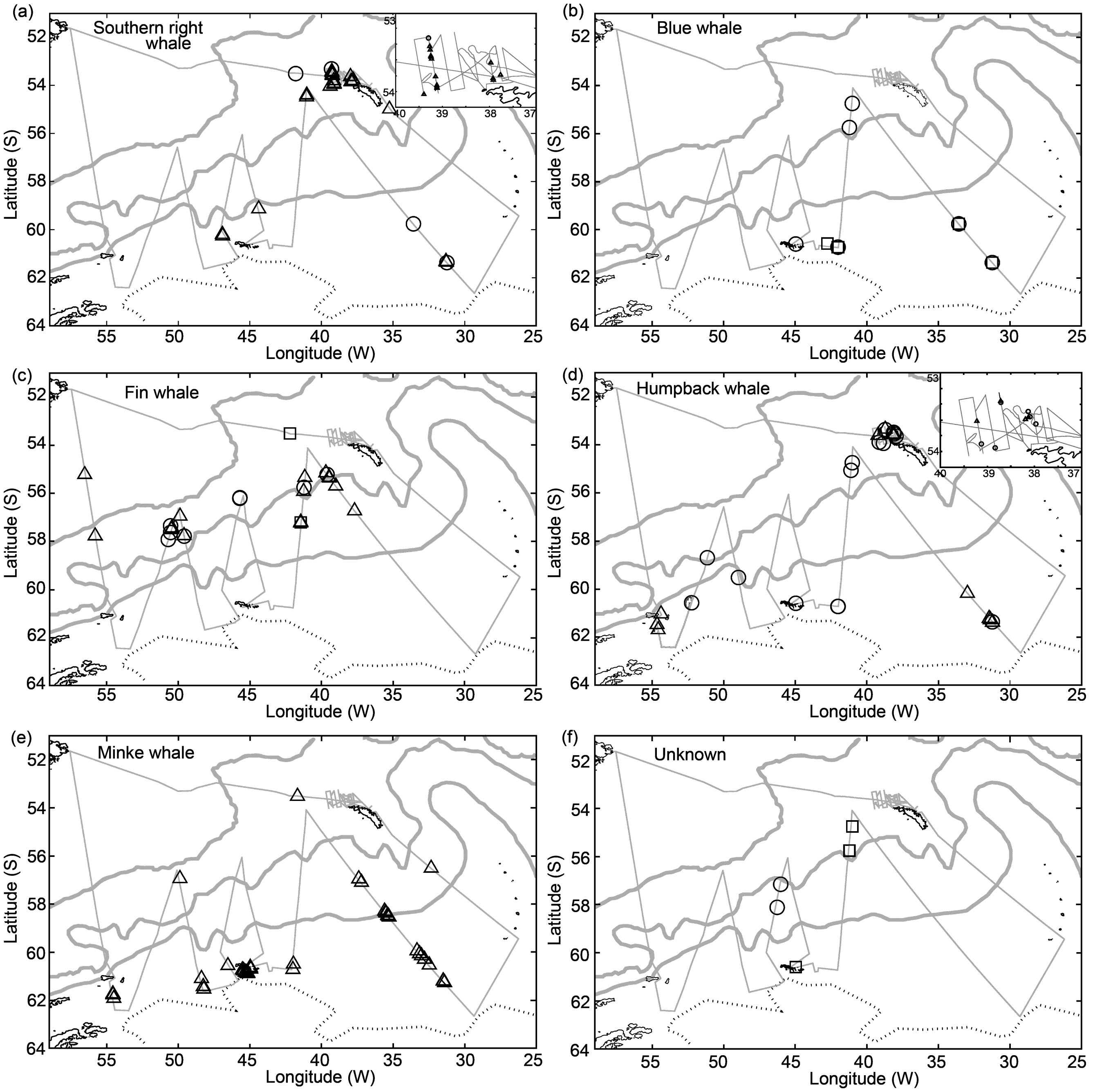

Fig. 3. Locations of acoustic (circles and squares) and visual (triangle) sightings: (a) southern right; (b) blue (circles are tonal call and squares D call locations); (c) fin (circles are low frequency and squares high frequency call locations); (d) humpback; (e) minke whales; (f) locations of 50Hz up (circles) and pulsing calls (squares). Insets on (a) and (d) show sightings in the WCB. Thin grey line is the cruise track, thick grey lines represent major fronts in the area: PF; sACCf; SB and the broken black line is the inferred ice edge on 1 February 2003 from the NSIDC satellite image (same as Fig. 1).

Globicephala melas and hourglass dolphins, *Lagenorhynchus cruciger*) were sighted. Fin whale calls were recorded twice by directional sonobuoys, but the visual observers sighted no fin whales at those times.

Higher frequency fin whale calls were detected by two additional sonobuoys (Fig. 3c). For both occurrences of these calls there were no lower frequency fin whale calls, but only fin whales were visually detected within an hour before or after the acoustic detection. One of these sightings was during a period when the visual observers were not on full-effort. Only 14 calls of this type were available for analysis. They were regularly repeated downswept calls that ranged on average from 102±15Hz to 51±3Hz over 0.6±0.1s, with the average sweep rate of 80±17Hz s^{-1} (Fig. 2e). Their intercall interval was 4.6±0.9s. Unfortunately, both recordings of the high frequency calls were made on omnidirectional sonobuoys so it was impossible to relate them to the visual fin whale detections. During the cruise, visual observers sighted 15 groups of fin whales, for a total of 36 animals.

Humpback whales

The areas where humpback whale calls were detected acoustically generally corresponded to areas of humpback sightings: around South Georgia, near the South Shetland Islands in the southwest, as well as in the southeast corners of the surveyed area (Fig. 3d). The calls attributed to humpback whales during this cruise were a variety of grunts and moans ranging approximately 100-600Hz (Fig. 2f). Grunts and moans that were detected repetitively in the above frequency range and lasted longer than 1s and that could not be attributed to any other species were subjectively assigned as humpback whale calls. Humpback whale calls were detected on 15 sonobuoys deployed during the cruise (Fig. 3d). A total of 12 groups and 38 humpback whales were visually detected during the JR82 cruise.

Minke whales

A total of 43 groups (76 total animals) of minke whales were visually detected during the JR82 cruise, most of them along the southern edge of the survey area close to the ice edge. No confirmed Antarctic minke whale calls were detected (Fig. 3e). In the southeastern section of the survey area, minke whales were seen further away from the ice edge, in the central sector of the Scotia Sea.

Other calls

Two other call types were heard on sonobuoys on multiple occasions, 50Hz upswept and pulsing calls. They cannot be linked positively to a particular baleen whale species, but it is likely that baleen whales produced these calls, as they contain typical baleen whale call characteristics: low-frequency and repetitiveness.

The 50Hz upswept calls were recorded by two sonobuoys deployed in the central Scotia Sea (Fig. 3f). There were no visual sightings of whales near the sonobuoys on which these calls were heard and there were higher frequency odontocete calls on one of the sonobuoys deployed nearby. The 50Hz upswept calls did not coincide with any other baleen whale calls. It was possible to determine frequency and temporal characteristics of 12 of these calls and they generally started at 26±4Hz, ended at 52±4Hz and lasted 0.5±0.1s (Fig. 2g). They were repeated at intervals ranging 62-78s, with usually 2-3 calls in a sequence.

Pulsing sounds were detected on three occasions (Fig. 3f). The pulsing was concentrated mainly in the 140-240Hz energy band, but it was highly variable within a pulsing bout (Fig. 2h). The average pulse duration and rate were calculated using 44 individual pulses and the duration was 0.31±0.04s while the pulse rate was 1.8±0.2pulses s^{-1}. The pulses were equally spaced throughout a call series and there was no evidence of slowing down or speeding up through the series. All three times these calls were detected by the same sonobuoys as blue whale 28Hz tonal calls and twice they were acoustically detected on the same sonobuoys as humpback whale calls.

DISCUSSION

This acoustic survey for baleen whales was the first of its type to be conducted in the Scotia Sea. In addition to multiple recordings of known baleen whale calls, two call types from unknown sources were recorded. The acoustic survey, in conjunction with the visual survey, enabled assessment of the spatial distributions of southern right, blue, fin, humpback and Antarctic minke whales in the area and comparison of the differences among the species. More work on call rates, gender bias and seasonal variation in calling is needed, however, to determine whether acoustics can be used to obtain reliable abundance estimates.

Sources of calls

Acoustic surveys offer an opportunity to study baleen whales even when whales are not available for observation by more traditional visual survey methods (e.g. due to darkness, high sea-state, low visibility). One of the problems acoustic surveys face is that calls cannot always be linked reliably to a particular species of whale since the animals often are not simultaneously seen and heard. Sometimes, however, it is possible to link the bearing of a calling animal and a visual sighting of a known species.

Up calls are well documented to be produced by southern right whales at other locations in the Southern Hemisphere (Cummings *et al.*, 1971; Payne and Payne, 1971; Clark, 1982; 1983). Southern right whales were also heard using directional sonobuoy and seen concurrently on one occasion during the cruise. Even though a group of sei whales was visually detected in the vicinity at the same time, they were at a different bearing to the detected calls. While little is known about sei whale calls, McDonald *et al.* (2005) reported sei whale calls off the Antarctic Peninsula to be of a higher frequency (around 200Hz) and have different characteristics to the up call reported here. The similarity of the calls detected during this survey to calls attributed to southern right whales in other reports and the evidence from the bearing measurements taken from acoustic and visual detection of these animals during this cruise, are strong evidence that southern right whales produced these up calls.

Since no blue whales were sighted during this cruise, previous reports of their calls in the Antarctic were relied upon to link the sounds heard to blue whales. Rankin *et al.* (2005) suggest that the 28Hz tonal call, similar to ones heard on multiple sonobuoys during this cruise, are a diagnostic feature in detecting blue whales. Given the flat tonal nature of the call, one possible mistake would be to confuse the ship's noise for a blue whale tonal, since the ship produced a tone at 27Hz while the bow thrusters were on at sampling stations. In this study additional identifying features were used, such as predictable repetitiveness of the call (Širović *et al.*, 2004), duration of the tonal being less than 10s or the presence of the downswept part of the call (28Hz downsweep, after Rankin *et al.*, 2005). Also, when possible, bearings were calculated to the 28Hz tonal calls and compared to the ship's bearing. Even though it is possible a calling blue whale and the ship could be on the same bearing, in instances when this happened we erred on the side of caution and did not report a blue whale call. From calls recorded while at sampling station with bow thrusters on, only ones that satisfied at least two of the above conditions were reported. The presence of 28Hz tonal calls was analysed independently of the presence of D calls and it was found that the two types of calls coincided at four sonobuoys. Downsweeps similar to these D calls have been reported as coming from blue whales at other locations worldwide (Thompson *et al.*, 1996; McDonald *et al.*, 2001; Mellinger and Clark, 2003; Rankin *et al.*, 2005). Confusion of blue whale D calls with calls from other species is more likely than for 28Hz tonals. Southern right whales, for example, are known to produce some low frequency downswept calls (e.g. Cummings *et al.*, 1972; Clark, 1983), but these are generally in the 200-100Hz frequency range and last less than 1.5s. Thus though there is some overlap with the location of right whale calls and blue whale D calls, it is not likely that the 1.0-3.7s duration calls heard in the frequency range below 100Hz can be attributed to southern right whales, but are indeed blue whale D calls. Confusion with high frequency fin whale calls is avoided because D calls are of a longer duration and are not repeated at regular intervals.

The fin whale calls recorded could not be linked to visual sightings of these animals, but the low frequency calls are similar to those reported for fin whales at other worldwide locations (Walker, 1963; Edds, 1988; Thompson *et al.*, 1992), although they differ from calls reported off the Western Antarctic Peninsula in their absence of the 89Hz component (Širović *et al.*, 2004). The high frequency calls are similar to the fin whale calls reported by Watkins (1981) but the frequencies are higher here (downsweep from 105 to 50Hz compared to 75 to 40Hz) and the duration is longer (0.6s compared to 0.3s). Two incidental sightings of fin whales around the time of these calls strengthens the case that fin whales produced these calls and their distribution followed the general pattern of fin whale distribution in the central Scotia Sea.

Calls similar to both 50Hz upswept and pulsing calls have been reported previously as having been produced by baleen whales (Winn and Perkins, 1976; Mellinger *et al.*, 2000; Rankin *et al.*, 2005) and their frequency and temporal characteristics are consistent with those generally reported for baleen whales. Pulsing calls were recorded using the same sonobuoys as blue whale calls, but it is not thought that blue whales produced these calls. Pulsing has previously been reported as being produced by common minke whales, but in those instances the pulsing rate was 2.2 pulses s^{-1} (Winn and Perkins, 1976), slightly higher than that reported here. Also, it has been implied that similar pulsing calls, with pulsing rates between 1.5 and 4.5 pulses s^{-1}, could be minke whale songs, as they have been recorded mostly in lower latitudes (Mellinger *et al.*, 2000; Gedamke *et al.*, 2001). If these pulses are from a minke whale, then this is the first recording of this species producing a song-like call at a high latitude. Even though similar pulsing sounds appear to be rather ubiquitous, they are not usually associated with visual sightings of common minke whales (Folkow and Blix, 1991; Mellinger *et al.*, 2000) and during this cruise they were recorded mostly in an area with no Antarctic minke whale sightings. It would be helpful to determine the source of this pulsing call, as well as the sources of pulsing sounds recorded elsewhere.

There were no baleen whale sightings in the vicinity of the sonobuoys on which 50Hz upswept calls were heard, but Rankin *et al.* (2005) reported similar upswept calls, from 23 to 57Hz with 1.6s duration, as coming from blue whales in the Antarctic. While the frequency range of the calls is similar, calls reported here are three times shorter. The frequency range of this call is lower than previously reported for minke or southern right whales. Although minke whales are not known to make upsweeps, the short duration of the calls means they resemble minke whale downsweep calls (Schevill and Watkins, 1972; Edds-Walton, 2000). Antarctic minke whale acoustics are very poorly understood and it is possible that they could be making these calls. Southern right whales also produce upsweeps, but their upsweeps tend to be higher in frequency and longer in duration, so it is unlikely the 50Hz upswept calls were produced by them. Edds (1988) reported upsweeps from fin whales in the St. Lawrence estuary and Thompson *et al.* (1992) reported that 17% of calls heard from fin whales in the Gulf of California were upsweeps. The much shorter duration of these calls than those of the blue whale reported in Rankin *et al.* (2005), the short intercall interval and their occurrence in the areas where fin whales mostly occurred during this survey make it possible that these calls were produced by fin whales. A more focused study, with dedicated ship time for visual observations and acoustic work with DIFAR sonobuoys, would be required to determine whether both the pulsing and 50Hz upswept calls are made by a species of baleen whale.

Whale distributions and environmental parameters

The locations of baleen whale calls and sightings provide a comparison of differences in spatial distribution among species. Comparison of these locations with major environmental parameters, such as the oceanographic fronts, the location of the ice edge and bathymetry, can offer insight into habitat use differences between the species. There was a difference in the distribution of fin whales in comparison with all other species of baleen whales. Fin whales were prevalent in the central part of the Scotia Sea, in deeper waters along the sACCf. This is in contrast to Tynan's (1998) observations from whaling data indicating that blue, fin and humpback whales are associated with the southern boundary of the ACC. All other species were found south of the southern boundary, around the South Orkneys and in areas of the Scotia Sea close to the ice edge. Humpback and southern right whales were found also in shallow areas around South Georgia, between the polar front and the sACCf, consistent with previous findings (Kellogg, 1929; Kasamatsu *et al.*, 1996).

During this survey no fin whales were detected near the ice edge, where all other baleen whale species were commonly located. This is consistent with the knowledge that fin whales are more pelagic in comparison with other baleen whales and generally are not associated with sea ice (Kellogg, 1929; Mackintosh, 1965). The association of fin whales with the sACCf average location in this survey is not surprising, but it is worthy of further investigation. The marginal ice zone along the retreating ice edge is known to be a biologically productive zone and this area is further enriched by the shallow upwelling of the Upper Circumpolar Deep Water (UCDW) associated with the southern boundary (Laws, 1985; Smith and Nelson, 1985; Tynan, 1998). Such a rich area has the potential to sustain a large animal biomass and diversity. The sACCf, on the other hand, is characterised by a deeper UCDW upwelling. Before reaching the central Scotia Sea this front passes along the continental shelf of the Antarctic Peninsula, where it is enriched with iron and other limiting micronutrients (Holm-Hansen *et al.*, 2004). While the productivity in the central Scotia Sea may be less than in the marginal ice zone, the combination of deep UCDW upwelling and micronutrient enrichment gives this deep water region potential for sustaining baleen whales. Fin whales, with their ability to make relatively deep dives (Panigada *et al.*, 1999), could potentially exploit the productivity brought by the deep upwelling and in turn avoid competition with other species that prefer the area near the southern boundary (Laws, 1977; Costa and Crocker, 1996).

Acoustic methods for population estimation are still under development, since parameters such as the whale calling rates and daily and seasonal calling patterns are not well understood (Barlow and Taylor, 2005). Direct comparison of acoustic and visual surveys is further complicated by a difference in range over which the two operate. While visual surveys cover a range of several km, a more typical range for acoustic survey of baleen whales with sonobuoys is several tens of km (McDonald, 2004). There are also differences in the availability of animals for either type of survey due to their diving preferences and differences in the frequency of calling. However, a simple comparison of the numbers of groups detected by each method can be done if we assume a single detection of a species by one sonobuoy represents one acoustic group. This introduces a low bias to the acoustic survey, and this bias could be reduced by using only DIFAR sonobuoys. Blue whales, for example, appear to be a better subject for acoustic surveys, as eight groups were detected acoustically and none visually. Minke and southern right whales, with zero and four acoustic and 43 and 20 visual groups, respectively, seem to be better suited for visual surveys. Humpback and fin whales fall in the middle, with 15 and 10 acoustic and 12 and 15 visual groups, respectively. There was a bias in this acoustic survey, however, since it was not independent of the visual survey and sonobuoys often were deployed deliberately after a visual sighting.

The efficiency of acoustic and visual surveys varies between species, as exemplified by blue and minke whales. While blue whales were heard on a number of occasions during the cruise, they were never seen. Due to the sound speed profile characteristics in polar regions, making the area an upward refracting environment (Richardson *et al.*, 1995), the area that was monitored acoustically was likely 1-2 orders of magnitude larger than the area surveyed visually. This could explain why blue whales were heard acoustically but were never seen by the visual observers as their low frequency calls propagate better than calls from other species. Also, a low density of blue whales in the Antarctic (Branch and Butterworth, 2001a) would give a low likelihood of a visual encounter with this species. Antarctic minke whales, on the other hand, were commonly seen during the survey, but were not heard. While they are the most abundant of the baleen whales in the Antarctic (Branch and Butterworth, 2001b), their known Antarctic calls are short and occur irregularly (Schevill and Watkins, 1972) and therefore can be difficult to detect with sonobuoys.

Acoustic surveys from ships complement visual surveys for cetaceans, since they provide larger scale coverage and can be conducted when the conditions are not appropriate for visual survey (e.g. darkness, rough seas, poor visibility). Sonobuoys are better suited for surveys of baleen whales than towed arrays, since ship noise interferes with low frequency whale calls and this noise diminishes as ships steam away from a sonobuoy. Concurrent visual and acoustic efforts are necessary, however, to investigate the sources of different call types, as well as to devise methods for population estimation using acoustics. Even though there are currently no means to estimate population sizes from a sonobuoy survey, it is possible to determine areas where certain call types are heard commonly and to estimate the spatial distribution of various baleen whale species if a consistent acoustic sampling programme is used.

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A note on divergent mtDNA lineages of bottlenose dolphins from coastal waters of southern Australia

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ABSTRACT

Bottlenose dolphins have a global distribution throughout tropical and temperate waters, both inshore and offshore. Many studies demonstrate the existence of at least two *Tursiops* species: *Tursiops truncatus*, consisting of inshore and offshore eco-types and *T. aduncus*, a coastal Indo-Pacific type known to extend south into temperate waters down the east coast of Australia. To clarify the taxonomic status of two populations (Port Phillip Bay and Gippsland Lakes) of coastal bottlenose dolphins along Australia's south coast (Victoria), a 346bp region of the mitochondrial-DNA (mtDNA) control region was sequenced from ten individuals and they were incorporated into phylogenetic analyses involving published sequences of other *Tursiops* spp., *Stenella* spp. and *Delphinus* spp., found worldwide. Both neighbour-joining and maximum parsimony trees place Victorian coastal haplotypes in a highly-supported group separate to those from the other dolphins, including those from the southern part of the Australian eastern coast. Victorian haplotypes are least divergent from *T. truncatus* (average 5.5%) and most divergent from *T. aduncus* (9.1%), with intermediate levels of divergence from *Stenella* and *Delphinus* spp. These data suggest that the Victorian coastal dolphins, similar to other world-wide coastal populations, are genetically unique, long isolated and therefore likely to be locally adapted. This has important implications for management and conservation.

KEYWORDS: GENETICS; TAXONOMY; CONSERVATION; BOTTLENOSE DOLPHIN; AUSTRALASIA

INTRODUCTION

Bottlenose dolphins (Family Delphinidae, Subfamily Delphininae, *Tursiops* genus) have a cosmopolitan distribution and show marked variation, despite being historically recognised as one species, the common bottlenose dolphin, *T. truncatus* (Montague 1821). Morphological and genetic studies have demonstrated the existence of several distinct *Tursiops* forms (inhabiting inshore and offshore regions) that differ in quantitative (and possible plastic) traits. Variable morphological traits include ventral spotting, beak length, body length (Ross and Cockcroft, 1990; Hale *et al.*, 2000; Wang *et al.*, 2000a), diet (Mead and Potter, 1995), haemoglobin type (Hersh and Duffield, 1990) and osteological characteristics (Wang *et al.*, 2000b). Genetic differentiation between 'types' has been observed using AFLP markers (Kingston and Rosel, 2004), cytochrome *b* sequences (LeDuc *et al.*, 1999) and mtDNA control region sequences (Möller and Beheregaray, 2001; Torres *et al.*, 2003). A smaller inshore form described as a separate species, *T. aduncus* (Ehrenberg 1932), occurs largely in warmer coastal waters of China and the Indo-Pacific region, but has recently been described (on the basis of mitochondrial haplotype) from the east coast of Australia (Möller and Beheregaray, 2001). Natoli *et al.* (2004) further suggest that an *aduncus*-type found in southern Africa may represent a third *Tursiops* species. While the coastal Indo-Pacific and distinct South African forms have both been described as species that are distinct from *T. truncatus*, the polytypic single-species perspective has been emphasised by others (e.g. Ross and Cockcroft, 1990). Based on several genetic markers, *T. aduncus* may be more closely related to *Stenella* and *Delphinus* species than to *T. truncatus* (LeDuc *et al.*, 1999; Natoli *et al.*, 2004). The often confusing taxonomic group has been named the '*Stenella-Tursiops-Delphinus-Lagenodelphis*' complex and the level of uncertainty regarding the taxonomy of the bottlenose dolphin worldwide has prompted its listing as a 'priority topic' for the International Whaling Commission (IWC) Scientific Committee's sub-committee on small cetaceans (Reeves *et al.*, 2004). What is clear however, is the emerging worldwide picture that coastal bottlenose dolphins often have local fine scale population structure with unique regional patterns of genetic differentiation and morphology. Historical founder events, long-term isolation and local and historical environmental effects, with reinforcement by philopatry, are the probable causal factors (Natoli *et al.*, 2004).

Australian bottlenose dolphins exhibit distinct regional morphological variation with respect to ventral spotting, body and beak length. One relevant factor may be that the resident populations assume an optimal body size for the local temperature regime, resulting in the formation of clines in body size. On this basis all Australian bottlenose dolphins were assigned to *T. truncatus* (Ross and Cockcroft, 1990). However, more recently *T. aduncus* mtDNA type has been reported from the bottlenose dolphins from coastal regions of eastern Australia (Möller and Beheregaray, 2001). To add to the complexity, Krützen *et al.* (2004) reported that the *Tursiops* population in Shark Bay on the northwest coast of Australia contains two distinct mtDNA lineages showing a level of sequence divergence similar to that seen between Chinese *T. truncatus* and *T. aduncus* (Wang *et al.*, 1999). Uncertainty remains about the taxonomy and population structure of bottlenose dolphins residing in coastal Victoria (southern Australia), in particular those in Port Phillip Bay (Hale, 2002; Scarpaci *et al.*, 2003). Their small physical size (average 2.5m) when compared to those found in Tasmania and further west along the south coast of Australia (3.05m and 2.83m respectively; Ross and Cockcroft, 1990), the absence of ventral spotting and reduced counter-shading, suggest that Port Phillip Bay dolphins may be *T. aduncus*,

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consistent with a recent prediction that *T. aduncus* may be continuously distributed around coastal waters of Australia (Möller and Beheregaray, 2001).

A resident Port Phillip Bay (PPB) population of 80-100 animals, at the southern end of the Bay, is considered to be vulnerable to extinction due to its small size, female natal philopatry, restricted home range and the large degree of associated human activity (Dunn *et al.*, 2001; Hale, 2002). In particular the population has shown high site fidelity to a region that has large amounts of boat traffic and a swim-with-dolphins tourism industry (Dunn *et al.*, 2001). Less direct human threats include urban development around this coastal region (pollution and vandalism), recreational and commercial fishing, channel dredging and heavy shipping traffic. While bottlenose dolphins are also known from one other Victorian coastal site, the Gippsland Lakes (Gips) around 320km east of PPB, little is documented about their population structure and biology.

To clarify their taxonomic status and population affinities, and thus contribute to improved population management, we report here the sequence a 346bp region of the mtDNA control region from ten dolphins from the PPB and Gips populations. These data are incorporated them into phylogenetic analyses involving published sequences of *T. aduncus, T. truncatus,* striped dolphin (*Stenella coeruleoalba*), long-beaked common dolphin (*Delphinus capensis*), and common dolphin (*D. delphis*) and the results discussed in the context of local and worldwide dolphin biology.

METHODS

Skin samples were collected via biopsy sampling (based on the system of Lambertson, 1987) from three individuals known[1] to be members of the local population in the southern end of PPB using a modified Junior Ranger Crossbow. Opportunistic sampling was also undertaken on dead dolphins washed ashore in either PPB (*n*=4) or Gips (*n*=3) as shown in Table 1 and Fig. 1 (additional data on all sampled animals is available from DRI).

Eight samples were preserved in a saline solution of 20% dimethyl-sulfoxide (DMSO), 0.25M EDTA, saturated with NaCl, pH7.5 (Suetin *et al.*, 1991) and two were stored in formaldehyde. Genomic DNA, from samples stored in the 20% DMSO solution, was extracted using a standard protocol (Sambrook *et al.*, 1989) following rinsing with RSB buffer (10mM Tris-Cl, 10mN NaCl, 25mM EDTA) (Davis *et al.*, 1986) to remove residual 20% DMSO solution. For the two samples stored in formaldehyde, DNA was extracted following the method of Rodriguez *et al.* (2002).

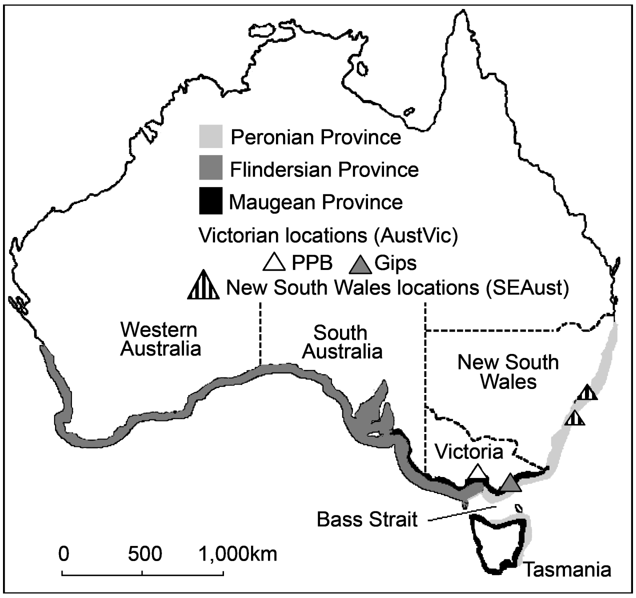

Fig. 1. Map of Australia, including marine bioregions for the south-east region and Australian sampled bottlenose dolphins.

A fragment of mtDNA control region was amplified by polymerase chain reaction (PCR) with primers Dlp 1.5 and Dlp 5 (Baker *et al.*, 1993). The PCR was carried out using *Expand High Fidelity PCR System* (Roche Molecular Biochemicals) to a final volume of 50μl. All PCRs were performed on an Applied Biosystems *GeneAmp PCR System 2700* using the regime reported by Möller and Beheregaray (2001). A *Wizard Purification System* (Promega) was used to purify the PCR product as per the manufacturer's instructions, which was used as template DNA in a cycle sequencing reaction. The thermal cycling conditions for the sequencing reaction consisted of a denaturing step for 30 seconds at 96°C, annealing step for 15 seconds at 50°C and an extension step for 4 minutes at 60°C. This cycle was repeated 25 times with a final hold at 4°C. Reagent concentrations and volumes used were; 6.0μl Terminator mix (Micromon), 100ng/μl template DNA, 5 μM Dlp 1.5 primer, and dH_2O to final volume of 20μl. Samples were analysed on an Applied Biosystems 3100 sequencer. Accuracy was confirmed by sequencing in both directions.

The 10 control region sequences from the Victorian dolphins were assigned to haplotypes (AustVic) (reduced to 346bp). They were aligned by eye with sequences of 4 *T. truncatus,* 4 *T. aduncus,* 2 *S. coeruleoalba,* 2 *D. capensis,* 2

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[1] Identified by Dolphin Research Institute (Hastings, Victoria (DRI)) personnel from a photographic database of individuals collected over a ten year period.

Table 1

Skin samples collected.

Code	Haplolype	Location	Source of sample	Date of collection	Sex	Age
PPB1	AustVic1	PPB	Boat strike	29/11/2001	F	3yrs
PPB2	AustVic2	PPB	Mentone Beach	12/12/2001	M	Adult
PPB4	AustVic2	PPB	PPB biopsy	23/06/2003	-	-
PPB6	AustVic2	PPB	PPB biopsy	24/06/2003	-	-
PPB3	AustVic3	PPB	Geelong	25/03/2002	M	Adult
PPB5	AustVic4	PPB	PPB biopsy	24/06/2003	-	-
Gips2	AustVic5	Gips	Bairnsdale	16/04/2002	F	Calf
PPB7	AustVic5	PPB	Werribee South	26/02/2003	M	Adult
Gips1	AustVic6	Gips	Bairnsdale	07/08/2002	M	Adult
Gips3	AustVic7	Gips	Raymond Island	17/08/2003	M	Sub-adult

Table 2

Control region sequences analysed.

Haplotype	Species	GenBank accession no.	Locality	Reference
Ttru6	*T. truncatus*	AF056224	Taiwan, Indo-Pacific	Wang *et al.* (1999)
Ttru10	*T. truncatus*	AF056228	Taiwan, Indo-Pacific	Wang *et al.* (1999)
Ttru13	*T. truncatus*	AF056231	Taiwan, Indo-Pacific	Wang *et al.* (1999)
Ttru22	*T. truncatus*	U20917	USA, NW Atlantic	Siemann (1994)
Tadu1	*T. aduncus*	AF056233	China and Taiwan, Indo-Pacific	Wang *et al.* (1999)
Tadu8	*T. aduncus*	AF056240	Taiwan, Indo-Pacific	Wang *et al.* (1999)
SEAust2	*T. aduncus*	AF287952	NSW, Australia, SW Pacific	Möller and Beheregaray (2001)
SEAust5	*T. aduncus*	AF287955	NSW, Australia, SW Pacific	Möller and Beheregaray (2001)
Lacu	*L. acutus*	AF113487	NW Atlantic	Cipriano (1997)
S.coer1	*S. coeruleoalba*	AY168600	-	Matzen *et al.*[1]
S.coer2	*S. coeruleoalba*	AY046549	Chinese waters	Yang *et al.*[2]
Dd10	*D. delphis*	AY168605	Azores Islands	Matzen *et al.*[3]
Z115	*D. delphis*	U02662	-	Rosel *et al.* (1994)
CDC2	*D. capensis*	AY185144	Chinese waters	Wang *et al.*[4]
CDC8	*D. capensis*	AY185142	Chinese waters	Wang *et al.*[4]
Oorca	*O. orca*	M60409	-	Hoelzel *et al.* (1991)
AustVic1		AY371171	Victoria, Australia, SW Pacific	This study
AustVic2		AY371172	Victoria, Australia, SW Pacific	This study
AustVic3		AY371173	Victoria, Australia, SW Pacific	This study
AustVic4		AY371174	Victoria, Australia, SW Pacific	This study
AustVic5		AY371175	Victoria, Australia, SW Pacific	This study
AustVic6		AY371176	Victoria, Australia, SW Pacific	This study
AustVic7		AY371177	Victoria, Australia, SW Pacific	This study

[1] Matzen Silva, J., Norberto, R., Matos, J., Mendonca, D., Simoes, F. and Azevedo, J. Direct sequence from GenBank accession number AY168600; [2] Yang, G., Ren, W.H., Niu, M.H. and Zhou, K. Sequence variability of the complete mitochondrial control region of striped dolphins (*Stenella coeruleoalba*). Direct sequence from GenBank accession number AY046549; [3] Matzen Silva, J., Norberto, R., Matos, J., Mendonca, D., Simoes, F. and Azevedo, J. Direct sequence from GenBank accession number AY168605; [4] Wang, J.Y., Yang, G., Liu, H., Zhou, K. and Wei, F.W. The preliminary application of mitochondrial DNA sequence variability in identification of common dolphins (genus Delphinus) in Chinese waters. Direct sequence from GenBank accession numbers AY185142 and AY185144.

D. delphis, 1 Atlantic white-sided dolphin (*Lagenorhynchus acutus)* and 1 killer whale (*Orcinus orca*) available on GenBank (Table 2).

Modeltest v3.5 (Posada and Crandall, 1998) was used to determine the most appropriate model and parameters for phylogenetic analysis of this data set. *PAUP* v4.0b10 (Swofford, 1998) was used to calculate sequence divergence values among haplotypes and to infer their phylogenetic relationships using both neighbour-joining (N-J) and maximum parsimony methods. All trees were generated using unweighted character analysis. A N-J tree was estimated using the HKY +G model (G=0.1156) (Hasegawa *et al.*, 1985) with gamma distribution (shape parameter = 0.2490) and observed ti/tv ratio (4.4082) as determined by *Modeltest* v3.5. All percentage differences cited are averages based on this model. Reliability of tree nodes for all trees was assessed using 1,000 bootstrap replicates. The *L. acutus* and *O. ocra* sequences were used as outgroups (Möller and Beheregaray, 2001; Pichler *et al.*, 2001).

RESULTS

Over the 346bp of the mtDNA control region, five polymorphic sites defined seven haplotypes among the 10 Victorian dolphin sequences. Four haplotypes (AustVic1-4) were only found in PPB, with AustVic2 having the highest frequency (three PPB individuals). AustVic 6 and 7 were each represented by a single Gips individual, while AustVic5 was recorded once in each location. When the AustVic sequences were aligned with the 15 from GenBank, there were a total of 52 variable sites and four fixed differences that characterise the Victorian coastal population (Table 3). All Victorian sequences diverged substantially from the *Tursiops* species sequences (Table 4), with the most similar being *T. truncatus*, from which they differed on average by 5.5% (Hasegawa *et al.*, 1985). Higher sequence divergence was observed between Victorian haplotypes and those of *T. aduncus* (9.1%). Regardless of the phylogenetic reconstruction method, the coastal Victorian sequences formed a strongly supported monophyletic grouping with respect to all other *Tursiops*, *Delphinus* and *Stenella* species (bootstrap values of 98% and 94% for the maximum parsimony and N-J trees, respectively; Fig. 2).

Table 4

Divergence from *Tursiops spp.* sequence (%).

	AustVic
AustVic	0.70%
SEAust (NSW)	9.70%
T. aduncus	9.10%
T. truncatus	5.50%
Stenella spp.	6.00%
Delphinus spp.	6.60%

DISCUSSION

The phylogenetic affinities of the resident PPB bottlenose dolphin population have been controversial, with authors variously describing them as, or predicting them to represent, *T. aduncus* and *T. truncatus* (Hale, 2002; Möller and Beheregaray, 2001; Scarpaci *et al.*, 2003). Our phylogenetic analyses suggest Victorian haplotypes do not cluster with those of other *Tursiops*, *Delphinus* or *Stenella* species. The average sequence divergence of these Victorian

Table 3

Relative position of variable nucleotide.

Haplotype	10	15	35	38	44	45	50	53	55	56	57	61	62	76	82	90	95	98	102	114	140	150	151	159	161	164	191	194	195	211	218	222	224	225	226	228	229	230	234	238	239	240	241	249	251	293	294	303	308	316	337	339	343
Ttru22	T	G	C	T	C	A	C	A	G	T	G	G	C	C	G	T	C	A	G	T	C	C	C	A	T	C	T	G	C	C	A	A	C	T	T	C	C	T	T	A	T	C	C	G	T	G	C	T	G	T	C	T	G
Ttru13	.	.	.	.	T	.	.	.	.	C	.	.	.	.	.	.	.	.	.	.	.	.	T	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	A	.	.	.	C	.	.	.	.	.
Ttru10	.	.	.	.	T	.	.	.	.	C	.	.	.	.	.	.	T	.	.	.	T	.	.	.	.	.	.	A	.	.	.	.	.	C	.	T	.	.	.	.	.	.	.	A	.	.	.	C	.	.	T	.	.
Ttru6	.	.	.	.	T	.	.	.	.	C	.	.	.	.	.	.	T	.	.	.	T	.	T	.	.	.	C	.	.	.	.	.	.	C	.	.	T	.	.	.	.	.	.	A	.	.	.	C	.	.	T	.	.
AustVic1	.	.	.	.	.	.	.	G	A	.	.	.	.	.	.	C	T	.	.	.	T	.	.	.	C	.	C	.	A	A	.	.	T	.	.	T	A	.	.	.	.	.	T	A	.	.	.	C	.	.	T	.	.
AustVic2	.	.	.	.	.	.	.	G	A	.	.	.	.	.	.	C	T	.	.	.	T	.	T	.	C	.	C	.	A	A	.	.	T	.	.	T	A	.	.	.	.	.	.	A	.	.	.	C	.	.	T	.	.
AustVic3	.	.	.	.	.	.	.	G	A	.	.	.	.	.	.	C	T	.	.	.	T	.	.	.	C	.	C	.	A	A	.	.	T	.	.	T	A	.	.	.	.	.	.	.	.	.	.	C	.	.	T	.	.
AustVic4	G	.	.	.	.	.	.	G	A	.	.	.	.	.	.	C	T	.	.	.	T	.	T	.	C	.	C	.	A	A	.	.	T	.	.	T	A	.	.	.	.	.	.	A	.	.	.	C	.	.	T	.	.
AustVic5	.	.	.	.	.	.	.	G	A	.	.	.	G	.	.	C	T	.	.	.	T	.	.	.	C	.	C	.	A	A	.	.	T	.	.	T	A	.	.	.	.	.	.	A	.	.	.	C	.	.	T	.	.
AustVic6	.	.	.	.	.	.	.	G	A	.	.	.	.	.	.	C	T	.	.	.	T	.	.	.	C	.	C	.	A	A	.	.	T	.	.	T	A	.	.	.	.	.	.	A	.	.	.	C	.	.	T	.	.
AustVic7	.	.	.	.	.	.	.	G	A	.	.	.	.	T	.	C	T	.	.	.	T	.	.	.	C	.	C	.	A	A	.	.	T	.	.	T	A	.	.	.	.	.	.	A	.	.	.	C	.	.	T	.	.
Tadu1	.	.	.	C	.	.	.	.	.	.	A	.	.	.	.	.	T	.	.	.	T	T	.	T	.	T	C	.	.	G	T	.	T	.	C	.	.	C	.	.	.	.	.	.	.	.	.	.	.	C	.	C	.
Tadu8	.	.	.	C	.	.	.	.	.	.	A	A	.	.	.	.	T	.	.	C	T	.	.	T	.	.	.	.	.	G	T	.	T	.	C	T	.	C	.	.	.	.	.	A	.	.	.	.	.	.	.	.	.
SEAust2	.	.	.	C	.	.	.	.	.	.	A	A	.	.	.	.	T	.	.	C	T	T	.	T	.	T	C	.	.	G	T	.	T	.	C	.	.	C	.	.	.	.	.	A	C	.	.	.	.	.	.	.	.
SEAust5	.	A	.	C	.	.	.	.	.	.	A	A	.	.	.	.	T	.	.	C	T	.	.	T	.	T	C	.	.	G	T	.	T	.	C	.	.	C	.	.	.	.	.	.	C	.	.	.	.	.	.	.	.
S.atten	.	.	T	.	T	T	T	G	A	.	.	.	.	.	.	.	T	G	.	.	T	.	T	.	.	.	C	.	.	A	.	G	T	C	.	.	.	.	.	T	C	T	.	.	.	.	.	C	.	C	T	.	.
S.coer1	.	.	.	.	.	.	.	.	.	.	A	.	.	.	.	.	T	T	.	.	T	.	T	.	.	.	C	C	.	A	-	.	T	.	C	T	.	C	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
S.coer2	.	.	.	.	.	.	.	.	.	.	A	.	.	.	.	.	T	T	.	A	T	.	T	.	.	.	.	A	.	A	-	.	T	.	C	T	.	C	.	.	.	.	.	.	.	.	.	.	.	.	T	.	.
CDC2	.	.	.	.	.	.	.	.	.	.	A	.	.	.	A	.	T	T	.	.	T	.	T	.	.	.	C	A	.	A	-	.	T	.	C	T	.	.	.	.	C	.	.	A	.	.	.	.	.	.	T	.	.
CDC8	.	.	.	.	.	.	.	.	.	.	A	.	.	.	.	.	T	T	.	A	T	.	T	.	.	.	.	A	.	A	-	.	T	.	C	T	.	C	.	.	.	.	.	.	.	.	.	.	.	.	T	.	.
Dd10	.	.	T	.	.	.	.	.	.	.	A	.	.	.	.	.	T	T	.	.	T	.	T	.	.	T	C	C	.	A	-	.	T	.	C	T	T	C	.	.	C	.	.	.	.	A	G	.	C	.	T	.	A
Z115	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	T	T	A	.	T	.	T	.	.	.	C	.	.	A	-	G	T	.	C	T	.	C	C	.	.	.	.	.	.	.	.	.	.	.	T	.	.

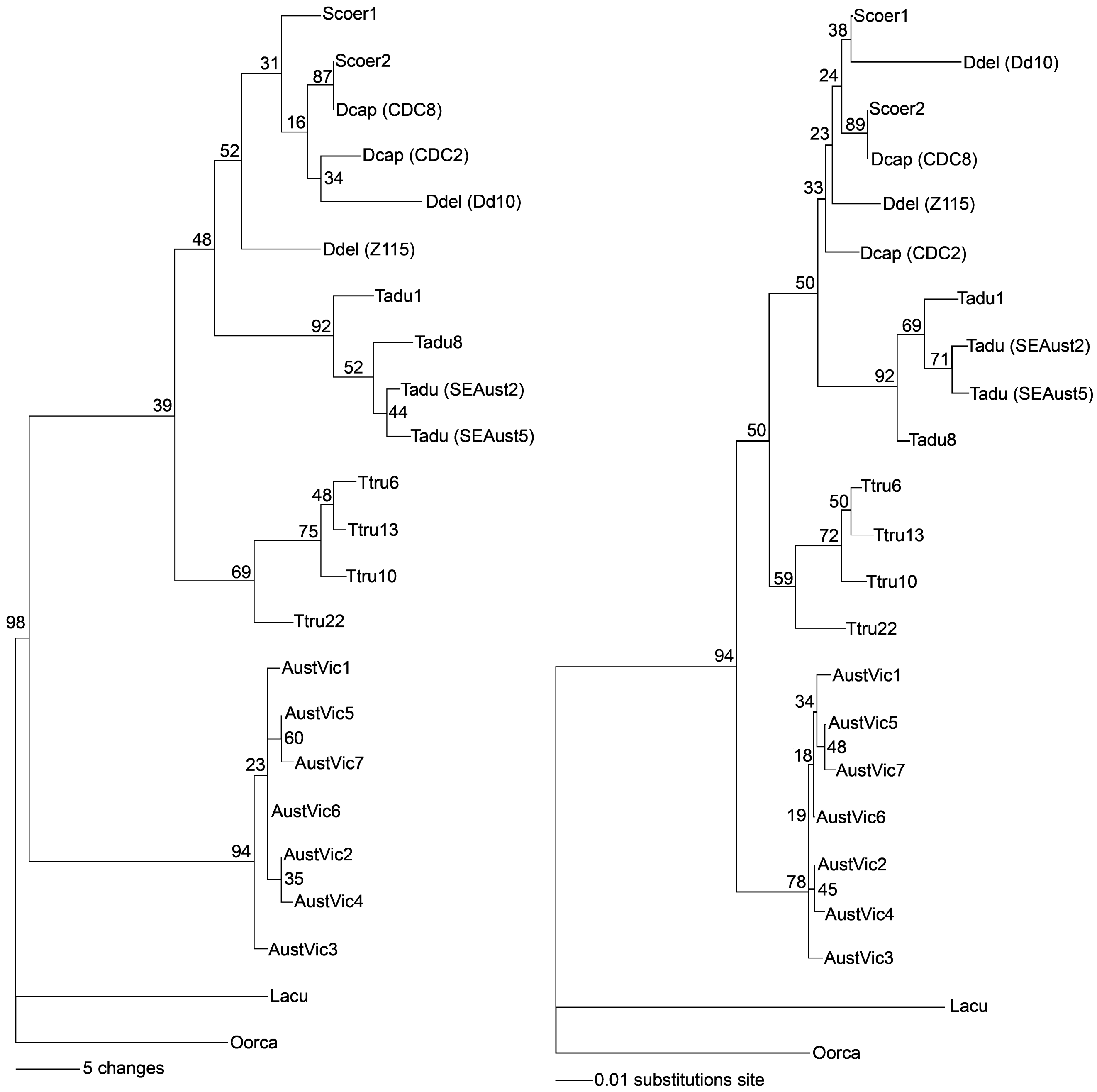

Fig. 2. Maximum parsimony (left) and N-J (right) bootstrap consensus trees based on mtDNA control region sequence of bottlenose dolphins from coastal Victoria (AustVic), and published *T. truncatus* (Ttru), *T. aduncus* (Tadu and SEAust), *S. coeruleoalba* (S.coer), *D. capensis* (CDC) and *D. delphis* (Z115 and Dd10) from different localities (50% majority-rule consensus). Outgroups *L. acutus* (Lacu) and *O. orca* (Oorca). Branch lengths are proportional to amount of genetic change and were calculated along strict consensus tree by PAUP (Swofford, 1998).

dolphins from the *T. truncatus* cluster is similar to that commonly observed between recognised species within each of the *Cephalorhynchus* (2.5-4%) and *Lagenorhynchus* (4.5-6.4%) genera (Pichler *et al.*, 2001), and higher than that between sympatric populations of short-beaked and long-beaked common dolphins, *Delphinus* sp. (1.09%, Rosel *et al.*, 1994). Our placement of taxa within the '*Stenella-Tursiops-Delphinus-Lagenodelphis*' complex agrees with that of LeDuc *et al.* (1999) using cytochrome b sequence, in that *T. aduncus* is more closely-related to *S. coeruleoalba* and *Delphinus* species than to *T. truncatus* (Fig 2). The overall level of mtDNA control region sequence divergence and presence of fixed polymorphisms in coastal Victorian dolphin haplotypes suggest that these populations may represent an undescribed taxon, requiring formal classification incorporating morphological and further genetic analysis.

How might such a divergent group have arisen? The establishment of coastal founder populations may be due to release of suitable habitat during inter-glacial periods (Natoli *et al.*, 2004). During glacial maxima, a Pleistocene landbridge connected Tasmania to mainland Australia, so PPB and Gips were formed only 18,000 years ago (CLIMAP, 1976; Waters and Roy, 2003). Resident dolphin population(s) therefore may have established relatively recently, during the postglacial period. The founders were unlikely to have been from recent ancestors of the eastern Australian coastal population, given the substantial contemporary haplotype divergence (9.7%). Comparable levels of sequence divergence observed between the genus *Lissodelphidae* and other members of its sub-family (7.7%-11.4%) lead Pichler *et al.* (2001) to suggest its early divergence in the history of the sub-family. In a similar way an early separation of Victorian coastal bottlenose dolphins may have occurred from the '*Stenella-Tursiops-Delphinus-Lagenodelphis*' complex. Our sampling has been neither widespread nor extensive and other dolphin groups with other affinity levels may occur in the region.

The distribution and divergence of the coastal Victorian population may be related to the occurrence of a number of marine bioregions that have been defined on the basis of physical and biotic parameters (Knox, 1963). The Maugean province (Fig. 1), which includes the area in which the study populations lie, is a cold-cool temperate region exhibiting a high level of diversity and endemism (Edyvane and Baker, 1995). Further sampling within and close-by on either side of this province will be important to see if and where dolphin phylogenetic barriers occur. The genetic uniqueness of coastal Victorian dolphins, and their possible origins from a cool-temperate bioregion, raises the question of if, and how well they are adapted to local environmental conditions. While the size of the coastal Victorian bottlenose dolphins may be a heritable trait related to its adaptation to water temperature (Ross and Cockcroft, 1990) it may also be a plastic developmental response, adaptive or otherwise, to the local environment. The possibility of local adaptation of cetaceans has been discussed in numerous reports where associations occur between population distributions or pod congregations and prey distributions, local marine habitat features (such as water depth and distance from shore), local currents, water temperatures, salinity changes and the presence of deep 'feeding' channels (Davis *et al.*, 2002; Selzer and Payne, 1988; Watts and Gaskin, 1985; Hastie *et al.*, 2004; Mead and Potter, 1995; Torres *et al.*, 2003; Wilson *et al.*, 1997). While many of these associations are likely to have an adaptive role, it is not known whether they are based on cultural (learned) behaviours or are long-term heritable adaptive characteristics of the populations. None-the-less, recent evidence of heritable and speedy adaptive divergence in many vertebrate species over latitudinal, altitudinal and environmental gradients (Stockwell *et al.*, 2003; Skelly, 2004), suggest that Victorian coastal bottlenose dolphins may be genetically well-adapted and hence an irreplaceable asset.

Given the extensive genetic divergence of the Victorian coastal bottlenose dolphins from other known *Tursiops* they arguably constitute a distinct entity worthy of separate management and conservation effort. The shared polymorphic sites and the existence of a shared haplotype among the PPB and Gips samples suggest close affinities between these locations, and relatively recent gene flow along this part of the coastline. However our sample size is insufficient to establish whether or not we are dealing with a large randomly mating group. The apparent small size of the Port Phillip Bay population, limited knowledge of the Gippsland Lakes population, and increasing anthropogenic threats make both populations vulnerable. Further sampling (including the southern Australian offshore dolphins, and more easterly and westerly populations), and analysis that incorporate morphology and nuclear genetic markers, is needed to elucidate local breeding structure and to determine the size and range of the population.

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Strandings, mortality and morbidity of Indo-Pacific humpback dolphins in Hong Kong, with emphasis on the role of organochlorine contaminants

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ABSTRACT

Factors related to mortality and disease in Indo-Pacific humpback dolphins (*Sousa chinensis*) from Hong Kong waters were investigated by detailed examination of dolphin specimens found stranded from 1995-2004. In total, 86 specimens were necropsied, but many of these were too badly decomposed to provide much information. Skin and blubber biopsies were also collected from six identified living individuals and concentrations of organochlorines (DDTs, PCBs and HCHs) were determined from blubber samples of stranded and biopsied dolphins. A large proportion of the strandings (53.2%) were young-of-the-year. The most commonly diagnosed causes of death were net entanglement and vessel collision. The pesticide DDT showed the highest concentrations and the ratio of DDT to its breakdown products (and other information) suggests that there may be a recent or nearby source of DDT into the dolphins' ecosystem. Concentrations of both DDTs and PCBs showed a pattern of increasing with age in males. In females, they increased until sexual maturity, then decreased, and finally increased again in late life. This is consistent with a hypothesised transfer of pollutants from mother to offspring during gestation and lactation. Inter-laboratory differences and effects of decomposition of specimens are two potential biases that may significantly affect the quality of the present data. In order to resolve the potential problems associated with these issues, a long-term biopsy collection programme has recently been initiated.

KEYWORDS: INDO-PACIFIC HUMPBACK DOLPHIN; BIOPSY SAMPLING; MORTALITY RATE; POLLUTANTS; ORGANOCHLORINES; CONSERVATION

INTRODUCTION

Mortality of small cetaceans is generally evaluated based on specimens obtained from strandings, or from those taken either directly or incidentally in fisheries. While fisheries catches provide fresh specimens, the catch is often biased in terms of age and sex. Strandings may give a better picture of 'natural' mortality; however, stranded specimens are often badly degraded from the actions of weathering and decomposition, and stranding rates may also show serious demographic and other biases (Reijnders *et al.*, 1999a; b). In Hong Kong, most strandings involve two species, the Indo-Pacific humpback dolphin (*Sousa chinensis*) and the finless porpoise (*Neophocaena phocaenoides*) (Parsons, 1998; Jefferson and Hung, 2004).

Humpback dolphins in Hong Kong face a number of potential threats. Although dolphins are known to get caught in fishing nets (Parsons and Jefferson, 2000), no large-scale fisheries interactions are known. Thus, strandings represent virtually the only source of carcasses for analysing mortality patterns, and for obtaining samples for analysis of various biological parameters. Therefore a programme was established in 1995 to document the occurrence of marine mammal strandings in Hong Kong, and to conduct necropsies of stranded specimens, when feasible (see Jefferson, 2000). Data and samples from the strandings are then analysed to examine patterns of mortality, life history and biology.

A long-term study into the effects of various environmental contaminants on humpback dolphins in Hong Kong has also commenced. This study integrates data from several sources, including sampling of stranded dolphins during necropsy, biopsy sampling of living dolphins and information obtained through our long-term programme of photo-identification of individual dolphins. By combining data from these various sources, a powerful programme has been initiated that avoids some of the biases and restrictions inherent in any single sampling design (see Wells *et al.*, 2003). For instance, photo-identification data can be used to monitor dermal disease, which may be associated with environmental contaminants (see Thompson and Hammond, 1992).

In this programme, three classes of contaminants were chosen for detailed examination, largely due to previous indications that they were especially problematic in this population (see Parsons and Chan, 1998; Parsons *et al.*, 1998; Minh *et al.*, 1999; Minh *et al.*, 2000a). The pesticide DDT (and its derivatives) was heavily used in past decades, because of its high toxicity to insects and its low cost. It has been banned in most developed countries, and also in China, but it may still be used illegally. Polychlorinated biphenyls (PCBs) are a group of several dozen compounds used in electrical equipment and in the manufacture of paints, plastics, adhesives, etc. (Clark, 1998). They are rarely used anymore, but their persistency ensures that they will continue to have damaging effects for many years. Lindane is another pesticide, which contains mostly hexachlorocyclohexane (HCH). It has toxic effects and it may still be used extensively in China (Clark, 1998).

The goals of this study were to determine the temporal and other patterns of humpback dolphin mortality in Hong Kong, and the main factors that are responsible for that mortality. In addition, we examined in detail the role of one particular threat to the dolphins, that of contamination of their environment by organochlorines.

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MATERIALS AND METHODS

Necropsy and sample collection

Even before the start of the current study, stranded humpback dolphin carcasses were examined in Hong Kong between 1993 and 1995 (see Parsons and Jefferson, 2000). In 1995, a dedicated stranding recovery programme was initiated. This involved soliciting stranding reports from the public, military and other government departments. The effort associated with soliciting and obtaining stranded carcasses was roughly similar throughout the study.

Over the course of the present study (September 1995 to December 2004) a total of 89 humpback dolphin mortalities in Hong Kong were confirmed. Necropsies were performed either in the laboratory (for fresh specimens) or in the field (for those that were badly decomposed or in relatively inaccessible locations). Basic biological data and samples were collected (see Parsons and Jefferson, 2000 for a detailed discussion of the stranding programme and sampling procedures). Veterinarians from Ocean Park Corporation or the Agriculture, Fisheries and Conservation Department (AFCD) of the Hong Kong Government were involved in many of the necropsies of fresh specimens. Specimens were classified as to their level of decomposition, codes 1-5, as outlined by Geraci and Lounsbury (1993).

In total, 86 specimens were necropsied and while most were also sampled for environmental contaminants, many specimens were badly decomposed and thus little usable information could be obtained from them. In addition, power failures caused several freezer breakdowns that resulted in significant additional decomposition of samples (see below). We generally followed the procedures of Jefferson *et al.* (1994) in conducting necropsies. Blubber samples, for organic contaminant analyses, were collected from the dorsal thoracic region, wrapped in aluminium foil and then frozen. In order to avoid cross-contamination, knives were thoroughly cleaned in soapy water and disinfectant between necropsies and storage containers were not reused. Gross pathology was noted during necropsies and (opportunistically) some samples were examined histopathologically. Blubber thickness was also measured on an opportunistic basis. For most specimens, 2-4 teeth from the middle of the lower left jaw were collected and age was estimated, as detailed in Jefferson (2000).

Biopsy sampling

For collection of biopsy samples from living dolphins, a Barnett Ranger RX-150 crossbow, with 150lb (68kg) draw weight was used. This crossbow shoots arrows at a speed of 69m s^{-1}. A red dot scope was used to assist in aiming and the senior author conducted all sampling. He had previous experience in crossbow biopsy sampling of four other species of cetaceans, as well as almost 10 years of experience observing the behaviour of the study animals. All biopsy sampling was conducted under appropriate permits from the Hong Kong Police Force and the AFCD.

Darts were ACC carbon fibre darts produced by *Ceta-Dart* and tips were made at the Scripps Institution of Oceanography (SIO) machine shop. Short 25mm biopsy tips were used (as opposed to longer 40mm tips). This was a conservative strategy, designed to reduce risk of injury or infection, but it yielded a smaller blubber core than was considered optimal for the studies on toxicology and reproductive biology (typically collecting only the outer one-half to two-thirds of the blubber layer). The tips had a sharpened, bevelled leading edge, which acted as a cutting surface, and there were three internal barbs to aid in sample retention.

The biopsy tips were soaked in bleach and 10% ethanol prior to being attached to the dart. This helped to reduce the chances of cross-contamination of samples and of infection. Shots were typically taken at target distances of 8-20m. The thoracic area just ahead of the dorsal fin was targeted. Photographs and video documentation were collected for all biopsy attempts (except for one successful attempt in which no video was obtained and another with no photographs).

When a biopsy sample was obtained, the tissue was removed from the biopsy tip by use of sterilised forceps. The skin sample was separated from the blubber using a single-edge razor blade, and the skin was stored in salt-saturated dimethyl sulfoxide (DMSO) solution, and then kept frozen. The blubber sample was bisected along its long axis. Both portions were frozen on dry ice and later in −30°C freezers, one for reproductive hormone studies and the other for determination of organic contaminant concentrations.

Contaminant analysis

For 59 specimens, three classes of contaminants in blubber tissue were examined in detail. These were DDT pesticide residues (DDTs), PCBs and HCHs. This selection was based on indications from earlier studies that these contaminants were the most critical, due to high levels in Hong Kong cetaceans and in some cases high known toxicity (Parsons and Chan, 1998; Minh *et al.*, 1999).

The analytical methods for PCBs and organochlorine pesticides (OCPs) for the biopsy samples followed those described in Richardson and Zheng (1999) and Zheng *et al.* (2004). Briefly, about 0.2g of subcutaneous blubber sample was spiked with 1ml each of internal standards, decachlorobiphenyl (1,012 ng ml^{-1}), C_{22} (8,160 ng ml^{-1}) and m-terphenyl (10,490 ng ml^{-1}). The sample was homogenised with 30ml dichloromethane (DCM) by a *K-Ultra-Turrax* T-25 homogeniser at a speed of 1,100rpm until all the blubber tissue was dissolved. After filtration with glass fibre of 70mm pore size (*Advantec*), the volume of each sample was reduced in a rotary evaporator and then passed through a silica gel column to remove impurities and lipids. After eluting PHCs from the column with 15ml of hexane, further elution from the column was conducted with a mixture of hexane:dichloromethane (8:2) and DCM for PCBs and OCPs, and PAHs.

Organochlorines in the second fraction were quantified by gas chromatography (GC-μECD; *Hewlett Packard* 6890 II series) equipped with an Agilent 7683 series automatic sampler. The GC column employed was a DB-5 capillary column (*J&W Scientific Inc.*, USA, 30m × 0.25mm internal diameter × 0.25μm film thickness). The column oven temperature was programmed at 110° held for 2min, increased to 180° at a rate of 10° min^{-1}, and then increased to 280° at a rate of 5° min^{-1} and held for 14 min. Injector and detector temperatures were set at 250°. Nitrogen was used as the carrier gas.

PCBs, HCHs, HCB, heptachlor, heptachlor epoxide, aldrin, dieldrin, endrin, kepone, chlordanes, and DDT and its metabolites were monitored. Peaks of individual compounds were identified from those of their corresponding external standards. Organochlorine concentrations were calculated from the peak areas of individual compounds relative to the peak area of the internal standard. The PCB standard (SRM 2262) used for peak identification was a mixture with known composition and content, containing 28 congeners (PCB 1, 8, 18, 28, 29, 44, 50, 52, 66, 77, 87, 101, 104, 105, 118, 126, 128, 138, 153, 154, 170, 180, 187, 188, 194, 195, 200, 206). Concentrations of the 28 PCB congeners were determined, and summed values were then multiplied by two to obtain total PCB concentrations (Leung *et al.*, 2005). A procedural blank was analysed with every set of six samples to check for interfering compounds and correction was made, if necessary. Total DDTs represented the sum of *p,p'*-DDT, *o,p*-DDT, *p,p'*-DDD, *o,p*-DDD, *p,p'*-DDE and *o,p*-DDE. Chlordanes (CHLs) included *cis*-chlordane, *trans*-chlordane, *cis*-nonachlor, *trans*-nonachlor, and oxychlordane, while total HCHs included alpha, beta, gamma and delta isomers. Recoveries of target analytes using this analytical method were 99 ± 2.0 % for PCBs, 95 ± 7.5 % for DDTs, 96 ± 7.7 % for HCHs, 100 ± 4.7 % for CHLs, and 94 ± 5.9 % for HCB.

For the samples from stranded dolphins, the analytical methods for OCPs were those described in Minh *et al.* (1999; 2000a; b; c) and Ramu *et al.* (2005). In brief, about 3-8g of blubber sample was homogenised with anhydrous Na_2SO_4 and extracted with Soxhlet apparatus for 7-8h, with a mixture of diethylether:hexane (3:1) (v/v). Samples were passed through a dry Florisil column for removing fat. After eluting OCs from the dry column with a mixture of acetonitrile and water and partitioning in a separatory funnel, hexane extracts were concentrated. The first fraction eluted with hexane contained HCB, PCBs, *p,p'*-DDE, and *trans*-nonachlor while the second fraction eluted with 20% dicholomethane in hexane contained chlordane compounds (oxychlordane, *trans*-chlordane, *cis*-chlordane, *cis*-nonachlor), *p,p'*-DDD, *p,p'*-DDT, HCHs and TCPMe. The third fraction was collected with 50% dichloromethane in hexane for TCPMeOH separation.

Organochlorines in the first and second fractions (except TCPMe) were quantified by GC-ECD (Hewlett Packard 5890 II Series) equipped with a moving needle-type inject port. The GC-column employed was DB-1 (J & W Scientific Inc., USA) fused with a silica capillary column (0.25mm X 30m) coated with 100% dimethyl polysiloxane at 0.25μm film thickness. The column oven temperature was programmed from 60°C to 160°C, held for 19min and then increased to 260°C at a rate of 2°C min^{-1} and held for 30min. Injector and detector temperatures were set at 260°C and 280°C, respectively. Helium and nitrogen were used as carriers and make-up gases, respectively. Organochlorine concentrations were calculated from the peak area of the sample to the corresponding external standard. The PCB standard used for quantification was an equivalent of the Kanechlor mixture (KC-300, KC-400, KC-500, KC-600) with known PCB composition and content. Concentrations of individually resolved peaks of PCB isomers and congeners were summed to obtain total PCB concentration. For TCPMe and TCPMeOH quantification, a GC-MS (Hewlett-Packard 5890 coupled with 5970 mass selective detector) was employed. Data acquisition was carried out by *HP* 5970C Data system, in which cluster ions were monitored at m/z 139, 253, 251, 362, 364 for TCPMeOH and 311, 313, 346, 348 for TCPMe.

Isomer-specific analysis of PCBs, including coplanar congeners, was conducted following the alkaline-alcohol digestion method (Tanabe *et al.*, 1987). Quantification was carried out using a GC-MS (Hewlett Packard 5890 II Series in coupled with 5970 mass selective detector). A Hewlett Packard 5970 data system was used for quantification, in which cluster ions were monitored at m/z 256, 292, 326, 360, 394 and 430 for tri-, tetra-, penta-, hexa-, hepta- and octa-chlorobiphenyls, respectively. Recoveries of OCs through analytical procedure are shown below. Concentrations were not corrected for recovery percentages.

There are some differences between Ramu's and Minh's method. Firstly after Soxhlet extraction, in Ramu's method, aliquot of the extract was subjected to gel permeation chromatography (GPC) GPC for lipid removal. The GPC fraction containing OCs was concentrated and passed through an activated Florisil column for clean-up and fractionation before quantification. Secondly, the PCB standard used for quantification was a mixture of 62 PCB isomers and congeners (BP-MS), instead of using Kanechlor mixture. Concentrations of individually resolved peaks of PCB isomers and congeners were summed to obtain total PCB concentrations. Most laboratory analyses were conducted by Prof. S. Tanabe and his colleagues (T.B. Minh and K. Ramu) of Ehime University in Japan (see Minh *et al.*, 1999; 2000a; b; c for laboratory protocols). For some additional specimens, frozen tissue samples were sent to a commercial ecotoxicology laboratory in Hong Kong (ALS Technichem [HK] Pty, Ltd.) for chemical analyses. The methods used there were the same as those of Minh *et al.* (1999).

Due to the three different laboratories conducting the analyses, there is significant potential for bias in comparing across datasets (Krahn *et al.*, 2003b; see below). Therefore, such comparisons were avoided and mainly comparisons were conducted in which each group had some data from different labs. Some of the data from the present dataset have been analysed previously in other studies (e.g. Minh *et al.*, 1999; Minh *et al.*, 2000a; b; c; Ramu *et al.*, 2005; Leung *et al.*, 2005).

RESULTS

Strandings and mortality rates

Since the first year of complete data (1996), there has been no consistent trend in the number of humpback dolphin strandings per year; the annual mean was 9.7 strandings (Fig. 1). In fact, the numbers have been relatively stable, with 6-14 strandings per year. This is especially true when compared with the number of finless porpoise strandings, which fluctuated more erratically in the last few years, and strandings of other species, which appear to be on the increase (Fig. 1).

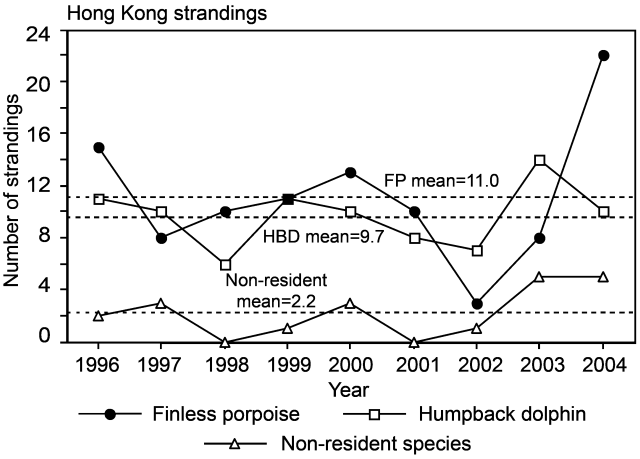

Fig. 1. The annual number of strandings of humpback dolphins (HBD), finless porpoises (FP) and other species in Hong Kong over the study period. The annual means are shown as dotted lines.

Only one humpback dolphin live stranding was recorded (SC03-08-08) during the study (although live strandings of finless porpoises, a rough-toothed dolphin (*Steno bredanensis*), false killer whale (*Pseudorca crassidens*) and sperm whale (*Physeter macrocephalus*) were also recorded). This was specimen SC03-08/08, which was found stranded alive by a local villager at Sam A Tseun, Double Haven, on 8 August 2003, and died after rehabilitation attempts at Ocean Park on 13 August. The animal was a 244cm sexually- and physically-mature female (with several ovarian scars and fully-fused vertebral centra), which was later aged at 27 growth layer groups (GLGs) (1 GLG is assumed to equal 1 year). At the time of death it weighed 148kg.

Young-of-the-year were defined as specimens <137cm in length as the estimated length at one year is 137cm. A very large proportion of all humpback dolphin strandings in Hong Kong were <137cm (Fig. 2). Of 79 specimens that could be placed into a length category, 42 (53.2%) were young-of-the-year. This is an apparently high proportion, although there are few other datasets available for comparison.

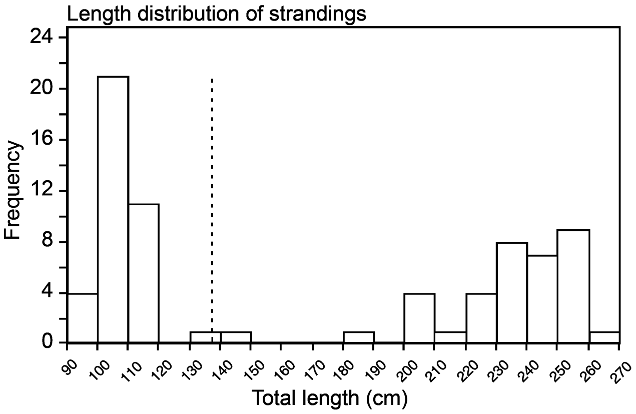

Fig. 2. Distribution of the total lengths of dolphins stranded in Hong Kong over the course of the study. The dotted line represents the criterion for considering specimens to be young-of-the-year (137cm total length).

Humpback dolphin strandings occurred throughout all months of the year (Fig. 3). Strandings of subadults and adults did not show any consistent pattern throughout the year. However, the monthly pattern of strandings of young-of-the-year showed a large peak during May-August (Fig. 3). As pointed out by Aguilar (1991), this can be viewed as an indicator of seasonal distribution of natural mortality (provided that certain conditions are met). Thus, it is clear that most of the natural mortality of young-of-the-year occurs in the four-month period from May to August, which is partly a reflection of the seasonality of calving (see Jefferson, 2000).

Of the animals that could be assigned to a sex, 62% were males (*n*=57). The sex ratio of stranded specimens was strongly biased towards males, both for specimens <150cm in length (1.60:1) and those >150cm (1.64:1). It should be noted that the gender of some specimens was not 100% certain, and these specimens were not used in the above analysis. If there are no sampling biases influencing this, then this indicates that more males than females died during the study period. This is an interesting finding, especially in light of the sex differences in patterns of contamination by organochlorines presented below.

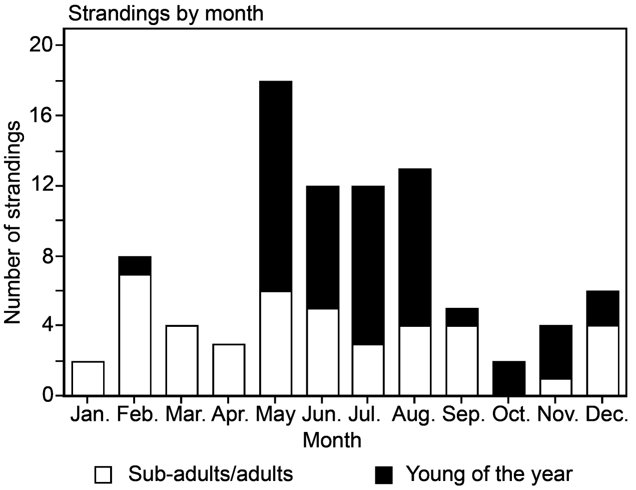

Fig. 3. The monthly distribution of humpback dolphin strandings in Hong Kong.

Causes of mortality and morbidity

Determination of cause of death was seriously hampered by the fact that most of the stranded specimens were badly decomposed. Of the 86 specimens for which the decomposition code could be determined, only one (1%) was code 1, 5 (6%) were code 2, 22 (26%) were code 3, 56 (65%) were code 4, and 2 (2%) were code 5. Since cause of death is nearly impossible to determine in most late code 3, code 4 and code 5 specimens, this left only a small number of specimens (<20%) in which determining the cause of death was feasible.

Of the 89 humpback dolphin strandings that occurred since the start of the study (through December 2004), cause of death could only be determined with certainty for 10 specimens, although a possible cause of death was diagnosed for three others. Three specimens were diagnosed as having died from net entanglement, four from vessel collisions, one from debris (in this case, net) ingestion, one from a heart or brain pathology, and one from a bone infection. For specimens that showed clear evidence of being struck by a vessel, there was the possibility that they died from some other cause and were then struck while floating after death. Therefore, specimens were only classified as dying from vessel collision if there was evidence that the animal was struck while still alive (e.g. blood infusion in the tissue around propeller cuts).

It was not possible to assign any deaths to high contaminant levels, but it was suspected that the high concentrations of contaminants (especially DDTs and PCBs) in some specimens may have led (directly or indirectly) to their deaths. Over the next few years it is hoped that a greater understanding of this issue will be achieved through new avenues of research (see below).

Dolphins are injured and even killed by nets and vessels, however not all serious injuries result in death. Several dolphins in our photo-identification catalogue show evidence of major injuries to the dorsal fin and back, apparently caused by boat propellers, vessel collisions, or rope/net cuts (Fig. 4). Between 2.9 and 6.8% of the animals show evidence of rope or net cuts and between 1.2 and 1.8% show evidence of propeller scars. Thus, it appears that up to 8.6% of animals have survived previous non-fatal encounters with human activities. It is rather remarkable that these animals can survive such serious injuries, which generally appear to heal well, despite Hong Kong's contaminated waters.

Fig. 4. Four photo-identified individuals showing evidence of human-caused injury to the dorsal fin and/or back.

The live-stranded dolphin showed evidence of epidermal disease when it stranded and necropsy confirmed extensive skin lesions consisting of fissures/cuts and severe bilateral thickening/hypertrophy of the epidermis along the flanks (see Fig. 5). This dolphin had previously been identified at sea from photos as CH76, which had been observed three times before it stranded, in both Hong Kong and Chinese waters. The first time was in Chinese waters just west of Lantau Island on 10 September 1998. It showed no evidence of dermal disease at this time. The second time was in the West Lantau area on 16 April 2002. The skin disease that the dolphin had when it stranded was clearly present in the photos taken in April 2002, as well as in photos from a sighting on 26 February 2003, and so the dolphin had the condition for at least 16 months. Laboratory analyses of a biopsy of infected skin showed parakeratosis and acanthosis, with a mild chronic inflammatory infiltrate in the papillary dermis and around the capillaries. There was no evidence of fungal or bacterial microrganisms, nor of any malignancy. The skin condition was not thought to be related to the cause of death, which was probably from a brain or heart pathology. Laboratory results of samples taken at necropsy for confirmation are pending and contaminant data are not yet available for this specimen.

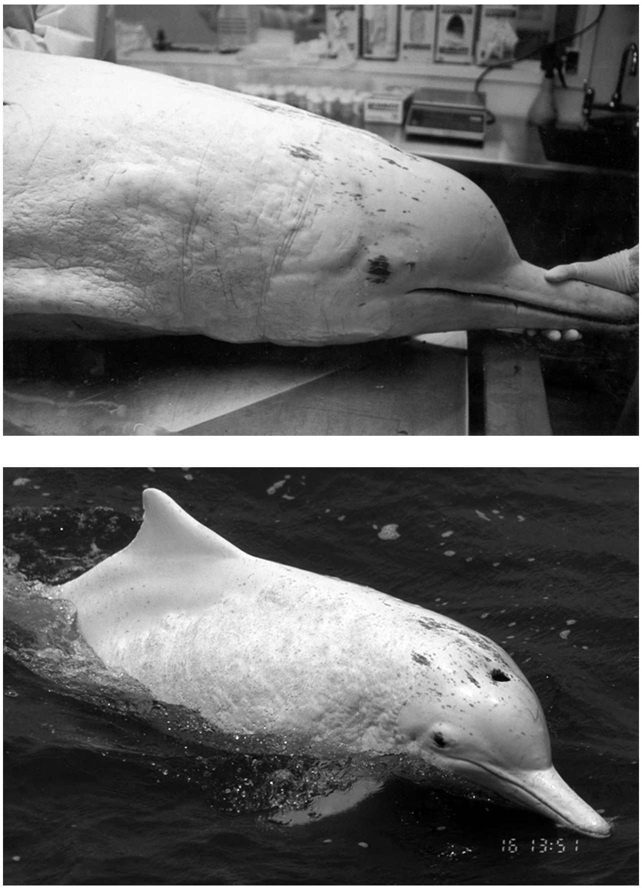

Fig. 5. Humpback dolphin live-stranded in August 2003 (SC03-08/08) showing evidence of a skin disease (see text). The lower photo shows the same dolphin on 16 April 2002, swimming off the west coast of Lantau Island, with evidence of the disease already present.

Contaminant concentrations

In general, for organochlorines, concentrations were high for cetaceans and on average males had concentrations several times higher than those of females. For ΣDDTs, males averaged 117.3μg g^{-1} wet wt. (± SD 125.66, range = 5-380, *n*=22) and females averaged 28.8μg g^{-1} wet wt. (± SD 19.11, range = 5-76, *n*=17). For ΣPCBs, males averaged 31.7μg g^{-1} wet wt. (± SD 23.21, range = 2-83, *n*=22) and females 10.8μg g^{-1} wet wt. (± SD 7.80, range = 1-30, *n*=17).

There was considerable variability, and often animals of the same sex and similar age showed widely scattered values (Fig. 6). ΣHCH concentrations for males averaged $0.9\mu g\ g^{-1}$ wet wt. (± SD 0.69, range = 0.1-2, *n*=16) and for females $0.2\mu g\ g^{-1}$ wet wt. (± SD 0.19, range = 0-0.5, *n*=6).

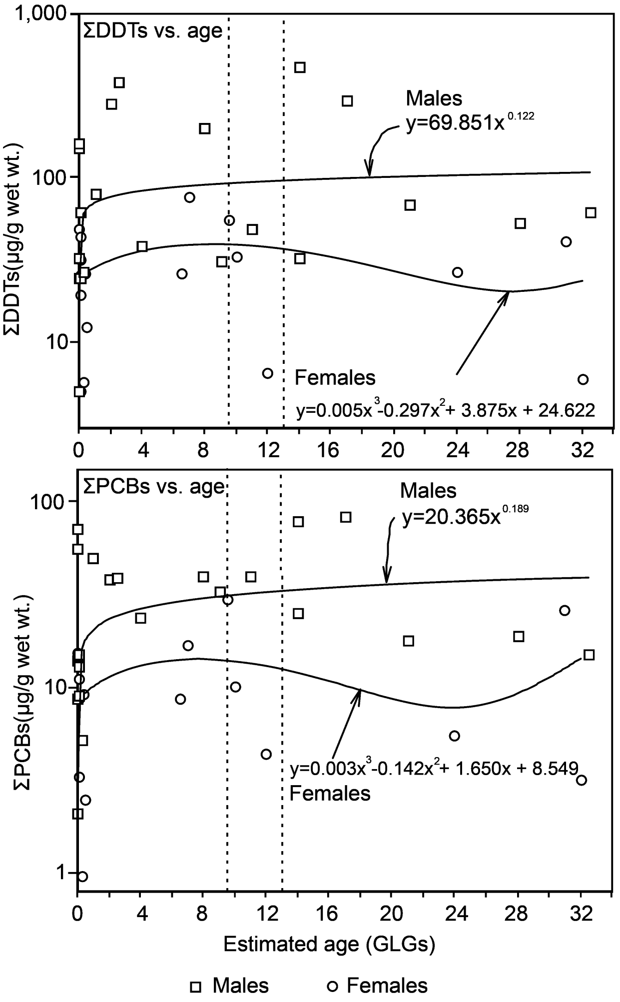

Fig. 6. Developmental patterns of ΣDDTs (upper) and ΣPCBs (lower) for male and female dolphins in Hong Kong. Contaminant data are presented on a logarithmic scale. The dotted lines represent the average age at sexual maturity for females and males.

For DDTs, most males had somewhat lower levels at birth, and then tended to have slightly increasing concentrations in later age classes (Fig. 6). The pattern for females was for much lower levels, which tended to increase somewhat until about 8-10 years of age, then to decrease until about 28 years and then to increase again (Fig. 6). When comparing the present data to those of bottlenose dolphins in the southeast United States (which have a similar life history – see Wells, 2000), DDT concentrations tend to be much higher for Hong Kong humpback dolphins, while PCBs are generally lower (except in adult females, in which they are slightly higher – Table 1). In both species, adult females had the lowest levels, but the reduction for adult females was not as pronounced in our data as it was for the bottlenose dolphin data (see Schwacke *et al.*, 2002; Hansen *et al.*, 2004).

Over time, DDT breaks down and is metabolised into DDD and DDE, and the relative proportions of these three compounds in the ΣDDTs can tell us something about the timing of input of the DDT into the system (see Aguilar, 1984; Parsons and Chan, 1998). On average, in this study only a small proportion of the ΣDDTs was made up of DDT and the largest amount was made up of DDE, although there was substantial variability (Fig. 7). The average proportion of DDT:DDD:DDE was 18.4%:28.5%:53.1%. The proportion of DDE is actually relatively low in comparison to that found in marine mammals from other regions of the Pacific, where it typically makes up between 70 and 95% (Prudente *et al.*, 1997). This suggests that the DDT in Hong Kong is from a relatively recent or nearby source, and may still be entering the dolphins' ecosystem, despite being banned in China in the early 1980s. Recent investigations indicate that a pesticide named Dicofol, currently being used in China to control mites in orange and eggplant growing areas, contains DDT as an impurity. A sample of Dicofol has been analysed and found to contain 2.4% DDT, which constitutes 1.8% of the active ingredient (PKSL). This is a serious concern, which needs to be addressed.

Development of PCB concentrations showed a broadly similar pattern to those of DDTs, with males having in some cases very high levels even at birth, and then a tendency to increase fairly rapidly (Fig. 6). Females also showed a similar pattern to DDTs, with an initial increase until about 8-10 years and then a decrease, and finally another increase late in life (Fig. 6). Unfortunately, there were not enough data to examine developmental patterns for HCHs.

There was a correlation between DDT and PCB concentrations; however this was not a one-to-one relationship (Fig. 8). Interestingly, DDTs (reaching nearly $500\mu g\ g^{-1}$ wet weight) tended to increase much more rapidly than PCBs, which remained below $100\mu g\ g^{-1}$ wet weight. Again, this is consistent with the idea that there may be a localised source of DDT into the western marine waters of Hong Kong (see Parsons and Chan, 1998).

Among the three classes of organochlorines analysed, DDTs made-up the largest fraction (68-78%) in all age classes, while PCBs only made-up 22-32%. HCHs made-up a negligible proportion (<0.01%) in all classes. However, there was an interesting difference between juveniles/adult males and adult females. Compared to the other age classes, adult females had a lower proportion of DDTs (68% vs. 76-78%), and a correspondingly higher proportion of PCBs (32% vs. 22-23%). A similar situation was found for several bottlenose dolphin populations in the southeast United States, and it is thought that this is due to DDT compounds being more efficiently transferred from mother to calf than PCBs (Hansen *et al.*, 2004).

Organochlorine concentrations in blubber samples of the biopsied dolphins are shown in Table 2. These are the first contaminant data we have been able to obtain from living, free-ranging dolphins of this population, and these data are not subject to the serious biases that may affect our stranding samples (see below). However, it must be noted that the biopsy sampling did not sample the more active inner layer that probably has the highest concentration of contaminants. The quality and reliability of the biopsy data are much higher than for strandings. When comparing data from biopsy samples with those from stranded samples of various levels of decomposition, indications are that the DDT levels are substantially lower in the biopsied dolphins than in the stranded specimens and it appears that in general decomposition and/or stranding increases the apparent concentrations of DDTs in the blubber (Table 3). There does not appear to be a similar relationship for PCBs and HCHs; however, it must be cautioned that this analysis is based on a very small sample. Further biopsy data are required to conduct a more reliable analysis.

Table 1

Summary statistics for major classes of OCs (μg g^{-1} wet weight) for Hong Kong humpback dolphins. Data from bottlenose dolphin populations along the US east coast are from Schwacke *et al.* (2002) and Hansen *et al.* (2004).

		Hong Kong					
Contaminant	Age class	*n*	Mean	SD	Range	Bottlenose dolphin means	Hong Kong levels
∑DDTs	Juveniles	31	67.4	83.50	3-380	17.8-28.8*	Much (2-4x) higher
	Adult males	7	132.7	164.63	5-470	12.6-51.9*	Much (5-11x) higher
	Adult females	6	28.1	17.60	7-55	4.0-4.4*	Much (6-7x) higher
∑PCBs	Juveniles	31	20.2	18.39	1-72	38.3-86.2	Much (2-4x) lower
	Adult males	7	37.1	27.98	11-83	70.3-91.2	Much (2x) lower
	Adult females	6	13.2	11.75	3-30	4.2-10.3	Similar to 3x higher

*Data in μg g^{-1} lipid weight basis.

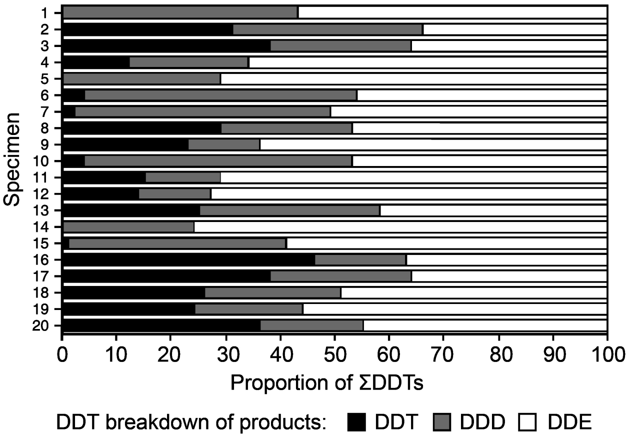

Fig. 7. Relative proportions of DDT and its metabolites in the total DDTs from dolphins stranded in Hong Kong.

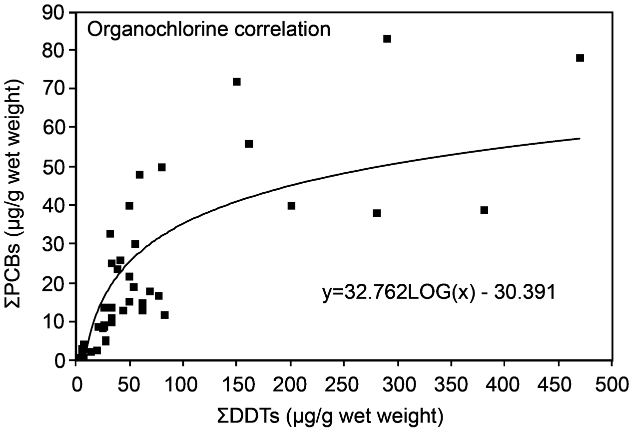

Fig. 8. Correlation between ΣDDTs and ΣPCBs in blubber samples from dolphins stranded in Hong Kong.

DISCUSSION

Potential biases

It is important to recognise the significant limitations of the currently available data on ecotoxicology for these animals.

Interlaboratory variability

Different laboratories use somewhat different techniques and equipment for conducting their work. Data on environmental contaminants in this study came from three different labs, and it is recognised that interlaboratory differences can be significant (Krahn *et al.*, 2003b). There were few cases of duplication to check the variability involved, but when duplication did occur it suggested that the variability could be significant. In two cases, two different labs examined blubber samples from the same specimen and arrived at quite different results (51 vs. 2.8μg g^{-1} for ΣDDTs and 1.7 vs. 9.4μg g^{-1} for ΣPCBs). These specimens were analysed at different times (years apart), and it is possible that intervening freezer breakdowns may have resulted in some real differences (see below), but nonetheless caution is required. Due to this potential problem, no attempts to analyse temporal trends in the contaminant dataset were made, since samples from different time periods were analysed by different labs. However, we do not believe that this possible bias will have a serious effect on the analyses presented here since, with one exception[1], all the comparisons presented use data from multiple labs in each group for comparison. The effect of the inter-laboratory variability will therefore be to exaggerate the variability in the compared groups and make determinations of differences more difficult. While this is not desirable, it is a more conservative and therefore more cautious approach than a situation in which the detection of apparent (but not real) differences were encouraged.

Effects of decomposition

As has been stated above, the vast majority of the specimens available for this study were badly decomposed (codes late 3 and 4). Decomposition is known to alter contaminant levels in an unpredictable manner (Borrell and Aguilar, 1990). In addition, the several freezer breakdowns resulted in significant additional decomposition of samples. Some evidence was found that DDT, but not PCB and HCH concentrations, may be significantly affected by decomposition. It is not possible to reliably evaluate the effects of the various levels of decomposition, but it must be considered when interpreting the data. Clearly, it would be better to deal with data from fresh specimens, where such problems are avoided.

Problems with using stranded specimens

The limitations of using samples collected from stranded specimens for contaminant studies must be acknowledged. Besides the obvious problems of decomposition (discussed above), there are potentially strong biases associated with the fact that specimens that strand are clearly not representative of the population as a whole. As many of these animals are sick, they are not good subjects for examining the levels of contaminants that the population is experiencing. This was clearly demonstrated by the results

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[1] The only exception is the situation in which we compared biopsy samples (all done by one lab) with stranding samples (all from two others).

of the study by Jepson *et al.* (2005). While these specimens represent the major source of data, alternative data sources are required.

Potential problems of stratification of blubber layer

The blubber biopsy samples collected in this project did not necessarily sample the entire blubber depth; the relatively short biopsy tips were used to avoid potential problems of penetrating the muscle layer below. Due to indications of stratification of contaminants within the blubber layer (e.g. see Krahn *et al.*, 2003a), there may be some bias in the biopsy contaminant results. These were minimised by splitting the blubber sample longitudinally, but some potential bias still remains.

While such potential biases may limit the reliability of the toxicology results of this study, the present study represents a first step and we view the results as preliminary. Despite this, we do not believe that the analyses presented here are significantly biased. An important lesson from this preliminary study is that future studies must attempt to overcome the potential problems discussed above. Significant advantages can be achieved through a dedicated programme of biopsy sampling (see below).

However, biopsy sampling also has the potential for some bias. This is mainly due to blubber stratification. How much this affects the data in Tables 2 and 3 is not yet known. However, by obtaining larger samples of biopsy data for comparison, and also by conducting specific studies comparing organochlorine concentrations from 'full-depth' blubber samples with subsamples taken from only the outer layers (e.g. see IWC, In press) it is hoped this can be further understood.

Levels and causes of mortality

While Cockcroft (1991) found that 28% of the humpback dolphins he examined from South Africa showed either recent or healed shark attack wounds, no evidence of such wounds was found on any of the dolphins examined in this study. Although at least three species of large, predatory shark potentially pose a threat to dolphins in Hong Kong, the great white (*Carcharodon carcharias*), tiger (*Galeocerdo cuvieri*) and bull (*Carcharinus leucas*) sharks (see Parsons and Jefferson, 2000), only the latter two are known to occur regularly in estuaries (where the dolphins are found). In fact, within Hong Kong, records of sharks in the western, estuarine waters are rare and we have not observed a shark in over 10 years of intensive surveys of these waters.

Comparison of the present results on strandings and mortality with those from other coastal and inshore dolphin populations is difficult since there are few other comparable published results.

Table 2

Concentrations of organochlorines (ng g^{-1} wet weight) in blubber biopsy samples collected in October and November 2004 in Hong Kong waters.

Specimen No.	HKB 1	HKB 2	HKB 4	HKB 5	HKB 6
Gender	Female	Male	Female	Male	Male
Repro Status	Unknown	Mature?	Mature?	Unknown	Unknown
Blubber wet (g)	0.09	0.16	0.09	0.11	0.10
∂ -HCH	27.33	25.94	46.11	15.36	8.50
ß-HCH	295.00	149.07	684.69	2,113.33	1,309.89
gamma-HCH	13.56	3.94	18.67	941.09	7.80
delta-HCH	7.89	3.56	7.89	15.55	128.30
∑ HCHs	343.78	182.51	757.36	3,085.33	1,454.49
HCB	8.00	30.50	17.00	40.82	117.10
Heptachlor	59.56	17.31	82.33	59.00	250.20
HE	495.78	139.44	215.11	285.27	106.60
Aldrin	10.44	12.88	75.89	12.00	87.40
Dieldrin	444.33	4,880.31	211.11	2,181.27	5,798.60
Endrin	113.89	149.44	2,626.67	217.36	17.10
Kepone	70.89	1,097.06	780.11	1,308.55	25.50
r- Chlordane	61.67	112.63	41.11	233.36	91.30
a-Chlordane	44.11	201.61	66.91	42.69	397.40
∑ Chlordanes	105.78	314.24	108.02	276.05	488.70
op-DDE	11.21	90.00	9.05	36.36	10.03
pp'-DDE	734.89	5,944.75	3,918.67	2,696.55	6,343.50
op'-DDD	28.33	548.38	60.67	95.00	158.40
pp'-DDD	315.44	3,706.25	1,883.78	891.27	2,497.10
op'-DDT	362.22	1,772.81	331.00	516.09	1,319.90
pp'-DDT	560.33	4,585.69	1,778.78	637.36	3,708.90
∑ DDTs	2,012.42	16,647.88	7,981.95	4,872.63	14,037.83
PCB 1	135.56	631.38	445.78	914.09	894.90
PCB 8	120.00	227.81	285.00	122.73	81.00
PCB 18	0.00	0.00	0.00	0.00	133.40
PCB 29	39.89	890.81	73.33	468.73	515.84
PCB 50	0.00	0.00	49.11	40.18	44.20
PCB 28	0.00	0.00	0.00	0.00	0.00
PCB 52	609.00	467.75	796.44	785.73	864.30
PCB 104	0.00	0.00	0.00	0.00	325.10
PCB 44	197.22	50.63	273.78	288.45	317.30
PCB 66	0.00	329.06	147.56	144.91	310.50
PCB 101	198.67	494.50	144.56	140.36	360.50
PCB 87	435.11	1,029.94	2,442.56	1,285.45	344.90
PCB 77	86.33	113.31	120.89	108.27	11,085.60
PCB 154	0.00	0.00	0.00	0.00	450.70
PCB 118	0.00	3,549.25	0.00	46.36	51.00
PCB 188	0.00	1,451.38	128.11	85.00	346.60
PCB 153	126.22	460.25	302.89	167.09	270.10
PCB 105	0.00	343.25	0.00	0.00	0.00
PCB 138	257.44	126.75	553.56	371.27	1,682.90
PCB 126	0.00	1,201.69	0.00	0.00	129.00
PCB 187	168.33	228.06	193.11	91.73	440.60
PCB 128	39.56	166.00	60.56	57.73	209.80
PCB 200	24.44	72.06	53.45	11.64	35.60
PCB 180	111.89	953.25	479.56	231.82	696.70
PCB 170	12.00	416.44	149.22	91.73	292.70
PCB 195	6.56	26.06	0.00	3.73	33.60
PCB 194	55.56	740.88	307.11	59.91	461.50
PCB 206	7.33	66.88	11.89	42.09	4.60
PCB 209	17.11	131.69	111.56	29.18	29.20
∑ PCBs	5,296.44	28,336.12	14,260.02	11,176.36	40,824.28

Table 3

Effects of decomposition level on organochlorine concentrations (µg g^{-1} wet weight). Code 1 specimens are from biopsy samples of living individuals.

		∑DDTs		∑PCBs		∑HCHs	
Decomp code	*n*	Mean ± SD	Range	Mean ± SD	Range	Mean ± SD	Range
1 (biopsy)[#]	5	9.1 ± 5.49	2.0-16.7	20.0 ± 12.88	5.3-28.3	1.2 ± 1.06	0.2-3.1
2	1	55.0	-	30.0	-	0.4	-
3	15	63.5 ± 111.30	5.1-470.0	20.3 ± 20.93	3.3-78.0	0.6 ± 0.48	0.0-1.4
4	27	82.3 ± 95.90	3.3-380.0	22.7 ± 21.06	0.8-83.0	0.7 ± 0.63	0.1-2.2
5	0	nd	-	nd	-	nd	-

[#] It should be recognised that, while any differences between code 1 and other samples are probably mainly a result of decomposition, there are other differences that could also explain them (see text for additional discussion).

The one exception is the long-term research programme on bottlenose dolphins along the west coast of Florida, USA, with stranding data extending back 18 years (see Wells, 2000; Wells *et al.*, 2004). Bottlenose dolphins in this area are ecologically similar to the Hong Kong/PRE humpback dolphin population, inhabiting mostly inshore waters, having similar life history characteristics and even sharing a spring to summer calving peak (see Wells, 2000). The yearly number of strandings in Florida (mean=17 – Hurst *et al.*, unpublished[2]) is broadly similar to that in Hong Kong (mean=9.7). Among the major diagnosed causes of death in Florida were fisheries/human interaction, and trauma of unknown possibly anthropogenic origin (see Hurst *et al.*, unpublished). Their results are similar to those presented here, indicating that fisheries interactions and vessel collisions may be the major causes of death.

There are some differences between the datasets, however. For Florida bottlenose dolphins, the proportion of males among the known-sex strandings (51.8% – Hurst *et al.*, unpublished) is substantially lower than in the study presented here, in which it comprises 62.1%. It thus appears that a higher proportion of males may be dying in Hong Kong waters vs. Florida waters. Finally, the proportion of young-of-the-year appears to be much higher in Hong Kong waters. For Florida, only 14.5% of strandings are <125cm neonates, and even when one considers the proportion of animals less than three years of age (<210cm), the proportion still only comprises 44% (Hurst *et al.*, unpublished). Along the Atlantic coast of the United States (Massachussetts to South Carolina), bottlenose dolphin young-of-the-year made up between 17.7 and 26.6% of strandings (Mead and Potter, 1990); in South Carolina, young-of-the-year (<184cm) made up 39.9% of strandings (McFee and Hopkins-Murphy, 2002); and in Texas they made up 20% (Fernandez and Hohn, 1998). By contrast, in Hong Kong 53.2% of all our strandings are of animals estimated to be less than one year old. Even more striking is that the vast majority of these animals are clearly less than a few months old. The much higher proportion of young calves among strandings in Hong Kong is consistent with the hypothesis that organochlorines are having a significant impact on dolphin survival (see below).

Effects of contaminants

In recent years, considerable work has been done on organochlorines and their effects on cetaceans (e.g. see Reijnders *et al.*, 1999a). Risk assessment studies have indicated that the high levels of organic contaminants in Hong Kong waters have probably caused damage to the marine environment and to seafood consumers (Connell *et al.*, 1998). Organic chemicals (including PCBs, hydrocarbons and pesticides such as DDT) are a potential threat to cetaceans, because they bioaccumulate in top predators and are passed from generation to generation; due to the absence or reduction of certain enzymes, cetaceans have a low capacity to metabolise (and thus detoxify) these compounds (Tanabe *et al.*, 1994).

Organochlorine concentrations in Hong Kong humpback dolphins are relatively high, and DDT and PCB levels are even higher than in the finless porpoise population that occurs in Hong Kong (Jefferson *et al.*, 2002a; Ramu *et al.*, 2005). This is not surprising, as the dolphins live in the estuary of the Pearl River, and are probably nearer the presumed source of the contaminants than are finless porpoises, which have a more southern and offshore distribution (see Jefferson *et al.*, 2002b). There is also evidence that DDT use still continues in some parts of the Pearl River Estuary (Fu *et al.*, 2003).

For a number of species, including some marine mammals, organochlorines have been reported to interfere with reproductive capacity (causing failed egg implantation, testis abnormalities, and reduced testosterone levels), cause immunosuppression (lowered resistance to disease), and have carcinogenic (cancer-causing) and teratogenic (developmental) effects (Tanabe and Tatsukawa, 1991; Busbee *et al.*, 1999; Reijnders, 2003). Exposure during early development can affect the endocrine, reproductive, immune and nervous systems, sometimes not expressing its effects until adulthood. Although direct cause-effect links have not been identified, it has been found that high concentrations of PCBs and DDE are correlated with lowered testosterone levels in the blood of Dall's porpoises (*Phocoenoides dalli*) in the North Pacific (Subramanian *et al.*, 1987). Similarly, Martineau *et al.* (1988) found that industrial contaminants were correlated with lesions and cancer-like tumours in white whales (*Delphinapterus leucas*) in the St. Lawrence Estuary; many of these were implicated in the animals' deaths. High levels of organochlorines were associated with suppressed immune response of bottlenose dolphins in the southeastern USA (Lahvis *et al.*, 1995). Cockcroft (1989) suggested that organochlorine concentrations of humpback dolphins in South Africa may be high enough to impair reproductive function of male humpback dolphins and to prove fatal to neonates of primiparous females[3]. High concentrations of organochlorine are also suspected to have been a causal factor in the die-offs of dolphins in the Mediterranean Sea and northeastern United States in recent years (Kannan *et al.*, 1993; Reijnders, 1996; Aguilar, 2000). While this link has not yet been clearly and unequivocally proven, there is good reason to be concerned about such factors (Kennedy, 1999). As Reijnders (2003) cautioned, the etiology of marine mammal disorders and the roles that contaminants might play remains uncertain and more detailed work is clearly required to clarify potential cause-effect relationships in cetaceans (e.g. Van Waerebeek, 1999).

Levels of organochlorines have been analysed in humpback dolphin tissues from only a few areas: South Africa (Cockcroft, unpublished[3]); India (Tanabe *et al.*, 1993; Tanabe *et al.*, 1996; Prudente *et al.*, 1997); Taiwan (Chou *et al.*, 2004) and Hong Kong (Parsons and Chan, 1998; Minh *et al.*, 1999; 2000a; b; c; this study). Although sample sizes have generally been very low, concentrations of at least certain organochlorines appear to be relatively high everywhere that they have been examined. Three adult male humpback dolphins from India showed PCB levels about an order of magnitude lower than in Hong Kong, although DDT levels were broadly similar (Tanabe *et al.*, 1993; Prudente *et al.*, 1997). A single adult male from Taiwan also had much lower PCB levels than specimens from Hong Kong (Chou *et al.*, 2004). Such comparisons of different studies must be viewed with caution, as

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[2] Hurst, G.E., Fauquier, D.A., Barros, N.B., Gorzelany, J.F., Lipscomb, T.P., Kinsel, M.J. and Wells, R.S. 2003. Bottlenose dolphin, (*Tursiops truncatus*), strandings and mortality on the west coast of Florida, 1985-2002. Unpublished abstract presented at the Fifteenth Biennial Conference on the Biology of Marine Mammals, Greensboro, NC, 14-19 December 2003.

[3] Cockcroft, V.G. 1989. Biology of Indo-Pacific humpback dolphins (*Sousa plumbea*) off Natal, South Africa. Paper presented at the Eighth Biennial Conference on the Biology of Marine Mammals, Pacific Grove, California. December 1989. Unpublished.

interlaboratory variability in methods and presentation may cause confounding factors (Krahn *et al.*, 2003b). However, the general pattern is likely to still be apparent.

In a recent probabilistic risk assessment of the effects of PCBs on bottlenose dolphin reproduction in the southeast United States, Schwacke *et al.* (2002) compared the levels of PCBs in three different populations and developed a predictive framework for examining health risks to the dolphins. Their results suggested that the levels of PCB exposure that the three populations were experiencing were causing serious impairment of reproductive success (reductions of 60-79% – Schwacke *et al.*, 2002). This may occur primarily through delayed age of primiparity, increased prevalence of stillbirths, increased neonatal mortality, or some combination of these. A study of concentrations of PCBs in known females and their young from the Sarasota Bay bottlenose dolphin population, confirmed that females ‘dump’ a large contaminant load to their offspring, especially the first-born (Wells *et al.*, 2005). It is therefore instructive to compare the levels of PCBs in different age classes between these two closely-related species (Table 1). While the mean concentrations of PCBs were generally lower in Hong Kong dolphins (vs. in the same age class of bottlenose dolphins) for juvenile and adult male age classes, the mean was somewhat higher for adult females, the age class that might be most influenced by these effects.

In general, the reduction of OC concentrations for adult female humpback dolphins (compared to adult males) was not nearly as strong as it was for adult female bottlenose dolphins, despite the very similar life history of the two species (Table 1). For DDTs, bottlenose dolphin females had levels only 8-13% those of males, while for humpback dolphins they were 21% those of adult males. Similarly for PCBs, bottlenose dolphin females had levels of 6-11% male levels, while humpback dolphin female levels were 36% those of males (see Schwacke *et al.*, 2002; Hansen *et al.*, 2004). We hypothesise that this may be due to reduced reproductive output (or at least reduced calf survival) of Hong Kong humpback dolphins, which would result in less opportunity for females to depurate and thereby reduce the levels of OCs that they possess. This is clearly just conjecture at this point and there are clearly other reproductive factors that could affect the levels of organochlorines (see Kajiwara *et al.*, 2002). However, the pattern of apparent high neonatal mortality observed is consistent with this idea. Further work is required to confirm or deny our hypothesis.

It has been suggested that the apparently high level of neonatal mortality seen among Hong Kong humpback dolphins (ca. 53% of strandings are young-of-the-year) is related to organochlorine contamination, although this cannot be confirmed at this point (Parsons and Chan, 1998; Jefferson, 2000). Concentrations of PCBs similar to those in blubber have been found in milk in the stomachs of calves from this population, clearly demonstrating the potential for mother-to-offspring transfer (Parsons and Chan, 1998). Cockcroft *et al.* (1989) provided evidence suggesting that in South African bottlenose dolphins, offspring receive a large portion of the mother’s OC load in the first seven weeks post-partum. Later, Kuss (1998) demonstrated what had previously only been hypothesised, that first-born bottlenose dolphin calves receive a much higher contaminant load from their mother’s milk than later-born calves. Their organochlorine concentrations were 2-5 times higher than those of a fourth-born calf of similar age (Kuss, 1998). Wells *et al.* (2005) provided further support for such a scenario. No data on birth order of calves were obtained in this study, but a similar phenomenon may be occurring. Some female humpback dolphins may have trouble successfully rearing their first calf, at least partially due to contaminant issues and thus cannot effectively offload their contaminant burden. If this were true, the succeeding calf would receive a similar contaminant load to the first-born. If it in turn did not survive, the cycle would continue. Again, at this point this is conjecture, but the data presented here have seemingly high levels of neonate mortality and apparently small differences in organochlorine concentrations between adult males and females (see above) which are consistent with such a scenario.

One important point to consider is that young calves appear to be especially vulnerable to the damaging effects of environmental contaminants and it is likely that increased amounts of organochlorines would affect calf survival. Especially for the organic contaminants, the ‘dumping’ of loads of contaminants to the offspring (in particular the first born) may be a very serious issue (see Tanabe *et al.*, unpublished[4]). The problem here is that the newborn (especially the first-born calf) gets overloaded with contaminants at a vulnerable stage of its growth, and this has been suggested to result in increased calf mortality. This phenomenon has been described for fin whales (*Balaenoptera physalus*) (Aguilar and Borrell, 1994), striped dolphins (*Stenella coeruleoalba*) (Tanabe *et al.*, unpublished; Borrell *et al.*, 1996), Indo-Pacific bottlenose dolphins (*Tursiops aduncus*) (Cockcroft *et al.*, 1989), long-beaked common dolphins (*Delphinus capensis*) (Cockcroft *et al.*, 1990), killer whales (*Orcinus orca*) (Ylitalo *et al.*, 2001), Dall’s porpoises (Subramanian *et al.*, 1987; 1988) and finless porpoises (Jefferson *et al.*, 2002a). The present data from humpback dolphins in Hong Kong suggest that this is also the case with these animals. This may explain the seemingly-high levels of neonatal mortality for Hong Kong’s dolphins (see above; Parsons and Jefferson, 2000; Ramu *et al.*, 2005). The reason why male neonates appear to have higher levels than females is unknown. However, it is possible that this is caused by some sex-related difference in the physiological process that occurs during gestation. This is worthy of further study.

Implications for conservation

This study has provided further suggestions that the high levels of some environmental contaminants in Hong Kong are probably impacting the health, survival and reproduction of the Pearl River Estuary humpback dolphin population. Parsons (2004) also came to the same conclusion and further suggested that other populations of humpback dolphins may be experiencing similar problems. However, the evidence for these effects is still largely circumstantial, even for Hong Kong. The existence of a series of problems (e.g. subtle and synergistic effects of contaminants, low quality of available specimen material from strandings, interlaboratory variability in contaminant concentrations) have made it difficult to evaluate how severe this issue is. Only a dedicated programme focusing on this issue and incorporating a plan to resolve these problems will move us forward in our knowledge.

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[4] Tanabe, S., Tanaka, H., Maruyama, K. and Tatsukawa, R. 1979. Elimination of chlorinated hydrocarbons from mother striped dolphins (*Stenella coeruleoalba*) through parturition and lactation. Unpublished report. [Available from TAJ].

Most importantly, although a great deal has been learnt about the Hong Kong population of humpback dolphins from strandings and associated necropsy of stranded specimens, the very extreme levels of decomposition of most stranded specimens have caused great frustration. Our level of understanding is such that a carefully-crafted biopsy collection programme is clearly the next step (and such a programme has recently been initiated). By obtaining biopsy samples from individuals that are well-known from photo-identification studies, knowledge can be advanced very rapidly. At least general age class information can be obtained by collecting samples mainly from animals in our long-term photo-identification database (some of which are of known age and sex, and most of which have at least a minimum known age). Wells *et al.* (2003; 2004) made a compelling argument for the ability to monitor effects of organic contaminants and even to use dolphins as monitors of ecosystem health by combining long-term ecological and observational data with periodic sampling of tissue from living dolphins. In Hong Kong, where environmental contamination is rampant and where humans consume large quantities of seafood, such an approach is even more warranted.

The small risk that is posed by biopsy sampling will be more than offset by the great advances in important conservation knowledge that is stood to be gained. Wells *et al.* (2005) may have said it best when they stated that:

> 'Long-term observational monitoring and periodic biological sampling provide a powerful, non-lethal approach to understanding relationships between organochlorine residue concentrations in tissues and reproductive parameters for coastal dolphins'.

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Trends in bottlenose dolphin (*Tursiops truncatus*) strandings in South Carolina, USA, 1997-2003: implications for the Southern North Carolina and South Carolina Management Units

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ABSTRACT

Trends in marine mammal stranding rates over multiple years can provide useful information on life history parameters, seasonal and spatial distribution and both natural and human-induced mortality rates when compared with baseline data. Data of bottlenose dolphin (*Tursiops truncatus*) stranding rates in South Carolina, USA from 1997-2003 were analysed. The objectives of this study were to: (1) compare recent trends in strandings with baseline data (1992-1996) for South Carolina; (2) compare strandings between the Southern North Carolina Management Unit (SNCMU) and the South Carolina Management Unit (SCMU); (3) determine annual, seasonal and spatial trends in bottlenose dolphin strandings; (4) investigate seasonal reproductive trends; and (5) determine the extent to which humans may affect stranding rates (human interactions). Bottlenose dolphins stranded in South Carolina are assumed to be from at least two of the seven management units recognised by the National Marine Fisheries Service in the Western North Atlantic: the SNCMU and the SCMU. During the study period, 302 bottlenose dolphin strandings were reported in South Carolina and stranding counts were analysed using a Generalised Linear Model. Results showed that there were significantly more bottlenose dolphin strandings in the spring and autumn as compared with summer and winter. The effect of season was highly significant for the number of neonate strandings, suggesting a bimodal reproductive cycle in spring and autumn for the study area. A significant increase in the number of strandings of all age classes was found in the autumn for the northern portion of the State (SNCMU), supporting the assumption that bottlenose dolphins from the north migrate into South Carolina waters during this time of year. Rope entanglements was the most common source of human interaction, with the crab pot fishery the most prevalent source of fishery mortality in South Carolina. This study demonstrates the usefulness of a long-term stranding database by increasing knowledge of temporal and spatial patterns and for monitoring neonate and human-induced mortality.

KEYWORDS: STRANDINGS; BOTTLENOSE DOLPHIN; TRENDS; DISTRIBUTION; REPRODUCTION; SEASONALITY; FISHERIES; NORTH AMERICA; ATLANTIC OCEAN

INTRODUCTION

The accumulation of stranding data over several years allows for the analysis of trends such as yearly, monthly and seasonal stranding rates, gender, length and age class and occurrences of human-induced mortality (human interaction). Analyses of bottlenose dolphin (*Tursiops truncatus*) strandings in the Western North Atlantic (WNA) have become more commonplace since the inception of a national marine mammal stranding program formally initiated by the National Marine Fisheries Service (NMFS) in 1991 (Swingle and Barco, 1997; McFee and Hopkins-Murphy, 2002; McLellan *et al.*, 2002; Stolen *et al.*, 2002; Stolen and Barlow, 2003). These stranding datasets have provided useful information for managers on bottlenose dolphin stock structure, can be used to detect unusual mortality events and serve to monitor the health of living populations. This paper presents additional data on trends of bottlenose dolphin strandings in South Carolina from 1997-2003.

The WNA coastal bottlenose dolphin 'stock' is still considered depleted as determined under the US Marine Mammal Protection Act (Waring *et al.*, 2004), eleven years after the designation (Federal Register, 1993). A stock is considered to be depleted when it falls below its optimum sustainable population, or the number of animals which will result in the maximum productivity of the stock (16 U.S.C. 1362, Sec. 3)[1]. Scott *et al.* (1988) suggested one contiguous population of migratory bottlenose dolphins based on the patterns of strandings during the epizootic of 1987-88 in which greater than 700 bottlenose dolphins died on the east coast of the United States. Since then, much has been learnt about bottlenose dolphin population structure, mainly through photo-identification studies, genetic analyses and air and ship-board surveys. The population structure appears to be more complex (Hohn, 1997; McLellan *et al.*, 2002) than previously described (Scott *et al.*, 1988). At present, the WNA coastal bottlenose dolphin stocks are divided into seven management units (Waring *et al.*, 2004) as defined by NMFS. Coastal bottlenose dolphins stranded in South Carolina are assumed to be from two of these management units: the southern North Carolina management unit (SNCMU) ranging from Cape Lookout, North Carolina to Murrell's Inlet, South Carolina; and the South Carolina management unit (SCMU) ranging from Murrell's Inlet south to the Savannah River (Fig. 1). The extent to which bottlenose dolphins from either management unit influence the stranding dynamics in the other is an issue that could help researchers better understand the stock structure and movement patterns in this region.

The objectives of this study were to: (1) compare recent trends in strandings with baseline data (1992-1996) for South Carolina; (2) compare strandings between the Southern North Carolina Management Unit (SNCMU) and the South Carolina Management Unit (SCMU); (3) determine annual, seasonal and spatial trends in bottlenose dolphin strandings; (4) investigate seasonal reproductive trends; and (5) determine the extent to which humans may affect stranding rates (human interactions).

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[1] 16 U.S.C. 1362 et seq. United States Congress. Marine Mammal Protection Act (MMPA) of 1972 as Amended.

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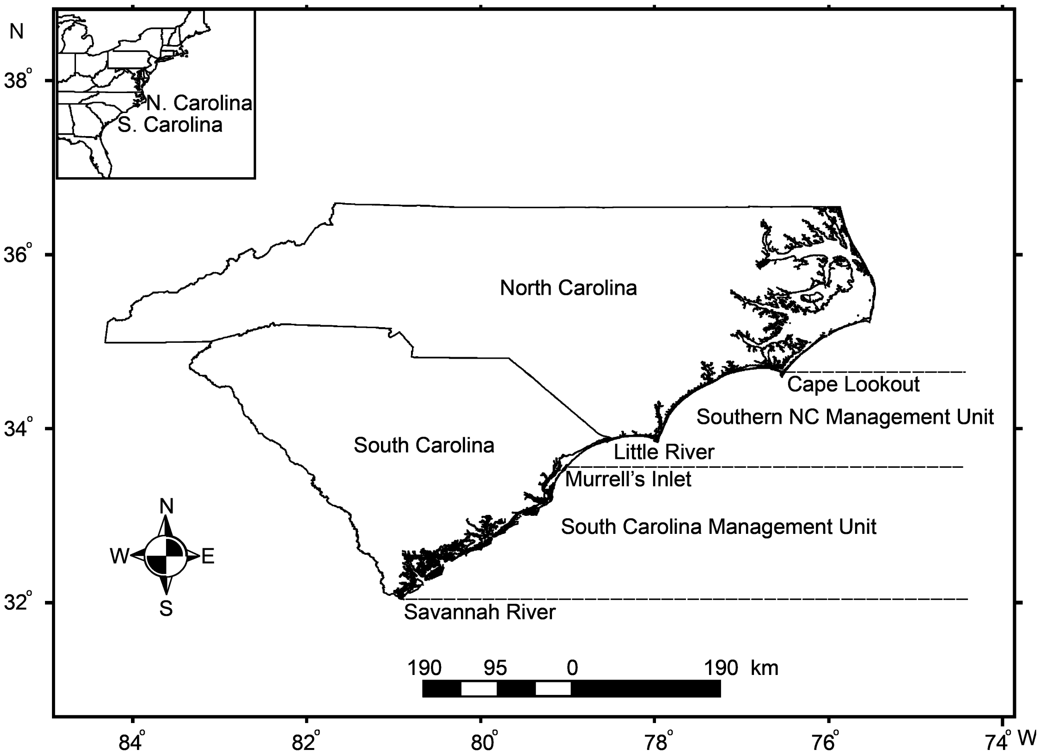


Fig. 1. Map of North Carolina and South Carolina, USA depicting the southern North Carolina Management Unit (Cape Lookout, NC to Murrell's Inlet, SC) and South Carolina Management Unit (Murrell's Inlet, SC to Savannah River).

METHODS

The South Carolina Marine Mammal Stranding Network (MMSN) has been a cooperative effort between the South Carolina Department of Natural Resources (SCDNR) and the National Ocean Service (NOS), Center for Coastal Environmental Health and Biomolecular Research (CCEHBR) in Charleston, South Carolina since 1991. For this study, the MMSN infrastructure and data collection methods have not changed since McFee and Hopkins-Murphy (2002) other than a change in State Coordinator on 1 August 2003. In short, strandings were reported by network volunteers and the public to SCDNR and NOS employees and basic information (Level A data: sex, length, species, stranding location, etc., as defined by Hoffman, 1991) on each carcass recorded. The extent to which humans may affect stranding rates (human interactions) was also evaluated. Bottlenose dolphins may show indications of human interaction in a number of ways: fishery-related mortality (e.g. rope wounds, gear attachment, hook and line, net markings), boat strikes, mutilation and blunt trauma. Additional data were included from necropsies of accessible animals.

Since the NMFS designation of the seven management units for the WNA bottlenose dolphins, analysis was conducted on stranded bottlenose dolphins that were assumed part of the South Carolina portion of the SNCMU (Little River Inlet, South Carolina south to Murrell's Inlet, South Carolina) and the SCMU (Murrell's Inlet south to Savannah River).

STATISTICAL METHODS

For analysing differences in expected stranding counts among seasons and management units, we applied a Generalised Linear Model (GLM) with a log link function and a Poisson error distribution. A Poisson log-linear model was most applicable for these types of data because the response outcome was a count and large counts were expected to be rare events. The fit of the model was evaluated by examining the residual deviance and Pearson Chi-Square statistic. These statistics divided by the degrees of freedom (df) were used to detect overdispersion and underdispersion in the model, indicating an inadequate model fit. When overdispersion was evident, a negative binomial error distribution in lieu of the Poisson model as a corrective measure was applied.

RESULTS

Yearly trends

During the period from 1997 to 2003, 302 bottlenose dolphin strandings were reported along the coast and estuaries of South Carolina. During this period, the number of bottlenose dolphin strandings ranged from 28 in 2002 to 68 in 2001, with a mean of 43.1 strandings per year. Strandings were notably higher in 2000 and 2001 (Fig. 2). In fact, the number of mortalities in 2000 and 2001 were significantly higher than what would be expected based on a statistical model of the number of strandings from previous years. Assuming that the number of strandings per year is a Poisson random variable with a mean calculated based on all prior years (1992-1999), the probability of observing 68 or more strandings (as in 2001) for a given year is less than 0.0001. The probability of observing 53 or more strandings (as in 2000) for a given year, is approximately 0.0005.

During the same period (1997-2003), the number of neonate (defined as a newborn having a folded dorsal fin or flukes or with unhealed umbilical remnants [or with both physical features]) strandings ranged from five in 1998 to 14 in both 2000 and 2001, with a mean of 8.3 strandings per year. The differences in the number of neonate strandings across years were not significant at the $\alpha=0.05$ level (χ^2 test, $p=0.08$).

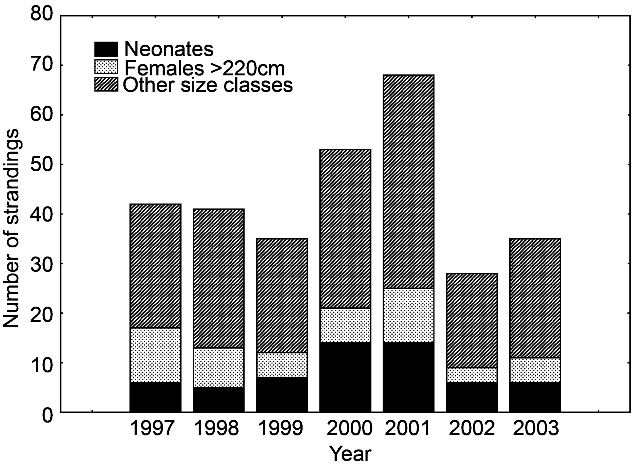


Fig. 2. Annual number of bottlenose dolphin strandings in South Carolina for the period 1997-2003.

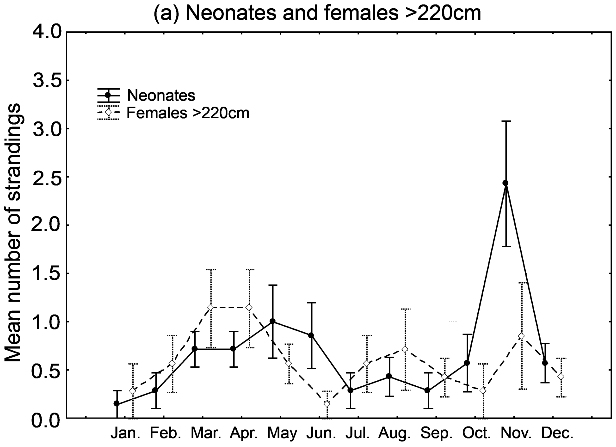
Monthly trends

Over the seven-year period, the greatest number of reports ($n=44$, or 14.6%) of bottlenose dolphin strandings occurred during November and the least in both February and September ($n=13$, or 4.3%). The effect of month on the total number of strandings for the 1997-2003 period was significant ($p=0.0012$). However, when data were divided into two classes representing neonates and a combined class of all other ages (Fig. 3), the significance of month on the expected number of strandings was variable. While month remained a significant factor for the number of neonate strandings ($p<0.001$), it was not a significant factor for the remaining age classes ($p=0.40$). The combined age class was then further divided into two subclasses: sexually mature (>220cm) females (Odell, 1975; Mead and Potter, 1990) and males and remaining females. The expected number of strandings between months did not vary for either of these subclasses ($p=0.38$ and $p=0.21$, respectively).

Seasonal trends

An equal number of bottlenose dolphin strandings occurred in spring (April-June) and autumn (October-December) ($n=85$, 28.1%). Bottlenose dolphin strandings were lowest in winter (January-March) ($n=62$, 20.5%). The Poisson GLM applied to examine the effect of season on the total number of strandings for the 1997-2003 period indicated overdispersion (deviance/df=1.79), so the alternative negative binomial model was employed. The effect of season on the total number of strandings for the 1997-2003 period was not significant ($p=0.16$). Data were then divided into two classes representing neonates and a combined class of all other ages. The effect of season was highly significant for the number of neonate strandings ($p=0.002$), Poisson model (deviance/df=1.16), yet the effect of season on the remaining age classes remained insignificant ($p=0.94$). These results are consistent with earlier analyses of stranding data from South Carolina for the previous 5-year period, which suggested that neonate strandings occurred more frequently in the spring and autumn months as compared to the winter and summer months (McFee and Hopkins-Murphy, 2002).

(a) Neonates and females >220cm



(b) Other age classes

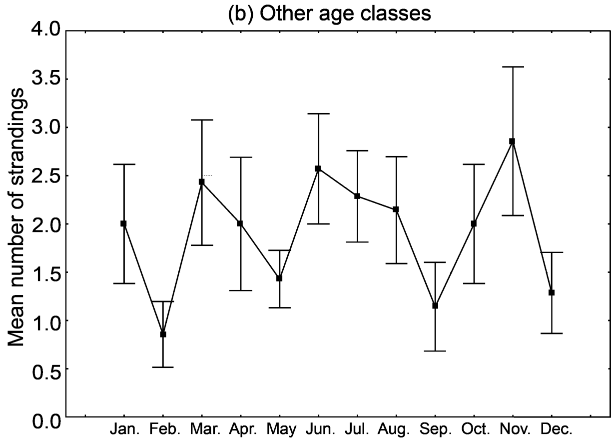


Fig. 3. Mean number of bottlenose dolphin strandings in South Carolina per month from 1997 to 2003. Graph (a) represents neonates and females greater than 220cm. Graph (b) represents all other age/sex classes. Whiskers represent standard errors.

To further explore the relationship between neonate strandings and season, spring/autumn versus winter/summer was contrasted. Differences between the two categories were highly significant ($p<0.001$), indicating an increased number of neonate strandings in the spring and autumn as compared to the winter and summer (Fig. 4). The highest number of neonate strandings was seen in autumn ($\bar{x} = 3.6$), although this did not differ significantly ($p=0.29$) from the mean number of neonate strandings for spring ($\bar{x} = 2.6$). The mean number of neonate strandings for the winter and summer seasons were significantly lower ($\bar{x} = 1.1$ and $\bar{x} = 1.0$, respectively).

The years 2000-2001 had an unusually high number of strandings, and in order to examine whether the inclusion of stranding data from these years could unduly influence results, the above analysis of neonate strandings across seasons, excluding data from 2000 and 2001, was repeated. While the results were less significant ($p=0.045$ for overall effect of season on number of neonate strandings) due to the reduced sample size, the overall conclusions did not change.

The Poisson model was used to determine if there was any effect of season in the SNCMU. The effect of season on the total number of strandings for the SNCMU was significant ($p=0.002$), confirming that there was a significant increase in strandings in autumn.

The seasonality of neonate strandings to determine if the bimodal distribution of neonate strandings (i.e. highest numbers in spring and autumn) was consistent across both management units was further examined. While neonate strandings were higher in the autumn for both management units (Fig. 5), only the SCMU appeared to show an increase in the number of strandings in the spring. A Poisson model was fitted using season and management zone as factors to determine whether or not the interaction term between the two factors would be significant. The interaction of season and management zone was significant (p<0.001), indicating seasonal strandings between the two management zones were dissimilar.

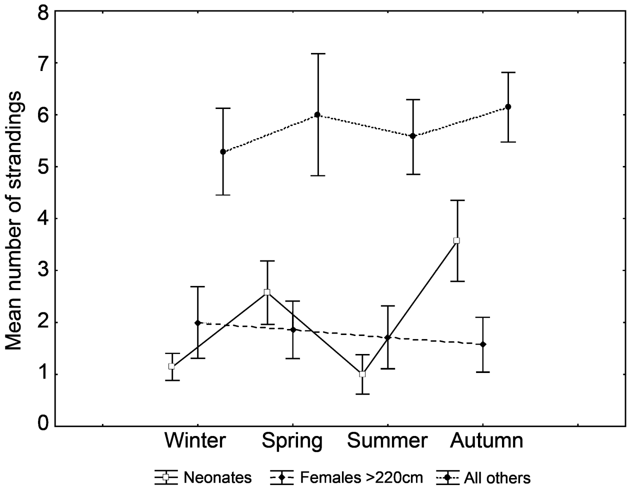


Fig. 4. Mean number of bottlenose dolphin strandings in South Carolina by season. Whiskers represent standard errors.

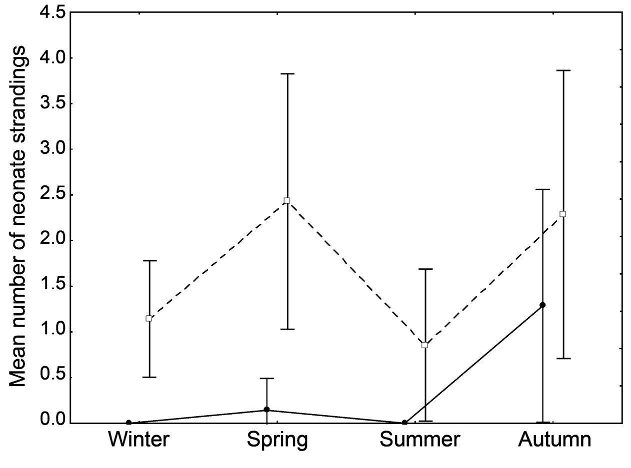


Fig. 5. Mean number of neonate strandings by season, divided into management zones. Whiskers represent standard errors.

Sex

The total number of stranded bottlenose dolphins with known sex was 229; 73 (24.2%) were of unknown sex. The sex ratio for 1997-2003 was 1.00:0.92, males (n=119) to females (n=110), not significantly different from parity (p=0.97).

Length classes

The total number of stranded bottlenose dolphins with known length was 271. Length data were stratified into five classes (McFee and Hopkins-Murphy, 2002):

class I	(neonates-defined as a newborn having a folded dorsal fin or flukes or with unhealed umbilical remnants [or with both physical features]; <120cm);
class II	(<184cm, young of the year);
class III	(185-200cm, calves);
class IV	(201-240cm, mostly physically immature, especially males); and
class V	(>240cm, mostly mature).

Where both sex and length were known (n=175), males and females were distributed proportionately across the length classes with the exception of class III and class IV. In class III, males dominated (80%), whereas in class IV females dominated (65.4%).

Neonates

Neonates represented 21.4% (n=58) of the total number (n=271) of strandings of bottlenose dolphins with known length, ranging from 14.3% in 1998 to 30.4% in 2000. Strandings were found in every month of the year, but occurred more frequently in autumn (n=25, 43.1%) and spring (n=18, 31.0%). November had the greatest number of strandings (n=16), accounting for 64% of autumn strandings. Twenty-six neonates (44.8%) were <100cm and 16 (61.5%) of these stranded during the spring and autumn. Forty-nine of the neonates were of known sex, with a 1:1 ratio between females (n=25) and males (n=24).

Forty-seven (81.0%) neonates stranded in the SCMU, with most strandings occurring in spring (n=16) and autumn (n=16). Of the 11 neonates that stranded in the South Carolina portion of the SNCMU, nine (81.8%) stranded in the autumn.

Females =220cm

Reproductively mature females (i.e. those ≥220cm) represented 47.3% (n=52) of the total number (n=110) of females stranded. The proportion of females ≥220cm stranded each year ranged from 36.4% (2002) to 55% (1997). The proportion of females ≥220cm stranded was consistent from season to season.

Comparison with baseline stranding information

Stranding counts for the 1997-2003 time period with the baseline data from 1992-1996 (McFee and Hopkins-Murphy, 2002) were compared. The mean number of strandings per year for the 1997-2003 period was higher than the baseline period (p=0.049). When separated into neonate and non-neonate categories, the increase in the number of neonate strandings per year was significant (p=0.02), while the increase in the number of non-neonate strandings per year was not significant (p=0.06).

Human interaction

The total number of stranded bottlenose dolphins where there was clear evidence supporting either human interaction (HI) or no human interaction was 143 out of 302 (some 47%). Approximately 25% (n=36) of these strandings showed evidence of HI while 107 showed no signs of HI; 97% of HI animals occurred in the SCMU (Table 1). Incidents of rope entanglements, including confirmed entanglements in crab pot lines (n=6), accounted for 44.4% of HI cases. Incidence of confirmed HI with bottlenose dolphins was highest in August (n=9) and most prevalent from May to August (n=24). Rope and crab pot entanglements were most prevalent in July and August (n=9) and four of the six boat strikes were in June/July. Twenty-nine of the 36 bottlenose dolphins showing signs of HI were of known sex, with a 1:1 ratio between males

Table 1

Summary of bottlenose dolphin strandings in South Carolina involved with human interaction from 1997-2003. 'CBD' refers to the number of bottlenose dolphin strandings where human interaction could not be determined.

	1997	1998	1999	2000	2001	2002	2003	Total
Total dolphins stranded	42	41	35	53	68	28	35	302
Human interactions (HI)								
Rope marks	5	3	0	1	0	0	1	10
Crab pot	2	0	1	0	1	0	2	6
Boat strike	0	1	2	1	2	0	0	6
Mutilation	2	0	1	0	1	0	0	4
Net marks	1	1	0	0	0	1	0	3
Trammel net	0	0	0	0	0	2	0	2
Shrimp fishery	0	1	0	0	0	1	0	2
Monofilament	0	0	0	1	1	0	0	2
Blunt trauma	0	0	0	1	0	0	0	1
Total HI	10	6	4	4	5	4	3	36
No HI	16	10	11	19	20	13	18	107
CBD	16	25	20	30	43	11	14	159
% HI (-CBD)	38.5 (*n*=26)	37.5 (*n*=16)	26.7 (*n*=15)	17.4 (*n*=23)	20 (*n*=25)	23.5 (*n*=17)	14.3 (*n*=21)	25.2 (*n*=143)

(*n*=15) and females (*n*=14). Some 73% of the males were <221cm in length ($\bar{x}$ = 198cm), whereas 50% of the females were <220cm ($\bar{x}$ =189cm).

DISCUSSION

The analysis of a larger dataset of bottlenose dolphin strandings in South Carolina combined with baseline data (McFee and Hopkins-Murphy, 2002) has helped to further elucidate stranding trends. While data from our current study show many of the same trends as the baseline data (e.g. length class distribution, gender distribution, seasonal distribution, geographic distribution), the larger dataset has allowed us to include data that may add to the knowledge of stock structure of bottlenose dolphins in the southeastern United States and reproductive seasonality in South Carolina. In particular, our analysis produced four main findings: (1) bottlenose dolphin strandings were unusually high for 2000 and 2001; (2) neonate strandings in the SCMU are bi-modally distributed, with peaks in spring and autumn; (3) more bottlenose dolphins strand in the SNCMU in the autumn; and (4) based on recovery of carcasses, rope entanglements (including confirmed crab pot interactions) are the dominant source of apparent human-induced mortality.

Results from the analysis of yearly trends depicted unusual increases in bottlenose dolphin stranding rates for 2000 and 2001 in South Carolina. A similar trend was observed for these two years in Florida, but no appreciable difference in stranding rates was observed in the neighbouring states of Georgia and North Carolina (Southeastern United States Marine Mammal Stranding Database). The increase in Florida bottlenose dolphin strandings was likely due to two unusual mortality events (UME's) declared by NMFS for the Indian River Lagoon (2001) and the Florida Panhandle (1999-2000). Elevated strandings in a localised geographic area are to be reviewed by a panel of marine mammal experts before a UME can be declared under the MMPA (16 U.S.C. 1421c, Sec. 404)[2]. A harmful algal bloom was suspected as the cause of the Florida Panhandle UME (NMFS, 2004; Flewelling *et al.*, 2005) in which at least 120 animals died. It is unclear what caused the Indian River Lagoon UME in which 39 animals died (NMFS, 2004).

In South Carolina, there was no apparent explanation for the increase in bottlenose dolphin strandings in 2000-2001 other than an increase in neonate strandings, although this increase was not significant across years. Formalin-fixed samples collected from fresh dead animals during 2000 and 2001 for histological analysis by the Armed Forces Institute of Pathology (Washington, DC) did not reveal related causes of death. Additionally, the number of human interaction cases for this period was not elevated.

Recent studies (Hohn, 1997; McLellan *et al.*, 2002; Gubbins *et al.*, 2003) suggest that bottlenose dolphin stock structure is more complicated than the previous concept of a single coastal migratory stock in the WNA (Scott *et al.*, 1988). The NOAA Fisheries now recognises seven management units of coastal bottlenose dolphins in the WNA (Marine Mammal Commission, 2003; Waring *et al.*, 2004). Bottlenose dolphins stranded in South Carolina are believed to be from two of these units, the SNCMU and the SCMU. While data were not available from bottlenose dolphins stranded in the North Carolina portion of the SNCMU (Cape Lookout, NC to Little River Inlet, SC) for this study, our results showed that strandings significantly increased in the autumn in the South Carolina portion (Little River Inlet, SC to Murrell's Inlet, SC) of the SNCMU suggesting an influx of migrating bottlenose dolphins, possibly from the north. In Virginia, bottlenose dolphins are nearly absent by mid-November but reappear in spring (Swingle, 1994; Barco *et al.*, 1999). Water temperature was negatively correlated with dolphin abundance in Virginia (Barco *et al.*, 1999) and has been suggested as a possible cue for migrations (Mead and Potter, 1990). Bottlenose dolphins were found in high abundance in the winter between Cape Hatteras, North Carolina and Cape Lookout, North Carolina in an aerial survey of marine mammals of the Southeast US continental shelf, although most of these appeared to be from the offshore morphotype of bottlenose dolphins (Garrison *et al.*, 2003). Counts of bottlenose dolphins from boat transect surveys conducted between 1995 and 1998 in the coastal waters between Little River Inlet, SC and Murrell's Inlet, SC also indicated a greater than an order of magnitude increase in abundance in late autumn

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[2] 16 U.S.C. 1421 et seq. United States Congress. Marine Mammal Protection Act (MMPA) of 1972 as Amended.

(Young and Peace, 1999). Monthly aerial survey data conducted from 1997-2003 by SCDNR from Murrell's Inlet, SC to Port Royal Sound, SC indicated a nearly 1.5× increase in bottlenose dolphin sightings during the autumn compared to that of the spring and summer and nearly a three-fold increase from winter (SCDNR unpublished data). It is plausible, therefore, that some of the SNCMU dolphins may migrate south into South Carolina (SC) in late autumn.

The increase in bottlenose dolphin strandings in autumn from Murrell's Inlet, SC to Little River Inlet, SC (i.e. southern portion of the SNCMU) can be partially explained by the large proportion (42.1%) of neonate strandings. Our results show that taken as whole for the state of South Carolina, there exists a bimodal neonate stranding cycle in the spring and autumn (Fig. 4). However, the two management units differ if reviewed separately. While the SCMU shows a bimodal neonate stranding cycle (spring and autumn), the southern portion of the SNCMU shows a unimodal distribution, with most neonate strandings in the autumn (Fig. 5). Thayer *et al.* (2003) noted that neonate strandings occurred more frequently in the spring, mostly north of Cape Lookout, NC, with a secondary, smaller scale peak of neonate strandings occurring south of Cape Lookout, NC in the autumn. This secondary peak in neonate strandings in the autumn south of Cape Lookout, NC supports what is observed in the southern portion of the SNCMU. Further investigation into the neonate stranding patterns of the North Carolina portion of the SNCMU is needed to determine if this is characteristic of the management unit as a whole.

Although bottlenose dolphins exhibit year-round calving cycles, reproductive seasonality can vary over large geographic regions or between local dolphin populations (Urian *et al.*, 1996). On the east coast of the United States, a bimodal neonate seasonal distribution was noted from the Indian River Lagoon, Florida (Urian *et al.*, 1996), while unimodal distributions were noted for North Carolina (Thayer *et al.*, 2003), the west coast of Florida (Waring *et al.*, 2004) and along the Texas coast (Fernandez and Hohn, 1998).

Fernandez and Hohn (1998) and Thayer *et al.* (2003) caution against the use of stranding data as an indicator of reproductive seasonality, as mortality of neonates may lie outside of the true birthing dates. Data from our study showed that 61.5% of the stranded neonates that were <100cm in length stranded in the spring and autumn. Assuming these animals were near-term foetuses or stillbirths, this, along with a bimodal neonate stranding cycle, would support a bimodal reproductive cycle in South Carolina.

The determination of human-induced mortality of bottlenose dolphins is difficult to assess. Many carcasses were too decomposed or lacked entangling gear. As a result, the number of HI cases may be underestimated. The results of this seven year study were similar to those of the baseline study (McFee and Hopkins-Murphy, 2002) in that rope entanglements was the most common source of HI and in the percentage of HI cases observed (25.2%; Table 1). HI cases are less frequent than in North Carolina and Virginia (53% and 49%, respectively), but more frequent than in Georgia (12%; Waring *et al.*, 2004). Entanglements of bottlenose dolphins in the crab pot fishery appear to be the most prevalent source of fishery-related mortality in South Carolina (Burdett and McFee, 2004). Mortality in fishing operations is the most common source of anthropogenic mortality for small cetaceans (IWC, 1994; Read and Murray, 2000; Friedlander *et al.*, 2001; McLellan *et al.*, 2002), but the fishery source varies from state to state. For instance, in North Carolina and Virginia, gill net fisheries appear to be the leading cause of anthropogenic mortality for bottlenose dolphins (Steve *et al.*, 2001; Read *et al.*, 2003; Read *et al.*, 2004; Rossman and Palka, 2004). In South Carolina, gillnet entanglements are rare as there are few gillnet fisheries. A study of the ocean American shad (*Alosa sapidissima*) fishery in South Carolina found no mortality of bottlenose dolphins in this fishery (McFee *et al.*, 1996) and the fishery was closed on 1 January 2005 (ASMFC, 1999). During the current study, two of the five bottlenose dolphins that showed signs of net entanglements were from a single trammel net set conducted by SCDNR's Marine Division in the Wando River, South Carolina. This mortality incident was the first in 15 years of dedicated trammel net fishing by SCDNR (~11,250 sets) (B. Roumillat, pers. comm.).

It has been suggested that bottlenose dolphin calves and subadults are more susceptible to human interactions than adults (Wells and Scott, 1994; Reynolds *et al.*, 2000). In our study, this was especially true with males even though mean length by gender was lower for females. This was similar to observations during the baseline study (McFee and Hopkins-Murphy, 2002). Interestingly, five of the six bottlenose dolphins that were struck by boats were <175cm and the other was a subadult (227cm). Inexperience around boats by primiparous females with dependent calves has been hypothesised for lower calf survivorship and the calf could hinder the avoidance capabilities of both mother and calf (Nowacek *et al.*, 2001). Curiosity, feeding behaviours, socialisation and inexperience around boats and fishery operations may also increase the vulnerability of calves to anthropogenic mortality.

Results from this seven year study into stranding rates of bottlenose dolphins in South Carolina demonstrated the value of a long-term database. Additional data from this study substantiated a bimodal reproductive cycle in South Carolina and significant seasonal changes in stranding rates were more easily recognised than from the baseline data alone. Future studies to elucidate more local reproductive strategies should include photo-identification studies currently being conducted in Charleston, Bulls Bay and North Inlet, South Carolina. Also, bottlenose dolphin stranding data from the entire southern North Carolina management unit should be compared with the South Carolina management unit to determine stranding trends of a broader geographical range. Results from the human interaction analyses clearly demonstrate the need to continue the investigation of anthropogenic mortality of bottlenose dolphins as these analyses are relevant to management decisions in the protection and conservation of this species.

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Cetaceans of the oceanic northern Gulf of Mexico: Distributions, group sizes and interspecific associations

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ABSTRACT

The Gulf of Mexico is a subtropical ocean basin with a diverse oceanic cetacean community. Cetacean research in the Gulf of Mexico has been driven by mandates of the US Marine Mammal Protection Act as well as concerns over the rapidly expanding oil and natural gas industry and related potential threats (e.g. seismic surveys, increased ship traffic, oil spills). Previously, cetacean distribution and abundances for specific Gulf of Mexico areas or species have been described based on work over periods of several years, and recently abundance estimates were made for the entire oceanic northern Gulf of Mexico (1996-2001). For each cetacean species, the paper describes distribution, group size, associated sea surface temperature and water depth and interspecific associations based on surveys conducted over 11 years that span the entire northern Gulf of Mexico. This dataset is the most comprehensive to date for the oceanic northern Gulf. Nine ship surveys totalling 45,462km of effort were conducted during spring seasons (1991-2001) in continental shelf-edge and oceanic waters ($\geqslant$100m) of the northern Gulf of Mexico. Eighteen species were identified from 1,868 sightings. Cetaceans were found throughout the area although some species had localised distributions or occurred in restricted ranges of water depths. Spinner dolphins (*Stenella longirostris*) had the largest mean group size ($n = 40$, $\bar{x} = 151.5$, SE = 30.90), followed by melon-headed whales (*Peponocephala electra*), clymene dolphins (*S. clymene*), pantropical spotted dolphins (*S. attenuata*), Fraser's dolphins (*Lagenodelphis hosei*) and striped dolphins (*S. coeruleoalba*) (range of means 46.1-99.6). Beaked whales (Ziphiidae), Bryde's whales (*Balaenoptera edeni/brydei*), sperm whales (*Physeter macrocephalus*) and pygmy/dwarf sperm whales (*Kogia* spp.) were found in the smallest groups ($\bar{x} < 3$). Twenty-seven sightings (1.4% of all sightings) were composed of two cetacean species. Common bottlenose dolphins (*Tursiops truncatus*) were recorded in mixed-species groups with more species than any other cetacean. Forty-five cetacean sightings (2.4% of all sightings) were associated with at least one bird species, and 21 (1.1% of all sightings) were associated with schools of fish. Contrary to previous reports, pantropical spotted dolphins were observed in association with both fish (including surface tunas) and seabirds, although to a lesser extent than for other tropical oceans. No mixed pantropical spotted and spinner dolphin groups were sighted despite their regular co-occurrence in other tropical oceans.

KEYWORDS: CETACEAN; GULF OF MEXICO; SURVEY-VESSEL; DISTRIBUTION; GROUP SIZE

INTRODUCTION

About 21 species of cetaceans regularly inhabit the northern Gulf of Mexico (i.e. waters within the boundary of the US Exclusive Economic Zone in the Gulf). The species are divided into two communities, the continental shelf community, comprised of the common bottlenose dolphin (*Tursiops truncatus*) and Atlantic spotted dolphin (*Stenella frontalis*), and the oceanic community, comprised of 19 additional species: the Bryde's whale (*Balaenoptera edeni/brydei*); sperm whale (*Physeter macrocephalus*); dwarf sperm whale (*Kogia sima*); pygmy sperm whale (*K. breviceps*); Cuvier's beaked whale (*Ziphius cavirostris*); Blainville's beaked whale *(Mesoplodon densirostris*); Gervais' beaked whale (*M. europaeus*); melon-headed whale (*Peponocephala electra*); pygmy killer whale (*Feresa attenuata*); false killer whale (*Pseudorca crassidens*); killer whale (*Orcinus orca*); short-finned pilot whale (*Globicephala macrorhynchus*); rough-toothed dolphin (*Steno bredanensis*); Risso's dolphin (*Grampus griseus*); Fraser's dolphin (*Lagenodelphis hosei*); pantropical spotted dolphin (*Stenella attenuata*); striped dolphin (*S. coeruleoalba*); spinner dolphin (*S. longirostris*) and clymene dolphin (*S. clymene*) (Mullin *et al.*, 1994a; b; 2004; Hansen *et al.*, 1996; Mullin and Hansen, 1999; Mullin and Hoggard, 2000; Fulling *et al.*, 2003). The cetacean community in the northern Gulf is essentially a tropical one. With the exceptions of Atlantic spotted dolphins and clymene dolphins, which are endemic to warm Atlantic Ocean waters, and common bottlenose dolphins, sperm whales and killer whales, which have nearly cosmopolitan distributions, all species occurring in the Gulf of Mexico inhabit deep, warm temperate to tropical waters throughout the world (Jefferson *et al.*, 1993).

Previous cetacean research in the Gulf of Mexico focused on abundance and distribution (Jefferson, 1996; Fulling *et al.*, 2003; Mullin *et al.*, 2004; Mullin and Fulling, 2004), habitat preferences (Baumgartner, 1997; Baumgartner *et al.*, 2001; Davis *et al.*, 1998; 2002), or detailed descriptions of sightings of specific species (Leatherwood *et al.*, 1993; Mullin *et al.*, 1994a; c; O'Sullivan and Mullin, 1997). Ballance and Pitman (1998) compared the cetacean communities (species composition, relative abundance, group sizes and associated species) in the eastern tropical Pacific Ocean, western tropical Indian Ocean and the Gulf of Mexico. They based their Gulf conclusions on results from spring cruises from 1991-1994 (Hansen *et al.*, 1995) and on personal observations by R.L. Pitman while participating in those cruises. Many of the conclusions on the Gulf cetaceans by Jefferson and Schiro (1997) and Mullin and Hansen (1999) were also based on the 1991-1994 data.

This paper summarises data from shipboard cetacean surveys of the shelf-edge and oceanic northern Gulf of Mexico conducted during nine spring seasons from 1991 to 2001 (the largest, most consistent dataset) to more adequately describe distribution, group sizes and interspecific associations for each cetacean species. The specific objectives are to describe: (1) the diversity of cetaceans; (2) the distribution of each species; (3) the group size, sea surface temperature and water depth for each species; and (4) the interspecific associations for each species. It also provides quantitative support for and amends comments on these topics for the Gulf of Mexico by Jefferson and Schiro (1997), Ballance and Pitman (1998) and Mullin and Hansen (1999).

METHODS

Study area

The study area was continental shelf-edge (100-200m deep) and oceanic waters (>200m deep) of the US Gulf of Mexico (398,960km^2) (Fig. 1). The Gulf is a subtropical ocean basin in which the biological and physical oceanography are dynamic both spatially and temporally (Baumgartner *et al.*, 2001; Biggs and Ressler, 2001; Davis *et al.*, 2002). In the eastern Gulf the near-surface circulation is dominated by the Loop Current (LC), an extension of the Gulf Stream that enters the Gulf of Mexico via the Yucatan Channel, turns anticyclonically and exits through the Straits of Florida (Wiseman and Sturges, 1999). Pairs of anticyclonic (warm-core) – cyclonic (cold-core) eddies are regularly found in the central and western Gulf.

The mean state of productivity of the oceanic Gulf of Mexico is low (<0.1mg chl · m^{-3}), but there are a number of physical features that make the habitat heterogeneous both spatially and temporally (Biggs and Ressler, 2001). Upwelling often occurs at the LC periphery, where cyclonic eddies frequently develop. The LC periodically sheds anticyclonic eddies, which after separation, move slowly westward until their advance is hindered by shoaling topography over the northwestern continental slope (Davis *et al.*, 2002). Another major influence on the Gulf of Mexico oceanography is the large freshwater inflow from the Mississippi River.

Major bathymetric features of the northern Gulf include: the wide continental shelf off the Florida peninsula and off northern Texas and western Louisiana; the narrow shelf off the Florida Panhandle near DeSoto Canyon, off the Mississippi River Delta region, and off southern Texas; the two major canyon systems, the Mississippi and DeSoto canyons; and the salt domes and basins on the northwestern continental slope (Baumgartner, 1997).

Data collection

Nine spring surveys were conducted during 1991-1994, 1996-1997 and 1999-2001. Surveys were conducted aboard NOAA ships *Oregon II* (52m) and *Gordon Gunter* (68m), and were approximately 44 days in duration (two ~22 day legs), beginning in mid-April and ending in early June. These surveys were conducted in conjunction with ichthyoplankton sampling along a trackline uniformly spaced throughout oceanic waters of the northern Gulf (Fig. 1). The trackline was transited 24h/day to accommodate plankton sampling at stations spaced 55.6km (30 n.miles) apart.

There was less survey effort in the extreme western and southeastern areas since plankton stations in the extreme west were considered of lower priority. Stations in this region were also sometimes dropped due to time constraints arising from inclement weather or mechanical problems. During some years, researchers from the State of Florida, in collaboration with our agency, sampled the stations in the southeastern Gulf, making those of lower priority as well. An additional 10-day leg that was a dedicated cetacean line-transect survey (no plankton sampling) was conducted during most years in northwestern (1992-1994) or northeastern (1996-1997) shelf-edge and continental slope waters (100-2,000m deep).

Data were collected by two teams of three observers on the ship's flying bridge, located 9.2m (*Oregon II*) and 14.5m (*Gunter*) above the water's surface. Data were collected during daylight hours in favourable weather conditions (i.e. Beaufort sea state <6, no rain) at a ship's speed of 10 knots (18km h^{-1}). Two observers searched for cetaceans using 25× 'bigeye' binoculars, and the third observer recorded data and searched near the ship using hand-held binoculars and unaided eye. Teams alternated 2 hour watches throughout the day, and observers rotated positions every 30-40min to avoid fatigue. Sightings made by the on-watch observer team while following standard line-transect protocol were 'on-effort'. Sightings made under other circumstances (e.g. while the ship was stopped for ichthyoplankton sampling) were 'off-effort'.

Data were recorded on a computer using a BASIC data acquisition program interfaced with the ship's GPS. For each cetacean sighting the following data were recorded: bearing from the bow; linear distance from the ship; species; group size; behaviour; presence of calves; presence of remoras (Echeneidae) and wounds from cookie-cutter sharks (*Isistius* spp.); sea surface temperature (SST); water depth; and the presence of associated seabird and fish species. A suite of environmental sensors (e.g. SST) were integrated into the ship's scientific computer system which was constantly displayed, allowing observers to record SST. Water depth for each sighting was obtained from nautical charts using the latitude and longitude of the sighting. Visibility conditions were recorded and updated at least every 30-40min, including Beaufort sea state, wind direction, weather and glare.

The ship was typically diverted if a sighting was within a 5,550m corridor perpendicular to the transect-line to confirm species identifications and to make group size estimates. For mixed-species cetacean groups, a separate group size estimate was made for each species. Group size was estimated by a consensus of the on-watch observers. Cetacean species were considered 'associated' or in a 'mixed-species group' if they were swimming in a mixed school, bowriding the research vessel together, behaving aggressively toward one another or behaving in a similar manner within 300-400m of one another.

Cetaceans were identified to the lowest taxonomic level possible based on descriptions in field guides and scientific literature (e.g. Jefferson *et al.*, 1993; Leatherwood *et al.*, 1983). Pygmy and dwarf sperm whales were not consistently distinguished, and mesoplodont whales were difficult to distinguish at sea; therefore findings are reported for *Kogia* spp. and *Mesoplodon* spp. Sightings of *Mesoplodon* sp. were probably Gervais' or Blainville's beaked whale, based on stranding records from the Gulf (Jefferson and Schiro, 1997; Mead, 1989; Schmidly, 1981). Male Blainville's beaked whales were identified in two sightings by their unique high arching mouthline (Jefferson *et al.*, 1993). Short-finned and long-finned pilot whales cannot easily be distinguished at sea, but based on stranding records and known distributions (Bernard and Reilly, 1999; Schmidly, 1981), it seems most likely all pilot whale sightings were short-finned and they are reported thus here. We also believe the only balaenopterid whale sighted during these surveys was the Bryde's whale; therefore sightings of Bryde's whales, Bryde's/sei whales and *Balaenoptera* sp. were combined and treated as Bryde's whales. Each whale in these sightings had a large, falcate dorsal fin similar to that of Bryde's or sei whales, but when observers clearly saw the dorsal surface of the rostrum of at least one whale in a sighting (11 of 17 sightings), three ridges were present, a diagnostic characteristic of Bryde's whales (Cummings, 1985). The five records of sei whales from the Gulf of Mexico are from strandings and are considered to be strays or accidental (Jefferson and Schiro, 1997). Finally, in some cases, animals could only be identified as unidentified Ziphiidae (Cuvier's beaked whale or *Mesoplodon* sp.), large whale (>7m long), small whale (non-dolphin, <7m), unidentified dolphin, *Stenella* sp., or odontocete.

Data analysis

All sightings used in analyses occurred in waters ≥100m. For group size summaries, off-effort and naked-eye sightings were deleted from the dataset (only on-effort sightings made with 25× binoculars were used), the latter because in most cases these sightings were believed to be a subset of a larger group that approached the ship to ride the bow. For distribution plots, all on-effort sightings were used. For analysis of mixed-species cetacean sightings, all sightings were used, including off-effort and naked-eye sightings. For SST data, temperatures not recorded to the nearest tenth of a degree due to observer error were deleted from the SST dataset. Descriptive statistics are reported as means and standard errors.

RESULTS

Effort

Line-transect effort for the nine spring surveys totalled 45,462km (Table 1, Fig. 1). Annual survey effort ranged from 4,048 to 5,844km. A total of 1,868 sightings were made, of which 1,736 were on-effort and 132 were off-effort. Annual total sightings ranged from 81 to 275.

Table 1

Survey effort and number of sightings by year.

Year	Effort (km)	Number of on-effort sightings	Number of off-effort sightings	Total number of sightings
1991	4,267	81	0	81
1992	5,756	236	16	252
1993	5,519	228	12	240
1994	5,601	259	16	275
1996	5,844	201	26	227
1997	5,724	205	15	220
1999	4,522	190	17	207
2000	4,048	181	10	191
2001	4,181	155	20	175
Grand total	45,462	1,736	132	1,868

Diversity

Eighteen species were identified (Table 2). These included male Blainville's beaked whales on two occasions and two distinct forms of *Kogia*, one with a large falcate dorsal fin and the other with a much more diminutive dorsal fin, that represent the two species, dwarf and pygmy sperm whales, respectively (Caldwell and Caldwell, 1989). Groups of pantropical spotted dolphins were the most commonly encountered species and made up about one third of all groups sighted. Sperm whales, which were frequently sighted, and Bryde's whales were the only great whales encountered.

Distribution, water depth and sea surface temperature

Cetaceans were found throughout the northern Gulf of Mexico; however, some species had more localised distributions (e.g. eastern, western) or occurred in more restricted ranges of water depths (Fig. 2a-l, Table 2). All five species in the genus *Stenella* regularly occurred in the northern Gulf. Atlantic spotted dolphins were found along the continental shelf break throughout the study area with the deepest sighting occurring at 362m. Pantropical spotted and striped dolphins had widespread distributions throughout oceanic waters in a wide range of depths. Spinner and clymene dolphins had nearly parapatric distributions, with most sightings of each species occurring east or west, respectively, of the Mississippi River. The mean depths of clymene, pantropical and striped dolphin sightings were twice that of spinner dolphins (Table 2).

Sperm whales were widely distributed but relatively concentrated near the mouth of the Mississippi and the area due west of the Florida Keys. *Kogia* spp. and Risso's dolphins were also widespread and occurred in a wide range of depths.

Common bottlenose dolphins occurred most commonly along the shelf-edge and upper continental slope. Most killer whales occurred in the central Gulf in waters >700m. There were few false killer whale sightings, but nearly all (9 of 11) occurred in the far eastern Gulf in a wide range of depths. Short-finned pilot whales were widespread throughout the continental slope of the western Gulf, west of 89°W, with the exception of one sighting near the Dry Tortugas in the eastern Gulf.

Melon-headed and pygmy killer whales occurred in waters >800m in a nearly identical range of depths, though the mean depth of pygmy killer whale sightings was about 1,000m deeper. Rough-toothed dolphins were widespread in

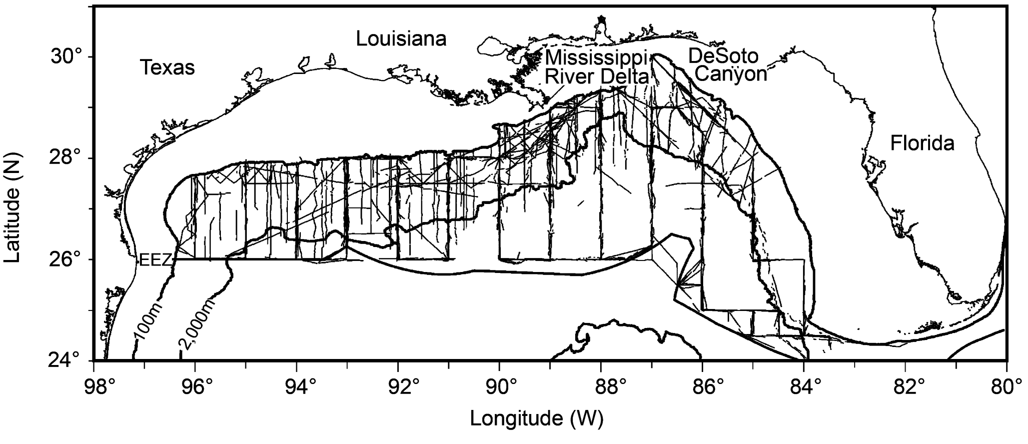
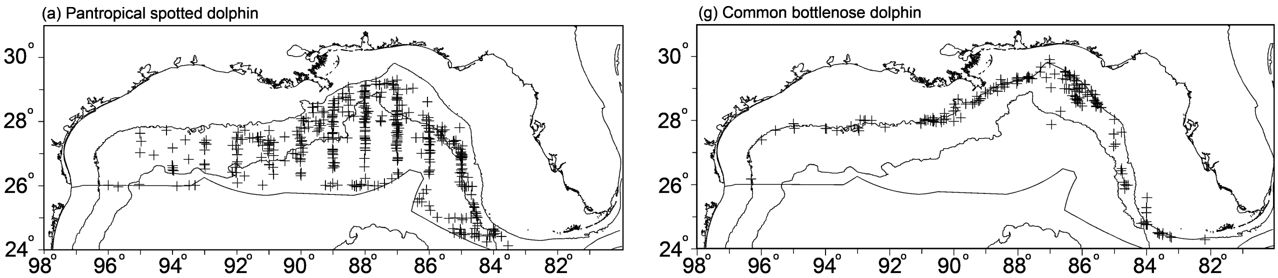
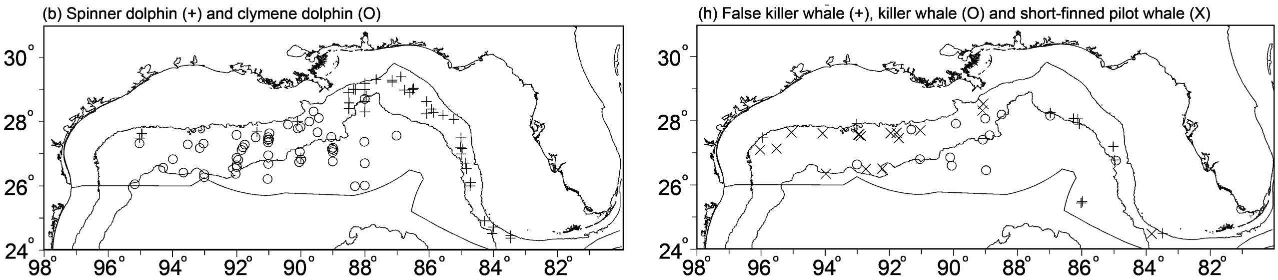


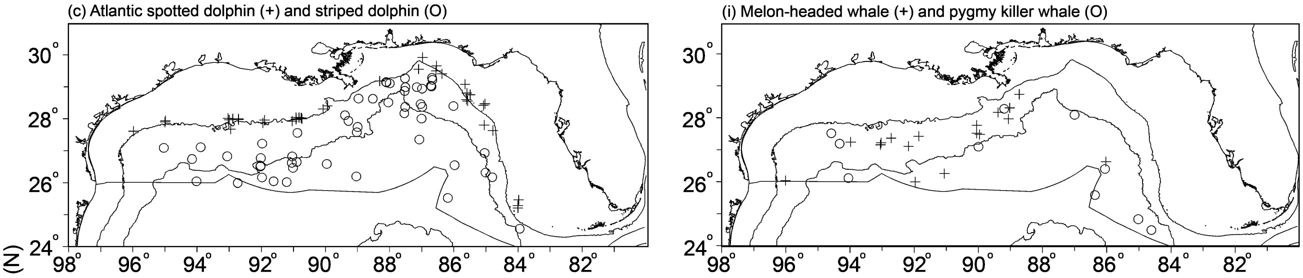
Fig. 1. Study area within the northern Gulf of Mexico. The 100m and 2,000m lines of bathymetry and the boundary of the US Exclusive Economic Zone (EEZ) are indicated by bold lines. Survey effort is indicated by the thinner lines.


(a) Pantropical spotted dolphin

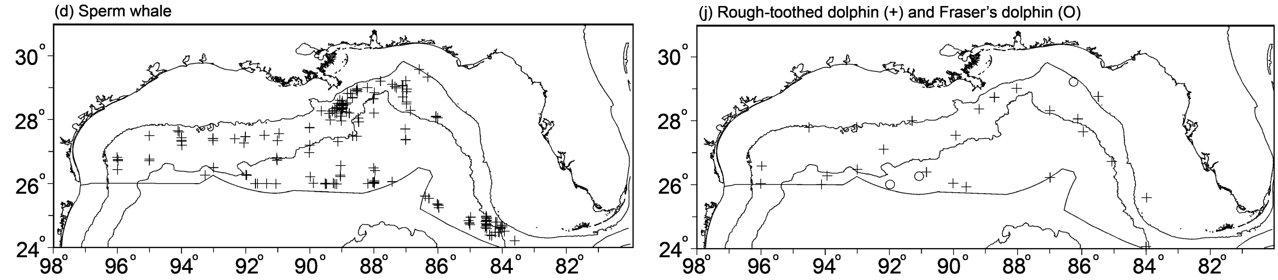
(g) Common bottlenose dolphin


(b) Spinner dolphin (+) and clymene dolphin (O)

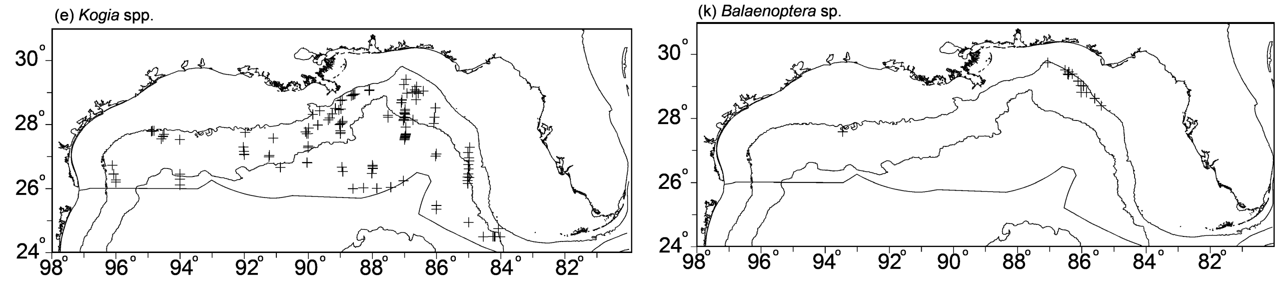
(h) False killer whale (+), killer whale (O) and short-finned pilot whale (X)


(c) Atlantic spotted dolphin (+) and striped dolphin (O)

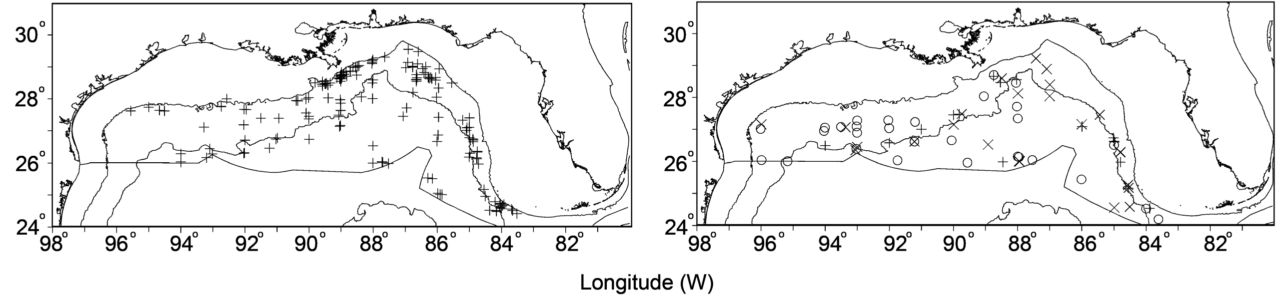
(i) Melon-headed whale (+) and pygmy killer whale (O)


(d) Sperm whale

(j) Rough-toothed dolphin (+) and Fraser's dolphin (O)


(e) *Kogia* spp.

(k) *Balaenoptera* sp.


(f) Risso's dolphin

(l) Cuvier's beaked whale (+), *Mesoplodon* spp. (O) and unidentified Ziphiidae (X)

Fig. 2. Sighting locations for each species/taxonomic group observed. Each symbol represents one sighting. The 200m and 2,000m lines of bathymetry and the boundary of the US Exclusive Economic Zone (EEZ) are shown. (a) Pantropical spotted dolphin (*n*=432); (b) Spinner dolphin (*n*=42) and clymene dolphin (*n*=50); (c) Atlantic spotted dolphin (*n*=39) and striped dolphin (*n*=52); (d) Sperm whale (*n*=172); (e) *Kogia* spp. (*n*=135); (f) Risso's dolphin (*n*=160); (g) Common bottlenose dolphin (*n*=179); (h) False killer whale (*n*=11), killer whale (*n*=13) and short-finned pilot whale (*n*=18); (i) Melon-headed whale (*n*=17) and pygmy killer whale (*n*=10); (j) Rough-toothed dolphin (*n*=24) and Fraser's dolphin (*n*=3); (k) *Balaenoptera* sp. (*n*=15); (l) Cuvier's beaked whale (*n*=16), *Mesoplodon* spp. (*n*=29) and unidentified Ziphiidae (*n*=24).

Table 2

Descriptive statistics for group size, sea surface temperature (SST), and depth of on-effort sightings for each species/taxonomic group. Sample sizes (*n*) may be different for the three categories within species due to deletion of naked-eye sightings from group size data and deletion of SSTs without decimals for SST data (see Methods for details).

	Group size					SST (°C)					Depth (m)				
Species	*n*	Mean	SE	Max	Min	*n*	Mean	SE	Max	Min	*n*	Mean	SE	Max	Min
Bryde's whale	14	2.0	0.33	5	1	9	23.31	0.497	25.9	21.5	15	226.3	7.94	302	199
Sperm whale	164	2.6	0.16	11	1	148	26.02	0.154	29.7	21.1	172	1,732.4	73.54	3,462	198
Kogia spp.	133	2.0	0.12	8	1	116	26.60	0.155	29.5	22.7	135	1,670.6	88.25	3,422	339
Cuvier's beaked whale	15	1.8	0.30	4	1	15	26.01	0.334	28.3	24.3	16	1,884.6	172.03	3,221	1,179
Mesoplodon spp.	29	2.3	0.25	7	1	26	26.95	0.296	28.9	23.1	29	1,791.6	143.24	3,257	796
Unidentified Ziphiid	19	1.7	0.20	4	1	21	26.48	0.471	29.2	22.5	24	1,876.9	185.14	3,386	531
Killer whale	13	6.5	1.37	12	1	11	26.66	0.476	28.6	22.7	13	1,865.8	195.46	2,818	732
False killer whale	11	27.6	7.38	70	3	7	26.79	0.494	28.7	25.1	11	1,301.5	329.96	3,294	167
Short-finned pilot whale	18	24.9	4.41	85	3	16	26.47	0.293	28.4	24.4	18	984.3	111.34	2,105	553
Melon-headed whale	17	99.6	16.44	275	22	15	26.47	0.354	28.7	24.1	17	1,401.5	160.29	3,203	824
Pygmy killer whale	10	18.5	7.39	84	4	8	26.84	0.394	28.2	24.5	10	2,405.7	330.73	3,422	893
Risso's dolphin	147	10.2	0.56	40	1	142	26.20	0.163	29.2	20.4	160	1,155.5	71.98	3,440	110
Rough-toothed dolphin	21	14.1	1.60	28	2	21	25.87	0.379	28.8	22.3	24	1,572.0	226.84	3,294	128
Fraser's dolphin	3	65.3	26.03	117	34	3	25.77	0.371	26.5	25.3	3	1,483.5	616.86	2,141	251
Common bottlenose dol.	151	20.6	2.49	220	1	154	25.25	0.175	29.5	19.4	179	312.4	18.90	2,950	102
Pantropical spotted dol.	381	71.3	3.45	650	3	377	25.94	0.084	29.1	21.1	432	1,912.2	45.49	3,488	280
Striped dolphin	51	46.1	4.74	150	8	45	25.30	0.260	28.6	22.2	52	1,638.3	109.43	3,206	404
Spinner dolphin	40	151.5	30.90	800	6	37	25.42	0.355	29.6	22.2	42	825.7	88.36	2,525	275
Clymene dolphin	44	89.5	11.48	325	2	43	25.93	0.227	29.2	22.1	50	1,692.2	93.72	3,065	688
Atlantic spotted dolphin	35	25.7	2.58	68	1	34	24.99	0.335	28.3	21.3	39	179.6	10.54	362	101

both distribution and range of water depths. Only three sightings of Fraser's dolphins were made. All sightings of Bryde's whales except one were concentrated along the northeastern shelf-edge in the DeSoto Canyon area, and were in a very narrow water depth range (199-302m), more narrow than for any other taxonomic group. Beaked whales (*Mesoplodon* spp., Cuvier's beaked whale, and unidentified Ziphiidae) were widely distributed in waters >500m deep. Mean SST ranged from 23.31°C for Bryde's whales to 26.95°C for *Mesoplodon* spp. (Table 2).

Group size

The beaked whales, Bryde's whale, sperm whale and *Kogia* spp. occurred in the smallest groups, all with mean group sizes <3 (Table 2). Killer whales were also found in small groups of ≤ 12 whales. Spinner dolphins had the largest mean group size (n=40, $\bar{x}$ = 151.5, SE = 30.90) of any species and the largest cetacean group observed during all surveys (800 dolphins). After spinner dolphins, the largest mean group sizes were those of melon-headed whales, clymene dolphins, pantropical spotted dolphins, Fraser's dolphins and striped dolphins (range of means 46.1-99.6).

Interspecific associations

The vast majority of sightings consisted of single species groups, however 27 of the 1,868 sightings (1.4%) comprised two cetacean species (Tables 3 and 4). The most frequent mixed-species group, common bottlenose and Atlantic spotted dolphins, comprised 33.3% of all mixed-species sightings but only 0.48% of all sightings (9 of 1,868). The other species most commonly sighted in mixed-species groups were rough-toothed dolphins, melon-headed whales, Risso's dolphins, false killer whales and Fraser's dolphins.

In five of the mixed-species cetacean groups, aggressive interactions were observed between the two species. Two common bottlenose and Atlantic spotted dolphin sightings involved both species bowriding. In one instance, the Atlantic spotted dolphins were riding first and snapped their jaws and made fast approaches at the common bottlenose dolphins when they came to the bow. In the second instance, both species approached the bow together, with common bottlenose dolphins swimming in front and tail slapping, and Atlantic spotted dolphins butting the common bottlenose dolphins with their rostrum/head. In two different sightings of mixed-species groups bowriding, rough-toothed dolphins chased Atlantic spotted dolphins in one case, and in another, they chased melon-headed whales away from the bow while jaw snapping. On one occasion, a pod of seven killer whales separated up to three dolphins from a group of about 120 pantropical spotted dolphins. They chased and herded a single dolphin for approximately 1.5 hours, ramming and tossing it into the air, finally killing it (see Pitman *et al.*, 2003).

Of the 1,868 cetacean sightings, 45 (2.4%) were associated with at least one seabird species/taxonomic group (Table 3). Cetacean and seabird sightings included the following species of cetacean: pantropical spotted dolphin (21 sightings); spinner dolphin (5); clymene dolphin (3); Risso's dolphin (2); false killer whale (2); and pygmy killer whale, melon-headed whale, sperm whale, rough-toothed dolphin and striped dolphin (1). The majority of pantropical or spinner dolphin and seabird sightings, 61.9% and 80.0%, respectively, were associated with terns (sooty terns, *Sterna fuscata*; black terns, *Chlidonias niger*; sooty/bridled terns, *S. fuscata/S. anaethetus*; and *Sterna* sp.). The largest seabird flocks contained ~50 birds each and were all associated with pantropical spotted dolphins. Species most commonly involved in cetacean sightings were sooty tern (10 sightings); *Sterna* spp. (8); storm petrels (band-rumped, *Oceanodroma castro;* Leach's, *Oceanodroma leucorhoa*; or Wilson's, *Oceanites oceanicus*) (6); Audubon shearwater (*Puffinus lherminieri*) (4); pomarine jaegar (*Stercorarius pomarinus*) (3); and sooty/bridled tern (3).

Twenty-one (1.1%) cetacean sightings associated with fish schools were observed. Pantropical spotted dolphins were most commonly sighted with fish (8 sightings); other cetacean species were sighted with fish only on one or two

Table 3

Species sighted in mixed-species cetacean groups, associated with birds, and/or associated with fish. Total number of sightings includes on- and off-effort sightings. Percent values represent percentage of total sightings for each species.

		Mixed cetacean		With birds		With fish	
Species	Total no. sightings	No. sightings	%	No. sightings	%	No. sightings	%
Bryde's whale	17	0	0.0	0	0.0	1	5.9
Sperm whale	186	1	0.5	1	0.5	0	0.0
Cuvier's beaked whale	18	0	0.0	0	0.0	1	5.6
Mesoplodon spp.	29	0	0.0	0	0.0	1	3.4
Killer whale	13	1	7.7	0	0.0	0	0.0
False killer whale	11	3	27.3	2	18.2	0	0.0
Short-finned pilot whale	18	1	5.6	0	0.0	0	0.0
Melon-headed whale	17	5	29.4	1	5.9	0	0.0
Pygmy killer whale	11	0	0.0	1	9.1	0	0.0
Risso's dolphin	163	4	2.5	2	1.2	0	0.0
Rough-toothed dolphin	25	6	24.0	1	4.0	1	4.0
Fraser's dolphin	3	2	66.7	0	0.0	0	0.0
Common bottlenose dolphin	195	16	8.2	0	0.0	2	1.0
Pantropical spotted dolphin	468	1	0.2	21	4.5	8	1.7
Striped dolphin	54	0	0.0	1	1.9	1	1.9
Spinner dolphin	43	0	0.0	5	11.6	2	4.7
Clymene dolphin	53	1	1.9	3	5.7	1	1.9
Atlantic spotted dolphin	45	10	22.2	0	0.0	0	0.0

occasions. Pantropical spotted dolphins were associated with tuna (*Thunnus* spp.), flyingfish (Exocetidae), a whale shark (*Rhincodon typus*) and unidentified small fish. Of the eight pantropical spotted dolphin sightings associated with fish, five were also associated with seabirds.

DISCUSSION

Diversity

All of the cetacean species sighted during spring surveys appear to be regular, if not abundant, inhabitants of the Gulf of Mexico (Würsig *et al.*, 2000), although some species were not sighted during every year. Other species previously reported from the Gulf but not observed during the spring surveys are considered to be accidental, stray or extralimital. Jefferson and Schiro (1997) discussed seven reliable reports of fin whales (*Balaenoptera physalus*), all from summer, fall and winter. There are records of North Atlantic right whales (*Eubalaena glacialis*; 3 sightings, 1 stranding), blue whales (*B. musculus*; 2 strandings), sei whales (5 strandings) and a Sowerby's beaked whale (*M. bidens*; 1 stranding) (Würsig *et al.*, 2000; Southeast Fisheries Science Center [SEFSC] unpublished data). Common minke whales (*B. acutorostrata*; 10 strandings) and humpback whales (*Megaptera novaeangliae*; 6 sightings) are rare visitors to the Gulf of Mexico, but with most confirmed records occurring during winter and spring, they likely strayed during migration (Jefferson and Schiro, 1997; Weller *et al.*, 1996; Würsig *et al.*, 2000).

Distribution

With a few exceptions, the species distributions reported here are similar to those previously published, most of which were based on subsets of our dataset (Baumgartner, 1997; Baumgartner *et al.*, 2001; Hansen *et al.*, 1996; Mullin *et al.*, 1994a; b; c; Mullin and Hansen, 1999; Mullin and Hoggard, 2000; O'Sullivan and Mullin, 1997). One exception is for the rough-toothed dolphin reported almost exclusively in oceanic waters west of the Mississippi for surveys conducted during 1990-1994 (Mullin and Hansen, 1999). During subsequent aerial (Mullin and Hoggard, 2000) and ship surveys, groups were sighted both east of the Mississippi (Fig. 2j) and in continental shelf waters <100m deep (Fulling *et al.*, 2003). It is also important to note that Atlantic spotted, common bottlenose and rough-toothed dolphins are known to inhabit waters <100m deep in the Gulf (Fulling *et al.*, 2003), so our surveys of waters ≥100m deep did not cover the entire range of the distributions for these species.

The species distributions from spring surveys cannot necessarily be applied to other seasons. Seasonal aerial surveys of continental slope waters in the northwestern Gulf from 1992 to 1994 (summer, fall, winter, spring; Mullin *et al.*, 2004) and in the northeastern Gulf from 1996 to 1998 (summer, winter; Mullin and Hoggard, 2000) provided some evidence of seasonal changes in species abundance in slope waters. For example, during the 1996-1998 aerial surveys, five groups of clymene dolphins (3 summer, 2 winter) were sighted in the northeastern Gulf, an area where none were seen during spring ship surveys. These sightings were spatially sympatric with those of spinner dolphins during summer and winter (Mullin and Hoggard, 2000).

While the seasonal results of the aerial studies were not definitive, they demonstrated that cetaceans remained diverse (10-15 species) and abundant throughout the year and that no common species vacated slope waters seasonally. We suggest that the spring distributions reported here are similar to distributions for other seasons for the majority of species, but further surveys that span the entire oceanic northern Gulf during additional seasons are needed.

Studies of cetacean habitats in the Gulf, based wholly or in part on subsets of cetacean sightings from our dataset, have shown physiography (bottom depth, bottom depth gradient), mesoscale oceanographic features and zooplankton biomass to be significant variables in identifying species-specific cetacean habitat (Baumgartner, 1997; Davis *et al.*, 1998; 2002; Baumgartner *et al.*, 2001). However, prior to this study, direct comparisons of the habitats of specific species or groups of species have not been made.

Table 4

Species sighted in mixed-species cetacean groups, including associated species and number of sightings.

Species	*n*	Associated species in mixed-species groups (number of sightings)				
Common bottlenose dolphin	16	Atlantic spotted dolphin (9)	Risso's dolphin (3)	False killer whale (2)	Rough-toothed dolphin (1)	Unidentified dolphin (1)
Atlantic spotted dolphin	10	Common bottlenose dolphin (9)	Rough-toothed dolphin (1)			
Rough-toothed dolphin	6	Melon-headed whale (3)	Common bottlenose dolphin (1)	Atlantic spotted dolphin (1)	False killer whale (1)	
Melon-headed whale	5	Rough-toothed dolphin (3)	Fraser's dolphin (2)			
Risso's dolphin	4	Common bottlenose dolphin (3)	Unidentified dolphin (1)			
False killer whale	3	Common bottlenose dolphin (2)	Rough-toothed dolphin (1)			
Fraser's dolphin	2	Melon-headed whale				
Sperm whale	1	Clymene dolphin				
Clymene dolphin	1	Sperm whale				
Killer whale	1	Pantropical spotted dolphin				
Pantropical spotted dolphin	1	Killer whale				
Short-finned pilot whale	1	Unidentified dolphin				
Unidentified dolphin	3	Risso's dolphin (1)	Short-finned pilot whale (1)	Common bottlenose dolphin (1)		

All five species of the genus *Stenella* are known to occur in the Atlantic Ocean, and, to date, the northern Gulf is the only area with a large number of sightings of each. While this genus may in fact be polyphyletic (Rice, 1998; LeDuc *et al.*, 1999), similar external morphology suggests at least some level of ecological overlap, such as in prey size and energetic requirements. The distributions within the Gulf hint that some of the *Stenella* may avoid interspecific competition by spatial partitioning. Atlantic spotted dolphins are essentially parapatric with the other four oceanic species. Clymene and spinner dolphins appear nearly parapatric, at least in spring. Spatially, spinner and pantropical spotted dolphins are sympatric in eastern slope waters (200-2,000m), but they do not generally co-occur in abyssal waters (>2,000m) where pantropical spotted dolphins are abundant (Mullin and Fulling, 2004). Pantropical spotted dolphins are sympatric with striped dolphins throughout the northern oceanic Gulf and both are sympatric with clymene dolphins in the western Gulf.

Other species with a limited distribution in the Gulf include the Bryde's whale (found in the northeastern Gulf) and the melon-headed and short-finned pilot whales (primarily in the western Gulf). Most of these distributions have an east-west component; in general, the eastern and western northern oceanic regions have different physiographic and oceanographic characteristics (Baumgartner, 1997; Biggs and Ressler, 2001). Habitat heterogeneity in these waters may provide the opportunity for niche partitioning but more quantitative studies are needed.

Atlantic spotted dolphins do not occur in the oceanic waters of the Gulf far from the shelf-edge, although they do occur in oceanic waters in other parts of the Atlantic Ocean, including north of Cape Hatteras, North Carolina (Bero, 2001; Mullin and Fulling, 2003) and around the Azores archipelago (Silva *et al.*, 2003). While more study is needed, initial results indicate that Atlantic spotted and pantropical spotted dolphins do not generally co-occur in these areas[1]. Similarly, common bottlenose dolphins in the Gulf were rare seaward of the upper continental slope (i.e. >1,000m) but more common in deep waters north of Cape Hatteras (Kenney, 1990) and in the eastern tropical Pacific Ocean (ETP) (Scott and Chivers, 1990). Why the distributions of Atlantic spotted and common bottlenose dolphins do not extend further seaward in the Gulf of Mexico is not known, but it may be due to the oligotrophic mean state of the oceanic Gulf compared to the Atlantic Ocean north of the Gulf Stream Front and areas of the ETP where productive waters may afford these traditionally coastal species the opportunity to exploit oceanic habitats. In addition, where it occurs, the pantropical spotted dolphin may competitively exclude the Atlantic spotted dolphin from oceanic habitats.

Group size, sea surface temperature and depth

It is difficult to compare our results with previous studies of cetacean group size, SST and water depth in the Gulf because study areas have varied. For example, some previous studies only covered waters to a depth of 1,000 or 2,000m (e.g. Davis *et al.*, 1998; Mullin *et al.*, 1994b). Our

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[1] A recent genetic study based on biopsy samples collected during research surveys has revealed four hybrids of the two species from the Gulf of Mexico and Atlantic. Personal communication from S.E. Kingston, NMFS/SEFSC, Marine Mammal Molecular Genetics Laboratory, 646 Cajundome Blvd. Rm. 219, Lafayette, LA 70506, USA, March 2004.

sample sizes are larger in most instances, and the ranges of group size, SST and depth tend to be broader than previously reported. Baumgartner *et al.* (2001) summarised data from three spring surveys (1992-1994, a subset of these data) for five cetacean species. The addition of sighting data from six additional surveys presented here did not affect group size descriptive statistics in most instances for these five species. In general, as with the distribution data, the present findings were similar to previous reports if differences in study area depth are taken into account.

The group size statistics reported here may be biased for some species. Groups were sighted during line-transect surveys and it is possible that larger groups were sighted disproportionally, particularly for those species with a large range of group sizes. For example, Mullin and Fulling (2004) estimated size-biased mean group sizes for pantropical spotted dolphin abundance estimates based on the regression of group size with perpendicular sighting distance (Buckland *et al.*, 2001), and found that the arithmetic mean overestimated mean group size by 27-52%. Sperm whale group sizes were estimated based on '10-minute' counts during line-transect surveys (once a sperm whale was sighted, all observers scanned 360° for 10 minutes to determine group size). Group sizes are certainly larger because sperm whale groups forage asynchronously (Whitehead, 1989; Whitehead and Weilgart, 1991; 2000; Whitehead, 1996). During a 2003 survey to obtain less biased estimates of sperm whale group size, 90-minute counts were conducted (observers scanned 360° for 90 minutes) that suggest mean group-sizes are at least 6-8 whales (SEFSC, unpublished data), considerably higher than the mean group-size of 2.6 reported here.

Interspecific associations

Similar to findings from vessel surveys, the percentage of mixed-species groups sighted during previous aerial surveys in the Gulf was low. Of 736 groups sighted during 12 seasonal aerial surveys conducted over the period from 1992-1998, only 9 sightings (1.4%) were of mixed-species groups (Mullin and Hoggard, 2000; Mullin *et al.*, 2004). However, there were mixed-species groups observed during aerial surveys that were not observed during ship surveys. Mullin *et al.* (1994b) sighted a mixed group of Risso's dolphins and *Globicephala* sp. during Gulf of Mexico aerial surveys. During another aerial survey study, Mullin *et al.* (2004) reported a mixed-species sighting of melon-headed whales, rough-toothed dolphins and Fraser's dolphins. No mixed groups of these three species were sighted during ship surveys, but rough-toothed and Fraser's dolphins were the only two species sighted with melon-headed whales, and the melon-headed whale was the only species sighted with Fraser's dolphins.

No dedicated seabird survey team was present during spring surveys, however, dedicated seabird surveys have been conducted in select areas of the oceanic Gulf (Davis and Fargion, 1996; Davis *et al.*, 2000). Although some species inhabit the Gulf year-round, the seasonal seabird composition varies (Hess and Ribic, 2000; Peake, 1999). Spring surveys produced the greatest species diversity of seabirds (28 species) and the second highest sighting rate after summer (Peake, 1999). Our findings on seabird species associated with cetaceans cannot necessarily be applied to other seasons; however, considering our observations were made during a time of high species diversity and high sighting rates, we suggest the general trend of few cetacean-seabird associated sightings applies year-round. Cetacean-seabird sightings during seasonal aerial surveys were also uncommon (Mullin and Hoggard, 2000; Mullin *et al.*, 2004).

The combinations of mixed-species groups reported here and the cetacean species that were observed associated with seabirds and fish are obviously not exhaustive. Additional effort may yield new combinations of associations, however, our results strongly suggest that interspecific interactions among cetaceans, seabirds and fish occur at low levels in the Gulf of Mexico.

Comparisons to areas outside the Atlantic Ocean

Most cetacean species that inhabit the oceanic Gulf are also distributed in warm waters throughout the world (Jefferson *et al.*, 1993). Comparisons of the relative abundances of cetacean species, group sizes, behaviours and associations (e.g. other cetacean species, birds, fish) from tropical regions throughout the world could provide an understanding of how they are affected by the biological and physical environment (Mullin *et al.*, 1994b). Ballance and Pitman (1998) compared cetacean communities in the ETP, western tropical Indian Ocean (WTIO) and the Gulf of Mexico. They noted that the major differences between the Gulf and ETP are that in the Gulf, pantropical spotted dolphins do not school with spinner dolphins, do not associate with surface tunas, are not accompanied by seabirds, and that the two species of *Stenella* exhibit largely parapatric distributions. The present data indicate these conclusions are essentially correct but can be quantified and refined.

Of 468 groups of pantropical spotted dolphins and 43 groups of spinner dolphins from our database, none were found in mixed-species groups with the other. Pantropical spotted dolphins in the Gulf were observed in association with fish in 4.5% of the sightings, including surface tunas, and were accompanied by seabirds in 0.2% of the sightings. The situation in the ETP and WTIO is very different where 58.9% and 58.3% of the pantropical spotted dolphin groups were found with seabirds and 33.5% and 58.3% were mixed with spinner dolphins, respectively (Au and Perryman, 1985; Au and Pitman, 1986; Ballance and Pitman, 1998).

Spinner dolphin sightings were widespread throughout continental slope waters of the eastern Gulf as were those of the pantropical spotted dolphin, so the two species are not parapatric. In addition, spinner dolphins were not associated with inshore waters, islands, banks or any other cetacean species. This supports the conclusion by Ballance and Pitman (1998) that association of spinner dolphins with these features in the open ocean is apparently not obligatory, as had been suggested previously (Norris *et al.*, 1994).

In the ETP, large flocks of seabirds accompanying dolphins, particularly pantropical spotted and spinner dolphins which are commonly associated with yellowfin tuna (*Thunnus albacares*), are a common and conspicuous sight. Purse-seine fishermen use the presence of seabird flocks as a reliable indication that tuna are accompanying the dolphins. Au and Perryman (1985) reported that 96.4%, 58.9% and 52.9% of groups of mixed pantropical spotted and spinner dolphins, pantropical spotted dolphins only and spinner dolphins only, respectively, occurred in association with seabird flocks in northern tropical waters of the ETP, and they assumed that their minimum flock size also indicated presence of tuna.

We found no indication that any interspecific interactions among any cetacean species, seabirds and tuna occurred in the Gulf at those levels. Our findings are more similar to those from the central and western Pacific, which also have the species involved in such associations present, but lack the dolphin-seabird-tuna interactions (Au and Pitman, 1986). A variety of tuna species occur in the Gulf including yellowfin tuna, which are commercially harvested mainly by longline (during the years our surveys occurred, 1991-2001, commercial landings of yellowfin ranged from 1,327.5 to 4,155.2 metric tons[2]). However, large-bodied diving seabirds such as boobies (*Sula* spp.) that associate with dolphins and tunas in the ETP and feed on prey driven to the surface by them, are uncommon in the northern oceanic Gulf (Hess and Ribic, 2000).

The Gulf mixed-species cetacean interactions more closely resemble those obtained by Ballance and Pitman (1998) for the WTIO. Overall, mixed-species cetacean groups comprised only 4% of the total sightings in the WTIO and 1.4% in the Gulf. Some of the frequent associations between mixed-species cetacean groups in the WTIO were different than those reported here, such as the pantropical spotted and spinner dolphin association. However, in both the Gulf and WTIO, common bottlenose dolphins were recorded in mixed-species groups frequently and with more species than any other cetacean. Seabirds were recorded with cetaceans at a low level for both the WTIO (7%) and the Gulf of Mexico (2%), and in both places terns, especially sooty terns (*S. fuscata*), were among the most frequently recorded flocks associated with cetaceans.

Scott and Chivers (1990) reported that common bottlenose dolphin groups in the ETP were sighted in mixed-species cetacean groups most prevalently with short-finned pilot whales, Risso’s dolphins, rough-toothed dolphins, pantropical spotted dolphins and spinner dolphins, and with at least eight other species. In the Gulf, they were recorded in mixed-species groups with four other cetacean species: Atlantic spotted dolphins; Risso’s dolphins; false killer whales; and rough-toothed dolphins. In the Gulf therefore, they were obviously sighted with far fewer species, and those they most commonly associated with in the Gulf and ETP were different. However, in contrast to the ETP, common bottlenose dolphins in the Gulf are not commonly found seaward of the upper continental slope. Therefore, in the northern oceanic Gulf, one of the species that is most likely to form mixed-species groups does not generally co-occur with many of the species it associates with in the ETP.

An important factor to consider in regional comparisons is the size of each area, and the spatial and temporal scale of the oceanographic processes found in each. Of the ETP, WTIO and Gulf, the ecology of the ETP has been most thoroughly studied. The ETP study area is about 19 million km^2 (Wade and Gerrodette, 1993), almost 50 times larger than the northern oceanic Gulf. The vast area of the ETP has at least several persistent oceanographic regions, including ‘tropical surface waters’ and ‘upwelling modified’, where cetacean communities with different characteristics reside (Au and Perryman, 1985; Reilly, 1990) that do not occur in the Gulf. *Delphinus* spp. are absent in the Gulf but in the ETP they are common and are most abundant in the upwelling modified regions. Regions of the ETP where spinner dolphin-pantropical spotted dolphin-tuna-seabird associations are the most prevalent are those tropical surface waters (warm, low salinity) where the thermocline is sharp and shallow, and dolphins and tuna feed more frequently close to the surface where seabirds have access to the prey (Au and Perryman, 1985; Au and Pitman, 1986; Reilly, 1990). Neither of these oceanographic conditions exist in the Gulf on a similar scale, and when they do, they are largely ephemeral (Biggs and Ressler, 2001).

While Ballance and Pitman (1998) suggested that cetacean group sizes are generally similar in the ETP and the Gulf, there is a difference in the frequency of large groups (i.e. >300 animals) that occur and in their maximum sizes. Only 15 groups were that large in the Gulf and all were <1,000 animals. Large groups are much more common in the ETP and routinely exceed 1,000 animals (Au and Perryman, 1985; Leatherwood *et al.*, 1983).

We suggest that it is important to identify the region of the ETP used in comparisons, and that the Gulf and ETP may be less different when the large area at the western edge of the tropical surface and upwelling modified waters in the ETP is used in the comparison. Ballance *et al.* (1997) described this area as ‘sooty tern-dominated’. In the ETP, <3% of all ‘sooty tern flocks’ (flocks with a large number of sooty terns) were associated with cetaceans, and waters where sooty tern flocks occurred were characterised by the deepest thermocline depth and the lowest surface productivity (Au and Perryman, 1985; Ballance *et al.*, 1997). A comparison of the oceanic northern Gulf and the sooty tern-dominated areas of the ETP may reveal fewer differences between the two. The seabirds that do occur routinely in the oceanic northern Gulf are terns, small shearwaters and storm petrels (Hess and Ribic, 2000). That is, small seabirds that can fly efficiently between patchy ephemeral food sources (Ballance *et al.*, 1997).

Comparisons to other areas of the Atlantic Ocean

During Cetacean and Turtle Assessment Program (CeTAP) surveys conducted between Cape Hatteras, North Carolina, and the northern Gulf of Maine during 1978-1982, 26 cetacean species were observed (CeTAP, 1982). Sixteen species were sighted in mixed-species groups, including sperm whales, common bottlenose dolphins, *Globicephala* spp., Risso’s dolphins and striped dolphins. One of the most frequent mixed-species sightings was of common bottlenose dolphins and *Globicephala* spp. (n=84), a combination which we have not seen in the Gulf of Mexico. Also, striped dolphins were sighted with many different species, including sperm whales, common bottlenose dolphins and Risso’s dolphins, but in the Gulf striped dolphins have not been sighted with any other cetacean species. Comparisons to CeTAP results should be made with caution however, as the term ‘association’ was used differently; in many instances during CeTAP, association simply meant animals sighted in the same general vicinity (Kenney, 1990).

During two ship surveys in the southeastern US Atlantic Ocean (US waters south of Maryland) conducted during summer 1998 and winter 2002, only 1.5% and 4.5% of all groups for the summer and winter surveys, respectively, were composed of mixed-species groups (SEFSC, unpublished data). The majority of mixed-species groups from the winter survey included species not found in the Gulf (*Delphinus* spp. and fin whale), whereas sightings from the summer survey included common bottlenose dolphins and *Globicephala* spp., again, a combination not seen in the Gulf. We hope that additional surveys in the southeastern US Atlantic will allow for better comparisons to this area, but preliminary findings suggest mixed-species groups occur at a low level, as they do in the Gulf.

In summary, the oceanic northern Gulf is physiographically complex and oceanographically dynamic, and has a diverse tropical cetacean community. The group

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[2] Personal communication from the National Marine Fisheries Service, Fisheries Statistics and Economics Division, Silver Spring, MD, March 2004.

sizes, interspecific associations and species distributions we characterise here are different from those in other tropical regions where most of the same species occur. The underlying ecological reasons for these differences between tropical regions and for the intra-Gulf species distributions we observed are fertile areas for future research.

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A review of cetacean interactions with longline gear

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ABSTRACT

Fishery-cetacean interactions, including those with longline gear, give rise to economic, ecological and social concerns. This paper reviews problems resulting from cetacean-longline interactions, considers potential strategies to reduce interactions and identifies research priorities and approaches. Depredation by cetaceans (removal and damage of hooked fish and bait from fishing gear) and damage and loss of fishing gear create economic problems; however, the magnitude of this problem is poorly understood. There is also insufficient information to determine whether there are population-level effects resulting from injury and mortality of cetaceans (from incidental entanglement and hooking and from deliberate actions to discourage depredation). Fishery-cetacean interactions may also: change cetacean foraging behaviour and distribution; increase fishing effort to make up for fish taken from gear by cetaceans; and create errors in fish stock assessments that do not account for cetacean depredation. Negative public perceptions of longline fishing can result from news of incidental and deliberate injury and mortality of cetaceans associated with longlining. Information on how to reduce cetacean interactions with longline gear is also limited, as is the understanding of the mechanisms responsible for them. Strategies already employed in some fleets include refraining from setting or cutting sets short when problematic species of cetaceans are observed and fleet coordination of daily fishing times and positions. Many fishermen perceive depredation as an inevitable part of fishing. This paper discusses a number of other possible cetacean avoidance strategies that warrant consideration, including: (1) fleet communication to enable vessels to avoid temporally and spatially unpredictable and sporadic hotspots of aggregations of cetaceans; (2) underwater acoustic masking devices to conceal the sound of the vessel, gear, and setting and hauling activities; (3) quieter vessels to reduce cetaceans' ability to target longline vessels; (4) encasement of caught fish to reduce cetacean access to or interest in the catch; (5) use of bait or gear with an unpleasant smell or taste to reduce the attractiveness of gear, bait and catch to cetaceans; (6) use of pre-recorded fishing vessel sounds played from stations throughout a fleet's fishing grounds to distract cetaceans from actual fishing vessels; (7) use of acoustic devices to mask returning cetacean echolocation signals; and (8) use of tethered sonobuoys to track cetaceans and enable fleet avoidance. Vessels with relatively low cetacean interaction rates should be examined for design and operational differences from vessels with high interaction rates, possibly allowing identification of effective avoidance methods. There is a need for experimentation in individual longline fisheries over several seasons to assess fishery-specific efficacy and commercial viability of cetacean avoidance strategies. This is necessary as different cetacean species likely respond differently to an avoidance method and cetaceans may habituate to an avoidance strategy, especially in fisheries interacting with resident cetaceans.

KEYWORDS: DEPREDATION; FISHERIES; INCIDENTAL CATCHES; ACOUSTICS; ECHOLOCATION; FEEDING

INTRODUCTION

Bycatch in marine fisheries is an increasingly prominent international ecological, social and economic issue (e.g. Alverson *et al.*, 1994; IUCN, 1996; Hall *et al.*, 2000; FAO, 1999a; FAO, 1999b; FAO, 2004; Gilman *et al.*, 2005). It has been recognised by many international organisations including the UN General Assembly, the United Nations Food and Agriculture Organisation (FAO), the World Conservation Union (IUCN), the International Whaling Commission (IWC), the Agreement on the Conservation of Small Cetaceans in the Baltic and North Seas Resolution on Incidental Take of Small Cetaceans (ASCOBANS) and the Agreement on the Conservation of Cetaceans of the Black Sea, Mediterranean Sea and contiguous Atlantic Area (ACCOBAMS).

Bycatch can harm ecosystems and the economic viability of commercial fisheries. In particular, some species of marine mammals, seabirds, sea turtles, sharks and other fish may be particularly vulnerable to increased mortality above natural levels because of their life history traits (e.g. Gilman and Freifeld, 2003) and this can lead to unsustainable levels of removal, affecting biodiversity. It also alters foraging habits of species that learn to utilise discarded bycatch (Hall *et al.*, 2000). In an attempt to reduce the amount of fisheries bycatch, some governments have introduced a range of restrictions with economic implications, such as closed areas, embargos and closures. Bycatch in one fishery can lead to a reduction in the target catch in another and bycatch of juvenile and undersized individuals of a commercial species can adversely affect future catch levels (Hall *et al.*, 2000). Bycatch is also a social issue, the disposal of millions of tons of fish is a waste of a valuable food source as well as a waste of animal lives; FAO (1999c) estimated that 1998 global marine fisheries fish discards totalled 20 million metric tons.

Interactions between marine mammals and fishing involve almost all existing fishing gear and typically result in negative economic, ecological and social consequences (e.g. Northridge, 1984; Perrin *et al.*, 1994; Northridge and Hofman, 1999; Reeves *et al.*, 1996; Reeves *et al.*, 2001; Read, 2002; Donoghue *et al.*, 2002; Australian Fisheries Management Authority, 2005). In addition to the primary interaction of bycatch, cetaceans may remove hooked fish and bait from fishing gear (referred to as depredation), fish confined in mariculture enclosures, and fish aggregated at natural and artificial constraints in river systems, such as below falls or fish ladders (Reeves *et al.*, 1996; Donoghue *et al.*, 2002). Other prominent issues resulting from marine mammal-fisheries interactions include the deliberate injury and mortality of marine mammals by fishermen and damage to and loss of fishing gear. This paper focuses on the problems of interactions between cetaceans and longline gear (Fig. 1) and potential strategies to abate them.

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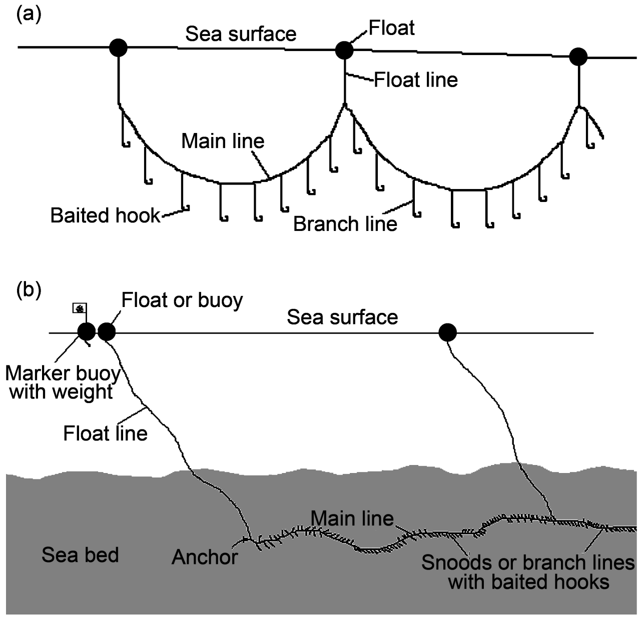

Fig. 1. Configuration of (a) pelagic and (b) demersal longline gear. Lengths and materials of float, main and branch lines; number of hooks between floats; amount and placement of weights on branch lines; depth of gear; types of hooks and bait; and methods of setting and hauling vary between fisheries and between vessels in a fishery. Longlining occurs throughout the world's oceans, has been used since the nineteenth century and ranges from small-scale domestic artisanal fisheries with small sometimes open vessels to modern mechanised industrialised fleets from distant-water fishing nations with large vessels. Pelagic longlines, where gear is suspended from line drifting at the sea-surface, mainly targets large tunas (*Thunnus* spp), swordfish (*Xiphus gladius*), other billfishes (*Istiorphoridae* spp) and dolphin fish (mahimahi) (*Coryphaena* spp), can be up to 100km long and carry up to 3,500 baited hooks. Demersal longlines, where gear is set on the seabed to target demersal species living at or near the seabed, such as Atlantic cod (*Gadus morhua*) and Pacific halibut (*Hippoglossus stenolepis*), might set up to 40,000 baited hooks per day.

PROBLEM IDENTIFICATION

Cetacean-longline interactions have been observed from as early as 1952 in the Japanese longline tuna fleet (Nishida and Shiba, 2002). Most cetacean-longline interactions are thought to be the result of odontocetes being attracted to the fishing gear or boat because of opportunities to remove bait or caught fish; this may occasionally (e.g. Northridge, 1984; Ashford *et al.*, 1996; Dawson *et al.*, 1998; Waring *et al.*, 1999; Baird *et al.*, 2002; Forney, 2004; Baird and Gorgone, 2005) also result in entanglement or hooking, injury and mortality of the cetaceans (Fig. 2). Odontocetes are thought to develop familiarity with the sounds of longline boats (including the engine, gear haulers, depth sounders and radio buoys) and target the catch and bait after homing in on the vessel or its gear. There is anecdotal evidence that some resident cetaceans can home-in on specific vessels, even singling out one vessel to target when several are fishing in the same area (e.g. Australian Fisheries Management Authority, 2005). Other observed cetacean behaviour includes following longline boats to gear that has been set soaking and waiting by buoys for the vessel to arrive and haul (Ashford *et al.*, 1996; Australian Fisheries Management Authority, 2005). The incidental entanglement and hooking of baleen whales has also occasionally been reported in longline gear (e.g. Bowman *et al.*, 1999; Forney, 2004), probably as a result of their swimming paths accidentally crossing gear.

Fig. 2. False killer whale hooked on a Hawaii pelagic longline hook. The linear mark on the side of the whale might be an abrasion from contact with a main or branch line (photo by US NOAA Fisheries Pacific Islands Regional Office).

Depredation

Depredation is usually identified when hauls reveal fish damaged in a particular way (e.g. Lauriano *et al.*, 2004). Fish damaged by cetaceans is usually distinguishable from shark-damaged fish with the latter typically being bitten in half with clean bites or multiple smaller bites. Some cetacean species (e.g. killer whales, *Orcinus orca*) often leave only the fish head up to the gills, or just the lips and upper jaw of the fish (Fig. 3) (Secchi and Vaske, 1998; Australian Fisheries Management Authority, 2005). Killer whales have also been observed to avoid the head and vertebral column and fins, preferentially eating only the flesh of hooked tuna and swordfish (Secchi and Vaske, 1998). Other species of odontocetes such as sperm whales (*Physeter macrocephalus*) are believed to pluck entire hooked fish, including the hook, off the line (Ashford *et al.*, 1996). Cetacean depredation on longline gear is believed to most frequently occur during gear hauling (e.g. Wang and Yang, 2002) but can also occur during the setting and soak of the line. This may be because depredation during hauling is easier and less costly energetically than diving deep to reach the hooked fish during the soak and set. In some areas, certain odontocetes have been observed to be less likely to depredate tuna entangled in fishing gear than tuna caught on a hook and not entangled (McPherson, 2003) although the reasons for this are not clear.

Killer whales have often been reported as interacting with longline fisheries taking a variety of fish species from gear (Northridge, 1984; Yano and Dahlheim, 1995; Ashford *et al.*, 1996; Secchi and Vaske, 1998; Donoghue *et al.*, 2002; Australian Fisheries Management Authority, 2005). In the tropical Pacific, there have been numerous observations of fishery interactions with false killer whales (*Pseudorca crassidens*), pilot whales (*Globicephala* spp.) and killer

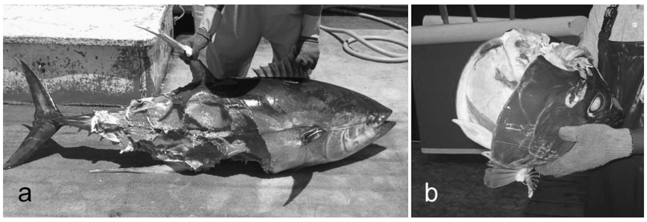

Fig. 3. Shark-depredated yellow fin tuna (left) and false killer whale-depredated tuna (right) from the Hawaii-based longline fishery (photos courtesy of US National Marine Fisheries Service Pacific Islands Regional Office).

whales and at least eight species of dolphins have been observed in the vicinity of longlines in the tropical Pacific, some of which may remove bait. Sperm whales have also been observed to take Patagonian toothfish (*Dissostichus eleginoides*) in the Southern Ocean and sablefish (*Anoplopoma fimbria*) and other fish species in the eastern Gulf of Alaska (Ashford *et al.*, 1996; Donoghue *et al.*, 2002).

Economic and social

Removal of or damage to fish clearly has economic implications for fishermen. Cetacean depredation in longline fisheries occurs worldwide; available estimates of depredation levels while extremely crude, suggest that it may result in substantial adverse economic effects in some fisheries (e.g. Nishida and Shiba, 2002; Donoghue *et al.*, 2002).

The few available estimates of cetacean depredation in longline fisheries employ a range of methods and quality of datasets to examine depredation levels, thus preventing appropriate comparisons between fisheries. Here, we present some of these estimates for information but do not attempt to review them. Sigler *et al.* (2002) estimated an annual 23% reduction in catch of sablefish in the Alaska demersal longline sablefish fishery due to depredation by sperm whales. Dalla Rosa and Secchi (2002) estimated between 5.6-100% (mean 45%) of total fish caught per set were damaged by killer whales in Brazil's pelagic longline tuna and swordfish fisheries. Nishida and Shiba (2002) estimated that between 1-19% of caught fish were depredated annually in Japanese longline fisheries operating in the Indian Ocean. Lawson (2002) estimated that 0.8% of caught fish in observed central and western Pacific longline fisheries are believed to be damaged by whale depredation. Depredation levels by killer whales have been reported to reach 100% in some hauls in the South Georgia demersal longline Patagonian toothfish fishery (Purves *et al.*, 2004).

Furthermore, cetacean-longline interactions often result in loss of or damage to fishing gear (Ashford *et al.*, 1996; Donoghue *et al.*, 2002) with resultant lost fishing time and increased vessel operating costs. This is a result of crew having to take the time to repair gear damaged and lost by cetaceans, time to move from areas with cetaceans and cost of complying with formal constraints such as area and seasonal closures.

A negative public perception of longline fishing has resulted in some cases, in response to the news of injury and mortality of marine mammals in longline gear. This may translate into poorer sales for such fisheries. The increase in eco-labelling efforts, such as these of the Marine Stewardship Council, have the potential to influence seafood consumer practices and to reduce demand and value of seafood caught in fisheries with relatively high rates of interaction with cetaceans (Wessells *et al.*, 1999).

Ecological

Potential effects on the status of cetaceans

While bycatch of cetaceans is a much larger problem in fishing gear such as gillnets and trawls (Perrin *et al.*, 1994), cetacean-longline interactions occasionally result in their entanglement and hooking, causing injury and sometimes mortality (e.g. Northridge, 1984; Ashford *et al.*, 1996; Waring *et al.*, 1999; Baird *et al.*, 2002; Forney, 2004; Baird and Gorgone, 2005). For instance, Forney (2004) estimates that from 1994-2002, the Hawaiian pelagic longline fleet resulted in the mortality and serious injury of about 48 whales and dolphins per year, which equates to one in every 250 sets.

In addition, in some areas the actual or perceived economic costs sustained by fishermen may incite them to harass and kill cetaceans by shooting them, using explosives or employing other harmful methods to try to prevent depredation and gear damage (e.g. Yano and Dahlheim, 1995; Hucke-Gaete *et al.*, 2002; Dalla Rosa and Secchi, 2002; Wang and Yang, 2002). It is possible that such mortality and injury may have important population-level consequences in terms of numbers and/or distribution, especially for small isolated populations of cetaceans, e.g. those associated with islands. For example, there is concern over the ecological effects of longline interactions with false killer whales around the Hawaiian Islands and Palmyra Atoll, which interact with several international pelagic longline fisheries including the Hawaii based fleet (Carretta *et al.*, 2005).

As also discussed below, the use of deterrent devices has the potential to alter the distribution of cetaceans by causing them to avoid their preferred feeding grounds; this may result in less than optimal feeding with the possibility of affecting the 'fitness' of the population (e.g. by lowering successful reproduction or increasing susceptibility to disease).

Altered cetacean foraging strategies

There are a number of possible ecological effects of the adapted foraging behaviour on cetaceans but their precise nature and level of effects are unclear. For example, in some cases cetaceans may feed on species of fish taken from longline gear that are not a normal component of their diet; this may result in their consuming a smaller number of their usual prey species. Depredation may also lead to a change in distribution if the longline fishing grounds are not in their usual feeding grounds.

Unexpected effects from avoidance strategies

Use of acoustic deterrents and acoustic masking devices to deter cetacean interactions with fishing gear will result in the addition of noise to the marine environment; it is not clear what ecological effects this could have on cetaceans and other species. For instance, clupeoid fishes, including herring (*Clupea harengus*), can hear the frequencies emitted by currently used 'pingers' (Nestler *et al.*, 1992, cited in Dawson *et al.*, 1998). Kraus *et al.* (1997) found that active pingers placed on gillnets to reduce porpoise bycatch resulted in a 6.5× lower catch of Atlantic herring. One possible explanation for this is that the herring moved away from the vicinity of the pingers (Dawson *et al.*, 1998). Despite recent advances, our knowledge of the short- and long-term responses of cetaceans to artificial sounds in the marine environment is limited (Reeves *et al.*, 1996). However, possible responses may range from hearing damage and ultimately strandings, (e.g. from close range exposure to intense noises such as Acoustic Harassment

Devices designed to scare pinnipeds away from mariculture facilities (Morton and Symonds, 2002) and military sonar (e.g. IWC, In press)) to temporary (e.g. Australian Fisheries Management Authority, 2005) or even perhaps long-term abandonment of some feeding grounds.

Ecological effects of depredation

The loss of fish due to depredation by cetaceans is generally not taken account of in fish stock assessments and the provision of management advice (e.g. total allowable catches). The degree to which this is important will clearly vary on a case-by-case basis, depending *inter alia* on whether the prey taken from the longlines are the same species, age/size and quantity that the cetacean would normally feed on. Similarly, any increased effort by fishermen to account for lost catches due to cetaceans may potentially confound fish assessments and place increased pressure on target fish species; it may also result in increased bycatches of other species such as seabirds, turtles and fish.

STRATEGIES TO REDUCE CETACEAN INTERACTIONS

There are a range of strategies that can or at least have the potential to reduce cetacean interactions with longline gear. Below we review a number of categories of approaches.

Fleet communication and coordination

The distribution of cetaceans (and other incidentally caught species groups such as seabirds and sea turtles), is often unpredictable and may be spatially contagious or aggregated. Consequently, fleet communication systems may be employed by the fishing industry to report near real-time observations of hotspots to enable a fishery to operate as a coordinated ‘One Fleet’ in order to reduce fleet-wide depredation by and bycatch of cetaceans (Gilman *et al.*, 2006). Gilman *et al.* (2006) describe case studies of industry fleet communication programmes of the US North Atlantic longline swordfish fishery, US North Pacific and Alaska trawl fisheries and US Alaska demersal longline fisheries, designed to reduce bycatch of seabirds, sea turtles and fish. Evidence suggests that these programmes substantially reduced fisheries bycatch and provided economic benefits that greatly outweighed operational costs. Fleet communication may be appropriate in fisheries where there are strong economic incentives to reduce depredation and bycatch and where such efforts can be monitored adequately via onboard observer coverage. Such an approach will be facilitated where vessels are coordinated by a fishery association. It is possible that fleet coordination of daily fishing positions and times (already a current practice in many fleets) may minimise per vessel depredation levels relative to vessels that fish in isolation, providing fishermen with an economic incentive to follow such a strategy.

Changes in fishing gear and methods

General approaches to altering fishing gear and fishing methods to reduce cetacean interactions fall into the following five categories. These are adapted from Gilman *et al.* (2005) who describe strategies to reduce seabird bycatch in longline fisheries. Methods need to be assessed for their efficacy in reducing cetacean bycatch and depredation, as well as their commercial viability (Gilman *et al.*, 2005); carrying out the appropriate testing is not simple and the question of habituation can not be ignored (IWC, 2000, pp.235-43; IWC, 2001).

Avoid areas and periods with peak cetacean abundance

At the simplest level, individual fishing vessels can avoid setting (or cut a set short) when problematic species of cetaceans are observed in the vicinity. It would be valuable for fishermen to learn to differentiate cetacean species in order to determine an appropriate response. Alternatively, when cetaceans are observed during a set, vessels could break a set and re-commence parallel and adjacent to the previously set line to attempt to lose cetaceans that might follow the first line to the end and not find the second line. In addition to visual detections, it is also possible to use sonobuoys and hydrophones to detect the presence and movement of some cetaceans (McPherson *et al.*, 2002) and in some cases identify the presence, species and even location and identification of specific pods of cetaceans. In theory this information can be used to avoid fishing in areas where depredation will probably be high (Donoghue *et al.*, 2002). Although suggested by some as a possible approach, telemetry is expensive, not sufficiently reliable and may give rise to objections with respect to attachment methods (Donoghue *et al.*, 2002). Better knowledge of the behaviour of cetaceans around gear may suggest other appropriate avoidance strategies. For example, if cetacean interactions are more common during daytime hours, then night hauling may be effective. Area and seasonal closures can also be used to help avoid known areas and periods of high concentrations of cetaceans, where these are predictable and this is discussed further in a following section.

Reduce cetacean detection of fishing gear and vessels

Vessels with lower cetacean bycatch and depredation rates than the rest of the fleet should be examined for their specific design and operational characteristics; this may suggest relatively simple solutions to reduce cetacean-longline interactions. For example, vessels that are observed to seldom experience depredation may have different acoustic signatures due to different hull shapes, materials (timber, fibreglass or steel) and electronic equipment.

If it is the sound of the vessel/operation that attracts the cetaceans, then underwater acoustic masking devices, quieter fishing vessels and/or equipment that disrupts cetacean echolocation may reduce cetacean detection of fishing gear. Creating a muffler for the hauler or isolating the hauler, transmission and gear hydraulics from the vessel hull with vibration isolating mounts may reduce vessel noise and reduce cetacean detection of fishing operations (Donoghue *et al.*, 2002; Australian Fisheries Management Authority, 2005). The introduction of a new relatively quieter vessel engine, with rubber mounts and Teflon coupling for sound insulation, to an Australian demersal longline vessel initially resulted in lower cetacean depredation compared to noisier vessels in the fleet. However, over time this vessel has come to experience the same depredation rates as the rest of the fleet, indicating that the resident killer whales learned to identify this new quieter vessel (Australian Fisheries Management Authority, 2005). Although it has been suggested that acoustic devices that masks returning echolocation signals may be an effective strategy to reduce cetacean-longline interactions, even if true, many design aspects remain unresolved (McPherson, 2003). McPherson (2003) suggested that an effective acoustic device for toothed whales will need to be: (a) impulsive (activated when toothed whale sounds are detected, versus continuously emitting sound) and broadband rather than tonal; (b) ultrasonic 20-100kHz; (c) loud enough to be aversive but not too loud that it causes permanent damage to cetaceans; and (d) varied sufficiently to avoid habituation. Development of such a prototype acoustic deterrent device was initiated for testing in the Australian longline fisheries, but development was discontinued due to concerns over cost effectiveness (McPherson *et al.*, 2002; McPherson, 2003).

Refraining from chumming during the set and not discarding offal and spent bait during the haul may also reduce cetacean detection of fishing vessels. Use of ‘decoy’ tactics (e.g. setting lines in a sinusoidal or wavy pattern rather than in a straight line and setting parts of the line without hooks) has also been suggested as a possible way to reduce cetacean interactions with longline gear (Donoghue *et al.*, 2002; Australian Fisheries Management Authority, 2005). Similarly, playing pre-recorded longline fishing vessel sounds from stations throughout a fleet’s fishing grounds may serve as a decoy to distract cetaceans from actual fishing vessels. Using a decoy fishing vessel to distract cetaceans away from fishing grounds with other fishing vessels has also been suggested as being effective, although even if it works, it might not be necessarily cost effective and the animals might quickly adapt to the strategy. There have been reports of vessels motoring over a competing vessel’s gear in an attempt to leave following whales behind (Straley *et al.*, 2002).

Limit cetacean access to catch and bait

It has been suggested that setting fishing gear at depths greater than 400m may reduce cetacean interactions, for those species where the maximum normal dive depths might be less than this (Donoghue *et al.*, 2002). However, this tactic would be commercially viable only in those fisheries targeting fish foraging predominantly at these depths. Even then, because cetaceans are known to wait for hauling in order to take fish at shallow depths, it is likely to be ineffective.

Some odontocete species have been observed to be less likely to depredate tuna entangled in fishing gear compared to tuna caught on a hook and not entangled (McPherson, 2003). This suggests that the development of gear that entangles or encapsulates caught fish could reduce depredation. It is unclear what mechanism causes this reduction in depredation but it is thought that it is either due to (1) a reduction in access to the fish or (2) a reduction in the desirability of the fish by making them appear dead. It should be remembered that while such an approach may decrease depredation it may result in entanglement of cetaceans.

Reduce the likelihood of hooking and entangling cetaceans

If lack of perception of the gear is the reason for the injury or death of cetaceans in longlines, making longlines more detectable by cetaceans could potentially reduce damage to them. Technology developed to reduce cetacean bycatch in other fisheries might be effectively modified for use with longline gear. However, making longline gear more detectable may also increase the incidence of depredation by odontocetes by drawing attention to the gear.

Some acoustic devices (small, low-intensity sound-generators called ‘pingers’), intended to provide a warning to alert cetaceans of the presence of fishing gear, have been demonstrated to significantly reduce entanglement bycatch of harbour porpoises (*Phocoena phocoena*) and short-beaked common dolphins (*Delphinus delphis*) in gillnets (e.g. Reeves *et al.*, 1996; Kraus *et al.*, 1997; Dawson *et al.*, 1998; Baldwin *et al.*, 2002; Barlow and Cameron, 2003; McPherson, 2003). The question as to whether porpoises habituate to the acoustic alarms over time (Dawson *et al.*, 1998; Gearin *et al.*, 2000; Cox *et al.*, 2001) requires further investigation. However, even if the animals do become accustomed to the pingers, the noise may still enable the animals to identify the presence of the fishing gear and avoid becoming entangled in it (McPherson, 2003). Methods to improve the detectability of gillnets to echolocating odontocetes have been tried to reduce bycatch (Read, 2002) e.g. by adding dense material such as barium sulphate to the nylon used to manufacture monofilament to increase reflectivity. The same technology could theoretically be applied to longline gear monofilament. Increasing the acoustical reflectivity of fishing gear will only reduce odontocete bycatch if these animals echolocate in the vicinity of the fishing gear and entanglement is occurring because the animals are not detecting the fishing gear in time to avoid it (Read, 2002). Acoustic warning devices and acoustically reflective fishing gear have not been tested in longline fisheries for any cetacean species.

Deter cetaceans from taking catch and bait

As noted above, in certain situations, pingers have been shown to reduce bycatch of some small cetacean species. Louder acoustic deterrents (e.g. Acoustic Harassment Devices used to scare and cause pain to primarily pinnipeds to prevent them coming close to aquaculture cages), are large, expensive in part due to battery maintenance, and may permanently damage cetaceans’ hearing. Acoustic deterrents may be impractical and cost prohibitive for use in longline gear, because a large number of units would be required to cover the entire length of gear. A towed device that broadcasts noise designed to mask the sounds of fishing vessels and imitate killer whale vocalizations when hunting has been suggested as a possible solution (Bakharev, No date), although cetacean habituation to this strategy is probable.

The use of bait or gear with an unpleasant smell or taste could help reduce the attractiveness of gear, bait and catch to cetaceans and could result in cetaceans developing a learned aversion to depredation behaviour. However, in addition to the need to test the effectiveness of this approach for cetaceans, it must also be assessed for any adverse effects on fish catches. There are several records of fishermen using devices , such as rifles, harpoons, and explosives, to intentionally injure or kill cetaceans (e.g. Yano and Dahlheim, 1995; Dalla Rosa and Secchi, 2002; Hucke-Gaete *et al.*, 2002; Wang and Yang, 2002). This raises ecological, ethical, social and legal concerns.

Formal constraints

National-level legal, regulatory and policy-derived formal constraints, combined with an effective surveillance and enforcement programme, can promote fishing industry compliance with laws, rules and policies to minimise cetacean bycatch. Seasonal or area closures and mandatory use of avoidance techniques, are examples of regulatory tools that might be used to manage cetacean bycatch (Hall *et al.*, 2000; Gilman *et al.*, 2005). Fishery management authorities could create a compensatory mitigation fee and exemption structure for cetacean bycatch, applicable to individual vessels or to an entire fleet, similar to a ‘polluter pays’ system (Gilman *et al.*, 2002). Alternatively, the fee structure could provide a positive reward-based incentive, where a higher subsidy, lower permit or license fee, earlier start to the fishing season, or lower taxes apply and a positive image is portrayed when a vessel or fleet meets standards for cetacean bycatch. This, combined with the threat of a fishery closure if performance standards are not met would provide a strong incentive for industry compliance to minimise cetacean interactions.

For example, the US Marine Mammal Protection Act (MMPA) is the primary legislation for the management of marine mammals in the USA. A maximum allowable level of anthropogenic mortality is determined for each stock of marine mammal, referred to as the Potential Biological Removal (Wade, 1998). If anthropogenic mortality levels from bycatch and other human sources of mortality exceed this level, then a take reduction plan is prepared, identifying measures to reduce mortality and serious injury from anthropogenic sources to below the threshold level.

Regional and international accords, regulations and policies

Multilateral treaties and accords that address cetacean interactions can obligate national governments to adopt enabling legislation to manage such interactions. Regional Fishery Management Organisations can adopt regulations and policies to manage interactions between fisheries and sensitive species to be implemented by member nations. Multilateral bodies can adopt advisory policies to encourage fishing nations to sustainably manage icetacean-longline interactions. However, determining what are sustainable levels requires good information on stock structure, anthropogenic removals and abundance; information that is often lacking.

Marine protected areas, area and seasonal closures

Area and seasonal closures are management tools that can complement employment of other strategies to reduce cetacean-longline interactions (e.g. Reeves *et al.*, 1996; Murray *et al.*, 2000; Read, 2002; Donoghue *et al.*, 2002). Closed areas can have substantial adverse economic effects, but remain a tool available to fishery managers in the absence of alternative effective methods. It may also be a more desirable option than a closed fishery.

Marine protected areas (MPAs) can be effective at reducing cetacean-fisheries interactions provided that the locations and times of occurrence of cetacean hotspots are known and predictable (Murray *et al.*, 2000). Furthermore, the hotspots must be a small component of the fleet's fishing grounds in order for temporal and area avoidance to be commercially viable.

The consequences of establishing MPAs need to be carefully considered, as resource use restrictions may displace effort to adjacent and potentially more sensitive and valuable areas, where weaker management frameworks may be in place. For instance, time and area closures for the Gulf of Maine gillnet fishery, designed to reduce bycatch of harbour porpoises, were ineffective due to displacement of fishing effort to areas with high harbour porpoise bycatch, as well as unpredicted inter-annual variability in timing and distribution of porpoise bycatch hotspots (Murray *et al.*, 2000). Closures implemented in the Northwest Atlantic for the US pelagic longline swordfish fleet to address sea turtle bycatch displaced longline effort to alternative grounds such as the South Atlantic, where bycatch rates of other sea turtle populations may have been problematic (Kotas *et al.*, 2004). One of the consequences of displacing longline fishing effort from an area closed off Newfoundland, due to concerns with bycatch of sea turtles, was an increase in the catch of 11 shark species and 10 depleted fish species (Baum *et al.*, 2003).

Similarly, closing of a fishery by one nation may also result in an increased effort by another nation's fleet with fewer controls to manage bycatch. For example, during a two-year closure of the Hawaii longline swordfish fishery due to concerns over bycatch of sea turtles, swordfish supply traditionally met by the Hawaii fleet to the US marketplace was replaced by imports from foreign longline fleets, including those from Mexico, Panama, Costa Rica and South Africa, which have substantially higher ratios of sea turtle captures to unit weight of swordfish catch than Hawaii and less stringent or no measures to manage seabird bycatch (Gilman and Freifeld, 2003; Bartram and Kaneko, 2004; Sarmiento, 2004).

Establishing MPAs within a nation's Exclusive Economic Zone to protect high-density areas for resident or migratory cetaceans is potentially an expedient method to reduce cetacean-longline interactions. However, establishing high seas MPAs to restrict fishing in cetacean foraging areas and migration routes, which would require extensive and dynamic boundaries and extensive buffers, may not be a viable short-term solution. This is due in part to the extensive time anticipated to resolve legal complications with international treaties, to achieve international consensus and political will and to acquire the requisite extensive resources for surveillance and enforcement to implement high-seas marine protected areas (Thiel and Gilman, 2001).

Some international bodies have succeeded in creating MPAs on the high seas. For example, the International Whaling Commission (IWC) has declared the Indian and large parts of the Southern Ocean as 'Sanctuaries' within which commercial whaling cannot occur; this covers around 30% of the world's oceans, mostly on the high seas. Conventions governing international shipping have designated large areas of the ocean that include high seas as Special Areas where stringent restrictions apply regarding discharges from ships. Furthermore, under the United Nations Convention on the Law of the Sea, the International Seabed Authority could protect areas from mineral extractions beyond national jurisdiction, where there is a risk of harm to the marine environment (Kelleher, 1999). Recent developments within the framework of the United Nations Convention on the Law of the Sea and associated conventions may make it possible to restrict future fisheries activities on the high seas that are shown to undermine marine conservation (Kelleher, 1999).

Improved practices for handling and release of cetaceans

Reducing injury and incidence of post-release mortality for cetaceans caught in longline gear may contribute to reducing the adverse ecological affects of cetacean-longline interactions, provided it is on a sufficient scale. For instance, there are prescribed best practices for disentangling whales caught in fishing gear (Lyman *et al.*, 1999) and formal networks to respond to entangled marine mammals (Bowman *et al.*, 1999).

Eco-labelling

Consumer demand can alter industry behaviour. A longline fishing industry can pursue certification or accreditation from an eco-labelling certification programme, in part, to demonstrate the employment of best practices to reduce cetacean interactions, assuming such best practices exist. The incentives to industry are a market-based incentive to increase demand for and value of their products and a social incentive to receive recognition from the public for complying with accepted norms (Wessells *et al.*, 1999). Eco-labelling can serve as an effective marketing tool for a fishing industry, when properly managed. For instance, certification under an eco-labelling scheme can be used as a marketing tool to develop and market an image and product differentiation, through advertising, sales promotion, public relations, direct marketing and media coverage. A company can differentiate their products from other seafood as originating from a fishery that follows internationally accepted practices to ensure environmental sustainability. This is a form of cause-related marketing and is a proven means to promote recognition and develop a positive company image and reputation.

For example, the Marine Stewardship Council is an international organisation that has a certification programme for seafood and uses a product label to distinguish environmentally responsible fishery management and practices. Principles and criteria adopted by the Marine Stewardship Council, used to assess the suitability of fisheries for certification, are intended to ensure that certified fisheries are sustainable and well managed (Marine Stewardship Council, 1998).

Industry self-policing

A longline industry can create a programme that makes information on individual vessel-cetacean interaction levels and compliance with relevant regulations available to the entire industry. This method is especially effective where regulations contain industry-wide penalties, such as a reduction in the length of a fishing season, closed areas, or complete fishery closure, should the fleet exceed cetacean bycatch rates. This self-policing programme uses peer pressure within the industry to criticise 'bad actors' and publicly acknowledge those who are operating in a responsible manner. For example, the North Pacific Longline Association initiated a seabird bycatch report card system among its members in 2000 (Fitzgerald *et al.*, 2004).

CONCLUSIONS AND NEXT STEPS

There is limited understanding of the mechanisms responsible for cetacean-longline interactions and the extent of ecological and economic repercussions from these interactions. Fishery-specific assessments are needed to determine reliable depredation levels and rates of cetacean injury and mortality. There is a need for reliable assessments of cetacean-longline interactions, derived from independent observer programmes where possible, which will benefit from training of observers and fishermen to correctly identify cetacean species and identify fish damaged by cetaceans versus other animals (e.g. sharks, squid, bony fish). A better understanding of the degree to which cetacean depredation is occurring during the set, soak and haul should help identify effective solutions.

Whilst there are several potential methods to reduce cetacean-longline interactions, there has been little research to test their efficacy and/or economic viability. To pursue these possibilities, we suggest that it is a priority to examine and compare vessels with relatively low cetacean depredation and bycatch rates with vessels with relatively high rates to identify design and operational differences. There may not be an effective way to reduce cetacean interactions with longline gear other than currently practiced strategies, such as avoiding fishing at times and locations when and where interactions are known to be frequent and shifting fishing position. However, several additional ideas to reduce cetacean-longline interactions warrant assessment.

The most appropriate avoidance measures for individual longline fleets may depend, in part, on the characteristics of the fishery, species and behaviour of cetaceans that interact with the fleet and available financial resources. There is a need for experimentation in individual longline fisheries over several seasons to assess fishery-specific efficacy and commercial viability of strategies to reduce cetacean interactions. This is necessary as different cetacean species likely respond differently to alternative avoidance methods (e.g. a single acoustic device is unlikely to be an effective deterrent for multiple cetacean species (McPherson, 2003)) and to address the question of possible cetacean habituation to the avoidance strategy (e.g. Dawson *et al.*, 1998), especially in fisheries that operate in grounds that overlap with resident cetaceans. Such evaluation must precede widespread advocacy for longline fleets to adopt specific avoidance methods.

Longline fishermen are some of the most qualified people to develop and improve methods to reduce cetacean-longline interactions. Longline fishermen have a large repository of knowledge and information related to this problem, which can be tapped into to contribute to finding effective and practical solutions (Gilman *et al.*, 2005). This has been demonstrated by successful collaborative research by the US Alaskan demersal longline fisheries (Melvin *et al.*, 2001), US Hawaii pelagic longliners (Gilman *et al.*, 2003, Gilman *et al.*, In press) and various industry-lead voluntary fleet communication protocols, to reduce fisheries bycatch (Gilman *et al.*, 2005; Gilman *et al.*, 2006). Incentive instruments should be instituted to encourage longline fishers to participate in developing and testing new mitigation methods (Gilman *et al.*, 2002). Fishermen and longline fishery associations are encouraged to become active participants in research and commercial demonstrations, implementing best practices and supporting adoption of regulations based on best available science.

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