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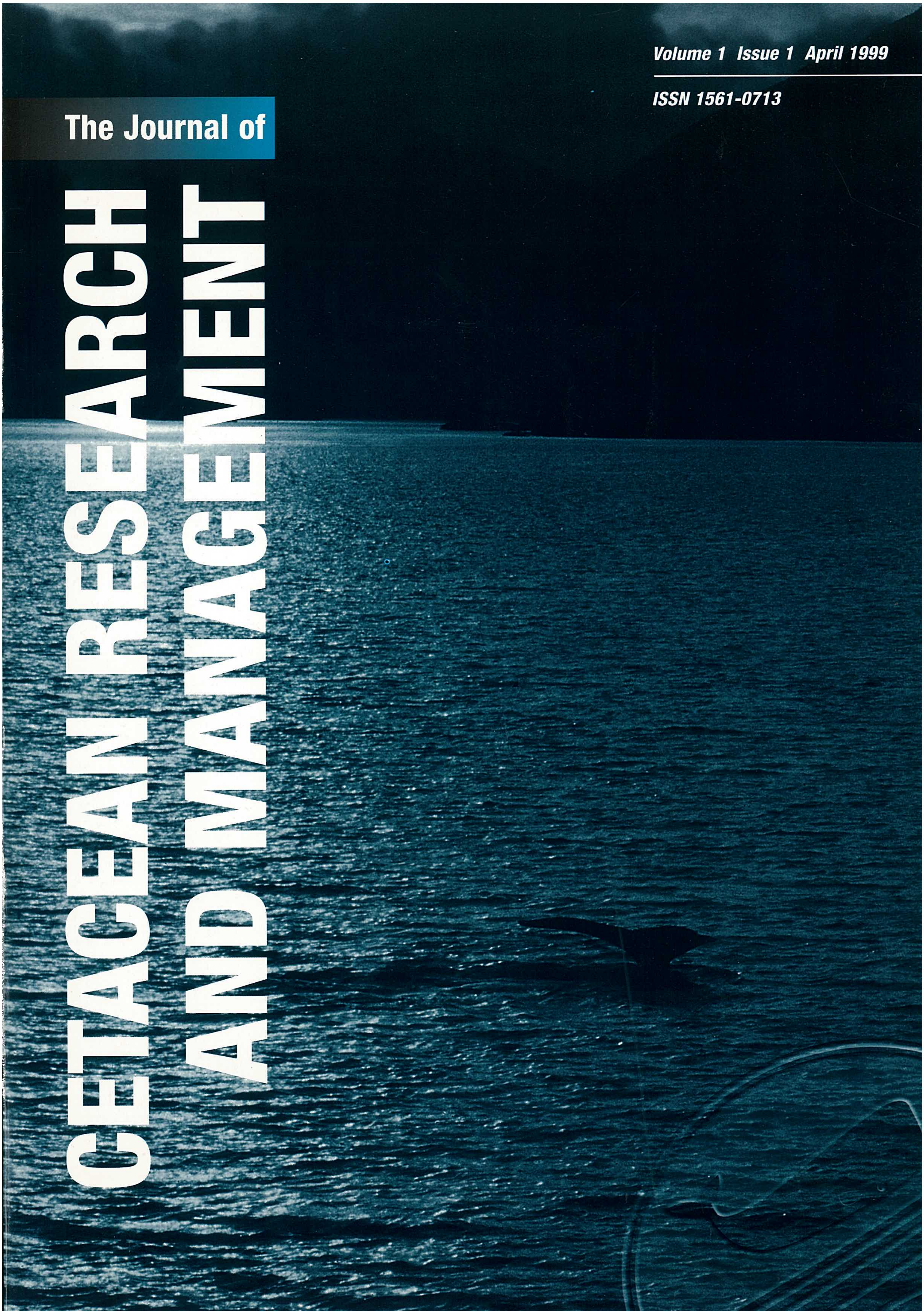
CETACEAN RESEARCH AND MANAGEMENT



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Editorial

Welcome to this, the first issue of the *Journal of Cetacean Research and Management.*

The Journal has been established to publish papers on those matters of most importance to the conservation and management of whales, dolphins and porpoises, and in particular papers that are relevant to the tasks of the Scientific Committee of the International Whaling Commission (IWC). These will include papers on:

- population assessment and trends
- population dynamics
- population biology
- taxonomy and stock identity
- risk averse management strategies
- direct and indirect exploitation
- environmental changes and threats in the context of cetaceans
- scientific aspects of whale watching and sanctuaries.

The Journal replaces the scientific sections of the *Reports of the International Whaling Commission.* That series began in 1950 (IWC, 1950), but at that time had little scientific content. The first report of the IWC Scientific Committee was published in 1955 (IWC, 1955). The first scientific papers presented to the Scientific Committee were not published in *Rep. int. Whal. Commn* until the beginning of the 1970s. In 1977, a full time editor was employed and *Rep. int. Whal. Commn* was professionally typeset. Before 1978, papers were more-or-less published as presented at the meeting. By the beginning of the 1980s, however, an anonymous review process was established to try to ensure the scientific quality of the papers published by the Commission. Altogether, over 1,500 papers have been published in *Rep. int. Whal. Commn* and its *special issue* series since 1950, mostly since 1970. References for all of the published and unpublished papers are available in database format (with the program *Papyrus*) from the Office of this Journal. Details of how to obtain IWC publications can be found on the IWC web page or from the IWC Office (details are given on the inside cover).

The rationale for the new Journal is discussed in Donovan (1999).

For those readers unfamiliar with the IWC and particularly the work of its Scientific Committee, a brief introduction is given below.

THE INTERNATIONAL WHALING COMMISSION

The International Whaling Commission was founded in 1946. It was established under the International Convention for the Regulation of Whaling which was signed in Washington DC on 2 December 1946 (IWC, 1999b). The Preamble to the Convention *inter alia* states that its purpose is to provide for the 'proper conservation of whale stocks and thus make possible the orderly development of the whaling industry'. Membership has grown from the original 15 nations to 40 nations today.

The Commission is the decision-making body established by the Convention and comprises one Commissioner from each government who has 'one vote and may be accompanied by one or more experts and advisers' (IWC, 1999b). It normally meets annually. There is also provision for observers to attend and at the 1998 Annual Meeting there were observers from 5 non-member governments, the European Community, 5 Inter-Governmental Organisations and 70 Non-Governmental organisations.

The report of the Commission's meeting ('The Chairman's Report') and other non-scientific material used to be published in *Rep. int. Whal. Commn.* It is now included in a new series called the *Annual Report of the International Whaling Commission* (IWC, 1999a).

The history of the Commission has been dealt with by a number of authors (e.g. Gambell, 1977; Donovan, 1992) and is not considered here. In short, much of the Commission's history has centred around the difficulties in finding a balance between its twofold aims i.e. 'conservation of whale stocks' and the 'orderly development of the whaling industry'.

THE SCIENTIFIC COMMITTEE

An important feature of the Convention is the emphasis it places on scientific advice. The Convention requires that amendments to the Schedule[1] 'shall be based on scientific findings' (IWC, 1999b). To this end, the Commission has established a Scientific Committee that normally meets once a year, immediately prior to the Commission meeting, to which it reports and makes recommendations.

The Scientific Committee comprises scientists nominated by member governments. In addition, in recent years it has invited other scientists to supplement its expertise in various areas. The size of the Committee, as well as the subject matter it addresses, has increased considerably over time. In 1954, it comprised 11 scientists from 7 member nations. At its most recent annual meeting (in Oman in 1998) it comprised over 115 participants (including some 30 invited participants); 22 member nations were represented. After 1955, the full Report of the Scientific Committee was published in *Rep. int. Whal. Commn.* It is now included as a supplement to this Journal. The report of the 1998 Meeting was published in April 1999 (*J. Cetacean Res. Manage. 1 (Suppl.):* 1- 284).

The subject matter considered by the Committee (and see IWC, 1999h) is largely determined by the scientific needs of the Commission. These are expressed in broad terms in the Convention text and are to:

- encourage, recommend, or, if necessary, organise studies and investigations relating to whales and whaling;
- collect and analyse statistical information concerning the current condition and trend of the whale stocks and the effects of whaling activities thereon;
- study, appraise and disseminate information concerning methods of maintaining and increasing the populations of whale stocks.

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[1] The Schedule to the Convention contains IWC regulations concerning whaling (e.g. definitions, catch limits, seasons, etc.). To amend a provision of the Schedule a three-quarters majority of those voting (excluding abstentions).

The following sections briefly summarise the main areas of scientific interest to the Commission at present. They are not intended to represent a comprehensive survey of the Committee's work but merely to provide an outline of this work for those unfamiliar with it.

Comprehensive Assessment of whale stocks

When the Commission adopted a proposal to set zero catch limits for commercial whaling (popularly known as the 'moratorium'), it had also agreed to a 'comprehensive assessment' of the effects of this decision on whale stocks (IWC, 1983). Similar terminology was adopted for the aboriginal whaling scheme the following year (IWC, 1984). The development of the concept of the 'Comprehensive Assessment' is reviewed in Donovan (1989). Finally, it was agreed that from a Scientific Committee viewpoint, 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 (IWC, 1987). Clearly, it was not possible to 'comprehensively assess' all whale stocks simultaneously, and the Committee has been working in an objective manner towards this, initially concentrating on stocks that have recently or are presently being subject to either commercial or aboriginal subsistence whaling (e.g. North Atlantic minke whales - IWC, 1991a; North Pacific minke whales - IWC, 1992c; Southern Hemisphere minke whales - IWC, 1991b; North Atlantic fin whales - IWC, 1992a; North Pacific Bryde's whales - IWC, 1997b; Bering-Chukchi-Beaufort Seas bowhead whales - IWC, 1992b; eastern North Pacific gray whales - IWC, 1993b). It is currently reviewing Southern Hemisphere baleen whales in this context, particularly humpback, blue and right whales (e.g. IWC, 1999e).

The Commission has a major research initiative in the Antarctic (SOWER - Southern Ocean Whale and Ecosystem Research Programme) with two main components, one concerning the abundance estimation of minke whales and other baleen whales south of 60ºS, and the second concerning the status of Southern Hemisphere blue whales (IWC, 1999j). The initial part of this latter component involves the development of methods to distinguish pygmy blue whales from true blue whales at sea (IWC, 1999e).

The Committee also recently reviewed the status of right whales (e.g. see IWC, 1999e). Whilst certain populations in the Southern Hemisphere, although still heavily depleted, are increasing, the same is not true for the Northern Hemisphere.

Of general concern to the assessment of any cetaceans is the question of stock identity (e.g. Donovan, 1991) and examination of this concept in the context of management plays an important role in much of the Committee's work (see IWC, 1999c, p.8).

The Revised Management Procedure for baleen whales

The history of the management of whaling and the IWC is summarised in Donovan (1995). After the adoption of the moratorium on commercial whaling, the Committee spent over eight years developing the Revised Management Procedure (RMP) for baleen whales (IWC, 1999i). In brief, this is a generic management procedure designed to estimate safe catch limits for commercial whaling (see Cooke, 1995). By way of extensive computer simulations, the RMP has been developed to take into account the inevitable uncertainty in scientific knowledge of whale populations and their environment. In addition, the Committee has developed guidelines and rules for how sighting surveys should be conducted and how the data are to be analysed if the resultant estimates are to be considered to be of sufficient quality to be used in calculating catch limits (IWC, 1997c). Similar guidelines and rules have been developed with respect to data requirements, quality and analysis (IWC, 1995b; 1997d).

These scientific aspects have been adopted by the Commission (IWC, 1993a). The implementation of the RMP for those stocks for which it has been tested is, of course, a political decision. 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). The RMS will not only include the scientific aspects such as the RMP, but a number of non-scientific issues, including inspection and enforcement (e.g. see IWC, 1999a).

Current scientific work on RMP matters largely centres on the simulation testing of its possible application for specific species and ocean areas: North Atlantic and Southern Hemisphere minke whales were first considered and at present North Pacific minke and Bryde's whales are being examined (IWC, 1999d).

Assessment of stocks subject to aboriginal subsistence whaling

The Commission has recognised aboriginal subsistence whaling as separate from commercial whaling. Such whaling is permitted from 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 (bowhead and gray whales). It is the responsibility of the Committee to provide scientific advice on safe catch limits for such stocks. The Committee has established a timetable (IWC, 1999c, p.37) for the future assessments it intends to carry out (1999 - the development of a research plan for Greenlandic stocks, bowhead whale stocks other than the Bering-Chukchi-Beaufort Seas stock; 2000 - North Atlantic humpback whales; 2001 - fin whales off Greenland; 2002 - minke whales off Greenland; 2003 - gray whales; 2004 - Bering-Chukchi-Beaufort Seas stock of bowhead whales).

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 that takes into account the different objectives for the management of such whaling as compared to commercial whaling. This is an iterative and ongoing effort. Given the results so far (IWC, 1999f), a likely potential scenario is that the Commission might 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.

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 threaten whale stocks. The Committee examined this issue in the context of the RMP and agreed that the RMP adequately addresses such concerns. However, it 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 (IWC, 1994). The Committee held two initial workshops, one on the effects of chemical pollutants on cetaceans and the other on the effects of climate change and ozone depletion - these have been subsequently followed up by the development of two multi-national, multi-disciplinary research proposals (IWC, 1999g). 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. SOWER 2000 will examine the influence of temporal and spatial variability in the physical and biological Antarctic environment on the distribution, abundance and migration of whales.

Scientific aspects of whale sanctuaries

As well as management measures governing catch and size limits, species and seasons, the IWC may also designate open and closed areas for whaling. A sanctuary in the Antarctic was established in 1938 (pre-IWC), south of 40°S and between 70°W and 160°W because commercial whaling had not taken place there and it was thought desirable that this situation was continued. The IWC adopted this sanctuary until 1955, when it was opened to whaling as a means of reducing the pressure of catches on the rest of the Antarctic whaling grounds.

An Indian Ocean Sanctuary (an area where commercial whaling is prohibited) was established by the IWC in 1979, extending south to 55°S. It was initially established for 10 years and its duration has since been extended twice. It will be reviewed again by the Commission in 2002 (IWC, 1999k).

In 1994, the Commission established a Southern Ocean Sanctuary. The northern boundary follows 40°S except in the Indian Ocean sector where it joins the southern boundary of that sanctuary at 55°S, and around South America and into the South Pacific where the boundary is at 60°S. It will be reviewed by the Commission in 2004 (IWC, 1999k).

In 1998, the Commission stated that the objectives of this Sanctuary were to provide for: the recovery of whale stocks, including the undertaking of appropriate research upon and monitoring of depleted populations; the continuation of the Comprehensive Assessment of the effects of setting zero catch limits on whale stocks; and the undertaking of research on the effects of environmental change on whale stocks (IWC, 1999a).

Small cetaceans

The Convention does not define a 'whale', although a list of the names of twelve whale species (in a number of languages) was annexed to the Final Act of the Convention. Some governments take the view that the Commission has the legal competence to regulate catches only of these named great whales. Others believe that all cetaceans, including the smaller dolphins and porpoises, also fall within IWC jurisdiction. Despite this, it has been agreed that the Scientific Committee can study and provide advice on small cetaceans. 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 (Bjørge *et al.*, 1994). The Committee has established a timetable for its future work (IWC, 1999c, p.44-5). In 1999 it will examine the status of white whales and narwhals and in its consideration of bycatch mitigation measures concentrate on acoustic deterrents. In 2000 it will examine the status of freshwater cetaceans and continue to discuss bycatch mitigation measures. After 2000, it will examine the status of Dall's porpoises, the systematics and population structure of *Tursiops*, the status of ziphiids in the Southern Ocean and the status of small cetaceans in the Caribbean Sea.

Scientific aspects of whalewatching

It is only recently that the Committee has been asked to examine scientific aspects of whalewatching by the Commission (IWC, 1995a). The Committee developed general guidelines for whalewatching and has identified four priority areas for future consideration: (a) a more detailed review of the approach distances, effort and activity limitations in place in existing operations for a range of species, and information on the basis for such controls; (b) an assessment of current studies of the effects of different approach distances and platforms; (c) a review of the quantitative methods used to assess the short-term reactions of cetaceans and the basis for judgements of adverse effects; and (d) comparative studies on different approaches/distances and other controls which may be required on areas important for feeding, resting and reproduction (IWC, 1997a).

Review and comment on Scientific Permits issued for scientific research

The right of national authorities to issue permits for the killing of whales for scientific purposes is given in Article VIII of the Convention (IWC, 1999b). Prior to 1982, over 100 permits had been issued by a number of governments including Canada, USA, USSR, South Africa and Japan. The issuance of such permits has become a major area of discussion since the moratorium and three countries (Japan, Norway and Iceland), have issued scientific permits as part of their research programmes since 1985. Currently permits are issued by Japan to take minke whales in areas of the Southern Hemisphere and the North Pacific. Governments must provide details of proposed permits for review by the Committee (IWC, 1999k). In recent years, the Committee and the Commission have developed a number of guidelines for the review of such proposals (e.g. see IWC, 1998b, pp. 103-5). The Japanese Southern Hemisphere programme is a long-term project and the results have recently been extensively reviewed by the Committee (IWC, 1998a). A similar review of the North Pacific programme is scheduled for the year 2000.

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The establishment of a new journal is a major undertaking. In addition to thanking the Editorial Staff (Helen, Elaine, Stella and Clare) and the Editorial Board, I would particularly like to thank the staff of Black Bear Press (especially Trevor Hann), for advice and patience.

G.P. Donovan
Editor

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Early descriptions of whales

Many of the early descriptions of whales and their behaviour and ecology, were published in languages other than English. These were often sections in books or articles that were more broad in scope, for example general works on zoology or geography. If translations into English exist at all, they are often not very precise with respect to the cetacean component. The Journal invites submissions of such descriptions. Submissions should include: full bibliographic information; a brief introduction to the author and the work in which the description is included; the full text in the original language; and a careful translation.

H. STRØM. 1762. PHYSICAL AND ECONOMIC DESCRIPTION OF THE DISTRICT OF SUNNMØRE IN THE DIOCESE OF BERGEN IN NORWAY, IST PART, SORØE. [*PHYSISK OG OECONOMISK BESKRIVELSE OVER FOGDERIET SØNDMØR BELIGGENDE I BERGENS STIFT I NORGE*, FØRSTE PART, SORØE] [UNIVERSITY PRESS].

Introduction

Hans Strøm was a Norwegian parson from the 18th century. Although the book is well known in Norway, few people have actually read it. The only edition available is the original from 1762. Following the publication of the book, Strøm was elected as a member of the Royal Swedish Academy of Science on a proposal from Carl Linne. In the book, he *inter alia* gave the first detailed description of the Norwegian coastal cod fishery including all equipment used. He also gave a very precise description of some aspects of whale feeding behaviour as can be seen from the extracts from Chapter 5 below.

English translation

Chapter 5: On the fisheries in Sunnmøre

....Several kinds of whales occur here, including the humpback whale, which is of greater size than the other kinds and has a hump or large bulge on its head.....

Rorqual whales are occasionally seen on their own, but also in company with the species mentioned above. It has an upright fin not far from the tail and is without doubt the "fin-fish" described in Mr. Egede's writings....

The herring whale is a small kind of whale that resembles the rorqual whale and has for many years driven the herring from the open sea towards our coasts every spring....

The killer whale is another small whale, which is easily recognized by the narrow, pointed fin about six feet high on its back. It is also called 'pole-whale' because of the tall, narrow dorsal fin, which resembles a post or an upright pole. And because it is a great hunter of common seals, it is also known as the 'seal-master', although it could equally well be called the 'porpoise-master', since it sometimes chases porpoises right up on to the shore.

Huge numbers of these kinds of whales, especially herring whales, appear every year just after Christmas and shortly before the arrival of the spring cod. They chase the spring herring through Bresund in indescribable numbers, and provide a fascinating spectacle as well as the opportunity for rich catches of herring. At one moment, they surface to breathe and expel jets of air through their blowholes, making an explosive sound; the next moment, they vanish down into the depths again, striking the water surface sharply with the tail as they do so, or diving head first with the tail pointing straight up into the air. Now they can be heard howling and bellowing across the water, now there are strange underwater squeaks and whistles*. Sometimes two whales can be seen mating; sometimes they breach, leaping into the air so that the whole body is a fathom or more above the sea and then falling back into the water with a great splash. But the real tragicomedy is played out with the herring, which they chase almost constantly. Often, three or four whales help each other to herd the fish and surround them, so that they cannot escape, since the whales are so close that they touch each other and swim upright in the water with open mouths, so near the surface that you can easily see them swallowing the herring. In this way unbelievable numbers of herring are not only swallowed but also suffocated° by the whales, which are sometimes so eager in the chase that they swim straight on to the shore. Usually they seem to manage to free themselves and swim off again. However, it happened a few years ago that one of the fin whales remained stranded until people were able to attach it with ropes and cables and thus capture it. In order to suffocate and kill the whale, they dropped a number of stones into its blowhole. It blew them high into the air with a loud blast, but finally had to give up the struggle.

Original text

Femte Kapitel: Om Søndmørs Fiske

Qval eller Hval forekommer her af adskillig Slags, saasom Tue-Qval, som er større end de andre hvale, og har en Tue eller stor Pukkel paa Hovedet.....

Rør-Qval sees enten af og til for sig selv, eller og i Selskab med de forbemeldte Hvale. Den har en opstaaende Finne hen ved Sporen og bliver uden Tvivl Hr. Egedes Finne-Fisk.....

Sild-Qval er et Slags smaa Hvale, som meest ligner Rør-Hvalen og har nu i mange Aar drevet Vaar-Silden fra Havet ind til vore Kyster.....

* This type of sound, which is locally known as fish-cries, is generally attributed to the whales, and is very unpleasant to listen to, especially for those who are unused to it or for the ignorant, who are often terrified by it.

° A few years ago, for instance, whales killed such huge numbers of herring near the farm Alnæss in Borgund parish that after the dead fish had sunk to the bottom of the sea, a large amount of oil continued to rise from them for several months, creating a dead calm even in strong winds. Many fishermen sailing past, who knew nothing of the reason for this, were not only amazed but sometimes even in danger, because squalls from land could catch their sails before they were visible on the water.

Den saa kaldte Staur-Hynning er ligeledes et Slags smaa Hvale og kiendes let deraf, at den har en smal, spids og vel 3 Alne høi Finne paa Ryggen. Den kaldes Staur-Hynning af sin høie og smale Ryg-Finne, som lignes ved en Staur): en opreist Stage; men fordi den er Kobbens store Forfølgere, kalles den og af nogle Kobbe-Herre, skiønt den med samme Ret kunde bære Navn af Nise-Herre, da den undertiden jager Nisen op paa det tørre Land.

Af disse Hvale, fornemmelig af Sild-Qvalene, indfinder sig aarlig et utroligt Antal, strax efter Juul og nyelig før Vaar-Torskens Ankomst, da de jage Vaar-Silden herind igiennem Breesund i en ubeskrivelig Mængde, og give ei alene Anledning til en overflødig Silde-Fangst, men og til adskillige fornøielige Syner; thi snart sees de at stikke op af Søen for at faae Luft, og at puste Luften fra sig igiennem Luft-Hullene med en hæftig Lyd, snart at stikke ned i Dybet igien og ved Nedfarten at Sporstøde (som det her kaldes) eller at støde ned med Hovedet og vende Sporen lige op i Veiret. Snart høres de at skraale og brøle over Vandet, snart at pibe og give en forunderlig Lyd fra sig under Vandet (*). Undertiden sees de at parre sig med sine Mager; undertiden løbe de Søeløst, som man siger, det er, springe med sin hele Krop 1 Favn eller mere op over Søe-Brynen, og falde ned igien med et hæftigt Knald. Men den rette Tragi-Comoedie spilles med den arme Sild, som næsten uophørlig forfølges, og det gemeenlig saaledes, at 3 eller 4 Hvale hielpe hinanden i at giænne og indslutte den paa alle Sider, at den ei kan undløbe, da de støde til hinanden og med aabne Kæfte stikke alle paa een Gang lige op i Veiret, og det saa høit, at man tydelig nok kan see dem sluge Silden i sig. Paa saadan Maade bliver en utrolig Mængde Sild ei alene opsluget men og qvalt (°) af Hvalene, som i at forfølge den ere undertiden saa hidsige, at de løbe lige ind paa Land; og skiønt de vel som oftest komme løse igien, saa hænde det sig dog for nogle Aar siden, at een af de saa kaldte Rør-Qvale blev staaende paa Grund, indtil man med Toug og Liner fik den fastgiort og fangen. For at faae den qvalt og dræbt, kastede man i dens Blæster eller Blæse-Huller en Deel Stene, hvilke den med et hæftigt Skraal pustede høit i Veiret, men maatte dog omsider opgive Aanden.

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(*) Dette Slags Lyd, som hos os egentlig kaldes Fiske-Liv, tilskrives i Almindelighed Hvalene og er meget fæl at anhøre, i sær for de uvante eller ukyndige, som derved ofte ere satte i Skræk.

(°) Saaledes blev for nogle Aar siden, ved den Gaard Alnæss i Borgunds Sogn, af Hvalene drebt saa stor en Mængde Sild, at, da samme sank ned paa Søe-Bunden, deraf i nogle Maaneder opsteeg en stærk Fedme, som dæmpede Bølgernes Kraft og foraarsagede et Havblik endog i stærk Blæst; saa at mange forbieseilende Fiskere, som ikke vedste Aarsagen dertil, bleve ei alene satte i Forundring, men og undertiden i Fare, saasom de fra Landet faldende Kaste-Vinde ofte laae i Seilet, førend de kunde mærkes paa Vandet.

An examination of the current knowledge on the stock structure of sperm whales (*Physeter macrocephalus*) worldwide[1]

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ABSTRACT

There is no clear picture of the worldwide stock structure of sperm whales in spite of a great deal of effort, especially in areas where there has been substantial modern whaling. Techniques to examine stock structure have included: the interpretation of catch and sighting distributions and catch per unit of effort; morphological examinations; biochemical and genetic analyses; comparisons of life history parameters; mark-recapture using artificial and natural marks; the occurrence of parasitic infestations; and the comparison of vocal repertoires. Methods which depended on the whaling industry were often limited by unequal distribution of effort and lack of standardised collection methods. Also, most analyses failed to consider the effect of social groupings. Recent research, independent of the whaling industry, has addressed some of these problems. However, the results are equally inconsistent. Variation between the results of different studies can be explained, at least partially, by the temporal scales of the measures used. In general, groups of female and immature sperm whales appear to be restricted to ranges of about 1,000km over periods of 10 years or so. Occasionally, they move much further. Male ranges are generally larger, especially latitudinally. Occasional movements across, and sometimes between, ocean basins seem to have resulted in remarkable global genetic uniformity. To effectively conserve and manage sperm whales in the face of substantial anthropogenic disturbance, we need new and good information on modal and exceptional movement patterns over a range of timescales.

KEYWORDS: SPERM WHALE; DISTRIBUTION; STOCK IDENTITY; MOVEMENTS; MORPHOMETRICS; MIGRATION; PHOTO-IDENTIFICATION; GENETICS; MARKING; MANAGEMENT

INTRODUCTION

This paper reviews published information on the worldwide stock structure of sperm whales (*Physeter macrocephalus*). It examines the range of methods employed in these studies and considers their effectiveness and shortcomings. The sometimes contradictory conclusions drawn from the same data in the same ocean are summarised. Finally, an overview of general conclusions reached with respect to sperm whale stock structure on a global basis is presented. To elucidate such a review, it is useful to begin with a discussion of what is meant by a 'stock'.

In his review of stock boundaries used by the International Whaling Commission (IWC), Donovan (1991) noted the importance of defining stocks in the context of the use to which they were being put. The term has been used variously to describe management stocks, biological stocks or geographical divisions, although clearly none of these can be taken in isolation. Stocks have been regarded, from an exploitation point of view, as population units that can be managed effectively (Donovan, 1991). Successful management must necessarily include some knowledge of the biology of a stock. Distinct sets of animals may occupy a single area at different times of the year and thus be temporally and genetically, though not geographically, discrete (possibly the case for equatorial populations of sperm whales as discussed in Rice, 1977). Additionally, members of different genetically distinct stocks may congregate in the same area at the same time, for example, on a feeding ground (perhaps the situation for Asian and American stocks of male sperm whales in the North Pacific described in Ohsumi and Masaki, 1977). In both of these cases, whaling in a localised region may have unexpected consequences. Unfortunately, for most whale species, there is a shortage of sufficient information to delineate biological stocks (Donovan, 1991).

In addition, there is no consensus on the degree of overlap or interchange between two 'separate' stocks that is acceptable before they are treated as a single stock. For example, Dufault and Whitehead (1993) defined 'stocks' in the eastern equatorial Pacific to be geographically distinct if they did not undergo random mixing over a two year period; however movement of a few percent per year from one stock area to the other was observed. Kasuya and Miyashita (1988) described stocks in the western North Pacific as separate if there was not a 'significant' (which they did not define) number of marked individuals moving between the two areas. They deemed movement between each of the stock areas and the intervening latitudes as unimportant and their suggested stock boundaries overlapped considerably. Best (1969b) and Gaskin (1973) described stocks which they thought could be considered distinct for management purposes although they presumed that interchange between them would likely make them genetically indistinguishable.

The current[2] IWC sperm whale management divisions (Donovan, 1991) comprise: the entire North Atlantic (~3,500km across); western (~4,000km across) and eastern (~2,000km across) divisions in the North Pacific separated by a rather controversial line; and nine divisions along lines of longitude in the Southern Hemisphere from the equator to the pack ice (ranging from 3,330-7,770km wide at the equator, to 1,110-2,590km at 60°S). The extent of any shore-based whaling operation was usually less than the area of a single management division due to a limitation in the distance whalers could travel from coastal stations. In contrast, pelagic whalers could take sperm whales from both sides of the North Pacific or from any of the nine stock divisions in the Antarctic.

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[1] A version of this paper was submitted to the IWC Scientific Committee as SC/49/O 7.

[2] Although 'current', this is largely by default. The IWC Scientific Committee has not reviewed sperm whale stock divisions for over a decade and sperm whales have not been caught in the Southern Hemisphere or the North Atlantic since 1981, or in the North Pacific since 1988.

In most studies examined in this review, the word 'stock' was used without formal definition, although, since the majority of studies were carried out in a whaling context, the concept of management stocks was implied. In this paper, the term 'stock' will be used as presented in the papers reviewed, usually referring to those animals caught from a specific station (in the case of coastal whaling) or within a specified region (in the case of pelagic whaling).

In recent years, the IWC Scientific Committee has concentrated on developing a 'Revised Management Procedure' for baleen whales (see Donovan, 1995). The fact that it has not considered sperm whales is in recognition of the difficulty in managing a species with such complex social organisation and behaviour.

Sperm whales are the most sexually dimorphic of the large whales, with males reaching lengths of 18m and females 12m. Males grow more rapidly than females beyond the age of four and there is evidence that their growth rate may accelerate at the onset of puberty which occurs at 11-12m or 19-20 years. Conversely, female growth rates slow down after sexual maturity which they attain at 8-9m or about nine years of age. Females attain physical maturity around 11m (28-29 years) and males at 15-16m or 35-45 years (Best, 1970). Females from the Northern and Southern Hemispheres are believed to be six months out of phase in their breeding cycles with peaks in ovulations from April to June in the North and October to December in the South (Best *et al.*, 1984). There is no evidence of seasonal cycling in spermatogenic activity in males (Best, 1969a; Mitchell and Kozicki, 1984) although there may be seasonality in testicular androgen production (Best, 1969a). Sperm whales are widely distributed throughout all deep (>1,000m) oceans of the world (Rice, 1989). Groups of adult females and their immature offspring of both sexes reside year-round in tropical and subtropical waters limited roughly by the 15°C sea surface isotherm and rarely range beyond 45-50°N or 40°S (Rice, 1989). These groups consist of approximately 20 individuals (Best, 1979; Whitehead *et al.*, 1991) from one or more permanent matrilineal units. Individuals from different units come together for periods of days (Whitehead *et al.*, 1991) or possibly much longer (Richard *et al.*, 1996). Males leave their natal groups at very approximately 6 years of age, ranging further poleward and becoming increasingly solitary as they age (Best, 1979; Richard *et al.*, 1996). Large mature males are commonly found right up to the edges of the polar pack ice. These large males, older than about 25 years, return to warmer waters to breed (Best, 1969a) on a schedule which is unknown. Distinctive features of the biology of sperm whales, such as the different latitudinal distribution of the sexes and the permanent groupings of females, are important considerations in trying to try to understand the stock structure of sperm whales.

TECHNIQUES USED TO STUDY STOCK STRUCTURE

Donovan (1991) considered a number of techniques and data sources that have been used in stock identity studies. These include: catch distributions; sightings distributions; mark-recapture data (using both artificial and natural marks); morphology; biochemical/genetic data; pollutant and parasite burdens; differences in life history parameters; and compatibility with models. These are discussed below with special reference to sperm whales.

Catch distributions

The largest data sources available relevant to questions of stock structure of sperm whales are catch data. The Townsend charts (Townsend, 1935), compiled from American whale-ship logbooks, depict the locations of whaling vessels during 36,908 sperm whale catch events worldwide between 1761-1920. These charts were employed by Bannister and Mitchell (1980), Best (1969b), Gaskin (1973) and Kasuya and Miyashita (1988) in their assessments of sperm whale stock structure. Kasuya and Miyashita (1988) also included catch locations representing more than 100,000 individual whales during the period 1940-1986. Thus, their analyses were based on a great deal of information over a rather long time period. Catch positions are available for almost all sperm whale catches since 1930, although the official data submitted by the USSR are now known to be false (e.g. IWC, 1999).

The use of catch distributions to elucidate stock structure has been criticised for being misleading unless effort is also considered (Best, 1975; Donovan, 1991). Bannister and Mitchell (1980) achieved this by also examining the charts of Maury (1851 *et seq.* cited in Bannister and Mitchell, 1980) which provide a measure of effort for 18th and early 19th century American whalers. Ohsumi and Masaki (1977) and Tillman (1977) presented analyses of catch per unit effort (CPUE) in their evaluations of North Pacific stocks.

Mark-recapture programmes

The marking of sperm whales using the 'Discovery'-type mark (a 23cm long stainless steel tube of 1.5cm diameter with a lead tip, fired from a modified 12-bore shotgun) began in 1934 (Rayner, 1940). Numbered marks were fired into whales at known geographical locations. Marks were recovered if the whale was subsequently killed and the mark found. Up to 1979, 3,558 sperm whales had been marked in the Southern Hemisphere under the USSR and international marking schemes (Brown, 1981). A total of 4,648 had been marked in the North Pacific by the Japanese and Soviet marking programmes as of 1980 (Ivashin, 1983). No large-scale marking programme was undertaken in the North Atlantic.

Any thorough examination of mark-recapture data must consider the level of effort of both marking and recovery (Donovan, 1991). A major weakness in using marking data for the examination of stock structure, was the general failure to distribute the marks widely (Best, 1975). For example, 50% of animals marked by Japan and the USSR in the North Pacific were marked in waters adjacent to the Japanese coast and the Kuril Islands and 67% of Soviet and 79% of Japanese recoveries were in this same area (Ivashin, 1983). In addition, doubt has been cast on the validity of the Soviet data (e.g. Best, 1989; IWC, 1999) requiring that caution be used in data interpretation. Discrepancies include marks reportedly fired at one species but recovered in another (e.g. Kasuya and Miyashita, 1988).

Another shortcoming was the low recovery rate of marks (e.g. the 3-7% reported by Ivashin, 1981; 1983) when expressed as the number of recoveries as a percentage of whales estimated to be successfully marked. Thus, the information gained may be considered small in comparison to the effort expended. A substantial number of mark recoveries exist for the North Pacific (Ivashin, 1983; Kasuya and Miyashita, 1988) and the Southern Ocean (Brown, 1981; Ivashin, 1981) although recovery effort also has been quite localised, especially in the North Pacific. In the North Atlantic, Aguilar (1985) used the recovery of a single Discovery-type mark plus the recoveries of two hand harpoons, lost when animals were struck but then escaped, to provide a view of the stock structure in this region where little other information exists.

Recently, the idea of using mark-recapture to reveal stock structure of sperm whales has been applied to photographically identified individuals in the South Pacific (Dufault and Whitehead, 1995). This technique has a number of advantages over Discovery-type marking programmes. The most important is that it allows for the possibility of multiple recaptures of the same individual since recapture is not dependent upon the death of the animal and the consequences of recapturing an animal shortly after marking disappear. The technique can be employed regardless of whether any whaling is taking place and can thus be used during the current hiatus in commercial whaling to provide a better understanding of stocks and, thus, better ability to manage them should whaling on sperm whales ever be resumed. At present photo-identification studies of sperm whales are rather localised, but it is of course possible to distribute effort more widely.

Morphological comparisons

Morphological (and often, therefore, genetic differences) can be of value for determining stock differentiation. Past morphological studies of sperm whales were often intensive and involved substantial sample sizes and large geographic ranges. A common technique was to compare the incidence of different forms of a given external character (e.g. colour pattern, type of fluke notch or the number of erupted teeth or dorsal humps of whales from different areas—see Best and Gambell, 1968; Clarke *et al.*, 1968; Veinger, 1980; Berzin and Veinger, 1981; Dufault and Whitehead, 1998). Internal characters (e.g. the shape of the spleen and number of sternal ribs, Berzin and Veinger, 1981) have also been used, as have characteristics of the tooth structure (Klevezal' and Tormosov, 1971). Observer subjectivity in the interpretation of many of these characters is problematic and there has been a general difficulty in finding an easily identifiable and quantifiable character which gives a definitive stock distinction (Donovan, 1991). This is particularly true for sperm whales, which for the most part, are remarkably similar in the different oceanic regions of the world (Best and Gambell, 1968; Clarke *et al.*, 1968; Gambell, 1972).

Some studies used morphometrics (e.g. skull measurements and total body length) rather than presence or absence of characters. For example, Clarke and Paliza (1972) compared growth coefficients (α) from the allometry equation, $y = bx^{\alpha}$ (where x is total length and y is a specific proportion), for measurements from several oceanic regions and Machin (1974) applied canonical analysis to the same set of data. The availability of sufficient data from the various regions was a limiting factor in these studies.

Biochemical and genetic analyses

In recent years biochemical and genetic analyses have become important in stock identity studies (e.g. see Hoelzel, 1991). There are to date, however, few studies in which this has been undertaken for sperm whales. Early biochemical analyses involved comparing blood types of individuals from different regions (Cushing *et al.*, 1963; Fujino, 1963). This method provided evidence for stock distinctions but there were numerous potential difficulties such as haemolysis and contamination of samples (Best, 1975). Later, allozyme studies on Pacific sperm whales (Wada, 1980) provided similar results to those of Fujino (1963).

A potentially important feature of such studies is that analyses must consider the social organisation of sperm whales. Females and immatures travel in permanent groups within which there is substantial genetic similarity (Richard *et al.*, 1996). Thus, any dataset including more than one member from any group is not independent, and statistical tests for heterogeneity that assume independence of samples (such as ANOVA) will be invalid. This is especially the case when sample sizes are small.

The first studies of sperm whales that examined DNA directly were those of Dillon (1996) and Lyrholm *et al.* (1996) who analysed mitochondrial DNA (mtDNA) control region sequences using DNA extracted from sloughed skin, samples collected using biopsy darts or tissue archives. These have been followed by research using highly variable nuclear microsatellite markers (Lyrholm *et al.*, 1999). Sequencing studies have found significant heterogeneity among social groups and rather little geographical structure (Dillon, 1996; Lyrholm and Gyllensten, 1998; Lyrholm *et al.*, 1999). Lyrholm *et al.* (1999) discuss the important finding that, in their studies, populations of sperm whales in different oceans are discriminated using mtDNA control region sequences which are maternally inherited, but not using nuclear markers which are inherited from both parents. Given the more extensive migrations of males than females, this finding is not unexpected. However, as mtDNA in sperm whales has particularly low diversity (Lyrholm *et al.*, 1996), a consequence is that these markers give rather little information on stock structure. This is in contrast to other cetacean species such as white whales, *Delphinapterus leucas*, (O'Corry-Crowe *et al.*, 1997) or humpbacks, *Megaptera novaeangliae*, (Baker *et al.*, 1993) where significant geographic structure has been found using mtDNA and similar sample sizes.

Other techniques

Parasitology

There do not appear to be any regional differences in the external parasites of sperm whales which can be used for stock delineation aside from latitudinal differences in cyamid species infestation and the presence of a diatom film which are merely indicative of the segregation of males to Antarctic waters (Best, 1979). Species of cyamids, copepods, barnacles and diatoms show no predilection for a particular ocean (Best, 1975). There is, however, some evidence that internal parasite fauna varies on a broad geographic basis (Berzin, 1972). Dailey and Vogelbein (1991) used helminth species of the genus *Corynosoma* to suggest the possibility of stock discrimination in the Antarctic although their sample size was too small to make firm conclusions.

Pollutants

Aguilar (1987) reviewed the use of pollutant burdens in the context of stock identity but this approach has not yet been applied to sperm whales.

Life history parameters

Comparisons of life history parameters such as pregnancy (Ohsumi and Masaki, 1977) and mortality (Holt, 1980) rates are another method that has been used in stock structure analysis. Potential problems of these studies include calculating parameters with suitable confidence limits to detect differences and, as with many other techniques, obtaining representative samples (Donovan, 1991).

Occurrence of markings

Marks caused by environmental agents such as predators, which may vary between regions depending on the levels of these agents, have been used to investigate stock separation. For example, the incidence of fluke damage has been compared between sperm whales from different locations (Berzin and Veinger, 1981; Dufault and Whitehead, 1998). Although the former study provided some evidence of differences between regions of the North Pacific, observed differences in the latter study could be accounted for almost entirely by variation between social groups and had little geographic foundation. Thus, the validity of results in the earlier study are called into question since the investigators in this study did not consider social grouping.

Vocal repertoires

Sperm whales produce patterned series of clicks, known as codas, which are used in communication (Watkins and Schevill, 1977). Coda repertoires may be different in different regions depending on their degree of isolation from one another and, thus, may indicate stock separation. Weilgart and Whitehead (1997) investigated differences in coda repertoires between sperm whales of the South Pacific and Caribbean on various spatial scales. These analyses confirmed increasing levels of dissimilarity with increasing distances which may be useful for the examination of stock separation.

Model fitting

In an attempt to settle the controversy over the dividing line between North Pacific stocks, Cooke and de la Mare (1983) used length distributions of whales caught in potential stock regions to find which proposed division best fit their model. One major problem with this technique is the assumption that the model and the data it uses are accurate (Donovan, 1991); for example, with respect to data, there are indications of misreporting of catch lengths (e.g. Best, 1989).

RESULTS OF STOCK STRUCTURE STUDIES

Despite the importance of stock identity to sperm whale management, relatively few studies were designed with the objective of addressing stock identity. Most of the data used were standard data collected during whaling operations (e.g. catch, sightings and CPUE distributions). Genetic studies were poorly developed during the peak of sperm whaling.

Within-ocean comparisons

North Pacific

As a result of the need to manage whaling operations, (e.g. both Japan and the former Soviet Union took large numbers of sperm whales), a considerable amount of time has been spent trying to elucidate the stock structure of sperm whales in the North Pacific; despite this, there is no clear picture to date. While it is likely that some stock segregation exists, it is unlikely that any stocks are completely discrete; the degree of any mixing is unknown. The exact number of stocks in the North Pacific is also controversial and the location of a boundary dividing management stocks has been the subject of much debate (see Donovan, 1991).

Catch and sightings data have shown discontinuities in distributions between western and eastern regions (Ohsumi and Masaki, 1977; Bannister and Mitchell, 1980; Kasuya and Miyashita, 1988) and latitudinally between different areas within the west (Bannister and Mitchell, 1980; Kasuya and Miyashita, 1988). CPUE data were found to show differing trends in western, central and eastern regions of this ocean (Tillman, 1977), although the interpretation of falsified Soviet data is no longer applicable. Mark-recapture studies have provided an abundance of markings and recoveries from the same area along the coast of Japan suggesting the possibility of some site fidelity (Ohsumi and Masaki, 1977; Ivashin, 1983; Kasuya and Miyashita, 1988) but the concentration of effort in this region is a confounding factor. Despite the level of effort in other areas of the North Pacific, instances of long-distance latitudinal and longitudinal movements have been found. Some morphological differences have been suggested between western and eastern regions (Veinger, 1980; Berzin and Veinger, 1981) and between areas within the west (Machin, 1974). Finally, biochemical studies suggest heterogeneity in western (Fujino, 1963) and lower central (Wada, 1980) portions.

Most authors have considered stock separation in the North Pacific to be longitudinal with an unquantified degree of intermingling near stock boundaries and in the Bering Sea. Ohsumi and Masaki (1977) analysed catch distributions reported by IWC member nations during the 1954-75 period (over 200,000 animals) as well as almost 180 mark recoveries from Japanese whaling during the 1949-75 period. Based on a discontinuity in female distribution, they proposed two female stocks divided at 160°W. They presumed the same division for males and suggested that the central and northern regions are areas of intermingling of 'surplus' (i.e. not part of the breeding population) males from the two stocks. Of their 71 female mark recoveries, 67 were marked and recovered near the coast of Japan, while two of the remaining four show movement across the proposed boundary. Male mark recoveries demonstrate much longitudinal movement including that between western and eastern regions.

Using 305 marks recovered by Japanese and Soviet whalers between 1949-1980, Ivashin (1983) concluded that there were western and eastern migration routes for both sexes in the North Pacific, but believed that it was not possible to define a border between them. He did not consider there to be mixing of males from the American and Asiatic regions in the Bering Sea but rather that this was a feeding area for the western males. The single mark recovery between the American region and the Bering Sea was from a female, although it is thought that they rarely enter this area.

Other authors proposed a third, central stock based on a number of differences among the three regions. Tillman (1977) defined Asian and American stocks near their respective coasts with the bulk of the North Pacific animals belonging to a central stock. His comparison of CPUE trends over the 1949-75 period is problematic as he found that on occasions the Japanese and Soviet data revealed differing trends (this may be explained by the falsification of the Soviet data); interpretation of such data can be confounded by possible shifts in whaling interest unrelated to sperm whale abundance. His analysis suggested that central male and Asian female stocks thus defined showed some decline (the others did not). He also recognised the importance of stock identity assumptions to such analyses and recommended further effort towards better stock delineation.

Based on an essentially qualitative review of the incidence of certain morphological characters, Berzin and Veinger (1981) suggested three (western, central and eastern) 'populations'. The most notable differences were between eastern and western regions with the central region being sometimes more like the west and sometimes more like the east. The lack of: (1) statistical analyses; (2) separation of the data by sex; and (3) consideration of sperm whale social groupings, renders their findings questionable. In an analysis of fluke notch morphology between the three proposed regions, Veinger (1980) had in fact suggested that unequal harvesting of sperm whale groupings could account for within region between-year differences but had failed to consider this for between-region comparisons.

In addition to these much-debated longitudinal divisions, there is also evidence for latitudinal separation, at least within the western portion of the North Pacific. Kasuya and Miyashita (1988) found a gap in female distribution between 30° and 40°N in this region and proposed two latitudinally segregating female stocks in the west and a single stock in the east. Support for a similar division for males came from 20 adult male mark recoveries that had suggested Bering Sea, Kuril Islands/coastal Japan and eastern North Pacific segregation. Their stock boundaries varied with season and oceanographic conditions. Despite considerable overlap, especially between male and female stock boundaries, they believed that interbreeding between stocks was rare. Further evidence for latitudinal stock separation in the west comes from discontinuities in distribution and CPUE from historical whaling records (Bannister and Mitchell, 1980), differences in morphologies (Machin, 1974) between Japan and the Bonin Islands and the possibility of blood type differences between coastal Japan and the Aleutian Islands (Fujino, 1963).

The most recent genetic analyses found no significant differences between areas of the North Pacific in the mtDNA control region or microsatellites of sperm whales once social structure had been accounted for (Lyrholm and Gyllensten, 1998; Lyrholm *et al.*, 1999). Failure to consider this important feature of sperm whale biology casts doubt on many of the results of earlier studies.

South Pacific

Much less information exists for the southern portion of the Pacific. There is some evidence for stock separation from catch and sightings data (Gaskin, 1973; Berzin, 1978), mark-recaptures (Brown, 1981; Ivashin, 1981; Dufault and Whitehead, 1995) and vocal repertoire comparisons (Weilgart and Whitehead, 1997). However the available morphological (Clarke *et al.*, 1968; Clarke and Paliza, 1972; Machin, 1974) and genetic (Dillon, 1996) information does not suggest stock separation.

Gaskin (1973), examined sighting and catch distributions of almost 10,000 individuals from the western South Pacific. From this he believed that it was possible to define two separate management stocks off New Zealand, one to the west and north from the Tasman Sea to the Fiji-Tonga region, varying with the season, and a second to the east off the Chatham Islands, with an eastern limit to both stocks of 170-150°W. However, he also believed that interchange of males and some intermingling of breeding schools north of New Zealand would maintain genetic homogeneity between the two stocks. The limited number of mark recoveries from this area do not contradict his ideas (Brown, 1981; Ivashin, 1981).

In the eastern South Pacific, mark-recapture of photo-identified individuals suggests geographic distinctiveness between stocks of female and immature sperm whales north and south of about 10°S and between equatorial stocks off the Galápagos Islands and mainland Ecuador, although a limited amount of movement has been observed between these latter two areas (Dufault and Whitehead, 1995). This supports the work of Berzin (1978) who proposed a separate Galápagos population between 10°N and 10°S based on sightings distributions. In contrast, intensive and extensive morphological investigations, some involving the examination of over 2,000 individuals, found no differences between sperm whales caught off Peru (at Paita and Pisco) and those caught off Chile (at Iquique and Talcahuano) along the western coast of South America from the equator to about 40°S (Clarke *et al.*, 1968; Clarke and Paliza, 1972; Machin, 1974).

On a broad basis within this ocean, mark-recapture suggests little or no movement of female and immature stocks between western and eastern regions (Dufault and Whitehead, 1995). Stock distinction within the South Pacific is supported by significant differences in the vocal repertoires of groups of females and immatures from western, eastern equatorial (north of 10°S), and southeastern (south of 10°S) areas of this ocean (Weilgart and Whitehead, 1997). No broad regional distinctions were detected from either genetic or morphological analyses. In a comparison of mtDNA haplotype distribution of female and immature sperm whales from these same three areas, all of the variation could be accounted for by differences within and between social groups (Dillon, 1996). No geographic differences in fluke notch morphology throughout the South Pacific were found except those which could be explained by differences between social groups (Dufault and Whitehead, 1998). In a synthesis of data collected on vocalisations, genetics and fluke markings from a survey of sperm whales of the South Pacific (Whitehead *et al.*, 1998), social grouping was found to be the strongest determinant of variation in all these attributes. Except for some between-area differences in vocal repertoires, no geographic structure was apparent.

North Atlantic

In the absence of any large-scale harvesting of sperm whales in this ocean, there have been few attempts to examine their stock structure. Best (1975) reviewed the published sighting information from merchant and whale-marking vessels in this region. He concluded that there are concentrations on either side of the North Atlantic with a connecting band between 30° and 60°N. From this limited information he suggested that the sperm whales in this ocean should be considered as a single stock for management purposes.

Aguilar (1985) examined data on movements in this Ocean. He included published reports on the recovery of an Azorean hand harpoon in a male sperm whale caught off Iceland (Martin, 1982) and the recovery of one Discovery-type mark from Nova Scotia in a male caught by a Spanish shore station (Mitchell, 1975). He presented a further incident of the recovery of an Azorean hand harpoon, this time off Spain, and concluded that all of the available evidence suggested a single North Atlantic stock. Aguilar and Sanpera (1982) found a decreasing trend in the average lengths of males caught by both Spain and Iceland though they caution that this does not mean that the catches came from the same stock since they have all followed the same history of exploitation. Holt (1980; unpub.) had examined the lengths of sperm whales caught in the Iceland, Azores and Madeira, Norway and Faroes fisheries to calculate mortality rates. Despite the limitations of such an approach, and particularly the lack of statistical power, the fact that the estimated rates were all similar does not contradict the hypothesis of a single North Atlantic stock.

The scale and scope of genetic analyses in this ocean are, as yet, insufficient to reach any conclusions on stock identity. Dillon's (1996) comparisons of mtDNA haplotype distributions included samples from the Caribbean, the southwestern North Atlantic, the Azores, the Canary Islands and off Nova Scotia but these five geographic areas were represented by only six social groups. Therefore, although there were different haplotypes in different areas, it is impossible to distinguish between group differences and area differences.

South Atlantic

Best (1969b) examined sperm whale catch and sightings distributions in the South Atlantic. An apparent discontinuity in the central region led him to suggest that for management purposes separate stocks should be considered on the east coast of South America and the west coast of South Africa. However, he noted that mixing of males in the Antarctic and breeding schools in the central regions may make the two stocks genetically indistinguishable. There are little other data available for this region. The scant mark-recovery data mostly demonstrate long-distance latitudinal movement of both males and females up the western coast of South Africa (Brown, 1981; Ivashin, 1981) which does not contradict the idea of separate stocks. Interestingly though, Brown's (1981) data also show a movement from the Indian Ocean past the southern tip of South Africa to about 200km from the eastern coast of South America providing not only evidence of inter-ocean movement but of longitudinal movement across almost the entire width of the South Atlantic.

Indian

Bannister (1974) examined aerial sightings survey data and two mark recoveries for the eastern Indian Ocean and concluded that sperm whales off the western and southern coasts of Australia were part of the same stock. Subsequent mark-recovery data concur with this conclusion (Brown, 1981).

In the western region, Gambell (1972) used the CPUE of pelagic factory ships and two mark recoveries to propose that the stock of sperm whales fished off Durban, South Africa is of a local nature extending out to about 70°E. Best (1974) concurred with these two assessments but suggested an eastern limit to the east African stock of 60°E and proposed further that there is a central Indian Ocean stock between 60° and 90°E. Mark-recovery data agree reasonably well with these delineations although there exist instances of sperm whales crossing all of these proposed boundaries (Brown, 1981).

Antarctic

Females and their young rarely travel south of 40°S and so only large males are found in Antarctic waters. It is thought that large males may intermingle on summer Antarctic 'feeding grounds'. The degree of mixing and the possibility of site fidelity are as yet unknown. Most mark recoveries in the Southern Ocean showed principally latitudinal movements, but twelve of 93 marks recovered up to 1979 showed movement across the boundaries of the nine IWC divisions, including one movement from the Indian to Atlantic Ocean (Brown, 1981). Thus, the potential exists for intermingling in the Antarctic of individuals from the three oceanic regions.

Cushing *et al.* (1963) suggested the possibility that individuals in Divisions III and IV of the Indian Ocean region of the Antarctic may be of different stocks, based on their respective frequencies of each of four blood sub-types. Their assessment, however, was based on only 17 samples (12 of which were from Division III) making it impossible to draw any firm conclusions.

Dailey and Vogelbein (1991) found some evidence that helminth species of the genus *Corynosoma* may be unique to the Atlantic, Pacific and Indian Ocean regions of the Antarctic. In this study, two ($n = 35$) individuals from the Pacific area were infected with *C. bullosum*, 18 (n = unspecified) from the Indian Ocean were infected with *C. mirabilis* and a single individual (n = unspecified) from the Atlantic region was infected with *C. singularis*. There was no co-occurrence of more than one of these species in the same ocean area. Although such data are inconclusive, they at least suggest the possibility of inter-ocean distinctiveness of these parasites. Of these three species, Berzin (1972) referred only to *C. mirabilis*, noting it occurred primarily in the Indian Ocean and describing its distribution as Divisions III, IV and V of the Antarctic (i.e. from 0° east to 170°W) which includes portions of the eastern South Atlantic and western South Pacific. Although sample sizes are small, making any conclusions tenuous, the results are interesting, particularly given the absence of any geographic specificity of external parasites.

Between-ocean comparisons

It has been generally assumed that sperm whale stocks in different oceans (and in different Hemispheres within the Atlantic and Pacific Oceans) are discrete and mixing between oceans has been presumed to be extremely rare, if it occurs at all. However, in practice this is based on rather limited and inconclusive data (Table 1). The major evidence for distinctiveness between the three major oceans comes from the almost complete lack of inter-ocean mark recoveries (Best, 1969b; Brown, 1981; Ivashin, 1981). Other supporting evidence includes the internal parasite information discussed above (Dailey and Vogelbein, 1991); and the analysis of coda vocalisations (for the Atlantic and the Pacific) in which groups of female and immature sperm whales from the South Pacific and Caribbean were found to have significantly different vocal repertoires (Weilgart and Whitehead, 1997). Best and Gambell (1968) cite some morphological evidence that sperm whales from the Atlantic coast of South Africa differ from those from the Indian Ocean coast (the former generally have a higher incidence of light markings) but the authors noted that observer differences could explain the apparent dissimilarities.

Evidence to support the view that limited intermingling can occur between oceans is also provided from marking data. Movement between the North and South Atlantic has been shown by two males travelling distances of approximately 4,000 and 7,400km (Ivashin, 1981). The same author reported that a single female was found to have moved between the North and South Pacific (2°52'N,

Table 1

Summary of types of evidence that have been considered to either support or contradict the hypothesis that mixing between sperm whales from different oceans does not occur. Note that none of this evidence can be regarded as unequivocal.

For	Against
(1) almost all marking data	(1) 4 mark returns
(2) internal parasites	(2) external parasites
(3) morphology	(3) morphology
(4) growth coefficients	(4) growth coefficients
(5) vocalisations	(5) nuclear genetics
(6) mtDNA genetics	(6) mtDNA genetics

94°55'W to 4°40'S, 82°50'W), a distance of about 1,580km. A sperm whale of unidentified sex (the mark was recovered during the processing rather than the flensing procedure) was found to have moved from the South Indian to the South Atlantic Ocean around the southernmost point of Africa (Brown, 1981).

External parasite fauna seems not to differ worldwide. Cyamids of the species *Neocyamus physeteris* have been found infesting sperm whales of the North (Buzeta, 1963) and South Atlantic (Best, 1969a) as well as the North and South Pacific (Buzeta, 1963). *Cyamus catodonti* have been found on sperm whales from the North Atlantic and North Pacific (Buzeta, 1963) and also from the Pacific, Atlantic and Indian Ocean sectors of the Antarctic (Best, 1979). The other two species of cyamid described for sperm whales come from single whales in the Indian (*C. boopis*) and South Pacific (*C. bahamondei*) Oceans. The former was thought to be specific to humpback whales on which they have been found on many occasions and in many different regions and this occurrence on a sperm whale is thought to be exceptional (Buzeta, 1963). Data on other external parasites are scarce, but there do not appear to be any clear distinctions between oceans in either copepod, barnacle or diatom infestations (see Berzin, 1972).

Morphological comparisons have revealed little differences between sperm whales worldwide. Best and Gambell's (1968) examination of colour patterns, tooth eruption, number of mandibular teeth, number of dorsal humps, incidence of deformed mandibles and incidence of double teeth, led them to conclude that 'sperm whales throughout the world are remarkably similar in their external characters'. In a similar study of external characters, Clarke *et al.* (1968), found no evidence indicating that sperm whales from different oceans are in general different in the traits, but noted that more data were needed.

Analysis of growth coefficients (i.e. rates of growth of certain parts of the body relative to growth in body length) has proved equivocal. Clarke and Paliza (1972) compared growth coefficients (for a number of measurements for five regions of the body: head, trunk, flippers, flukes and dorsal fin). With respect to adult males, the authors found that animals from South Georgia and in the pelagic Antarctic were similar to each other and different from those in the other areas considered (Japan and the Bonin Islands in the North Pacific; Durban, South Africa in the Indian Ocean; and Paita, Pisco and Iquique in the eastern South Pacific). They found no differences between these other regions for males or females. From this they hypothesised that sperm whales from the Atlantic (the only ocean not included in their analysis) may be so different from other oceans that the Atlantic component in the animals from South Georgia and the Antarctic made them look similar to one another and different from all the rest. Critical to their analyses were assumptions made concerning the maximum proportion of physically mature individuals in their samples and of constancy in the growth coefficient of each character through the entire growth phase of an individual beyond eight or nine metres. These assumptions are based mostly (for the former) or entirely (for the latter) on samples from lower latitudes. However, the length distributions of the South Georgia and Antarctic pelagic samples when compared to the other regions (fig. 1 of Clarke and Paliza, 1972), show, perhaps unsurprisingly, that samples from these high latitudes represent the biggest males in the population; extrapolation from these regions may not be appropriate; their result may simply reflect a distinction between the largest, mature males and younger, smaller ones. Clearly, further samples from the Atlantic would be needed to confirm or refute this hypothesis.

Machin (1974) applied canonical analysis to Clarke and Paliza's (1972) data. Prior to a between-region comparison, Machin performed a principal components analysis on the measurements for individuals from each region to isolate those which were most informative. In his between-region analysis, however, insufficient data from some regions forced him to use only seven of the 27 possible measurements – and these seldom corresponded to those considered most informative. Unlike Clarke and Paliza (1972) he found three distinct female groups: Paita/Pisco/Iquique; South Africa; and Japan/Bonin Islands. However, sample sizes were small (< 10 for four out of six areas) so these conclusions should be treated with caution. In addition, as in many of the studies, no consideration was given to social groupings. Observed differences may reflect uneven sampling of groups if the growth coefficients were genetically determined. Machin's results were less clear for males, perhaps because the most-informative characters were better represented for females than males. A distinction was found between: South Georgia, South Africa, the Antarctic and the rest; Japan and the Bonin Islands; and between South Georgia/Antarctic and South Africa for the first three canonical variates respectively.

Neither Clarke and Paliza (1972) nor Machin (1974) provided features for practical distinction between individuals from different stocks. The former study found that males from South Georgia generally grew faster in the head region and slower between the dorsal fin and flukes than those at lower latitudes, whilst the latter found only overall differences in body proportions.

Three sequencing studies have examined oceanic differences in sperm whale DNA. Dillon (1996) and Lyrholm and Gyllensten (1998) both used control region sequences of mtDNA. These studies were similar in techniques used, sample sizes (182 *vs* 231 individuals) and geographic coverage (3 oceans each), and both considered social structure in their analyses, although Dillon sequenced more of the control region (600 *vs* 330 base pairs). However, whereas Dillon (1996) found no significant difference between oceans ($P = 0.56$ using nested analysis of molecular variance), the population differentiation found by Lyrholm and Gyllensten (1998) was highly significant ($P = 0.0007$ from an exact test). In contrast to their results with maternally-inherited mtDNA, Lyrholm *et al.* (1999) report negligible, and statistically insignificant, differences between sperm whales in different oceans using nuclear microsatellites, which are inherited from both parents. They conclude that movements between oceans have been more common among males than females.

DISCUSSION

General overview of distribution

Commercial whaling data have provided a great deal of information on sperm whale distribution (e.g. Townsend, 1935) but not stock identity. They show that sperm whales concentrated in certain areas (termed 'grounds' by whalers) of approximately 1,000km across that are often associated with oceanic islands or other areas where the depth drops quickly from the coast (Clarke, 1956). More recent studies have suggested that sperm whale concentrations are correlated with oceanographic features including high secondary productivity and steep underwater topography (Jaquet and Whitehead, 1996). Sperm whale stocks are commonly viewed as being of a local nature with most individuals remaining in or returning to the same grounds (Berzin, 1972; Gambell, 1972; Ivashin, 1983). However, some interchange is considered likely even between stocks which can be considered discrete for management purposes (Best, 1969b; Gaskin, 1973; Dufault and Whitehead, 1995).

It is generally thought that northern stocks of sperm whales do not interbreed to any large degree with southern ones, since female breeding cycles are six months out of phase (Best, 1974) and the socially mature males are only present with females during the respective breeding seasons. However, Clarke (1956) suggested that females moving between hemispheres could alter their breeding rhythm and Best *et al.* (1984) noted that spontaneous ovulations can occur outside a female's usual breeding cycle. In addition, the absence of evidence of seasonal cycles in spermatogenesis suggests that males travelling between hemispheres could breed with either northern or southern females. In summary, physiological data do not preclude genetic exchange between hemispheres.

Within the Northern Hemisphere, the Atlantic is largely separated from the Pacific by land rendering interchange between these two areas to be doubtful. In the Southern Hemisphere, it is unlikely that any but the largest males range far enough south to round the tip of South America (Rice, 1989) and thus the Atlantic and Pacific can be for the most part considered geographically isolated. Movement has been observed between the Indian and Atlantic Oceans around the southern point of Africa (Brown, 1981) and interchange may also be feasible between the Indian and Pacific Oceans (Clarke and Paliza, 1972; Rice, 1989) although there is, as yet, no proof that this occurs.

Marking data have revealed lengthy latitudinal movements by large males (Best, 1969b) as well as some extensive longitudinal movements within (Ohsumi and Masaki, 1975; Aguilar, 1985) and between (Brown, 1981) ocean basins. Thus, the potential exists for some genetic exchange over large geographic scales. However, the fact that the vast majority of mark-recaptures have been within the same ocean basin and usually within the same whaling ground suggests that such large-scale movements are rare.

Temporal scales of stock structure measures

The different methods of examining sperm whale stock structure provide insights on different timescales. Catch and sightings survey data, for example, provide a single data point within the lifetime of an individual. Particularly where effort covers a wide area and a long time period, such data are useful for demonstrating general patterns of where and when sperm whales are likely to be found and may be related to the suitability of the habitat. However, discontinuities in distribution do not necessitate complete segregation and such studies are unable to provide information on movements between concentrations of animals. For example, photo-identification data have shown that groups of females and immature sperm whales can travel distances of 40-55km within a 12 hour period during times of presumed low feeding success (Whitehead, 1996); they could thus travel between areas of preferred habitat separated by 1,000km or so in roughly 10-20 days. Male movements are likely in the same order of magnitude; three males in the Southern Hemisphere travelled 55-250km during three days between marking and recapture (Ivashin, 1981).

Discovery-type marking programmes can provide direct evidence of movements in that they provide information on the location of individual animals on two separate occasions. Recoveries have generally been made within 10 years of marking and, thus, give a medium timescale view of movements on the order of a single generation or less. Studies using mark-recapture of photo-identified individuals clearly have the advantage that they can generate multiple sightings of a single individual. To date, these studies are also based on medium timescales of 10 years or so. When sperm whale stock structure is examined over temporal scales of this magnitude, it is clear that stock delineation may not be a simple matter of drawing lines between concentrations of animals. Many exceptions to the general pattern of distribution begin to emerge, including not only short-distance (1,000km) movements between concentrations of animals, but also long-distance movements across and between ocean basins.

Studies of genetics, or of traits which are presumed to be genetically determined, present a perspective over the timescale of generations. When sperm whale stock structure is examined over this scale, few distinctions are evident. This implies that, on the timescale of generations, there may be enough mixing to make individual stocks indistinguishable. A single individual moving between populations per generation would be sufficient to prevent complete genetic differentiation between these populations (Slatkin, 1987). However, movement would necessarily have to be greater than this in order to prevent any detectable differences. That few obvious differences have so far been found in the genetics and morphologies of sperm whales worldwide implies that inter-oceanic movements may occur more frequently than has thus been detected, perhaps on the order of a few individuals every generation or so. Discrepancies between studies using maternally inherited mtDNA and those using nuclear DNA (contributed by both parents) suggest these movements are more common for males.

CONCLUSIONS

In summary, it seems that groups of female and immature sperm whales are usually restricted to ranges of about 1,000km over periods of a decade or so. Sometimes, they will move much further. Male ranges are, in general, larger, especially latitudinally. Long-distance movements across and, occasionally, between ocean basins have resulted in remarkable genetic and morphological uniformity in sperm whales worldwide, especially in biparentally-inherited genes.

To effectively manage and conserve sperm whale populations, information is needed on the likely geographical extent of the effects of local perturbations, be they caused by direct exploitation, anthropogenic environmental change or extreme natural events, such as El Niño. This requires knowledge of movement patterns over a variety of timescales, including not only the modal behaviour (normal geographical ranges over years, decades and lifetimes), but also the relatively uncommon long-distance movements which are vital in determining genetic structure and rates of recolonisation of depleted areas.

Such data could come from several sources. Satellite tags can give detailed movement patterns of individuals over periods of months (e.g. Mate, 1989; Dietz and Heide-Jørgensen, 1995), which could be particularly useful in tracing the breeding migrations of mature males, if sample sizes are sufficient. Photo-identification becomes especially valuable when a substantial portion of individuals from a given region is identified, as is now the case for the sperm whales off the Galápagos Islands (Whitehead *et al.*, 1997), and can be continued over long periods. For sperm whales, the logistics of wide-scale photo-identification are difficult due to their deep-water, cosmopolitan distribution, but a great deal of progress has been made and we may soon have useful information on movement patterns over periods of 10 years and more. Over longer timescales, the most useful information could potentially come from additional studies of highly variable genetic markers, such as microsatellites.

Once we have a reasonable picture of the modal and exceptional movement patterns of sperm whales over a range of timescales, we can begin to construct reasonably realistic population models. Such models could be based on traditional, or newly defined, stock boundaries, and include rates of interchange between stocks. Alternatively, basin-wide, geographically specific models incorporating the movement patterns of sperm whales could be constructed. As sperm whale movement patterns are related to feeding success (Jaquet, 1996; Whitehead, 1996), models incorporating density-dependent habitat selection (e.g. MacCall, 1990) may be particularly appropriate (Whitehead *et al.*, 1997).

In the absence of sufficient data to construct such models, knowledge of stock structure in sperm whales is constrained to be little better than anecdotal. This calls into question our ability either to manage any resumption of substantial sperm whaling, or to predict the population effects of a disturbance such as that caused by a large pollution event or epizootic. Alternative strategies that incorporate uncertainty in stock boundaries into a management procedure have yet to be explored in the case of sperm whales.

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Inferences on the dynamics of Southern Hemisphere minke whales from ADAPT analyses of catch-at-age information[1]

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ABSTRACT

The dispute over the last two decades in the IWC Scientific Committee as to whether inferences of utility for management purposes can be drawn from catch-at-age information for Southern Hemisphere minke whales is reviewed, particularly in the context of whether or not such data are able to reveal if this population was increasing prior to the start of major commercial harvests in the early 1970s. Butterworth *et al.* (1996) developed an ADAPT VPA estimation procedure to address this last question. This paper extends that procedure to take account of assumed separability of the fishing mortality matrix for the periods of the commercial and of the Japanese scientific take (although only for ages above 15 for the former). A base-case estimator is motivated from the many possible variants of the procedure, and applied to catch-at-age and survey abundance estimates for Areas IV and V, both separately and in combination. The survey estimates used include results from both international and Japanese research programmes. Bootstrap methods are used to estimate precision, and a number of sensitivity tests for the Area IV assessment are performed. Estimates are provided of the extent to which this precision is expected to improve given the further data to be collected before the end of the Japanese scientific programme (JARPA) as currently conceived; this is achieved by using the current Area IV assessment as a basis to develop an operating model of the population for evaluation (by simulation) of the information content of future data. The Area IV base-case assessment shows satisfactory behaviour under retrospective analysis, and is consistent with the separability assumptions made. It provides an estimate of 5.5%yr^{-1} (90% confidence interval [1.4%; 9.1%]) for the historic (increasing) trend in minke whale recruitment over the period 1947-1968 prior to the exploitation of this resource. The positivity of this estimate and the associated interval is robust to a number of sensitivity tests. The point estimate of this trend for Area V is larger, but less precisely estimated. Important implications (both qualitative and quantitative) for management of the resource that follow from these results are discussed. The point estimate of age-independent natural mortality M for Area IV is 0.057yr^{-1}. The root mean square error of this estimate by the end of the JARPA programme is estimated to be about 0.022yr^{-1} (much of this reflecting negative bias related to assumptions concerning the slope of the commercial selectivity-at-age vector for large ages). The point estimates of M for Area V, and for the two Areas combined, are lower. A notable result of the Area IV assessment is a marked drop in recruitment from 1970 to the mid-1980s, for which some possible reasons are advanced. Patterns of inter-annual change in recruitment (as distinct from overall trends) are well estimated from the data, indicating that the availability of catch-at-age data leads to the provision of a much finer probe to detect possible links between minke whale dynamics and environmental factors than would survey estimates of total abundance alone.

KEYWORDS: MINKE WHALE; TRENDS; MODELLING; RECRUITMENT RATE; INDEX OF ABUNDANCE; SOUTHERN HEMISPHERE; SCIENTIFIC PERMITS; DIRECT CAPTURE; SURVEY-VESSEL

INTRODUCTION

The question of whether inferences of utility for management purposes can be drawn from catch-at-age information for Southern Hemisphere minke whales has been in dispute in the Scientific Committee of the International Whaling Commission for the last two decades. Some 20 years ago, predispositions towards an M (natural mortality rate) value of about 0.1yr^{-1}, based on an interspecific relationship between M and maximum male length for cetaceans put forward by Ohsumi (1979a), led to the inference from these data (specifically from the slope of the descending limb of the catch curve -a plot of the log of catch numbers against age - which exceeded the value then used for M by about 0.04yr^{-1}) that this minke whale population had been increasing prior to exploitation (e.g. Ohsumi, 1979b). This, together with other evidence which at that time was considered to point in the same direction (e.g. minke whale earplug transition phase analyses which suggested a decline in the age at maturity prior to exploitation; Masaki, 1979[6]), contributed to the theory that Southern Hemisphere minke whales had increased prior to the start of (substantial) minke whale exploitation off Antarctica in the early 1970s. This inferred increase in numbers (and drop in the age at sexual maturity) was seen as a plausible response to the additional food made available to krill feeders through the earlier large reduction in numbers of other Antarctic whale species -the blue whale in particularby excessive harvests. Indeed, at the end of the 1970s, the IWC Scientific Committee had stated this as an established fact (IWC, 1980, pp.50, 99).

In the early 1980s, inferences from these catch-at-age data were used as a basis to estimate productivity levels and hence recommend sustainable catches for Southern Hemisphere minke whales (e.g. IWC, 1983, p.93). However, in a watershed debate at the Scientific Committee's 1984 meeting (IWC, 1985, pp.41, 77-8), it was agreed that the productivity estimates forthcoming from the two methods in use at that time to analyse the catch-at-age information

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[1] An earlier version of this paper was submitted to the IWC Scientific Committee as SC/M97/6.

[6] The reality of this decline was subsequently called into question (e.g. Cooke. 1985a) although more recent analyses using a longer time-series of data have strengthened the case that a real decline did occur (e.g. Butterworth *et al.*. 1997).

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should be rejected. These conclusions were reached primarily on the basis of contributions by de la Mare (1985a; b), which showed that the methods could produce unreliable results if minke whale natural mortality was age-dependent, and also argued that the high slope of the minke whale catch curve for large ages was plausibly attributed to an increasing natural mortality with age.

During that same period, Sakuramoto and Tanaka (1985; 1986) developed a multi-cohort model for the analysis of these catch-at-age data, the results from which suggested pre-exploitation annual rates of increase in recruitment of 3-4%. However, Cooke (1985b) countered that the values estimated were entirely dependent on certain assumptions made for the computations, such as the value used for natural mortality *M.* Further reservations raised about the approach (including the confounding of interpretation of the data by possible trends in selectivity-at-age) are recorded in IWC (1986, pp. 41, 68) and IWC (1987, pp.40, 69, 80-1).

In 1987, following the imposition of a moratorium on commercial whaling by the IWC, Japan proposed a feasibility study (see IWC, 1989b) for what came to be called the 'Japanese Whale Research Programme under Special Permit in the Antarctic' or JARPA. The Convention governing the IWC makes allowance for national Governments to issue such permits for catches of whales for scientific research purposes (e.g. see Donovan, 1992). JARPA incorporated both catches and sighting surveys of minke whales, which were to take place each austral summer season in the Antarctic, alternately in Areas IV and V (700E-130oE and 130°E-170°W, respectively, see Donovan, 1991). After two seasons of feasibility studies, JARPA proper commenced in Area IV in the 1989/90 season.

The primary purpose of JARPA was stated to be the estimation of the age-specific natural mortality of minke whales. This was to be achieved by obtaining representative samples of the age structure of the population through random sampling, combined with systematic sighting surveys. The programme was motivated on the argument that the main reason the Scientific Committee had failed to reach agreement in immediately preceding years on catch limit recommendations for Southern Hemisphere minke whales, had been its inability to agree upon the value of natural mortality and its age-specific patterns (IWC, 1988, p.139).

The validity of this argument was contested at the 1987 meeting of the Scientific Committee, as was the ability of the methodology proposed to estimate natural mortality (see IWC, 1988, pp.55-7, 139-49). Key contributions to these opposing views were provided by de la Mare (1989), who showed that simultaneous estimation of a time series of recruitment rates and age-dependent mortality rates was not possible from catch-at-age data alone. Further, de la Mare (1990) argued that even if, in addition, annual abundance estimates with a CV of 0.15 could be achieved, JARPA would not provide estimates of natural mortality sufficiently precise to determine historical recruitment trends or refine sustainable yield prediction, even if continued for 30 years. It may seem surprising to readers familiar with the behaviour of Virtual Population Analyses (VPAs) of catch-at-age data for fish stocks that historic (in contrast to recent) trends in recruitment are not automatically well determined because of the backwards convergence property of VPA. The reason is that such backwards convergence requires that the cumulative fishing mortality over the whole life-span of a cohort is reasonably high, but Southern Hemisphere minke whales have been too lightly exploited for this to be the case.

This dispute as to the utility of catch-at-age information, and particularly the further such information which has become available through JARPA's lethal sampling (without which information on ages cannot be obtained), for drawing inferences about the population dynamics of Southern Hemisphere minke whales, has continued unresolved to the present (see IWC, 1989a, pp.37-8; IWC, 1990, pp.64-6; IWC, 1991, pp.72-4; IWC, 1992a, p.73; IWC, 1992b, pp.263-4; IWC, 1995a, pp.81-2; and further papers referenced therein).

Butterworth and Punt (1990) entered this debate with the demonstration that, at least deterministically, the provision of further catch-at-age data through JARPA could resolve whether or not there had been an historic increasing trend in minke whale recruitment, given temporal invariance of selectivity-at-age (above a certain age) and natural mortality-at-age. Essentially this follows because an increasing recruitment trend cannot continue indefinitely, so that the large slope of the descending limb of the catch curve will decrease in time if there was an historic increase, but will remain unchanged if it reflects only age-specific natural mortality and selectivity effects. Butterworth and Punt (1990) used simulated age-structure data from a generalised operating model to assess the likely precision with which a crude VPA-like approach might be able to estimate such a possible historic increase rate. They concluded that it would be unable to discriminate an annual increase rate of 4% from zero even after 25 years of data. However, improvements to their estimator developed in Bergh *et al.* (1991a; b) gave more promising results, and they suggested moving to estimator tests based on the actual catch-at-age data available (from both JARPA and earlier commercial whaling).

In taking up this last suggestion, Butterworth *et al.* (1996) also introduced an ADAPT (Gavaris, 1988) approach for the joint analysis of catch-at-age and abundance survey data for these minke whales. A key feature of their implementation was to group the catch-at-age data into cells including a number of years and of ages - combinations of three years and three ages were chosen -to handle the problem of small sample sizes and (essentially by transformation of the time variable) to reduce the catch-at-age matrix to a size (in terms of these new 'age' groups) typical of that considered in most age-data-based fishery assessments.

Shortcomings of the Butterworth *et al.* (1996) approach were that it involved external specification of selectivity-at-age values for the most recent year analysed, and also that it assumed an absence of sampling variability in the catch-at-age data for that same year. This led to poor performance of the estimator, as demonstrated by the results of retrospective analysis[7] in Butterworth and Punt (1996), who therefore extended the original approach to estimate the selectivity-at-age vector for the scientific permit catches directly from the data, and to account for sampling variability, by assuming separability of the fishing mortality matrix for the period of the scientific catches. This led to greatly improved results on retrospective analysis.

This paper takes that extension yet further, by admitting separability for the fishing mortality matrix for the commercial catch above a certain age as well. It also takes

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[7] Retrospective analysis involves repeating assessments using only the data available up to some earlier year. and checking whether or not estimated trends in, say. recruitment remain similar to those of the current assessment (thus reflecting acceptable performance) rather than evidencing systematic deviations.

Table 1

The catches-at-age matrices for minke whales used for the analyses of this paper. Both commercial and scientific permit catches are included, with the matrices developed in terms of the procedures detailed in the Appendix. Each matrix is expressed in terms of combination years and combination ages (three-year groupings, where the notation is such that the three seasons 1969/70 to 1971/72 are referenced as 1971, and ages 1 to 3 as 2, etc.)

	Age																		
Year	2	5	8	11	14	17	20	23	26	29	32	35	38	41	44	47	50	53	Total
Area IV																			
1971	121	256	314	310	352	319	284	235	146	95	99	45	30	25	3	7	17	4	2,663
1974	820	1,508	1,773	1,716	1,423	1,261	895	723	470	345	170	110	92	18	15	13	7	0	11,358
1977	80	329	437	633	618	529	283	234	125	79	48	11	25	6	0	2	6	0	3,444
1980	213	493	626	730	776	751	596	469	294	228	138	117	64	47	36	23	18	0	5,617
1983	235	499	606	808	709	886	664	506	346	216	84	47	34	32	7	7	3	0	5,689
1986	68	181	330	478	598	676	598	539	358	234	116	92	51	20	15	6	0	0	4,359
1989	110	91	62	54	48	62	56	30	37	21	9	10	7	5	1	0	0	0	603
1992	48	35	38	28	18	19	20	15	19	14	12	8	4	2	2	2	1	1	288
1995	95	82	83	93	52	37	36	29	43	22	24	25	11	6	3	9	5	5	660
Area V																			
1974	21	62	129	133	131	89	74	48	30	3	10	4	0	0	0	0	0	0	734
1977	38	279	374	488	502	439	320	188	146	98	40	34	9	13	12	0	0	2	2,982
1980	58	179	323	344	395	464	264	246	259	198	84	81	37	23	26	25	0	0	3,006
1983	117	382	479	584	700	678	527	376	285	150	103	60	34	23	11	6	2	1	4,518
1986	61	151	202	307	357	497	426	314	275	164	75	64	15	14	3	4	2	3	2,936
1989	23	33	24	33	38	25	21	16	4	11	5	4	4	0	0	0	0	0	241
1992	33	55	65	70	58	56	57	59	52	35	26	21	16	8	5	2	0	1	619
1995	31	25	44	45	37	29	30	19	22	15	10	14	7	3	0	0	0	0	330

JARPA in addition to IWC/IDCR and SOWER[8] estimates of abundance into account in applying this extended approach to data for Area IV and Area V.

The paper first develops the data to be analysed, and then provides technical details of the estimation process advanced and of associated options which have been encoded. The choice of options for a 'base-case' estimator is motivated, and this is then applied to provide assessments for Areas IV and V both separately and in combination, together with associated bootstrap estimates of precision. A number of sensitivity tests are applied to the Area IV assessment, which is also used as the basis for simulation evaluation of the likely level of precision possible for some key population parameters (e.g. natural mortality, *M*) by the end of the JARPA programme as currently conceived (the 2003/04 season for Area IV).

Note that most of the analyses of this paper are based on the three-year-three-age grouping referenced above. The associated notation convention used refers, for example, to the three seasons 1969/70 to 1971/72 as '1971', and to ages 1 to 3 as age '2'. The words 'year/age' are used in the paper for both 'true' years/ages and 'combination' years/ages, with clarification provided in the text as to which is intended in cases where this is not obvious from the context.

DATA

The catch-at-age matrices used for the analyses of this paper are developed in the same way as for Butterworth *et al.* (1996). Details are given in the Appendix. Table 1 provides the results for both sexes combined for Areas IV and V separately, where these results are in terms of the combinations of three years and of three ages used as the base-case grouping in this paper.

Failure to use an age-length key in scaling the scientific catch age distribution upwards from numbers aged to numbers caught could introduce bias if ear-plug readability depends on animal age, because such scaling implicitly assumes that the animals aged constitute an unbiased sample from the age distribution of the whole catch (a problem which the use of an age-length key could circumvent). Table 2 gives results for readability as a function of length for the scientific catch from Area IV. There is some suggestion that there may be such an effect, with plugs for the smallest/youngest animals somewhat less likely to be readable (an average readability of 79% for animals < 8m, compared to 89% for larger animals) - a matter whose possible consequences for the analyses of this paper are addressed later.

Table 2

Readability (%) of minke ear plugs for total age as a function of animal length for JARPA samples from Area IV from 1987/88-1995/96 for males and females combined.

Body length (m)	Total sample	Readability
4.5 - 4.9	7	100
5.0 - 5.4	50	86
5.5 - 5.9	95	83
6.0 - 6.4	48	67
6.5 - 6.9	79	67
7.0 - 7.4	75	83
7.5 - 7.9	126	83
8.0 - 8.4	407	91
8.5 - 8.9	430	88
9.0 - 9.4	188	88
9.5 - 9.9	39	85
10.0 - 10.4	2	100

There are two sources of information for abundance estimates: the IWC surveys, and the survey component of JARPA. The estimates from these surveys used in this analysis, with associated CVs, are listed in Table 3. Because

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[8] The International Decade of Cetacean Research (IDCR) commenced in the mid-1970s. The major component of this IWC initiative came to be a set of annual surveys carried out off Antarctica, whose primary aim was the estimation of abundance of the Southern Hemisphere minke whale population. Every year since the 1978/79 austral summer season, from 2-4 vessels have undertaken sighting surveys in a region off Antarctica which has covered from 40-70 degrees of longitude, and generally most of the open ocean area from ice-edge to latitude 60°S, with abundance estimates evaluated from the observations made using line transect methodology. Since 1996/97, these surveys have fallen under the IWC's Southern Ocean Whale and Ecosystem Research Programme (SOWER). For the purpose of this paper, the IDCR and SOWER surveys are collectively termed 'IWC surveys'.

the analysis relies on comparability of such estimates over time, the IWC estimates used are those for 'equivalent northern boundaries' as developed for the 'additional variance' estimation of Punt *et al.* (1997). Although there have been IWC surveys in Areas IV and V subsequent to 1988/89, these have not covered the full extent of an Area in a single season. Pending agreement on how most appropriately to combine such estimates to reflect results pertinent to a complete single Area, they have not been taken into account in the analyses of this paper.

Table 3

Abundance estimates, with CV's in parenthesis, used in analyses in this paper. The sources of the various estimates and other pertinent details are given in the text.

Survey	Combination year to which applied	Estimate (CV)
Area IV		
IWC 1978/79	1980	68,381 (0.155)
IWC 1988/89	1989	58,215 (0.326)
JARPA 1989/90	1989	24,868 (0.168)
JARPA 1991/92	1992	25,951 (0.293)
JARPA 1993/94	1995	26,359 (0.161)
JARPA 1995/96	1995	21,213 (0.180)
Area V		
IWC 1980/81	1980	135,422 (0.216)
IWC 1985/86	1986	160,741 (0.187)
JARPA 1990/91	1992	77,560 (0.201)
JARPA 1992/93	1992	54,970 (0.189)
JARPA 1994/95	1995	84.230 (0.507)
Areas IV + V		
IWC 1978/79 + 1980/81	1980	203,803 (0.153)
IWC 1988/89 + 1985/86	1989	218,956 (0.162)
JARPA 1991/92 + $\left\{\begin{array}{l}1990/91\\1992/93\end{array}\right.$	1992	87,868 (0.131)
JARPA $\left.\begin{array}{l}1993/94\\1995/96\end{array}\right\}$ +1994/95	1995	107,746 (0.397)

The JARPA estimates of abundance based on SSV[9] data given in table 6 of Nishiwaki *et al.* (1997) have been used for this analysis. These were preferred to those based on the SV data because they provide a longer time series and are generally more precise. Nishiwaki *et al.* (1997) list a number of reasons why the JARPA estimates are not expected to be comparable to those from the IWC surveys (e.g. the former involve a form of closing mode survey, whereas the latter are standardised to passing (IO) mode). In particular, the JARPA protocol whereby survey starts from a pre-fixed position each day, whether or not survey of all the trackline to that point had been completed on the previous day, leads to undersampling of higher densities areas and hence a negative bias in JARPA abundance estimates compared to those from the IWC surveys (see Burt and Borchers, 1997 and IWC, 1998). Accordingly, this analysis treats the JARPA estimates as relative abundance indices, with the relative bias between the IWC and JARPA estimates being estimated in the model fitting process.

For the case where Areas IV and V are analysed together, combined abundance estimates have been developed by adding those for seasons relatively close in time (see Table 3). For the JARPA estimates in this case, combinations have been developed consistent with the combination-years chosen. In a three-year period, there are two JARPA estimates for one Area, and one for the other; the procedure used is to take an inverse-variance-weighted average of the first two, and then to add that result to the third. This procedure does mean, however, that the 1989/90 JARPA survey result for Area IV is not taken into account in this combined analysis.

ESTIMATION METHODS

The ADAPT estimator considered in this paper involves specifications for the population dynamics, the parameterisation of fishing and natural mortality, and the likelihood. Each of these components is considered in turn. Note that 'year' and 'age' as used below refer to 'combination year' and 'combination age' unless otherwise specified. To assist in giving illustrations to the reader, the specifications have been written for combinations at the three-year and three-ages level for Area IV, but could easily be generalised for other choices for these periods or for other Areas.

Basic population dynamics

The basic population dynamics are taken to be governed by the following equations:

$$N_{y+3,a+3} = (N_{y,a} - C_{y,a})\exp(-M_a) \qquad 2 \le a \le m-3 \qquad (1)$$

$$F_{y,a} = C_{y,a} / N_{y,a} \qquad (2)$$

where:

$N_{y,a}$ is the number of minke whales (normally both sexes combined) of age a present at the start of year y;

$C_{y,a}$ is the number of such whales taken during year y;

M_a is the (possibly age-dependent) rate of natural mortality;

$F_{y,a}$ is the actual rate of fishing mortality on animals of age a during year y[10,11];

m is the oldest age considered in the analysis (taken here, as in Butterworth *et al.* (1996), to be $m=29$ - sample sizes for larger ages are very small, and furthermore such ages are less reliably estimated because of the difficulties of counting large numbers of closely spaced layers in ear plugs).

Whale catches in the Antarctic are limited to a shortish period around the end of the calendar year, so that it is customary to model the population dynamics assuming a pulse fishery at the start of the year as in Equation (1). Strictly, this justification no longer holds when time-steps in excess of one year (as here) are considered. However, for the cases investigated here, both M and F are sufficiently small that Equation (1) still represents a reasonable approximation.

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[9] The JARPA Programme has incorporated both sighting-and-sampling (i.e. whale catching) survey vessels (SSVs), and (at a later stage) vessels dedicated to sighting surveys only (SVs).

[10] Note that although the $F_{y,a}$ and M_a as defined by Equation (2) apply to three-year periods, any numerical values will be quoted will be in units yr^{-1} (i.e. dividing the actual values obtained by 3), as is conventional (and more readily interpretable) practice.

[11] The word 'actual' is used here in the context of the assumptions being made that every animal in the catch is aged without error, so that given the assumptions of Equation (3), the difference between $C_{y,a}$ and $C^E_{y,a}$ is caused by sampling variability only. These assumptions are relaxed later in the paper where, for example, the consequences of possible ageing error are considered in sensitivity tests.

Model parameterisation

The parameters needed to compute the numbers-at-age matrix are the terminal actual fishing mortalities $\{F_{y,m}: y = 71,74..n\}$ and $\{F_{n,a}: a = 2,5,..m-3\}$. Fishing mortality is assumed to be separable (in expectation). Different selectivity patterns are assumed for the years of commercial and scientific catches:

$$F^E_{y,a} = \begin{cases} S^c_a F_y & \text{if } y < 89 \\ S^s_a F_y & \text{otherwise} \end{cases} \qquad (3)$$

where: S^c_a is selectivity-at-age for the period of commercial catches ($S^c_m = 1$);

S^s_a is selectivity-at-age for the period of scientific catches ($S^s_m = 1$);

F_y is the fishing mortality for year y on age m (i.e. the fully-selected fishing mortality in cases where $S^{c/s}_a \leq 1$ for $a \neq m$)[10]; and

$F^E_{y,a}$ is the expected rate of fishing mortality on animals of age a during year y, which differs from the actual rate $F_{y,a}$; the difference arises because the actual catch made ($C_{y,a}$) differs from that expected in terms of Equation (3) ($C^E_{y,a} = F^E_{y,a} N_{y,a}$) because of sampling variability[11].

Natural mortality is assumed to change linearly between ages 2 and 29, to be constant from ages 29 to 41, and to be infinite thereafter[12]:

$$M_a = \begin{cases} M_2 + \tau(a-2) & \text{if } 2 \leq a \leq 29 \\ M_2 + 27\tau & \text{if } 29 < a \leq 41 \\ \infty & \text{if } a \geq 44 \end{cases} \qquad (4)$$

One sensitivity test admits quadratic behaviour between ages 2 to 29. This dependence is specified by the three parameters: M_2, M_{29} and the age at which the parabola has a minimum (biologically a maximum would not seem realistic, as natural mortality would be expected to increase for both the youngest and oldest ages). A further set of sensitivity tests considers the possibility of time-dependence in M by generalising Equation (1):

$$N_{y+3,a+3} = (N_{y,a} - C_{y,a})\exp(-\tilde{M}_y M_a) \qquad 2 \leq a \leq m-3 \qquad (5)$$

where: $\tilde{M}_y$ is a factor related to the 'overall' level of natural mortality during year y, standardised by setting $\tilde{M}_{68} = 1$.

The values for the $\tilde{M}_y$ are pre-specified, rather than estimated.

For the case for which m is chosen to be 29, the total number of possible estimable parameters is therefore 38[13]:

(i) the eighteen terminal fishing mortalities: $\{F_{95,2}, F_{95,5}, \ldots, F_{95,26}\}$; $\{F_{71,29}, F_{74,29}, \ldots, F_{95,29}\}$;
(ii) the nine free selectivities-at-age for the period of commercial catches: $\{S^c_a: a = 2,5,\ldots,26\}$ where $S^c_{29} = 1$;
(iii) the nine free selectivities-at-age for the period of scientific catches: $\{S^s_a: a = 2,5,\ldots,26\}$ where $S^s_{29} = 1$; and
(iv) the two parameters which define the natural mortality schedule: M_2 and τ.

The associated computer code has been written to allow a variety of simplifications of this parameterisation, so as to reduce the number of parameters and hence achieve a sufficiently parsimonious model:

(a) natural mortality is independent of age (i.e. $\tau = 0$);
(b) the commercial catch information for ages 2 to 14 is excluded from the likelihood, so that it is not necessary to estimate $\{S^c_a: a = 2,5,..,14\}$;
(c) selectivity for the commercial catches is flat ($S^c_a = 1$) above age a^c_{flat} (reduces the number of parameters by $(29 - a^c_{flat}) / 3$);
(d) selectivity for the scientific catches is flat ($S^s_a = 1$) above age a^a_{flat} (reduces the number of parameters by $(29 - a^s_{flat}) / 3$);
(e) selectivity-at-age for the commercial catches for ages between 17 and a^c_{low} is the same (reduces the number of parameters by $(a^c_{low} - 17) / 3$);
(f) selectivity-at-age for the scientific catches for ages between 2 and a^s_{low} is the same (reduces the number of parameters by $(a^s_{low} - 2) / 3$);
(g) selectivity-at-age for the commercial/scientific catches changes linearly between age $a^{c/s}_{slop}$ and age 29, i.e.

$$S^{c/s}_a = 1 - \beta^{c/s}(29 - a) \qquad (6)$$

(reduces the number of parameters by $26 - a^{c/s}_{slop}) / 3$);

(h) for some of the years of commercial catch, the terminal fishing mortalities $F_{y,29}$ can be set by formula rather than treated as estimable parameters - the options possible are first

$$F_{y,29} = F_{y,26} \qquad \text{for } y = 71,\ldots y^* \text{ where } y^* \leq 86 \qquad (7)$$

and secondly

$$F_{y,29} = \alpha F_{y,26} \qquad \text{for } y = 71,\ldots y^* \qquad (8)$$

$$\text{where} \quad \alpha = \sum_{y=y^*+3}^{86} (F_{y,29} / F_{y,26}) / [(86 - y^*)/3]$$

i.e. α is the average F_{29} / F_{26} ratio for the other years of commercial catch.

Note that the choice of $m = 29$ together with an effective absence of catches prior to $y = 71$ means that recruitment ($N_{y,2}$) cannot be estimated further back in time than year $y = 44$ for Area IV. Given $C_{y,29}$ and estimates of $F_{y,29}$, the consequent estimates of $N_{y,29}$ from Equation (2) can be projected forwards as well as backwards along their respective cohorts using Equation (1), thus providing numbers-at-age estimates up to age 44. Note that this formulation therefore assumes the input $C_{y,a}$ values to be exact in terms of the equations for the dynamics, thus ignoring the variance associated with their estimation by scaling upwards, or using an age-length key based upon the lesser number of animals actually aged each year (see Appendix).

The likelihood function

The likelihood function contains contributions from three sources: the estimates of absolute abundance from the IWC surveys in Area IV in 1978/79 and 1988/89 (and, in principle, could include estimates from similar surveys in subsequent years); the estimates of relative abundance from the JARPA surveys; and the catch-at-age data. The

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[12] The natural mortality rates for ages 2-44 are also constrained to lie between 0.01 and 0.25yr^{-1} when treated as estimable parameters.

[13] This total omits the F_y parameters, whose explicit estimation is not required for the procedures following.

abundance surveys of the latter research programme are treated as providing relative rather than absolute abundance values for reasons discussed in the preceding section.

The contribution of the absolute (IWC) abundance estimates to the negative of the logarithm of likelihood function (ignoring constants) is given by:

$$\ell nL_1 = \sum_y \frac{1}{2(\sigma_y^N)^2}\left(\ell \mathrm{n} N_y^{obs} - \ell \mathrm{n} \hat{N}_y\right)^2 \tag{9}$$

where: N_y^{obs} is the abundance estimate for year y;

σ_y^N is the standard error of the logarithm of N_y^{obs} (approximated by $\sqrt{CV_y^2 + CV_{add}^2}$);

CV_y is the coefficient of variation of N_y^{obs};

CV_{add} is the 'additional standard error'[14]; and

$\hat{N}_y$ is the model-estimate of the 1+ abundance for year y[15]:

$$\hat{N}_y = \sum_{a=2}^{44} \hat{N}_{y,a} \tag{10}$$

The contribution of the relative (JARPA) abundance data to the negative of the logarithm of the likelihood function (ignoring constants) is given by:

$$\ell \mathrm{n} L_2 = \sum_y \frac{1}{2(\sigma_y^R)^2}\left(\ell n R_y^{obs} - \ell n(q\hat{N}_y)\right)^2 \tag{11}$$

where: R_y^{obs} is the relative abundance index for year y;

σ_y^R is the standard error of the logarithm of R_y^{obs} (approximated by a combination of its CV and an 'additional standard error' as for Equation (9) above); and

q is the relative bias of estimates from JARPA compared to those from IWC surveys.

If some 'prior' information is available about q, and this can be expressed in the form of a lognormal LN(q^{obs};σ_q^2) distribution, then an extra term can be added to the negative of the logarithm of the likelihood function:

$$\ell \mathrm{n} L_2^* = \frac{1}{2\sigma_q^2}(\ell \mathrm{n} q^{obs} - \ell \mathrm{n} q)^2 \tag{12}$$

The maximum likelihood estimate of q can be obtained analytically using the formula[16]:

$$\ell \mathrm{n}\hat{q} = \left(\ell n q^{obs} / \sigma_q^2 + \sum_y \ell n(R_y^{obs} / \hat{N}_y) / (\sigma_y^R)^2\right) / \left(1/\sigma_q^2 + \sum_y 1/(\sigma_y^R)^2\right) \tag{13}$$

For case (b) above where a fixed selectivity pattern is assumed to apply to the commercial catch for ages 17 and above only, then assuming a multinomial distribution of the catch-at-age for each year, the contributions of the commercial and scientific catches to the log-likelihood (ignoring constants) are given by:

$$\ell n L_3^c = \sum_{y=71}^{86} \lambda_y \sum_{a=17}^{m} C_{y,a}^* \,\ell \mathrm{n} \hat{p}_{y,a} \tag{14a}$$

$$\ell n L_3^s = \sum_{y=89}^{95} \lambda_y \sum_{a=2}^{m} C_{y,a}^* \,\ell \mathrm{n} \hat{p}_{y,a} \tag{14b}$$

where: $C_{y,a}^*$ is the effective[17] number of animals of age a caught during year y, computed as $C_{y,a}C_y^* / C_y$[18];

C_y is the total catch in numbers during year y;

C_y^* is the number of animals actually aged, with ages which are included in the likelihood for year y (for the scientific catches, this is the total number of animals whose actual (as distinct from combination) ages were assessed to lie between 1 and 30, while for the commercial catches it is the total number of animals whose actual ages were assessed to lie between 16 and 30);

λ_y is a factor to account for over-dispersion (assuming that the catch-at-age distributions are not under-dispersed implies that $0 < \lambda_y \leq 1$); and

$\hat{p}_{y,a}$ is the model-estimate of the expected proportion of the catch during year y which consists of animals of age a (these formulae follow from the assumptions of Equation (3) for the expected rate of fishing mortality):

$$\hat{p}_{y,a} = \begin{cases} S_a^c N_{y,a} \Big/ \sum_{a'=17}^{29} S_{a'}^c N_{y,a'} & \text{if } y < 89 \\ S_a^s N_{y,a} \Big/ \sum_{a'=2}^{29} S_{a'}^s N_{y,a'} & \text{otherwise.} \end{cases} \tag{15}$$

For simplicity, it is assumed that λ_y is constant (λ^c) for all of the years of commercial catches and also (a potentially different) constant (λ^s) for all of the years of scientific permit catches. For the analyses in which $\lambda^{c/s}$ is not taken to be equal to 1, the estimation involves an iterative reweighting approach. First, the values for the parameters of the model are obtained by maximising a likelihood function in which

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[14] This additional variance arises from the fact that the variance estimates provided by surveys relate only to the sampling variability of those surveys. What is relevant for fitting population models to abundance data is the total variability of survey estimates about the underlying true abundance trend. This is affected not only by survey sampling variability, but also by other factors such as inter-annual changes in the proportion of the population in the area surveyed at the time of the survey. For further details, see IWC (1997).

[15] Numbers-at-age are not computed for ages 41 and 44 for 1979 because, as indicated above, the available data do not permit estimation of recruitment for the associated cohorts. A (small) correction factor obtained by regressing on ($\hat{N}_{y,41} + \hat{N}_{y,44}/\hat{N}_y$) year is therefore applied to the estimate for 1979, which is computed using Equation (10) with the summation extending only to $a = 38$.

[16] If the 'prior' information about q is ignored, the terms involving σ_q are dropped from Equation (13).

[17] The multinomial distributions assumed by the likelihood formulations of Equations (14) require specification of the number of samples for each year and age which can be considered as effectively independent.

[18] Strictly for the scientific catch, $C_{y,a}^*$ should be the actual number of whales caught in year y and assigned to be age a; however, this formula will provide virtually identical results and has the convenience of being reasonably applicable for both the scientific and commercial catches.

$\lambda^{c/s}$ is taken to be equal to 1 for all years. The following formula (see McAllister and Ianelli, 1997, appendix 2) is then applied to provide updated estimates for the λ's:

$$\lambda^{c/s} = \sum_y 1 \Bigg/ \sum_y \left\{ \frac{C_y^* \sum_a (\rho_{y,a} - \hat{\rho}_{y,a})^2}{\sum_a \hat{\rho}_{y,a}(1 - \hat{\rho}_{y,a})} \right\} \qquad (16)$$

where $\rho_{y,a}$ is the observed proportion of the catch during year y which consists of animals of age a:

$$\rho_{y,a} = \begin{cases} C_{y,a}^* \Big/ \sum\limits_{a'=17}^{29} C_{y,a'}^* & \text{if } y < 89 \\ C_{y,a}^* \Big/ \sum\limits_{a'=2}^{29} C_{y,a'}^* & \text{otherwise} \end{cases} \qquad (17)$$

The summations over year and age in Equation (16) depend on the period considered. For example, to estimate a value for λ^c for the years of commercial catches, the summations over year cover the years 1971 to 1986 and summations over age cover ages 17 to m. The estimation is then repeated replacing λ^c by the updated estimates unless the estimate of λ^c exceeds 1 (corresponding to under-dispersion) in which case it is set equal to 1. This process is repeated until convergence takes place.

Bootstrap estimation of precision

Bootstrap estimates of precision are calculated using an extension of the approach described in Butterworth *et al.* (1996). The procedure involves generating a large number of artificial datasets (typically 100) and fitting the model to each. Each artificial dataset contains a pseudo catch-at-age matrix, and pseudo absolute and relative abundance indices.

The pseudo vector of catches-at-age for year y is obtained by generating a sample from the multinomial distribution with probabilities defined from the actual catch-at-age for year y (Table 1) and then scaling the resultant age-frequency upwards to the total catch for year y. The sample size for year y used when generating the age-frequency is set equal to the actual number of animals aged during that year[19]. This procedure does not reflect the actual practice for the commercial catches (which involves the use of an age-length key - see Appendix) exactly. However, it will constitute an adequate approximation provided the shape of the length distribution of the subsample of all the whales aged does not differ markedly from that for all whales caught, i.e. provided certain length ranges in the catch are not highly disproportionately under- or over-sampled in the ageing exercise.

Two of the sensitivity tests concerned with the estimation of precision consider the impact of ageing error. This is implemented by adding such error to the multinomial sample generated from the actual catch-at-age data (i.e. before scaling upwards to the total catch) using the equation:

$$a' = a(1 + \varepsilon) \qquad \varepsilon \sim N(0; \sigma_e^2) \qquad (18)$$

where: a' is the observed age of an animal of actual age a, and
σ_e reflects the extent of ageing error.

Ageing error is added independently to each age and a' is bounded to lie between 1 and 53 (generated ages outside this range are set equal to 1 and 53 respectively). Two choices for σ_e, in addition to the base-case choice of 0, are considered. The choice $\sigma_e = 0.066$ corresponds to the extent of the error estimated for age readings by Kato (Tanaka and Fujise, 1997) while the choice $\sigma_e = 0.132$ is double this size.

The pseudo absolute abundance estimates are drawn from lognormal distributions defined by the point estimates and CVs in Table 3. The pseudo relative abundance indices are generated similarly. If a 'prior' for the relative bias factor q for the relative abundance indices is used, each bootstrap dataset contains a pseudo relative bias factor generated from a lognormal distribution with a median given by q^{obs} and a CV of σ_q.

The specification of the base-case estimator

The preceding section indicates that a large number of variants of the ADAPT estimator developed could be applied to the available data. To facilitate interpretation of results, a preferred base-case estimator has been developed. Sensitivity tests are detailed later, which systematically explore the consequences of alternative choices for many aspects of this base-case estimator.

As in Butterworth *et al.* (1996), the base-case-estimator operates on a three-age-three-year grouping basis, with a maximum age $m = 29$ in the VPA. As there is no independent information on the JARPA-IWC survey relative bias factor q, σ_q is set to ∞ (i.e. effectively, L_2^* - see Equation (12) - is omitted from the likelihood). All but the first terminal fishing mortality for the maximum age m considered are treated as estimable parameters. Thus, for $y = 71$ for Area IV, $F_{y,29}$ is fixed by use of Equation (7). This choice was made as otherwise essentially only one datum ($C_{71,29}$) is available upon which to base an estimate of $F_{71,29}$.

Natural mortality M

The base-case estimator assumes M to be an estimable parameter, independent of age a (i.e. $\tau = 0$ in Equation (4)). The reason for this is not that this is thought to be the situation in reality, but rather that preceding studies (e.g. Butterworth *et al.* (1996)) have suggested that such an estimator performs better than one which attempts estimation also of a linear trend of M with age a. This was because the lesser bias of this latter estimator tends to be more than offset by the additional variance arising from estimation of a further parameter from the data.

Selectivities-at-age: S_a^c and S_a^s

For the commercial catches, a consistent selectivity-at-age pattern is assumed to apply from age $a = 17$ and above only (see Equation (14a)). This assumption was made because Sakuramoto and Tanaka (1985) present arguments that the commercial selectivity pattern for ages below 15 varied between seasons. The commercial selectivity slope parameter β (which is taken to apply to the age range $a = 23$ to 29, i.e. $a_{slop}^c = 23$ in Equation (6)) was set to zero, so that, for example, $S_{26}^c = 1$ where $S_{29}^c = 1$ by definition. There are two reasons for this choice. First, although the commercial whalers would clearly have wished to select for larger (and hence older) animals, minke whale growth is (on average) very limited at older ages, with less than 0.5m growth to be expected after an animal reaches an age of 10 years. Best (1984) presents results indicating that shipboard estimates of

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[19] If the catch-at-age data appear to be over-dispersed, account of this is taken in the bootstrap generation process by reducing the actual sample size by multiplying by the over-dispersion factor (λ).

minke whale length had a root mean square error (RMSE) of some 0.8m. Thus, the whalers would clearly have been unable to preferentially select older animals amongst those of age, say, 20 and above on the basis of apparent size[20].

The commercial whaling fleet did not catch at random throughout an Area (as the scientific take intends), but rather concentrated in regions of higher minke whale density near to the ice-edge. Thus non-uniform commercial selectivity-at-age could result if there is age-specific segregation of the animals. Table 4 presents results for the average age of the whales sampled in JARPA between 80° and 130° E over the January-March period (covering the peak of commercial whaling operations) as a function of latitude. This section of Area IV was chosen as the continental edge and ice-edge run roughly east-west for this longitude range, so that latitude is a good proxy for distance from the ice-edge. From 61°S southward, there is a clear tendency for average age to increase, suggesting that older animals are more likely to be found closer to the ice-edge. This in turn suggests that the slope parameter β cannot be negative, i.e. that S_{26}^c is not greater than 1. The base-case estimator sets $\beta^c = 0$ ($S_{26}^c = 1$), with the implications for bias should β^c in fact be positive that are discussed below[20]. [Table 4 also indicates high average ages in latitudes 59°-61°S; this may be an artefact of small sample sizes, but does merit further investigation.]

Table 4

Average age by latitude of minke whales (both male and female) sampled in JARPA surveys between longitudes 80°-130°E over the January-March period from 1987/88 to 1995/96.

Latitude range (°S)	Sample size	Average age (yrs)
59-60	6	16.3
60-61	47	17.4
61-62	63	10.5
62-63	58	10.3
63-64	138	14.9
64-65	190	13.4
65-66	280	15.5
66+	7	16.9

Given that the scientific take intends a random sample, the scientific selectivity-at-age function (S_a^s) is taken to be flat for large ages a. The evidence for non-uniform selectivity-at-age at younger ages for both the commercial (age 17 and above) and scientific (age 2 and above) catches was examined for Area IV by the use of likelihood ratio tests. Starting with a uniform function (all $S_a^{c/s} = 1$), these parameters were successively freed and treated as estimable, starting with the parameter for the youngest age under consideration. This exercise suggested that the first two selectivities in each set (S_{17}^c and S_{20}^c; S_2^s and S_5^s) were less than 1. Furthermore, however, over a wide range of age-independent values for M (0.02 to 0.14yr^{-1}), no difference significant at the 5% level between S_{17}^c and S_{20}^c, and between S_2^s and S_5^s was detected. Thus the base-case estimator allowed two estimable selectivity-at-age parameters: $S_{17}^c = S_{20}^c \leq S_{23}^c = 1$ and $S_2^2 = S_5^s \leq S_8^s = 1$, with likelihood ratio tests indicating these distinctions (from values of 1) to be justified at the 5% level. Some difference between the selectivities at these and at higher ages seems possible for the commercial catch given the distributional patterns of both animals and whaling operations as discussed above. For the scientific take, similar differences might also be expected, with some of the smaller (younger) minke whales remaining to the north of the JARPA survey area (as indicated by long-established evidence from high 'proportion takeable' estimates from IWC surveys - see, for example, estimates listed in Chapman, 1985). The formulation of the base-case estimator for the selectivity-at-age of the scientific take is consistent with the results of Cooke *et al.* (1997), whose multiple regression analysis found no evidence for heterogeneity with respect to Area, time within a season, latitude or school size in the scientific take for animals over 9 years of age.

Additional variance (CV_{add})

Repetition of the analysis of Punt *et al.* (1997) at the Area level yields a point estimate $CV_{add} = 0$, with an approximate 95% confidence interval of [0; 0.31]. Hence, noting this point estimate, the base-case estimator uses the CV estimates of Table 3 *without* any additional variance added (see Equation (9) and following).

In summary

Note that the base-case estimator for Area IV thus has 21 estimable parameters:

(i) seventeen terminal fishing mortalities, $\{F_{95,2}, F_{95,5}, \ldots, F_{95,26}\}$; $\{F_{74,29}, \ldots, F_{95,29}\}$;
(ii) one selectivity-at-age for the period of commercial catches, $\{S_{17}^c = S_{20}^c \leq 1\}$;
(iii) one selectivity-at-age for the period of scientific catches, $\{S_2^s = S_5^s \leq 1\}$;
(iv) the relative bias of the JARPA survey estimates of abundance, q; and
(v) the age-independent natural mortality, M.

Sensitivity tests for the base-case assessment

Base-case assessments are provided by application of the base-case estimator developed above to the catch-at-age and abundance data in Tables 1 and 3. A number of sensitivity tests for the resultant Area IV assessment are also pursued.

(i) Age-dependence of M - the estimation of linear and quadratic dependence on age a is examined.
(ii) Commercial selectivity slope (β^c) - alternative fixed values (to 1) for S_{26}^c are examined, and this is also treated as an estimable parameter. This test is conducted for the cases both of M independent of age a and M linear in a. Given the choice $a_{slop}^c = 23$, fixing S_{26}^c specifies S_{23}^c. This sensitivity test then assumes that $S_{17}^c = S_{20}^c \leq S_{23}^c$, rather than ≤ 1 as for the base-case.
(iii) Some older animals 'hidden' in the pack-ice - Table 4 indicates a trend towards older animals closer to the edge of the pack-ice, and it is known that minke whales are present within the pack-ice region (e.g. Ensor, 1989), where they can be neither surveyed (nor sampled) by IWC, JARPA or commercial whalers. This suggests that the probability that a minke whale is 'hidden' in this way may increase with age, which

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[20] P. Best (pers. comm.) and T. Polacheck (pers. comm.) point out that this argument holds only for selection of whales from different schools. Within a school, likely ability to make comparisons on relative size suggests that whalers would have been able to select the larger animals more successfully than we infer from the results of Best (1984). This suggests β^c greater than rather than equal to zero, the implications of which are discussed later in the paper.

would correspond to a decreasing slope in selectivity-at-age for both the commercial and scientific catches (since both would be equally affected by such a possibility). This is investigated by setting (see Equation 6) $\beta^c = \beta^s$ to values differing from 1, with $a^c_{slop} = 23$ and $a^s_{slop} = 11$. As for the base-case, S^s_8 was equated to S^s_{11} with $S^s_2 = S^s_5$ estimated for these sensitivity tests, while for the commercial selectivities, $S^c_{17} = S^c_{20}$ was estimated, though no longer subject to the constraint that it did not exceed S^c_{23}[21].

(iv) Retrospective analysis - this standard VPA diagnostic procedure (comparing trends with those for analyses carried out with only those data available at some earlier times) is followed for analyses up to combination-years $y = 92$ and $y = 89$.

(v) Absolute abundance estimates - although the IWC estimates are used as absolute in the analysis, they may be biased for various reasons (e.g. animals to the north of the common boundary line used for the IWC estimates listed in Table 3); thus the consequences both of doubling and of halving the IWC estimates is explored.

(vi) Lesser readability of earplugs from younger animals (Kato *et al.*, 1991) in the scientific take - as noted above, this may lead to an underestimate of the scientific catch-at-age of younger animals - as a simple way of examining the consequences of this, the contributions of ages $a = 2$ and 5 are omitted from the pertinent contribution to the likelihood (L^s_3 - see Equation (14b)).

(vii) Greater inter-annual consistency in the commercial selectivity-at-age - age $a = 14$ is included in the pertinent contribution to the likelihood (L^c_3 - see Equation (14a)), with S^c_{14} treated as an additional estimable parameter subject to $S^c_{14} \leq S^c_{17} = S^c_{20} \leq 1$.

(viii) Separate assessments for males and females - this is problematic because although the catch-at-age matrices are readily disaggregated by sex, the same is not the case for the sighting survey estimates of abundance; as a crude first attempt, sex-disaggregated assessments have been conducted for Area IV by halving the abundance estimates in Table 3, and multiplying their CVs by $\sqrt{2}$.

(ix) Technical modifications - the consequences of the alternative choices of $m = 26$ and $m = 32$ for the oldest age considered in the VPA ($m = 29$ for base-case) are examined, as well as those of choosing a four-age-four-year instead of a three-age-three-year grouping.

(x) Alternative treatment of the JARPA abundance estimates - as a result of biases introduced by the survey protocol applied (Burt and Borchers, 1997), these estimates may also give biased indications of trends in relative abundance (IWC, 1998). Two sensitivity tests examine imposing an annual 2% increasing/decreasing trend on the abundance estimates, while another examines the consequences of assuming that the JARPA estimates are proportional to the square root of $\hat{N}$ rather than $\hat{N}$ itself.

(xi) Time trends in M — allowance is made for the possibility that M (assumed in this test to be independent of age) is time dependent by changing M linearly with time from 1944 to 1968 and then linearly (but with a change of slope) from 1968 to 1995 (see Equation 5).

ASSESSMENT RESULTS AND DISCUSSION

Area IV

For this Area, preliminary analyses estimated λ to be greater than 1 for the periods of both the commercial and the scientific permit catches. Since the possibility of under-dispersion is excluded (this hardly seems likely, and would overweight data if incorrectly assumed), λ has been taken to be equal to 1 for all of the analyses for Area IV. Fig. 1 (see also Table 6) shows estimated recruitment ($N_{y,a}$) trends for the base-case estimator computed for various alternative age-independent values of M ranging from 0.02 to 0.14yr^{-1}. This range captures a wide set of possible historic (1947-68) recruitment trends - from rapidly increasing to continuously declining. The plots are normalised to the corresponding estimates of recruitment in 1968 for ease of trend comparison, as absolute recruitment levels differ greatly for the different values of M.

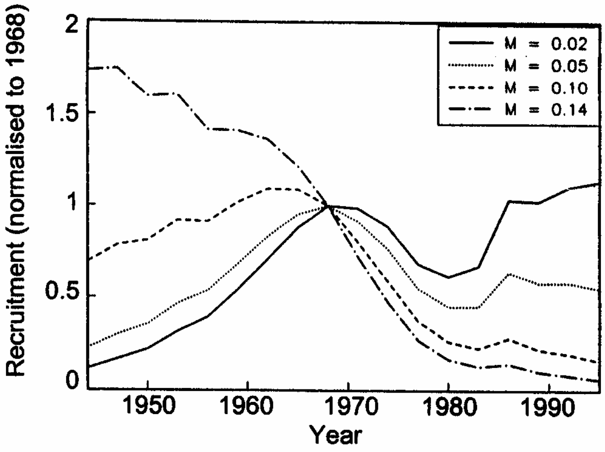

Fig. 1. Estimates of recruitment ($N_{y,2}$) for Area IV plotted against year for fixed values of age-independent natural mortality $M = 0.02$, 0.05, 0.10 and 0.14yr^{-1}. Each series is normalised to its 1968 level.

The recruitment trend for the base-case estimator itself, which estimates the value of an age-independent value of M from the data (obtaining an estimate 0.057yr^{-1}) is shown overleaf in Fig. 2. Fig. 3 illustrates how the estimator is able to distinguish amongst alternative values of M based upon the survey abundance estimates. Fig. 3a shows the trends in total population size from 1980 to 1995 (here corresponding to estimated numbers-at-age $N_{y,a}$ summed from $a = 2$ to $a = 44$, using the procedure of footnote 15 to extrapolate where necessary) for different values of age-independent M, with this trend changing from positive to negative as M is increased. The total abundance estimates fitted are shown in Fig. 3b, together with the corresponding base-case estimate of the total abundance trend (note that the JARPA estimates as shown in this plot are adjusted by the estimate of the relative bias factor q). The trend of these estimates is slightly downward, essentially allowing the base-case estimator to 'choose' from amongst the possibilities shown in Fig. 3a.

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[21] This is a simple initial investigation of the consequences of this possibility, which ignores the fact that if some animals are 'hidden' in this manner, the total population numbers to which survey estimates are fitted – see Equations (10) and (11) – should be summations of true numbers-at-age downweighted in an age-dependent manner to allow for the fact that older animals are preferentially unavailable to the surveys. Given, however, that key results of interest (see Table 8) show little sensitivity to changes in absolute estimates of abundance (sensitivity test (v)), failure to take this downweighting into account seems unlikely to have much impact on those results.

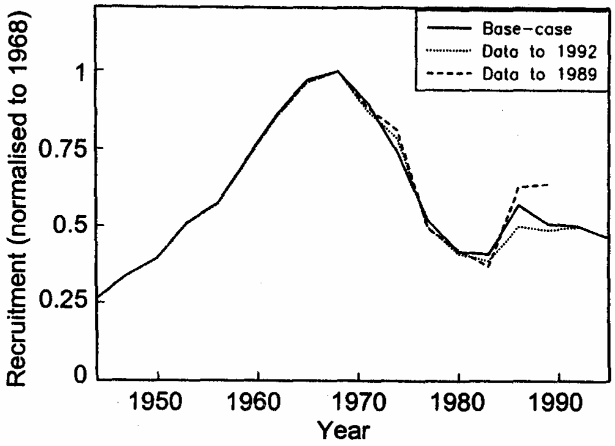

Fig. 2. Estimates of recruitment ($N_{y,2}$) for Area IV plotted against year as in Fig. 1 for the base-case estimator, for which M is assumed to be independent of age with a value estimated by fitting the data (and yielding $M = 0.057\text{yr}^{-1}$), are shown by the full line. The other lines show retrospective analyses, which involve applying the base-case estimator to the data available up to 1992, and up to 1989 only - in both cases fixing $M = 0.057\text{yr}^{-1}$.

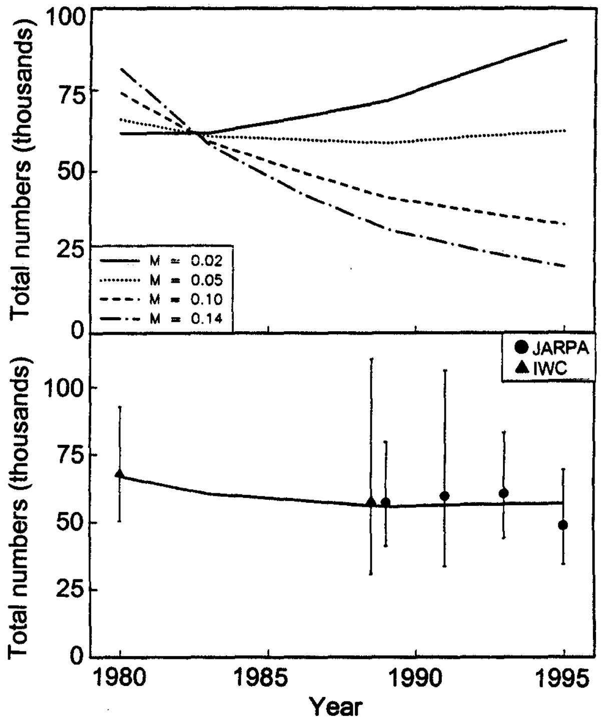

Fig. 3. Plots of estimated total population size ($\sum_{a=2}^{44} N_{y,a}$) against year for Area IV for fixed values of age-independent natural mortality $M = 0.02, 0.05, 0.10$ and 0.14yr^{-1} are shown in the upper panel. The plot for the base-case estimator, which estimates $M = 0.057\text{yr}^{-1}$ is shown in the lower panel, together with the abundance estimates input to this estimation procedure. The JARPA abundance estimates have been scaled to be comparable to the IWC estimates by use of the base-case estimate of the relative bias factor $q = 0.431$. The error bars show 90% CI's for these abundance estimates under the assumption of distribution lognormality.

Fig. 2 also includes the results of a retrospective analysis, showing recruitment trend estimates based on data available up to 1992 only and to 1989 only. There are no indications of a systematic trend in the estimates of year-to-year changes in recruitment as more data became available, consistent with an absence of model mis-specification. [The retrospective analysis is run for the same value of $M = 0.057\text{yr}^{-1}$ as estimated by the base-case estimator for data through to 1995. If M is treated as an estimable parameter in these retrospective fits, different values to 0.057 result, essentially 'rotating' the plots in Fig. 2 somewhat. This is to be expected, as M is not that precisely estimated, even given data up to 1995 - see Table 9. But the objective of the retrospective analysis is rather to address the issue of consistency over time in estimates of inter-annual changes (within this overall 'rotational' degree of freedom), and these changes do seem well estimated by the available data.] The numbers-at-age ($N_{y,a}$) matrix for Area IV estimated by the base-case estimator is given in Table 5a, with estimates of the commercial and scientific selectivity-at-age vectors (S^c_a and S^s_a respectively), together with the estimate of the relative bias factor q for the JARPA/IWC abundance estimates, given in Table 5b. Table 5c gives values for the 'apparent' selectivity-at-age $S^*_{y,a}$. This statistic is developed by first calculating a 'fully-selected' fishing mortality F^*_y for each year; this was taken to be the average fishing mortality over ages $a = 23$ to 29 for the years of commercial catch, and $a = 8$ to 29 for those of the scientific take. The 'apparent' selectivity for age a in year y is then given by:

$$S^*_{y,a} = F_{y,a} / F^*_y \tag{19}$$

If the model used for the base-case estimator was mis-specified, one would expect to see systematic patterns in $S^*_{y,a}$ in Table 5c over age ranges for which the underlying selectivity ($S^{c/s}_a$) was constant. There is no obvious indication of such patterns in this Table.

Another assumption to be tested is that of independence of the age samples, as tacitly assumed by the forms of Equations (14a) and (14b) with λ taken to be 1. If there was positive correlation in these samples, these equations would give undue weight to these data, leading to negatively biased estimates of variance for quantities of interest whose values are estimated in the assessment. This test was effected by considering, as an approximate measure[22] of goodness of fit, a χ^2 statistic for the catch-at-age data:

$$\chi^2 = \sum_{y=71}^{86}\sum_{a=17}^{m}\frac{(C^*_{y,a} - C^*_y\hat{p}_{y,a})^2}{C^*_y\hat{p}_{y,a}} + \sum_{y=89}^{95}\sum_{a=2}^{m}\frac{(C^*_{y,a} - C^*_y\hat{p}_{y,a})^2}{C^*_y\hat{p}_{y,a}} \tag{20}$$

For the base-case assessment, the value of χ^2 is 31.41 (df = 40). The null hypothesis that the catches included in the analysis are multinomially distributed about the model predictions therefore cannot be rejected ($P > 0.75$), so that there is no statistically significant evidence of non-independence in the age samples in this instance. Repeating the assessment including commercial catch-at-age data for all ages gives a significant result under this test, consistent with the assumption that the commercial selectivity varied from year to year for the younger ages.

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[22] This statistic is described as approximate because the resultant inferences fail to take into account that absolute abundance estimates and relative abundance indices are also fitted in the estimation process.

Table 5

Results for the application of the base-case estimator to the data for Area IV. The symbols used are defined in the text.

(a) Numbers-at-age matrix $N_{y,a}$ ($\hat{M} = 0.057$).

	Age															
Year	2	5	8	11	14	17	20	23	26	29	32	35	38	41	44	Total
1944	5,494	-	-	-	-	-	-	-	-	-	-	-	-	-	-	5,494
1947	7,100	4,633	-	-	-	-	-	-	-	-	-	-	-	-	-	11,734
1950	8,327	5,988	3,907	-	-	-	-	-	-	-	-	-	-	-	-	18,222
1953	10,722	7,022	5,050	3,295	-	-	-	-	-	-	-	-	-	-	-	26,090
1956	12,041	9,042	5,922	4,259	2,779	-	-	-	-	-	-	-	-	-	-	34,043
1959	15,098	10,154	7,626	4,994	3,592	2,344	-	-	-	-	-	-	-	-	-	43,808
1962	18,083	12,733	8,563	6,431	4,212	3,029	1,977	-	-	-	-	-	-	-	-	55,028
1965	20,322	15,250	10,738	7,222	5,424	3,552	2,554	1,667	-	-	-	-	-	-	-	66,729
1968	20,913	17,138	12,861	9,056	6,090	4,574	2,996	2,154	1,406	-	-	-	-	-	-	77,188
1971	18,825	17,637	14,453	10,846	7,637	5,136	3,857	2,526	1,817	1,186	-	-	-	-	-	83,920
1974	15,468	15,773	14,657	11,924	8,886	6,144	4,063	3,014	1,933	1,409	919	-	-	-	-	84,190
1977	10,904	12,354	12,031	10,866	8,609	6,294	4,118	2,671	1,932	1,233	897	632	-	-	-	72,540
1980	8,756	9,128	10,141	9,777	8,630	6,739	4,862	3,234	2,056	1,524	974	716	523	-	-	67,061
1983	8,592	7,205	7,283	8,025	7,630	6,624	5,050	3,598	2,331	1,486	1,094	705	505	387	-	60,513
1986	11,942	7,048	5,655	5,630	6,086	5,837	4,839	3,699	2,607	1,674	1,071	851	555	397	299	58,192
1989	10,640	10,014	5,791	4,491	4,346	4,629	4,352	3,576	2,665	1,897	1,215	806	641	425	318	55,804
1992	10,486	8,880	8,368	4,832	3,742	3,624	3,851	3,623	2,991	2,216	1,582	1,017	671	534	354	56,772
1995	9,721	8,803	7,459	7,025	4,052	3,141	3,041	3,231	3,043	2,506	1,857	1,324	851	563	449	57,063

(b) Selectivity and relative bias.

	Age									
	2	5	8	11	14	17	20	23	26	29
Selectivity - commercial S_a^c	-	-	-	-	-	0.865	0.865	1	1	1
- scientific S_a^s	0.823	0.823	1	1	1	1	1	1	1	1
Relative bias q (JARPA = q.IWC)	0.431									

(c) 'Apparent' selectivity $S^*_{y,a}$

	Age									
Year	2	5	8	11	14	17	20	23	26	29
1971	0.08	0.17	0.26	0.34	0.55	0.74	0.87	1.10	0.95	0.95
1974	0.22	0.39	0.50	0.59	0.66	0.85	0.91	0.99	1.00	1.01
1977	0.10	0.37	0.51	0.81	1.00	1.17	0.96	1.22	0.90	0.89
1980	0.17	0.37	0.42	0.51	0.62	0.76	0.84	1.00	0.98	1.02
1983	0.19	0.48	0.58	0.70	0.64	0.92	0.91	0.97	1.03	1.00
1986	0.04	0.18	0.41	0.60	0.70	0.82	0.88	1.04	0.98	0.99
1989	0.89	0.78	0.91	1.02	0.94	1.15	1.10	0.72	1.20	0.96
1992	0.86	0.73	0.86	1.07	0.90	0.99	0.99	0.80	1.19	1.21
1995	0.83	0.80	0.95	1.14	1.09	1.01	1.08	0.78	1.21	0.74

Sensitivity tests

Given the large number of statistics generated by an assessment, a key sub-set of five was chosen to characterise results in order to facilitate comparisons in sensitivity tests. These are:

(i) the historic recruitment trend, as given by the slope of a linear regression of $\ell n\, N_{y,2}$ against year y for $y = 1947$ to 1968, and expressed in (true yr)$^{-1}$;

(ii) $N_{83,2}$ / $N_{68,2}$ - usually reflecting the lowest value to which recruitment drops after the 1968 peak, expressed as a fraction of that peak value;

(iii) $N_{95,2}$ / $N_{68,2}$ - current recruitment as a fraction of the 1968 peak value;

(iv) age-averaged natural mortality, $\overline{M}$ - for cases of age-dependent M, this is calculated as:

$$\overline{M} = (M_2 + M_5 + M_8 + \ldots + M_{29}) / 10; \text{ and} \qquad (21)$$

(v) the recent trend in total population size, as reflected by the slope of a linear regression of $\ell n \left[\sum_{a=2}^{38} N_{y,a} \right]$ against year y for $y = 1980$ to 1995, and expressed in (true yr)$^{-1}$.

Table 6 (overleaf) shows results for these statistics for a variety of options for the specification of M and its age dependence. While changing the (age-independent) value of M makes key qualitative changes to the results (as also evident from Fig. 1), minimal differences result when attempts are made to estimate linear or quadratic dependence of M on age a. There is a weak indication of a generally increasing trend of M with age, but likelihood ratio tests do not provide statistical justification for estimation of the additional parameter(s) involved (maximal ℓnL increases of 0.13 and 0.52 for introduction of linear and quadratic dependence respectively).

Table 6

Sensitivity of the base-case assessment for Area IV to alternative specifications for natural mortality M and its age-dependence. The statistics reported are defined in detail in the text. Units, where pertinent, are yr^{-1} (i.e. true years, not combination years).

	$N_{y,2}$ incr. rate 47-68	$N_{83,2}/N_{68,2}$	$N_{95,2}/N_{68,2}$	$\overline{M}$	N_y incr. rate 80-95	M_2	M_{17}	M_{29}	-ℓn L
Constant with a									
$M = 0.02$	0.088	0.672	1.134	0.020	+0.025	0.020	0.020	0.020	17.46
$M = 0.05$	0.061	0.451	0.549	0.050	-0.004	0.050	0.050	0.050	16.51
$M = 0.057$ (base-case)	0.055	0.411	0.465	0.057	-0.011	0.057	0.057	0.057	16.48
$M = 0.10$	0.015	0.226	0.161	0.100	-0.054	0.100	0.100	0.100	17.86
$M = 0.14$	-0.023	0.129	0.059	0.140	-0.094	0.140	0.140	0.140	21.64
Linear in a	0.049	0.407	0.471	0.058	-0.013	0.045	0.060	0.071	16.35
Quadratic in a									
Minimum at $a = 2$	0.047	0.412	0.477	0.060	-0.013	0.047	0.058	0.084	16.13
Minimum at $a = 17$	0.054	0.409	0.421	0.066	-0.012	0.095	0.050	0.079	15.96
Minimum at $a = 29$	0.055	0.411	0.465	0.057	-0.011	0.057	0.057	0.057	16.48

Table 7

Sensitivity of the base-case assessment for Area IV to alternative specifications for the selectivity-at-age functions. In (a), only the commercial selectivity slope parameterβ^c (see Equation 6) is considered, where this slope applies to the age range a=23 to 29, i.e. sensitivity test (ii) as detailed in the text. For ease of understanding, rather than β itself, the value of S^c_{26} is given (note: $S^c_{29} = 1$ by definition). In (b), all results are for the case where M_a is independent of a. The first set of results show the consequences of successively freeing additional S^c_a parameters for constraint-free estimation. The second set is for sensitivity test (iii), which allows for the possibility that some of the older animals are 'hidden' in the pack-ice, with consequent negative slopes for both commercial and scientific selectivities-at-age.

(a)

Estimator variant	$N_{y,2}$ incr. rate 47-68	$N_{83,2}/N_{68,2}$	$N_{95,2}/N_{68,2}$	$\overline{M}$	N_y incr. rate 80-95	M_2	M_{29}	-ℓn L
M_a indep. of a								
$S^c_{26} = 0.80$	0.102	0.475	0.621	0.046	+0.005	0.046	0.046	26.15
$S^c_{26} = 1.00$ (base-case)	0.055	0.411	0.465	0.057	-0.011	0.057	0.057	16.48
$S^c_{26} = 1.20$	0.030	0.420	0.490	0.053	-0.014	0.053	0.053	18.06
$S^c_{26} = 1.05$ (estimated)	0.049	0.420	0.482	0.055	-0.011	0.055	0.055	16.22
M_a linear in a								
$S^c_{26} = 0.80$	0.086	0.447	0.613	0.052	-0.002	0.010	0.094	24.99
$S^c_{26} = 1.00$	0.049	0.407	0.471	0.058	-0.013	0.045	0.071	16.35
$S^c_{26} = 1.20$	0.038	0.419	0.465	0.052	-0.013	0.071	0.033	17.74
$S^c_{26} = 1.04$ (estimated)	0.049	0.422	0.491	0.055	-0.011	0.049	0.060	16.20

(b)

Estimator variant	$N_{y,2}$ incr. rate 47-68	$N_{83,2}/N_{68,2}$	$N_{95,2}/N_{68,2}$	$\overline{M}$	N_y incr. rate 80-95	S^c_{17}	S^c_{20}	S^c_{23}	S^c_{26}	-ℓn L
Selectivity parameters estimated										
$S^c_{17} = S^c_{20}$ (base-case)	0.055	0.411	0.465	0.057	-0.011	0.865	0.865	1	1	16.48
$S^c_{17} = S^c_{20}$, S^c_{26}	0.049	0.420	0.482	0.055	-0.011	0.978	0.978	1.099	1.049	16.22
$S^c_{17} = S^c_{20}$, S^c_{23}, S^c_{26}	0.050	0.426	0.493	0.054	-0.011	0.962	0.962	1.087	1.024	16.17
S^c_{17}, S^c_{20}, S^c_{23}, S^c_{26}	0.056	0.401	0.445	0.059	-0.012	0.813	0.884	0.990	0.976	15.87
Some older animals 'hidden' in the pack-ice										
$S^c_{26} = S^s_{26} = 0.9$	0.044	0.456	0.535	0.088	-0.004	0.634	0.634	0.800	0.900	20.51
$S^c_{26} = S^s_{26} = 1$ (base-case)	0.055	0.411	0.465	0.057	-0.011	0.865	0.865	1	1	16.48
$S^c_{26} = S^s_{26} = 1.05$	0.053	0.386	0.427	0.050	-0.014	0.989	0.989	1.100	1.050	15.98
$S^c_{26} = S^s_{26}$ (estimated)	0.053	0.385	0.427	0.048	-0.014	1.017	1.017	1.122	1.061	15.95
$S^c_{26} = S^s_{26} = 1.1$	0.053	0.381	0.427	0.042	-0.014	1.115	1.115	1.200	1.100	16.07
$S^c_{26} = S^s_{26} = 1.2$	0.049	0.362	0.407	0.031	-0.016	1.385	1.385	1.400	1.200	17.58

Table 7a shows similar results when the possibility of a commercial selectivity slope that is not flat (i.e. β^c of Equation (6) is not zero) at older ages is admitted. This Table gives results for the cases both where M is independent of age a and where it is linear in a, while Fig. 4 shows the former set of results graphically. The key feature of these results is that the estimate of the historic recruitment trend is quite sensitive to the value assumed for β^c (or equivalently S^c_{26}), becoming larger or smaller as S^c_{26} is less than or greater than 1 (recall earlier arguments based on whale and whaling distributions that S^c_{26} is likely not in excess of 1). When S^c_{26} is treated as an estimable parameter, the resultant estimates are slightly above 1, but likelihood ratio tests do not provide statistical justification for the additional estimable parameter (increases in ℓnL of 0.26 and 0.15 for the M_a constant with a and the M_a linear in a cases considered, respectively). When linear dependence of M_a on a is allowed, the estimate of this linear selectivity trend changes from positive to negative over the range of S^c_{26} considered. However, the negative trends occur only for S^c_{26} values in excess of 1, a situation considered unlikely for reasons discussed above.

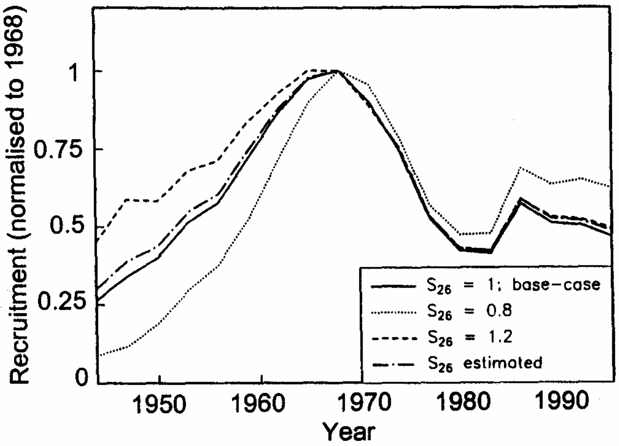

Fig. 4. Sensitivity of the base-case estimates of recruitment ($N_{y,2}$) for Area IV to the commercial selectivity slope parameter (see Equation 6). Results are shown for $S^c_{26} = 0.8$, 1.0 (the base-case), 1.2 and for the best estimate from fitting to the data of $S^c_{26} = 1.05$. Each series is normalised to its 1968 level.

During the 1998 meeting of the IWC Scientific Committee, considerable debate took place concerning the results shown in Table 7a (IWC, 1999). Particular concern was expressed that those results had been conditioned on the constraint $S^c_{17} = S^c_{20} \leq S^c_{23}$, thus precluding the possibility of any dome in the commercial selectivity-at-age having its maximum at an age below 23. This is because a decreasing slope in the commercial selectivity, particularly if it commenced at ages less than 23, would lead to estimates of lesser rates of increase in the historic recruitment trend. To investigate this, the base-case calculations (with M_a constant with a) have been repeated while successively freeing additional commercial selectivity-at-age (S^c_a) parameters for constraint-free estimation. The results shown in Table 7b confirm that there is no justification in likelihood-ratio terms for attempting to estimate these additional parameters given the available data, but nevertheless also indicate that the associated point estimates provide a virtually unchanged estimate of the historic recruitment trend and no indication of a maximum in the commercial selectivity-at-age at an age below $a = 23$.

Sensitivity test (iii) relating to the possibility of some older animals 'hidden' in the pack-ice also addresses this question, as it offers a mechanism which would result in the commercial (but then also the scientific) selectivity-at-age decreasing for greater ages. The results of this test are also shown in Table 7b, and again indicate very little sensitivity of the estimate of the historic recruitment trend to this factor, with likelihood maximisation again favouring an estimate of $S^c_{26} = S^s_{26}$ slightly greater than 1, i.e. only a small drop in selectivity with age[23]. The reason for this perhaps surprising result is that the existence of such 'hidden' animals changes the estimate of M, not that of the historic recruitment trend. This is as would be expected from the analyses of Butterworth and Punt (1990), which showed (see particularly equation 10 of that paper) that given temporal invariance of selectivity-at-age (above a certain age) and natural mortality-at-age, the collection of future catch-at-age data could, in principle, allow the estimation of the historic recruitment trend for Southern Hemisphere minke whales. Essentially, the contradiction of the inference of an increasing historic recruitment trend for minke whales on the basis of trends in selectivity-at-age requires that any decrease in this selectivity at larger ages is notably greater for the commercial than for the scientific catch - a scenario for which no obvious potential mechanism immediately suggests itself.

Results for the remaining sensitivity tests are shown in Table 8. Changing the values of the IWC abundance estimates does make a considerable difference to recent recruitment estimates compared to those for the 1968 peak. Increasing the abundance estimates (the more likely direction, given the need to allow both for animals north of the survey area and for the possibility that not all animals on the trackline are sighted) suggests that recent recruitment levels are not as far below the 1968 peak as for the base-case estimator. Other sensitivity test results of some note in Table 8 are that omission of ages $a = 2$ and 5 from L^s_3 (the surrogate test for possible bias in the number of young animals in the scientific take as a result of possible lower readability of earplugs from younger animals) leads to a slight increase in the estimated historic recruitment increase rate, and decrease in the estimated natural mortality rate, while the first of these estimated rates drops under a four- rather than a three-year grouping.

The results are sensitive to imposing a trend with time on the JARPA estimates of relative abundance. However, they are rather less sensitive to variation of the assumption of a linear relationship between these estimates and abundance (primarily because the existing JARPA estimates for Area IV are essentially without trend over time). Estimates of recruitment trends for recent years are not particularly sensitive to time trends in natural mortality. However, the estimate of the increase rate in $N_{y,2}$ from 1947 to 1968 is sensitive to such trends, becoming larger if M has increased over time. Indeed, it is possible to virtually eliminate the positive trend in $N_{y,2}$ from 1947 to 1968 by assuming that natural mortality decreased steadily from 0.143yr^{-1} in 1944 to 0.057yr^{-1} in 1968. Thus, if complete freedom is allowed in trends in natural mortality M over time, it becomes impossible to draw any inference about past recruitment trends. However, hypotheses about systematic changes in M would not seem to merit much credibility unless linked to independent supporting evidence or rationale. Only one such

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[23] Naturally, only values of $S^c_{26} = S^s_{26} > 1$ are consistent with the hypothesis of some older animals 'hidden' in the pack-ice; results for a value lower than this are shown purely for the purposes of illustrating the behaviour of the log-likelihood.

Table 8

Further sensitivity tests of the base-case assessment for Area IV.

Variant	$N_{y,2}$ incr. rate 47-68	$N_{83,2}/N_{68,2}$	$N_{95,2}/N_{68,2}$	$\overline{M}$	N_y incr. rate 80-95
Base-case	0.055	0.411	0.465	0.057	-0.011
Retrospective to 92	0.055	0.389	-	0.057[1]	-0.018[2]
Retrospective to 89	0.055	0.371	-	0.057[1]	-0.015[3]
Halve abundance estimates	0.049	0.265	0.272	0.057[1]	-0.038
Double abundance estimates	0.059	0.525	0.615	0.057[1]	0.000
Omit a=2,5 from L_3^s	0.068	0.499	-[4]	0.042	-0.005[3,4]
Include a=14 in L_3^c (i.e. estimate S_{14}^c)	0.057	0.425	0.492	0.054	-0.009
Males only	0.047	0.451	0.444	0.059	-0.012
Females only	0.049	0.324	0.398	0.067	-0.019
$m = 26$	0.057	0.401	0.434	0.056	-0.012[5]
$m = 32$	0.068	0.424	0.493	0.053	-0.007
4-year grouping	0.032[6]	0.591[7]	0.381[8]	0.054	-0.016[9]
$R_y^{obs} \rightarrow R_y^{obs} e^{0.02y}$	0.063	0.463	0.588	0.048	-0.002
$R_y^{obs} \rightarrow R_y^{obs} e^{-0.02y}$	0.046	0.362	0.363	0.066	-0.021
$R_y^{obs} \propto \sqrt{\hat{N}_y}$	0.060	0.445	0.545	0.051	-0.005
$\widetilde{M}_{44} = 0.8; \widetilde{M}_{95} = 1.2$ [10]	0.066	0.435	0.485	0.051	-0.012
$\widetilde{M}_{44} = 1.2; \widetilde{M}_{95} = 0.8$	0.040	0.376	0.428	0.065	-0.011
$\widetilde{M}_{44} = 2.5; \widetilde{M}_{95} = 1$	0.007	0.399	0.452	0.057	-0.011

[1] M fixed at same value as for base-case (0.057 yr^{-1}). [2] To 92 only. [3] To 89 only. [4] Statistics for y=95 not reliable as data exclusion essentially precludes recent recruitment estimation. [5] N_y to age 35 only. [6] 47/48-50/51 to 63/64-66/67. [7] 79/80-82/83 compared to 67/68-70/71. [8] 91/92-94/95 compared to 67/68-70/71. [9] 79/80-82/83 to 91/92-94/95 with N_y involving summation to combination age 37-40. [10] $\widetilde{M}_{68} = 1$ - see Equation (5).

Table 9

Bootstrap estimates of precision for the base-case estimator and certain variants thereof applied to data for Area IV. Figures given are medians, with 90% confidence intervals in parenthesis.

Estimator	$N_{y,2}$ incr. rate 47-68	$N_{83,2}/N_{68,2}$	$N_{95,2}/N_{68,2}$	$\overline{M}$	N_y incr. rate 80-95	M_2	M_{29}	S_{26}^c
Base-case	0.054 [0.014;0.091]	0.380 [0.214; 0.729]	0.393 [0.147; 1.334]	0.059 [0.018; 0.101]	-0.016 [-0.056;0.032]	-	-	-
$CV_{add} = 0.1$	0.054 [0.015; 0.098]	0.389 [0.205; 0.785]	0.405 [0.133; 1.586]	0.060 [0.010; 0.105]	-0.016 [-0.060;0.038]	-	-	-
Omit a=2,5 from L_3^s	0.066 [0.007; 0.100]	0.446 [0.187; 0.882]	-[1]	0.048 [0.010; 0.112]	-[1]	-	-	-
Estimate S_{26}^c	0.045 [0.005; 0.092]	0.424 [0.225; 0.741]	0.429 [0.158; 1.393]	0.057 [0.015; 0.101]	-0.015 [-0.053;0.030]	-	-	1.028 [0.965; 1.172]
M_a linear in a	0.045 [0.002; 0.092]	0.369 [0.213; 0.730]	0.380 [0.146; 1.214]	0.065 [0.019; 0.105]	-0.021 [-0.065;0.029]	0.046 [0.010; 0.113]	0.075 [0.010; 0.135]	-
M_a linear in a; estimate $S_{26}^c \leq 1$	0.045 [0.002; 0.092]	0.363 [0.212; 0.722]	0.380 [0.148; 1.230]	0.065 [0.019; 0.105]	-0.021 [-0.065;0.028]	0.045 [0.010; 0.113]	0.076 [0.010; 0.140]	1 [0.947; 1.000]
M_a linear in a; estimate S_{26}^c	0.041 [0.000; 0.091]	0.373 [0.214; 0.703]	0.405 [0.149; 1.260]	0.060 [0.018; 0.104]	-0.018 [-0.065;0.027]	0.053 [0.010; 0.117]	0.066 [0.010; 0.137]	1.027 [0.944; 1.163]
Ageing error; σ_e=0.066	0.051 [0.012; 0.088]	0.386 [0.226; 0.721]	0.415 [0.145; 1.290]	0.060 [0.021; 0.106]	-0.017 [-0.054;0.029]	-	-	-
Ageing error; σ_e=0.132	0.047 [0.000; 0.083]	0.413 [0.236; 0.799]	0.421 [0.151; 1.158]	0.060 [0.018; 0.102]	-0.019 [-0.057;0.026]	-	-	-

[1] Statistics for y=95 not reliable as data exclusion essentially precludes recent recruitment estimation.

associated mechanism immediately suggests itself: M is density dependent, increasing as the population size grows. As noted above then, this suggests an even faster historic rate of increase in recruitment than estimated when assuming M to be time-independent, rather than that there was no such increase.

Precision

Bootstrap estimates of precision have been calculated based on 100 replicates. The resultant 90% confidence intervals for the five key statistics identified above for the base-case Area IV assessment are shown in Table 9, with the associated recruitment trend plot with confidence intervals in Fig. 5. A likelihood profile indicates a 90% confidence interval for M of [0.013; 0.100] compared to the [0.018; 0.101] from the bootstrap procedure; their similarity suggests that the bootstrap computations are reasonably reliable.

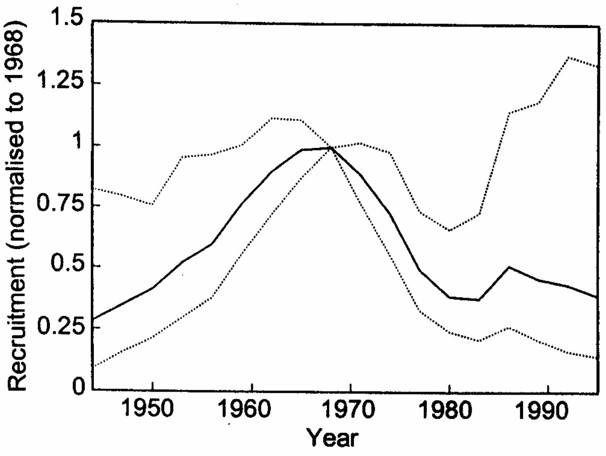

Fig. 5. Bootstrap estimates of medians (solid line), and 5%- and 95%-iles (dotted lines), for recruitment $N_{y,2}$ (relative to its estimated 1968 level for the corresponding bootstrap replicate) for Area IV for the base-case estimator.

Estimates of precision for a number of variants of the base-case estimator are also shown in Table 9. These include variants which attempt to estimate a linear dependence of natural mortality with age and the slope of the commercial selectivity at large age a, as well as those which allow for 'additional variation' in the abundance estimates and consider the impact of ageing error. Results of note are that, almost without exception, confidence intervals for the historic (1947-68) recruitment trend exclude the possibility of a decline. When the commercial selectivity slope is estimated, the confidence limits on S^c_{26} remain reasonably close to 1. Confidence interval estimates were not attempted for the variant of the base-case shown in Table 7b that estimates all four commercial selectivity parameters (S^c_{17}, S^c_{20}, S^c_{23} and S^c_{26}) without constraint, as numerical aspects of the bootstrap procedure used may be unreliable in this situation because these extra parameters constitute a subspace in which the likelihood is rather flat. However, for the case indicated as 'Estimate S^c_{26}' in the Table (corresponding to sensitivity test (ii)), the constraint boundary $S^c_{17} = S^c_{20} \leq S^c_{23}$was not hit for any of the 100 bootstraps. Hence, further to the Table 7b results which indicate no evidence for a commercial selectivity maximum below age $a = 23$ in point estimate terms, this suggests that this conclusion is supported at a high level of statistical significance.

Table 9 also shows that if additional variance at the level $CV_{add} = 0.1$[24] is introduced into the calculations, confidence intervals increase slightly but not substantially. Attempts to estimate age-dependence in M generally result in lower confidence bounds hitting the constraint boundary 0.01yr^{-1}. The impact of ageing error is minimal.

Extension to Area V

Results for the application of the base-case estimator to the data for Area V are given in Table 10. The estimator sets the age-independent estimate of M on the constraint boundary of 0.01yr^{-1}. The resultant estimated recruitment trend, together with those for some other fixed values of M, is shown in Fig. 6. The very low estimate of $N_{y,47}$ is an artefact of the small sample size for the catch-at-age at high ages - specifically $a = 29$ - for year $y = 74$ (see Table 1b), coupled with the application of Equation (7), and hence is not shown in the figure.

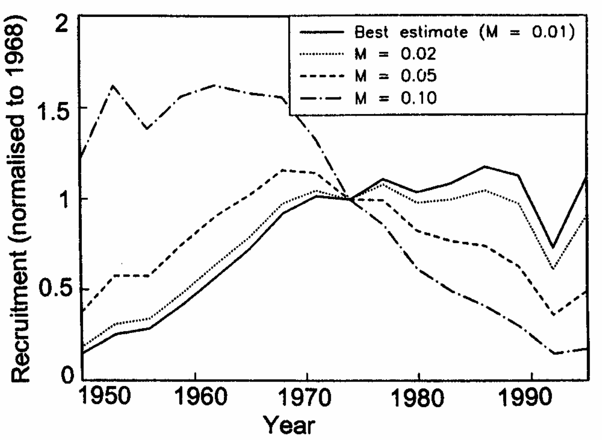

Fig. 6. Estimates of recruitment ($N_{y,2}$) for Area V plotted against year for fixed values of age-independent natural mortality $M = 0.02$, 0.05 and 0.10yr^{-1}. The full line shows the result for the base-case estimator, which sets M on the constraint boundary value of 0.01yr^{-1}. Each series is normalised to its 1968 level.

For this Area, the estimate of λ^c for the period of commercial catches is less than 1 (point estimate 0.688), so that account needs to be taken of over-dispersion in the bootstrap procedure. Bootstrap confidence interval estimates reported in Table 11 show that the precision of estimates is not as good as for Area IV, and do not exclude the possibility of a downward trend in historic recruitment over the 1947-68 period.

When the data for Areas IV and V are combined, the catch-at-age data are again over-dispersed. However, in contrast to the situation for Area V alone, both the commercial (λ^c = 0.742) and scientific take (λ^s = 0.702) data are now estimated to be over-dispersed. One possible reason for this is that even if the scientific catches-at-age reflect random samples within the Areas in which they were collected, bias (and possibly also apparent over-dispersion) can be introduced on combining data from the two Areas, as the sampling proportions differ because of the different sizes of the populations in these Areas. The base-case estimator chooses an age-independent M value of 0.030yr^{-1}, although the associated lower confidence bound hits the constraint boundary of 0.01yr^{-1} (see Table 11). The associated recruitment trend estimate, together with those for some other fixed age-independent values of M, is shown in Fig. 7. For this case, the confidence limits do exclude the possibility of a downward trend in historic recruitment.

The base-case estimator's formulation of two estimable selectivity-at-age parameters ($S^c_{17} = S^c_{20}$ and $S^s_2 = S^s_5$), which was based on analysis of results for Area IV data alone, could have been re-evaluated for the assessments above. However, it was decided to maintain the same format here in the interests of comparability.

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[24] Although the point estimate of CV_{add} at the Area level provided by the procedure of Punt *et al.* (1997) is 0, a coarse Bayesian analysis based on a U[0,1] prior provides a posterior median of about 0.08, so that 0.1 seems a reasonable value to examine for sensitivity purposes.

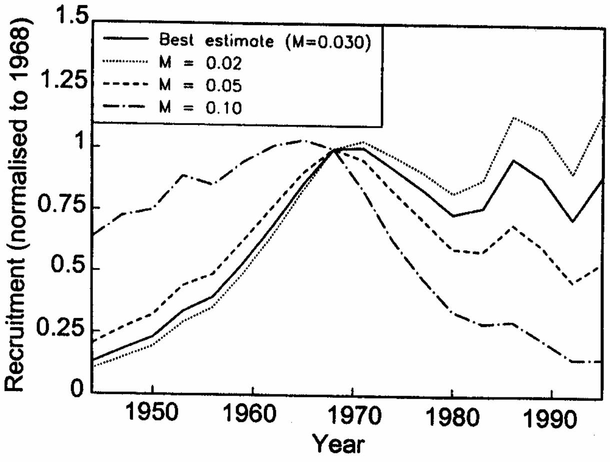

Fig. 7. Estimates of recruitment ($N_{y,2}$) for an assessment of the data for Area IV and Area V combined (see text for details) for fixed values of natural mortality $M = 0.02$, 0.05 and 0.10yr^{-1}. The full line shows the result for the base-case estimator, which estimates $M = 0.030$yr^{-1}. Each series is normalised to its 1968 level.

THE POTENTIAL IMPROVEMENT IN ESTIMATION PERFORMANCE FOR AREA IV GIVEN FURTHER DATA

Methods

Addressing this issue by means of simulation testing requires the development of an operating model of the actual underlying resource dynamics, from which (pseudo) data can be generated to which estimators are then applied to assess their statistical properties. Sensibly, such a model must be consistent with ('conditioned upon') existing data.

The base-case operating model chosen for this exercise reflects the population parameter sets estimated by a variant of the base-case estimator applied to 100 replicate pseudo datasets generated by the bootstrap procedure described above. The estimator variant used is deliberately chosen to be more complex than the base-case estimator itself, so as to better test this estimator for robustness to reasonable deviations from its assumptions that could apply in practice. Thus, this variant:

(i) assumes M varies linearly with age a to a = 29 (and is constant thereafter), in contrast to the base-case estimator's assumption of independence of a;

Table 10

Results for the application of the base-case estimator to the data for Area V.

(a) Numbers-at-age matrix $N_{y,a}$ ($\hat{M} = 0.010$ - constraint boundary).

Year	Age 2	5	8	11	14	17	20	23	26	29	32	35	38	41	44	Total
1947	295	-	-	-	-	-	-	-	-	-	-	-	-	-	-	295
1950	2,774	287	-	-	-	-	-	-	-	-	-	-	-	-	-	3,060
1953	4,824	2,691	278	-	-	-	-	-	-	-	-	-	-	-	-	7,793
1956	5,425	4,681	2,612	270	-	-	-	-	-	-	-	-	-	-	-	12,987
1959	7,971	5,264	4,542	2,535	262	-	-	-	-	-	-	-	-	-	-	20,573
1962	10,832	7,735	5,108	4,408	2,460	254	-	-	-	-	-	-	-	-	-	30,797
1965	13,789	10,511	7,506	4,957	4,278	2,387	247	-	-	-	-	-	-	-	-	43,674
1968	17,535	13,381	10,200	7,284	4,810	4,151	2,316	239	-	-	-	-	-	-	-	59,917
1971	19,410	17,016	12,985	9,899	7,068	4,668	4,028	2,248	232	-	-	-	-	-	-	77,554
1974	19,035	18,835	16,512	12,601	9,606	6,859	4,530	3,909	2,181	225	-	-	-	-	-	94,294
1977	21,200	18,451	18,217	15,898	12,099	9,195	6,570	4,324	3,746	2,088	216	-	-	-	-	112,005
1980	19,816	20,535	17,635	17,315	14,954	11,254	8,497	6,065	4,014	3,494	1,931	171	-	-	-	125,681
1983	20,742	19,173	19,754	16,799	16,469	14,128	10,471	7,989	5,647	3,644	3,199	1,792	88	-	-	139,894
1986	22,492	20,014	18,235	18,705	15,736	15,302	13,052	9,650	7,387	5,203	3,390	3,004	1,681	52	-	153,903
1989	21,538	21,767	19,276	17,499	17,853	14,923	14,367	12,253	9,059	6,901	4,890	3,217	2,853	1,617	37	168,052
1992	13,894	20,879	21,091	18,682	16,950	17,289	14,457	13,922	11,874	8,787	6,686	4,741	3,118	2,765	1,569	176,703
1995	21,406	13,450	20,208	20,404	18,061	16,391	16,723	13,974	13,453	11,472	8,494	6,463	4,580	3,010	2,676	190,766

(b) Selectivity and relative bias.

	Age 2	5	8	11	14	17	20	23	26	29
Selectivity - commercial S_a^c	-	-	-	-	-	0.984	0.984	1	1	1
- scientific S_a^s	0.768	0.768	1	1	1	1	1	1	1	1
Relative bias q (JARPA = q.IDCR)	0.370									

(c) 'Apparent' selectivity $S^*_{y,a}$

Year	Age 2	5	8	11	14	17	20	23	26	29
1974	0.09	0.25	0.60	0.80	1.03	0.99	1.24	0.94	1.03	1.03
1977	0.04	0.35	0.48	0.71	0.97	1.11	1.13	1.01	0.90	1.09
1980	0.06	0.16	0.34	0.37	0.49	0.77	0.58	0.75	1.20	1.05
1983	0.12	0.43	0.52	0.75	0.92	1.04	1.09	1.02	1.09	0.89
1986	0.08	0.22	0.33	0.49	0.67	0.96	0.97	0.96	1.10	0.93
1989	0.72	1.02	0.85	1.27	1.43	1.14	1.01	0.90	0.28	1.12
1992	0.64	0.71	0.82	1.00	0.92	0.86	1.05	1.12	1.18	1.06
1995	0.81	1.05	1.22	1.23	1.14	0.98	1.01	0.78	0.91	0.73

Table 11

Comparative point estimates for application of the base-case estimator to data for Area IV, Area V and the two Areas combined. Figures in parenthesis are bootstrap 90% confidence intervals.

Area	$N_{y,2}$ incr. rate 47-68	$N_{83,2}/N_{68,2}$	$N_{95,2}/N_{68,2}$	$\overline{M}$	N_y incr. rate 80-95
IV	0.055	0.411	0.465	0.057	-0.011
	[0.014; 0.091]	[0.214; 0.729]	[0.147; 1.334]	[0.018; 0.101]	[-0.056; +0.032]
V	0.139	1.159	1.103	0.010[1]	+0.025
	[-0.016; 0.108]	[0.192; 1.330]	[0.052; 1.797]	[0.010[1]; 0.133]	[-0.104; +0.032]
IV + V	0.083	0.764	0.894	0.030	+0.012
	[0.047; 0.110]	[0.449; 1.142]	[0.320; 1.911]	[0.010[1]; 0.073]	[-0.029; +0.037]

[1] Constraint boundary.

Table 12

Results of simulation trials for the base-case estimator for Area IV.

		Operating model					
Statistic		Simple (=Estimator)	Base-case	Double future catches	Continue to 2013	Base-case but estimate linear trend in M	Base-case but estimate selectivity slope
$N_{y,2}$ incr. rate 47-68	Mean true	0.053	0.063	0.063	0.063	0.063	0.063
	Mean est.	0.050	0.049	0.049	0.047	0.046	0.049
	RMSE	0.014	0.024	0.024	0.023	0.025	0.024
$N_{83,2}/N_{68,2}$	Mean true	0.415	0.359	0.359	0.359	0.359	0.359
	Mean est.	0.396	0.388	0.380	0.379	0.386	0.388
	RMSE	0.100	0.095	0.092	0.068	0.093	0.095
$N_{95,2}/N_{68,2}$	Mean true	0.520	0.413	0.413	0.413	0.413	0.413
	Mean est.	0.473	0.452	0.428	0.431	0.450	0.452
	RMSE	0.231	0.188	0.170	0.118	0.186	0.188
$\overline{M}$	Mean true	0.060	0.079	0.079	0.079	0.079	0.079
	Mean est.	0.062	0.063	0.063	0.065	0.063	0.063
	RMSE	0.015	0.022	0.022	0.017	0.022	0.022
N_y incr. rate 80-95	Mean true	-0.015	-0.016	-0.016	-0.016	-0.016	-0.016
	Mean est.	-0.017	-0.016	-0.016	-0.018	-0.017	-0.016
	RMSE	0.016	0.015	0.016	0.009	0.015	0.015

(ii) allows $\hat{S}^s_2 \leq \hat{S}^s_5 \leq \hat{S}^s_8 \leq 1$ and $\hat{S}^c_{17} \leq \hat{S}^c_{20} \leq \hat{S}^c_{23} \leq 1$, compared to the base-case estimator's assumptions that $\hat{S}^s_2 = \hat{S}^s_5 \leq \hat{S}^s_8 = 1$ and $\hat{S}^c_{17} = \hat{S}^c_{20} \leq \hat{S}^c_{23} = 1$;

(iii) to avoid a large fraction of replicates with $\hat{S}^c_{23} = 1$ forced by the constraint boundary, rejects pseudo datasets for which this occurs and regenerates data to provide 100 sets for which $\hat{S}^c_{23}$ is strictly less than or equal to 1.

The base-case estimator was then applied to the actual catch-at-age and abundance data for Area IV (see Tables 1 and 3), together with future data for each replicate dataset generated in the manner outlined below.

(i) JARPA abundance estimates with expectation given by the true total abundance in the year concerned multiplied by the estimate of q for the bootstrap replicate in question, and lognormal error of CV = 0.2 (the average of the values attained in the previous JARPA SSV surveys in Area IV - see Table 3 - so that as for the base-case estimator, the assumption is made that $CV_{add} = 0$), for the seasons 1997/98, 1999/2000, 2001/02 and 2003/04 (i.e. until the end of the research programme as currently envisaged)[8,25].

(ii) A total of 330 whales are taken in each of these four seasons, of which 86% (the average for the previous scientific take) is aged and provides an age distribution generated from a multinomial distribution whose probabilities are proportional to the true numbers-at-age multiplied by the estimated scientific selectivity-at-age ($\hat{S}^s_a$) pattern for that replicate[26].

Finally, some assumption is needed concerning recruitment to enter the population in the future. Similarly to procedures followed in Butterworth *et al.* (1989; 1992), this is assumed to have expectation and variability as reflected by recent past values, so that for each replicate:

$$N^{true}_{y,2} = \gamma e^{w} \qquad w \text{ from } N(0;\sigma^2_w) \tag{22}$$

where $$\gamma = \left\{ \prod_{y=77}^{95} \hat{N}_{y,2} \right\}^{1/7}$$

$$\sigma^2_w = \frac{1}{6} \sum_{y=77}^{95} [\ell n\, \hat{N}_{y,2} - \ell n\, \gamma]^2$$

In addition to this 'base-case' test, a number of variants are also considered to examine sensitivity. These comprise:

(i) use of the base-case estimator, rather than the more complex variant above, to provide the operating model, so as to examine the estimator's capabilities under 'optimal' conditions;

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[25] Given lack of clarity about the Areas to be surveyed in future IWC cruises, results from such have not been taken into account.

[26] Account is not taken in this process for over-dispersion because there is no evidence for over-dispersion for Area IV. The impact of ageing error is also ignored here because the results in Table 9 indicate it to be insubstantial.

(ii) doubling the level of scientific take for the four future seasons in question, to ascertain the extent to which this might improve estimation performance;

(iii) continuing the programme for a further 9 years (i.e. up to a 2013/14 take and survey in Area IV) to ascertain the consequences for estimation precision;

(iv) amending the base-case estimator to one which attempts estimation of a linear trend of M with age a, to ascertain the trade-off between the consequent lesser bias, but likely greater variance from estimation of an additional parameter; and

(v) amending the base-case estimator to one which attempts estimation of a commercial selectivity slope which is non-negative.

Results and discussion

Results of the calculations detailed above are reported in Table 12 for the subset of five key statistics identified earlier. They are shown as the mean of the 100 'true' (operating model) values, the mean of the corresponding 100 estimates provided by the estimator and the root mean square error (RMSE):

$$\sqrt{\frac{1}{100}\sum_{r=1}^{100}\left(x_r^{est} - x_r^{true}\right)^2} \qquad (23)$$

where x_r^{est} and x_r^{true} are respectively the estimated and true values of quantity x for bootstrap replicate r. Furthermore, scatter plots showing (x_r^{true}, x_r^{est}) data pairs for two of the key statistics - the historic recruitment ($N_{y,2}$) rate of increase over the 1947-68 period and the age-averaged natural mortality $\overline{M}$ (see Equation (21)) - are shown in Figs 8 and 9.

It is convenient to commence comment on the results with reference to the 'optimal' case where the operating model corresponds to the base-case estimator (the 'Simple' operating model of Table 12). The scatter plots (Figs 8 and 9) do indicate some tendency towards positive bias at smaller, and negative bias at larger, true values for the two statistics to which these plots correspond. Such behaviour is not surprising because, in the absence of any future data, the estimates are equal to those given by the base-case estimator (dotted lines in Figs 8 and 9) so that the impact of future data is generally to 'move' an estimate from its current value towards the true value (assuming that the estimator is unbiased). The RMSEs for these two statistics (the historic recruitment trend and $\overline{M}$) are 1.4% and 1.5% (yr^{-1}), compared to values now (i.e. without the future four JARPA cruises in Area IV) of 2.3% and 2.5% respectively.

For the base-case operating model, the estimates of the historic recruitment trend and $\overline{M}$ are negatively biased (by 1.4% and 1.6% (yr^{-1}) respectively). The RMSEs for these two statistics are 2.4% and 2.2% (yr^{-1}) respectively. Compared to current values for these RMSEs, these estimates for 2003/4 reflect effectively no improvement for the historic recruitment trend, but an improvement in performance for $\overline{M}$ of 0.2%.

The sensitivity tests reported in Table 12 indicate little improvement in estimation performance for four of the five statistics if catches for the next four JARPA programmes in Area IV are doubled. Attempts to estimate a linear trend of natural mortality M with age a or the slope in selectivity with age for the period of commercial catches bring effectively no benefits in RMSE terms. The reason for this latter result is that the selectivity slope is determined essentially by the historic commercial catch-at-age data, which naturally remain invariant whatever future data are generated for the

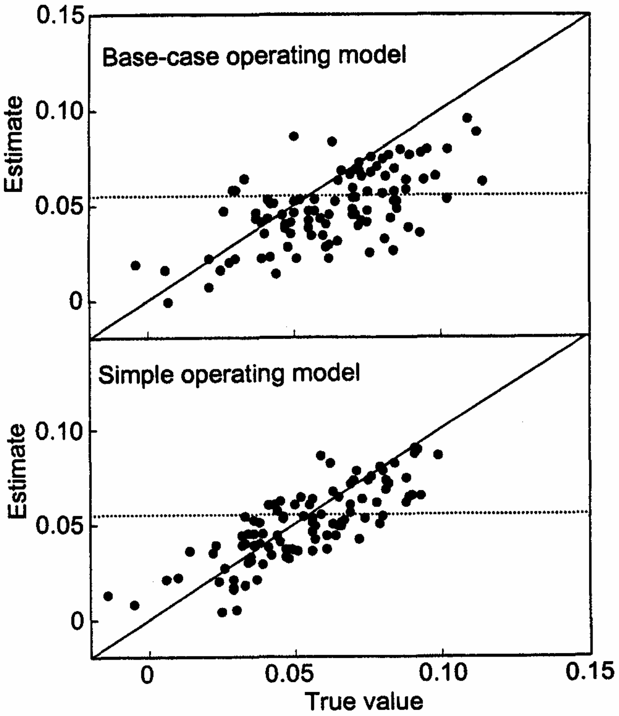

Fig. 8. A scatter plot of estimates of the historic recruitment ($N_{y,2}$) rate of increase over the 1947-68 period for Area IV provided by the base-case estimator against the corresponding true values for data sets generated by an operating model. Results are shown for the base-case operating model in the upper panel, and for the 'simple' operating model (corresponding to the base-case estimator) in the lower panel. The solid line reflects estimate = true, while the dotted lines indicate the estimate in the absence of future catch-at-age data and JARPA abundance estimates.

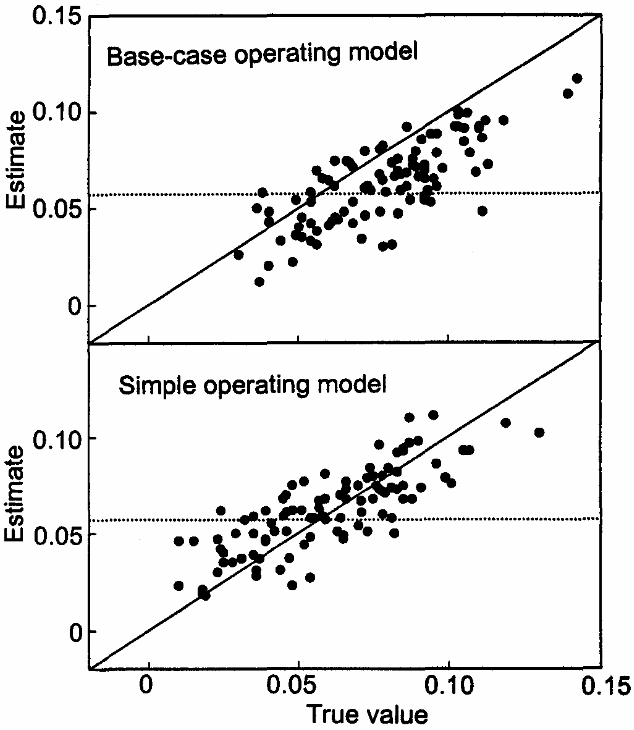

Fig. 9. Scatter plots as in Fig. 8, but here for the age-averaged natural mortality $\overline{M}$.

simulations; results for this option in Table 12 are identical to those for the base-case estimator because the best estimate of the selectivity slope β (subject here to a non-negative constraint) is $\hat{\beta} = 0$ (see Table 7) as assumed for the base-case estimator. Where distinct improvements are to be found is in continuing the programme for a longer period, which yields marked improvements in the RMSE for total population trend and recent relative recruitment level estimates, and also improves M estimation.

The reasons for the differing extents of improvement in the estimates of the historic recruitment trend and $\overline{M}$ relate to the interactions between the influences of historic commercial catch-at-age data, assumptions about the slope (β) of the commercial selectivity-at-age at older ages, and future information on abundance and catch-at-age from the JARPA programme. If the assumption of the base-case estimator that $S^c_{23} = S^c_{26} = 1$ (i.e. that the commercial selectivity-at-age was flat ($\beta = 0$) at older ages) is correct, then future data from JARPA will secure a continuing decrease over time in the RMSE's for both the historic recruitment trend and $\overline{M}$ estimates. However, if the possibility that $S^c_{26} < 1$ is admitted, the only data which have a bearing on the estimate of (the commercial catches-at-age for older ages) have already been collected. Although when S^c_{26} is treated as an estimable parameter subject to the constraint $S^c_{26} \leq 1$, these data provide a best estimate of $S^c_{26} = 1$, alternative possibilities with $S^c_{26} < 1$ are not excluded, and these alternatives cannot be resolved by the future data to be collected in the JARPA programme. These alternative possibilities also introduce negative bias into the estimate of the historic recruitment trend provided by the base-case estimator. The contribution of this bias to the RMSE will not decrease over time because future data do not address it, so that the extent to which this RMSE can drop given future JARPA data is limited. In contrast, the estimate of $\overline{M}$ depends 'equally' on data throughout the period under analysis. Thus although the base-case $\overline{M}$ estimate becomes negatively biased given the possibility that $S^c_{26} < 1$, the size of this bias (as well as the associated estimation variance and hence the RMSE) will continue to decrease over time as more JARPA data become available.

CONCLUDING REMARKS

The introduction referenced the major debate that commenced some 20 years ago concerning interpretation of the catch curve for Southern Hemisphere minke whales: whether the large negative slope at higher ages reflected a population increasing prior to exploitation, or rather simply a large natural mortality (or decreased selectivity) for those ages. The additional data provided by the JARPA programme would appear now to have contributed to resolution of this issue. The base-case estimator for Area IV indicates an upward trend in minke whale recruitment prior to the onset of exploitation (the 1947-68 period) of 5.5% per annum, with a 90% confidence interval of [1.4%; 9.1%]. This estimate is sensitive to assumptions about the slope of the commercial selectivity-at-age for large age and to trends in the natural mortality rate over time. However, arguments based upon the distributional pattern by age of the whales and the operational pattern of the commercial whaling fleet suggest that this slope would not be negative, and hence that the recruitment trend estimate quoted above is negatively biased. Even if this commercial selectivity did decrease as a result of preferentially older animals being unavailable in the pack-ice, the selectivity for the scientific catch would decrease similarly, with the result that the conclusion concerning the historic recruitment trend is unaffected. Furthermore, if this commercial selectivity slope is estimated from the data without the constraint that it cannot be negative, the 90% confidence interval for the recruitment trend estimate remains entirely positive. (This result requires effectively only the weak assumption of separability in expectation of the commercial fishing mortality for ages from 17 to 29.) Similarly, the most likely reason for the natural mortality to change with time - density dependence - would also introduce negative bias into this recruitment trend estimate. Analysis of the Area V data provides a higher point estimate for this recruitment trend, but with poorer precision that does not exclude the possibility of negative values, though combining data for Areas IV and V again produces a statistically significant positive historic trend estimate. Note that not all the available IWC abundance data have been included in these computations - incorporation of such extra data would improve estimation precision.

Resolution of the issue of whether and at what rate Southern Hemisphere minke whales may have increased prior to exploitation is of management importance for two reasons. First, the rate of increase relates to the matter of a range of plausible values for MSY rate (*MSYR*)[27] for minke whales which is a key input to Revised Management Procedure *Implementation Simulation Trials* (IWC, 1993; 1994; 1995b), but one for which there is currently little definitive evidence. Secondly, whether or not the earlier heavy depletion of the large baleen whales (e.g. blue whales) in the Southern Hemisphere by excessive catches may have resulted in a biological interaction response in the form of an increase in the then unexploited minke whales is of importance in interpreting future data and formulating management goals for the Southern Ocean ecosystem overall.

For Area IV, the present estimate of (age independent) M from the assessment is 5.7%yr^{-1}. By the planned end of the current JARPA programme, the RMSE of this estimate should be reduced from 2.5% at present to 2.2% - where both these values are to quite some extent reflective of negative bias arising from possible positive slope in the commercial selectivity-at-age (S^c_a) at older ages which the base-case estimator assumes to be zero. Data for Area V suggest a lower value for M, but the results are less precise than for Area IV. Combining data for the two Areas yields an estimate for M of 3.0%yr^{-1}. Given the data available, there is effectively no advantage for estimating population trend statistics in attempting to estimate trends in M with age, rather than assuming M to be age-invariant (even if it does depend on age in reality).

A notable feature of the base-case assessment results, particularly for Area IV and to a lesser extent for Areas IV and V combined (see Figs 2, 6 and 7), is the marked drop in recruitment indicated over the period from 1970 to the mid-1980s (the higher the value of M, the larger this drop). This drop does not constitute any cause for concern about the population: for example, given the base-case assessment for Area IV, and the current population size of some 57,000 animals, the recruitment ($N_{y,2}$) needed for a stable population is about 9,000, which is similar to the lower recruitment levels experienced since the drop (see Table 5a). The size of this drop in recruitment may also in part reflect the use of negatively biased estimates of absolute abundance from the

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[27] *MSYR* is the ratio of *MSY* to *MSYL*, the last being the population size at which *MSY* is achieved.

IWC surveys (see Table 8), but even so some further explanation for this feature needs to be sought. Some possibilities are:

(i) super-compensation (a drop in the absolute recruitment level - see Holt, 1985; Butterworth and Best, 1990) as the population approached its new larger (e.g. following depletion of 'competitors') carrying capacity;
(ii) increased competition from those 'competitors' as they recover following protection from harvesting;
(iii) poorer environmental conditions for reproductive success (in which case, one would seek independent corroborative evidence); and
(iv) violation of certain assumptions underlying the estimator.

Possibilities (i) and (ii) are investigated further in Butterworth and Punt (1999). One possibility in regard to (iv) is that the Areas for which the assessments are conducted may not encompass (as near as makes no odds) closed populations, and further that there have been systematic temporal trends across Areas in the migration of certain age groups over the period analysed. Insofar as this may have happened between Areas IV and V, the difficulty is resolved by assessing the two Areas combined. However, this does introduce a further technical complication, as bias can be introduced on combining random samples of differing age-distributions from two Areas, if the associated sampling proportions differ because of the different sizes of the populations in these Areas. Further investigations might address the matter of adjusting the estimation process to correct for this effect.

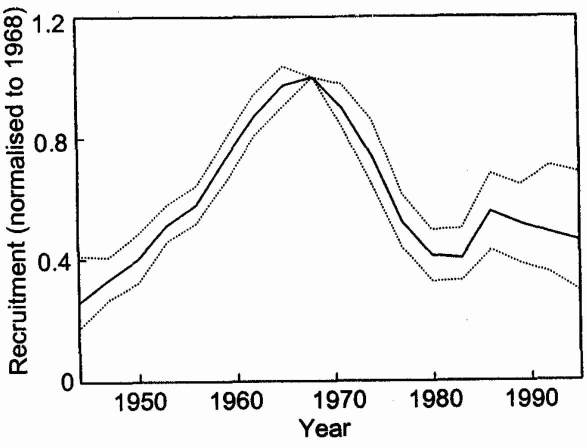

Fig. 10. Bootstrap estimates of medians (solid line), and 5%- and 95%-iles (dotted lines), for recruitment $N_{y,2}$ (relative to its estimated 1968 level for the corresponding bootstrap replicate) for Area IV for the base-case estimator when M is fixed at its corresponding best estimate of $0.057yr^{-1}$. Whereas the confidence intervals in Fig. 5 reflect sampling variability in both survey abundance estimates (and hence particularly uncertainty in the estimate of M) and the catch-at-age data, the intervals for this plot reflect only the latter source of variability.

Even if the low precision of the abundance estimates leads (for the moment) to relatively poor precision in estimates of M, and hence still to relatively large confidence intervals in overall recruitment trend estimation, what is clear from these analyses is that the availability of catch-at-age data allows good estimation of patterns of inter-annual changes in recruitment. This is suggested by Figs 1 and 2, and more clearly demonstrated by Fig. 10. This last Figure shows confidence intervals for relative recruitments for Area IV as estimated by the base-case estimator, but conditional on that estimator's best estimate of an age-independent value of M = 0.057yr-1. Note that these intervals are relatively narrow, and in particular much reduced compared to those in Fig. 5 which also incorporate uncertainty in the estimate of M. The availability of catch-at-age data for this population thus allows for the provision of a much finer probe for the investigation of possible links of environmental factors to minke whale reproductive success (and hence population 'health') than would survey estimates of total abundance alone.

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Appendix

SPECIFICATION OF THE CATCH-AT -AGE MATRICES

The catch-at-age matrix for Area IV used in this paper is obtained by pooling the annual sex-specific catch-at-age matrices and then combining the results into combination ages and combination years.

The catches-at-age by sex are computed differently for the periods of commercial and scientific catches because a much greater fraction (86% compared to 32%, on average) of the scientific catch is aged. The annual catch-at-age vector for each sex for the scientific catch is obtained by scaling the sex-specific age-frequency obtained from aged animals upwards to the total catch by sex, i.e.:

$$\begin{aligned} C^m_{y,a} &= C^m_y \, C^{m*}_{y,a} \Big/ \sum_{a'} C^{m*}_{y,a'} \\ C^f_{y,a} &= C^f_y \, C^{f*}_{y,a} \Big/ \sum_{a'} C^{f*}_{y,a'} \end{aligned} \qquad (A.1)$$

where: $C^{m/f}_{y,a}$ is the estimated catch of males / females of age a during year y,

where: $C^{m/f*}_{y,a}$ is the number of males / females caught during year y and assigned to be age a, and

where: $C^{m/f}_{y}$ is the total catch of males / females during year y.

The single animal in the 1989/90 Area IV catch which was not sexed is allocated *pro rata* between males and females. The small sample size for the scientific catch makes the application of more complicated methods such as that used for the commercial catches of little benefit.

The catches-at-age by sex for the period of commercial catch are obtained by applying annual sex-specific age-length keys constructed from the subset of the catches aged by Japanese scientists to the sex-specific length-frequencies for Japan and the (former) USSR:

$$\begin{aligned} C^m_{y,a} &= \sum_{l} A^{m,l}_{y,a} \, C^{m,l}_y \\ C^f_{y,a} &= \sum_{l} A^{f,l}_{y,a} \, C^{f,l}_y \end{aligned} \qquad (A.2)$$

where: $C^{m/f,l}_{y}$ is the catch during year y of males/females in (1m) length-class l, and

$A^{m/f,l}_{y,a}$ is the probability that a male/female in length-class l caught during year y is of age a (i.e. the relative frequency of males/females of age a in the column of the age-length key for year y for length-class l), as determined by ageing by Japanese scientists.

The age-length keys do not include data for all length-classes. This is generally not a major concern for the analyses of this paper, but there are some instances where animals in those length-classes were caught. To overcome this problem, the age-frequency for the 'nearest' length-class is used when applying Equation (A.2). The 'nearest' length-class is selected by examining whether data are available for any of the adjacent length-classes (starting with greater length) and examining length-classes further from the length-class for which age-frequency information is needed until a length-class for which data are available is found. The seven unsexed animals in the Area IV commercial catch are allocated *pro rata* between males and females.

The same overall approach is applied to provide the catch-at-age matrix used for Area V.

An initial examination of possible inferences concerning MSYR for Southern Hemisphere minke whales from recruitment trends estimated in catch-at-age analyses[1]

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ABSTRACT

A slightly modified version of the BALEEN II population dynamics model, which makes allowance for time trends in carrying capacity K, is fitted to the recruitment time series provided by the base-case ADAPT VPA assessment of the catch-at-age and survey abundance data for minke whales in Area IV reported in Butterworth *et al.* (1999). The initial increasing trend of these recruitment estimates from 1944-1968 is well fitted by the model, yielding an estimate of $MSYR_{\text{mat}}$ of some 13% (or $MSYR_{1+}$ of about 6%) which is reasonably robust to changes in a number of assumptions such as variation in the period over which K is assumed to increase. The post-1970 drop in recruitment indicated by the base-case ADAPT VPA assessment cannot be explained by the effects of catches and super-compensation alone, and requires the additional assumption of a recent decline in K. However, the need for this last assumption diminishes if allowance is made for likely negative bias in the absolute abundance estimates from the IWC surveys input to the ADAPT VPA assessments.

KEYWORDS: MINKE WHALE; INDEX OF ABUNDANCE; TRENDS; MODELLING; MSY RATE; RECRUITMENT RATE

INTRODUCTION

Butterworth *et al.* (1999) present estimates of trends in recruitment (strictly 2 year olds, given the three-year, three-age grouping system for catch-at-age data which they consider) for minke whales in Areas IV and V of the Antarctic[2], based upon the joint analysis of catch-at-age and survey abundance data. Their base-case estimator for Area IV reflects an increasing trend in recruitment of 5.5% per annum over the 1947-68 period. A further feature of their results is the marked drop in recruitment indicated from 1970 to the mid-1980s.

Butterworth *et al.* (1999) comment that this increasing trend in recruitment relates to the matter of a range of plausible values for MSY rate (*MSYR*[3]) for minke whales, which is a key input to the Revised Management Procedure *Implementation Simulation Trials*[4] (IWC, 1993; 1994; 1995), and suggest that the trend may reflect an increase in carrying capacity for minke whales linked, perhaps, to the concurrent heavy depletion of populations of large baleen whales in the Southern Ocean. They further speculate that a possible explanation for the subsequent drop in recruitment after 1970 might be the phenomenon of super-compensation (Holt, 1985; Butterworth and Best, 1990). This is a reduction in the absolute recruitment level as a population nears its carrying capacity, as illustrated, for example, in the stock-recruitment plots of Fig. 1 for $MSYR_{mat}$ values of 4% or greater.

This paper presents an initial quantitative examination of these suppositions by fitting a modified version of the BALEEN II population model (de la Mare, 1989; Punt, 1996) to the time series of recruitment estimates from two of the Area IV minke whale ADAPT VPA assessments of Butterworth *et al.* (1999). These fits are based on maximising a likelihood function. A variety of alternative parametrizations of the time-dependence in carrying capacity are examined. The primary purposes are to draw inferences about the possible value of *MSYR*, and to ascertain whether the combined effects of catches (which effectively commenced in 1970, and contribute to a reduction in recruitment through the removal of some adult females) and super-compensation are alone sufficient to explain the post-1970 recruitment trends evident in the results of the ADAPT VPA analyses.

METHODS

Modifications to the population dynamics model

Two modifications have been made to the standard BALEEN II model (de la Mare, 1989; Punt, 1996) for these analyses. These involve (i) the function relating the number of births to the number of mature females; and (ii) the time-dependence of carrying capacity.

The number of births in the BALEEN II model is governed by the equation[5]:

$$N_{y,0}^{m/f} = \begin{cases} f_{-\infty} P_y^M (1+A) & \text{if } P_y^D = 0 \\ \max(0, f_{-\infty} P_y^M (1+A(1-(P_y^D / K_y^D)^z)) & \text{otherwise} \end{cases} \qquad (1)$$

where: $N_{y,0}^{m/f}$ is the number of male/female calves at the start of year y;

$f_{-\infty}$ is the pregnancy rate at carrying capacity;

P_y^M is the number of females which have reached the age at first parturition (termed here the 'mature' females, for convenience) at the start of year y;

A is the resilience parameter (which is the primary determinant of the *MSYR*);

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[1] An earlier version of this paper was submitted to the IWC Scientific Committee as SC/49/SH22.

[2] Area IV = 70°E-130°E and Area V = 130°E-170°W; see Donovan (1991).

[3] The ratio of *MSY* to the population level, *MSYL*, at which it is achieved. The value depends upon the component of the population considered to be under harvest, as detailed later in the paper.

[4] This is because procedure performance in such trials is critically dependent on the population's productivity level, which is not well known for minke whales.

[5] Allowance is made here for the possibility that the component of the population to which density-dependence is functionally related becomes zero even though some mature females remain.

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z is the degree of compensation;

P_y^D is the size, at the start of year y, of the component of the population to which density dependence is functionally related (taken here to be the number of 'mature' females P_y^M); and

K_y^D is the carrying capacity, at the start of year y, for the component of the population to which density dependence is functionally related.

This relationship is illustrated in the top panel of Fig. 1 for various values of the *MSYR* in terms of the mature component of the population ($MSYR_{\text{mat}}$). As this figure shows, it leads to zero births for sizes of the pertinent component of the population larger than $(1 + A^{-1})^{1/z}K_y^D$. If the population overshoots carrying capacity, or if carrying capacity declines rapidly over time, the number of births drops quickly to zero for relatively little overshoot, which seems unrealistic biologically. To eliminate this problem, if the number of 'mature' females exceeds their (current) carrying capacity, the assumption is made here that the number of births is equal to the number expected at carrying capacity, i.e.:

$$N_{y,0}^{m/f} = \begin{cases} f_{-\infty} P_y^M (1+A) & \text{if } P_y^D = 0 \\ f_{-\infty} P_y^M (1 + A(1-(P_y^D / K_y^D)^z)) & \text{if } 0 < P_y^D < K_y^D \\ f_{-\infty} K_y^M & \text{if } P_y^D \geq K_y^D \end{cases} \quad (2)$$

as illustrated in the lower panel of Fig. 1.

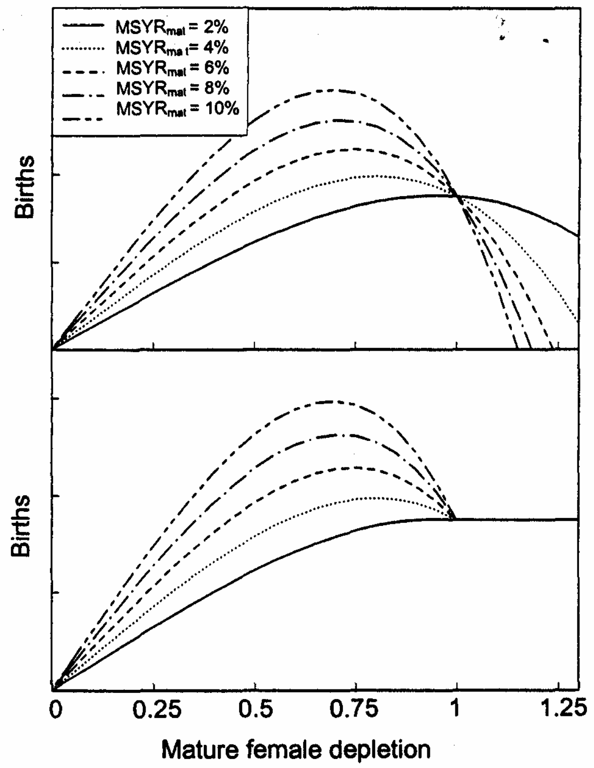

Fig. 1. The upper panel shows plots of births as functions of mature female depletion for the standard BALEEN II model, as given by Equation (1). The plots are evaluated for the values of biological parameters specified in the text, and shown for different values of $MSYR_{\text{mat}}$. The lower panel shows the modification adopted for this paper (Equation 2), for which the number of births remains constant for depletions above 1 (i.e. for $P^D > K^D$).

The second modification to the BALEEN II model relates to the time-dependence of carrying capacity, *K*. The current version of BALEEN II allows *K* to change in a piecewise linear fashion where the years in which changes in *K* occur are pre-specified. This has been generalised here to allow *K* to change in a non-linear fashion between pre-specified years. For example, if *K* changes between the years y_i and y_{i+1}, the time dependence of *K* is given by:

$$K_y = a + by^{\beta} \qquad y_i \leq y \leq y_{i+1} \quad (3)$$

where *a* and *b* are chosen to effect continuity at the end points of this period.

Specification of a scenario regarding the time dependence of *K* therefore involves choosing a value for β and selecting the years in which the relationship between *K* and time changes (i.e. $\{y_i\text{: } i = 1,2,\ldots,m\}$). For simplicity, it is assumed that *K* is constant from the first year considered in the analysis (1920) to year y_1, and also constant from year y_m to the last year considered in the analysis (1996).

Likelihood function

The population dynamics model is fitted to the estimates of age 2 abundance from the ADAPT VPA assessments (Butterworth *et al.*, 1999) by assuming that these estimates are normally distributed about the modified BALEEN II model estimates[6]. Additive (normal) rather than multiplicative (log normal) error is assumed because bootstrap estimates of variance for these abundance estimates are more suggestive of the former - see fig. 10 of Butterworth *et al.* (1999). This leads to minimisation of the following negative log likelihood (after removal of constants) for $MSYR_{\text{mat}}$, K_{1920}^D and $\{K_i^D/K_1^D\text{: } i = 2,\ldots\}$[7]:

$$-\ell nL = n\ell n\hat{\sigma} + n/2 \quad (4)$$

where: $\hat{\sigma}$ is the 'residual' standard deviation, and is given by

$$\hat{\sigma} = \sqrt{\frac{1}{n}\sum_{y}(\tilde{N}_{y,2} - \tilde{N}_{y,2}^{VPA})^2} \; ; \quad (5)$$

$\tilde{N}_{y,2}^{VPA}$ is the ADAPT VPA estimate of the abundance of animals assigned to age 2 and year *y* under the three-year, three-age grouping system used by Butterworth *et al.* (1999);

$\tilde{N}_{y,2}$ is the model quantity corresponding to $\tilde{N}_{y,2}^{VPA}$

$$\tilde{N}_{y,2} = \sum_{y'=y-1}^{y+1}(R_{y',2}^f + R_{y',2}^m + U_{y',2}^f + U_{y',2}^m) \; ; \quad (6)$$

$R_{y,2}^{m/f}$ is the number of recruited males/females of age 2 at the start of year *y*;

$U_{y,2}^{m/f}$ is the number of unrecruited males/females of age 2 at the start of year *y*; and

n is the number of years for which ADAPT VPA estimates of age 2 abundance are available.

For the purposes of the preliminary examination, the estimates of $MSYR_{\text{mat}}$ are constrained to lie in the range [0, 15%] while the estimates of K_i^D/K_1^D are forced to lie in the range [0, 15].

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[6] The information on abundance from the IWC cruises and from the JARPA programme are not included in the likelihood function, as they are already taken into account in the ADAPT VPA assessments used to obtain the estimates of age 2 abundance.

[7] By definition $K_{1920}^D = K_1^D$.

Catch data and biological parameter values

Analyses in this paper consider minke whales in Area IV and use the annual catch data for this Area. The (age- and sex-independent) rate of natural mortality, M, is set equal to 0.057 yr^{-1} (the value estimated for the base-case ADAPT VPA assessment of Butterworth *et al.* (1999), for which the corresponding estimates of age 2 abundance are given in Table 1). The proportion of 'mature' females is defined by a logistic curve where 50% of animals reach first parturition at 8.5 years and 95% by 11.5 years. The first age at which an animal may reach first parturition is set equal to 3 years. Density-dependence is assumed to act on the mature female component of the population.

It is necessary to account for the commercial and scientific take catches differently because the selectivity patterns for these two periods are quite different (see table 5(c) of Butterworth *et al.*, 1999). This has been achieved here by assuming that the commercial catches were taken uniformally from the mature component of the population, while the scientific catches were taken uniformally from the 1+ component of the population[8].

Variance estimation

Three alternative methods are used to quantify uncertainty. Two of these condition on the ADAPT VPA point estimates (the recruitment estimates and the (age-independent) value for M) while the third considers the imprecision in the ADAPT VPA output.

For the analyses conditioned on the ADAPT VPA point estimates, the (conditioned) parametric bootstrap approach is used to estimate coefficients of variation and, in conjunction with the percentile method, to estimate 95% confidence intervals. The (conditioned) parametric bootstrap approach is described in detail by Punt and Butterworth (1991), so that only the details of how the artificial datasets are generated will be outlined here. The age 2 abundance for year y and artificial data set U, $\tilde{N}^{VPA,U}_{y,2}$, is generated using the formula:

$$\tilde{N}^{VPA,U}_{y,2} = \hat{\tilde{N}}_{y,2} + \varepsilon^U_y \qquad \varepsilon^U_y \sim N(0;\hat{\sigma}^2) \qquad (7)$$

where: $\hat{\tilde{N}}_{y,2}$ is the estimate of $\tilde{N}^{VPA}_{y,2}$ obtained by fitting the model to the actual ADAPT VPA output; and

$\hat{\sigma}$ is the estimate of the residual standard deviation obtained by fitting the model to the actual ADAPT VPA output, and is sufficiently small compared to the recruitment estimates themselves, that the potential problem of Equation (7) generating negative values does not arise in practice.

The profile likelihood method (Press *et al.*, 1988; Venzon and Moolgavkor, 1988; Schnute, 1989) is also used to calculate a 95% confidence interval for $MSYR_{\text{mat}}$. This method is, however, not used for any other model outputs because it is highly intensive computationally (especially for model outputs which are not estimable parameters of the model).

The ADAPT VPA output upon which the estimation is conditioned is subject to considerable imprecision (see fig. 5 and table 11 of Butterworth *et al.*, 1999). The impact of this imprecision can be examined by applying the estimation procedure of Equation (4) above, to each of 100 ADAPT VPA bootstrap outputs. Each of these contain a time-series of recruitment estimates and a value of the (age-independent) rate of natural mortality. Coefficients of variation and 95% intervals for the estimated quantities can be calculated from the 100 sets of results obtained by fitting to the 100 sets of outputs.

Specification of analyses

In order to fully define an analysis, it is necessary to provide specifications for the following (the options considered in this paper are given in parenthesis).

(a) The number of years of ADAPT VPA age 2 abundance estimates to consider (1944-1968; 1944-1995). The rationale for considering these two periods is explained below.

(b) The value of the parameter in Equation (3) which determines the extent of non-linearity in the time-dependence of K over the period, $y_1 \leq y \leq y_2$, β (0.5, 1, 2). The choice $\beta = 1$ (i.e. linearity) has been made for the base-case on the basis of simplicity.

(c) The years in which the relationship between K and time changes (a variety of choices involving either two or three changes are considered).

(d) The value of $MSYL_{\text{mat}}$ (0.5, 0.6, 0.7, 0.8).

RESULTS AND DISCUSSION

Two ADAPT VPA assessments from Butterworth *et al.* (1999) are considered in this initial examination. The first corresponds to their base-case estimator, while the second is for the case when the absolute estimates of abundance (from dedicated IWC surveys) input to that estimator are doubled. There are two particular reasons for considering this second case. The first is that the IWC cruise abundance estimates are likely to be negatively biased to some extent (IWC, 1991, pp.58-9) as a result of factors such as the incomplete area coverage by these surveys, and the assumption in the analysis of their results that all whales on the trackline are seen (i.e. that $g(0) = 1$). For example, the 'equivalent northern boundaries' abundance estimates of Punt *et al.* (1997) used for the computations of Butterworth *et al.* (1999) pertain to open ocean areas south of latitude 60°S only, and furthermore to only portions of those regions (some 80% for Area IV and 60% for Area V). Secondly, the estimated recruitment trend after 1970 is notably different in this case, reflecting a much smaller drop in relative terms. The two ADAPT VPA recruitment series considered are listed in Table 1.

The analyses of the paper are conducted in two stages. In the first, only the initial increasing recruitment trend (over 1944-68) from the ADAPT assessment is fitted by the modified BALEEN II model, and under very simple assumptions concerning the time trend in K: constant to year y_1, increasing (usually linearly) until year y_2, and thereafter constant again at the higher value reached. The purpose of this exercise is twofold: first to see whether or not inferences about the value of $MSYR$ drawn from such model fits are robust to variations in the model assumptions, and this in circumstances where such $MSYR$ estimates are not perhaps biased by lack of fit for years subsequent to 1968 as a result of model misspecification; and secondly to examine how well such model fits are able to predict the post-1970 recruitment estimates provided by the ADAPT VPA assessments.

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[8] This reflects the maximum flexibility which the available computer code for the BALEEN II model admits.

The results of this exercise for the base-case ADAPT VPA assessment are shown in Table 2a for various choices for y_1, y_2, $MSYL_{\text{mat}}$ and β (the parameter determining the linearity or otherwise of the increasing trend in K between years y_1 and y_2 - see Equation 3). Essentially variations are performed on a base-case specified by the choice of $MSYL_{\text{mat}}$ equal to the value of 0.6 conventionally assumed by the IWC Scientific Committee, $\beta = 1$ (linearity for simplicity), and $y_1 = 1930$, $y_2 = 1960$ corresponding roughly to the period of heavy harvesting of the other baleen whale species around Antarctica (e.g. see Allen, 1980).

The results for a fit are summarised in the tables by 12 statistics (13 if carrying capacity is assumed to change three times rather than twice during the period 1920-1996):

Table 1

Estimates of the abundance of age 2 animals in Area IV (pooled into three-year groupings) based on two of the ADAPT VPA analyses in Butterworth *et al.* (1999).

	Analysis	
Year	Base-case	Double abundance estimates
1944	5,494	8,652
1947	7,100	11,174
1950	8,327	13,111
1953	10,722	16,840
1956	12,041	18,942
1959	15,098	24,083
1962	18,083	29,764
1965	20,322	33,887
1968	20,913	36,226
1971	18,825	34,288
1974	15,468	29,439
1977	10,904	21,967
1980	8,756	18,371
1983	8,592	19,023
1986	11,942	27,102
1989	10,640	24,187
1992	10,486	23,945
1995	9,721	22,266

(a) $MSYR_{\text{mat}}$ - *MSYR* in terms of uniform-selectivity harvesting of the mature component of the population (expressed as a percentage);

(b) $MSYR_{1+}$ - *MSYR* in terms of uniform-selectivity harvesting of the 1+ component of the population (expressed as a percentage);

(c) K_i/K_1 - the ratio of the carrying capacity at the start of year y_i to that at the start of 1920;

(d) $-\ell nL$ - the negative log likelihood (see Equation 4);

(e) σ - the estimate of the residual standard deviation (see Equation 5);

(f) P_y^m/K_y^M - the ratio of number of mature females at the start of year y to the corresponding carrying capacity (presented for $y = 1968$, 1983 and 1995);

(g) N_y^{1+} - the total (1+) population size at the start of year y (presented for $y = 1968$ and 1995); and

(h) $N_{y,2}/N_{68,2}$ - the ratio of the age 2 abundance at the start of year y (see Equation 6) to that at the start of 1968 (presented for $y = 1983$ and 1995).

Note that values for statistics (g) and (h) are available for the ADAPT VPA results as reported in Butterworth *et al.* (1999), so that these values can be compared with those forthcoming from fitting the modified BALEEN II model.

The choice made for a base-case in fact provides one of the best of the fits to the data amongst those reported in Table 2a. The only variations which provide slight improvements are those which increase $MSYL_{\text{mat}}$ to 0.7 or have K increasing quadratically rather than linearly with time over the 1930-1960 period.

The base-case fit, and those for two other variants, are shown in Fig. 2. The instance where the increase in K commences in 1920 rather than 1930 results in a markedly misspecified fit - the worst of all the variants considered in

Table 2

Summary statistics for fits of the modified Baleen II model to the estimates of age 2 abundance (1944-1968) for minke whales in Area IV from ADAPT VPA. The row 'Observed' contains values for some of the summary statistics from the output of the ADAPT VPA analyses. Profile likelihood 95% confidence interval estimates for $MSYR_{\text{mat}}$ are given in square parentheses.

									P_y^M/K_y^M			N_y^{1+}		$N_{y,2}/N_{68,2}$	
y_1	y_2	$MSYL_{\text{mat}}$	β	K_2/K_1	$MSYR_{\text{mat}}$	$MSYR_{1+}$	$-\ell nL$	σ	1968	1983	1995	1968	1995	1983	1995
(a) Base-case recruitment estimates															
Observed												77,188*	57,063	0.411	0.465
1930	1960	0.6	1	10.79	13.36 [12.33 14.39]	6.02	108.04	245	0.784	0.851	1.093	80,131	82,859	0.778	0.503
1930	1960	0.5	1	14.63	13.12 [11.48 14.24]	5.97	111.88	304	0.648	0.811	1.029	79,925	92,155	0.893	0.645
1930	1960	0.7	1	8.45	13.42 [12.52 14.20]	6.02	107.39	237	0.899	0.798	1.152	80,328	83,036	0.841	0.439
1930	1960	0.8	1	6.95	13.32 [12.28 14.42]	5.98	113.17	326	0.987	0.779	1.178	80,581	79,692	0.953	0.393
1930	1960	0.6	0.5	11.35	13.40 [12.32 14.44]	6.03	108.65	254	0.785	0.851	1.093	80,106	82,821	0.777	0.502
1930	1960	0.6	2	9.08	13.30 [12.30 14.24]	6.00	106.91	230	0.786	0.849	1.092	80,290	83,027	0.782	0.505
1920	1960	0.6	1	14.98	9.99 [8.42 11.04]	4.89	128.21	752	0.692	0.832	1.063	81,140	93,400	0.940	0.613
1930	1955	0.6	1	11.28	13.29 [12.03 14.48]	6.00	111.19	292	0.779	0.857	1.092	80,103	82,868	0.774	0.505
1930	1965	0.6	1	11.45	14.93 [13.56 15.00+]	6.50	110.78	286	0.827	0.821	1.113	79,935	82,678	0.778	0.473
1930	1970	0.6	1	12.50	14.99+[13.74 15.00+]	6.52	114.18	345	0.787	0.911	1.106	80,003	82,110	0.763	0.520
(b) 'Double abundance estimates' recruitment															
Observed												127,346*	130,939	0.525	0.615
1930	1960	0.6	1	12.52	13.71 [12.36 15.00+]	6.13	120.00	477	0.731	1.033	0.967	132,132	128,473	0.496	0.653

* The ADAPT VPA computes this quantity for ages up to 27 only.

\+ Constraint boundary.

terms of the σ values listed in Table 2 - and would therefore seem not to merit further consideration. Notable then is the fact that all the remaining variants considered yield $MSYR_{mat}$ estimates in excess of 13%, corresponding to $MSYR_{1+}$ estimates above 6%.

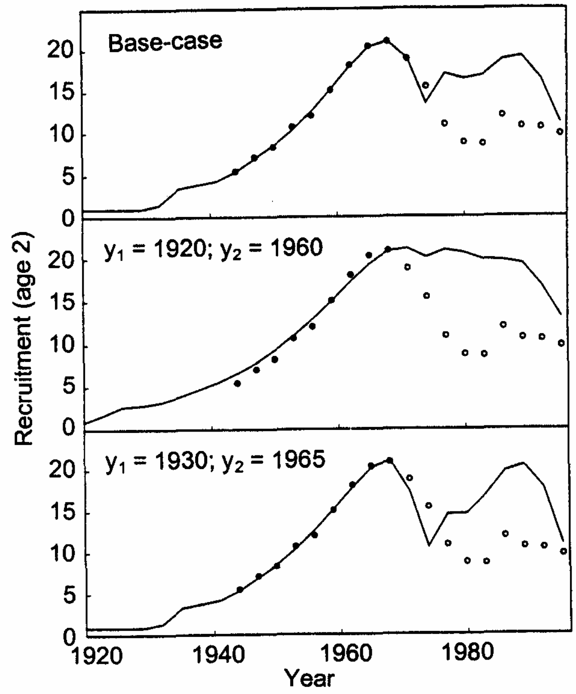

Fig. 2. Estimates of recruitment for minke whales in Area IV (age 2 abundance in thousands pooled into three-year groupings) from the base-case ADAPT VPA assessment (dots) and based on the results of fits of the BALEEN II model to the data (solid lines) The fits shown here take account of the ADAPT estimates from 1944-1968 (solid dots) only, omitting consideration of those from 1971-1995 (open dots). Results are shown for three alternative prescriptions for specifying time-dependence in carrying capacity K, which is constant to year y_1, increases to year y_2 and then is constant again (the values for y_1 and y_2 are shown in each panel).

Also apparent both from the fits shown in Fig. 2, and the tabulated values of $N_{y,2}/N_{68,2}$ in Table 2a, is that although the combination of the effect of catches and super-compensation (given the high *MSYR* estimate) do result in a drop of recruitment in the modified BALEEN II model fits after 1970, these drops are not as large as the ADAPT VPA base-case assessment results suggest. However, in Table 2b which reports results for the ADAPT VPA assessment for which the absolute abundance estimates input are doubled, this marked lack of fit essentially disappears.

Table 3 reports bootstrap CVs and 95% confidence interval estimates for all the statistics of the base-case fit considered, while profile likelihood estimates of this confidence interval for $MSYR_{mat}$ are provided for all the variants considered in Table 2. The two methods for confidence interval estimation provide virtually identical results for $MSYR_{mat}$ for the base-case. All these results reflect high precision, but are based on point estimates of recruitment and M from the ADAPT VPA. When the imprecision of these last estimates is also taken into account, CV estimates increase markedly[9] – to 20% for *MSYR* estimates, for example. Nevertheless the lower 5%-ile for $MSYR_{mat}$ remains notably large at 6.7%.

The second stage of this examination is even more preliminary, and considers what further changes in K after 1960 are necessary to have the modified BALEEN II model better reflect the post-1970 recruitment trends indicated by the ADAPT VPA assessment results. Clearly the large drop in recruitment for the base-case ADAPT assessment requires some decline in K after 1960 (the base-case choice for y_2 in Table 2). The further options considered are for this decline to continue to y_3 = 1980 or 1990, after which K again stays constant.

Table 3

Point estimates, bootstrap coefficients of variation and percentile method 95% confidence intervals (in square parentheses) for ten quantities of interest for the Area IV base-case analysis. A profile likelihood 95% confidence interval for $MSYR_{mat}$ is given in round parentheses. Results are shown both for analyses which ignore and which account for the imprecision in the ADAPT VPA estimates of recruitment and M.

Quantity	Point estimate	Ignore recruitment and M imprecision		With recruitment and M imprecision	
		CV	95% CI	CV	95% CI
K_2/K_1	10.79	0.041	[10.05 11.75]	0.491	[1.11 14.99*]
$MSYR_{mat}$	13.36	0.036	[12.36 14.32] (12.33 14.39)	0.197	[6.72 15.00*]
$MSYR_{1+}$	6.02	0.025	[5.70 6.32]	0.198	[3.34 6.70]
P^M_{68} / K^M_{68}	0.784	0.025	[0.742 0.819]	0.146	[0.600 0.997]
P^M_{83} / K^M_{83}	0.851	0.019	[0.817 0.879]	0.060	[0.729 0.932]
P^M_{95} / K^M_{95}	1.093	0.005	[1.084 1.103]	0.056	[0.904 1.149]
N^{1+}_{68}	80,131	0.006	[79,164 81,100]	0.332	[49,095 159,317]
N^{1+}_{95}	82,859	0.008	[81,886 84,317]	0.283	[61,583 160,059]
$N_{83,2} / N_{68,2}$	0.778	0.019	[0.752 0.808]	0.171	[0.563 1.122]
$N_{95,2} / N_{68,2}$	0.503	0.023	[0.483 0.529]	0.403	[0.176 1.012]

* Constraint boundary.

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[9] The intervals calculated in this way are not strictly confidence intervals, as they do not take the imprecision arising from the fit of the modified BALEEN II model to a specific set of input values into account. However, as is evident from comparison of the results in Table 3, this source of imprecision is totally dominated by that related to the imprecision of the ADAPT VPA estimates of M and recruitment, so that these estimated intervals should be reasonably representative of the overall confidence interval, and hence are, for convenience, reflected as such in Table 3.

The results of this exercise are reported in Table 4a and also shown in Fig. 3. The choice *y3* = 1980 reflects a marginally better fit. However *y3* = 1990 seems biologically more realistic. Although difficult to establish any direct cause-effect relationship, it is not inconceivable that the carrying capacity for minke whales might have been decreasing over more recent decades, perhaps reflecting some combination of partial recovery of the larger baleen whale populations under protection, increases in other, possibly competing, predators (such as crabeater seals) or changes in the physical environment (IWC, 1997); but if so, a longer period for this decrease would seem more likely than this process having come to a halt as early as 1980.

Results in Table 4a for the base-case ADAPT VPA assessment indicate that a drop of about 50% in *K* for minke whales since 1960 is necessary for the modified BALEEN II model to provide a satisfactory fit to the ADAPT recruitment trends. However, for the ADAPT variant for which absolute abundance estimates input are doubled, hardly any post-1960 change in *K* is necessary to provide a reasonable

Table 4

Summary statistics for fits of the modified BALEEN II model to the estimates of age 2 abundance (1944-1995) for minke whales in Area IV from ADAPT VPA. The analyses in this Table all assume that $MSYL_{mat}$ = 0.6, y_1=1930 and β=1. The row 'Observed' contains values for some of the summary statistics from the output of the ADAPT VPA analyses.

								P_y^M / K_y^M			N_y^{1+}		$N_{y,2} / N_{68,2}$	
y_2	y_3	K_2/K_1	K_3/K_1	$MSYR_{mat}$	$MSYR_{1+}$	$-\ell nL$	σ	1968	1983	1995	1968	1995	1983	1995
(a) Base-case recruitment estimates														
Observed											77,188*	57063	0.411	0.465
1960	1980	10.60	5.30	9.82 [8.09 11.53]	4.83	272.23	1,167	0.677	1.135	0.920	81,507	57,242	0.377	0.515
1960	1990	11.49	7.23	12.32 [10.83 14.03]	5.69	272.19	1,165	0.749	0.986	1.029	80,567	57,353	0.426	0.390
(b) 'Double abundance estimates' recruitment														
Observed											127,346*	130,939	0.525	0.615
1960	1980	11.35	12.80	13.92 [11.43 15.00+]	6.20	292.23	2,034	0.762	0.979	1.000	130,580	135,360	0.531	0.652
1960	1990	9.66	9.89	12.23 [10.87 14.80]	5.66	294.74	2,181	0.756	0.988	0.977	132,164	134,461	0.539	0.700

* The ADAPT VPA computes this quantity for ages up to 27 only.
\+ Constraint boundary.

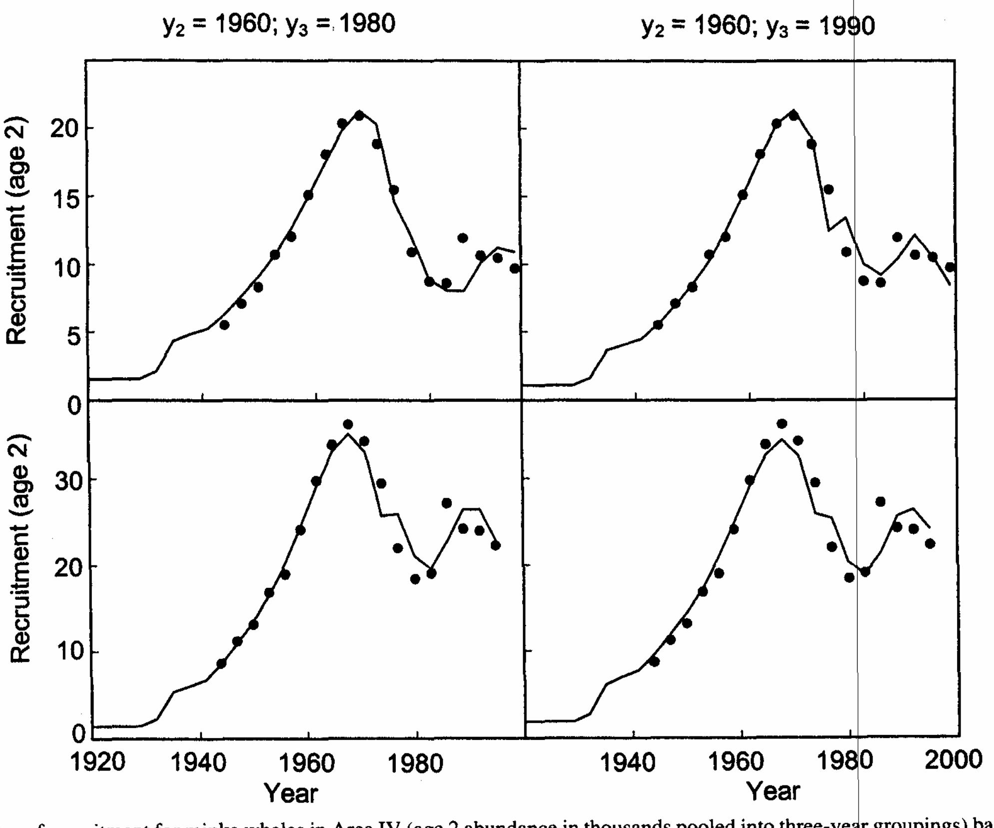

Fig. 3. Estimates of recruitment for minke whales in Area IV (age 2 abundance in thousands pooled into three-year groupings) based on ADAPT VPA assessments (solid dots) and on the results of fits of the BALEEN II model to the data (solid lines). Results are shown for fits to ADAPT VPA estimates based on two alternative analyses ('base-case' = upper panels and 'double abundance estimates' = lower panels), and for two alternative prescriptions for specifying the time-dependence in carrying capacity *K*, both of which have this first increasing from year y_1 = 1930 to year y_2, then decreasing to year y_3 after which it remains constant (the values for y_2 and y_3 are shown above the relevant panels).

fit (see Table 4b and Fig. 3). The results in Table 4 are reflective of $MSYR_{mat}$ estimates in the region of 10-14% (corresponding to $MSYR_{1+}$ of about 5-6%).

CONCLUSIONS

The most surprising result of what was conceived as no more than an exploratory exercise, is its substantial success as reflected by the good fits shown in Fig. 3, which are based only on relatively simple trends assumed for K. The base-case ADAPT VPA assessment results do require some downward trend in K in recent years to be fit adequately by the modified BALEEN II model, but the need for this adjustment is diminished if the quite plausible assumption of some negative bias in the IWC survey abundance estimates is admitted.

Thus, it seems that the post-1970 recruitment trends as estimated by the ADAPT VPA can largely (perhaps completely) be attributed to the effects of catches and super-compensation, and also that inferences can be drawn from these trends about likely values of *MSYR*.

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Blue whale (*Balaenoptera musculus*) occurrence off the Galápagos Islands, 1978-1995

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ABSTRACT

Twenty-three blue whale (*Balaenoptera musculus*) sightings made in the vicinity of the Galápagos Islands (~00°S, 90°W) between 1978-1995 are analysed. Blue whales occurred seasonally in the austral winter/spring months. A significant proportion of the sightings (13 or 56.5%) had a tendency to occur on the same day or on consecutive days in a given year. Five (21.7%) of the sightings were of groups of three or more individuals. Distribution was to the west and southwest of the Galápagos archipelago, where a plume of cool, upwelling-enriched surface water with high planktonic biomass develops during this season. Blue whales were observed feeding on surface swarms of the euphausiid *Nyctiphanes simplex* in 1993. Defecation was commonly seen. The external appearance of these whales suggests they were true blue whales (*B.m. intermedia*). Much of the evidence from this study suggests a Southern Hemisphere stock feeding west of the Galápagos during the austral winter/spring months. Alternatively, they may belong to a presumed eastern tropical Pacific stock of blue whales which exploits the productive habitats of the Costa Rica Dome and the Peruvian/Ecuadorian coast.

KEYWORDS: BLUE WHALE; PACIFIC OCEAN; SOUTH AMERICA; SANCTUARIES; OCEANOGRAPHY; SURVEY - VESSEL; INCIDENTAL SIGHTINGS; PHOTO-ID; FEEDING; EUPHAUSIIDS; HABITAT; FEEDING GROUNDS; MOVEMENTS

INTRODUCTION

All major blue whale (*Balaenoptera musculus*) populations were severely depleted by whaling operations which lasted until 1966, when they were afforded full worldwide protection by the IWC (Yochem and Leatherwood, 1985; Klinowska, 1991). In spite of this measure, and taking into account the difficulties in estimating abundance and trends in severely depleted species, their global numbers still appear to be depressed except for a stock inhabiting the eastern North Pacific from California to Baja California, whose numbers appear to be increasing (Baskin, 1993; Barlow, 1994; Barlow *et al.*, 1995; Clapham *et al.*, 1999). Hence, observations from areas where their presence is less well known are valuable in understanding their current distribution and status.

Information on blue whale occurrence in the general area of the Galápagos Islands can be summarised as follows. In 1975, a Soviet/American expedition to the eastern tropical Pacific (ETP) aboard the whaling vessel *Vnushitely* sighted aggregations of blue whales, twice in late March and once in mid-June, in a small area bounded by 08°55'N-09°07'N and 93°34'W-93°55'W (Berzin, 1978; also reported in Wade and Friedrichsen, 1979). Based on their 'behaviour and markings', Berzin (1978) identified them as pygmy blue whales (*B.m. brevicauda*), and assigned them to the 'Galapagos biostock' (a term he applied to cetacean populations presumably resident to the ETP that are characterised by their smaller body sizes). Perhaps this has led some authors (e.g. Yochem and Leatherwood, 1985; Klinowska, 1991) to state that these sightings were made 'near the Galápagos Islands', when in fact they were made in the vicinity of a productive oceanic eddy known as the Costa Rica Dome (~09°N, 89°W), some 1,100km north of the Galápagos Islands, where blue whales appear to be present year-round (Reilly and Thayer, 1990). A distinct concentration of blue whale sightings, nonetheless, has been reported off the Galápagos Islands as well (Reilly and Thayer, 1990).

Unlike sperm whales (*Physeter macrocephalus*), blue whales apparently were never hunted off the Galápagos Islands. The only expedition in the modern whaling era to visit the Galápagos was the floating factory *Tioga* in 1912, but unfortunately the catch by that expedition has not been recorded (Risting, 1922; Clarke, 1962). The waters around the Galápagos Islands are now part of a Cetacean Sanctuary created by the Government of Ecuador in 1990, covering its entire 200 mile zone of control (Evans, 1991; Merlen, 1992).

This paper discusses 23 blue whale sightings from two sources, covering the years 1978 to 1995 and discusses the possible population affinities and sub-specific identity of the whales, their behaviour and their distribution off the Galápagos in relation to the local regime of oceanic biological production.

MATERIALS AND METHODS

Study area

The Galápagos Islands are an oceanic archipelago that straddles the equator between 01°40'N-01°25'S and 89°15'W-92°00'W. The nearest land, continental Ecuador (to whom they belong), is approximately 960km to the east. They are the product of 'hotspot activity' (ocean floor volcanism) and are formed by the emerging tips of submarine volcanoes that rise from the 40,000km^2 wide Galápagos Platform, at a depth of 1,300m (Jackson, 1993).

The local climate in the Galápagos reflects large-scale oceanographic and atmospheric conditions in the ETP. There are two main seasons: from about December to May there is a hot/wet period and from about July to October there is a cool/dry period, locally known as *garúa*. The region has a strong austral character and an unusually dry climate. This is

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because the Intertropical Convergence Zone is situated north of the equator in the ETP, leaving the islands under the regime of the southeast trade winds (Chavez and Brusca, 1991). The 'thermal' equator also lies north of the geographic equator in the ETP (Fiedler *et al.*, 1992). Sea surface temperature ranges from 16-28°C, depending on season and site (Jackson, 1993).

The Galápagos are located in a region where horizontal currents and their associated water masses are particularly dynamic. The main current systems affecting the islands are: (a) the cool westward surface South Equatorial Current which bathes the Galápagos region most of the year, fed by the Peru Current System and driven by the southeast trade winds; (b) the cool eastward subsurface Equatorial Undercurrent, which is 'trapped' along the equator and is modified significantly by the Galápagos when it collides with the westernmost islands, Fernandina and Isabela, causing local topographically-induced upwelling; and (c) the warm surface North Equatorial Countercurrent, which seasonally flows eastward north of the Galápagos. A rather abrupt boundary between the water masses in the North Equatorial Countercurrent and the South Equatorial Current is known as the Equatorial Front. The Equatorial Front has a marked seasonal variation, with displacements to the north and south. At the Galápagos, it is typically between the equator and 1°N (Chavez and Brusca, 1991). Upwelling, which occurs throughout the year but increases during the cold season, brings cool, nutrient-rich waters to the surface, creating the conditions for elevated biological production (Houvenaghel, 1978; 1984). A productive oceanic habitat extends seasonally several hundreds of kilometres downstream (west) of the Galápagos (Feldman, 1986).

These mean conditions are modified periodically by the El Niño phenomenon, which causes significant changes in circulation in the tropical Pacific, increased water temperatures, decreased productivity (e.g. Fiedler *et al.*, 1992) and has important 'negative' effects on the marine life of the islands (e.g. Robinson and del Pino, 1985; Trillmich and Limberger, 1985; Smith and Whitehead, 1993).

Data sources and collection

(a) SWFSC sightings database, 1975-1993

S.B. Reilly of the National Marine Fisheries Service, Southwest Fisheries Science Center (SWFSC, La Jolla, CA, USA), compiled a sightings database for the years 1975-1993. It comprises sightings made by scientific observers aboard US research and tuna vessels operating in the ETP, as well as sightings collected by Inter-American Tropical Tuna Commission (IATTC, La Jolla, CA, USA) scientific technicians aboard US and non-US commercial tuna vessels. Reilly and Thayer's (1990) study of blue whale distribution in the ETP was based on 211 sightings through 1988 from this database, of which seven were made near the Galápagos Islands. Further SWFSC ETP cruises through 1993 resulted in 11 additional sightings from the Galápagos area being added to this database (Table 1).

Because blue whale distribution in the ETP is highly clustered in four productive upwelling areas (the Costa Rica Dome, the coast of Baja California, the Galápagos Islands and the coasts of Ecuador and northern Peru), sightings for the Galápagos in the SWFSC database were easily separated visually from those for the other areas when plotted on a map (e.g. fig. 1 of Reilly and Thayer, 1990). A criterion used in assisting this selection was to only include those sightings made south of 5°N and west of 85°W. These seemingly arbitrary boundaries are useful for two reasons. First, they are at approximately the mid-point between the two other nearby centres of blue whale abundance: the Costa Rica Dome to the north and the South American coast to the east. Blue whale sightings relative to search effort decrease as one moves away from these three centres (e.g. fig. 3 in Reilly and Thayer, 1990). Second, these boundaries approximately correspond with natural areas of lower productivity separating the productive upwelling habitats (cf. Longhurst, 1998, p.281). Indeed, other cetacean species in the ETP have similar gaps in their distribution (e.g. Wade and Gerrodette, 1993; Dizon *et al.*, 1994) that mirror the productivity gradients. The computed search effort around the Galápagos area for the years 1975-1988 combined was at least 185km

Table 1

Blue whale (*Balaenoptera musculus*) sightings off the Galápagos Islands, 1978-1995.

Date and time	Position	Number of individuals	Distance to Galápagos centre (km)	Source and vessel
9 Apr. 1978, 0701hrs	01°23'S, 93°40'W	1	362.2	SWFSC, tuna vessel
6 Oct. 1980	00°35'N, 92°37'W	6	264.2	SWFSC, tuna vessel
15 Jun. 1981, 0850hrs	02°05'S, 94°13'W	3	445.2	SWFSC, RV *Oceanographer*
15 Jun. 1981, 0912hrs	02°06'S, 94°09'W	1	439	SWFSC, RV *Oceanographer*
15 Jun. 1981, 0927hrs	02°06'S, 94°06'W	2	433.8	SWFSC, RV *Oceanographer*
15 Jun. 1981	02°05'S, 94°12'W	2	443.2	SWFSC, tuna vessel
21 Sep. 1981	02°27'S, 93°18'W	1	374.8	SWFSC, tuna vessel
19 Sep. 1986, 1616hrs	01°32'N, 101°32'W	2	1,244.6	SWFSC, RV *D.S. Jordan*
20 Sep. 1987	03°13'N, 106°06'W	1	1,780	SWFSC, tuna vessel
21 Oct. 1988, 1353hrs	02°52'S, 96°19'W	5	694.2	SWFSC, RV *McArthur*
24 Sep. 1989, 0826hrs	01°14'S, 91°19'W	2	117.5	SWFSC, RV *McArthur*
24 Sep. 1989, 0904hrs	01°16'S, 91°17'W	2	117.2	SWFSC, RV *McArthur*
20 Nov. 1989, 0739hrs	00°53'S, 109°28'W	2	2,105.8	SWFSC, RV *McArthur*
22 Sep. 1990, 1120hrs	01°48'S, 91°53'W	1	206.1	SWFSC, RV *McArthur*
22 Sep. 1990, 1340hrs	01°50'S, 91°32'W	1	182.2	SWFSC, RV *McArthur*
19 Oct. 1990, 1349hrs	03°38'S, 100°06'W	1	1,117.7	SWFSC, RV *McArthur*
21 Oct. 1990, 0847hrs	03°43'S, 95°39'W	2	670.4	SWFSC, RV *McArthur*
23 Oct. 1990, 1220hrs	09°07'S, 93°40'W	1	1,015.3	SWFSC, RV *McArthur*
15 Jun. 1993, 1550-1850hrs	01°10'S, 91°22'W	1	117.3	WCI, RV *Odyssey*
17 Aug. 1993, 0825-1800hrs	00°10'S, 91°41'W	6	133.9	WCI, RV *Odyssey*
18 Aug. 1993, 0900-1800hrs	00°02'S, 91°38'W	9	134.3	WCI, RV *Odyssey*
13 Sep. 1993, 1448-1800hrs	01°14'S, 91°40'W	1	148.6	WCI, RV *Odyssey*
Early Sep. 1995	01°11'S, 90°48'W	2	78.5	D. Day, pers. commn.

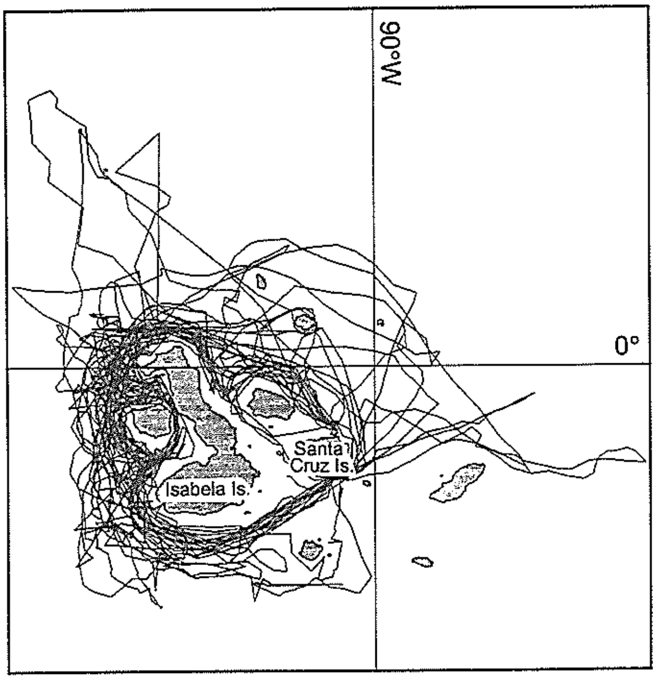

Fig. 1. Tracklines of 16 cruises off the Galápagos Islands, March 1993-March 1994, aboard R/V *Odyssey*.

per 1º latitude-longitude blocks (range: 185-1,850km). Search effort extended to 130°W, but was limited west of 100°W (see fig. 2 in Reilly and Thayer, 1990).

(b) WCI database

The second source of blue whale sightings is a database at the Whale Conservation Institute (WCI), Lincoln, MA, USA. This database consists of sightings made during 16 marine mammal cruises, conducted between March 1993 and March 1994 in waters of the Galápagos Islands, aboard the 28m ketch R/V *Odyssey* (Palacios, 1994). Fig. 1 shows the tracklines of the 16 cruises, which were spaced roughly at monthly intervals and searched mainly within the 'Galápagos Marine Reserve' [which is defined as the waters within 15 n.miles (28km) from a line joining the extremities of the islands (Comisión Permanente para las Islas Galápagos, 1992)]. One additional sighting, collected during a naturalist trip in early September 1995, was contributed by D. Day (*in litt.*, 18 January 1996), a WCI associate living in Puerto Ayora, Isla Santa Cruz, Islas Galápagos, Ecuador (Table 1).

Although topographically-induced upwelling occurs close to shore as a result of the Equatorial Undercurrent colliding with the steep slopes of the western islands, the westward flow of the South Equatorial Current carries this enriched water downstream of the Galápagos, creating a productive offshore habitat in water depths greater than 2,000m. Therefore, the great circle distance from each sighting (in both databases) to the centre of the Galápagos Islands [00°32'S, 90°31'W (Snell *et al.*, 1995)] was computed as a measure of the dispersion of the sightings about the archipelago (Table 1).

Whenever blue whales were sighted during the *Odyssey* cruises, the ship was diverted from its course to close on the animals and stay with them for as long as daylight conditions permitted. Behavioural data, identification photographs and

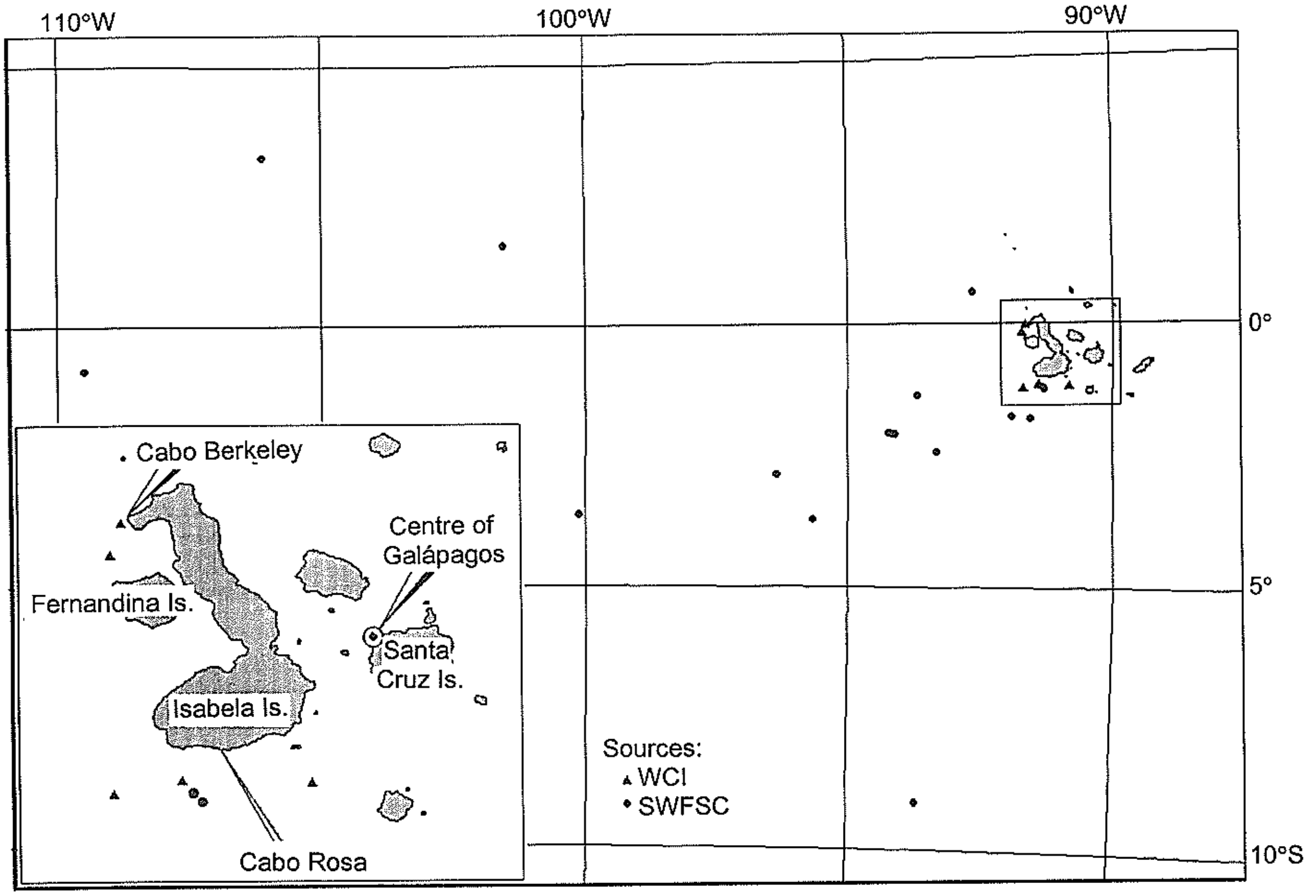

Fig. 2. Twenty-three blue whale sightings made off the Galápagos Islands, 1978-1995.

zooplankton samples were collected. Two skin biopsies from a presumed mother-calf pair were taken with biopsy darts for genetic studies (to be performed by T. Lyrholm, Department of Medical Genetics, Biomedical Center, Uppsala University, Stockholm, Sweden).

During one of these sightings (18 August 1993), a number of whales were observed dispersed over a large area. In order to estimate the number of whales present, the vessel was allowed to drift behind the whales, with the bow pointing towards them. Two observers conducted five-minute scans from a crow's nest on the main mast, 18m above the waterline, with 7.5X binoculars with a built-in compass. During each scan, observers gave the distance and the bearing of surfacing whales on either the port or the starboard bow to a third person who recorded this information. The scans were conducted over a two-hour period, with five-minute rest intervals between them. The maximum number of surfacings in each five-minute scan was averaged over the two-hour period to obtain an estimate of the total number of whales present in the area. A 'group' was defined as an aggregation of three or more animals within 100m of each other (but 'group size' could be as low as one individual, see below).

RESULTS

Seasonal and spatial distribution of the sightings

Eighteen blue whale sightings were included in the analysis after applying the above criterion to the SWFSC database. There were five sightings in the WCI database, for a total of 23 sightings involving 55 whales (Table 1). Except for one sighting on 9 April 1978, all sightings occurred in the austral winter and spring months (June through November). A significant proportion of the sightings (13 or 56.5%) had a tendency to occur on the same day or on consecutive days in a given year (4 sightings on 15 June 1981, 2 on 24 September 1989, 2 on 22 September 1990, 3 on 19-23 October 1990 and 2 on 17-18 August 1993).

Group size ranged from 1-6 animals. It was estimated that nine whales were present in the area during the sighting of 18 August 1993. The modal group size for all sightings was one, with single whales accounting for 43.5% (10) of the sightings. Pairs accounted for 34.8% (8 sightings) and groups of three or more accounted for 21.7% (5 sightings).

The spatial distribution of the sightings is presented in Fig. 2. All sightings were distributed on the western side of the Galápagos. Their distance to the centre of the archipelago ranged from 78.5-2,106km. The closest sighting to shore was made on 18 August 1993, 5.5km off Cabo Berkeley, Isabela Island. Seven of the sightings were made off the southern shore of Isabela Island. The four 1993 sightings collected aboard the R/V *Odyssey*, were made in water 2,000-3,500m deep with Beaufort sea states of 3-5. Sea surface temperature ranged from 16.7-20.9°C for these sightings.

Observations collected during the 1993 sightings aboard the R/V *Odyssey*

Physical appearance

Detailed data on the appearance and behaviour of the blue whales sighted from the R/V *Odyssey* in 1993 were collected and are summarised here. At least two pairs in the group of six individuals seen on 17 August consisted of large calves accompanied by adults (presumably their mothers, Fig. 3a); all other animals appeared to be adults, but lengths were not estimated. Coloration and pigmentation patterns were quite variable among individuals, but in general they appeared light grey, sometimes with a purplish hue. The backs were silvery grey with darker mottling; the extent of the mottling varied from light to heavy. The heads were darker and 'chevron' patterns behind the blowhole demarcated the unmottled head from the mottled back.

The calf in one of the mother-calf pairs had several small remoras of an unidentified species on the head and the back. Sessile barnacles (probably *Xenobalanus globicipitis*) clung from the tip of the dorsal fin of this animal and from the trailing edge of the flukes of another individual. One of the whales seen on 17 August had what appeared to be 'white scarring' (*sensu* Sears *et al.*, 1990) along the apex of the back in front of the dorsal fin and on its right flank (Fig. 3b). The vertebral processes were apparent behind the dorsal fin of the single animal seen on 13 September, indicating some malnourishment.

Behaviour

The single animals seen on 15 June and 13 September tended to be wary of the approaching vessel and changed directions frequently. The six individuals seen on 17 August were mostly in pairs and allowed close approach. Identification photographs and skin biopsies of one of the mother-calf pairs were obtained; one of the calves approached the vessel on two occasions. The *Odyssey* remained in the area overnight and the next morning encountered blue whales not far from where they had been seen the previous day (see Table 1). It was apparent that the number of whales had increased and that they were dispersed over a larger area. They appeared to be travelling on a general southward heading and most animals swam singly or in pairs. Rather than attempting to approach them, five-minute scans were conducted as described in the Methods.

'Side-fluking' (swimming on one side and exposing one lobe of the flukes) was frequently observed at the surface during these sightings. 'Fluking-up' (raising the flukes completely out of the water as an animal makes a deeper dive) was also seen several times, and the whales usually defecated on these occasions, leaving a large brownish-orange discoloration in the water. Large swarms of a small crustacean of similar colour to the faeces were observed in the immediate vicinity of the whales. Samples were collected with a dip-net and were identified as the euphausiid *Nyctiphanes simplex* (now in the Planktonic Invertebrates Collection of the Scripps Institution of Oceanography, La Jolla, CA, USA, under accession number PIC-960515-0001).

Photo-identification

Photographs of the flanks of six animals were compared to a catalogue of over 1,070 individuals from the eastern North Pacific population, collected in their summering grounds off the United States (compiled by Cascadia Research Collective, Olympia, WA, USA). No matches were found between the Galápagos and the North Pacific blue whales from this catalogue (J. Calambokidis, pers. comm.). A document containing photographs of the six blue whales identified off the Galápagos in 1993 (Palacios, 1998) is deposited at the SWFSC's cetacean photo-identification database (under the care of J. Barlow).

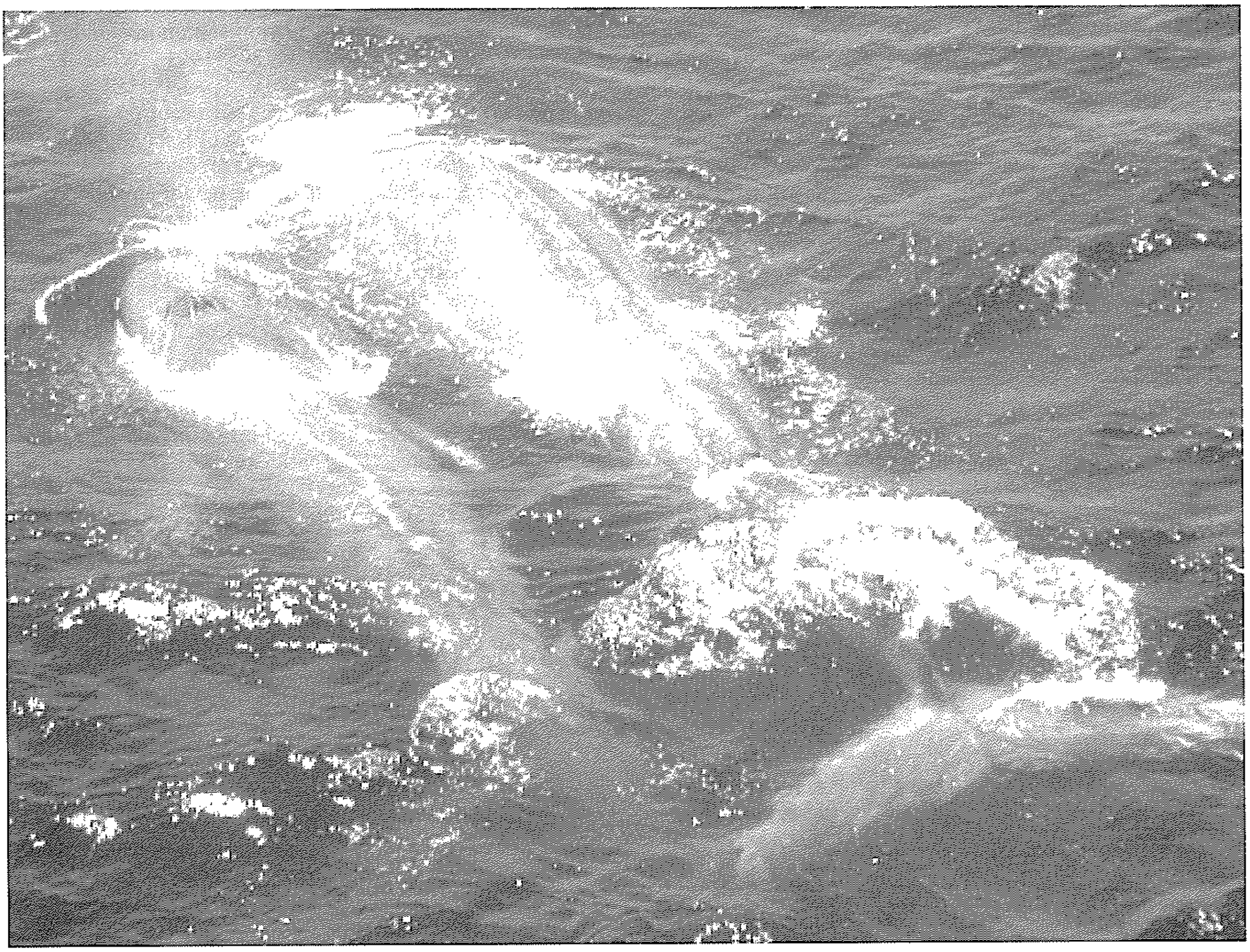

Fig. 3. (a) Mother-calf pair seen on 17 August 1993 north of Fernandina Island.

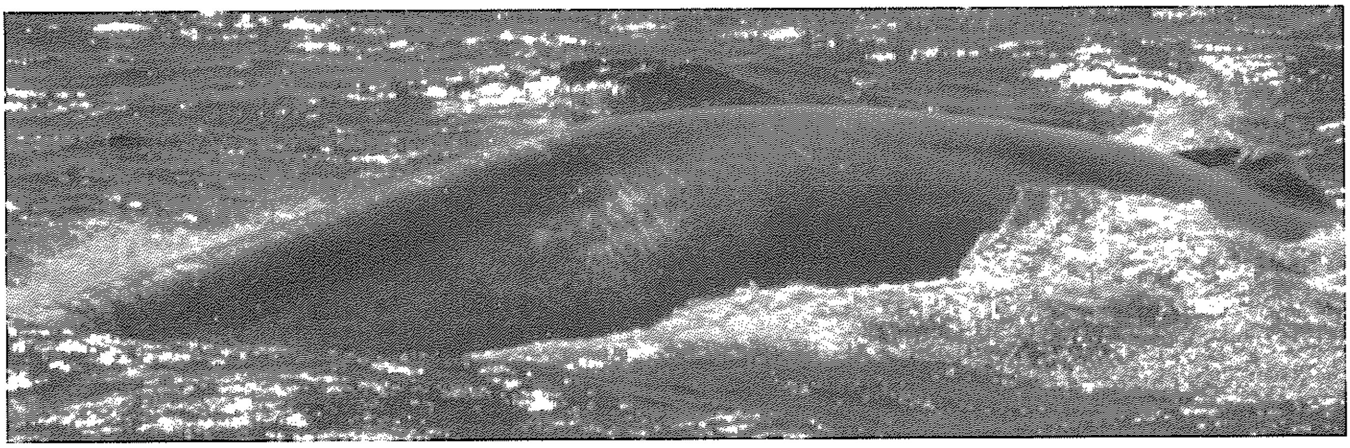

Fig. 3. (b) Presumed 'white-scarring' on the right flank and along the apex of the back of an individual seen on 17 August 1993.

DISCUSSION

Seasonality and distribution

The sightings showed a marked seasonality; all but one occurred during the austral winter and spring months. Although search effort was not uniform during the year (Reilly and Thayer, 1990; Palacios, 1994), the lack of blue whale sightings in the reports of several other researchers that have recorded cetacean presence off the Galápagos at other times of the year constitute additional evidence of seasonality (Clarke, 1962; Norris, 1967; Balridge, 1968; Whitehead, 1986; Le Boeuf *et al.*, 1988; Lyrholm *et al.*, 1992). For example, no blue whales were seen in 3,975 daylight hours of searching for and studying whales off the Galápagos between 1985-1995 during the months of January-June by a research team from Dalhousie University, Canada (H. Whitehead, pers. comm.).

The tendency for the sightings to occur on the same day or on consecutive days in a given year suggests that blue whales congregate off the Galápagos. This is supported by the relatively large fraction of groups (5 of 23) with three or more whales, as was found in Reilly and Thayer's (1990) study. This is similar to Berzin's (1978) and Wade and Friedrichsen's (1979) observations of blue whale aggregations in the Costa Rica Dome area during the first part of the year.

The area of blue whale occupation in the Galápagos extends from a few kilometres off the islands to at least 2,000km offshore, mostly west and southwest of the islands of Isabela and Fernandina (Table 1, Fig. 2). As a result of upwelling to the west of these islands and the increased westward flow of the South Equatorial Current during the austral winter/spring months, a productive habitat, clearly visible in satellite images as a plume of high phytoplankton biomass extending for hundreds of kilometres, develops seasonally downstream (west) of the Galápagos (Feldman, 1986). This distinct portion of the ocean has been termed the 'Pacific Equatorial Divergence Province' by Longhurst (1998). Several of the offshore sightings occurred near the south and north (poleward) edges of the productive plume. This distribution may be associated with the banded distribution of the equatorial zooplankton community (and that of euphausiids in particular) parallel to the plume of maximum phytoplankton biomass, with higher trophic levels being further away from the phytoplankton maximum (e.g. Vinogradov, 1981; Mackas *et al.*, 1991; White *et al.*, 1995).

The fact that several sightings also occurred near shore (including those off the southern coast of Isabela), in the core area of upwelling [where biological production has not yet developed because the nutrient-rich, newly upwelled water has not been organically conditioned (Barber and Ryther, 1969; Houvenaghel, 1978; 1984)], is perhaps related to the reproductive activity of the euphausiid *Nyctiphanes simplex* (on which the blue whales were feeding, as discussed below). This species requires the cooler waters found near centres of upwelling for breeding (Brinton, 1979; Gómez-Gutiérrez *et al.*, 1995).

It is interesting to note that blue whales had not been reported locally, either from sightings (Day, 1994) or from strandings (Palacios, 1995), prior to the 1993 observations aboard the R/V *Odyssey*, despite regular tourist vessel

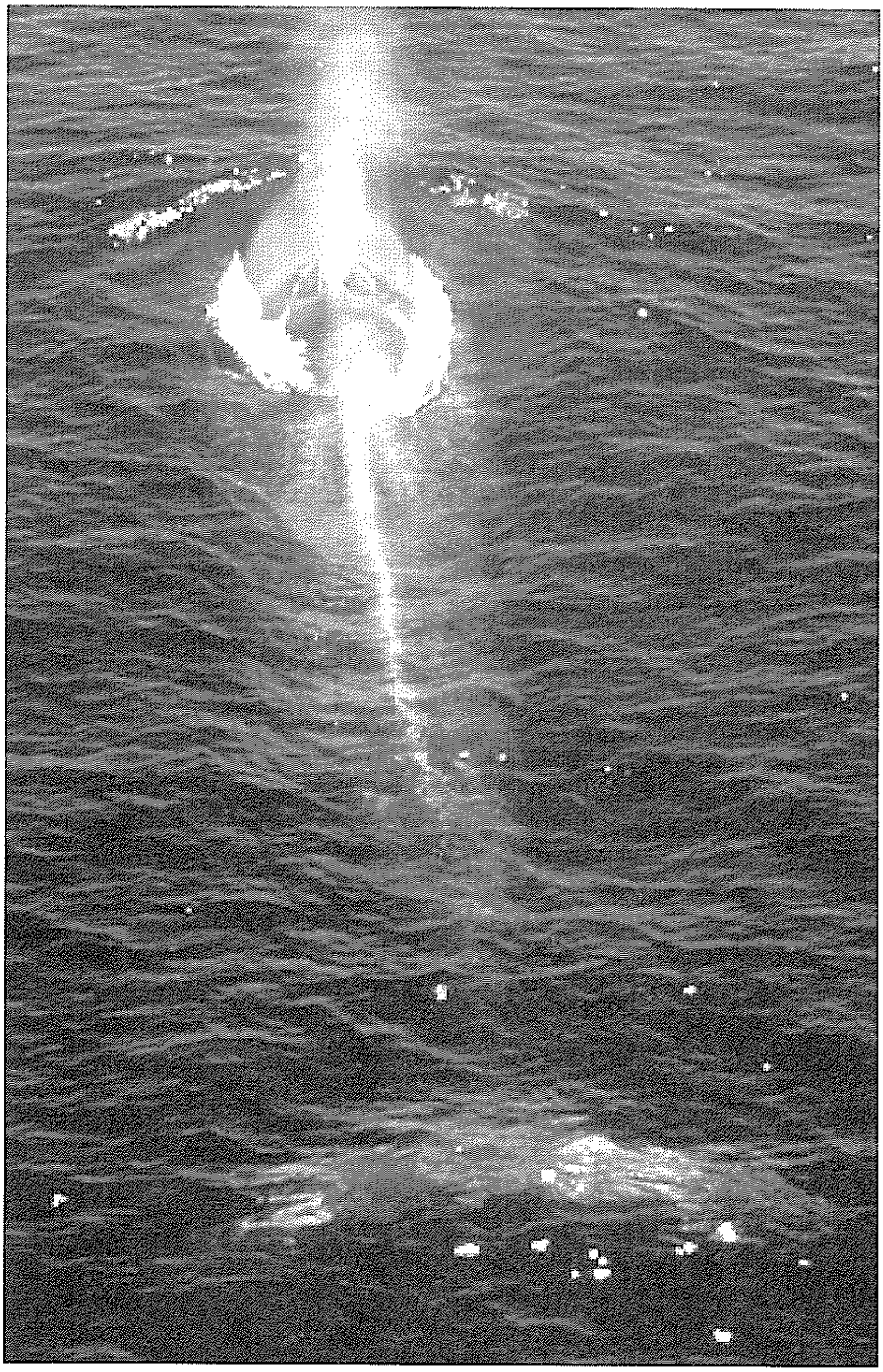

Fig. 4. (a)-(d) Several aspects of the external appearance of the blue whales from multiple sightings during 1993. Presumably these are true blue whales. Notice the small remoras on the head of the animal on the left (photographs (a)-(b) by D. Day, (c) by L. Leonhardt and (d) by the author).

operation in some of these localities and the presence of experienced observers in the Galápagos for over 25 years (D. Day, G. Merlen and T. de Roy, pers. comm.). This is probably because the main blue whale aggregations appear to be well offshore. Since then, local incidental blue whale sightings have been reported by other sources: two blue whales were seen southeast of Cabo Rosa, Isabela Island, in early September 1995 (H.M. Snell, pers. comm.). Merlen (1998) also recorded a blue whale south of Fernandina Island in 1997.

Feeding observations

Based on the distribution of blue whale sightings in four productive areas of the eastern tropical Pacific (the Baja California and the Peruvian/Ecuadorian coasts, the Costa Rica Dome and the Galápagos Islands), Reilly and Thayer (1990) hypothesised that blue whales may select habitats which permit foraging while in their low latitude grounds. These habitats are all characterised by coastal or equatorial upwelling and high standing stocks of euphausiids. The side-fluking behaviour, defecation and dip-netted samples during the 1993 sightings strongly suggest that the whales were feeding on surface swarms of *N. simplex*. Blue whales have also been reported feeding in two other low latitude grounds: the southwest Gulf of California (Sears, 1987; Gendron and Sears, 1989; 1993), and off northeastern Sri Lanka, Indian Ocean (e.g. Leatherwood, 1986; Alling *et al.*, 1990). Therefore, Reilly and Thayer's hypothesis for the ETP may well apply to other productive habitats in the tropical/subtropical oceans (cf. Ballance and Pitman, 1998).

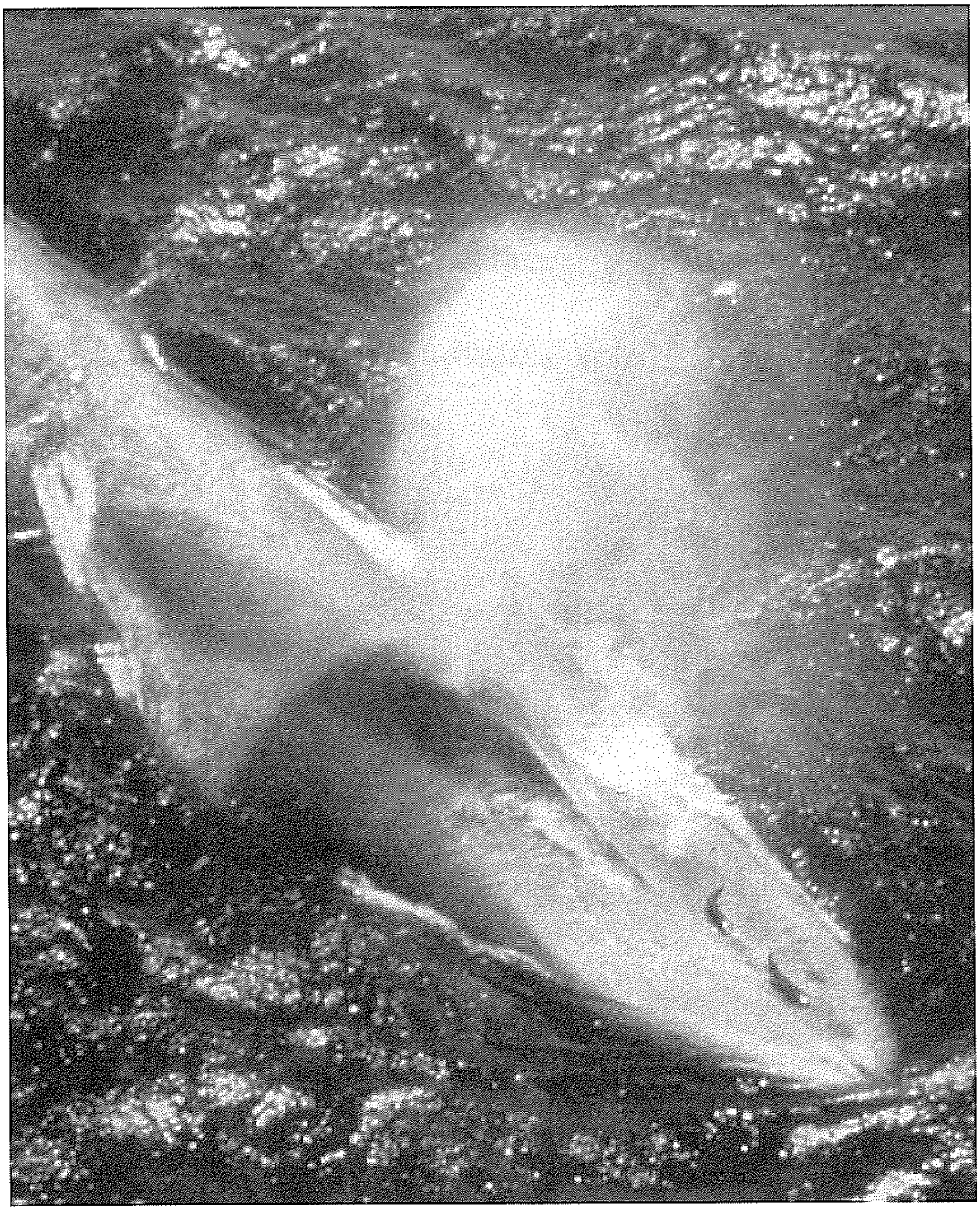

Fig. 4. (b) See legend on p. 46. Note the white scarring.

N. simplex is a neritic euphausiid that thrives in the cool, upwelling-modified extensions of the California and Peru Currents in the ETP. A third population centre to the west of the Galápagos Islands is supported by the equatorial divergence and the South Equatorial Current-Equatorial Undercurrent system (Brinton, 1979). It is one of the most important euphausiids in terms of biomass off central Chile (Antezana, 1970), in the Gulf of California (Gendron, 1992) and off the west coast of Baja California (Brinton, 1979; Gómez-Gutiérrez *et al.*, 1995). Surface swarming in *N. simplex* has been related to reproductive activity during the spring months (Gendron, 1992). There is a close relationship between this phenomenon and blue whale abundance in the southwest Gulf of California (Gendron and Sears, 1989; 1993; Gendron, 1992). Before blue whales were reported feeding on this euphausiid in the Gulf of California (Sears, 1987), *N. simplex* had not been reported as part of their diet (see review by Yochem and Leatherwood, 1985). Off the Galápagos, several other euphausiid species, particularly in the genus *Euphausia*, with important population centres to the west of the Islands (Cornejo de González, 1977; Brinton, 1979), could also constitute prey for blue whales.

'White scarring'

White scarring similar to that on the animal in Fig. 3b has been observed on the backs of blue whales in the Gulf of St. Lawrence, western North Atlantic, and has been attributed to contact with ice as a whale comes to the surface to breathe among ice floes (Sears *et al.*, 1990). In the event that the scarring on the Galápagos animal was indeed caused by ice, this would indicate that this individual had visited polar latitudes previously.

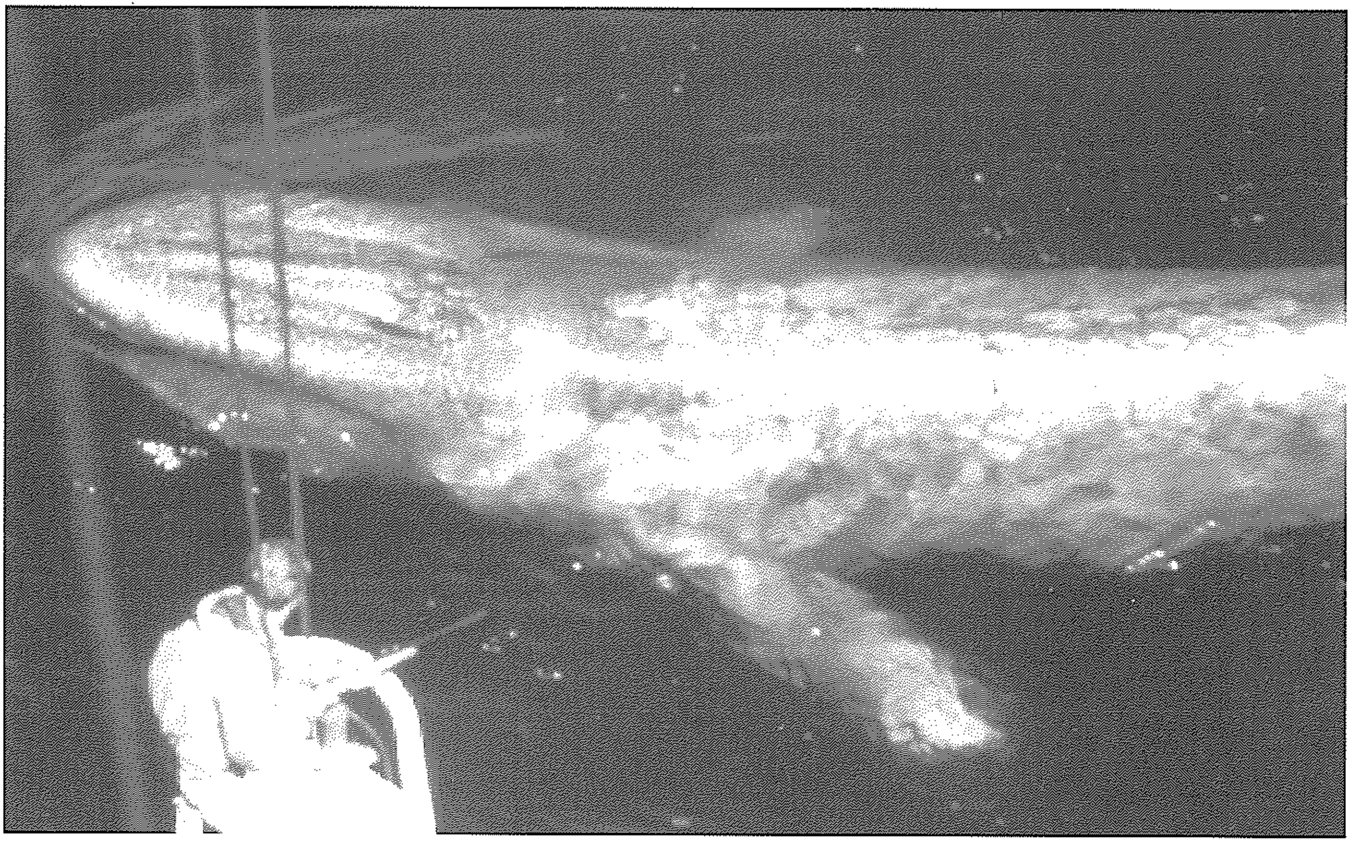

Fig. 4. (c) See legend on p. 46.

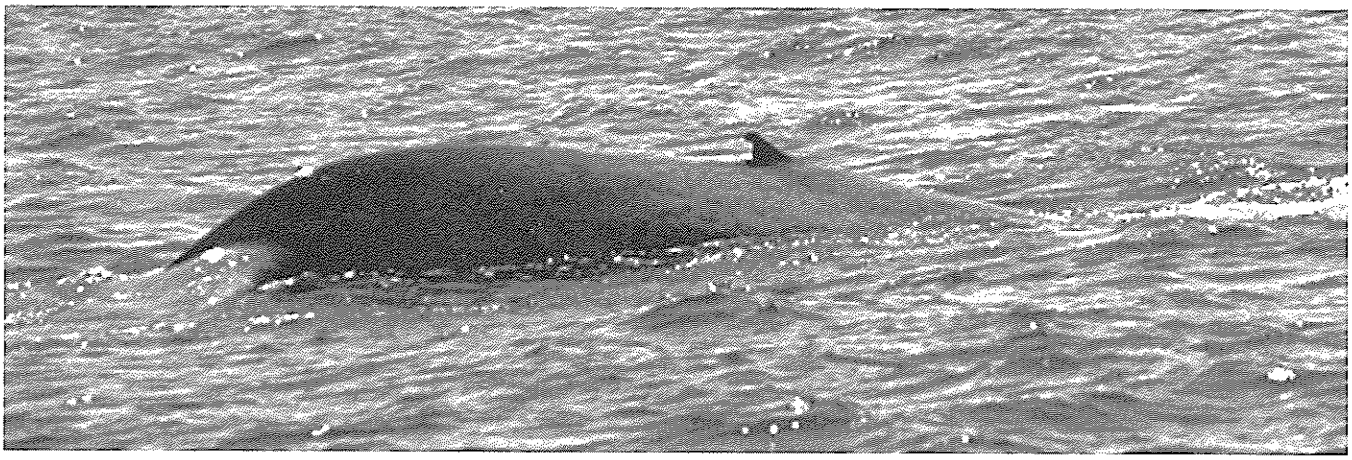

Fig. 4. (d) See legend on p. 46.

Population affinities and sub-specific identity

Although the migratory habits of blue whales are poorly understood, it has been traditionally postulated that they move between the cold and productive waters of the polar regions, where they feed in spring and summer, and the subtropical and tropical waters of the lower latitudes, where they breed in winter (e.g. Mackintosh, 1965; 1966). On these grounds it could be interpreted that the blue whales sighted off the Galápagos belong to a Southern Hemisphere stock, which visits the islands as part of its low latitude distribution during the austral winter and spring months. This is supported by the observation of two calves on 17 August 1993. The absence of matches with photographically identified blue whales in the eastern North Pacific and the possibility that the scarring observed on one individual could have resulted from contact with ice, all constitute additional support for assigning the animals discussed here to a southern stock of blue whales.

However, this view is confounded by the direct feeding observations of 1993 and their distribution in four areas of high productivity in the ETP, which indicate that blue whales select low latitude grounds which enable them to feed (Reilly and Thayer, 1990). This contrasts with Gaskin's (1982) view that 'the breeding grounds of rorquals are determined by relatively simple parameters of which [warm] sea temperature is probably the most important'. In addition, recent theoretical thermoregulation models suggest that the reason for the low latitude migration in blue whales should be other than calving, since even their neonates should be able to tolerate the temperatures of polar seas (Lavigne *et al.*, 1990; Watts *et al.*, 1993).

Year-round sightings of blue whales in the vicinity of the Costa Rica Dome have been interpreted as belonging to a resident stock (Reilly and Thayer, 1990). Actual peaks in sightings and catches during the summer months off Peru (Ramirez, 1983; Donovan, 1984) appear to indicate these whales are not from a southern stock. Thus, as an alternative hypothesis, it is possible that the blue whales off the Galápagos Islands are linked to those in these two nearby areas, i.e. as part of a resident ETP stock that exploits seasonally abundant peaks in euphausiid production.

The issue of stock identity is further complicated by the purported presence of both true (*B.m. intermedia*) and pygmy blue whales in the region. Pygmy blue whales were identified in the vicinity of the Costa Rica Dome (Berzin, 1978) and probably off the coast of Peru (Donovan, 1984). However, true blue whales were also caught off Peru (see summary in Donovan, 1984). Although reliable characteristics for distinguishing true from pygmy blue whales in the field have not been developed (Donovan *et al.*, 1996), it is believed some experienced observers are capable of separating them by their behaviour and body proportions (see review by Kato *et al.*, 1995). Photographs of the animals seen in the Galápagos during 1993 (Figs 4a-d) were examined by H. Kato (National Research Institute of Far Seas Fisheries, Japan) and his impression was that they were true blue whales. The dorsal profile of the head in the whales in Fig. 4 of this paper, particularly at the rostrum level, appears to be narrower than that of fig. 1c in Kato *et al.* (1995) of a pygmy blue whale off Australia.

The question of population identity of the whales seen off the Galápagos must, however, remain open until more adequate information is gathered, particularly on the genetic structure of the blue whales that occupy the different areas of the ETP, and their relationship to whales in high latitude summer grounds both in the northern and Southern Hemisphere. Sub-specific identification is the subject of a major IWC research effort that includes photo-identification, genetic and acoustic studies involving animals in several areas of concentration in both Antarctic and sub-tropical waters (e.g. see IWC, 1997; 1998, pp.78-80). Satellite telemetry is another useful tool (e.g. Mate *et al.*, 1997), which may help elucidate the population identity of blue whales in the ETP by demonstrating poleward movements or year-round residency. Finally, combining the techniques above with studies of their prey and their habitat (e.g. Fiedler *et al.*, 1997) may advance knowledge of their ecology in low latitude grounds.

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On assessment of the Bering-Chukchi-Beaufort Seas stock of bowhead whales (*Balaena mysticetus*) using a Bayesian approach

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ABSTRACT

This paper explores a number of issues surrounding the current assessment of the Bering-Chukchi-Beaufort (B-C-B) Seas stock of bowhead whales and provides a 'preferred' set of specifications for this assessment. A Bayesian approach appears to be preferable. However, the Bayesian Synthesis method is subject to the Borel paradox. Reverting to a 'standard' Bayesian approach which places all 'indirect' information in priors (rather than representing this information as likelihoods) would overcome this problem. The basis for the prior distributions used should be documented clearly, and the sources of information for the B-C-B bowhead stock divided into 'indirect' and 'direct'. Simulation results and 'in principle' arguments support the choice of a current population size rather than the pre-exploitation equilibrium size for the parameter to scale the population size (i.e. a 'backwards' rather than a 'forwards' approach). Arguments are presented that the most appropriate choice for a productivity-related parameter, for which a prior has to be specified, is the maximum steady rate of increase. A method for treating the N_4/P_4 estimates as relative indices of abundance, allowing for prior information about the relationship between absolute abundance and those estimates, and accounting for the correlation among the indices of relative abundance derived from the N_4 and P_4 data is developed. Two 'preferred approaches' for assessing the resource both lead to estimates for the lower 5th percentile of the replacement yield that are greater than the current annual strike limit of 67 for the B-C-B stock.

KEYWORDS: BOWHEAD WHALE; POPN ASSESSMENT; TRENDS; BIOLOGICAL PARAMETERS; MODELLING; WHALING-ABORIGINAL; ARCTIC

INTRODUCTION

Bowhead whales (*Balaena mysticetus*) of the Bering-Chukchi-Beaufort Seas (B-C-B) stock are subject to subsistence whaling in Alaska and Chukotka. Thus the assessment of this stock is important for providing management advice to the International Whaling Commission (IWC), the intergovernmental body that establishes catch limits. The present regulations state that the total number of landed whales for seasons 1998-2002 shall not exceed 280, with no more than 67 struck in anyone year (IWC, 1999).

Recent assessments of this stock have been conducted using both conditioned maximum likelihood (e.g. Butterworth and Punt, 1992; 1995; Punt and Butterworth, 1996; 1997a) and Bayesian methods (e.g. Givens *et al.*, 1995; Givens and Thompson, 1996). The Bayesian assessments have been based on Bayesian Synthesis (e.g. Raftery *et al.*, 1995a) and standard Bayesian methods (e.g. Punt and Butterworth, 1997a; Breiwick, 1997). These Bayesian analyses involve the development of a coherent joint posterior distribution for seven population model parameters: the total (1+) pre-exploitation size of the resource, K_{1+}; *MSYR; MSYL;* the age-at-maturity, a_m; the survival rate of adults in the absence of exploitation, $S_{adult} = \exp(-M_{adult})$; the survival rate of juveniles in the absence of exploitation, $S_{juv} = \exp(-M_{juv})$; and the greatest age at which juvenile natural mortality applies, *a*. The assessment conducted by the IWC Scientific Committee (hereafter 'Scientific Committee') at its 1994 meeting (IWC, 1995) used pre-model distributions [1] for each of these parameters, as well as pre-model distributions for the recent rate of population increase *(ROI)*, the 1988 (1+) population size *(P1988)*, the maximum pregnancy rate $(f^{max})^2$, and the proportion of mature animals and calves in the population from 1985 to 1992.

There are three main reasons for using a Bayesian approach for stock assessment: (a) it provides a relatively straightforward means to represent the full range of uncertainty (both parameter uncertainty and model-structure uncertainty); (b) information based on 'expert opinion' and inferences about other stocks/species can be incorporated explicitly into the stock assessment within a statistically defensible framework; and (c) the output of the analysis is exactly the information needed to parameterise operating models for evaluating alternative candidate management procedures (viz. the probability of alternative states of nature). Thus, unlike the situation for maximum likelihood approaches, it is not necessary to argue that the joint distribution obtained for parameter estimates can be assumed to represent these probabilities, because it is exactly these probabilities which a Bayesian approach provides.

The principles underlying Bayesian Synthesis have been criticised as this method is subject to the Borel paradox (Wolpert, 1995; Bravington, 1996). Put simply, the Borel paradox arises because there are (through the relationships provided by the population dynamics model) two different prior distributions for the same quantity (Raftery and Givens, 1997). Concern has also been expressed within the Scientific Committee about some of the prior distributions selected for the 1994 assessment (IWC, 1995) - see

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[1] The term 'pre-model distribution' will be reserved in this paper for references to Bayesian Synthesis applications. The more common terms 'prior' and 'likelihood' will be used when discussing issues related to standard Bayesian assessments.

[2] The term 'pregnancy rate' refers to the fraction of females past the age-at-first-parturition that give birth in a year (Punt, 1996; 1999). This definition differs from usage in some other earlier papers (e.g. de la Mare, 1989; Punt and Butterworth, 1991) in that it applies to births of both sexes rather than to females only.

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Butterworth (1995), Punt and Butterworth (1996; 1997a), and discussion of points raised therein in the section 'Priors and Likelihoods' below.

The information used in a Bayesian assessment can be obtained from both 'direct' and 'indirect' sources (Bravington, 1996). 'Direct' information means observations from the population being assessed (e.g. the 'proportion' data for the B-C-B bowhead stock). 'Indirect' information involves inferences that do not depend on the population being assessed (e.g. inferences concerning natural mortality from estimates for other baleen whale species and stocks). The difference between these two sources of information is critical to an understanding of Bayesian stock assessments, as the two need to be treated quite differently within such analyses.

The parameters for which prior (pre-model) distributions were specified in the 1994 B-C-B bowhead assessments (IWC, 1995) are conventional inputs for HITTER-FITTER (de la Mare, 1989) with its underlying BALEEN II model (Punt, 1996; 1999). However, when specifying prior distributions, it is often better to select 'natural parameterisations'. The choice of parameterisation should be made to ease the specification of the priors. Some choices for parameters are simpler for scientists to relate to practical experience, and should therefore be preferred. For example, we argue later that specifying a prior for the average number of years an animal lives after reaching maturity may be more 'natural' than doing this for an adult natural mortality rate.

Punt and Hilborn (1997) advocate using parameters that do not depend on a separate parameter that scales the population size. This is because such parameters are then comparable among stocks/species, making it considerably easier to construct priors on the basis of inferences for other stocks/species. This practice also means that the biological parameters are independent of the parameter that scales the population size. The parameters chosen for the 1994 B-C-B bowhead stock assessment (IWC, 1995) confonn to this suggestion.

In several instances, the use of an 'uninformative' prior is advocated. This is perhaps somewhat misleading (and perhaps even unhelpful) because it is not always clear to what extent a particular prior is uninformative. For example, the selection of a uniform prior for *MSYR* may be 'uninformative' with respect to *MSYR*, but it will certainly not be uninformative with respect to the current replacement yield (a possibly more important quantity from the management viewpoint). In most cases where we advocate that a prior be chosen to be uninformative, we suggest that it should be uniform. However, several alternatives exist (e.g. uniform on a log-scale). The selection of a metric for uninformative priors can have a substantial impact on assessment results. There is therefore a need for the metric to be explicitly considered when specifying uninformative priors. For example, if comparing the options of uniform on the given or a log-scale, the key question to be addressed is on which of the two scales do intervals of equal length correspond to equally likely ranges of possible values.

This paper first considers the appropriate framework (Bayesian Synthesis or 'standard' Bayesian) for conducting the assessment of the B-C-B bowhead stock. It then compares the 'backwards' and 'forwards' approaches[3] by means of simulation and considers the information about each model parameter and data type in turn to suggest how these should be treated in a Bayesian assessment of the B-C-B bowhead stock. Finally, the results for two 'preferred' variants are presented and discussed.

BA YES IAN SYNTHESIS OR BAYESIAN ANALYSIS

Bayesian stock assessment and risk analysis methods have been applied in the fisheries field for several years (e.g. Walters and Hilborn, 1976; Bergh and Butterworth, 1987; Sainsbury, 1988; Collie and Walters, 1991; Thompson, 1992; Hilborn *et al.*, 1994; McAllister *et al.*, 1994; Walters and Ludwig, 1994; Walters and Punt, 1994). The assessment method applied to the South African fur seal population by Butterworth *et al.* (1987) and more recently by Givens *et al.* (1993; 1995) for the B-C-B bowhead stock differs from other Bayesian assessments because it is based on a Bayesian Synthesis approach rather than a standard Bayesian analysis. As such, these assessments are subject to the Borel paradox (Wolpert, 1995).

Bravington's (1996) appraisal of Bayesian Synthesis highlights the Borel paradox and suggests that sensitivity to this paradox can be explored through relabelling of model inputs and outputs. This suggestion is both sensible and adequate but it is required only if the assessment has been provided with more priors than are actually needed. (As detailed in the following section, one of the two sources of the Borel paradox in the 1994 B-C-B assessment was removed by the Scientific Committee's decision in 1997 not to include a prior on S_{juv} (IWC, 1998c).)

Bayesian analysis deals with priors and likelihoods in different ways. However, the 1994 B-C-B bowhead assessment treats some priors (e.g. that for the maximum pregnancy rate) as likelihoods. This practice is dangerous and can readily be shown to lead to erroneous results (e.g. Bravington, 1996). Raftery and Poole (1997) and Poole and Raftery (1998) provide suggestions on how to combine priors in a manner that overcomes this problem. However, for the B-C-B stock of bowhead whales, the most obvious solution to this problem is to place all of the 'indirect' information into the prior distributions and to represent all of the data for the B-C-B bowhead stock in the fonn of a likelihood function. In this situation (which we will refer to as a 'standard' Bayesian assessment), the Borel paradox is not a concern provided the joint prior is of the same dimension as the parameter vector. Naturally, one cannot use a 'standard' Bayesian assessment if there really is 'indirect' information about both model inputs and outputs. However, we will argue below that the basis for some of the priors used in the 1994 B-C-B bowhead assessment is so weak that it is perhaps better to ignore certain of these priors and thus be able to take advantage of adopting a 'standard' Bayesian approach.

THE 'REFERENCE' ANALYSIS

In 1997, the Scientific Committee specified a 'reference case' for comparing alternative approaches to the assessment of the B-C-B bowhead stock (IWC, 1998b and see Tables 1 and 2). The 1994 B-C-B bowhead assessment (IWC, 1995) incorporated priors for $MSYR_{mat}$, $MSYL_{mat}$, a_m, a, S_{adult}, S_{juv} and f_{max}. However, given values for any six of these seven parameters, the value for the seventh can be derived from the BALEEN II population dynamics model (Punt, 1999). The use of all seven priors therefore leads to an instance of the Borel paradox. The specifications of the 'reference case' resolve this problem as no prior is placed on S_{juv} and instead

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[3] The 'backwards' approach effectively projects population trajectories backwards from a population estimate generated from a prior for a population size in a recent year, whereas the 'forwards' methodology generates a population size for the year in which exploitation started from a prior for the pre-exploitation equilibrium population *K*, and projects this forwards in time by means of the population model.

the values for the parameters S_{adult}, a_m, a, $MSYR$, $MSYL$ and f_{max} and the relationships within BALEEN II are used to compute a value for S_{juv}. For ease of presentation, the analyses presented in this paper are all variants of this 'reference case'. The results of the assessments are summarised by eight management-related quantities, the first seven of which were identified by IWC (1998c).

Table 1

Historical catches for the Bering-Chukchi-Beaufort Seas stock of bowhead whales (source: J.M. Breiwick, pers. comm.).

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

Table 2

The prior distributions and data assumed when conducting the 'reference case' assessment of the Bering-Chukchi-Beaufort Seas stock of bowhead whales (IWC, 1998c) - see text for definition of the parameters listed. (t_n is a t random variable with n degrees of freedom.)

Parameter	Prior distribution/likelihood
Prior	
S_{adult}	N(0.99; 0.02^2) $S_{juv} \leq S_{adult} \leq 0.995$
Maximum pregnancy rate, f_{max}	$1/f_{max} \sim$ U[2.5; 4]
Transition age, a	1,2, … , 9 equally likely
Age-at-maturity, a_m	N(20;3^2) $13.5 \leq a_m \leq 26.5$
K_{1+}	$\ell n K_{1+} \sim U[\ell n 7000, \ell n 31000]$
$MSYL_{1+}$	U[0.4; 0.8]
$MSYR_{1+}$	U[0.01; 0.07]
Data source	
1993 population size, P_{1993}	N(8200, 564^2)
1978-93 *ROI*[1]	$\exp(0.0319+0.0076t_8) - 1$
Propn of calves[2] 1985-92	$0.052 + 0.0164t_5$
Propn of matures[2] 1985-92	$0.411 + 0.0286t_5$

[1] J.E. Zeh (pers. comm.). [2] Givens *et al.* (1995).

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

P^{1+}_{1998}/K_{1+} - the ratio (expressed as percentage) of the size of the 1+ component of the population at the start of 1998 to K_{1+}.

P^{f}_{1998}/K^{f} - the ratio (expressed as percentage) of the size of the mature female component of the population at the start of 1998 to the corresponding pre-exploitation size.

$P^{1+}_{1998}/MSYL_{1+}$ - the ratio (expressed as percentage) of the size of the 1+ component of the population at the start of 1998 to *MSYL*.

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

RY (1998) - the replacement yield for 1998.

Q_0 (1998) - the value of the quantity Q_0 (Wade and Givens, 1997) for 1998:

$$Q_0(1998) = \begin{cases} 0.9\,MSY_{1+} & \text{if } P^{1+}_{1998}/K_{1+} > MSYL_{1+} \\ \min(RY(1998) & \\ -1, 0.9\,MSY_{1+}) & \text{otherwise} \end{cases}$$

$$\text{where} \quad MSY_{1+} = MSYR_{1+}\,MSYL_{1+}\,K_{1+}$$

Slope - the annual rate of increase of the 1+ population from 1978 to 1993, expressed as a percentage.

The posterior distribution is approximated numerically using a variant of the Sampling-Importance-Resampling (SIR) algorithm. This involves drawing Z_1 sets of parameter values from the joint prior distribution[4] and then calculating the likelihood corresponding to each vector. The likelihood is set equal to zero if the value for S_{juv} is greater than that for S_{adult} or if the population is rendered extinct. The posterior is then based on $Z_2 = 5{,}000$ draws (with replacement) from the Z_1 sets of parameter values, where the probability of selecting a given parameter set is proportional to its likelihood. The maximum weight (the ratio of the likelihood for most likely set of parameter values to the total likelihood over all sets of parameter values) is used to assess whether the SIR algorithm has converged adequately to the posterior distribution.

The results for the 'reference case'

Table 3 lists post-model-pre-data and posterior distributions for the 'backwards' and 'forwards' approaches. Results are shown in Table 3 for the 'forwards' approach for Z_1 = 1,000,000 ('reference case') and Z_1 =2,500,000. The maximum weight for anyone draw for the reference case 'backwards' analysis (0.00066) suggests that Z_1 = 250,000 is more than sufficient to obtain an adequate numerical representation of the posterior. In contrast, the maximum weight for the reference case 'forwards' analysis (0.02286) is perhaps larger than desirable. Increasing Z_1 from 1,000,000 to 2,500,000 decreases the maximum weight to 0.00894, which seems adequate. The results for these two choices of Z_1, however, differ only marginally (Table 3).

The posterior distributions differ markedly from the post-model-pre-data distributions (both in terms of precision and central tendency). The post-model-pre-data distributions for 'backwards' are more similar to the posteriors because the 'backwards' projections include the prior information

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[4] Unless stated otherwise, z_1 for the analyses of this paper is 250,000 for the 'backwards' analyses and 1,000,000 for the 'forwards' analyses.

Table 3

Estimates of eight management-related quantities for the Bering-Chukchi-Beaufort Seas stock of bowhead whales. The point estimates given are posterior medians, followed by posterior means in round parentheses. Posterior 90% credibility intervals are given in square parentheses. Results are shown for the 'forwards' and 'backwards' approaches to implementing the method (see text for details).

	K_{1+}	$RY(1998)$	$Q_0(1998)$	P^{1+}_{1998}/K_{1+}	P^{f}_{1998}/K^{f}	$P^{1+}_{1998}/MSYL_{1+}$	$MSYR_{1+}$	$Slope$
Post-model-pre-data								
Forwards	20953 (21406)	45 (54)	235 (260)	98.5 (92.7)	95.6 (88.9)	137.2 (135.7)	1.86 (2.00)	0.00 (0.17)
	[13834 30399]	[20 140]	[110 566]	[55.9 100.0]	[43.8 101.8]	[87.9 173.5]	[1.07 3.66]	[-0.07 1.24]
Backwards	14956 (14897)	154 (159)	149 (156)	55.7 (57.4)	39.8 (40.5)	84.0 (84.7)	1.72 (1.87)	1.60 (1.74)
	[11401 18328]	[95 258]	[91 262]	[38.4 87.8]	[28.1 59.0]	[55.3 122.1]	[1.06 3.48]	[0.92 3.39]
Forwards								
Reference case	13995 (14223)	180 (180)	171 (174)	64.1 (63.9)	43.5 (43.7)	94.5 (93.0)	2.04 (2.05)	1.94 (1.95)
	[11547 17918]	[110 250]	[104 249]	[47.5 85.4]	[36.1 55.8]	[69.9 119.3]	[1.12 3.35]	[0.99 3.10]
Z_1=2,500,000	13967 (14170)	183 (181)	174 (175)	64.0 (63.8)	43.6 (43.7)	94.0 (92.7)	2.04 (2.07)	1.96 (1.96)
	[11758 17847]	[110 250]	[106 250]	[47.8 85.4]	[35.9 54.4]	[69.4 115.7]	[1.13 3.40]	[1.01 3.15]
With plus-group	13363 (13553)	168 (168)	168 (169)	65.5 (66.4)	41.9 (42.4)	97.0 (96.5)	2.04 (2.10)	1.87 (1.91)
	[11078 17411]	[106 242]	[104 259]	[48.6 90.7]	[35.0 55.3]	[73.0 125.8]	[1.16 4.17]	[0.99 3.33]
$S_{\max} = 0.999$	13523 (13794)	195 (191)	188 (185)	65.6 (65.8)	43.7 (44.3)	95.1 (94.7)	2.20 (2.23)	2.14 (2.14)
	[11425 17670]	[115 268]	[109 265]	[48.5 85.1]	[36.4 54.0]	[72.0 117.3]	[1.18 3.37]	[1.06 3.29]
Alt Preg constraint	13870 (14092)	176 (175)	172 (173)	64.4 (65.2)	43.8 (44.9)	96.2 (96.4)	2.07 (2.09)	1.94 (1.94)
	[11577 17823]	[110 246]	[105 254]	[48.1 90.5]	[36.3 60.7]	[72.1 127.1]	[1.15 3.60]	[1.02 3.13]
Backwards								
Reference case	12631 (12863)	211 (209)	209 (207)	71.2 (70.9)	45.9 (46.1)	100.2 (99.5)	2.59 (2.58)	2.49 (2.48)
	[10924 16531]	[141 273]	[136 279]	[53.5 90.1]	[37.8 57.9]	[76.8 122.8]	[1.51 3.78]	[1.39 3.67]
With plus-group	11833 (12055)	193 (191)	206 (204)	75.2 (74.9)	43.9 (44.4)	104.9 (104.1)	2.67 (2.68)	2.49 (2.48)
	[10158 15829]	[132 253]	[137 270]	[56.5 93.3]	[36.3 56.3]	[81.4 125.5]	[1.58 3.97]	[1.44 3.61]
$S_{\max} = 0.999$	12500 (12719)	215 (212)	215 (212)	72.1 (71.8)	45.8 (46.2)	101.5 (100.9)	2.67 (2.66)	2.59 (2.56)
	[10843 16409]	[145 275]	[139 281]	[54.6 91.1]	[38.0 58.3]	[78.5 124.1]	[1.55 3.89]	[1.43 3.74]
Alt Preg constraint	12547 (12775)	206 (204)	208 (206)	71.6 (71.4)	46.2 (46.6)	101.9 (101.7)	2.62 (2.61)	2.50 (2.47)
	[10710 16468]	[137 270]	[133 277]	[54.0 91.0]	[38.3 59.4]	[78.8 126.4]	[1.54 3.89]	[1.40 3.68]

about P_{1993} whereas the 'forwards' projections do not. Similarly to previous studies that have compared results from 'backwards' and 'forwards' (e.g. Butterworth and Punt, 1995; Givens and Thompson, 1996), the results for 'backwards' are more optimistic in terms of stock productivity that those for 'forwards'. This is reflected by higher values for all of the quantities (except K_{1+} which shows a compensating decrease). It is noteworthy that the posterior for *Slope* for 'backwards' is closer to the estimate inferred from the data (see Table 2) than that for 'forwards'. Both variants suggest that the population is close to the *MSY* level (in terms of the 1+ component of the population) and both analyses suggest that the lower 5%iles of the distributions for Q_0 and the current replacement yield are substantially larger than the current annual strike limit for the B-C-B stock of 67 animals.

Previous analyses based on 'backwards' and 'forwards' have obtained posteriors for *Slope* that are closer to the actual data (e.g. Punt and Butterworth, 1997a provides 'reference case' median estimates of 2.81 and 2.28% respectively). Three sensitivity tests were conducted to examine which of the changes made in IWC (1998c) to the prior distributions might have led to the change to the posterior for the *Slope* statistic. These three sensitivity tests involved (i) dropping the specification that the survival rate is zero for animals aged 100 years ('With plus-group'), (ii) increasing the upper limit for adult survival, $S_{\max}$, from 0.995 to 0.999 ('$S_{\max}$ = 0.999'), and (iii) decreasing the lower limit of the prior for the maximum calving interval from 2.5 to 2 years ('Alt preg constraint'). The first and third of these changes have little impact on *Slope* (Table 3). Increasing $S_{\max}$ from 0.995 to 0.999 brings the results in closer agreement with those from previous analyses, but there are still notable differences between the posterior for *Slope* for the '$S_{\max}$ = 0.999' sensitivity test and the posteriors from previous analyses, so that the reasons for these differences from the previous results are not immediately obvious.

COMPARING ALTERNATIVE STOCK ASSESSMENT METHODS

Punt and Butterworth (1997a) evaluated the relative performances of three alternative estimation procedures (two maximum likelihood methods and the 'forwards' Bayesian Synthesis approach) for the B-C-B bowhead stock by means of a Monte Carlo simulation exercise. The evaluation involved generating 100 sets of artificial abundance and 'proportion' data, applying each estimation approach to each data set, and then comparing point estimates (posterior medians for these Bayesian methods) with true values. The results of the simulation trials were summarised in Punt and Butterworth (1997a) by the biases and root-mean-square errors (RMSEs) (expressed in relative terms) of four quantities (indicated by Q below) of interest to management:

$$\hat{Q}^U = (1+\beta)Q^{True,U} + \varepsilon^U \tag{1}$$

and

$$\mathrm{RMSE}(Q) = \sqrt{\frac{1}{100}\sum_{U=1}^{100}\left(\hat{Q}^U / Q^{True,U} - 1\right)^2} \tag{2}$$

where $Q^{True,U}$ is the true value of quantity Q in simulation U,

$\hat{Q}^U$ is the estimate of Q in simulation U,

β is the relative bias, and

ε is assumed to be a normally distributed random variate.

The analyses of this paper involve applying the simulation testing framework developed by Punt and Butterworth (1997a) to compare the estimation ability of the 'backwards' and 'forwards' approaches to Bayesian analysis[5]. Punt and Butterworth (1997a) considered eleven trials, the first nine of which involved fixed values for the biological parameters. Here we consider only the remaining two trials, which involved generating true values for the biological parameters from the posterior distributions obtained from either the 'forwards' or the 'backwards' variants of the Bayesian assessment.

IWC (1997) noted that previous simulation evaluations had made no attempt to compare estimation methods for the B-C-B bowhead stock with respect to their estimates of precision. Both estimation procedures are Bayesian, and so can readily be applied to provide comparable 90% credibility intervals. The intervals are compared for each management quantity using three measures of performance: (a) the probability that the 90% credibility interval includes the true value, (b) the probability that the true value is smaller than the lower 90% limit and (c) the probability that the true value is larger than the upper 90% limit. If the estimation procedure performed 'perfectly', the values for these quantities would be 0.90, 0.05 and 0.05.

Table 4 lists the relative biases and RMSEs for the 'forwards' and 'backwards' approaches for six quantities of interest to management $(K_{1+}$, $MSYR_{1+}$, Q_0 (1998), $P^f_{1998}/K^f, P^{+1}_{1998}/MSYL_{1+}$, and RY (1998). Figs 1 and 2 plot the actual and estimated values for four of the six quantities for the two trials. Results are not shown in these figures for *RY* (1998) and $p^{1+}_{1998}/MSYL_{1+}$ because they are qualitatively the same as those for Q_0 (1998) and P^f_{1998}/K^f respectively. Not surprisingly, the performance of the 'forwards' estimation approach is better when 'forwards' rather than 'backwards' is used to generate the true data, although it remains poor in both cases. But importantly, whichever approach is used to generate the data, the 'backwards' estimation approach outperforms its 'forwards' counterpart in terms of both RMSEs and the absolute size of the bias. Both approaches tend to provide 'conservative' (i.e. negatively biased) estimates of the management quantities upon which catch limits would be based (Table 4; Figs 1 and 2) .

In terms of coverage probability, the 'backwards' approach again performs better than the 'forwards' approach (Table 5 on p. 60). The poor performance of the 'forwards' approach is attributable to the fact that the estimate of the upper 90% credibility value is far too low for all of the quantities except K_{1+} for which the lower limit is too high.

This comparison overestimates the confidence to be placed in the Bayesian credibility intervals because all the estimators assume the exact form of the true population dynamics model, and further because the assumption of deterministic dynamics made by all the estimation procedures is correct. Had the simulations allowed for process error effects (such as variation in the juvenile survival rate or uncertainty about historical catches), it is likely that the credibility intervals would have been shown to be overly narrow. Punt and Butterworth (1993) demonstrate that coefficients of variation estimated using bootstrap procedures for hake assessments can be negatively biased by some tens of percent when observation errors (but not process errors) are taken into account.

Table 4

Percentage biases and root mean square errors (in parentheses) for two estimators and two management-related quantities (see text for details).

	Estimation procedure	
Simulation trial	Forwards	Backwards
Backwards		
K_{1+}	15.9 (21.5)	4.7 (12.6)
$MSYR_{1+}$	-37.0 (36.1)	-17.2 (25.2)
Q_0 (1998)	-31.1 (31.7)	-13.5 (21.0)
P^f_{1998}/K^f	-14.8 (16.5)	-8.3 (11.9)
$P^{1+}_{1998}/MSYL_{1+}$	-15.6 (18.0)	-7.7 (13.6)
RY (1998)	-29.5 (30.6)	-13.6 (20.4)
Forwards		
K_{1+}	8.2 (15.7)	-1.2 (10.2)
$MSYR_{1+}$	-28.3 (28.8)	-7.6 (27.3)
Q_0 (1998)	-23.6 (26.5)	-5.5 (24.9)
P^f_{1998}/K^f	-9.8 (12.9)	-4.1 (10.1)
$P^{1+}_{1998}/MSYL_{1+}$	-10.8 (15.1)	-4.0 (13.2)
RY (1998)	-22.9 (25.5)	-7.1 (22.3)

PRIORS AND LIKELIHOODS

The analyses presented above illustrate the need to identify those quantities for which some of the available information comes from 'indirect' sources (e.g. inferences from data for other stocks/species), and those for which all of the information comes from 'direct' sources. In a 'standard' Bayesian assessment, the former quantities must be included as priors, while the information contained in the latter should form part of the likelihood[6]. In the 1994 B-C-B bowhead assessment (IWC, 1995), two of the prior distributions (those for $f_{\max}$ and P_{1988}) were treated as 'data' rather than priors in the analysis even though they were based, in part, on 'indirect' evidence. The contribution of P_{1988} to the likelihood function included 'indirect' information (for example, about whale numbers and behaviour - e.g. Raftery and Zeh, 1991) as well as information from the 'direct' count data collected at Point Barrow, Alaska. The likelihood contribution for $f_{\max}$ was not based on any direct information about the pregnancy rate of bowhead whales at very low population size, but rather on inferences about what this rate might be, taking account of perceptions/observations for other baleen whale species (IWC, 1992; 1995).

The first step needed in this process is to list the various sources of information which could contribute to the assessment, and then to clarify which are data (and so should be incorporated into the likelihood function) and which constitute 'indirect' information (and must therefore form part of the (joint) prior distribution). Sainsbury *et al.* (1998) highlight the point that this step in the process of conducting a Bayesian assessment has often been missing

> 'there should be much more careful documentation of the steps involved in successive updating (i.e. the initial definition of the prior, the information used to calculate a posterior that in turn is the prior for the next iteration of the analysis)'.

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[6] It is often computationally more efficient to update priors based solely on 'indirect' data with the 'direct' data for the parameters concerned - this does not impact the final results at all.

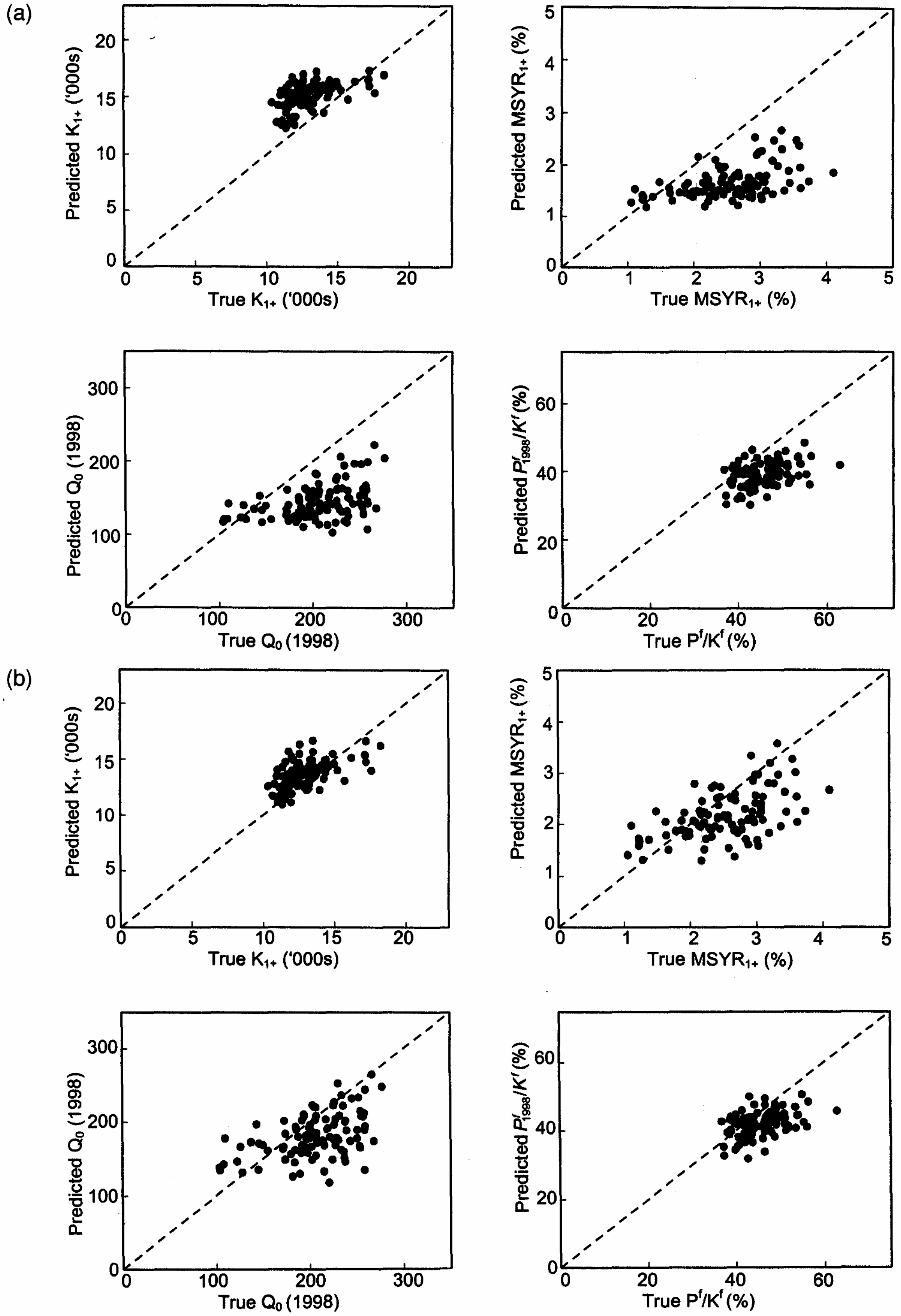

Fig. 1. Plots of predicted and true values for K_{1+}, $MSYR_{1+}$, P^f_{1998}/K^f, and Q_0 (1998) for the 'backwards' simulation trial. Results are shown for (a) the 'forwards' and (b) the 'backwards' estimation approaches.

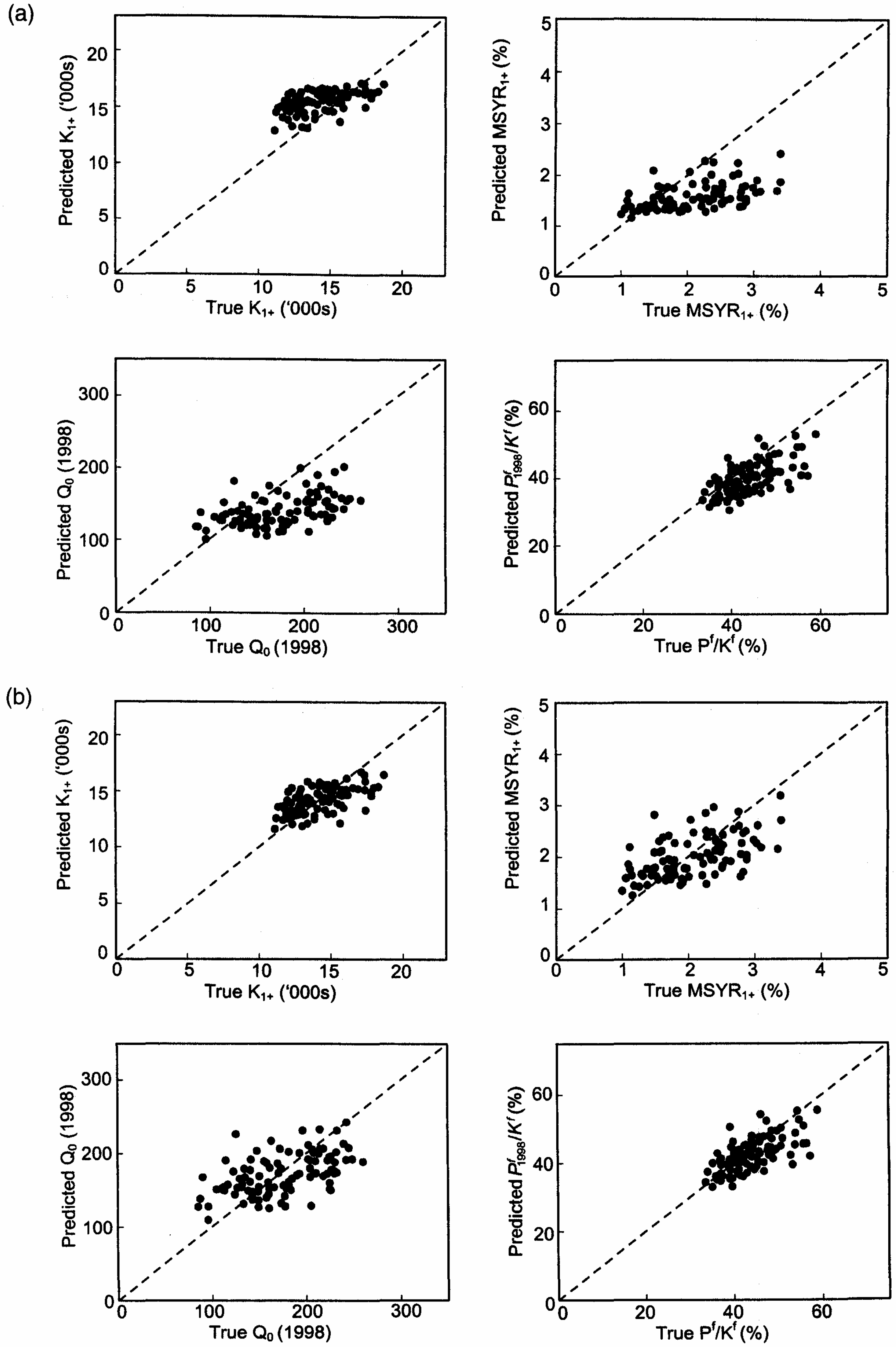

Fig. 2. Plots of predicted and true values for K_{1+}, $MSYR_{1+}$, P^{f}_{1998}/K^{f}, and Q_0 (1998) for the 'forwards' simulation trial. Results are shown for (a) the 'forwards' and (b) the 'backwards' estimation approaches.

Table 5

Performance statistics to measure the quality of 90% credibility intervals for six management quantities obtained using two Bayesian estimation procedures. The three statistics for each trial/estimator are: the probability that the 90% credibility interval includes the true value, the probability that the true value is smaller than the lower 90% limit and the probability that the true value is larger than the upper 90% limit.

	Estimation procedure					
Simulation trial	Forwards			Backwards		
Backwards						
K_{1+}	0.62	0.38	0.00	0.86	0.12	0.02
$MSYR_{1+}$	0.59	0.00	0.41	0.86	0.01	0.13
Q_0 (1998)	0.63	0.00	0.37	0.91	0.00	0.09
P^f_{1998} / K^f	0.65	0.00	0.35	0.89	0.00	0.11
$P^{1+}_{1998} / MSYL_{1+}$	0.69	0.01	0.30	0.91	0.01	0.08
RY (1998)	0.66	0.00	0.34	0.89	0.00	0.11
Forwards						
K_{1+}	0.81	0.17	0.02	0.94	0.00	0.06
$MSYR_{1+}$	0.81	0.01	0.18	0.94	0.06	0.00
Q_0 (1998)	0.80	0.03	0.17	0.92	0.05	0.03
P^f_{1998} / K^f	0.80	0.00	0.20	0.94	0.01	0.05
$P^{1+}_{1998} / MSYL_{1+}$	0.84	0.01	0.15	0.97	0.01	0.02
RY (1998)	0.81	0.02	0.17	0.91	0.04	0.05

The 1994 application of the Bayesian Synthesis method (IWC, 1995) was based on seven input pre-model (prior) distributions and five terms in the likelihood function. The basis for each of the prior distributions based on 'indirect' data is discussed below, including comments on some of the updates reflected by the 'reference case' specifications of 'IWC (1998c). This section does not deal in detail with the derivation of the 'direct' data (e.g. the 'proportion' data) because they were derived using standard statistical procedures, but does comment on alternative approaches to including the abundance data in the likelihood function.

Absolute abundance

All stock assessments must incorporate a parameter that scales the overall abundance. Punt and Hilborn (1997) note that this parameter is of particular importance in most assessments, but that data for other stocks/species can rarely be used to construct an informative prior for it. In many stock assessments, this parameter is chosen to be *K* (the pre-exploitation equilibrium biomass), although it is possible to select the biomass/numbers/exploitation rate in any year as this scaling parameter. For stock assessment methods based on (conditional) maximum likelihood estimation, the choice of this parameter (whether, for example, *K* or the current biomass) is irrelevant because the likelihood is invariant to transformations of the model parameters. However, for a Bayesian approach, this choice can be very important and the results may be highly sensitive to it because a Bayesian assessment is not invariant to such transformations.

Two approaches to the B-C-B bowhead Bayesian Synthesis assessment have been a focus for discussion. The 'forwards' approach requires a prior distribution for K_{1+} and projects population trajectories forwards from realisations generated from this prior distribution. In contrast, the 'backwards' approach uses realisations from a prior distribution for a recent estimate of absolute abundance to essentially extrapolate trajectories back to 1848; thus it provides an implicit distribution for K_{1+}, and so avoids the need for an explicit specification of a prior distribution for this parameter. Punt and Bu,tterworth (1997a) show that the results of the 'backwards' approach are not notably sensitive to the year (within the period of the past two decades) for which abundance estimates are available which is selected to provide the recent estimate of abundance.

Considerable attention has been directed towards identifying the reason for the difference in the results for these two approaches (see Table 3). Much of the debate initially centred on the justification of the basis used to provide the 'direct' component of the prior distribution for K_{1+}. For the 1994 assessment (IWC, 1995), this was based on an application of the DeLury (1947) estimation procedure to historical (1849-1870) catch per unit effort (CPUE) data. Butterworth and Punt (1995) criticised the derivation of this prior because the DeLury method effectively assumes that $MSYR$ = 0 and because the general acceptance of CPUE as an index of abundance has proved problematic in the past in the Scientific Committee (IWC, 1988, p.35; IWC, 1989). Punt and Butterworth (1996) and Givens and Thompson (1996) show, however, that including the 'direct' component of the K_{1+} prior in the likelihood when applying the 'backwards' method has virtually no impact on the results. Subsequently, Raftery and Poole (1997) showed that the reason for the differences between the results for 'forwards' and 'backwards' is attributable to differences in the joint region of support for P1993, K_{1+}, and *MSYR* for the two approaches

This is a case in which there are two priors for the same quantity (the parameter that scales the population). However, although the full pooling approach of Raftery and Poole (1997) and Poole and Raftery (1998) removes the associated problem of the Borel paradox, in doing so it introduces a new one, namely how to choose the pooling weight that is to be placed on the two priors (K_{1+} and P_{1993}) when conducting full pooling[7]. Clearly results are sensitive to the weight chosen, as demonstrated by the differences in results for the two extreme choices for this weight (corresponding to 'backwards' and 'forwards') which are shown in Table 3. In addition, the assumption of *a priori* independence between K_{1+} and *MSYR* underlying the inclusion of 'forwards' in full-pooling is violated because, prior to inclusion of the data in the assessment, some combinations of K_{1+} and *MSYR* can be rejected as implausible (see below for further details). Rather than attempting to combine these two priors, we prefer instead to choose the more appropriate of the two.

This choice initially seems rather arbitrary because both seem reasonable *a priori*. However, the simulation results of Table 4 are available to guide a choice in this matter. These suggest that the assumption underlying the 'backwards' approach is more appropriate as it leads to lower MSEs and less biased 90% credibility intervals. There are also two 'in principle' reasons for preferring a current rather than a historical population size as the parameter which scales the

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[7] Logarithmic pooling, which is the approach generalised in full pooling, given two priors p_1 and p_2 for the same parameter, provides a pooled prior proportional to $p_1^{\alpha} p_2^{(1-\alpha)}$, where the pooling weight α reflects the relative reliability accorded to the two sources of information that underlie the two priors specified. Raftery and Poole (1997) argue for $\alpha = 0.5$ when pooling priors for P_{1993} and K_{1+} on the basis of invariance under relabeling of inputs and outputs (initial and current population sizes), suggesting also that two priors that are agreed by the same 'expert' (the IWC Scientific Committee) should accordingly be deemed equally reliable. We disagree with these views, judging for the various reasons put forward in this paper that the (or indeed any) prior advanced for K_{1+} in the particular case of the B-C-B bowhead population is much less reliable than that for P_{1993}.

population size. The first is that there is no need when applying the 'backwards' approach to specify that the population is not currently extinct, because this is incorporated implicitly in the prior for current population size. If a 'forwards' approach is taken, it is necessary to place a prior distribution on current depletion (or current population size) and incorporate it as a bound in the likelihood function. The second reason is that, in the absence of data, the 'backwards' approach does not update any of the prior distributions (i.e. the post-model-pre-data distributions for *MSYR*, *MSYL*, a_m, a and S_{adult} are identical to their priors[8]). In contrast, the 'forwards' approach updates the joint prior distribution substantially (*inter alia* because combinations of low K_{1+} and low *MSYR* correspond to extinction and can thus be excluded). Intuitively, it would seem undesirable to update prior distributions in the absence of direct data. The greater difference between the post-model-pre-data distribution and the prior for $MSYR_{1+}$ for 'backwards' than 'forwards' (contrast the prior in Table 2 with post-model-pre-data distributions in Table 3) would seem to contradict this. However, there are two factors that determine the post-model-pre-data distribution. The first is the impact of rejecting parameter combinations that give rise to juvenile survival rates exceeding S_{adult}, and the second is the impact of the effect just discussed. The post-model-pre-data distribution for $MSYR_{1+}$ for 'backwards' reflects only the first while that for 'forwards' reflects both. As expected, the post-model-pre-data distribution for 'forwards' gives greater probability to higher values for *MSYR*.

Another seemingly undesirable property of the 'forwards' approach is that once a single abundance estimate becomes available, the joint distribution for the biological parameters (including *MSYR*) is updated. This seems intuitively undesirable because a single abundance estimate does not provide any information about *MSYR*. The past application of the 'Hitting with fixed MSYR' methodology by the Scientific Committee constitutes specific concurrence with this assertion. Even though an estimate of absolute abundance is available, all values for *MSYR* remain equally likely[9] because there is always some combination of *MSYR* and K_{1+} which 'hits' the estimate of abundance exactly. As a consequence, the likelihood is the same for all values of *MSYR*, but the associated prior is updated in the Bayesian integration under the 'forwards' approach. This is because the non-linearity of the relationship between *MSYR* and K_{1+} (given a single estimate of abundance) means that equal intervals on the K_{1+} axis do not correspond to equal intervals on the *MSYR* axis (Butterworth and Punt, 1997, illustrate what amounts to this point). In contrast to this situation for the 'forwards' approach, the effect of a single estimate of abundance on the 'backwards' approach is to update the prior for current abundance without having any impact on the distribution for *MSYR*.

A concern with the 'backwards' approach is its use of the N(7800; 1300^2) prior for P_{1993}. The basis for this prior is unclear because there is no obvious independent information that could be used to construct an informative prior for P_{1993}. However, the 'backwards' approach can be applied using an 'uninformative' U[0, ∞) prior for P_{1993}. As the likelihood for P_{1993} would be very informative compared to any sensible 'uninformative' prior for P_{1993}, the results are unlikely to be very sensitive to the choice of an 'uninformative' prior for P_{1993}.

MSYR

The second parameter that all stock assessments have to incorporate is one that determines the overall productivity of the resource. In the BALEEN II population dynamics model, this is the resilience parameter (*A*). The 1994 B-C-B bowhead assessment (IWC, 1995) placed a prior distribution on MSYR_{mat} rather than on *A* (presumably because scientists are familiar with values for MSYR, which facilitates comparison among stocks/species, unlike the situation for *A*). Other possible choices for the productivity parameter include the increase rate at low population size, λ_{max}, and the current rate of increase, *ROI* (Punt, 1999).

The U[1%; 7%] prior for $MSYR_{mat}$ selected by the Scientific Committee (IWC, 1995) is consistent with that used in the development of the *Catch Limit Algorithm* for commercial whaling. Some concern has been expressed over the validity of the approach taken and its consistency in previous discussions about $MSYR_{mat}$ (IWC, 1995, p.148). Butterworth and Punt (1995) point out that the upper 2.5%ile of the posterior for $MSYR_{mat}$ under the 'backwards' approach suggests that values of $MSYR_{mat}$ higher than the upper bound of 7% permitted by its prior above are not incompatible with the other information available. Gelman *et al.* (1995) suggest that all plausible values for the model parameters should be assigned non-zero prior probability. One reason for this is that if the prior assigns zero probability to the value of some parameter, this value is always assigned zero probability in the posterior distribution. Punt and Butterworth (1996) argue that any prior for $MSYR_{mat}$ for the B-C-B bowhead stock should be viewed as 'uninformative', because the dissimilarities of bowheads and other baleen whale species render inferences for bowheads drawn from those other species questionable. Consequently, they advocate that the prior be chosen to be uniform and over a wider range than specified by IWC (1995). This suggestion was implicitly accepted by IWC (1998c) where a U[1%, 7%] prior for MSYR_{1+} (corresponding to an upper bound for MSYR_{mat} considerably larger than 7%) is specified (see Table 2).

Punt and Butterworth (1997a) developed an approach to Bayesian analysis ('less both') that ignores both of the priors for K_{1+} and *MSYR*. It involves generating values for current population size and the current rate of increase of the population (*ROI*) from prior distributions, and then selecting values for K_{1+} and *MSYR* to 'hit' the values generated for P_{1988} and *ROI* exactly. An assumption (not explicitly stated by Punt and Butterworth (1997a)) underlying this approach is that there is an 'indirect' prior for *ROI* which is U(-∞, ∞). The approach is thus equivalent to placing all of the direct information about *ROI* into the likelihood (for example, in the manner indicated in equation (3) following) and generating values for current population size from its prior and for *ROI* from U(-∞, ∞).

Punt (1999) outlines an approach for placing a prior on λ_{max} instead of on $MSYR_{1+}$ when conducting a Bayesian assessment. Best (1993) provides estimates of annual increase rates at low population size for a range of severely depleted stocks of baleen whales. Ignoring the estimate for the B-C-B bowhead stock (to avoid using the abundance data

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[8] This is an oversimplification to better make the essential point, which relates in particular to the update of the *MSYR* prior under 'forwards'. The reason it is not exactly correct as stated, however, is that even before the BALEEN II population model trajectories are computed, certain combinations of these biological parameters are impossible because of incompatibility with the demographics underlying the BALEEN II model, so that this aspect alone converts the independent priors into a joint distribution with some non-zero (but typically small) covariances.

[9] For the purposes of simplicity of presentation, this argument has ignored the possibility of oscillatory trajectories.

for this stock twice in the analysis) and the estimate for the Eastern North Pacific gray whale (which is not currently at a small fraction of its pre-exploitation equilibrium size), and taking the lower rate of increase when more than one estimate is provided for a given population, leads to seven estimated rates of increase at low population size (Table 6). The mean of these estimated annual rates is 0.085 (SD 0.024).

Table 6

Estimated annual rates of increase (with 95% confidence intervals) for several severely depleted stocks of baleen whales (source: Best, 1993).

Stock	Point estimate	95% CI
South African Right	0.068	[0.048, 0.086]
Argentine Right	0.073	[0.038, 0.108]
W. Australian Right	0.127	[0.076, 0.178]
NW. Atlantic Humpback	0.094	[-0.12, 0.30]
W. Australian Humpback	0.088	[0.030, 0.146]
E. Australian Humpback	0.097	[0.06, 0.13]
NE. Atlantic Blue	0.051	[0.026, 0.076]

Some account needs to be taken of the likely difference in productivity between bowheads and other baleen whales when using the information in Table 6 to develop a prior for the maximum steady rate of increase for the bowhead stock. Accordingly a range of alternative prior distributions for λ_{max} are considered for the sensitivity tests of this paper. These prior distributions should bound most interpretations of the information.

(a) $N(0.085, 0.024^2)$ – Using the empirical distribution as summarised by a normal distribution.
(b) U[0, 0.127] – A uniform distribution which covers the range of estimates and includes all non-negative values for λ_{max} lower than the largest value in Table 6.
(c) U[0, 0.051] – A uniform distribution with an upper bound equal to the lowest value in Table 6 – this reflects the perception that bowheads are among the least productive of the baleen whales.
(d) U[0.005, 0.051] - A uniform distribution with an upper bound equal to the lowest value in Table 6 and a lower bound chosen to exclude the possibility of a very unproductive stock.

Note that some of the estimates in Table 6 pertain to increase rates for stocks that are probably not currently at 'very low' levels (e.g. Best (1993) reports that the West Australian humpback population is currently 16 – 21% of its pre-exploitation equilibrium level). Use of such estimates therefore leads to the prior being biased towards low values.

Table 7 lists results for the 'reference case' 'backwards' analysis and the four sensitivity tests that place a prior on λ_{max} instead of on $MSYR_{1+}$. The results are notably sensitive to the choice of the prior for λ_{max}. This is not surprising because λ_{max} is closely related to $MSYR_{1+}$ and it is well known that the results of the B-C-B bowhead assessment are sensitive to the choice of the prior (particularly the choice of its upper bound) for $MSYR_{1+}$. The sensitivity test which places a $N(0.082;\ 0.024^2)$ prior on λ_{max} leads to more optimistic results (in terms of resource productivity) than the 'reference case', while the sensitivity tests which place an upper bound of 0.051 on λ_{max} lead to less optimistic results. It is notable, however, that the lower 5%iles of the *RY* and Q_0 distributions remain larger than 67, even for the most pessimistic assessment. The posteriors for the two most pessimistic cases suggest that the stock is most likely below *MSYL* in terms of the 1+ component of the population.

The prior distribution for $MSYR_{1+}$ upon which the 'reference case' is based was inferred from estimates of λ_{max}. The results in Table 7 suggest that considerable care needs to be taken in choosing species/stocks when constructing a prior for *MSYR* by inference because the results are very sensitive to which stocks/species are chosen.

With respect to the selection among *MSYR*, λ_{max}, and *ROI* as the parameter to choose (and with which probably to associate a uniform prior) to reflect the productivity of the resource, it should be noted that most of the estimates of *MSYR* for baleen whales that have been put forward (e.g., see summary in Butterworth and Punt, 1992) have been argued from inferences from increase rates at low population size. Such inferences depend implicitly on the values assumed for the biological parameters (such as *MSYL*) (Butterworth and Best, 1990). To avoid this need, we prefer here to place a prior on λ_{max} and let the population dynamics model make the link to *MSYR*, whose quantitative relationship to λ_{max} will vary across the ranges of values for the various biological parameters. On the other hand, bowheads have been argued to be dissimilar to other baleen whale species because of their unusually high age at maturity, which renders the defensibility of a prior on *MSYR* or λ_{max} based on those other species somewhat questionable. Furthermore, the current replacement yield (*RY*) is an output of the assessment of particular importance, and this is closely related to the product of the current population size and *ROI*. A uniform prior on *ROI* would be less informative about *RY* than would such a prior on *MSYR* or λ_{max}. However, there is no basis for

Table 7

Estimates of eight management-related quantities for the Bering-Chukchi-Beaufort Seas stock of bowhead whales based on the 'backwards' approach. The point estimates given are posterior medians, followed by posterior means in round parentheses. Posterior 90% credibility intervals are given in square parentheses. This table includes results for analyses that place a prior on λ_{max} rather than on *MSYR*.

	K_{1+}	*RY* (1998)	Q_0 (1998)	P^{1+}_{1998}/K_{1+}	P^{f}_{1998}/K^{f}	$P^{1+}_{1998}/MSYL_{1+}$	$MSYR_{1+}$	*Slope*
Reference case	12631 (12863)	211 (209)	209 (207)	71.2 (70.9)	45.9 (46.1)	100.2 (99.5)	2.59 (2.58)	2.49 (2.48)
	[10924 16531]	[141 273]	[136 279]	[53.5 90.1]	[37.8 57.9]	[76.8 122.8]	[1.51 3.78]	[1.39 3.67]
$\lambda_{max} \sim N(0.082;0.024^2)$	12178 (12375)	216 (214)	221 (217)	74.1 (73.8)	47.2 (47.6)	104.8 (104.2)	2.82 (2.81)	2.72 (2.69)
	[10687 15754]	[152 277]	[148 285]	[57.0 91.8]	[38.8 60.5]	[83.7 125.8]	[1.74 3.96]	[1.63 3.77]
$\lambda_{max} \sim U[0, 0.127]$	12631 (13109)	207 (203)	206 (201)	70.4 (69.8)	45.4 (45.8)	100.2 (99.2)	2.58 (2.52)	2.48 (2.42)
	[10893 18579]	[123 272]	[118 276]	[50.4 89.4]	[36.9 57.9]	[75.6 123.5]	[1.27 3.81]	[1.16 3.67]
$\lambda_{max} \sim U[0, 0.051]$	13767 (14412)	193 (185)	183 (176)	64.1 (62.7)	42.8 (42.6)	90.8 (89.3)	2.10 (2.01)	2.02 (1.92)
	[12365 21022]	[94 256]	[90 242]	[44.5 78.5]	[34.9 51.3]	[68.9 107.2]	[0.96 2.79]	[0.82 2.73]
$\lambda_{max} \sim U[0.005, 0.051]$	13755 (14326)	193 (187)	183 (177)	63.9 (62.9)	42.7 (42.6)	90.6 (89.3)	2.11 (2.02)	2.03 (1.93)
	[12386 20129]	[97 254]	[93 241]	[45.1 78.6]	[34.9 51.4]	[69.1 108.1]	[0.99 2.79]	[0.85 2.71]

specifying a prior on *ROI* (which depends on the current status of the resource) so on balance we advocate placing a prior on λ_{max}.

The choice of a prior for λ_{max} is complicated by a lack of data (see Table 6). We tentatively prefer a U[0, 0.127] prior. This prior implicitly acknowledges the perception that bowheads are likely to be relatively unproductive compared to other baleen whales by including values for λ_{max} lower than the lowest value in Table 6, but equally does not exclude higher values which are not incompatible with the data on the bowhead rate of increase.

Natural mortality

The derivation of the priors for S_{adult} and S_{juv} in 1994 (IWC, 1995) is poorly documented. The basis for the choice of the prior for S_{adult} appears to be inferences from the capture of a very large animal at Wainright in 1993 with two stone harpoons of a pattern generally out of use by the start of the 20th century, the age determination study by Nerini (1983), and estimates of natural mortality for adult right whales (IWC, 1995). IWC (1992) used values of 0.01yr^{-1} and 0.02yr^{-1} in Hitter-Fitter runs for the B-C-B bowhead stock primarily (it appears) because higher values were incompatible with estimates of the proportion of the population which is immature. Fig. 3 shows the marginal prior distribution assumed for S_{adult} by IWC (1995), as well as the corresponding distribution for the number of further years for which 5% of the population will survive after maturing. The upper tail of this distribution (5% point = 562yrs) is clearly unrealistic. The Scientific Committee could, in its reconsideration of priors for the B-C-B bowhead assessment, perhaps consider a prior on longevity rather than on adult natural mortality because this is arguably a more 'natural' parameter. Any prior on longevity would exclude unrealistically long lifespans and hence (effectively) place an upper bound on S_{adult}. In suggesting the 'reference' priors in Table 2, IWC (1998c) explicitly dealt with this issue by placing an upper bound of 0.995 on S_{adult} and by imposing a maximum age of 100 years.

Whitcher *et al.* (1996) and J.L. Laake (pers. commn) provide separate preliminary estimates of the survival rate of adult bowhead whales using data from aerial photographs of identified whales. These estimates are 0.970 (SD 0.054) [M-profile-1] and 0.995 (SD 0.055) [M-profile-2] respectively (see Fig. 4, upper panel). The prior distribution for S_{adult} selected by IWC (1995) (see Fig. 4, lower panel, for its marginal[10]) was not based (explicitly at least) on these data, so that this prior distribution and the aerial-photography-based distributions for the estimates can legitimately be considered to be independent. These aerial-photography-based distributions can therefore be included along with the abundance and 'proportion' information in the 'direct' data used when applying Bayesian methods. Naturally, because the Whitcher and Laake estimates are based on the same data, they cannot both be included in the same analysis.

The incorporation of these data can be achieved in two ways. The prior distribution of IWC (1995) for S_{adult} can be updated using Bayes' theorem, or this prior distribution can be left unchanged and an extra component added to the likelihood function. These two procedures will give identical results. The first is computationally more efficient and so has been applied here.

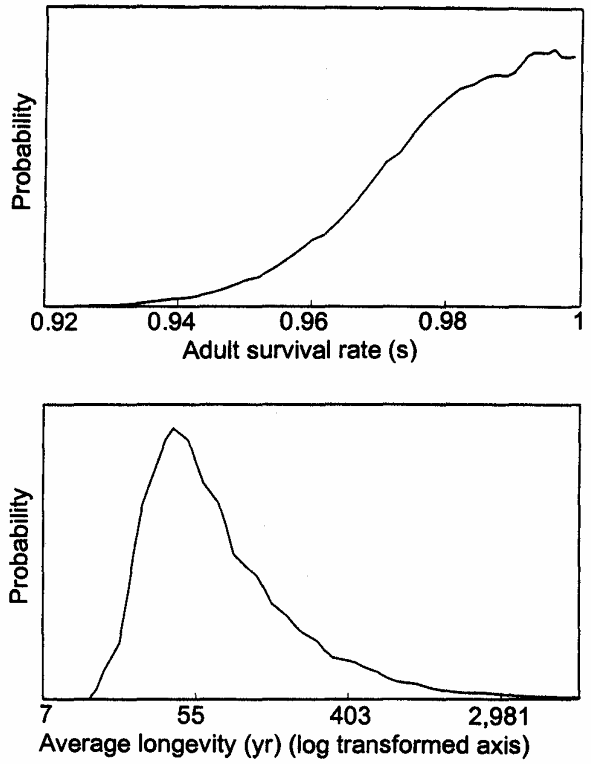

Fig. 3. Marginal prior distributions for adult survival rate S_{adult} (upper panel - from IWC (1995), see Table 2) and the number of years for which 5% of the population survive after reaching maturity (lower panel).

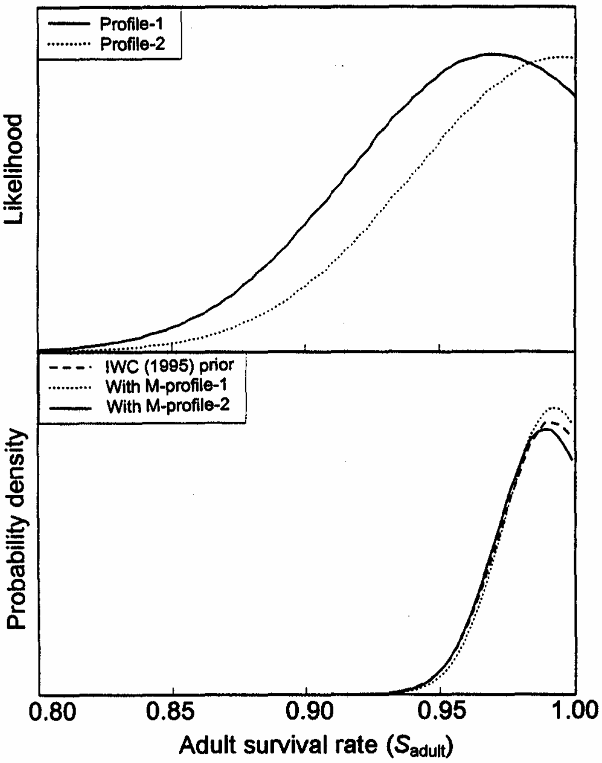

Fig. 4. The upper panel shows the two likelihood profiles derived for S_{adult} from analyses of aerial photography data, while the lower panel shows the marginal prior distribution for S_{adult} specified by IWC (1995) and two prior distributions for S_{adult} obtained by updating the IWC (1995) prior by means of the likelihood profiles in the upper panel.

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[10] This is a marginal distribution because IWC (1995) specified a joint pre-model distribution for S_{adult} and S_{juv}.

Butterworth (1995) raises the issue that the priors for age-at-maturity (a_m), natural mortality (M) and maximum fecundity should be correlated because, *a priori*, one expects that a high value for a_m would be linked to low values for M (e.g. Gunderson and Dygert, 1988). One of the impacts of the independence of the priors for a_m and S_{adult} (under the assumptions of IWC (1995)) is that there is a greater prior probability than seems reasonable that the age-at-maturity lies in the upper tail of its prior (say at the maximum of 26 years) and simultaneously that the adult survival rate lies in the lower tail of its prior (corresponding, say, to an average age that a bowhead lives after maturity of only 8 years or less).

IWC (1992) notes that there is no direct evidence about S_{juv}. The prior selected by IWC (1995) is based on the (seemingly reasonable) assumption that juvenile natural mortality is less than adult natural mortality (although it should be noted that there are also arguments that the reverse applies for fur seals, at least, because of the stress placed on the adults by the cost of reproduction—I. Boyd, pers. commn). However, the actual prior for S_{juv} is essentially arbitrary. This is hardly surprising because there are precious few (if any) reliable estimates of S_{juv} for baleen whales. Punt and Butterworth (1996) and Wade (1999) propose methods that avoid the need for specifying priors for both of S_{adult} and S_{juv}. The method proposed by Wade (1999) involves generating values for $MSYR$, $MSYL$, S_{adult}, a, a_m and f_{max} from their priors and then calculating a value for S_{juv}. If the value for S_{juv} is greater than the value for S_{adult}, the set of parameters is assigned zero likelihood. This approach was adopted by IWC (1998c), thus avoiding the need to specify a prior for S_{juv} in Table 2. It also implicitly forces a relationship (and hence correlation) between a_m and natural mortality and hence partially resolves the problem caused by the *a priori* assumption that a_m and S_{adult} are independent.

Including the data on S_{adult} from analysis of aerial photographs of identified bowheads hardly impacts the results of the assessment. This is a consequence of the highly informative prior distribution assumed for S_{adult} and the comparatively uninformative nature of the data. The lower panel of Fig. 4 shows the distributions for S_{adult} obtained by updating its prior distribution using the likelihoods in the upper panel. The updated distributions are very similar to the original distribution, confirming the uninformative nature of the data given the prior assumed for S_{adult}.

George *et al.* (1998) provided estimates of age for 42 bowheads using the aspartic acid racemization technique. Four of the animals were estimated to be older than 100 years. These data should be used in future to update the prior for S_{adult}.

Age-at-recruitment

The assessment assumes that recruitment occurs at age 1 and that the historical harvest has been taken with uniform selectivity from the 1 + component of the population. This is equivalent to assuming a delta-function prior for the age-at-recruitment at age 1. However, the age-at-recruitment is likely to have changed over time because, during the early years of the commercial fishery, whalers presumably targeted large animals (IWC, 1992). Following the demise of this fishery, aboriginal exploitation targeted smaller animals (IWC, 1992). The current formulation of the Baleen II model cannot allow for changes to the age-at-recruitment explicitly. It can, however, divide catches into those from the mature component of the population and those from the recruited (in this case the 1 +) component. The available data should be examined to see if an appropriate division of the historical harvests can be made between those to be assumed to be taken uniformly from the 1+ component and those taken similarly from the mature population, for a better reflection of the historical reality.

Age-at-maturity

The length at maturity for bowheads (averaged over both sexes) is approximately 13m (Withrow and Angliss, 1992). The prior assumed for a_m by IWC (1995) is based on converting a length of 13m to age. Information from carbon isotope ageing of baleen plates suggests that bowheads reach 13m between 18 and 20 years of age (Schell *et al.*, 1989). The prior for age-at-maturity, a normal distribution with mean 20 and standard deviation 3, constrained to lie between 13.5 and 26.5, was chosen to encompass the best estimates of 18-20 years and to incorporate a minimum value of 14 years (the lower limit for age-at-maturity obtained by Schell *et al.*, 1989). It is therefore based primarily on 'direct' information from ageing. The prior is probably overly precise because no account was taken of uncertainty in ageing methods and of the assumption that the length at maturity is 13m. Such information would have to be reflected as 'indirect' information.

Age of transition from juvenile to adult natural mortality rate

The prior for the greatest age at which juvenile natural mortality is assumed to apply, a, is based on a suggestion by Givens *et al.* (1995). They argued that because nothing is known about this parameter, a discrete uniform distribution from 1-9 years would be appropriate. The upper limit for this prior was selected to be less than 10 years, the lower limit of the prior assumed by Givens *et al.* (1995) for a_m. When the Scientific Committee (IWC, 1995) selected a prior for a_m which differed from that suggested by Givens *et al.* (1995), no changes were made to the prior for a. The available data are uninformative about the value for this parameter (Givens *et al.*, 1995).

Maximum pregnancy rate

The prior for the maximum pregnancy rate in IWC (1995) (taken to be the maximum possible pregnancy rate by Punt and Butterworth (1996)) was modified by the Scientific Committee in 1997 (IWC, 1998c). The lower bound for f_{max} of 0.25 was supported by evidence from photographically identified B-C-B bowheads. IWC (IWC, 1998c) does not provide a basis for the assumption of a uniform distribution on $1/f_{max}$, nor for the upper bound of 0.4. IWC (1995, p.146) does, however, refer to a 3-4 year calving interval under optimal conditions, although it is not completely clear how this is intended to relate to the maximum pregnancy rate. The prior selected by IWC (1998c) is markedly more informative than that suggested by Givens *et al.* (1995), which had most of its mass between 0.14 and 0.5 but also had some mass between 0.5 and 1.

The BALEEN II population dynamics model assumes that density dependence acts on fecundity (de la Mare, 1989; Punt, 1999)[11]. It differentiates between a pregnancy rate, which is density-dependent, and a constant 0-year-old natural mortality rate that is pre-specified. It is unclear to what extent this has been considered in previous assessments.

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[11] A variant of the BALEEN II model exists which allows for the assumption that density dependence acts on natural mortality rather than fecundity (Punt, 1996), and has been applied in an assessment of the B-C-B bowhead stock (Punt and Butterworth, 1996).

MSYL

The prior for this quantity is based on the arguments of Givens *et al.* (1995). It encompasses the range of values considered during the development of the *CLA* for commercial whaling. The prior chosen for $MSYL_{1+}$ (U[0.4; 0.8]) is centred on the Scientific Committee's choice in general past practice of $MSYL = 0.6$. This choice was based primarily on empirical evidence (e.g. Fowler, 1981) that the *per capita* growth rate of large mammal populations as a function of population size has a negative second derivative -see Butterworth and Best (1994) for a more detailed historical summary. However, the evidence and justification for this view has more recently been called into question (de la Mare, 1994; IWC, 1994; MacCall and Tatsukawa, 1994). IWC (1995) specified this prior for $MSYL_{mat}$, but this was changed to $MSYL_{1+}$ in IWC (1998c), in the light of arguments reflected in IWC (1998a).

Table 8

Data used in the construction of an index of abundance for the Bering-Chukchi-Beaufort Seas stock of bowhead whales (source: Zeh *et al.*, 1995). The N_4/P_4 estimates are based on analyses conducted by Zeh *et al.* (1995).

	N_4		P_4		N_4/P_4	
Year	Estimate	SE	Estimate	SE	Estimate	CV
1978	3,383	289	N/A		5,019	0.294
1980	2,737	488	N/A		4,061	0.336
1981	3,231	716	0.750	0.108	4,308	0.266
1982	4,612	798	N/A		6,843	0.333
1983	4,399	839	N/A		6,527	0.343
1985	3,134	583	0.519	0.131	6,039	0.317
1986	4,006	574	0.518	0.062	7,734	0.187
1987	3,615	534	N/A		5,364	0.320
1988	4,862	436	0.739	0.053	6,579	0.115
1993	7,249	505	0.933	0.013	7,770	0.071

Including the abundance data in the likelihood function

The data available for the assessment of the B-C-B bowhead stock are the estimates of the proportions of mature animals and calves in the population from 1985 to 1992 (the 'proportion' data) and the estimates of 1+ abundance from surveys conducted at Point Barrow, Alaska (the 'abundance' data).

The 'proportion' data are included in the likelihood function by assuming that the observations are *t* distributed with 5 degrees of freedom (IWC, 1995). The model-estimates are taken to be average of the predicted proportions for 1988 and 1989. Only the proportions of calves and of mature animals are included in the likelihood function and these proportions are assumed to be independent of each other.

Zeh *et al.* (1995) present a series of estimates of abundance for the B-C-B bowhead stock based on visual and acoustic counts of bowheads off Point Barrow (reproduced here as Table 8)[12]. Bayes Empirical Bayes (B-E-B) estimates of abundance are available for 1988 and 1993 (Raftery and Zeh, 1991; 1998; Zeh *et al.*, 1995). The B-E-B estimates are constructed from the data from the visual and acoustic surveys but also utilise prior information. For example, the B-E-B estimate for 1993 is based on a prior of 7,800 (SD 1,300) and a likelihood of approximately $N(8{,}293; 626^2)$. For ease of presentation, the former will be referred to as the B-E-B prior and the latter as the B-E-B likelihood. The following discussion deals only with the B-E-B likelihood because the B-E-B prior does not comprise part of the likelihood function[13].

Several alternative prescriptions are available to incorporate the abundance data in the likelihood function. Following past practice (IWC, 1995; 1998c), we assume that the N_4/P_4 estimates in Table 8 provide information on relative abundance while the B-E-B estimate for 1993 is an estimate of absolute abundance. Prescriptions (b) and (c) examine the implications of assuming that the N_4/P_4 estimates provide information on absolute abundance.

(a) The B-E-B likelihood for 1993 (or 1988) is assumed to provide information on absolute rather than relative abundance (IWC, 1992) and the N_4/P_4 estimates are used to obtain an estimate of the rate of increase in 1+ abundance. These two sources of information are then treated as being independent when constructing the likelihood function. The contribution of the abundance data to the negative of the logarithm of the likelihood function (excluding constants) in this case is given by:

$$-\ell nL = \frac{1}{2(\sigma_{1993}^{BEB})^2}\left(N_{1993}^{BEB} - \hat{N}_{1993}\right)^2 + \frac{9}{2}\ell n\left(1 + \tfrac{1}{8}(ROI^{obs} - R\hat{O}I)^2 / \sigma_{ROI}^2\right) \qquad (3)$$

where	N_y^{BEB}	is the B-E-B estimate of abundance for year y (assumed to apply to the 1+ component of the population and to be equal to the mode of the likelihood at 8,293 for $y = 1993$),
	$\hat{N}_y$	is the estimate of the number of 1+ animals at the start of year y from the population model,
	σ_y^{BEB}	is the standard error of N_y^{BEB} (taken to be 626, the likelihood standard deviation, for $y = 1993$),
	ROI^{obs}	is the estimate of the 1978-93 rate of increase, which is assumed to have a t_8 distribution (see Table 2),
	$R\hat{O}I$	is an estimate of ROI based on a regression of $\{\hat{N}_y ; y = 1978, 79, ... 93\}$ on y, and
	σ_{ROI}	is the standard error of ROI^{obs}.

(b) The data in Appendix A are assumed to provide independent estimates of absolute abundance; in terms of this assumption, the B-E-B likelihood would provide exact duplicate information to that already contained in the corresponding entry in the survey series, and hence is ignored. The contribution of the abundance data to the negative of the logarithm of the likelihood function (excluding constants) in this case is given by[14]:

$$-\ell nL = \sum_y \frac{1}{2(\sigma_y^{surv})^2}\left(\ell n N_y^{surv} - \ell n\hat{N}_y\right)^2 \qquad (4)$$

where	N_y^{surv}	is the estimate of abundance for year y based on the survey and acoustic data

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[12] 'Additional variance' (IWC, 1997) will be ignored because Zeh *et al.* (1995) and Cooke (1996) report that these abundance estimates and their *CV*s are consistent with the assumption that any such variance is of negligible size.

[13] Except when applying the 'forwards' approach to Bayesian Synthesis, for which the analysis is subject to the Borel paradox.

[14] The choice of log-normal error is based on a suggestion by Buckland (1992).

(assumed to apply to the 1+ component of the population), and

σ_y^{surv} is the standard error of the logarithm of N_y^{surv}.

(c) As for (b), except that account is taken of the covariance among the estimates of abundance (see Appendix A). The contribution of the abundance data to the negative of the logarithm of the likelihood function (excluding constants) is then given by (in vector-matrix notation):

$$-\ell nL = \tfrac{1}{2}(\ell n\underline{N}^{surv} - \ell n\hat{\underline{N}})^{T}(\Sigma^{surv})^{-1}(\ell n\underline{N}^{surv} - \ell n\hat{\underline{N}}) \quad (5)$$

where Σ^{surv} is the variance-covariance matrix for the logarithms of the survey estimates.

(d) The survey data are assumed to provide independent indices of relative abundance, with the B-E-B likelihood ignored for the same reason as in (b). The contribution of the abundance data to the negative of the logarithm of the likelihood function (excluding constants) in this case is:

$$-\ell nL = \sum_y \frac{1}{2(\sigma_y^{surv})^2}\left(\ell nN_y^{surv} - \ell n(b\hat{N}_y)\right)^2 \quad (6)$$

where b is the survey bias.

For this case, it is necessary to specify a prior for b. In the absence of information about b, an uninformative prior $\ell nb \sim U[-\infty, \infty]$ is assumed for this parameter.

(e) As for (d), except that account is taken of the covariance among the estimates of abundance. The contribution of the abundance data to the negative of the logarithm of the likelihood function (excluding constants) in this case is given by:

$$-\ell nL = \tfrac{1}{2}(\ell n\underline{N}^{surv} - \ell n(b\hat{\underline{N}}))^{T}(\Sigma^{surv})^{-1}$$
$$(\ell n\underline{N}^{surv} - \ell n(b\hat{\underline{N}})) \quad (7)$$

(f) The likelihood for the 1993 B-E-B estimate and the survey-based estimate for 1993 provide an estimate of the survey bias factor b of 0.936 (CV = 0.026)[15]. Following Butterworth *et al.* (1999) and Butterworth and Punt (1992), this estimate can be incorporated into the likelihood function as independent information about b. For the case in which the covariance among the estimates is ignored, this leads to the following negative log-likelihood:

$$-\ell nL = \frac{1}{2\sigma_b^2}(\ell n\tilde{b} - \ell nb)^2 +$$
$$\sum_y \frac{1}{2(\sigma_y^{surv})^2}\left(\ell nN_y^{surv} - \ell n(b\hat{N}_y)\right)^2 \quad (8)$$

where $\tilde{b}$ is the estimate of the survey bias factor (0.936) and,

σ_b is the CV of $\tilde{b}$ (0.026).

(g) As for (f), except that account is taken of the covariance among the estimates of abundance. The contribution of the abundance data to the negative of the logarithm of the likelihood function (excluding constants) in this case is given by:

$$-\ell nL = \frac{1}{2\sigma_b^2}(\ell n\tilde{b} - \ell nb)^2 +$$
$$\tfrac{1}{2}(\ell n\underline{N}^{surv} - \ell n(b\hat{\underline{N}}))^{T}(\Sigma^{surv})^{-1}(\ell n\underline{N}^{surv} - \ell n(b\hat{\underline{N}})) \quad (9)$$

Approach (a) above forms part of the 'reference case', while approaches (b)-(g) provide increasingly sophisticated treatments of the data. Equation (9) provides the most complete treatment of the data as it assumes: that the data in Appendix A provide an index of relative rather than absolute abundance; that those estimates are correlated; and that the likelihood for the B-E-B estimate provides information on absolute abundance. The likelihood for the 1993 B-E-B estimate is not explicitly included in Equation (9) as much of the information underlying this likelihood is already included in the survey estimate for 1993. Zeh and Givens (1997) illustrate that including both the likelihood of the B-E-B estimate and the information corresponding to the data on trend in an analysis can lead to severely biased estimates of quantities of importance to management. If data were available on the likelihood for the 1988 B-E-B estimate of abundance, Equation (9) could be extended by including a second term related to the associated estimate of survey bias.

Table 9 presents results for analyses based on the 'backwards' approach. Results are shown in this table for the 'reference' method for incorporating the abundance data in the likelihood function (Equation 3) and six alternative methods (see Equations 4 to 9). The results based on Equations 4-9 indicate a slightly less productive population and hence lower values for RY (1998) and Qo (1998). It should be noted that the abundance estimates for these latter analyses are not identical to those upon which ROI is based (contrast the estimates in Tables 8 and A.1). However, this is not the only reason for the differences in Table 9 because Punt and Butterworth (1996) show that incorporating the N_4/P_4 data in Table 8 into the assessment as absolute indices of abundance (cf. Equation 4) also leads to less optimistic results.

The results become slightly less optimistic if account is taken of the correlation among the estimates of abundance. Treating the abundance estimates as relative (Equations 6 and 7) rather than as absolute indices of abundance (Equations 4 and 5) or including a prior for the bias factor (Equations 8 and 9) increases the widths of the 90% credibility intervals slightly. However, the posterior means and medians are not impacted markedly by this change. Including a prior on the bias factor (our preferred approach) leads to results that are intermediate in terms of the widths of the 90% credibility intervals between those which treat all of the abundance estimates as absolute and those which treat all of the abundance data as relative. The posterior medians for Slope, RY (1998) and Q_0 (1998) for our preferred approach are also intermediate.

CONDUCTING THE POPULATION PROJECTION FOR RECENT YEARS ONLY

Assessments of the B-C-B bowhead stock have been conducted under the assumptions that, at the start of the catch series (1848), the population was at pre-exploitation equilibrium and that the carrying capacity of the bowhead population has not changed over time. An alternative to this set of assumptions is to assume instead that the population had a stable age-structure in some more recent year (see Punt (1999) for details of how this is implemented *for* the Baleen II model). The assessments of the Eastern North Pacific stock of gray whales are based on this latter assumption (Punt and Butterworth, 1997b; Wade, 1997; 1999).

One arguable advantage of this approach to conducting assessments of the B-C-B bowhead stock is that it becomes possible to place a (joint) prior distribution on K_{1+} and the $_{1+}$

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[15] This *CV* follows from the *CV*s for the N_4/P_4 and B-E-B estimates for 1993 assuming that these estimates are uncorrelated.

Table 9

Estimates of eight management-related quantities for the Bering-Chukchi-Beaufort Seas stock of bowhead whales based on the 'backwards' approach. The point estimates given are posterior medians, followed by posterior means in round parentheses. Posterior 90% credibility intervals are given in square parentheses. The analyses in this table differ in how the abundance data are included in the likelihood function.

	K_{1+}	RY (1998)	Q_0 (1998)	P^{1+}_{1998}/K_{1+}	P^{f}_{1998}/K^{f}	$P^{1+}_{1998}/MSYL_{1+}$	$MSYR_{1+}$	*Slope*
Post-model-pre-data	14,956 (14,897)	154 (159)	149 (156)	55.7 (57.4)	39.8 (40.5)	84.0 (84.7)	1.72 (1.87)	1.60 (1.74)
	[11,401 18,328]	[95 258]	[91 262]	[38.4 87.8]	[28.1 59.0]	[55.3 122.1]	[1.06 3.48]	[0.92 3.39]
Reference case	12,631 (12,863)	211 (209)	209 (207)	71.2 (70.9)	45.9 (46.1)	100.2 (99.5)	2.59 (2.58)	2.49 (2.48)
	[10,924 16,531]	[141 273]	[136 279]	[53.5 90.1]	[37.8 57.9]	[76.8 122.8]	[1.51 3.78]	[1.39 3.67]
Eqn. 4 likelihood	12,776 (13,026)	210 (206)	203 (201)	64.7 (64.6)	41.1 (41.5)	92.0 (91.4)	2.51 (2.51)	2.47 (2.47)
	[10,900 16,577]	[127 277]	[122 280]	[47.0 86.6]	[34.1 53.0]	[68.2 117.1]	[1.43 3.90]	[1.33 3.80]
Eqn. 5 likelihood	13,137 (13,397)	203 (198)	195 (192)	62.9 (63.0)	40.5 (41.1)	90.0 (89.8)	2.36 (2.37)	2.31 (2.31)
	[11,062 17,125]	[114 275]	[111 274]	[45.3 84.8]	[33.7 52.2]	[66.3 115.6]	[1.27 3.68]	[1.15 3.67]
Eqn. 6 likelihood	12,838 (13,084)	202 (199)	201 (199)	65.5 (65.6)	42.2 (42.8)	92.7 (92.4)	2.49 (2.50)	2.41 (2.41)
	[10,836 16,816]	[124 279]	[121 282]	[44.3 91.7]	[29.6 61.4]	[64.4 124.0]	[1.39 3.91]	[1.26 3.82]
Eqn. 7 likelihood	13,184 (13,413)	194 (192)	193 (191)	63.6 (64.1)	41.8 (42.3)	90.7 (90.8)	2.34 (2.37)	2.25 (2.28)
	[10,952 17,286]	[117 276]	[113 280]	[43.0 91.3]	[29.2 60.7]	[62.8 123.1]	[1.28 3.83]	[1.16 3.75]
Eqn. 8 likelihood	12,854 (13,066)	208 (203)	204 (202)	68.3 (68.2)	44.0 (44.4)	96.3 (96.1)	2.49 (2.51)	2.42 (2.42)
	[10,749 16,878]	[127 269]	[122 285]	[49.1 91.0]	[36.0 56.9]	[71.7 121.4]	[1.38 4.04]	[1.28 3.82]
Eqn. 9 likelihood	13,195 (13,429)	200 (196)	195 (193)	66.2 (66.5)	43.4 (44.0)	94.9 (94.4)	2.33 (2.36)	2.25 (2.27)
	[10,981 17,327]	[119 267]	[114 279]	[47.8 89.8]	[35.7 56.4]	[69.4 121.8]	[1.27 3.85]	[1.15 3.71]

Table 10

Estimates of eight management-related quantities for the Bering-Chukchi-Beaufort Seas stock of bowhead whales based on the 'backwards' approach. The point estimates given are posterior medians, followed by posterior means in round parenthesis. Posterior 90% credibility intervals are given in square parenthesis. This table includes results for analyses that start the population trajectories from a more recent year (y_1) rather than from an assumed pre-exploitation equilibrium in 1848.

	K_{1+}	RY (1998)	Q_0 (1998)	P^{1+}_{1998}/K_{1+}	P^{f}_{1998}/K^{f}	$P^{1+}_{1998}/MSYL_{1+}$	$MSYR_{1+}$	*Slope*
Reference case	12,631 (12,863)	211 (209)	209 (207)	71.2 (70.9)	45.9 (46.1)	100.2 (99.5)	2.59 (2.58)	2.49 (2.48)
	[10,924 16,531]	[141 273]	[136 279]	[53.5 90.1]	[37.8 57.9]	[76.8 122.8]	[1.51 3.78]	[1.39 3.67]
y_1 = 1930	17,920 (18,710)	241 (245)	239 (245)	50.7 (54.1)	31.9 (34.9)	73.7 (76.8)	2.46 (2.47)	2.55 (2.53)
	[10,002 30,097]	[127 401]	[136 399]	[30.8 91.5]	[19.2 63.8]	[43.7 123.0]	[1.48 3.68]	[1.41 3.81]
y_1 = 1950	16,190 (16,482)	234 (238)	234 (239)	56.5 (59.3)	35.7 (38.4)	80.5 (83.4)	2.51 (2.52)	2.54 (2.53)
Max K_{1+} = 25,000	[9,637 24,453]	[118 397]	[132 393]	[37.7 93.2]	[23.5 67.2]	[52.7 124.4]	[1.49 3.69]	[1.35 3.79]
y_1 = 1950	18,541 (19,032)	244 (248)	242 (248)	49.3 (53.3)	30.9 (34.3)	71.8 (75.4)	2.48 (2.48)	2.57 (2.54)
Max K_{1+} = 31,000	[10,038 30,114]	[125 402]	[137 400]	[30.7 91.9]	[19.1 63.8]	[43.5 123.0]	[1.48 3.68]	[1.39 3.83]
y_1 = 1950	23,188 (25,191)	253 (256)	251 (256)	39.6 (44.8)	24.6 (28.7)	57.5 (63.9)	2.42 (2.42)	2.58 (2.56)
Max K_{1+} = 50,000	[10,276 48,051]	[134 411]	[141 409]	[19.7 90.2]	[12.2 62.4]	[28.6 121.4]	[1.44 3.62]	[1.44 3.77]
y_1 = 1960	18.415 (19.027)	247 (247)	243 (248)	49.5 (53.4)	30.9 (34.4)	72.0 (75.6)	2.48 (2.48)	2.57 (2.55)
	[9.847 30.148]	[124 401]	[135 398]	[30.7 92.3]	[19.0 65.1]	[43.5 123.0]	[1.50 3.66]	[1.39 3.82]
y_1 = 1970	18.417 (19.044)	247 (248)	244 (248)	49.6 (53.3)	31.1 (34.3)	72.0 (75.5)	2.49 (2.48)	2.58 (2.55)
	[9.921 30.202]	[124 401]	[136 399]	[30.8 91.8]	[19.0 64.4]	[43.5 123.0]	[1.49 3.65]	[1.37 3.79]

population size in 1993, P_{1993}[16]. Thus, the problem of having to choose between the 'backwards' and 'forwards' approaches is eliminated. Other arguable advantages are that results are no longer dependent on values for catches during the early period of the fishery, which have had to be estimated in the absence of specific records, and that the possibility of regime shifts (tantamount to changes in K over time) is admitted. Four alternative choices for the first year in the analysis, y_1, are considered (1930, 1950, 1960, and 1970). The prior for K_{1+} is taken to be that for the 'reference case', $\ell n K_{1+} \sim U[\ell n 7000, \ell n 31000]$. The sensitivity of the results to the choice for the upper end of the prior for K_{1+} is explored by changing it from 31,000 to 25,000 and to 50,000.

Table 10 lists results for six sensitivity tests that do not start the population projections from deterministic pre-exploitation equilibrium in 1848, but assume instead that the population had a stable age-structure in some more recent year. For comparability with the 'reference case', the sensitivity tests are based on the 'reference' likelihood of Equation 3. The results are not particularly sensitive to the choice of y_1. However, there are notable differences between the results for the 'reference case' and those for the six sensitivity tests. For example, the posterior distributions for Q_0 (1998) and RY (1998) have longer tails at high values and the posterior for the pre-exploitation size does not differ much from its prior. One consequence of the latter result is that the depletion- and population size-related results depend strongly on the upper bound of the prior assumed for K_{1+}. For example, the posterior median for P^{1+}_{1998}/K_{1+} drops from 56.5 to 39.6 (%) as the upper bound for K_{1+} is increased from 25,000 to 50,000. In contrast, the posterior medians for RY (1998), Q_0 (1998), *Slope*, and $MSYR_{1+}$ do not depend notably on the upper bound for K_{1+}.

Thus, not unexpectedly, dropping the assumption that the population was at its pre-exploitation level in 1848 (and that all the historical catches are known exactly) leads to much wider 90% credibility intervals for all quantities except *Slope* and $MSYR_{1+}$. This effect is perhaps most notable for RY (1998) for which the 90% credibility interval is (roughly) [125, 400] for the sensitivity tests compared to [141, 273] for the 'reference case'. It is perhaps notable that the lower 5%ile for Q_0 (1998) hardly differs among the analyses

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[16] This needs to be a joint prior distribution because the *a priori* constraint that $P_{1993} < K$ must be imposed (there being negligible probability that possible oscillatory behaviour of the population trajectory as a result of time-lags in the dynamics could see the population above K in recent years).

although the upper 95%ile differs markedly between the 'reference case' and the sensitivity tests. The posterior median for the *Slope* statistic for the sensitivity tests is slightly closer to the 'observed' value in Table 2.

OUR PREFERRED ANALYSIS

The advantages of starting the population projections in some more recent year are that it is not necessary to assume that the carrying capacity of the bowhead population has remained unchanged over the last 150 years and that all the historical catches are known exactly. We believe that analyses should be conducted for both options, i.e. assuming that the population was at its pre-exploitation level in 1848 and assuming that it had a stable age-structure in some more recent year. Results are presented for the case $y_1 = 1950$ for the analyses that start the projections in a recent year as such results are not very sensitive to the choice for y_1. The results for this assessment are shown for the 'reference case' prior for K_{1+}. This choice is essentially arbitrary, so little confidence can be placed in the results for the depletion- and population size-related quantities because the posteriors for these quantities depend critically on the choice of a prior distribution for K_{1+}, which is barely updated by the data (Table 10). However, Table 10 does also show that the key management-related quantities RY (1998) and Q_0 (1998) are relatively insensitive to variations in the specification of a prior for K_{1+}, so that this approach retains utility.

We prefer the 'backwards' to the 'forwards' approach for three main reasons: the simulation test results show a clear preference for 'backwards', any assessment based on 'forwards' which also places a prior on the abundance in a recent year is subject to the Borel paradox, and 'forwards' updates the prior for *MSYR* before any data are included in the assessment. As noted above, although the full pooling approach of Raftery and Poole (1997) and Poole and Raftery (1998) resolves the Borel paradox, in doing so it introduces a new problem of how to choose pooling weights (i.e. how to specify their relative reliabilities of the priors for K_{1+} and P_{1993}). λ_{max} (the maximum rate of population increase, which occurs at low population size) is our preferred choice for the productivity parameter, because nearly all the data available from other whale species upon which to base a productivity prior constitute observations of this quantity. We tentatively suggest a U[0, 0.127] prior for λ_{max} for reasons discussed above.

We prefer the likelihood defined by Equation (9) because it treats the abundance estimates in Table A.1 as relative indices of abundance and because it incorporates the (independent) information about the bias factor explicitly in the likelihood. Equation (9) is preferred to Equation (8) because it takes account of the correlation among the abundance estimates.

Table 11 lists results for the 'reference case' 'backwards' analysis and the two 'preferred' variants. In addition to providing results for the eight quantities listed above, results are also shown for S_{juv}, S_{adult}, a_m, f_{max}, P_{1993}, $MSYL/K_{1+}$ $MSYR_{mat}$, and λ_{max}. The results for $MSYL/K_{1+}$, $MSYR_{mat}$ and λ_{max} are presented as percentages. As expected from the results of Table 9 which show that the use of the Equation 9 likelihood leads to notably lower estimates of productivity, the results for the 'preferred' analyses are less optimistic than those for the 'reference case'. The lesser productivity of the resource is reflected by lower posterior medians for *MSYR* and λ_{max}. This appears to be a reflection primarily of lower values for S_{juv} and $MSYL/K_{1+}$ - the posterior medians for which drop from 0.94 and 0.72 respectively for the 'reference case' to 0.93 and 0.70/0.69 for the two 'preferred' variants. Although the results for the population size- and depletion-related quantities from the $y_1 = 1950$ variant are unreliable owing to their sensitivity to the choice of a prior for K_{1+}, the posteriors for the biological parameters are remarkably similar for the two preferred analyses. The lower 5%iles for RY (1998) and Q_0 (1998), although insensitive to the choice of y_1, are notably lower than those for the 'reference case' (only about 80 compared to some 140). This is a consequence of a smaller current population size and lower productivity. However, these lower 5%iles are all larger than the current annual strike limit for the B-C-B stock of 67.

Table 11

Estimates of the eight management-related quantities considered previously and eight further biological parameters/variables for the Bering-Chukchi-Beaufort Seas stock of bowhead whales based on the 'backwards' approach. The point estimates given are posterior medians, followed by posterior means in round parentheses. Posterior 90% credibility intervals are given in square parentheses. Results are shown in this table for the reference case and the two 'preferred' analyses.

	Estimation procedure					
Quantity	'Backwards' reference case		Preferred - y_1=1848		Preferred - y_1=1950	
K_{1+}	12,631 (12,863)	[10,924 16,531]	13,353 (1,3935)	[10,998 20,881]	17,979 (18,660)	[9,692 30,322]
RY (1998)	211 (209)	[141 273]	195 (186)	[84 265]	207 (216)	[83 413]
Q_0 (1998)	209 (207)	[136 279]	189 (183)	[81 275]	206 (215)	[82 412]
P_{1998}^{1+}/K_{1+}	71.2 (70.9)	[53.5 90.1]	65.2 (64.4)	[41.0 88.5]	49.6 (52.7)	[29.5 91.5]
P_{1998}^{f}/K^{f}	45.9 (46.1)	[37.8 57.9]	42.9 (43.2)	[33.1 56.3]	32.6 (35.4)	[19.4 66.2]
$P_{1998}^{1+}/MSYL_{1+}$	100.2 (99.5)	[76.8 122.8]	94.1 (92.9)	[65.1 121.3]	73.5 (76.6)	[43.3 124.5]
$MSYR_{1+}$	2.59 (2.58)	[1.51 3.78]	2.27 (2.25)	[0.88 3.78]	2.22 (2.21)	[0.94 3.65]
Slope	2.49 (2.48)	[1.39 3.67]	2.19 (2.15)	[0.75 3.63]	2.24 (2.23)	[0.74 3.87]
$MSYL/K_{1+}$	0.72 (0.71)	[0.62 0.80]	0.70 (0.69)	[0.57 0.79]	0.69 (0.69)	[0.56 0.79]
S_{juv}	0.937 (0.926)	[0.827 0.985]	0.928 (0.917)	[0.810 0.983]	0.928 (0.917)	[0.813 0.983]
S_{adult}	0.988 (0.987)	[0.975 0.995]	0.986 (0.985)	[0.970 0.995]	0.986 (0.985)	[0.971 0.995]
a_m	20 (20)	[16 25]	20 (20)	[16 25]	20 (20)	[16 25]
f_{max}	0.31 (0.31)	[0.26 0.39]	0.31 (0.32)	[0.26 0.39]	0.30 (0.31)	[0.26 0.39]
λ_{max}	5.14 (5.16)	[3.63 6.95]	4.74 (4.78)	[2.95 7.09]	4.77 (4.77)	[3.00 6.88]
P_{1993}	8,212 (8,195)	[7,262 9,250]	7,984 (7,988)	[7,246 8,887]	8,009 (8,016)	[7,230 9,031]
$MSYR_{mat}$	4.86 (4.89)	[2.77 7.55]	4.21 (4.22)	[1.64 7.33]	4.12 (4.14)	[1.72 7.16]

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Appendix A

CONSTRUCTING INDICES OF ABUNDANCE FOR THE B-C-B BOWHEAD STOCK

The data available for the construction of indices of abundance for the B-C-B bowhead stock include estimates of N_4 (the observed number of bowheads passing within visual range) for ten years and estimates of P_4 (the observed proportion passing within visual range) for five of these years (Table 8). Previous analyses of these data (e.g. Raftery *et al.* (1995b); Zeh *et al.* (1995)) have assumed that the proportion passing within visual range for the years for which estimates of P_4 are not available is equal to the average over the years for which such estimates are available. Cooke (1996) criticised the methods used by Raftery *et al.* (1995b) and Zeh *et al.* (1995) because they treat the observation and process errors in an *ad hoc* manner. He proposed the following statistical model for the analysis of the data in Table 8:

$$N_{4y} = P_y p_y e^{v_y} \qquad v_y \sim N(0;\sigma^2_{v,y}) \qquad \text{(A.1)}$$

$$P_{4y} = p_y e^{\varepsilon_y} \qquad \varepsilon_y \sim N(0;\sigma^2_{\varepsilon,y}) \qquad \text{(A.2)}$$

$$p_y = \pi e^{\eta_y} \qquad \eta_y \sim N(0;\sigma^2_\eta) \qquad \text{(A.3)}$$

where N_{4y} is the estimate of N_4 for year y,
P_{4y} is the estimate of P_4 for year y,
P_y is the size of the 1+ component of the population in year y,
p_y is the proportion of the 1+ component of the population within visual range in year y,
π is the mean proportion of the 1+ component of the population within visual range (the actual proportion varies from year to year as a consequence of process error),
$\sigma^2_{v,y}$ is the variance of the logarithm of N_{4y} (reflecting observation error),
$\sigma^2_{\varepsilon,y}$ is the variance of the logarithm of P_{4y} (reflecting observation error), and
σ^2_η is the process error variance.

The parameters of this model are P_y and p_y for each of the ten years, π, and σ^2_η. The estimates of the 22 parameters of this model are obtained by maximum likelihood. This involves finding the values for the parameters that minimise the following negative log-likelihood (after removal of constants):

$$-\ell nL = \sum_y \frac{(\ell n N_{4y} - \ell n(P_y p_y))^2}{2\sigma^2_{v,y}} + \sum_y \frac{(\ell n P_{4y} - \ell n p_y)^2}{2\sigma^2_{\varepsilon,y}} + \sum_y \frac{(\ell n p_y - \ell n \pi)^2}{2\sigma^2_\eta} + \tfrac{1}{2}\ell n\left\|1 + \sigma_\eta U\right\|$$

where U is the reduced information matrix (which accounts for the impact of the estimation of the nuisance parameters - see Seber and Wild, 1989).

The first and third summations are over all ten years and the second summation is over the five years for which estimates of P_4 are available. The maximum likelihood estimate of p_y for those years for which estimates of P_4 are not available is π.

Table A.1 lists the estimates of the P_y, the estimates of the asymptotic standard errors of ℓnP_y and the correlation matrix for ℓnP_y that result from the implementation of Cooke' s approach.

Table A.1

Estimates, CVs (actually standard errors of the logarithms), and the correlation matrix for the indices of abundance for the Bering-Chukchi-Beaufort bowhead stock. Values are based on the estimation procedure described in Appendix 1.

Year	Estimate	CV	Correlation matrix									
1978	4,820	0.273	1.000									
1980	3,900	0.314	0.166	1.000								
1981	4,389	0.253	0.054	0.047	1.000							
1982	6,572	0.311	0.168	0.146	0.047	1.000						
1983	6,268	0.321	0.163	0.141	0.046	0.143	1.000					
1985	5,132	0.269	0.126	0.109	0.025	0.110	0.107	1.000				
1986	7,251	0.186	0.080	0.070	0.012	0.070	0.068	0.108	1.000			
1987	5,151	0.298	0.175	0.152	0.049	0.154	0.149	0.115	0.074	1.000		
1988	6,609	0.113	0.038	0.033	0.012	0.033	0.032	0.018	0.009	0.035	1.000	
1993	7,778	0.071	0.002	0.001	0.001	0.001	0.001	-0.002	-0.002	0.001	0.001	1.000

Trends in harbour porpoise abundance off central California, 1986-95: evidence for interannual changes in distribution?[1]

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ABSTRACT

This paper presents an updated analysis of trends in the abundance of harbour porpoise, *Phocoena phocoena*, in central and northern California, for the period 1986-95. The most recent survey effort (1995) was comparable to previous years, and regional patterns of density were similar to those found on past surveys, with densities lowest south of Monterey Bay, intermediate from Monterey Bay to the Russian River and highest off northern California. An analysis of covariance model was constructed to test for a trend in abundance while accounting for the effects of sea state, cloud cover and area. The results are qualitatively similar to those obtained for the 1986-93 time series, but encounter rates were higher in 1995, and the estimated rate of decline over the entire time period changed from 9.4% to 5.9% per year. The decreasing trend is no longer significant at $\alpha = 0.10$ ($p = 0.149$). A power analysis based on Monte Carlo simulations revealed that power remains low to detect trends of less than 10% per year. Possible effects of oceanographic conditions, as measured by the September average sea surface temperature anomaly (SSTa), on porpoise abundance are investigated using two different techniques. Correlation tests indicate an inverse relationship between SSTa and relative porpoise abundance for the eight survey years. The correlation is greatest when considering the change between survey years (decreases in relative abundance and increases in SSTa), rather than the individual values of relative abundance and SSTa. An alternate, Poisson-based generalised additive model (GAM) of porpoise sighting rates in relation to area, sea state, cloud cover, year and SSTa indicates a significant, non-linear effect of sea surface temperature on porpoise sighting rates, with no significant year effect once SSTa is included. These results suggest that harbour porpoise may exhibit interannual movement in and out of the study area in relation to changing oceanographic conditions.

KEYWORDS: HARBOUR PORPOISE; INDEX OF ABUNDANCE; DISTRIBUTION; MOVEMENTS; NORTH PACIFIC; SURVEY-AERIAL; TRENDS; OCEANOGRAPHY

INTRODUCTION

The abundance of the harbour porpoise, *Phocoena phocoena*, in nearshore waters off central California, was recently reported to have declined between 1986 and 1993 based on aerial surveys designed to monitor the relative abundance of this species (Forney, 1995). The observed trend was statistically significant at $\alpha = 0.10$ ($p = 0.078$), but there was a large degree of uncertainty around the point estimate of a 9.4% per year decline (coefficient of variation, CV = 0.56). Several plausible explanations were presented for the observed trend, including natural and human-caused factors contributing to a true reduction in population size, and changes in the geographical distribution of harbour porpoises in this region. However, the available data were insufficient to attribute the decline to any of the possible causes.

An eighth aerial survey, conducted in 1995, has completed a 10-year time series for this population. This paper presents an updated trend analysis for 1986-95, including a power analysis to evaluate the likelihood of detecting trends in this 10-year time series. Power is similar to the values predicted in Forney *et al.* (1991), but overall it is still too low to reliably detect small changes in abundance. A Poisson-based generalised additive model (GAM) is explored as an alternative to the previously used ANCOVA model. Finally, one of the possible explanations for the observed decline in abundance - distributional shifts of this population in relation to oceanographic changes - is investigated using correlation tests and generalised additive models.

METHODS

A complete description of the field methods and the ANCOVA analysis is given in Forney *et al.* (1991), and only a brief summary is provided here.

Field methods

Aerial line transect surveys were conducted from late summer to early autumn (15 August-15 November) in 1986-91, 1993 and 1995. In each survey year, a set of 26 transects between Point Conception and the Russian River (Fig. 1a) was replicated as often as weather permitted (generally 4-8 times) to monitor the central California harbour porpoise population. Beginning in 1989, a set of 17 additional transects between the Russian River and the California-Oregon border (Fig. 1b) was surveyed 1-3 times per field season, to monitor the northern California population. The transects followed a zigzag pattern designed to survey systematically between the coast and the 92m (50 fathom) isobath, which is the depth range in which the majority of harbour porpoise are expected to be found in this region (Barlow, 1988). The only deviation from this design occurred outside of San Francisco Bay, where the 92m (50 fathom) contour is located too far offshore for safe operation of the survey aircraft; in this region, the transect lines only extended to the 55m (30 fathom) contour. Total transect length was 916km, and under good weather conditions all transects could be surveyed in two days. The survey platform was a high-wing, twin-engine *Partenavia* P-68 aircraft outfitted with two bubble windows for lateral viewing and a belly port for downward viewing. The survey team consisted of three observers (left, right and belly) and one data recorder. Line transect methods were followed, with sighting distances calculated from the declination angle to the sighting when abeam of the aircraft (obtained with a hand-held clinometer) and the aircraft's altitude. Surveys were flown at 167-185km/hr (90-100 knots) airspeed and 213m (700ft) altitude. Flights were conducted only when weather conditions were good (Beaufort sea states 0-3, with mostly clear or partly cloudy skies). Sighting information and environmental conditions were recorded and updated throughout the survey using a laptop computer connected to the aircraft's LORAN navigation system.

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[1] A version of this paper was submitted to the IWC Scientific Committee as SC/48/SM5.

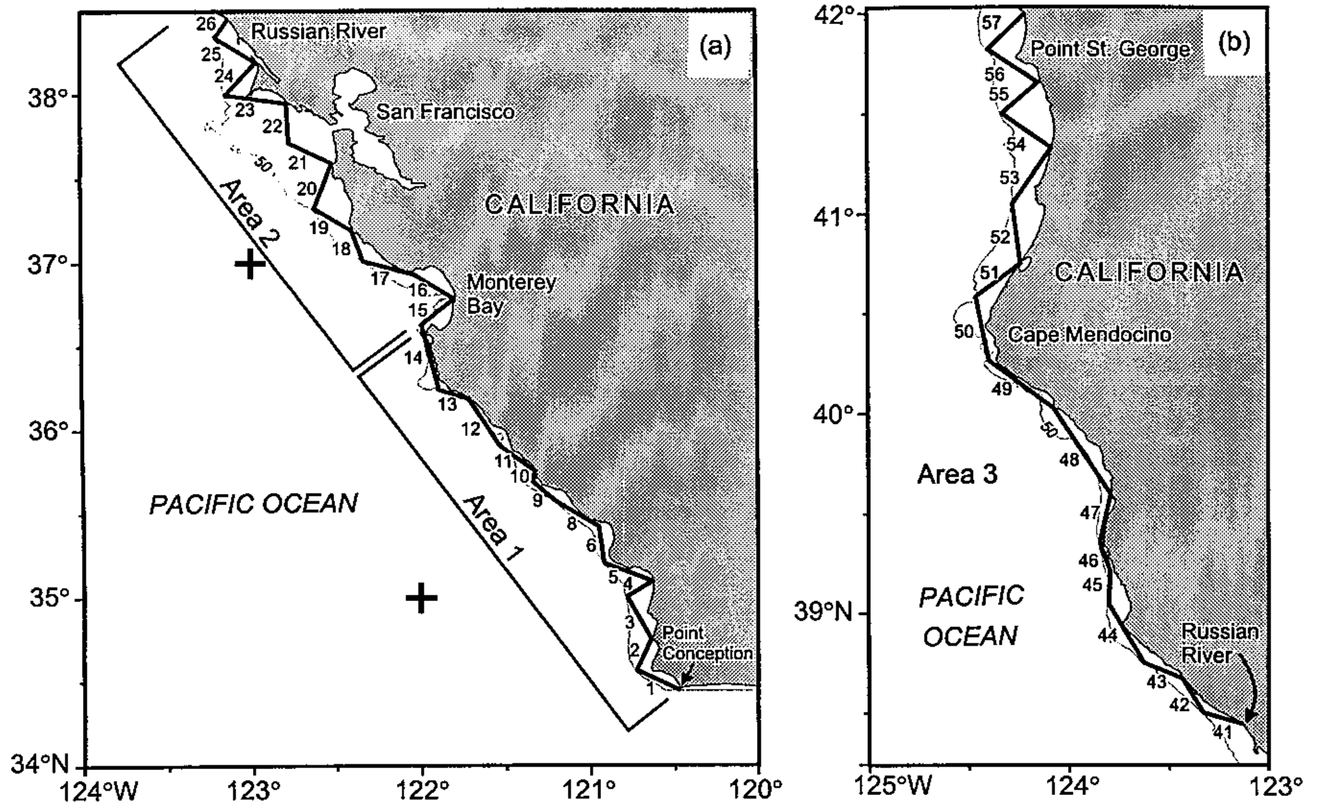

Fig. 1. Flight transects and defined areas for aerial surveys for harbour porpoise, *Phocoena phocoena*: (1a) central California (Transects 1-26, Areas 1 and 2); and (1b) northern California (Transects 41-57, Area 3). Transect 7 was combined with transect 8 after 1986 and is not shown. Crosses indicate locations for SSTa data.

The ANCOVA model

The number of harbour porpoises seen per kilometre (porpoise km^{-1}) of search effort was used as a measure of relative abundance. These data were stratified by Beaufort sea state (0-1, 2 and 3), area (transects 1-14 and 15-26 in central California, and 41-57 in northern California; see Fig. 1), and percent cloud cover ($<25\%$; $\geq 25\%$). Data values were log-transformed, and a stepwise selection procedure was used to construct an analysis of covariance model of the form:

$$P = \mu + \beta_1 + \beta_2 + \ldots + \delta(y - \bar{y}) + \varepsilon \qquad (1)$$

where P is the log-transformed value of the number of porpoises $\mathrm{km}^{-1} + 0.001$, μ is the mean value of P, the β are factors influencing apparent porpoise abundance (such as sea state), δ is the coefficient for the covariate year (y), $\bar{y}$ is the mean year and ε is a random error term. This additive model for the log-transformed data is equivalent to a multiplicative model for the actual data. (Stratification variables such as sea state are expected to change the fraction of animals observed, and thus have a multiplicative effect). Interaction terms were included in the stepwise procedure for values previously included in the model. Variability caused by unequal survey coverage in each combination of sea state, percent cloud cover and geographic area was included in the model by weighting by the number of kilometres flown. The analysis was done separately for central California alone (Transects 1-26) and for both central and northern California (Transects 1-26 and 41-57).

Simulation methods

Once the best model had been selected (see results), Monte Carlo simulations were performed as described in Forney *et al.* (1991) to determine the power of the ANCOVA to detect a given trend in porpoise abundance correctly. Only central California data were included in the simulations. Increasing and decreasing trends of 5% and 10% per year over 10 and 12 years were simulated, as well as a situation with 'no trend' to evaluate α-levels in this procedure. The random datasets were generated using the parameters and error structure obtained for the actual data from the best model. First, the expected logarithmic value of porpoises km^{-1} for each combination of conditions was calculated from the fitted parameters. A random error term for each expected value was then drawn from a normal distribution with a mean of zero and standard deviation equal to the standard error from the ANCOVA results of the best model (without year). To allow weighted analysis of the simulated data, this error term was weighted inversely, i.e., multiplied times $\sqrt{(1/w)}$, where w is the number of kilometres flown under the given conditions. For each simulation, a set of 96 values of w representing each of the 96 combinations of the predictor variables, was obtained by randomly selecting the actual numbers of kilometres flown from one of the eight survey years. Complete yearly sets were chosen rather than individual values to avoid unlikely combinations of kilometres flown.

A yearly trend was incorporated into the simulation data by multiplying the calculated value of porpoises km^{-1} by a factor representing the desired exponential change in porpoise abundance. To make the simulated data more realistic, all values were rounded to yield only integer values of porpoises over the given number of kilometres flown. In addition, to prevent infeasible values of porpoises km^{-1}, a new error term was drawn if the original one resulted in a back-transformed value of porpoises km^{-1} that was negative or greater than 0.4. The highest value observed in central California in 1986-95 was 0.24 porpoises km^{-1}; multiplying this value by the maximum simulated increasing trend, yields an upper limit of approximately 0.4 porpoises km^{-1}. In the simulations, less than 5% of all error terms were redrawn because they failed to meet these criteria.

Tests of oceanographic correlates

No direct measurements of oceanographic conditions at the time of the surveys were available for this analysis. Therefore, the monthly mean sea surface temperature anomalies (SSTa) for September and October, estimated by the US National Weather Service (NWS) for all years from satellite, buoy and shipboard measurements of sea surface temperature[2], were obtained as an approximate indicator of oceanographic conditions off central California during the survey period. The most representative stations were located at 35°N,122°W and 37°N,123°W for Areas 1 and 2, respectively, and the average value at these stations for September and October was used as an index of oceanographic conditions for each year. [Note: Although these two stations are farther offshore than the central California study area, the NWS contour maps indicated that nearshore SSTa were identical or very similar to those at these stations.] Two different types of analyses were performed to investigate a possible environmental component to the observed patterns of abundance: correlation tests and a GAM, as described below.

Two Pearson's correlation tests were performed on SSTa and the relative abundance of harbour porpoise in central California, adjusted for the effects of sea state and cloud cover using the best-fit coefficients from the ANCOVA model. First, the values of SSTa and relative porpoise abundance were compared to investigate a potential relationship between high and low values of each variable. Second, the differences in SSTa and relative porpoise abundance between successive survey years were compared to test for a relationship between the direction and magnitude of *changes* in these two variables.

The Poisson-based generalised additive model

As an alternative to the previously used ANCOVA model, a Poisson-based GAM was explored to test for trends in harbour porpoise abundance, and to investigate possible non-linear effects of the sea surface temperature anomaly. Animal count data often follow a Poisson distribution, and therefore a Poisson model may be more appropriate for the survey data in this analysis. GAMs (Hastie and Tibshirani, 1990) differ from the more familiar generalised linear models (GLM) (McCullagh and Nelder, 1989) in that the response variable (y) is modelled as the sum of nonparametric functions of the predictor variables ($x_1, x_2, \ldots, x_n$), rather than the sum of linear relationships. A general equation describing a GAM (Hastie and Tibshirani, 1990) is:

$$y = c + \sum_{i=1}^{n} f(x_i) \qquad (2)$$

In the framework of GLMs and GAMs, a Poisson process can be modelled by specifying the log-link function $\eta = \log(\mu)$ with variance $V(\mu) = \mu$ between the mean, $E(Y) = \mu$, and the sum of the predictor functions, η (McCullagh and Nelder, 1989).

In the analysis presented below, a GAM of the form:

$$s = \tau + offset(\log(km)) + \sum_{i=1}^{n} f(x_i) \qquad (3)$$

was created, with the number of sightings (s) modelled as a Poisson-distributed variable predicted by an overall mean (τ), plus an offset for the number of kilometres surveyed, plus the sum of nonparametric functions of the predictor variables, x_i. The x variables included in the stepwise model selection procedure were area, sea state and cloud cover (as ordered categorical variables) and year and SSTa (as numerical variables). Because the number of kilometres surveyed under each combination of conditions varied, the logarithm of the kilometres flown was included in the model as an offset (i.e. with coefficient = 1; McCullagh and Nelder, 1989). The individual functions of the model were derived using cubic smoothing splines (Hastie and Tibshirani, 1990) and the level of smoothing was determined by specifying the degrees of freedom to use in the fitting algorithm. One degree of freedom corresponds to a linear fit, and additional degrees of freedom allow the smoothed function to track the actual data points more closely. For this analysis, the level of smoothing was set at 3 degrees of freedom to allow non-linear relationships while restricting unrealistic detail in the shape of the functions. The goodness of fit for these models is measured in terms of the residual deviance, calculated as $D = \Sigma r_D^2$ with $r_D = \text{sign}(y-\hat{\mu})\ \{2(y\log(y/\hat{\mu}) - y + \hat{\mu})\}^{1/2}$, where y is each observation, $\hat{\mu}$ is the calculated mean and sign $(y - \hat{\mu})$ is either plus or minus, depending on the sign of the parenthetical expression (McCullagh and Nelder, 1989). Individual models were then compared using analysis of deviance, which is analogous to the more familiar analysis of variance used for normal distributions.

The above model uses the number of sightings, rather than the number of porpoises, as the response variable, because preliminary analyses revealed that the number of porpoises was overdispersed (dispersion parameter >5) and not adequately represented by the Poisson distribution, which assumes that dispersion is about one. The number of sightings is only a valid alternate measure of relative abundance if group sizes did not vary between years. To establish this, a test was first performed using a similar GAM with group size as the response variable and area, sea state, cloud cover and year as predictor variables.

RESULTS

In central California, a total of 3,015km of survey effort was completed in 1995, which is slightly below the average for all previous years (Table 1 overleaf). However, a higher proportion (67.5%) of the survey was completed with good viewing conditions. A total of 221 porpoises were seen in 113 groups in central California. Survey effort in northern California was lower than in previous years (611km, 61.2% in good conditions), mainly because weather opportunities were more limited. A total of 192 porpoises were seen in 116 groups off northern California.

The best-fitting ANCOVA model for the 1986-95 time series, as determined by the stepwise procedure, was the same as in the previous analysis of the shorter time series (Forney, 1995), with the exception of the annual trend. Area, sea state and cloud cover categories were highly significant predictors of relative porpoise abundance, but year was not significant at $\alpha = 0.10$ ($p = 0.143$; Table 2). No interaction terms were significant. Potential inter-observer effects could not be included in the model since this would have resulted

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[2] National Oceanic and Atmospheric Administration, National Weather Service, San Francisco Forecast Office, 21 Grace Hopper Avenue, Stop 5, Monterey, California, 93143-5505.

Table 1

Summary of harbour porpoise (*Phocoena phocoena*) aerial survey data collected 1986-1995 in central and northern California. Areas 1, 2 and 3 correspond to Transects 1-14, 15-26, and 41-57, respectively (see Fig. 1). % good conditions is defined as 100 times the total km surveyed with Beaufort sea states 0-2 and <25% cloud cover, divided by the total number of km flown in all conditions. '-' indicates that no surveys were flown; SD is the standard deviation.

	1986	1987	1988	1989	1990	1991	1993	1995
Area 1								
No. of sightings	36	28	15	22	18	12	9	15
No. of porpoise	62	47	20	44	29	20	17	33
Mean group size (±SD)	1.72 (±0.91)	1.68 (±1.79)	1.33 (±0.49)	2.00 (±1.41)	1.61 (±1.04)	1.67 (±0.65)	1.89 (±0.93)	2.20 (±1.01)
Km surveyed	1,767	1,618	1,834	1,653	1,887	1,066	1,941	1,342
% good conditions	56.4%	66.7%	31.3%	32.4%	60.3%	56.5%	68.7%	68.0%
Area 2								
No. of sightings	63	44	88	60	57	43	69	98
No. of porpoise	104	76	154	134	126	76	149	188
Mean group size (±SD)	1.65 (±1.17)	1.73 (±1.11)	1.75 (±1.18)	2.23 (±1.51)	2.21 (±1.47)	1.77 (±1.11)	2.24 (±1.61)	1.92 (±1.06)
Km surveyed	1,282	1,463	2,086	1,607	1,751	669	1,919	1,673
% good conditions	55.9%	34.3%	36.0%	42.1%	32.0%	58.9%	59.9%	67.1%
Area 3								
No. of sightings	-	-	-	44	173	87	143	116
No. of porpoise	-	-	-	76	296	166	246	192
Mean group size (±SD)	-	-	-	1.73 (±1.21)	1.71 (±1.27)	1.91 (±1.02)	1.72 (±1.40)	1.66 (±0.98)
Km surveyed	-	-	-	804	1,084	612	966	611
% good conditions	-	-	-	34.1%	67.3%	77.9%	88.0%	61.2%

in a large number of missing values and over-stratification of the data. However, preliminary nonparametric tests (two-factor extension of the Kruskal-Wallis analysis of variance; Scheirer *et al.*, 1976; Zar, 1984) indicated that sighting rates (under clear skies and stratified by area to account for regional differences in porpoise density) did not differ significantly ($p > 0.50$ and $p > 0.10$ for Beaufort sea states of 0-2 and 3, respectively) for the eleven main observers in this study, defined as those who completed at least 3,000km of search effort. As in the previous analyses, visual inspection of residual values from the model in a quantile-quantile plot (Sokal and Rohlf, 1995) revealed a deviation from normality only in the extreme tails of the distribution (where $z > 2$), indicating that the log-transformation was still appropriate for inference at $\alpha \geq 0.05$. The ANCOVA results are similar for models including central and northern California combined (Table 2).

The results of the power analysis are consistent with past findings of relatively low power. For the eight surveys over ten years, this analysis would be expected to detect a decreasing trend of 10% per year about 76% of the time, or a 5% annual decrease only 32% of the time (at $\alpha = 0.10$). If α is increased to 20%, then power increases to 84% and 45%, respectively, for the 10% and 5% annual decline. Thus power remains low for this trend analysis, and the lack of significance is not surprising. The chance of obtaining a covariate representing a decline over 10 years (of any magnitude and regardless of significance; this is equivalent to $\alpha = 1.0$), if the population were in fact increasing (γ-error; Forney *et al.*, 1991) was determined to be 16% for a population increasing at 5% per year and 2% for a population increasing at 10% per year. These simulation results are illustrated in Fig. 2 for the 10-year time series. When the simulated population was stable, covariates resulting in increasing and decreasing trends were obtained with equal probability, indicating that the procedure is not biased.

Based on the parameters of the ANCOVA, the number of porpoises km^{-1} of search effort was adjusted for the effects of sea state and cloud cover to produce a plot of relative porpoise abundance through time (Fig. 3). There is a large degree of variability in the point estimates, corresponding to the low power. Despite this variability, an inverse relationship between relative abundance and the mean September/October sea surface temperature (measured in terms of the anomaly from the long-term mean) is nonetheless apparent (Fig. 4 overleaf). The Pearson's correlation tests revealed a weak correlation between sea surface temperature and relative abundance (Pearson's $r = -0.567, p = 0.1426$) and a stronger correlation that borders

Table 2

Results of the analysis of covariance for central California and combined central and northern California aerial survey data. The dependent variable is the log-transformed number of porpoise per km, and the independent variables tested are area, sea state, cloud cover and year. df = degrees of freedom; F = F-ratio; p = probability value; R-squared = proportion of variance explained by model.

	Central California			Central and Northern California		
Source	df	F	p	df	F	p
Model	5	19.73	0.0001	6	28.34	0.0001
Area	1	62.48	0.0001	2	58.40	0.0001
Sea state	2	14.34	0.0001	2	18.23	0.0001
Cloud cover	1	18.28	0.0001	1	19.83	0.0001
Year	1	2.12	0.1489	1	1.88	0.1730
Error	84			102		
R-Squared		0.540			0.625	
Year coefficient (standard error)		-0.060 (0.041)			-0.050 (0.037)	
Annual rate of change		-5.9%			-5.0%	

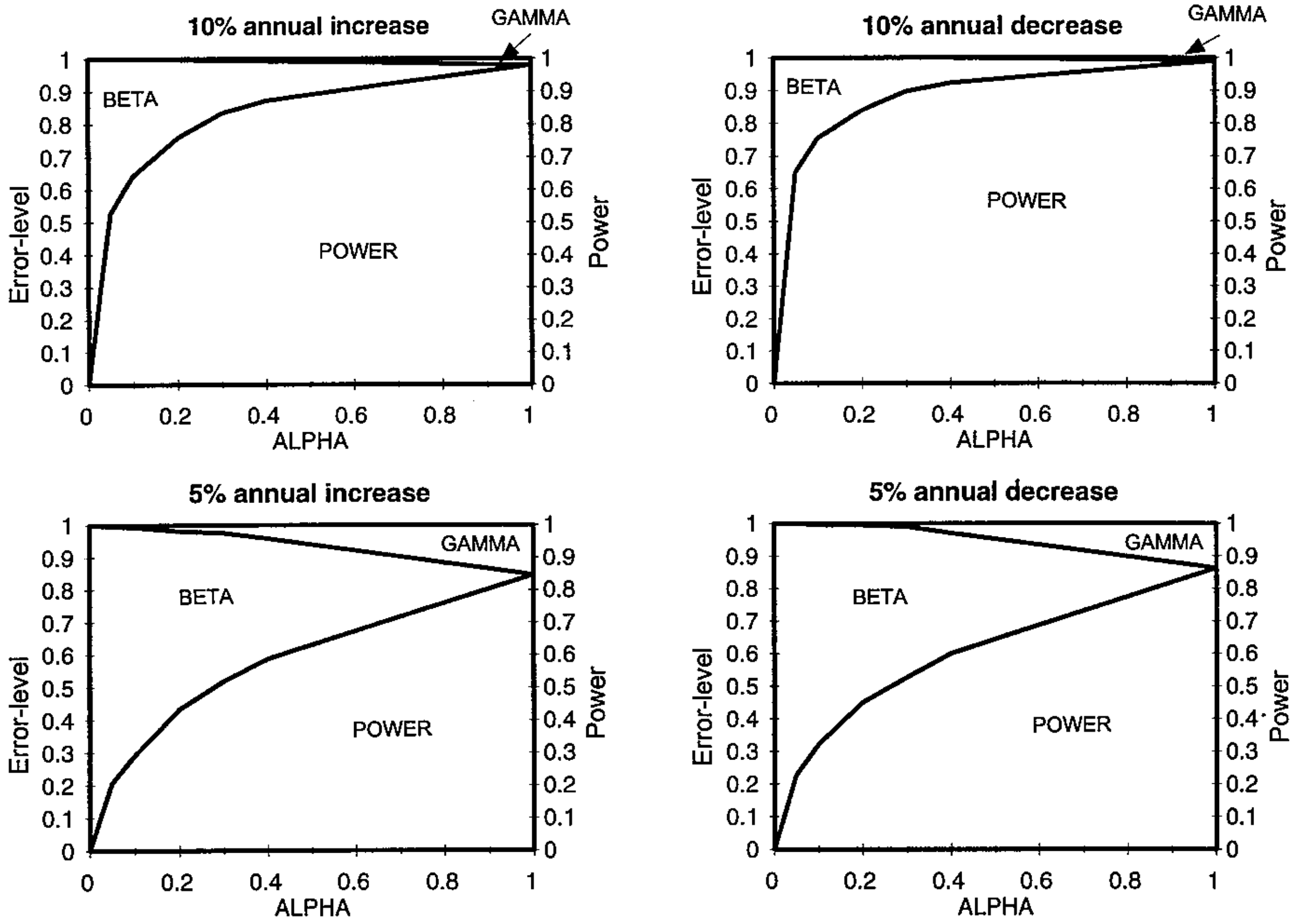

Fig. 2. Graphical representation of the results of the power simulations for the trend analysis of the 1986-95 harbour porpoise aerial surveys for rates of change of ±5% and ±10% per year. Areas represent probability levels as follows: ALPHA is the chosen α-error (the probability of detecting a significant trend when in fact none is present), BETA is the resulting β-error (the probability of not detecting a trend that is present) and GAMMA is the resulting γ-error (Forney *et al.*, 1991: the probability of detecting a trend in the wrong direction). POWER to detect trends correctly is 1-(BETA + GAMMA).

on statistical significance between the direction and magnitude of the change in these two variables between successive survey years ($r = -0.744$, $p = 0.055$). Given that only a rough measure of average oceanographic conditions was available for these analyses, these correlations are surprisingly high. The results suggest that although sea surface temperature itself may not be strongly correlated with harbour porpoise abundance, changes in sea surface temperature do appear to correlate negatively with changes in porpoise abundance between successive years.

The results of the GAMs (Table 3) provide further insights into the possible nature of the observed decline in abundance and the potential relationship between relative porpoise abundance and oceanographic conditions. The test of group size as a function of area, sea state, cloud cover and year, indicated that group size did not vary significantly between years ($p = 0.254$), confirming that sighting rates are a suitable proxy for relative abundance in this analysis. The model of porpoise sighting rates including area, sea state, cloud cover and year as predictors (but excluding the SSTa) resulted in a year effect of similar significance to that of the ANCOVA model ($p = 0.119$). The pattern of relative abundance by year (Fig. 5b) is also qualitatively similar to that derived from the ANCOVA model (Fig. 3), with a decreasing trend between 1986 and 1993, and a subsequent increase in 1995. However, in the GAM, the SSTa was more significant ($p = 0.022$) and was included in the stepwise selection procedure instead of year. After the inclusion of the SSTa, the year pattern is less pronounced (Fig. 5c) and the level of statistical significance decreases considerably ($p = 0.570$). The non-linear function of porpoise sightings in relation to the SSTa (Fig. 5) indicates that sighting rates are greatest in the coolest years, decrease slowly as temperatures

Table 3

Results of the Poisson generalised additive model for central California aerial survey data. The dependent variable is the number of porpoise sightings, and the independent variables tested are area, sea state, cloud cover, year and sea-surface-temperature anomaly. The number of km flown is included in the model as an offset. df = degrees of freedom, F = F-ratio, p = probability value.

Source	df	Deviance	F	p
Best Model				
Model	7	900.80	55.25	<0.0001
Area	1	76.93	33.03	<0.0001
Sea state	2	130.86	27.68	<0.0001
Cloud cover	1	62.74	26.83	<0.0001
SST anomaly	3	23.54	3.36	0.022
Residual	82	186.95		
Best Model plusYear				
Model	10	905.54	38.69	<0.0001
Area	1	73.07	31.23	<0.0001
Sea state	2	127.95	26.96	<0.0001
Cloud cover	1	59.45	25.31	<0.0001
SST anomaly	3	13.90	1.98	0.124
Year	3	4.74	0.68	0.570
Residual	79	182.20		

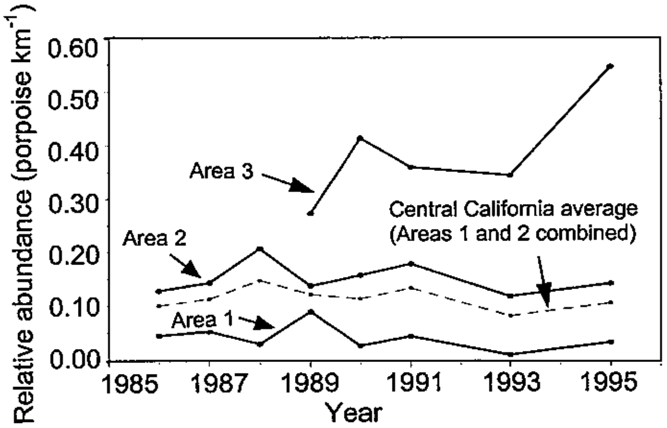

Fig. 3. Relative abundance of harbour porpoise for the period 1986-95. Relative abundance is defined as the number of porpoise observed per kilometre surveyed, adjusted for the effects of sea state and cloud cover on sighting rates. Areas correspond to those shown in Fig. 1. The combined relative abundance for central California was calculated as the average of the adjusted values of porpoise km^{-1} for Areas 1 and 2, weighted by the proportion of the 6,951km^2 central California study area encompassed by each (33.6% for Area 1, 66.4% for Area 2).

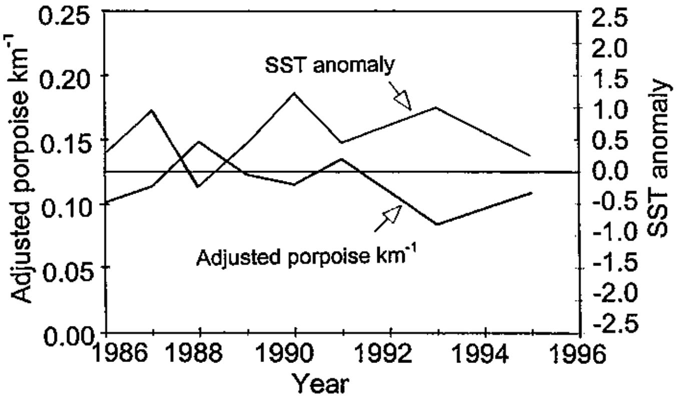

Fig. 4. Relative abundance of harbour porpoise in central California (thick line; calculated as for Fig. 3) and mean sea surface temperature anomaly (thin line; averaged for September and October at two stations along the central California coast) for 1986-95.

increase to about the mean climatological values and drop off rapidly as the anomaly exceeds about +1.0°C (Fig. 5). These combined results support the hypothesis that oceanographic changes may be responsible for the observed interannual trend.

DISCUSSION

The updated trend analysis for harbour porpoise abundance off central California in 1986-95 shows a reduced magnitude compared to the previously documented downward trend (Forney, 1995), and this trend is no longer significant at $\alpha = 0.10$. Inclusion of data for northern California yields similar results (5.0% per year decline, $p = 0.1730$; Table 2). [Note: Although the 1995 index of relative abundance of harbour porpoise in northern California was very high (Fig. 3), this point has a large uncertainty because of low survey effort.] The implications of this decreasing trend are not clear, but a potential link to oceanographic conditions (Forney, 1995) is suggested by the correlation between SSTa and porpoise abundance, and by the results of the GAM. The correlation is strongest when considering the direction of change in the two measurements: when the SSTa became more positive (i.e. water temperature increased from one survey year to the next), the relative abundance of harbour porpoise tended to decrease, and *vice versa*. In contrast, the actual value of the SSTa was less well correlated with the relative abundance of harbour porpoise. In part, this lack of correlation may be due to the presence of non-linear effects, as determined by the GAM: porpoise sighting rates appear to decline rapidly in warmer than average conditions, but exhibit only a slight decreasing trend in cold to average years (Fig. 5). These results underscore the importance of investigating non-linear effects of environmental variables in models of species abundance.

A caveat to the above relates to the nature of the measure of oceanographic conditions used in this analysis, the mean SSTa averaged for the months of September and October at two stations off central California (for the northern and southern parts of the study area, respectively). This rough measure of general sea surface temperature was used because no detailed oceanographic information was available on a scale comparable to the aerial survey data. Depending on the likely response time of harbour porpoise in relation to oceanographic changes, a two month average may not be the most appropriate choice. The choice of September and October was based on the timing of the surveys (15 August to 15 November, with most effort in September and October) and the documented summer/autumn increase in harbour porpoise densities in Monterey Bay (Sekiguchi, 1995). Although this choice seems reasonable, it is arbitrary. Thus the interpretation of these data is limited by our lack of understanding about temporal and geographic scales of movement of harbour porpoise.

Pollutant studies have revealed differences in pollutant ratios in harbour porpoises from central California and Oregon/Washington, suggesting that north-south movement is limited (Calambokidis and Barlow, 1991); however, no samples from northern California were available for that study. Insufficient data are available to establish whether harbour porpoises may use deeper waters outside the central California study area to a variable extent during different years, because systematic surveys have only been conducted in nearshore waters. In recent years, harbour porpoises have occasionally been observed in deeper waters off California during the summer/autumn period (J. Calambokidis, pers. comm.; J. Barlow, pers. comm.), but such observations have been rare despite considerable search effort for other cetaceans in these offshore areas.

The potential influence of variability in oceanographic conditions on the measured abundance of harbour porpoises is an important consideration when evaluating the status of this species. The central California population probably was depleted during the 1970s and 1980s when incidental mortality in coastal set gillnet fisheries was high (Barlow and Hanan, 1995). After a substantial reduction in fishery mortality beginning in the late 1980s, the population was expected to recover. The subsequent decline documented for the period 1986-93 (Forney, 1995) was therefore surprising. The analysis presented here provides some support for one of the potential explanations: that the observed patterns may reflect distributional changes resulting from interannual variability in oceanographic conditions, rather than a true decline in abundance. However, the evidence at this point is far from conclusive and targeted studies will be necessary to confirm or reject this possibility.

Indices of oceanographic conditions (such as SSTa or measures of productivity) may provide additional explanatory power, but they should be collected in conjunction with the sighting data in order to be more meaningful. For this reason, shipboard surveys on which

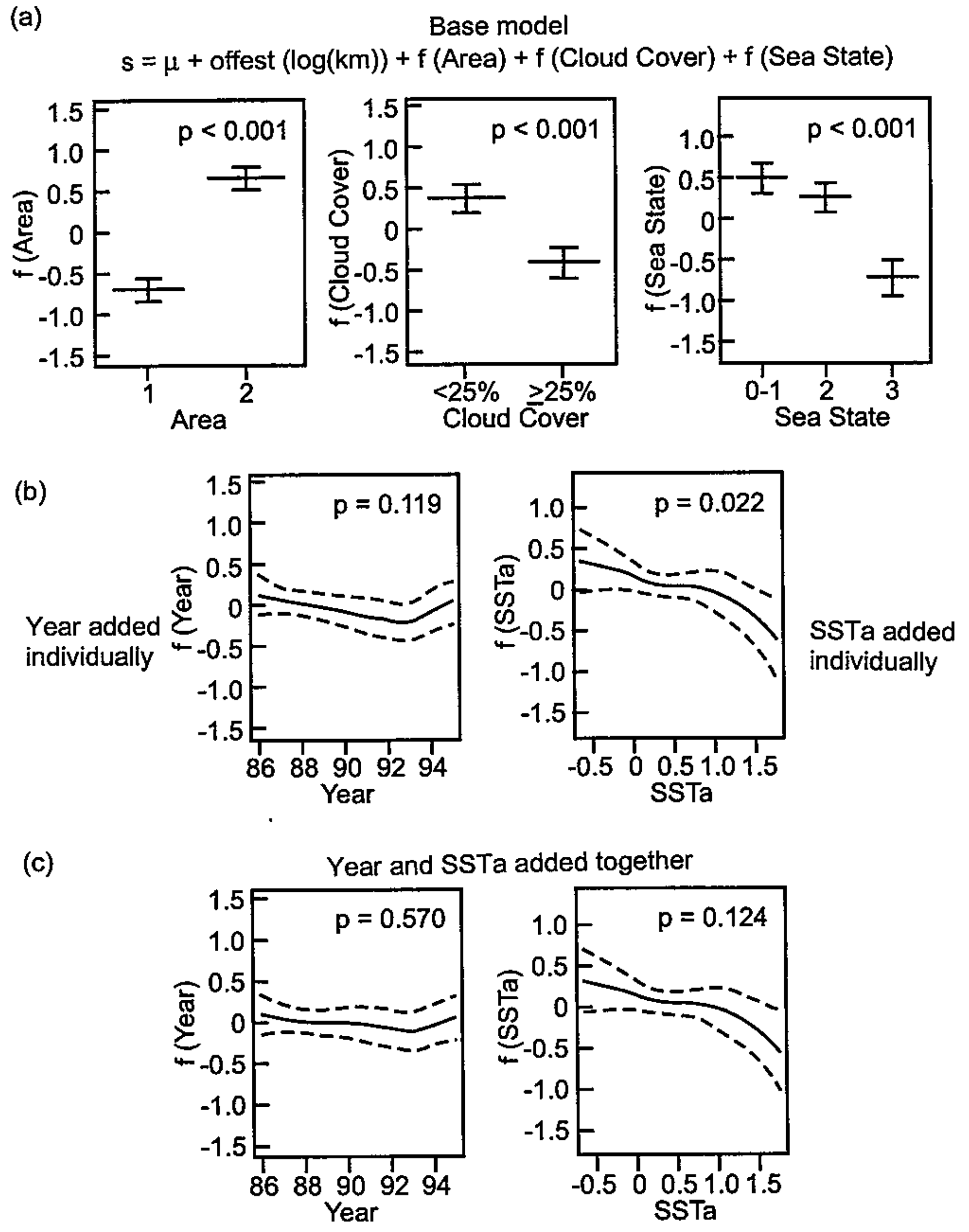

Fig. 5. Graphical results and probability values for variables included in the Poisson generalised additive model of the number of porpoise sightings for central California: (a) 'Base model', including effects of area, sea state and cloud cover; (b) effects of year and SSTa when added individually to the base model; and (c) effects of year and SSTa when both are included in the model. Dashed lines are 2× standard error bands for the fitted functions with three degrees of freedom.

oceanographic data are collected along with the sighting data would be more effective than aerial surveys. Future studies should also attempt to address movement patterns and possible changes in depth distribution of California harbour porpoises, but until suitable methods of capturing and radio-tagging free swimming harbour porpoises in this region have been perfected, this goal may remain elusive.

The continued low power of the ANCOVA analysis and the large amount of unexplained variability that remains in the data will continue to make the detection of trends very difficult. GAMs may provide greater power to detect trends in the future because of their greater flexibility to include non-linear relationships. The Poisson model using the number of sightings as a response variable yielded similar results to the previous ANCOVA model that used the logarithm of the number of porpoise km^{-1}. However, these models are not entirely comparable because one implicitly includes group size information and the other assumes group sizes to be constant across years. The present analysis revealed that the Poisson distribution does not adequately model trends in total harbour porpoise abundance, because the number of porpoises is overdispersed. More sophisticated GAMs, such as those using a negative binomial distribution family (Chambers and Hastie, 1992), may be required in the future to allow individual-based trend analyses.

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Review of the biology and exploitation of striped dolphins in Japan

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ABSTRACT

The biology, distribution, abundance and exploitation of striped dolphins off Japan are reviewed in an attempt to collate the available information required for a better understanding of the status of populations exploited by Japanese fisheries. Striped dolphins are found in summer in three geographical aggregations in the Pacific waters off Japan, between 20° and 42°N. Occurrence is seasonal in the northern part of the range. They are uncommon in the Sea of Japan, East China Sea and Ryukyuan waters. School structure is believed to be fluid. Weaned juveniles usually leave their natal schools to aggregate with individuals of similar age. Adults move between schools depending on sex and reproductive status. They have been harvested along the Japanese coast since at least the 19th century. An annual catch of up to 21,000 continued from the end of World War II to the end of 1950s. This has been followed by a gradual decline in catches despite demand for dolphin meat. Changes in life history parameters such as female age at sexual maturity and perhaps in female reproductive cycles have occurred over time. Japanese multispecies dolphin fisheries now receive an annual quota of 725 striped dolphins. Fragmented information on morphology, life history, pollutant levels and genetics suggests that the striped dolphins taken by Japanese fisheries are from more than one population, with varying proportions among fisheries and perhaps over time. Further study is needed to clarify population structure, immigration among populations, site fidelity and the function of dolphin 'schools'.

KEYWORDS: STRIPED DOLPHIN; FISHERIES; DIRECT CAPTURE; POPULATION PARAMETERS; GROWTH; PACIFIC OCEAN; STOCK IDENTITY; MOVEMENTS; POLLUTANTS; SOCIAL BEHAVIOUR; REGULATIONS; REPRODUCTION; TRENDS.

INTRODUCTION

Striped dolphins, *Stenella coeruleoalba* (Meyen, 1833), have been commercially hunted in Japan by either drive or hand-harpoon fisheries since at least the 19th century. Statistics are incomplete for the period before World War II. Since then, the catch has declined from over 21,000 dolphins to less than 1,000 after 1980. It is continuing in three regions (Fig. 1 shows all places referred to in the text): Taiji and adjacent areas of the Wakayama Prefecture; Futo on the Izu Peninsula of Shizuoka Prefecture; and Choshi in Chiba Prefecture (Kishiro and Kasuya, 1993). In 1993, the Japanese government established catch limits for all the dolphin fisheries and dolphin species (Kasuya and Kishiro, 1995).

The large harvest of striped dolphins has prompted numerous studies on both biology and management (e.g. Nishiwaki and Yagi, 1953; Kasuya, 1972; 1985; Miyazaki and Nishiwaki, 1978; O'Shea *et al.*, 1980; Honda *et al.*, 1982; Itano *et al.*, 1984a; b; Miyazaki, 1984). Conservation concerns led to a number of studies of distribution and abundance in the western North Pacific (e.g. Kasuya, 1976a; Kasuya and Miyashita, 1989; Miyashita, 1993).

The Scientific Committee of the International Whaling Commission (IWC) has been greatly concerned about the status of the population, and reviewed the topic several times since 1976 (IWC, 1977). The most recent review was in 1992 (IWC, 1993). They noted the decline in catches over about 30 years, changes in reproductive parameters in a manner consistent with a density-dependent response, and depletion of a possible coastal stock by the fishery. This concern was reiterated the following year (IWC, 1994).

This review summarises existing knowledge on the biology, population, exploitation and management of striped dolphins off Japan, and presents an interpretation of the results of these studies in the hope of assisting the scientific consideration of the current status of population(s) involved in the fishery.

DISTRIBUTION

An analysis by Kasuya (1982) indicated that striped dolphins inhabit warm offshore waters above 18°C in surface temperature; this was based on data collected in the western North Pacific mainly from spring to autumn. Off Japan, water of this temperature moves seasonally by latitude; i.e. between 42°N off Hokkaido and 33°N off Shikoku and Kyushu in the Pacific, and between 44°N at the Soya Strait and 32°N off western Kyushu in the Sea of Japan/East China Sea Area (Fig. 1). However, the distribution of the striped dolphin is probably influenced by more factors than surface water temperature, and its apparent temperature preference may change seasonally, as observed for the short-finned pilot whale (Kasuya *et al.*, 1988). This would explain why striped dolphins are found in all seasons of the year off Taiji (34°N), where the winter temperature is lower than the range given above.

Miyashita (1993) studied the distribution of striped dolphins in the western North Pacific in August and September, when the sea surface temperature was highest and the northerly movement had probably reached its peak. The northern limit of distribution was around 42°N in offshore waters east of 145°E. It is unlikely that animals would be found further north in coastal waters west of 145°E, where the cold Oyashio Current approaches from the north, but a limited number of sightings in relation to effort has prevented confirmation.

In winter, survey data have shown striped dolphins to be found from 10°-35°N and 120°-145°E (Miyashita *et al.*, 1996), including waters from the Kii Peninsula/Shikoku area to the eastern offshore waters of the southern Ryukyu Islands at around 23°N. However, these winter surveys have not covered the main fishing grounds of the current striped-dolphin fisheries, which operate in the winter season.

A 104-day sighting survey in the Sea of Japan and East China Sea in July and August made no striped dolphin

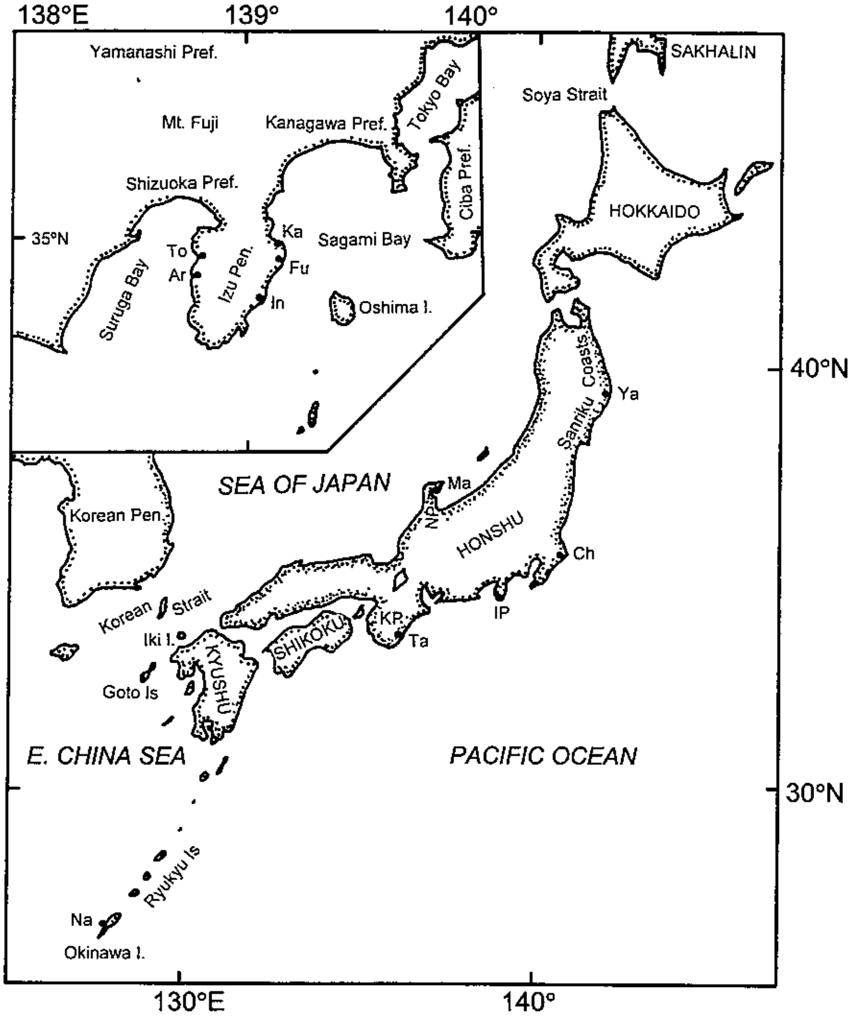

Fig. 1. Geography of area covered by the present review. Details of Izu area is shown in the inset map. Ar: Arari; Ch: Choshi; Fu: Futo; In: Inatori; IP: Izu Peninsula; Ka: Kawana; KP: Kii Peninsula; Ma: Mawaki; Na: Nago; NP: Noto Peninsula; Ta: Taiji; To: Toi; Ya: Yamada.

sightings (Iwasaki *et al.*, 1995). A similar survey from July to September in the Yellow Sea and East China Sea also resulted in no sightings (Miyashita *et al.*, 1995) as had several summer cruises in the Sea of Japan in earlier years (Kasuya, unpublished). Striped dolphins are also absent from the strandings records along the coasts of the Sea of Japan (Yamada, 1993) except for one mass stranding in May 1998 near Shimonoseki City, at the western end of Honshu (Anon., 1998).

This information suggests that striped dolphins are rare in the Sea of Japan. Winter occurrence is unlikely given the cold environment. It also concurs with their absence in the opportunistic driving operations in the Goto Islands or surveys made in the East China Sea in connection with the dolphin/fishery conflict in the Iki Island area (Anon., 1968).

There have been no confirmed striped dolphin sightings off Okinawa Island in the southern Ryukyu Islands (Uchida, 1985). They were similarly absent in the area in summer in more recent surveys (Iwasaki *et al.*, 1995) and only one sighting was made in winter in the northern part of the Ryukyu Islands (Miyashita *et al.*, 1996).

In China Taiwan there are only two records of striped dolphins, one was a landed animal at Suao north-eastern Taiwan (Yang, 1976) and the other was a skull found in a collection at National Taiwan Ocean University (Mizue, 1988 cited in Zhou *et al.*, 1995). Striped dolphins are apparently uncommon there (Yang, 1976). No confirmed striped dolphin specimens were found in 41 stranding incidents representing 15 cetacean species off Taiwan from 1990-1995 (Chou *et al.*, 1995), although they are apparently more common off Hong Kong (Parsons *et al.*, 1995).

In summary, striped dolphins are common along the Pacific coast of Japan south of 42°N, but they are uncommon or absent in the Sea of Japan, East China Sea and waters around the Ryukyu Islands (Fig. 2).

PAST DOLPHIN FISHERIES

Striped dolphins have been hunted in hand-harpoon and drive fisheries in Japan. The hand-harpoon, with a detachable head, has been known since the Jomon era (10,000-300BC) and has been used in the hunting of several marine species of suitable size, including dolphins and porpoises (Yamaura, 1996). The hunting of delphinoids using this technique was placed under the licensing systems of prefecture governments in 1989 (Kasuya, 1992).

Drive fisheries are effective for gregarious species; off Japan these are the tropical and temperate delphinids, including the striped dolphin. At least 52 Japanese villages have operated dolphin drive fisheries since the late 14th century; 6 on the Sea of Japan coast, 23 on the coast of the Korean Strait and the East China Sea, 1 at Okinawa Island and 22 on the Pacific coast (see Kishiro and Kasuya, 1993; Kasuya, 1994). They are all south of Yamada Town (39°28'N) on the Pacific coast or of Mawaki (37°20'N) on the Sea of Japan coast (Fig. 1). Except for three villages, Futo and Kawana on the Izu Peninsula and Taiji on the Kii

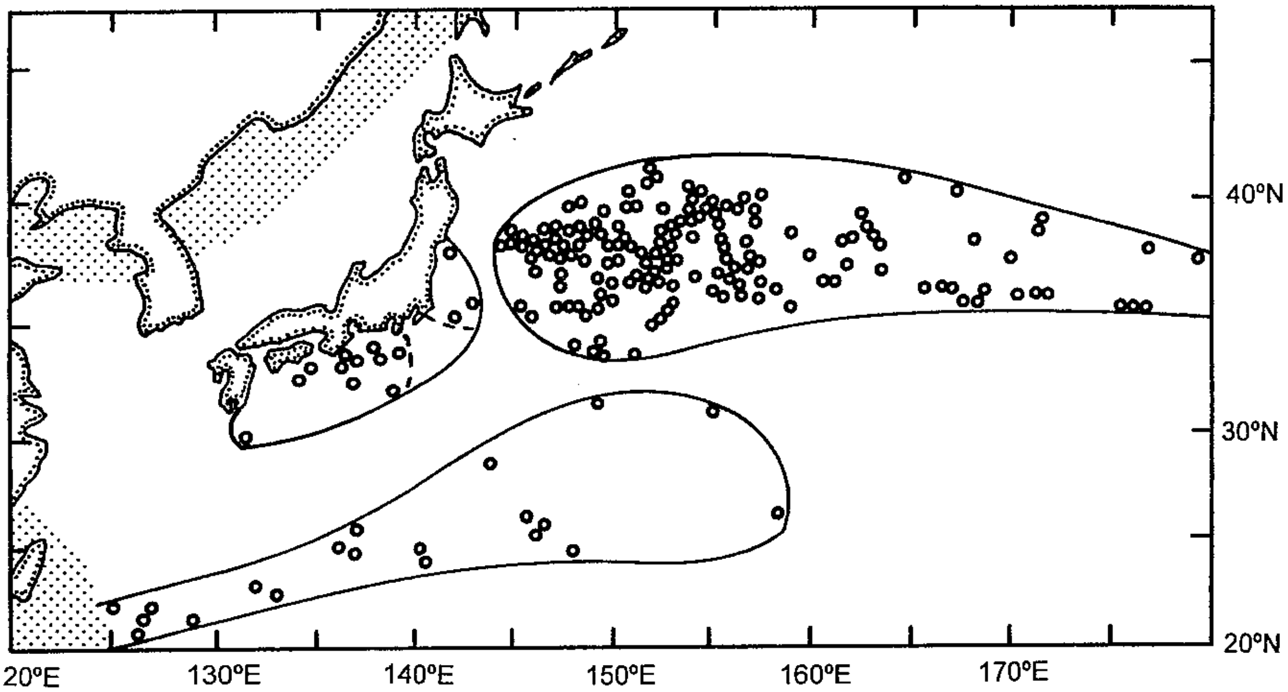

Fig. 2. Distribution of striped dolphins in the western North Pacific in July-September. Each circle represents a striped dolphin school in Miyashita (1993). Solid lines indicate my interpretation of three concentrations of striped dolphins in the western North Pacific, dotted lines sub-areas within the inshore concentration, and shaded area waters of insufficient data. Density of sighting effort is higher in coastal waters at 35°-43°N and west of 145°E, where sighting of striped dolphins are scarcer. Reproduced from figs 2-4 of Miyashita (1993) with permission.

Peninsula, most ceased operation before 1982, when the government placed drive fisheries under prefecture licensing systems.

The species taken by the earlier drive fisheries are unknown and no striped dolphin catch statistics exist. However, striped dolphins are unlikely to have been the major target of the fisheries in the Sea of Japan and East China Sea (including Okinawa), if the delphinid fauna has remained similar. This is partially supported by the absence of striped dolphin remains at the Mawaki archaeological site of dolphin hunting in the Jomon era, where many remains of common (*Delphinus delphis*), Pacific white-sided (*Lagenorhynchus obliquidens*) and bottlenose dolphins (*Tursiops truncatus*) and pilot whales (*Globicephala* sp.) were found (Hiraguchi, 1993). The exploitation of striped dolphins in villages around Taiji in central Japan is recorded in old scrolls (Yuboku, *ca.* 1660).

EXISTING FISHERIES FOR STRIPED DOLPHINS

Current Japanese fisheries for striped dolphins are limited to drive fisheries on the Izu Peninsula and in Wakayama Prefecture and hand-harpoon fisheries in Chiba and Wakayama Prefectures. Opportunistic driving at Nago, Okinawa and a subsequent crossbow fishery have reported no catches of striped dolphins (Fig. 1).

Drive fisheries on the Izu coast, Shizuoka Prefecture

(1) Operating bodies

The Izu Peninsula (Fig. 1) is surrounded by rugged shorelines. It is 55km in length and has a maximum width of 35km. It projects southward from the Pacific coast of central Japan at 35°N, 139°E and separates Sagami Bay to the east and Suruga Bay to the west. Ohsumi (1972) described the method of dolphin driving on each side of the Peninsula.

Such fisheries on the Izu coasts have been known since 1619 (Shibusawa, 1982). In the late 19th century, Kawashima (1894) recorded over 20 villages operating opportunistic dolphin drive fisheries. After World War II, scientists confirmed that the catches were almost exclusively striped dolphins which were called *mairuka* ('true' or 'common' dolphin) by the local fishermen. A species of the same vernacular name was the major target of the drive fishery that operated in the late 19th century on the Izu coast (Kawashima, 1894). The target species was described as weighing 90-200kg and was found in schools of over 1,000 individuals. The drives were carried out mainly in winter. All this leads to the conclusion that *mairuka* is likely to have referred to the striped dolphin since at least the late 19th century.

Following Kawashima's summary (1894), the Bureau of Fisheries (1911) reviewed the dolphin harvest. They recorded drive fisheries at eight villages on the Izu Peninsula but it is not clear if this was an exhaustive list or merely selected examples. A decline in the number of operating groups occurred during the early 20th century (see below), but little is known of the pre-War operations.

During World War II and the post-war period, the Izu fishery underwent expansion both in the number of operating groups and the number of dolphins taken (Shizuoka Board of Education, 1986; 1987; Nakamura, 1988), as a response to the difficulty of offshore fishing during the war and to the food shortage after the war. Postwar operations took place at the five villages of Arari, Futo, Inatori, Kawana and Toi (Nakamura, 1988). Of these, only Futo had not been recorded by Kawashima (1894).

Inatori resumed the fishery in 1947, after 50 years' cessation and Toi in 1946/47, after a cessation of unknown length (Nakamura, 1988). Both villages again ceased operations, sometime before 1961, when the fishery was investigated by M. Nishiwaki and S. Ohsumi (Kasuya, 1985).

Arari, which was very dependent on the dolphin drive fishery during the war, made its last significant catch in 1961 (Miyazaki, 1983; Kasuya, 1985) and was reported to have dissolved its driving team in 1973 (Shizuoka Board of

Education, 1987). However, it acquired an operating license in 1982 when the fishery came under the licensing system of the prefecture (Kishiro and Kasuya, 1993).

Kawana began a drive fishery for dolphins (presumably striped dolphins) in December 1882. Its last drive was made in 1983. It is unknown when the Futo drive fishery began. The first record is of a confrontation between driving vessels from Futo and Kawana in 1903 (Nakamura, 1988). Both teams considered the other as a competitor when I started examining their catches in 1961. However, they combined operations in autumn 1968 and this co-operation lasted until autumn 1983. Futo is now the only village operating a regular dolphin drive on the Izu coast (Shizuoka Board of Education, 1986; 1987).

(2) Change in the technology

The equipment used in the Izu drive fishery has changed over time (Kasuya and Miyazaki, 1982; Kasuya, 1985; Shizuoka Board of Education, 1986; 1987; Nakamura, 1988). In the early days, sail assisted rowing boats operated within several n.miles from the coast (Kawashima, 1894; Kasuya and Miyazaki, 1982). The use of motor driven vessels began in the 1920s and resulted in an expansion of the searching range to 20 n.miles from the port or the entire Sagami Bay area (Kasuya, 1985). The Shizuoka Bureau of Education (1987) reported that motor driven vessels were introduced to Kawana in 1900 and that the number increased slowly until 1925 when it underwent a nearly four-fold increase within a single year. A similar improvement probably occurred around the same time in the other Izu villages. Although no records are available, it seems likely that improvements to the efficiency of these vessels continued after their introduction in the 1920s.

Three high-speed motor vessels were introduced to Kawana in 1962, and occasionally searching expanded outside Sagami Bay, reaching up to 50 n.miles from port (Kasuya and Miyazaki, 1982). When first introduced, the maximum speed was 13 knots. This had increased to 40 knots by the time of the last operation in 1983 (Shizuoka Board of Education, 1987). Futo soon followed Kawana in the use of such high-speed boats.

In 1968, when Kawana and Futo began cooperative operations, four high-speed boats, two from each village were used, and this continued until these operations ceased in 1983. The last Izu drive fishery at Futo used two high speed boats from 1984-86 and has used one since then (Miyazaki, 1983; Kishiro and Kasuya, 1993). In addition, the fishery often utilises reports of dolphin sightings by other fishing vessels. In recent years, Kawana fishermen have sent information on sightings of striped dolphins to Futo fishermen and received 3% of the profit obtained from their drives (Shizuoka Board of Education, 1987).

(3) Regulations

Kishiro and Kasuya (1993) summarised regulations and the operation of the fishery. In 1951, Shizuoka Prefecture introduced a license system for all nominal drive fisheries in the prefecture (actual drives were known only for dolphins), and banned the establishment of new driving teams. In 1959, the fishing season was limited to the September-March period for the three license holders of the prefecture. The first effective catch limit was established in 1991, when a limit of 657 dolphins (species not specified) proposed by the Fisheries Agency for the entire Shizuoka Prefecture was accepted by the prefecture for the Futo fishermen. Quotas by species were first established in 1993. The fishery currently operates (Kasuya, 1997) with a quota of 600 dolphins comprising 70 striped dolphins, 75 bottlenose dolphins and 455 pantropical spotted dolphins (*Stenella attenuata*).

Although the fishing season extends from September to March, the Futo fishery actually ends in December.

Drive fishery off Taiji, Wakayama Prefecture

(1) Operating groups

Exploitation of various cetacean species at Taiji and the nearby area has continued since at least the early 17th century. The right to drive dolphins had already been authorised in the 19th century (S. Matsui, pers. comm.) and an opportunistic dolphin drive was recorded in 1933 (Hamanaka, 1979; Kasuya and Marsh, 1984; Kishiro and Kasuya, 1993). The current dolphin drive team was started in 1969 (for short-finned pilot whales) by a group of fishermen using eight vessels and a method learned from the Izu fishermen. Striped dolphins were included in 1973. Another drive team of seven vessels started in 1979. The two competing teams merged in 1982 and operated using a total of 15 vessels. The number of vessels decreased to 14 in the 1984/85 season (Kishiro and Kasuya, 1993).

(2) Method of operation

No significant changes in recent driving technology have been documented for the Taiji fishery, and the size of vessels has remained unchanged (Kishiro and Kasuya, 1993). However, the same authors reported increase in daily searching effort in recent years. Daily searching activity used only half (6-7 vessels) of the total vessels (15 vessels) until at least the 1984/85 season. Use of the full fleet started in 1990/91 or earlier.

Another factor affecting the searching effort of the team is cooperation with other fisheries vessels. Initially the drive team used to receive news of dolphin sightings in exchange for gratuities, but it started to pay for the information around 1988, when small-type whaling returned to Taiji and began to compete with the driving team for short-finned pilot whales (*Globicephala macrorhynchus*) and Risso's dolphins (*Grampus griseus*). Whaling vessels may also buy such information from particular fishing or whale-watching vessels. This will clearly increase the searching efficiency of the drive fishery, but quantifying this is difficult.

(3) Regulations

Wakayama Prefecture placed the Taiji drive fishery under its license system in 1982. The fishing season was limited to October-April and voluntary catch limits of 500 short-finned pilot whales and 5,000 other delphinids (without specification of species) were set. These became obligatory in 1986. The number of licensed vessels decreased from 15 to 14 in the 1986/87 season in concurrence with the actual decline that occurred in 1984/85.

In 1991, the catch limit was reduced to 2,900 delphinids including a maximum of 500 short-finned pilot whales. This was further reduced in 1992 to a total of 2,500 delphinids including a maximum of 1,000 striped dolphins and 300 short-finned pilot whales. This was the first catch limit set for striped dolphins in Japan.

In 1993, the Government set catch limits for six species of delphinids (Risso's, pantropical spotted, striped and bottlenose dolphins, false killer whales, *Pseudorca crassidens* and short-finned pilot whales) and the Dall's porpoise, *Phocoenoides dalli*, for the drive and hand-harpoon fisheries. The take of other small cetaceans by these fisheries is prohibited. The current drive fishery at Taiji operates with a total limit of 2,380 dolphins and a season of October to February, with an extension for short-finned pilot whales until the end of April. The quota comprises 450 striped dolphins, 890 bottlenose dolphins, 400 pantropical spotted dolphins, 300 Risso's dolphins, 40 false killer whales and 300 short-finned pilot whales (Kasuya, 1997).

Hand-harpoon fishery at Choshi, Chiba Prefecture

Ohsumi (1972) reported annual landings of 200-3,000 dolphins in Chiba Prefecture during 1957-1970. Kasuya and Miyazaki (1982) reported on a hand-harpoon fishery off Choshi, Chiba Prefecture (Fig. 1), for various dolphin species (including striped dolphins) and estimated the mean annual catch at 1,500 striped dolphins.

This hand-harpoon fishery now operates from November-April, using 14 vessels, with a catch limit of 80 striped dolphins.

Hand-harpoon fishery in Wakayama Prefecture

The fishermen of Taiji used to harpoon striped dolphins and other delphinids for local consumption. Their annual catches of striped dolphins ranged from a few hundreds to 2,000 individuals from 1963-1973 (Kasuya, 1985). When the drive team expanded operations to striped dolphins in 1973, the hand-harpoon fishery became unprofitable; and only about 15 vessels obtained licenses in 1989 when the hand-harpoon fishery for dolphins came under control of the Regional Fishery Adjustment Commission.

However, about 147 vessels from the Wakayama Prefecture, including some from Taiji, started harpooning dolphins in 1991 off the coast of Wakayama Prefecture. This became a political issue, and all the vessels finally obtained licenses. The fishery now operates from February to August with a total quota of 520 dolphins, comprising 100 striped dolphins, 100 bottlenose dolphins, 70 pantropical spotted dolphins, and 250 Risso's dolphins.

CATCH STATISTICS

Table 1 presents statistics of dolphins taken at Futo provided to me in the late 1970s by the coastal division of the Fisheries Agency. Table 2 (overleaf) reports all the catch statistics of striped dolphins available in published reports. Further details of the statistics are described below.

Izu coasts

Tobayama (1969) examined the species composition of dolphins taken in drive fisheries on the Izu coast for selected seasons. Kasuya and Miyazaki (1982) estimated that about 96.7% of the catch was composed of striped dolphins. They reported the mean annual catch (and the range) for the Izu coast between 1942-53 as Arari, 7,394 (277-20,131) and Kawana, 2,003 (0-5,311).

Catches by other villages on Izu coasts (e.g. Futo, Inatori and Toi) are not available for that period; it is known that Futo was relatively inactive.

Ohsumi (1972) presented catch statistics for 'dolphins' by prefecture in 1957 to 1970. The annual catch for Shizuoka Prefecture (almost exclusively along the Izu coast) fluctuated between 3,601 and 21,432. Kasuya and Miyazaki (1982) used correction factors derived from Tobayama (1969) to analyse Ohsumi's (1972) data by species: the estimated average annual catch of striped dolphins off Japan in the late 1950s to early 1960s was: Izu, 11,000; Chiba, 1,500; Taiji, 630; other areas, 1,000; Total, 14,000.

Miyazaki *et al.* (1974) were the first to report statistics for striped dolphins at Arari (1950-1970), Kawana and Futo (1949-1973) and Taiji (1963-1972). Kasuya (1976b) presented earlier catches missing in Miyazaki *et al.* (1974), i.e. for Arari (1942-1956) and Kawana (1942-1953).

Table 1

Japanese catch of striped dolphins by prefecture. •: no data; +: negatively biased due to incomplete coverage; -: positively biased due to inclusion of species other than striped dolphins.

Year	Chiba[1]	Shizuoka[2]	Wakayama[3]	Total
1942	•	21,591+	+	21,591
1943	•	7,763+	+	7,763
1944	•	7,660+	+	7,660
1945	•	7,319+	+	7,319
1946	•	8,180+	+	8,180
1947	•	95+	+	95
1948	•	5,892+	+	5,892
1949	•	13,441+	+	13,441
1950	•	15,186+	+	15,186
1951	•	11,899+	+	11,899
1952	•	8,152+	+	8,152
1953	•	4,059+	+	4,059
1954	•	298+	+	298
1955	•	2,669+	+	2,669
1956	•	8,991+	+	8,991
1957	•	3,172	+	3,172
1958	•	3,681	+	3,681
1959	•	21,953	+	21,953
1960	•	4,418	+	4,418
1961	•	10,569	+	10,569
1962	•	8,554	+	8,554
1963	•	8,509	331-	8,840
1964	•	6,428	934-	7,362
1965	•	9,696	642-	10,338
1966	•	8,371	422-	8,793
1967	•	3,664	819-	4,483
1968	•	9,250	400-	9,650
1969	•	3,130	499-	3,629
1970	•	5,348	997-	6,345
1971	•	3,315	1,717-	5,032
1972	•	7,235	700-	7,935
1973	•	6,799	727-	7,526
1974	•	11,715	967-	12,682
1975	•	5,996	759-	6,755
1976	•	5,175	1,053-	6,228
1977	•	4,020	562-	4,582
1978	•	2,028	1,644-	3,672
1979	•	1,300	893	2,193
1980	•	5,220	11,017	16,237
1981	•	73	4,710	4,783
1982	•	246	1,758	2,004
1983	•	40	2,179	2,219
1984	•	925	2,812	3,737
1985	•	578	2,639	3,217
1986	10	0	2,760	2,770
1987	20	0	369	389
1988	38	356	1,767	2,161
1989	48	102	1,000	1,150
1990	67	0	796	863
1991	14	32	971	1,017
1992	0	0	1,045	1,045
1993	6	0	538	544
1994	7	0	528	535
1995	6	0	533	539
1996	0	0	303	300
1997	0	0	702	702

[1] Hand harpoon fishery off Choshi from Japanese Progress Reports to IWC (no data for operation before 1986).

[2] Drive fishery off the Izu coast from Kishiro and Kasuya (1993) before 1992, and Japanese Progress Reports to IWC (1992-1996 fishing seasons).

[3] All fisheries taking striped dolphins, from Kishiro and Kasuya (1993) before 1992, and Japanese Progress Report to IWC (1992-1994 fishing seasons).

Table 2

Catch of all 'dolphins' at Futo, Izu coast, during the early stage of post World War II operations. Provided by Coastal Division, Fisheries Agency.

Year	Dolphins	Year	Dolphins
1950	0*	1961	8,606
1951	0*	1962	4,132
1952	120*	1963	4,599
1953	31*	1964	3,795
1954	0*	1965	8,757
1955	117*	1966	7,154
1956	484*	1967	1,250
1957	421*	1968	3,382
1958	1,060	1969	1,775
1959	2,848	1970	2,867
1960	3,172	1971	3,131

*: These figures are not included in Miyazaki *et al.* (1974) and Kishiro and Kasuya (1993), but are included in Table 2 of this study.

Miyazaki (1983) and Kishiro and Kasuya (1993) updated these statistics using data collected by the Fisheries Agency. Thus the striped dolphin statistics for the Izu fishery cover the following seasons: Arari, 1942-1970 (last significant drive in 1961); Kawana, 1942-1983 (last drive in 1983); Futo, 1949-1991 (missing years in 1950s); Inatori, missing (no operation since the 1960s).

Arari recorded a large catch of 20,131 individuals in 1942, the first year for which statistics are available, suggesting that it had started operations considerably earlier. Annual catches at Futo were small at 0-500 in 1950-1957 before increasing to 1,200-8,700 in the 1960s (Table 2). This suggests that the Futo team resumed post-war operations in the late 1940s or early 1950s. The currently available statistics for the drive fisheries off the Izu coast are complete from 1958 as summarised by Kishiro and Kasuya (1993). Some fragmentary 19th century statistics are available in Kawashima (1894). Other villages on the Izu coast may have operated driving dolphins for some pre-World War II period, but no statistics are available.

Taiji, Wakayama Prefecture

Miyazaki (1980) compiled statistics of striped dolphins landed at the Taiji wholesale market for 1963-1979. He used the numbers of dolphin viscera sold at the market as an indicator of the number of dolphins landed. However, because viscera were not separable between striped and pantropical spotted dolphins in the records, his striped dolphin statistics could have included small numbers of the latter species.

The Fisheries Agency started to collect statistics by species for each prefecture in 1979, and these data were used in Miyazaki (1983). Kishiro and Kasuya (1993) further extended the time range of the statistics using Fisheries Agency statistics.

Earlier statistics for Taiji could include striped dolphins taken by the hand-harpoon fishery and in small-type whaling. However, only drive and hand-harpoon fisheries now take the species there.

LIFE HISTORY STUDIES

Age determination

Most of the studies of life history of striped dolphins off Japan used carcasses from the drive fishery at Kawana and Futo on the Izu coast. Nishiwaki and Yagi (1953) made the first attempt to determine the rate of deposition of dentine layers by injecting lead acetate as a marker. However, the short survival time of the dolphins meant that no conclusions could be drawn. Using samples obtained from October to January, Kasuya (1972) examined the innermost dentine in the pulp cavity and found that alternation from opaque to translucent dentine occurred during November-December ($n = 275$ for November-January). A similar conclusion (December-January) was reached by Miyazaki (1977a; $n = 209$ for November-January). Their conclusion of annual dentine deposition of dentinal layers (one opaque and one translucent layer = one Growth Layer Group – GLG – see IWC, 1980) assumed that dentine will alternate from translucent to opaque layers sometime in early summer.

Kasuya (1976a) found cessation of dentine deposition at various ages over 10 GLGs after which age the use of cementum layers is necessary for unbiased age estimation. Some of the earlier studies based only on dentine layers (e.g. Kasuya, 1972; Miyazaki, 1977a; b; Miyazaki and Nishiwaki, 1978) are thus questionable for individuals over 10 GLGs.

Neonatal length

A simple comparison of the largest foetus and the smallest neonate found from samples collected from the Izu fishery gave a range of 90-110cm for neonatal length but the number of foetuses (73) was much greater than neonates (17) which might lead to a biased estimate (Kasuya, 1972). Kasuya (1972) corrected for this and estimated the mean neonatal length at 99.8cm. A similar analysis by Miyazaki (1977a) using different samples but again from the Izu fishery (68 foetuses at 95-108cm and 20 neonates at 98-115cm) resulted in almost the same estimate (100.5cm).

Body length frequency and mean growth curve

Kasuya (1972) reported the maximum body length of 567 females examined on the Izu coast from 1967-1970 as 243-247cm and the modal length as 223-227cm; corresponding values for males ($n = 391$) were 258-262cm and 238-242cm. The maximum body lengths from 47 animals killed for research purposes in the northern offshore concentration in 1992 (Fig. 2) were 251cm (females) and 257cm (males) (Iwasaki and Kasuya, 1993), similar to those from off the Izu coast (Kasuya, 1972).

Iwasaki and Goto (1997), using samples collected at Taiji for the 1991/92-1994/95 seasons, reported the maximum body length and modal length of females at 238cm and 210-219cm ($n = 412$) and of males at 249cm and 220-229cm ($n = 301$). They believed that the striped dolphins taken off Taiji were smaller than those studied by Kasuya (1972) on the Izu coast. The body length difference is about 10cm in females and 15cm in males and appears to be significant (see *Stock Identity*).

The mean asymptotic length of striped dolphins has been estimated from an age/length relationship for the Izu sample representing six schools in 1971-1975 (Kasuya, 1976a). The mean growth curve was determined visually to reach a plateau at age 21 years or at 236cm ($n = 41$, $SD = 6.1$) for males and 17 years or at 225.3cm ($n = 89$, $SD = 15.3$) for females. However, Miyazaki (1984), combining an Izu sample (28 schools in 1970-1973) and about 10% of the sample from Taiji (2 schools by driving plus catches by the hand-harpoon fishery in 1973, 1979 and 1980; see Fig. 8 for samples), estimated the corresponding figures as 17 years and 238.9cm for males and 11 years and 225.7cm for females. As the two studies agreed on the asymptotic body lengths but not the ages, this suggests disagreement in age reading or interpretation of growth curves. Little if any growth occurred after 11 years (females) or 17 years (males) in Kasuya (1976a) and the disagreement may be insignificant. A similar analysis by Miyazaki (1977a) is not considered here because it is based on ageing by dentinal layers.

Subsequently, Miyazaki (1984) constructed mean growth curves using larger sample sizes ($n = 3{,}362$) from the Izu fishery in 1970-1973 plus the additional samples from Taiji referred to above (Fig. 3). Individuals aged around 40 years in his sample would have been born between 1930-1940, and those around 17 years between 1953-1963. If the mean asymptotic length had significantly increased between the above two time periods in response to a decline in density then one might expect some increase in the mean body lengths for animals > 17 years on the mean growth curve. No such change is evident in the growth curves of Miyazaki (1984) (Fig. 3) or of Kasuya (1976a). This does not exclude the possibility, however, that density dependent growth changes either only occurred before physical maturity or that changes in asymptotic body lengths occurred for individuals born after 1953-1963 or before 1930.

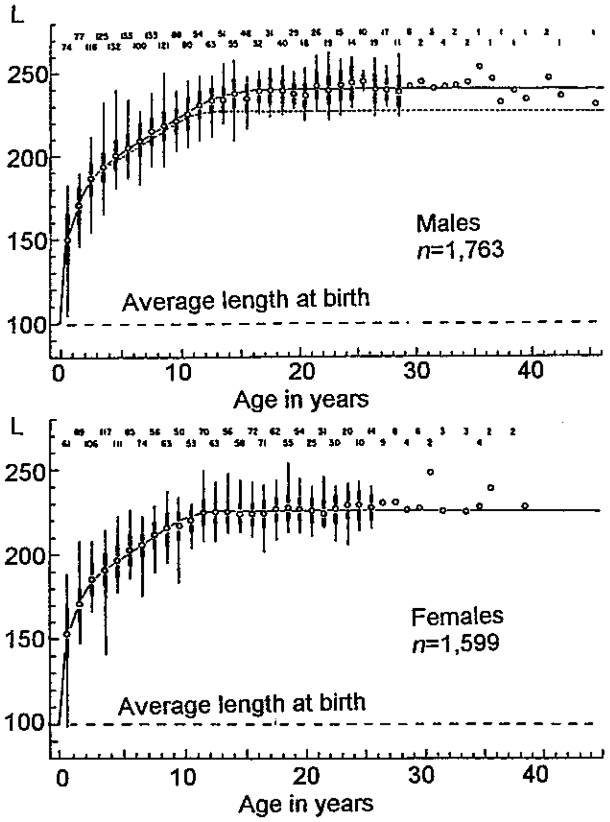

Fig. 3. Mean growth curve of striped dolphins constructed using samples obtained at Izu and Taiji in 1970-1980. Open circles indicate mean, vertical line range and black box two standard deviations. L = body length in cm. Numbers are sample sizes. Reproduced from figs 4 and 5 of Miyazakai (1984) with permission.

Similar analyses have been made in an attempt to look at density-dependent responses, usually with inconclusive results, for southern minke whales (Kato, 1987), North Pacific sperm whales (Kasuya, 1991), long-finned pilot whales (Bloch *et al.*, 1993) and Baird's beaked whales (Kasuya *et al.*, 1997). It has also been suggested that density-dependent improvements as a result of growth changes may be reflected in the age at sexual maturity rather than the lengths at sexual maturity or physical maturity (e.g. Read and Gaskin, 1990). Kasuya (1985) identified possible density-dependent changes in the age at sexual maturity for female striped dolphins born between the late 1950s and early 1970s (see *Sexual maturation of females*).

Sexual maturation of males

(1) Definition and age at maturation

Male sexual maturity was studied by Miyazaki (1977a) using ages based on dentine GLGs and by Miyazaki (1984) using cementum. Both studies used a similar sample set obtained from the Izu coast, with some additional samples from Taiji (see Fig. 8).

Classification of testicular maturity by Miyazaki (1977a; 1984) was in two steps. First he examined an unspecified number of tubules at the testicular centre and classified the testes into three categories: 'immature' without spermatogenetic tubules; 'puberty' with spermatocytes and without spermatozoa; and 'mature' with at least one spermatozoon. He further classified 'mature' testes, by examining 20 tubules, into: 'MI' having spermatozoa in one tubule; 'MII' spermatozoa in 2-19 tubules; and 'MIII' spermatozoa in all tubules examined. His maturity stages against testicular weight and age are shown in Table 3.

Table 3

Comparison of maturity, testis weight (g) and age (year) of male striped dolphins between authors.

Miyazaki (1977; 1984)			Iwasaki and Goto (1997)	
Stages	Weight	Age	Stages	Weight
Immature	<10	<15	Immature	<10
Puberty	4-40	2-14	Early maturing	5-37
MI	7-90	6-30	Late maturing	15-64
MII	15-200	6-30	Mature	12-229
MIII	40-225	7-46		

Testicular weight increased rapidly between 6-16 years, after which the correlation was weak (Kasuya, 1976a; Miyazaki, 1984). Spermatogenesis started between 2-10 years, and half of the males had reached his mature stage at age 8.8 years (Miyazaki, 1984).

The weights of testes at the M1, MII and MIII stages did not change greatly with age, but Miyazaki (1984) found that the proportion of MIII animals increased with age. At 16.5 years, half of the males were at the MIII stage and for most males at the MIII stage, the weight of single testis was > 80g. He also observed that males driven with females near oestrous tended to contain more males > 16.5 years than those taken with mature females at other reproductive stages. From this he concluded that MIII coincided with the attainment of social maturity.

In any analysis of male maturity, it is important to try to disentangle the effects of the male maturation process, seasonal cycles in males and male behaviour relative to the female cycle (also see *Seasonality in reproduction*).

Komyo (1983) studied the diameter of seminiferous tubules and the density of spermatozoa in the epididymal fluid using samples from the Izu coast. He confirmed histologically that the maturity stage did not vary among positions in an individual testis. The mean tubule diameter increased in three phases: (1) a rapid growth phase at testis weight < 40g; (2) slower growth at 40-110g; and (3) a plateau (about 200μm) at testis weight > 110g. The smallest testis with spermatozoa in the epididymis was 7.2g and the largest testis without spermatozoa was 57.2g. The highest sperm density (135×10^6/ml) was found at a testes weight of 50-60g. The density of epididymal sperms increased rapidly at a testis weight of 40-60g. By 100g it had reached a plateau of about 55×10^6/m although with wide individual variation of 25-100 ($\times 10^6$/ml). Komyo (1983) believed that males with epididymal sperm density $\geq 25 \times 10^6$/ml could be reproductively successful. Such densities could be found at testis weights >34.5g; all males with testes >86.2g had such densities. These testicular weights roughly agree with the social maturity classification of Miyazaki (1984). Age was not analysed by Komyo (1983).

Iwasaki and Goto (1997) determined four maturity stages of males taken off Taiji in winter 1993/94 and 1994/95 based on proportion of spermatogenetic tubules in the testicular centre (Kasuya and Marsh, 1984): (1) 'immature', no spermatogenetic tubules; (2) 'early maturing', >0% and <50%; (3) 'late maturing', >50% and <100%; and (4) 'mature', 100%. From this they concluded that half of the males were 'mature' when the mean weight of the two testes reached 40g. Ages were not estimated in this study.

There are difficulties in comparing these two approaches to assigning maturity stages. The use of a particular phase in the spermatogenetic cycle to classify maturation stages requires caution; the spermatogenetic cycle last only weeks and the phase varies between positions in a tubule, whilst the process of testicular maturation lasts for years. Further questions arise in the context of sample size; sampling of fewer tubules may result in a greater instability in classification.

No analyses trying to relate changes in age at the attainment of male sexual maturity with population density changes over time have been undertaken.

(2) Body length at maturation

Iwasaki and Goto (1997) found in the Taiji sample that spermatogenesis started at body lengths of 190-229cm. The smallest 'mature' male was 200-209cm and the largest male in the earlier stages 230-239cm; 50% of males were 'mature' at 224.4cm. It should be remembered that estimates of average body length at sexual maturity will be influenced by the age composition of the sample, e.g. a sample with a high proportion of juveniles (see *Segregation of juveniles*) may result in a greater estimated body length at sexual maturity.

Miyazaki (1984) found that 50% of his sample had spermatozoa in the testis (i.e. his MI to MIII stages) by age 8.8 years and obtained mean body length of 219cm by fitting this age to the mean growth curve. However, this body length is not necessarily equal to the length at which 50% of individuals are in the MI-MIII stages, because growth decreases after sexual maturity, and there is great individual variation in body length.

The two body-length estimates are not directly comparable due to differences in the definition of maturity chosen and the methods employed.

Again no attempts to examine this parameter in the context of a density-dependent response have been made.

Sexual maturation of females

Sexual maturity has been determined by the presence of at least one corpus luteum or albicans in the ovaries representing ovulation. About 70% of females having one corpus luteum or albicans were either pregnant or lactating (Miyazaki, 1984). This suggests that at least 70% of females conceived at their first ovulation; many of the remaining 30% will experience a second ovulation in the same season and have a high probability of conception. Since gestation time is believed to be about one year (see *Female reproductive cycle*), the age at first reproduction is close to one year after the first ovulation.

(1) Geographical variation

Using a sample from the Izu fishery in 1968-1971 ($n = 26$ for 8-10 layers) and ageing by dentine layers, Kasuya (1972) concluded that sexual maturity occurred at 8-10 years, with an average of 8.8 years. A similar study by Miyazaki (1977a) gave the age range of 4-12 and an average age of 8.8 years using a larger sample from the Izu fishery ($n = 363$ for 4-12 layers). These results were similar to those of a later study by Kasuya (1976a) who used cementum layers (mature at 5-12 years with an average of 8.5 years, $n = 110$ for the age range).

The smallest sexually mature female taken in the Izu fishery was 188-192cm long and the largest immature female was 218-222cm long ($n = 567$ for all postnatals), with 212cm as a rough estimation of body length at 50% maturity (Kasuya, 1972). Miyazaki's (1977a) estimate of 8.8 years, corresponded to 216cm on his mean female growth curve.

Using samples from Taiji for the 1991/91-1994/95 seasons, Iwasaki and Goto (1997) reported that the smallest mature females were around 190-199cm and the largest immatures around 220-229cm ($n = 259$). The reason for the differences in these ranges from the Izu sample (Kasuya, 1972) is difficult to ascertain given the differences in length groupings. They calculated mean length at sexual maturation at 199.8cm, about 12cm smaller than the corresponding figure for the Izu sample in 1968-1971.

(2) Density-dependent changes

Kasuya (1985), using samples from the Izu coast, examined historical changes in female age at sexual maturity. He compared the average age at sexual maturity (determined as the age at which 50% of individuals are mature) and variation between year classes in age at maturation. The average maturation age declined from about 9.4 years in 1956-58 cohorts to about 7.5 years in 1968-70 cohorts. The age of the youngest mature female also declined: females matured at >8 years for the 1956-62 cohorts, 7-9 years for the 1963-67 cohorts and 5-9 years for the 1968-71 cohorts. He interpreted these changes to reflect improvement in growth due to increased *per capita* food availability resulting from depletion of striped dolphin stocks off the Izu coast.

There are a number of potential confounding factors that may affect interpretation of the apparent density dependent response of striped dolphins. For example, the observed acceleration of growth occurred while the fishery moved offshore. A lowered proportion of a 'coastal stock' in the catch could either mask or enhance real changes in the coastal population if growth-parameter differences exist between the populations. One proposed mechanism for density-dependent responses is that *per capita* food supply increases as abundance decreases. However, if an unexploited dolphin population competed with the coastal striped dolphins for resources, then this might suppress acceleration of growth in the striped dolphin stock. The drive fishery for pantropical spotted dolphins started in 1959, possibly due to a decline in the availability of striped dolphins, and continued at a low level (Miyazaki *et al.*, 1974; Kasuya, 1985). The absolute effect of this harvest is unknown, but it may have enhanced the density-dependent response of striped dolphins if they competed for resources. In addition, possible changes in food availability for striped dolphins due to fishing activities needs further investigation.

At least one species of squid in the diet of striped dolphins is also known to be harvested by Japanese coastal fisheries (see *Food habits*).

No attempts to relate changes in body length at the attainment of sexual maturity over time with population abundance have been made.

Female reproductive cycle

(1) Gestation period

The short fishing season (October to December) and apparently extended breeding season means that it is not possible to reliably estimate the foetal growth curve of striped dolphins off Japan based on monthly samples of foetal body lengths. The need to disentangle seasonal growth of foetuses, school specific foetal length compositions and the effect of foetal size on the timing of migration to fishing grounds also confound efforts to determine the female reproductive cycle and foetal growth (see *Seasonality in reproduction*).

Kasuya (1972) observed that foetal body lengths in October-December samples from the Izu coast were continuous from <5cm to >100cm with three modes at <10cm, 40-60cm and 70-105cm. He concluded that their breeding was diffusely seasonal and that the gestation period was about 12 months. The 40-60cm mode of foetal lengths would represent conception in the early summer. Miyazaki (1984) plotted monthly foetal modes from an October-January sample plus a May sample from Nishiwaki and Yagi (1953) from Arari (see Fig. 5 on p. 91). A linear regression of the five means he believed to represent growth of foetuses conceived in February and March was used to obtain a gestation time of 13.4 months.

There appears to be a general positive correlation between neonatal body length and gestation period in toothed whales (e.g. Kasuya, 1985). The mean neonatal length and observed gestation period of the finless porpoise, *Neophocaena phocaenoides*, were about 78cm and about 11 months, respectively; those of Commerson's dolphins, *Cephalorhynchus commersonii*, about 100cm and 11.3 month; and those of bottlenose dolphins 117-128cm and 12.2 months (see Kasuya, 1995). This suggests that the gestation time of striped dolphins will be about 11-12 months.

(2) Age-dependent changes in female reproductive cycle

Kasuya (1985) examined age-dependent changes in the female reproductive cycle off the Izu coast using proportions of various reproductive classes in a sample from 1960-1980. Three parameters (mean length of lactation, resting period and calving interval) increased with age and the regression coefficient was significantly different from zero. However, the magnitude of the change in the calving interval (which showed the most distinct change) was so small that the 2-year cycle detected at age <15 years did not increase to 3 years until age >40 (uncorrected for sample bias, see below). Thus any age-dependent decline in reproductive activity of females seems inconsequential.

The oldest pregnant female was 48 years, and the oldest lactating and simultaneously pregnant female 42 years (Kasuya, 1985). There were only three females >48 years, of which two were resting (57 and 49 years) and one lactating (49 years). These data suggest that striped dolphins off the Izu coast in 1960-1980 had no significant post-reproductive survival (Marsh and Kasuya, 1986).

(3) Length of calving cycle

The average calving cycle was analysed by Kasuya (1972; 1976a and 1985) and by Miyazaki (1984). The first two and the last studies were similar in that they used the crude proportion of females in each reproductive stage and a mean gestation time of 1 year (Kasuya, 1972 and Kasuya, 1976a) or 1.1 years (Miyazaki, 1984). Kasuya (1985) however, attempted to correct the imbalance of the ratio of neonates and foetuses (see below). These results are shown in Table 4.

The estimate of calving interval by Kasuya (1972) was speculative in that it was based on only three drives by the Izu fishery. Although Kasuya (1976a) increased the sample to 165 females from the Izu fishery, it was still too small. Miyazaki's (1984) analysis used a greater sample (699 adult females) from the Izu coast combined with about 10% of sample from Taiji (see below).

Kasuya (1985) reanalysed data from 14 drives from the Izu coast during the period 1967-1980. These included the samples used in his earlier studies. He compared the number of pregnant females (412) with the number of calves aged <1 (262) in the same sample. If mortality is ignored, then these two values should be similar; however, calves represented only about 63% of foetuses. Incidentally, this imbalance was reversed in the case of pantropical spotted dolphins (Kasuya, 1985).

These imbalances might result from: (1) the timing of sampling and parturition; (2) geographical segregation of females by reproductive class; or (3) errors due to small sample sizes. Neonatal mortality or loss of neonates during the drive could not explain the opposing imbalances for striped and spotted dolphins. In the absence of conclusive evidence, Kasuya (1985) assumed that for striped dolphins either lactating females were under sampled or pregnant females were over sampled.

Results of his analysis were similar to those of Miyazaki (1984) who had used a greater sample size and no correction (Table 4). This suggested that the imbalance was largely due to small sample sizes. Thus it appears that the mean calving interval of striped dolphins off the Izu coast from the late 1960s to the early 1980s was about 3 years.

(4) Density dependent change in female cycle

Kasuya (1985) examined historical changes in the female reproductive cycle and found that the mean estimated calving interval of striped dolphins off the Izu coast had declined by about 1.24 years from 1955 to 1977. The regression coefficient was not statistically different from zero ($0.05 < p < 0.1$). Although the estimated resting period

Table 4

Estimates of the reproductive cycle of female striped dolphins off Japan (in years).

Author	Preg.	PL	Lactation	Resting	Total
Kasuya (1972)	◄ 1 ►		1.5	0.3-0.5	c.3
Kasuya (1976a)	0.86	0.14	0.33	0.08	1.41
Miyazaski (1984)	◄ 1.1 ►		1.36	0.69	3.17
Kasuya (1985)	0.82-0.88	0.18-0.12	1.48-1.36	0.33-0.22	2.81-2.58

and mean lactation period also showed apparent declines, the regression coefficients were not significantly different from zero ($0.1 < p < 0.2$). The only statistically significant change observed was an increase in proportion of females that were pregnant and simultaneously lactating. Thus, although one might have expected a historical increase in female reproductive activity off the Izu coast, the available data do not confirm this perhaps due to the small sample size.

The Izu fishing season has tended to start earlier in later years (see *Fishing season and migration*) and foetal lengths tended to be smaller in the early part of the fishing season whilst testis weight was greater (see *Seasonality in reproduction*). Possible effects of these factors on the analysis of historical changes in the female reproductive cycle (Kasuya, 1985) remain to be investigated.

The annual ovulation rates estimated from an age-corpora relationship were 0.414 (5-25 years, Kasuya, 1976a) and 0.4944 (7-28 years, Miyazaki, 1984), thereby giving an upper bound for the potential annual pregnancy rate.

Seasonality in reproduction

(1) Parturition peaks

The calving season was estimated by fitting foetal lengths of multiple years to a mean foetal growth curve, which was constructed from an assumption of a gestation period of about 1 year and average neonatal length of 100cm. Parturition thus estimated occurred in all months of the year, with two distinct peaks in May-July and October-January (Kasuya, 1982: Izu sample in October-December), in December-April and July-September (Miyazaki, 1977a: Izu sample and a few Taiji specimens in December-February and June), or January-April and June-November (Iwasaki and Goto, 1997: Taiji sample in October-January). This disagreement is most probably due to inter-annual variation in breeding season and different timing of migration into the fishing area by gestation stage.

The estimated calving season using neonate data resulted in indistinct modes from May-August and November-December (Miyazaki, 1977a), probably due to uncertainty in the estimation of postnatal growth, low sample sizes and greater individual variation. Miyazaki's (1977a) conclusion of three mating peaks (February-May, July-September and December) was based on the accumulation of information from foetuses and juveniles below the age of 2 years and should be considered with caution.

In summary, the calving pattern is not well understood at present. For a better understanding, foetal length data for a wider geographical range, more months of the year and a greater number of years are required to resolve problems surrounding annual and school specific variations in mating, timing of migration and the possibility of the inclusion of more than one population in the fishery (see below).

(2) Apparent school specific pattern in the season

The presence of school-specific foetal length compositions was identified by Kasuya (1972) and further supported by Miyazaki and Nishiwaki (1978) based on 26 striped dolphin schools from off the Izu coast (Fig. 4). All of the pregnant females in 11 schools were in early pregnancy, most of the pregnant females in seven schools were in late pregnancy, whilst there were two, almost equal, foetal modes in the remaining eight schools. The apparent pregnancy rates in these last schools tended to be lower for schools of the other two types. Thus, length frequencies of foetuses are school specific, and this character is most distinct in schools of high apparent pregnancy rate. Kasuya (1972) interpreted this as suggesting that oestrus may be one of the key factors in establishing a new association of females (Kasuya, 1972).

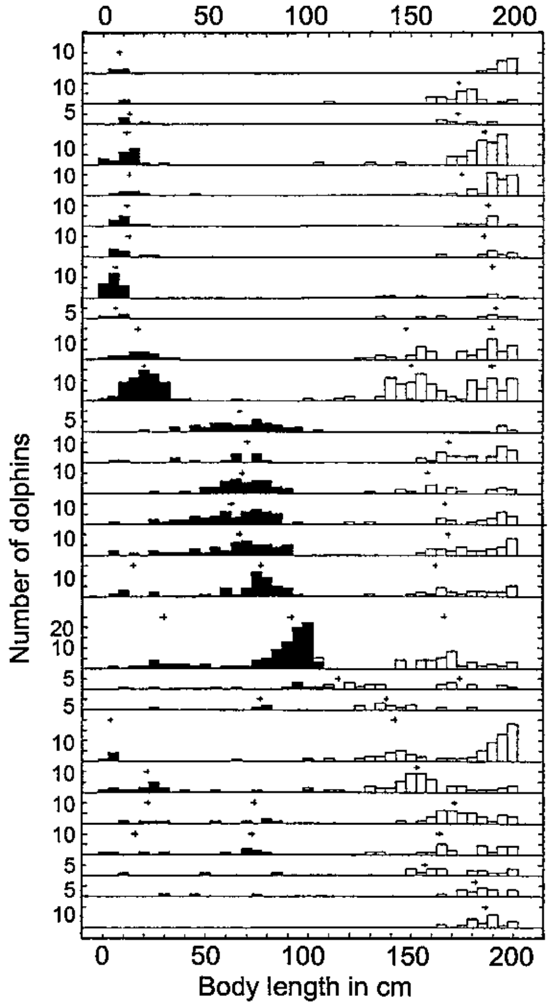

Fig. 4. Body length composition of foetuses (black squares) and juveniles (white squares) of striped dolphins for each school from the Izu coasts in October-December, 1968-1973. Larger postnatals over 2m in body length are not indicated. Reproduced from fig. 21 of Miyazaki and Nishiwaki (1978) with permission.

Miyazaki's (1977a) six years of foetal records revealed apparent annual variation in the timing of parturition, i.e. samples from certain years showed a single peak while other samples showed double peaks of similar strength. This was also evident in Iwasaki and Goto's (1997) Taiji sample, where 1994/95 samples suggested a calving season from April-October (peak in August), whilst the equivalent period from the 1993/94 samples was from October-July (peak in February). Such a situation could occur even in the absence of variation in the calving season, if the timing of migration is related to reproductive class (see below), or if more than one population (with different breeding seasons) migrate to the fishing ground.

An interesting feature of Miyazaki's (1984) data is the between-month variation in foetal length frequencies. While the October samples had more foetuses in the 0-40cm class than the 50-100cm, the reverse was true for December whilst the November sample was intermediate (Fig. 5). This suggests that females in early pregnancy tend to migrate into the fishing grounds early in the season while those with near-term foetuses arrive later in the season.

Using a sample from the Izu coast, Miyazaki (1977a) analysed 'mature' (> 15yrs) males by season and found that those taken in October had the greatest average testis weight (*ca* 140g). This value decreased to *ca* 80g in November and *ca* 30g in December (Fig. 6). This suggests a degree of correlation between male reproductive activity and the stage in the oestrus cycle of females they were caught with. This may reflect seasonality in male reproduction or a pattern of male-female association determined by reproductive cycle (also see *Sexual maturation of males*).

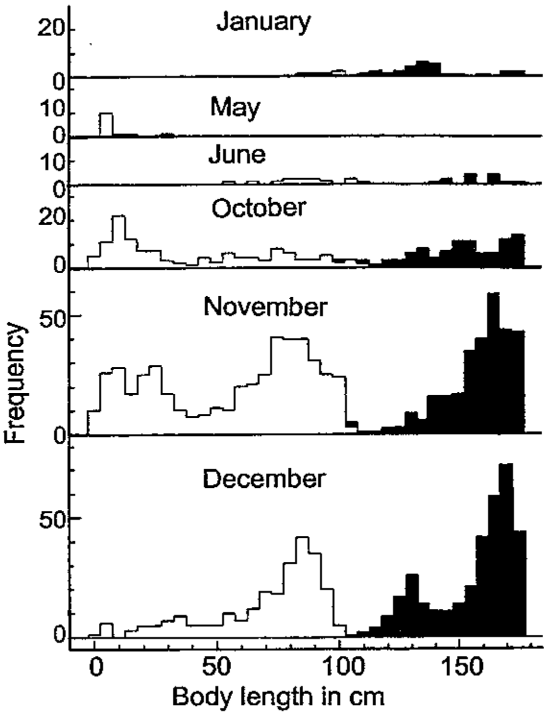

Fig. 5. Monthly body length composition of foetuses and juveniles of striped dolphins from the Izu coast (May and October-January) and Taiji (January and June). The May sample is from Arari cited from Nishiwaki and Yagi (1953). Reproduced from fig. 2 of Miyazaki (1984) with permission.

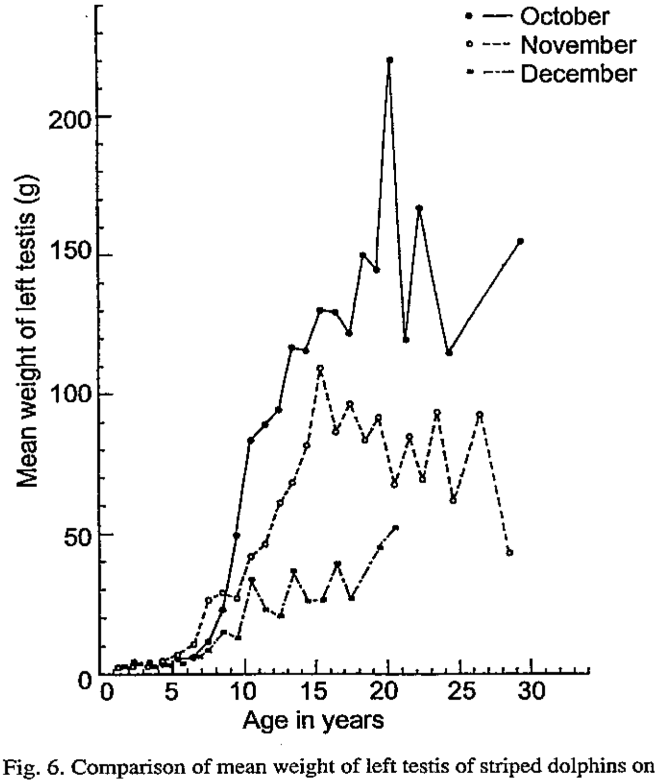

Fig. 6. Comparison of mean weight of left testis of striped dolphins on age. Samples were taken off the Izu coast by drive fishery (October-December, 1968-1973). Ages were determined from dentinal growth layers. Reproduced from fig. 8 of Miyazakai (1997a) with permission.

The Taiji samples of Miyazaki (1984) had only near term foetuses (taken in January and June) while his Arari sample (from Nishiwaki and Yagi, 1953) had small foetuses (May). The 1994/95 Taiji sample of Iwasaki and Goto (1997) had a distinct peak at 20-45cm (3 drives in November-January), and their 1991/92 and 1993/94 samples had a peak at 80-100cm (10 drives in October-January). That these Taiji samples do not show any clear season-dependent foetal size composition may reflect the small sample size rather than any lack of pattern. Further work is needed to clarify this.

Weaning

Miyazaki (1977a) examined the stomachs of 45 juveniles to determine the presence of milk in the stomach. The smallest individual with solid food remains was 133cm, and the largest individual with milk was 176cm. There were 23 individuals in this length range of which five had only milk in their stomachs (142-176cm), four had both milk and solid food remains (133-159cm) and 12 with solid food remains only (135-174cm).

The youngest individual with solid food was 0.25 years old and the oldest individual with milk was 1.25 years old (Miyazaki, 1977a). Of the 12 animals in this age range, three had only milk (0.25-0.75 year), two both milk and solid food remains (0.5-1.25 years) and seven only solid food remains (0.25-1.25 years).

These data suggest that calves start taking solid food at age 0.25-0.5 years and may continue to take both milk and solid food to age 0.75-1.25 years. However, this method can bias weaning age downward, as acknowledged by Miyazaki (1977a), because milk mixed with solid food is hard to identify.

Miyazaki's (1977a) also estimated weaning age by comparing the numbers of lactating females and juveniles driven together; this gives an upper bound of the age at completion of weaning. If calves are lost during the drive, or if a calf nurses from multiple females (not confirmed for the species), this method is likely to overestimate age at weaning. The age thus calculated was 1-2.5 years (17 schools), and the lower bound showed fair agreement with the first estimate. It can thus be concluded that suckling continues to at least close to 1 year but may often last to almost 2 years in the population studied.

In an analysis of school structure, Miyazaki and Nishiwaki (1978) showed that weaned juveniles started to live with other immatures at between 1 and 2 years and that the number of such individuals increased rapidly to 3-4 years of age, i.e. with the formation of juvenile schools (see *Segregation of juveniles*). Although there is no estimate of the length of time between the completion of weaning and the departure of calves from the mothers' school, it does not appear to be very great.

SCHOOL STRUCTURE

The structure of striped dolphin schools was first examined by Kasuya (1972). Subsequently, Miyazaki (1977b) and Miyazaki and Nishiwaki (1978) elaborated on this using a larger sample size from the Izu fishery. One potential confounding factor was that the drive fishermen may have combined some schools for driving or, in rare cases, only part of a larger aggregation might have been driven; such information is not usually available. Thus the school size and the size of a drive were not distinguished by the above studies; each drive was usually described as a 'school'.

Sex ratio

The estimated foetal sex ratio (male:female) was 58:57 (Kasuya, 1972), 152:163 (Kasuya, 1985), or 269:247 (Miyazaki, 1977a and Miyazaki, 1984); none differ statistically from parity ($p > 0.05$).

The overall postnatal sex ratio was also close to parity: 1,774:1,681 (Miyazaki, 1984). The apparently low proportion of males from ages 3-10 years (Miyazaki and Nishiwaki, 1978; Kasuya, 1985) reflects the tendency of males to leave adult schools after weaning to form juvenile schools, which had a lower probability of being driven than adult schools.

Both Miyazaki (1984) and Kasuya (1976a; 1985) identified a slight decrease in the proportion of males after age 35 years. Although this could be a reflection of a slightly higher natural mortality rate in males, there is no significant difference in the maximum age between sexes, i.e. 57 years for both sexes. There were five males and females aged between 45 and 57 years (Kasuya, 1985).

In conclusion, there appears to be little, if any, difference in natural mortality rates by sex among striped dolphins off Japan. This is in contrast to the result for pantropical spotted dolphins aged by the same author, where the oldest observed ages were 42 years in males and 45 years in females and the proportion of females increased steadily from 45% in foetuses to close to 100% at age 35-45 years (Kasuya, 1985).

School size

The number of individuals found in a single 'drive' ranged between 25 and 2,327 and the mean school size was 415; about 86% of the drives contained less than 500 individuals (Miyazaki, 1977b) (Fig. 7). The question of changes in school size over years has not been examined.

Miyazaki (1977b) analysed schools taken by the drive fishery on the Izu coast by month and area. In winter (November-January), the fishery operated on both the east and west coasts, but it operated only on the west coast in spring (April-May) and only before 1960. The average number of dolphins per drive in winter (*ca* 300) did not differ between the coasts, but the school size (*ca* 150) in spring operations on the west coast was significantly smaller than in the winter operation in the same area.

Schools found in the early morning were often large, suggesting merging of schools during feeding at night and splitting of schools in daytime (Miyazaki and Nishiwaki, 1978). By contrast, the diurnal pattern in school size observed for pantropical spotted, spinner and short-beaked common dolphins in the eastern Pacific was for larger school sizes late afternoon and smaller in the early morning (Scott and Cattanach, 1998).

Segregation of juveniles

Many of the striped dolphin schools taken off the Izu coast contained a large proportion of adults of both sexes as well as immature individuals, particularly of suckling age (these are termed 'adult schools' (see below)), but showed a deficiency in post-weaning juveniles. Other schools were composed mostly of immatures of both sexes between 2 and 12 years of age (usually with excess males) (Fig. 8). The proportion of immatures was discontinuous between the two types of schools (Miyazaki and Nishiwaki, 1978). This suggests that calves leave their natal school after weaning to associate with other immature individuals and thus form 'juvenile schools'. The proportion of mature females in these schools was usually negligible, although there were some males of later growth stages. Therefore, it appears that females join the adult schools at the onset of puberty, not pregnancy or parturition.

In juvenile schools, males exceeded females of the same age. This high proportion of males (*ca* 75% on average) implies a stronger tendency of males to leave the natal school combined with their higher age at maturation. Peak ages in these 'immature schools' are variable between schools, suggesting that formation of such schools is at least partly a function of age. The maximum size of juvenile schools was close to 1,000, but many were less than 100 individuals.

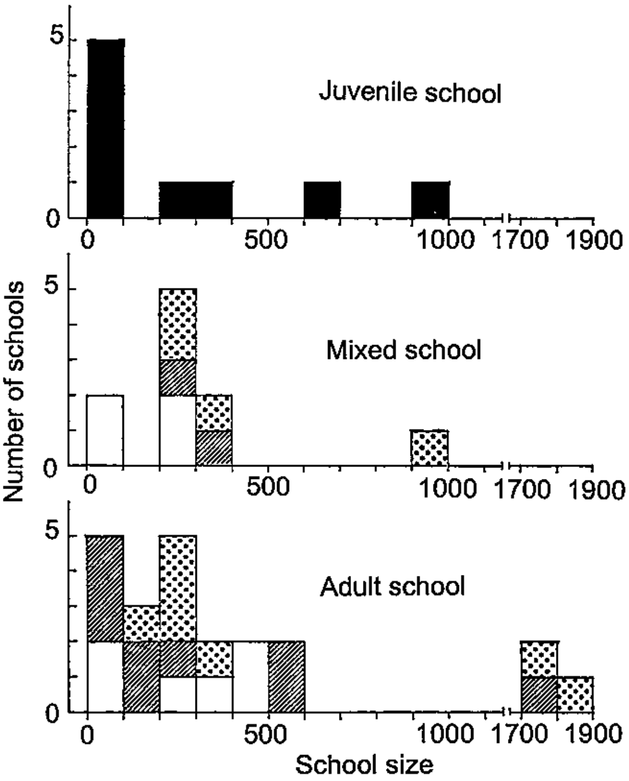

Fig. 7. School size frequencies of striped dolphins for juvenile (top), mixed (middle) and adult schools (bottom). The last two school types are further divided into mating (hatched), non-mating (dotted) and unclassified (white) schools (Miyazaki and Nishiwaki, 1978). Data are from drive fishery off the Izu coast in October-December, 1963-1973. Reproduced from fig. 10 of Miyazaki and Nishiwaki (1978) with permission.

Adult schools

'Adult schools' contained sexually mature males and females at various reproductive stages and their dependent calves. Although there was a deficiency of individuals aged 2-11, there were always some animals in this age range. Most ($n = 19$) adult schools contained less than 600 individuals, but some ($n = 3$) over 1,700 individuals (Fig. 7).

The composition of adult schools was variable and parametric values continuous among schools. Thus attempts by Miyazaki and Nishiwaki (1978) to draw a clear picture of the formation of adult schools or the movement of adults between them was unsuccessful.

Ten of the 41 schools examined by Miyazaki and Nishiwaki (1978) had characteristics of both juvenile and adult schools. This suggests the merging of several schools either as a natural process or by the fishery in an effort to combine several nearby schools for a drive.

Age composition and mortality

If dolphins mixed freely within a population and the fishery was not selective, then the age composition of the catch would reflect both the total mortality rate and yearly changes in recruitment. An alternative 'extreme' situation might be the situation if a drive fishery took place on resident killer whales (*Orcinus orca*) studied off the Vancouver Island area, which form matrilineal pods and where the offspring are believed to remain in their natal pods for life (e.g. Bigg *et al.*, 1990). Fishing mortality caused by a drive fishery on such pods would not directly alter the age composition of other pods, except through changes in recruitment and in natural mortality rate responding to decreased density.

The situation for striped dolphins off Japan is somewhat intermediate between the above two extremes. They have been exploited partially by hand-harpoon fisheries which are strongly selective for weaned juveniles (ages 2-7 years) (see Fig. 8 of this study and fig. 25 of Kasuya, 1978) and largely by drive fisheries which are the least selective (see fig. 25 of Kasuya, 1978). As noted earlier, the drive fishery may combine some small schools before the drive or may drive only part of a large aggregation. The social structure of Japanese striped dolphins is considerably more fluid than for resident killer whales. There appears to be considerable movement of individuals between schools by age and reproductive status (see *School structure*). The age composition of samples < 10 years is strongly affected by the probability of encountering juvenile schools and can not be reliably analysed at present.

Fig. 9 presents the age composition of striped dolphins taken by drive fisheries off the Izu coast from 1971-1977 (8 schools). Kasuya (1985) stated that the slope of the age composition changed from medium (10-22 years), low (20-34 years) and high (> 32 years), and suggested that the first two segments possibly reflected changes in total mortality rate and/or in recruitment caused by fishing operations after World War II, whilst the last portion reflected an increase in age-dependent natural mortality rate. The 'apparent annual mortality rates' calculated from the catch composition using method of Robson and Chapman (1961) are 0.1074 (11-22 years), 0.0622 (20-34 years) and 0.1408 (> 32 years) for females and 0.1486 (11-22 years), 0.0534 (20-34 years) and 0.1419 (> 32 years) for males (Kasuya, 1985). The catch curve of pantropical spotted dolphins in the same study (Kasuya, 1985) showed two phases for the adult ages; lower apparent mortality rates of

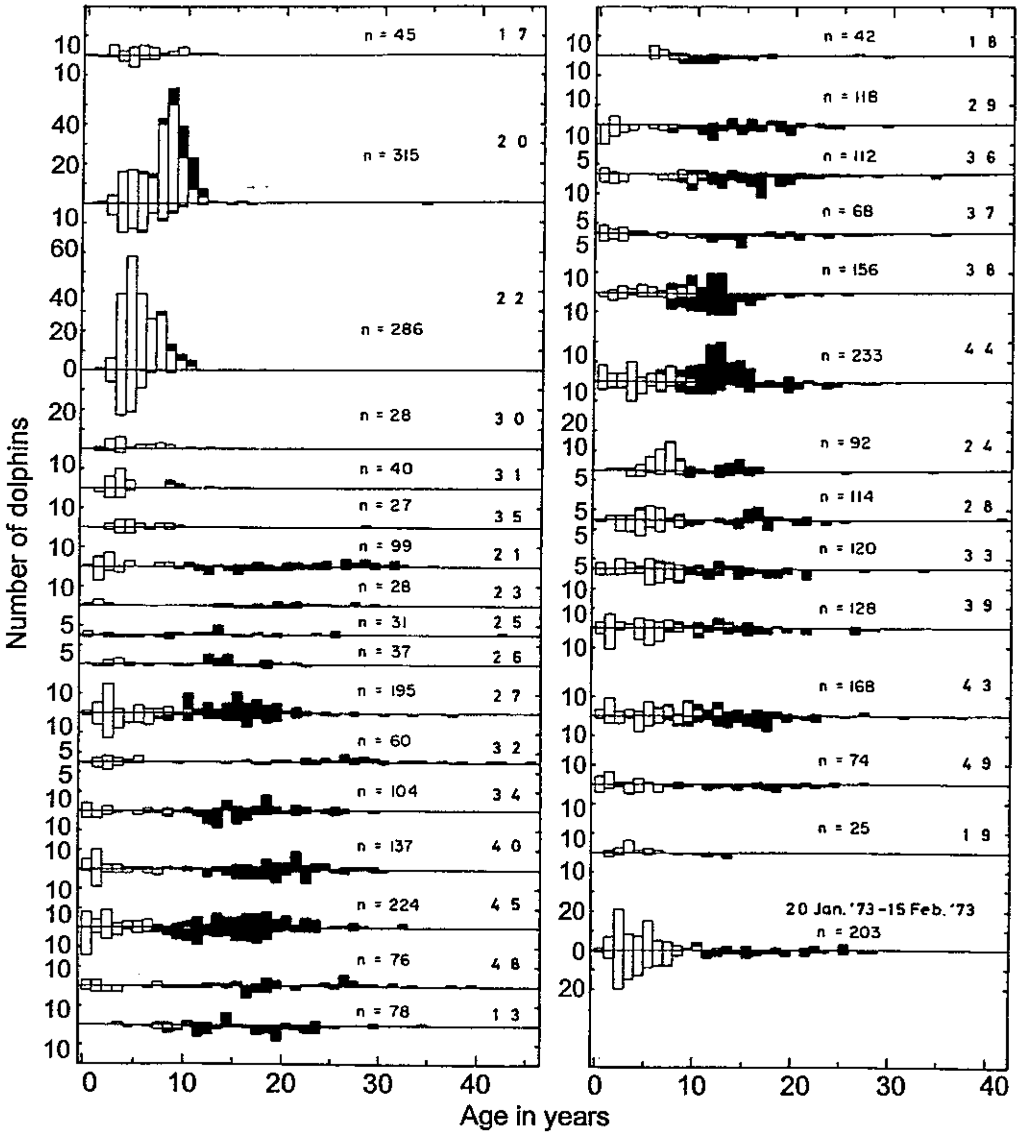

Fig. 8. Age composition of striped dolphin schools taken by drive fishery off the Izu coast in 1971-1977. School nos 13-45 are from the Izu coast (October-December, 1970-1973), nos 46-49 are from Taiji (January, June and December, 1975-1980). Catch of hand-harpoon fishery off Taiji is shown in the right bottom. Reproduced from fig. 1 of Miyazaki (1984) with permission.

0.0563 (females at 11-26 years) and 0.0590 (males at 7-22 years) for intermediate ages, and 0.1348 (females >24 years) and 0.1618 (males >20 years) for higher ages.

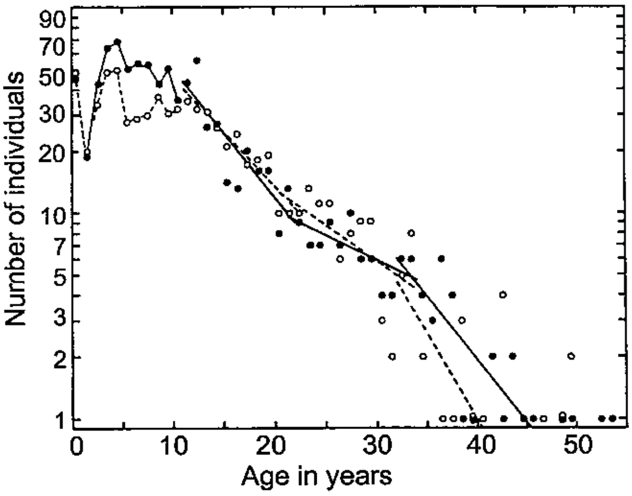

Fig. 9. Age composition of striped dolphins taken by drive fisheries off the Izu coast in November-December, 1971-1977. Eight schools are combined. Reproduced from fig. 10 of Kasuya (1985) with permission.

A qualitative comparison of apparent mortality rates for the two species, bearing in mind greater longevity of striped dolphins, suggests the following: (1) the greater apparent mortality rates in older individuals of both species is a reflection of higher natural mortality rates among old individuals; and (2) the apparent mortality rates of striped dolphins at intermediate ages (11-34 years) compared with corresponding figures of pantropical spotted dolphins probably reflects higher fishery related mortality rate and/or increased recruitment.

Feeding

There has been relatively little work carried out on the feeding of striped dolphins in Japanese waters. Miyazaki *et al.* (1973) studied the stomach contents of 27 striped dolphins from two schools taken off the Izu coast in December 1970. Nineteen dolphins had half-digested squid remains representing 35 individuals of two species, *Tadarodes pacificus* in both schools and *Symplectoteuthis luminosa* (c.f. *Eucleoteuthis luminosa*) in one school. Squid beaks (1,805 in total) were present in all the stomachs.

All 27 stomachs contained half-digested shrimps representing a total of 1,971 shrimps of four genera and three families. Of these *Bentheogennema borealis* was the most dominant (85.6% by number).

Only eight stomachs contained half-digested fish remains; these represented 30 individuals. In addition to these, fish otoliths (5,410 in total) and urohyals (1,448 in total) were found in the stomachs. Miyazaki *et al.* (1973) identified fish species using urohyals and partially digested food remains. Myctophidae (64.0%) was the most dominant in the urohyals, which was followed by Nemichthyidae (13.1%), Emmelichthyidae (8.1%) and Chauliodontidae (7.5%).

The authors concluded that the striped dolphins feed mainly on fish. It would be desirable, however, to consider the difference of digestion time among urohyals, squid beaks and shrimps and effect on their numbers found in the stomachs. The quantity, not the number, of these food items also needs to be considered.

Of the food species identified by Miyazaki *et al.* (1973) only one squid species, *Tadarodes pacifica*, is commercially exploited off Japan.

POLLUTANTS

Honda *et al.* (1982) studied the distribution of various heavy metals in the body tissues (muscle, liver, blubber and bone) of striped dolphins. Iron, manganese, copper, nickel and cadmium were highest in the liver, and zinc and lead were highest in bone.

Mercury and selenium in striped dolphins were first studied by Arima and Nagakura (1979) using samples collected in 1973 on the Izu coast. Mercury content in the skeletal muscle increased with age linearly from about 0.95ppm wet weight at 0 year to 9.43ppm at 30 years of age; selenium (0.22-0.48ppm) also increased linearly with mercury. A positive correlation between these metals was confirmed in tissues other than skeletal muscle (Itano *et al.*, 1984b) and by other studies of skeletal muscle (Itano *et al.*, 1984a).

Itano *et al.* (1984a) reported the mercury and selenium content in skeletal muscle of 55 striped dolphins collected in 1977-1979 off Japan (Fig. 10). They found that an increase in methylmercury ceased at around age 10 years while that of total mercury continued to increase further. From this they postulated that the species might have a demethylation mechanism. Levels of total mercury and selenium were low in neonates (mercury:1-2ppm; selenium: 0.5-1ppm) and increased almost linearly until age around 20 years, when the increase levelled off. The levels were not different between sexes and did not vary with the reproductive status of individuals in the same sample set. However, levels of selenium and mercury showed a large variation between schools. Dolphins taken in 1977 (Izu) and 1980 (Taiji) had muscle levels of 18-30ppm (total mercury) and 3.5-7.5ppm (selenium) at ages over 15 years, which were discontinuously higher than the corresponding figures (total mercury: 9-16ppm; selenium: 0.5-2.5ppm) for dolphins taken in 1978 (Taiji) and 1979 (Taiji). The tendency was the same for ages below 15 years if compared between individuals of same age. The number of sampled schools is not given in their publication (also see *Stock identity*).

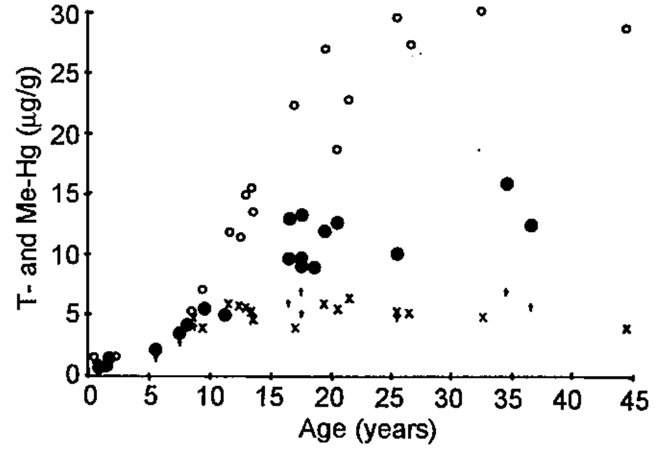

Fig. 10. Age dependent change in mercury levels in skeletal muscles of striped dolphins. Circles represent total mercury and × and † methylmercury. White circles and Xs represent samples from Kawana in October 1977 and Taiji in December 1980, and black circles and †s those from Taiji in December 1978 and 1979. Reproduced from fig. 1 of Itano *et al.* (1984a) with permission.

Tanabe *et al.* (1981b) studied the anatomical distribution of chlorinated hydrocarbons in postnatal striped dolphins and concluded that over 90% of the total burdens were deposited in the blubber, which comprised 17% of body weight. O'Shea *et al.* (1980) first studied organochlorine pollutants in the blubber of striped dolphins off Japan using samples from the Izu coast in 1968-1975. The levels of PCBs and total DDT were 1.2-4.8ppm and 1.26-18.04ppm, respectively, in wet blubber weight. Later, Tanabe *et al.* (1981a), Tanabe *et al.* (1982) and Tanabe (1985) studied the transfer of PCBs and DDTs from mother to offspring through the placenta and milk. The organochlorine content in female blubber sharply declined after age of 8-10 years, while that of males remained almost constant.

Loganathan *et al.* (1990) studied historical changes in organochlorine levels using two sets of adult male samples (aged 15-37 years) from off Taiji in 1978-1979 and 1986-1996. Ranges for the latter sample were (ppm in wet weight, mean in parentheses); PCB: 17-37 (28), DDTs: 23-51 (37), HCHs: 130-460 (270), HCB: 90-290 (150). These mean levels of PCBs and DDTs were the same as the earlier levels (PCBs: 29ppm; DDTs: 38ppm), but the levels of HCHs and HCB were considerably lower than the mean levels 10 years previously, 410ppm (HCHs) and 240ppm (HCB).

MIGRATION AND STOCK IDENTITY

Fishing season and migration

Ohsumi (1972) was the first to consider migration and stock identity in striped dolphins taken by the drive fisheries off the Izu coast and the hand-harpoon fishery off Taiji. He hypothesised that these fisheries exploited a single population of striped dolphins.

Miyazaki *et al.* (1974) analysed catch statistics to examine seasonality in striped dolphin fisheries off Japan. Taiji exhibited a peak in October-February, the west coast of Izu in December-February and April-June and the east coast of Izu in October-December. They concurred with the hypothesis that the Taiji and Izu fisheries exploited a single population. However, it should be recognised that the absence of catches in the summer in these regions does not necessarily mean the absence of striped dolphins. Even before the establishment of current fishing season regulations, the Taiji fishermen used to switch to more profitable trolling or net fisheries in the spring and summer months. The demand for dolphin meat was lower in spring and summer in the Kanagawa, Shizuoka and Yamanashi Prefectures on which the Izu fishery depended.

Miyazaki *et al.* (1974) also found that the annual catch of striped dolphins off the Izu coast was negatively correlated with the offshore distance of the Kuroshio Front. From this and from the results of sightings cruises made at *ca* 35°N and 141°E in September-October, they concluded that the fishery hunted striped dolphins that inhabited the northern front area of the Kuroshio Current; thus the advance of that current to the coast should increase the availability of dolphins to the fishery. However, Miyazaki's (1983) study, using a longer series of data, somewhat confounded this interpretation: the correlation was negative from 1961-66, positive after 1974, whilst no correlation was observed for the period 1967-73. The reasons for this are unknown.

Miyazaki (1983) identified two catch peaks (September/October and November/December), in terms of both number of individuals and number of schools, driven on the east coast of the Izu Peninsula. Although not referred to by the author, his data reveal a gradual advancement in the fishing season: the season started in December during 1950-52 at Kawana and Futo (east coast), but it began in November (1953), October (1956-77), and finally September in 1977-81 (no data for 1954-55). There has been no operation in January since 1969. A similar pattern can be seen for Arari (west coast), i.e. the proportion of the March-July catch decreased since 1942 whilst that for December-January increased. It is unknown whether this was due to a response of the fisheries to the market (higher prices for earlier catches) or to a change in the availability of dolphins to the fishery.

Using sightings data, Kasuya and Miyashita (1989) and Miyashita (1993) identified three geographic concentrations of striped dolphins in the western North Pacific in August-September: a northern offshore concentration; an inshore concentration; and a less distinct southern offshore concentration. The density of striped dolphins was apparently low between the concentrations and in northern inshore waters (west of 144°E and 35°-41°N) where striped dolphins from the Izu ground might be thought to summer.

Fig. 2 represents distribution of striped dolphin sightings in July through September based on data from Miyashita (1993) with my own interpretation of the concentrations (solid lines). The inshore concentration is limited to within about 200 n.miles from the Pacific coast, and apparently separated into two portions, north of 35°N and south of 33°20'N (dotted lines in Fig. 2). The southern portion of the inshore concentration showed no clear seasonal movements (Miyashita, 1997). Its range does not seem to cover the Izu fishery, but probably covered the Taiji fishery. Striped dolphins that summer in the northern part of the inshore concentration will enter the Izu area in the autumn/winter season.

Miyashita (1997) examined the monthly range of these concentrations from June to March. From spring to summer, the southern boundary of the northern offshore concentration moved from south to north: 32°N (June), 33°N (July), 34°N (August), and 36°N (September), whilst the western boundary of the concentration remained at 145°E. In October, the southwestern limit moved to the southwest, to 33°N and 141°E, i.e. approaching the recent operating area of the Izu fishery (34-35°N, 139°-140°E). It therefore is possible that the northern offshore concentration approaches the current Izu fishing grounds in autumn and is harvested by the fishery. However, this does not necessarily mean that the Izu fishery exploits only individuals from the northern offshore concentration.

Stock identity

The question of what comprises a 'stock' or 'population' is complex and no general accepted definition exists. Donovan (1991) emphasised that the nature of the definition was to some extent a function of the use to which it is being put (c.f. 'biological' and 'management' stocks). The situation for cetaceans is rarely simple and the structure of population(s) or stock(s) of striped dolphins off Japan remains unresolved. Previous discussions of stock identity for this region have not defined what is meant by either a 'stock' or 'population'. For example, it is possible to assume that several local populations of incomplete isolation constitute a metapopulation of wider geographical range (Hanski and Simberloff, 1997). These local populations, which may or may not be under different selection pressure, may have some limited degree of genetic exchange and may experience extinction due to natural or human related causes, followed possibly by recolonisation from other areas. The concept of a 'management stock(s)' for this fishery is complicated by a lack of understanding as to how the unit of harvest in the Japanese drive fishery often called 'school', functions within the 'population(s)' of striped dolphins. Consideration of these fundamental concepts is outside the scope of this review. The terms 'population' or 'stock' are used in the rather general sense that has been used in previous studies.

As noted in Donovan (1991), consideration of stock identity requires consideration of information for a suite of techniques. Information relating to stock identity of striped dolphins is summarised below. For geographical names see Fig. 1.

(1) Distribution

Kasuya and Miyashita (1989) considered that the three summer concentrations of striped dolphins off Japan might represent separate populations. They recognised the large abundance of the northern offshore concentration (see *Abundance*) and suggested that if these individuals were involved in the Izu fishery the fishery would not have experienced such a drastic decline. They proposed that for safe management, the northern offshore concentration should be assumed to be a different stock from that harvested and depleted by the Izu fishery.

(2) Osteology and growth

Amano *et al.* (1997) analysed geographical and temporal differences in skull morphology of striped dolphins in the western North Pacific based on:

1. an early Taiji/Izu sample (45 individuals from Taiji and Izu in 1958-1979);
2. a recent Taiji sample (24 from Taiji in 1992); and
3. a recent northern offshore sample (21 from research takes in the northern offshore concentration in August 1992, see Iwasaki and Kasuya, 1993).

They identified significant sexual dimorphism in the early Taiji/Izu sample as described by Ito and Miyazaki (1990), but did not find this in the recent Taiji and northern offshore samples. Males of the three sample sets were distinguishable from each other by canonical variate analysis, but females were different only between the recent Taiji sample and other two samples combined.

Amano *et al.* (1997) found it difficult to reach any firm conclusions, particularly given the small samples and the greater uncertainty for females. However, they considered that the difference between the early Taiji/Izu sample and recent Taiji sample was real, and that the recent northern offshore sample also differed from the two coastal sample sets. The small sample sizes precluded comparison between early samples from Taiji and Izu. The degree of sexual dimorphism differs between populations of striped dolphins, and this can provide useful stock identity information (Archer, 1996). It is quite possible to find interpopulation differences only in males.

Iwasaki and Goto (1997) compared the body lengths of three striped dolphin samples: (1) a recent Taiji sample from 1991/92 and 1994/95; (2) a recent northern offshore sample from 1992 (Iwasaki and Kasuya, 1993); and (3) an early Izu sample (Kasuya, 1972). Lengths in the recent Taiji sample were smaller than those in the early Izu sample or the recent northern offshore sample (see Body length frequency and mean growth curve). Whilst growth may change in response to density, length differences between the two recent samples are also of relevance to stock identity.

(3) Genetics

Wada (1983) studied isozymes of 10 enzymes encoded by 15 genetic loci of 40 striped dolphins using samples collected from a single school driven on the Izu coast in 1980. Two loci (13.3%) were polymorphic and average heterozygosity for all 15 loci was 0.021. He thought that this low heterozygosity might reflect interbreeding. Because the tissues were collected from livers that had already been removed from the carcasses, it was not possible to examine the data in terms of growth and reproductive status. Subsequently, Shimura and Numachi (1987) examined 19 genetic loci encoding 12 enzymes of 370 striped dolphins taken on the Izu coast, which presumably represented multiple schools but this information was not given in the paper. The proportion of polymorphic loci (26.3%) and the average heterozygosity (0.089) were much greater than the values reported by Wada (1983) and were similar to values found for pantropical spotted dolphins from the same fishery and intermediate between values for bottlenose dolphins and Dall's porpoises (Shimura and Numachi, 1987).

Yoshida and Iwasaki (1997) analysed the control region of mitochondrial DNA of 43 striped dolphins from the northern offshore concentration in August 1992 and 34 animals from the Taiji area in September/November 1992. They identified 61 haplotypes, 36 of which were represented by 36 offshore specimens, 21 by 27 inshore specimens, and the remaining four (7%) shared by four offshore and 6 inshore individuals (13.7% of the total sample). The authors found no statistically significant genetic differences between the two sample sets, but felt that the very high haplotype diversity could have masked any true differences and they identified the need for further analyses that took into account social structure.

(4) Pollutants

Itano *et al.* (1984a) found distinct yearly variations in total mercury and selenium contents in the skeletal muscle of adult striped dolphins (see *Pollutants*): high in Izu (1977) and Taiji (1980) samples and low in Taiji (1978 and 1979) samples. Although the details of the sampled schools are not available, the number of schools is probably small and the differences might be school specific. It seems likely that the between-school differences in heavy metal levels probably reflect differences in prey species or major feeding grounds in the last 15-20 years. In view of the fluid school structure of the species (see *School structure*), then it is not an unreasonable hypothesis that these differences are indicative of different stock structure. However, as indicated in Reijnders *et al.* (1999), the age and sex structure of the sampled animals must be considered when examining differences in pollutant levels. Having said that, these results are not incompatible with the hypotheses that more than one population was involved in the Taiji fishery in the late 1970s and that the composition of populations was at least partially different between the Izu and Taiji fisheries.

(5) Synthesis

This section summarises the available information on stock structure in terms of reasonable hypotheses and supporting evidence (in parentheses). The term 'past' or 'early' denotes any period during 1959-1980 and 'recent' or 'current' that after 1990.

1. Striped dolphins in the present northern offshore concentration may be different from those taken by the current Taiji fishery (osteology, growth and DNA) and also from those taken by the past Taiji fishery (osteology).
2. Part of the current harvest at Taiji may be from a population that was not exploited by the past Izu fishery (osteology).

(3) The past Taiji fishery may have exploited at least two populations, one of which could also have been taken by the Izu fishery of the time (mercury level).
(4) The northern offshore concentration has not constituted a major portion of the catch of the Izu fishery (catch trend, distribution and osteology), although some degree of involvement cannot be excluded (seasonal distribution).

The above four hypotheses do not conflict with each other. One possible scenario for population structure exploited by the Japanese striped dolphin fisheries is that at least two coastal populations were involved in the fishery. The Taiji fishery exploited both of them, while the Izu fishery exploited at least one; the involvement of the northern offshore population with the fishery was small, if any. This would explain the observation that the Taiji fishery made a large catch in the earlier days of the operation, when the Izu fishery had already declined, and subsequently experienced major decline. There is accumulating evidence for local populations on the small and large scale for many small cetaceans (e.g. Perrin *et al.*, 1991; 1994; Perryman and Westlake, 1998). Further study is needed to understand stock structure of striped dolphins off Japan.

ABUNDANCE AND CATCH TREND

Kasuya (1976a) and Kasuya and Miyazaki (1982) concluded that the population of striped dolphins off Japan had been declining and could not sustain the catch levels of the early 1970s. Although their conclusion has been supported by a later decline in the fishery on the Izu coast, there are identified problems with the estimation methods they used at that time. For example, their model assumed that maximum productivity is achieved at 50% of carrying capacity (although there was little evidence to support or refute this; there are cases suggesting otherwise - Fowler, 1994). In addition, the use of fishing mortality rates derived from catch curves has been shown to be unreliable in most fishery situations.

Kasuya (1985) analysed historical changes in life history parameters and catch statistics of the Izu fishery. He concluded that the catch off the Izu coast had shown a major decline from about 10,000 in the early 1960s to less than 1,000 in the early 1980s, when the fishery was operated at Kawana and Futo using the same number of searching vessels (Kishiro and Kasuya, 1993), but with increasing speed (Shizuoka Board of Education, 1987). He believed that this decline was compatible with changes in reproductive parameters that one might expect as a result of a density dependent response. Kishiro and Kasuya (1993) concurred with this interpretation and estimated that the Japanese drive fishery had depleted the coastal stocks of striped dolphins to less than 10% of their post-World War II level.

Kasuya and Kishiro (1995) examined the catch statistics of the Taiji dolphin fisheries in the context of possible environmental factors. They found no correlation between variation in catches and variation in the Kuroshio Current or squid landings off the Wakayama Prefecture. However, they did find a statistically significant decline in the catch of striped dolphins (1979-1991) and short-finned pilot whales (1979-1994). The decline could not be explained by the fishing regulations; pilot whale catches rarely, if ever, achieved the catch limits, while no limits were set for striped dolphins during the period. The catch of striped dolphins decreased from over 12,000 in 1979 to below 1,000 since 1990. Thus, there is clear evidence that the availability of striped dolphins to the Taiji fishery has declined.

Miyashita (1993) estimated the abundance of striped dolphins for the three geographical concentrations in the western North Pacific (Fig. 2) using sighting data obtained during August and September from 1982-1996. The estimates were 497,725 (CV=0.179) individuals for the northern offshore concentration (32°-42°N, 145°E-180°), 52,682 (CV = 0.952) for the southern offshore concentration (23°-30°N, 127°E-180), and 19,631 (CV=0.696) for the inshore area (coastal waters north of 30°N and west of 145°E). The boundary for the estimation was placed for calculation purposes at the middle of the density hiatus, and the inshore area included vacant coastal waters north of the Izu ground; the author left open the question as to whether the population exploited by the Izu fishery was included in this estimate. It can be seen that the confidence intervals for the inshore and southern offshore areas are very large.

The above estimates were made during the peak of the summer migration of striped dolphins: this was not unreasonable because surveys were undertaken in favourable weather conditions and bias associated with seasonal movements was minimised. However, it left an important question unanswered. Where is the summering ground of the individuals that migrate to the fishing grounds during the winter season?

DISCUSSION

Trends in catch and striped dolphin availability

The dolphin fishery on the Izu coast has existed since at least the 17th century and appears to have exploited striped dolphins since at least the late 19th century. In addition to the observed decline in catches over time, two other historical trends can be seen. One is the decrease in the number of operating fisheries (the expansion of fisheries during and after the World War II was followed by rapid decline) and the other is the expansion of the operating area from the coast to outside the Sagami Bay.

A greater than 10-fold decline in the catch off the Izu coast occurred from 1961-1983, and the fishery almost collapsed. The trend did not change even for the 1968-1983 period when two drive teams co-operated, using four searching vessels that were continuously improved in speed. It is clear that the availability of striped dolphins to the fishery must have declined to $<10\%$ of original during the period.

In terms of explanations for this decline in availability, changes in the migration pattern of striped dolphins due to oceanographic changes or declines in food availability appear unlikely, because: (1) there have been no identified oceanographic changes extending for 30 years (Miyazaki, 1983; Kasuya and Miyashita, 1988); (2) striped dolphins off the Izu coast appear to be generalist feeders that do not appear to consume prey of high economic value (see *Feeding*); and (3) the age at sexual maturity has changed in a way one might expect of a population with improved nutrition (see *Sexual maturation of females*).

The importation of Dall's porpoises products from northern Japan to Kanagawa, Shizuoka, and Yamanashi Prefectures, where striped dolphins from Izu fishery were consumed, occurred in the 1970s (Kasuya and Miyashita, 1989). The total Japanese catch of Dall's porpoises and striped dolphins ranged between 10,000 and 15,000 during the early 1970s (Kasuya, 1982), near the level of the striped dolphin catch in the 1960s. It appears that the importation of Dall's porpoise products did not saturate the market for the

Izu fishery. However, this does not preclude the possibility that if Dall's porpoises had not been supplied to consumers, the price of striped dolphins might have been higher, leading to higher catches in the Izu fishery with more severe consequences for the striped dolphin population(s) exploited there.

The first dolphin drive team in Taiji began to take striped dolphins in 1973; a second team began in 1979. The maximum catch (> 12,000) occurred in 1980. The two drive teams merged in 1982, retaining the same fleet of 15 vessels (later it decreased to 14). The catch of striped dolphins showed a significant decline between 1980 and 1991 (from *ca* 12,000 to < 1,000) before a quota was set for the fishery (Kasuya and Kishiro, 1995). This decline occurred while the actual number of vessels used for daily searching almost doubled. Therefore, the availability of striped dolphins to the Taiji fishery as well as the Izu fishery must have declined after 1980.

Indices of abundance

Following suggestions by the IWC Scientific Committee (IWC, 1993), the Government of Japan collected daily operation records for the drive fisheries at Taiji and Izu, i.e. the number of searching vessels, searching hours, number of dolphin schools and individuals sighted, and dolphins actually taken (Kishiro and Kasuya, 1993). The low sighting rate makes analysis of the data from the Izu fishery difficult. Two difficulties with the use of such data for the Taiji fishery can be identified as discussed below.

The first reason lies in the nature of sighting rates. The number of dolphin schools/individuals sighted per unit of effort of search is only useful as an index of abundance in the fishing ground if the fishing mode remains constant over the period. However, in the early period of the fishery, almost every sighting was driven and all the individuals killed. This changed after the establishment of catch limits by species in 1993 as some schools were not driven because the animals present were small. In addition, large individuals within a driven school could be selectively killed and remaining individuals released. Finally, some striped dolphin schools might not be driven because the catch limit had been reached, although searching was continuing for other species. Thus, there is a possibility that recent sighting rates might be biassed upwards. In any event, simple comparison of abundance indices before and after 1993 is problematic.

A second problem is the need to quantify the effect of informer vessels that sell sightings information to the drive team. After Kawana ceased operations in 1984, Futo fishermen paid 3% of the profit to Kawana fishermen for sighting information that led to a successful drive (Nakamura, 1988). In Taiji, the drive team buys sighting information from other fishing vessels. The price seems to have been high since 1988, when competition with small-type whaling vessels resumed. Although this practice has probably occurred throughout the period of drive fisheries, the difficulty lies in quantifying its changing role over time.

Catch limits and inspection system

The current Japanese catch limit for the drive fishery is expressed as the maximum number of individuals to be killed by the fishery, and the catches are sold by weight. In addition, for Taiji the prefectural permit requests that 'whales' below 2m are released, although there is some confusion as to whether the striped dolphin is classified as a 'whale'. Irrespective of this, there are good economic reasons for the fishermen to select large individuals now that catch limits are in force. Unlike previous practice, it is now common for a greater number of striped dolphins to be driven than are to be landed; larger animals are killed and smaller ones released. If, as the author has observed, juveniles die in the enclosure 'naturally' they are discarded and not considered as part of the catch. Even if released alive, it seems likely that their probability of survival will decrease to an unknown degree.

This is suggested by *inter alia* the fact that the striped dolphin is known to be a difficult species to maintain in captivity. Attempts by aquariums to keep animals alive after transporting them from drives have all failed, although this method did not significantly affect survival of bottlenose dolphins. This explains the absence of striped dolphins in Japanese aquaria (Kasuya *et al.*, 1984). Similarly, of 11 striped dolphins (mostly adults) obtained from drives for radio tracking experiments, three had dummy radio-tags attached. Despite the attendance of aquarium personnel, all died in pens within 15 days of the drive, although some of them had started to feed. Subsequent necropsy revealed symptoms of stress, but it was not possible to determine if irreversible physiological changes had begun during the drive (Dr. T. Kotani and F. Hashimoto, September 1997, pers. comm.).

Given the possible mortality of released animals identified above and the unknown effects of social disruption caused by the selective removal of large animals from schools and the concerns about the status of the stock (e.g. IWC, 1993), it is clear that the manner in which catch limits are set should be reviewed as a matter of some urgency.

Further aspects of catch limits/inspection that warrant further consideration concerns the hand-harpoon fishery for striped dolphins. A total of nearly 150 vessels in Chiba and Wakayama Prefectures are licensed for this fishery even though the catch limit is only 180 animals. Catches can be processed at the sea and are not examined by scientists or inspectors prior to flensing. The potential for unreliable reporting and quota overruns is thus not insignificant.

Stock identity and dolphin movement

Although little is known about the population structure of the striped dolphins exploited in the western North Pacific, there is evidence to suggest that more than one population may be exploited in Japan. Irrespective of genetic mixing levels, the possibility of some degree of site fidelity, particularly at the extremes of the geographical range of a population, can make determination of sustainable catch limits difficult with the possibility of local 'extinction'. Some of the coastal population 'units' involved in the Japanese coastal fisheries may have been hunted to extremely low levels or even local 'extinction'; thus the composition of the population(s) in the fishing grounds may have changed during the long history (> 100yrs) of the fisheries. Northern coastal waters west of 145°E, which are now known to be almost vacant of striped dolphins, may have once been summering grounds for coastal population units depleted by the Izu fishery. The Taiji ground lies to the southwest of the Izu grounds, and the fishery operated mostly from autumn to spring seasons. The available information supports some partial overlap of exploited populations with the Izu fishery.

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A note on cephalopods from the stomachs of Dall's porpoises (*Phocoenoides dalli*) from the Northwestern Pacific and Bering Sea, 1978-1982

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ABSTRACT

Cephalopod prey were identified from the stomachs of 100 Dall's porpoise (*Phocoenoides dalli*) incidentally taken by commercial salmon gillnets and research vessels from 1978 to 1982 in the western North Pacific Ocean and Bering Sea. Eighty-four porpoise were collected in June and July during the salmon fishing season; the remainder were collected in August-September. Seven cephalopod families (Enoploteuthidae, Onychoteuthidae, Gonatidae, Histioteuthidae, Chiroteuthidae, Cranchiidae and Bolitaenidae) were identified in the stomachs. Gonatids were the most abundant, comprising 98% of the beaks. *Gonatopsis borealis* was the most abundant species, occurring in 85 stomachs. The gonatids occur in meso- and epipelagic waters and many approach the surface at night when the porpoise are feeding.

KEYWORDS: DALL'S PORPOISE; SQUID; FOOD/PREY; FEEDING; NORTHERN HEMISPHERE; PACIFIC OCEAN

INTRODUCTION

A cooperative programme between the United States and Japan on the incidental take of Dall's porpoises (*Phocoenoides dalli*) in the Japanese High Seas Salmon fishery was initiated in 1978. As part of this, a study of the feeding habits of the Dall's porpoise was carried out. This paper presents information on the cephalopod portion of stomach contents of Dall's porpoises collected from 1978 through 1982. Crawford (1982) reported on fish remains from the 1978-79 collection ($n = 472$). He noted that cephalopods comprised some 90% of stomach contents by volume.

The salmon mothership fishery area is located in the northwestern North Pacific Ocean from 46-56°N and 168-175°E, and between 56-59°N and about 173°E-175°W north of 56-59°N in the Bering Sea. Surface water temperatures in this sub-Arctic water mass, in June and July, range from 6-9°C in the Pacific and 4-7°C in the Bering Sea (Oceanographic Monthly Summary, 1982). A small number of Dall's porpoises were collected to the southwest of these areas in August and September 1982, between 42-50°N and 158-170°E. Surface water temperatures here were noticeably higher, mostly 14° and 15°C, but the range was between 10° and 17°C (Oceanographic Monthly Summary, 1982).

The oceanography of the region is described by Favorite *et al.* (1976). Jefferts (1988) describes the distribution of the North Pacific epi-and meso-pelagic cephalopods related to water masses.

MATERIALS AND METHODS

When the salmon gillnets were hauled, the dead porpoises were brought aboard and, after being weighed and measured, the stomachs were removed and usually preserved by freezing for later examination (28 taken in 1978 were preserved in formalin). Most stomachs were frozen upon removal and transported to the National Marine Mammal Laboratory (NMML), Northwest and Alaska Fisheries Center, NMFS, Seattle, Washington.

For a complete description of the methods used for examining Dall's porpoise stomachs, see Crawford[2] (1982). Stomachs were thawed and the contents removed, then weighed and the volume determined by water displacement. Through a process of water flushing and sieving through graduated screens, the material was cleaned and sorted, then stored in 50% isopropyl alcohol (Treacy and Crawford, 1981; Crawford, 1982). Fish and cephalopod remains were separated at this time. Otoliths and statoliths were stored dry.

Cephalopod remains were initially sorted into fleshy parts (bodies and crowns), buccal masses and upper and lower beaks. Beaks were then sorted into recognisable categories preliminary to final designation. Most identifications were based on the examination of lower beaks, as the bodies and crowns in most instances lacked the tentacle and arm components necessary for identification.

The major identification problem encountered during this study was the lack of suckers and hooks on arms and tentacles, and in most instances absence of tentacles other than stubs. The major cause of this is probably related to length of time (12-24 hours) between entanglement and dissection of the porpoise. However, another factor which may have contributed to the lack of hooks and suckers on remnants of arms and tentacles is the method used to separate stomach contents. Although washing stomach contents through a sieve may not be a problem with fish remains and otoliths/statoliths, it may contribute to the absence (i.e. destruction) of features needed to identify cephalopod specimens. For future studies, therefore, we recommend that cephalopod bodies and crowns be carefully removed and cleaned prior to or as the stomach contents undergo the initial flushing, to preserve any remaining suckers and hooks on the arms and tentacles.

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[2] T.W. Crawford made the original examination of the Dall's porpoise stomachs collected in 1978-79 and, with the assistance of L. Tsunoda, those collected through 1982.

The identification of beaks was made through comparison with identified specimens in the NMML voucher collection and through the use of keys and descriptive material (Akimuskin, 1963; Panina, 1966; Iverson and Pinkas, 1971; Clarke, 1980; 1986).

The size of the squid portion of the stomach contents collection precluded examination of the entire collection and a sub-sample was selected. We asked the investigators who did the initial separation of squid from the fish samples, to set aside the few relatively intact squid for us, otherwise the sub-sample was randomly selected making sure samples came from each area.

Distribution of samples examined from the fishery by year was: 1978 (26), 1979 (11), 1980 (1), 1981 (19), and 1982 (17). In addition, the stomachs of 25 *dalli*-type and 1 *truei*-type of Dall's porpoise collected by T. Kasuya during an August/September 1982 Japanese research cruise were examined. In all, the cephalopod portion of the contents of 100 stomachs were examined and are reported on in this paper.

RESULTS

The samples examined were from four localities (Fig. 1; Table 1). The Western North Pacific (WNP) sample was taken from 21 August to 10 September 1982. The cephalopod stomach contents of the one *truei*-type porpoise taken in the WNP did not differ significantly from the contents of the 25 *dalli*-type porpoises and is not treated separately. Two of the remaining localities were located within the US Fisheries Conservation Zone (US FCZ) and sampling dates are based on when each locality opened for fishing. The Southern North Pacific (SNP) opened on 1 June and the Central Western Aleutians (CWA) on 10 June. Little fishing effort occurs in the SNP area after the main fishing area (CWA) opens. The remaining location is the southern Bering Sea (SBS) which opened on 25 June. Samples from these three localities were all taken in June and July, 1978-1982.

The cephalopod fauna of the region is well documented (Kodolov, 1970; Nesis, 1973; 1987; Ogi, 1980; Bublitz, 1981; Kubodera and Okutani, 1981a, b; Fiscus and Mercer, 1982; Kubodera and Jefferts, 1984a; b; Jefferts, 1988; Okutani *et al.*, 1988 and Okutani and Nemoto, 1964).

In addition to the cited publications, we were fortunate to have specimens collected in or adjacent to the fishery area by Roger Mercer (Resource Assessment and Conservation Engineering Division, Northwest and Alaska Fisheries Center, National Marine Fisheries Service, Seattle, Washington) in July 1982. Mercer fished six deep midwater trawl stations. The specimens were identified by Drs. K. Jefferts and T. Kubodera, and the first author. Of particular importance to the present project was the acquisition of seven species of gonatids (three new to the NMML collection) from these stations.

The family Gonatidae dominates the cephalopod fauna of epi- and meso-pelagic waters in the subArctic Pacific and Bering Sea (Okutani *et al.*, 1988).

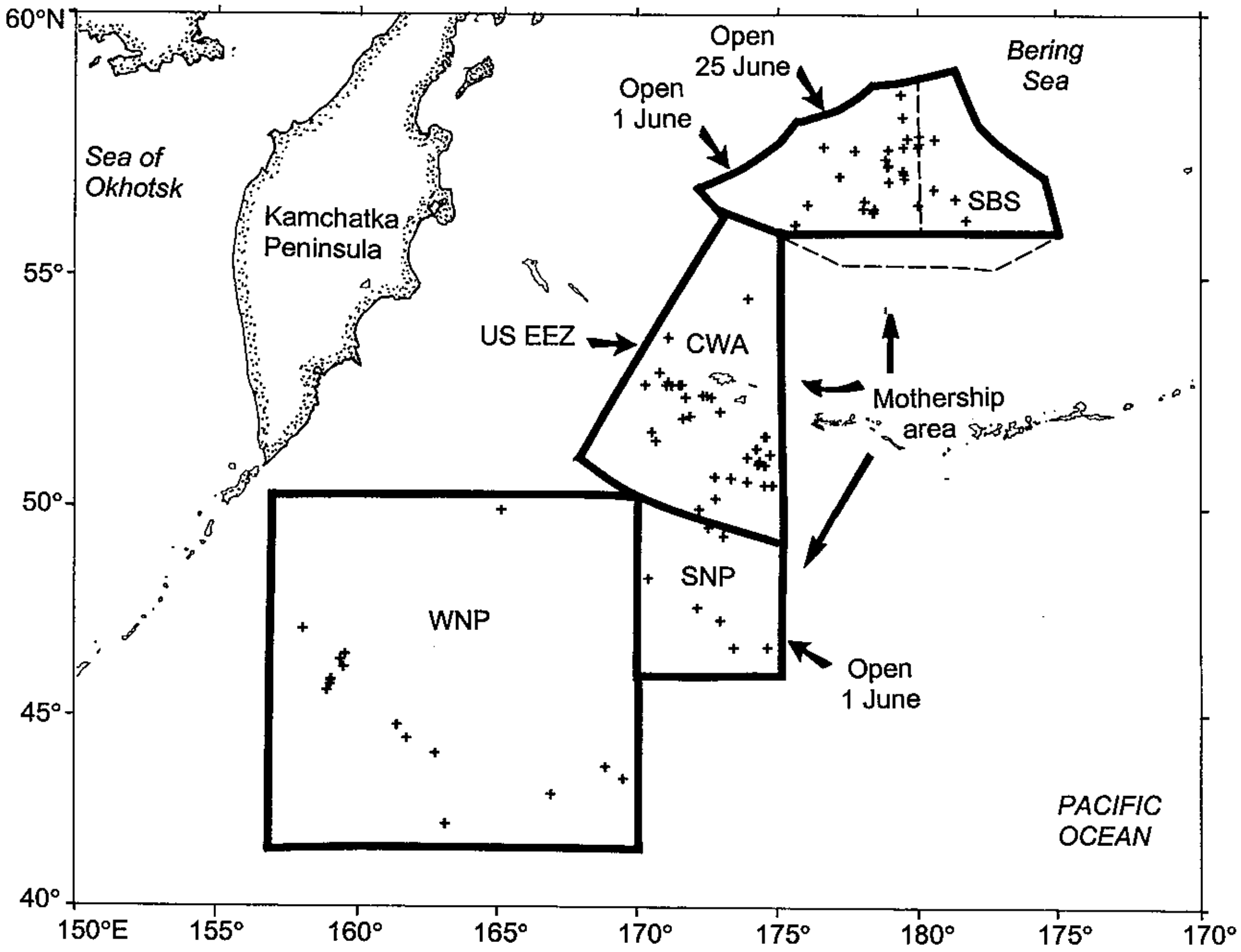

Fig. 1. Approximate locations where Dall's porpoise (*Phocoenoides dalli*) were taken in the Japanese high seas salmon gillnet fishery and by a Japanese research vessel in the North Pacific Ocean and Bering Sea 1978-1982, from which cephalopod prey were identified. The four localities are: WNP = Western North Pacific (26 stomachs); SNP = Southern North Pacific (7 stomachs); CWA = Central Western Aleutians (35 stomachs); SBS = Southern Bering Sea (32 stomachs).

Table 1

Cephalopods from the stomachs of Dall's porpoise (*Phocoenoides dalli*) taken in the Japanese high seas salmon gillnet fishery and by a Japanese research vessel in the western North Pacific Ocean.

	Western N. Pacific $n = 26$[1]		Southern N. Pacific $n = 7$		Central western Aleutians $n = 35$		Southern Bering Sea $n = 32$		All four localities totals $n = 100$		
									Occ.	Bks.	
Cephalopods	Occ.[2]	Bks.[3]	Occ.	Bks.	Occ.	Bks.	Occ.	Bks.	%	No.	%
Enoploteuthidae											
Abraliopsis sp.	13	33							13	33	.4
Onychoteuthidae											
Onychoteuthis borealijaponicus	4	13							4	13	0.2
Gonatidae	7	166			3	54	3	44	13	264	3.5
Gonatus berryi	20	177	4	7	25	506	22	299	71	929	12.3
Gonatus onyx			2	6	4	74	7	41	13	121	1.6
Gonatus pyros	22	660	7	52	27	388	22	349	78	1,449	19.2
Gonatus madokai					4	5			4	5	0.1
Gonatus middenorffi	2	4			12	28	8	11	22	43	0.5
Gonatus spp.	7	34	3	23	22	472	17	128	49	657	8.7
Eogonatus tinro	16	55	6	16	20	112	22	205	64	388	5.1
Gonatopsis borealis	20	267	5	51	29	901	31	781	85	2,000	26.6
Gon/Berry	12	184	2	6	19	681	9	444	42	1,315	17.4
Berryteuthis magister					1	1	1	10	2	11	0.1
Berryteuthis anonychus	1	1	2	3	6	26	10	154	19	184	2.4
Histioteuthidae											
Histioteuthis sp.			1	1					1	1	<.1
Chiroteuthidae											
Chiroteuthis sp.					1	1			1	1	<.1
Chranchiidae			2	3					2	3	<.1
Galiteuthis sp.							2	2	2	2	<.1
Taonius sp.	1	1	1	5	12	63	6	18	20	87	1.1
Bolitaenidae											
Japetella sp.					1	1			1	1	<.1
Unidentified squids	2	8	1	2	2	2	1	1	6	13	0.2

[1] n = number of stomachs examined. [2] Occ. = number of occurrences in stomachs. [3] Bks = total lower beaks found in all stomachs per locality.

Kubodera and Jefferts (1984a; b), reporting on catches of primarily larval and juvenile cephalopods in the northern North Pacific and Bering Sea, found that the family made up 93% of the catch in the western sector of the North Pacific, 50% in the eastern sector and 99% in the Bering Sea. Based on total lower beaks counted in all stomachs examined (Table 1), gonatids comprised 96% of the cephalopods from the WNP sample, 94% of the SNP, 98% of the CWA and 99% of the SBS samples. These values are in reasonable agreement with gonatid catches for the western North Pacific and Bering Sea sectors of Kubodera and Jefferts (1984a; b) where gonatids comprised 93% and 99% of the catch respectively.

The family Gonatidae contains four Genera (Clarke, 1986; Okutani *et al.*, 1988): *Gonatus* with 10 species, six of which are found in the area; *Eogonatus* with one species; *Gonatopsis* with five described species and undescribed species, at least two of which are found in the region; and *Berryteuthis* with two species, both of which are found in the region. Okutani *et al.* (1988) discuss and provide distributional maps of all species.

Species accounts

Enoploteuthidae

***ABRALIOPSIS* SP.**

This species was found only in the stomachs of porpoises taken in late summer in the WNP (Table 1). Thirteen of the 26 stomachs examined contained *Abraliopsis*. No identifiable body fragments were found; the beaks most closely resembled those of *Abraliopsis felis*. Nesis (1987) recorded *A. felis* from Baja California and Washington, in the northeastern Pacific westward to the area east of Japan and the Kurile Islands.

Onychoteuthidae

***ONYCHOTEUTHIS BOREALIJAPONICUS* (OKADA, 1927)**

This species was only found in four stomachs including that of 1 *truei*-type porpoise, from the WNP in August-September. The largest specimen, taken on 22 August 1982, had a gladius length (which approximates mantle length, ML) of 155mm, and a lower rostral length (LRL) of 4mm. Beaks of other specimens were no larger. These specimens represented immature squids. Most maturing *O. borealijaponicus* (MLs of 290mm+) were probably north of these latitudes at this season (Naito *et al.*, 1977a; Fiscus and Mercer, 1982).

Gonatidae

A number of beaks could be recognised only as gonatids. There were seven porpoise stomachs with Gonatid beaks in the WNP, 3 in the CWA and 3 in the SBS.

***GONATUS BERRYI* (NAEF, 1923)**

G. berryi beaks were found in stomachs of *P. dalli* from all four localities: WNP-20; SNP-4; CWA-25; and SBS-22.

This species has been reported from the fishery area by Kubodera and Okutani (1981b), Jefferts (1983), and Kubodera and Jefferts (1984a; b). Nesis (1987) recorded *G. berryi* from the northern shelf slope in the Bering Sea to the southern Kuriles. Bublitz (1981) records this species from the eastern Bering Sea.

GONATUS ONYX (YOUNG, 1972)

This species was found in stomachs from three localities: SNP-2; CWA-4; and SBS-7. Kubodera and Jefferts (1984a; b) reported *G. onyx* across the northern North Pacific and into the Bering and Okhotsk Seas. Both Jefferts (1983) and Roper and Young (1975) reported it most frequently from depths less than 800m at night (it is known to approach the surface at night). *G. onyx* may have occurred more frequently in the stomachs than indicated, as the beaks at some growth stages can be confused with other species of *Gonatus*.

GONATUS PYROS (YOUNG, 1972)

Beaks of this species were found in stomachs from all four localities: WNP-22; SNP-7; CWA-27; and SBS-22. One relatively intact specimen was taken in the SNP. The species has been reported from the US FCZ by Jefferts (1983). Although Kubodera and Jefferts (1984a; b) reported a westernmost limit of about 174°E, our samples were from as far west as 155°E. Nesis (1987) reports *G. pyros* from the central Bering Sea to eastern Honshu, Japan, and eastward to California in mesopelagic and lower epipelagic waters.

GONATUS MADOKAI (KUBODERA AND OKUTANI, 1977)

G. madokai beaks were only found in four stomachs from the CWA. This species is reported across the northern North Pacific and into the Bering and Okhotsk Sea (Kubodera and Jefferts, 1984a; b). Kubodera and Okutani (1981a) reported a catch of only 50 (8-72mm in size) *G. madokai* in surface tows compared to 500 *G. middendorffi*. Okutani *et al.* (1988) mentioned that *G. madokai* is most abundant at depths of 150-200m at night whereas *G. middendorffi* is regularly taken in near surface tows at night. It would appear that *G. madokai* is probably mesopelagic in the adult stage whereas *G. middendorffi* is an epipelagic species.

GONATUS MIDDENDORFFI (KUBODERA AND OKUTANI, 1981B)

The beaks of this species were found in stomachs from three areas: WNP-2; CWA-12; and SBS-8. None were found in the seven porpoises from the SNP area in early June. Kubodera and Jefferts (1984a; b) reported the species from the western North Pacific and Bering Sea. Fiscus and Mercer (1982) reported three adult *G. middendorffi* taken in surface gillnets from the fishery area. T. Kubodera (pers. comm. March 1983) mentioned that this species is much more abundant in North Pacific waters than is *G. madokai*. Nesis (1987) lists this species as *G. kamtschaticus* (Middendorff 1849).

GONATUS SPP

Beaks, identifiable only as *Gonatus*, were found in stomachs from all localities: WNP-7; SNP-3; CWA-22; and SBS-17. Some of these beaks may represent different stages of beaks from species already discussed and some may represent beaks of unknown or undescribed *Gonatus* sp.

EOGONATUS TINRO (NESIS, 1972)

Beaks of this species were found in stomachs from all four localities: WNP-16; SNP-6; CWA-20; and SBS-22. Body and crown fragments of three were taken from one *P. dalli* stomach from the SNP. *E. tinro* has been reported from the eastern Bering Sea by Bublitz (1981). The three specimens in the NMML collection were taken by Mercer, two from the SBS and one from the northern North Pacific. Nesis (1987) lists this genus as a subgenus in the genus *Gonatus*, distributed from the northern slope of the Bering Sea to the Okhotsk Sea and from the Kurile Islands and British Columbia.

GONATOPSIS BOREALIS (SASAKI, 1923)

This was the most frequently occurring species in the samples. It was identified in 85 of the 100 stomachs examined and in all four localities

The bodies and crowns (head with attached arms) of *G. borealis* apparently resist the digestive juices of marine mammal stomachs to a greater degree than other gonatids. Hence bodies, body fragments and crowns of this species persist in the stomachs long after the fragments and crowns of other gonatids have been digested.

MLs were obtained from 22 relatively intact specimens which ranged in size from 85 to 200mm. LRL measurements were taken from 27 beaks. A comparison of these measurements with beaks of *G. borealis* in the NMML collection, suggests that the squid ranged from about 140 to 265mm ML. Kubodera *et al.* (1983) reported that this species was numerically the third most abundant (20%) taken in surface gillnets in the subArctic Pacific, behind *Ommastrephes bartrami* (about 46%) and *O. borealijaponicus* (33%). They reported that the MLs of *G. borealis* taken in surface gillnets in June and July ranged in size from 130-260mm. This does not differ greatly from the measurements of specimens found in the Dall's porpoise.

'GON/BERRY'

Beaks in this category exhibit characteristics of *G. borealis* and the two *Berryteuthis* species and cannot be separated to species. The category was found in 42 stomachs from all four localities. Many of the beaks were very small.

BERRYTEUTHIS MAGISTER (BERRY, 1913)

Eleven specimens were identified during the present study. One on 20 June 1978 south of Attu Island (CWA) and ten from a single porpoise taken on 9 July 1982 from the SBS.

Larval and juvenile specimens have been taken in surface and near surface tows (Kubodera and Okutani, 1981b; Kubodera and Jefferts, 1984a; b), and from the stomachs of *Uria lomvia* (thick-billed murre) taken in the Japanese high seas salmon fishery gillnets (Ogi, 1980). Kubodera *et al.* (1983) reported that this species (mature or maturing) was rarely caught in surface gillnets, noting that it occurred in 16 stations (49 squids) from May to July in the years 1977-81. Fiscus and Mercer (1982) reported only one male taken in August 1971 (ML 152mm) in surface gillnet catches.

Naito *et al.* (1977a) reported this species as abundant around Attu Island in the western Aleutian Islands where its spawning ground is located on the slope in 200 to 500m. The spawning season occurs from June to October.

B. magister probably settles to the bottom at about the 55-80mm size range. Okutani *et al.* (1988) citing Naito *et al.* (1977b) used the figure < 100mm. One of us (CHF) took 42 specimens (55-363mm ML) in two bottom trawls on the eastern Bering Sea shelf on 26 June 1973 at a depth of 292m; 26 of the specimens were less than 100mm ML. Naito *et al.* (1977b) reported that commercially taken *B. magister* off Attu ranged in size as follows: males 195-265mm ML; females 235-335mm ML.

The species, because of its habit of settling to the bottom at a relatively small size, is available for only a short time to *P. dalli* which appear to be feeding in the epipelagic water layer in these localities in June and July.

BERRYTEUTHIS ANONYCHUS (PEARCY AND VOSS, 1963)

This species was identified from stomachs taken in all four localities, although occurrence was low except in the Bering Sea: WNP-1; SNP-2; CWA-6; and SBS-10. It probably occurred more frequently, however, as it is very difficult to separate small beaks of *G. borealis* and *B. magister* from beaks of this species. Identification of *B. anonychus* beaks is based on the size at which the beak wing darkens. Maturing specimens (ML of about 80mm) can be easily separated from similarly sized *G. borealis* and *B. magister*. If the beak wing is lost, which often happens because of its fragility, then the beak is relegated to the 'Gon/Berry' category. Mercer obtained numerous specimens of this species from a trawl station west of the SBS locality on 25 July, 1982. The species has been reported throughout the four localities sampled (Kubodera and Okutani, 1981b; Kubodera and Jefferts, 1984a; b).

Histioteuthidae

HISTIOTEUTHIS SP.

One lower beak of a ?*Histioteuthis* was identified in a stomach taken in the SNP, on 17 June 1978. Voss (1969) lists six species of the genus from the North Pacific. Akimuskin (1963) mentions that *H. (Stigmatoteuthis) dofleini* probably approaches the surface at night. Kodolov (1970) reported 2 ?*Histioteuthis* sp. taken in Aleutian waters. This beak is a good match to the immature *H. dofleini* beak illustrated in Clarke (1986, fig. 66, p.137), and compares favourably with several mature *H. dofleini* beaks in the NMML collection. It represents the first record of *Histioteuthis* from the stomach of a *P. dalli*.

Chiroteuthidae

CHIROTEUTHIS SP.

One lower beak (*Chiroteuthis* sp.) was identified in the stomach of a porpoise taken in the CWA on 21 June 1978. The beak, based on an LRL of 4.8mm, was from an adult or nearly adult squid. Kodolov (1970) lists *Chiroteuthis veranyi* (*veranyi* not presently used for Pacific species) from the stomachs of sperm whales taken in the vicinity of the western Aleutians. Fiscus and Mercer (1982) reported one *Chiroteuthis* sp. taken in a surface gillnet on 27 March 1968 (49° 46'N, 176° 29'W). Roper and Young (1975) reported an upward movement of this species at night. Jefferts (1988) listed *Chiroteuthis calyx* as a holo-subArctic species. The beak reported here represents the first occurrence of this species identified from the stomach of *P. dalli*.

Cranchiidae

Cranchiid gladii were identified in the stomachs of 2 *P. dalli* from the SNP. The largest gladius, which measured 376mm in length, was from the stomach of a porpoise taken on 17 June 1978. Two gladii (one incomplete, the other 284mm) were found in the stomach of another porpoise taken nearby on the same day, as were the beaks of 5 *Taonius* sp.

GALITEUTHIS SP.

One pair of *Galiteuthis* sp. beaks was found in the stomach of an animal taken in the SBS on 12 July 1981. The lower beak (LRL 6mm) represented a mature squid. A dorsal beak, *Galiteuthis* sp.?, was found in a stomach from the SBS on 17 July 1981. Both Okutani and Nemoto (1964) and Jefferts (1983) reported *Galiteuthis* from the US FCZ; the former from the stomach of a sperm whale and the latter from sampling nets. Mercer took two *G. phyllura* in a haul on 27 July 1982 just north of the western Aleutian Islands. The *Galiteuthis* beaks found in the Dall's porpoise were probably *G. phyllura*. They represent the first record of the genus from *P. dalli* stomachs.

TAONIUS SP.

Taonius sp. beaks were identified from the stomachs of 20 animals: WNP-1; SNP-1; CWA-12; SBS-6. Okutani and Nemoto (1964) from the stomachs of sperm whales and Jefferts (1983) from sampling nets, report *T. pavo* from the vicinity of the western Aleutian Islands and in the North Pacific south of the Aleutians. Mercer caught *T. pavo* in two midwater trawl sets north of the western Aleutian Islands, in 1982. These *Taonius* beaks from the *P. dalli* stomachs are most likely *T. pavo*. Although a cranchiid is listed from the stomach of a Dall's porpoise taken off California (Kajimura *et al.*, 1980), the present beaks represent the first record of *Taonius* sp. identified from *P. dalli* stomachs.

Bolitaenidae

JAPETELLA SP.

A pair of *Japetella* sp. beaks were identified from the stomach of a *P. dalli* taken on 14 June 1978 in the CWA. Jefferts (1983) reported *J. heathi* as occurring across the North Pacific Ocean westward to south of the western Aleutian Islands. Fiscus and Mercer (1982) reported an adult *Japetella* taken in a surface gillnet south of the western Aleutian Islands. Akimuskin (1963) reported this species from off the Kurile Islands. Kubodera and Okutani (1981a) reported 8 larval *Japetella* from surface tows. Nesis (1987) refers to this species as *J. diaphana heathi*. This pair of *Japetella* beaks represents the first record of its occurrence in *P. dalli* stomachs.

Unidentified beaks

Thirteen beaks from all four localities could not be identified.

DISCUSSION

There is no evidence that Dall's porpoises can catch and then break up large prey before swallowing it. Therefore the size of its prey is limited to those fish and cephalopods that it can swallow whole. Kajimura *et al.* (1980) and Crawford (1982) described the size and shape of Dall's porpoise prey and list earlier records of prey consumed elsewhere in the North Pacific Ocean and Bering Sea. Fish otoliths were found in all 472 stomachs Crawford examined (average per stomach 386) and he suggested that the volume of fish consumed is underrepresented due to their rapid digestion. He also reported that the contents of the largest stomach that he examined weighed 2.5kg and had a volume of 2,542ml. The largest cephalopods found in stomachs during the present study were two cranchiids represented by gladii measuring 284 and 376mm in length. MLs of *G. borealis*, the most frequently encountered prey, ranged in size from 85-265mm in length.

Surface water temperatures in the SNP and CWA localities in June and July ranged from 6°-9°C and in the SBS from 4° to 7°C but were noticeably higher in the WNP in August and September ranging from 10° to 17°C. *Abraliopsis* and *Onychoteuthis* were identified only in stomachs of *P. dalli* taken in the warmer surface waters of the WNP.

There was no evidence of 'secondary cephalopod contamination' in the stomachs examined, i.e., of cephalopods first being the prey of fish or cephalopods which in turn were eaten by the porpoise.

Cephalopods representing 7 families (Enoploteuthidae, Onychoteuthidae, Gonatidae, Histioteuthidae, Chiroteuthidae, Cranchiidae, and Bolitaenidae) were identified from the examined stomachs. The occurrence of cephalopods, other than Gonatids in the porpoise stomachs was insignificant, comprising only 2% of the total numbers of beaks examined from the stomachs of porpoise taken in all localities.

Thus members of the family Gonatidae contributed significantly to the prey of *P. dalli* in all localities sampled. Most gonatids identified here are inhabitants of the meso- and epipelagic depth zones and many approach the surface at night. Hence they are readily available to Dall's porpoises.

The identification of species in the genus *Gonatus* was based on comparisons of beaks from known voucher specimens in the NMML collection. Differences separating some species are slight and specimens and beaks of all described *Gonatus* and several undescribed species were not available for comparison. It is entirely possible that when more specimens from other species in the genus become available for study, that some changes in species designation and percent of total sample may occur in this group.

G. borealis was identified in 85 of the 100 stomachs examined, ranking first in occurrence and in total count of all beaks examined. Both *B. magister* and *B. anonychus* are probably underrepresented in the samples for reasons mentioned in the results section; however, adult *B. magister*, most of which leave the epipelagic zone at a relatively early age (small size), are probably not readily available to Dall's porpoises.

Abraliopsis and *Onychoteuthis* were only identified in the stomachs from the WNP. These two genera do not normally occur north of the subArctic water boundary. The genera, *Histioteuthis*, *Chiroteuthis*, *Galiteuthis* and *Japetella* probably represent only opportunistic prey in the four localities. *Taonius*, which was found in 20 stomachs, from all localities, may occur in sufficient numbers in the upper mesopelagic and epipelagic zones to form a regular part of the Dall's porpoise diet.

Kuramochi *et al.* (1993) reported on the stomach contents of 32 *dalli*-type porpoises taken from the same areas in 1984-85. They report many of the same genera listed here.

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C. Brooks made the initial sort of cephalopod materials used for this paper; his assistance is gratefully acknowledged. T.W. Crawford was most helpful in locating certain samples. L. Tsunoda provided samples as needed and selected several relatively intact specimens which proved invaluable in species determination. K. Jefferts examined several specimens and provided identifications which greatly facilitated our work. We would like to express our thanks to the personnel of the Japanese high seas salmon mothership fishing fleets for their support throughout this project.

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Examination of the reliability of catch statistics in the Japanese coastal sperm whale fishery[1]

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ABSTRACT

Catch statistics are important for the assessment of whale stocks. The paper reviews earlier questions over the reliability of statistics from the Japanese land based sperm whale fishery, and presents some new information for the periods 1959-65 and 1983-84. The available data suggest that aspects of post-World War II statistics are unreliable to an unknown extent in terms of total numbers, length and sex ratio. The level of unreliability appears to vary by month, year and whaling company. Suggestions for future work to try to determine the likely levels of unreliability are presented. This is important to enable an accurate assessment of the status of North Pacific sperm whales.

KEYWORDS: SPERM WHALE; REGULATIONS; STATISTICS; WHALING-MODERN; PACIFIC OCEAN; SEX RATIO

INTRODUCTION

Catches of sperm whales by Japanese traditional coastal whaling were negligible (Dainihon-Suisankai, 1896) until large-scale exploitation of sperm whales (*Physeter macrocephalus*), using sailing ships and hand harpoons, began off Japan about 1820. It was probably associated with the breeding schools of the southwestern North Pacific stock (see Kasuya and Miyashita, 1988). The fishery declined in the subsequent 30 years, partly due to a decrease in availability throughout the western North Pacific (Tillman and Breiwick, 1983) and partly due to social factors (Davis *et al.*, 1997). Quantitative assessment of changes in the sperm whale population during this period requires further investigation (Whitehead, 1995).

Modern whaling methods (using steam vessels with harpoon cannons) were introduced to the western North Pacific in 1889 by Russian companies. The whaling company, Nippon Enyogyogyo Kaisha, established in Japan in 1899, was the founder of Japanese modern whaling (Akashi, 1910; Tønnessen and Johnsen, 1982). Japanese catches of sperm whales were low before World War II, but increased in the post-war period (Fig. 1).

Official data for Japanese modern coastal whaling are available from 1910; the total take for the period 1910-1988 was about 88,000 sperm whales (e.g. Kasahara, 1950; Kasuya, 1991). However, as discussed below, the reliability of aspects of these data has been questioned.

Earlier assessments of North Pacific sperm whale stocks by the Scientific Committee of the International Whaling Commission (IWC) were unable to address questions regarding the uncertainty in the data (e.g. Cooke *et al.*, 1983a; Shirakihara *et al.*, 1983), making an interpretation of the results problematic (IWC, 1983). An important advance in the assessment process within the IWC Scientific Committee in recent years has been the explicit decision to take uncertainty into account (e.g. see Donovan, 1995). The aim of this study is to examine the available catch data for the Japanese coastal sperm whale fishery and to discuss their reliability. Any future assessment of North Pacific sperm whale stocks (e.g. see IWC, 1997) must take this uncertainty about historic data into account.

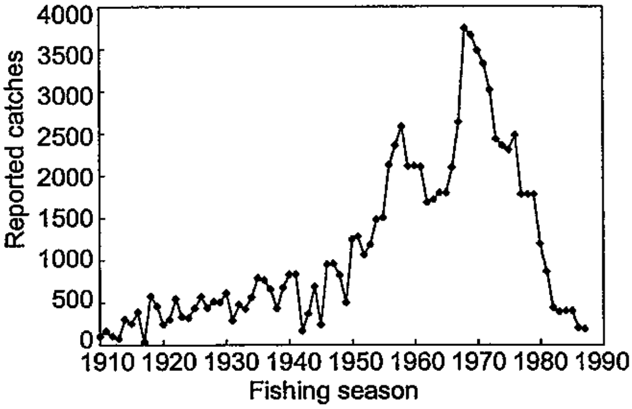

Fig. 1. Official statistics of sperm whales taken by Japanese land based whaling (based on table 1 of Kato, 1996). Regulations in force include minimum length limits (1938-), national catch limits (1959-1966, 1969-1970), agreement by North Pacific whaling countries (1971), IWC limits (1972-) and IWC limits by sex (1973-). The fishery last operated in March 1988.

Previous questions of reliability

Total catches

Tønnessen and Johnsen (1982) reported that considerable differences existed between the catch data published by the Bureau of International Whaling Statistics (BIWS) for the Japanese coastal seasons between 1920-1930 and the records of the Whales Research Institute (WRI) in Tokyo. They presented the correct statistics from the WRI prepared by the late H. Omura, its former director. Table 1 shows the differences in catch totals for each species (over the 10 year period) between the two sets of data. Tønnessen and Johnsen (1982) also commented that the differences for 1911-19 and 1931-40 were 'insignificant'. Gray and right whale statistics present in their table are not analysed here.

A simple comparison of the total catches over the 1920-30 period reveals over-reporting of only 106 sperm whales (2.1%) in the BIWS (Table 1). However, the annual variation is very large for each species, for sperm whales ranging from +277 to –226 in absolute numbers or from +56% to –30% in any one year. Fig. 2 shows the annual percentage of under- or over-reporting by species. There appears to be little pattern, either by species or by year, although significant under-reporting is confined to blue and sperm whales whilst over-reporting occurs for all species. Sei whale catches are over-reported except for 1924-1926.

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[1] A version of this paper was submitted to the IWC Scientific Committee as SC/50/CAWS10.

Table 1

Comparison of Japanese coastal whaling catches (1920-1930) from BIWS and corrected WRI (table 46 of Tønnessen and Johnsen, 1982) data. The percentage difference is the absolute difference (Abs.) expressed as a percentage of the WRI value.

	Blue				Fin				Humpback				Sei				Sperm			
	Catch		Difference		Catch		Difference		Catch		Difference		Catch		Difference		Catch		Difference	
Year	BIWS	WRI	Abs.	%	BIWS	WRI	Abs.	%	BIWS	WRI	Abs.	%	BIWS	WRI	Abs.	%	BIWS	WRI	Abs.	%
1920	35	37	-2	-5.4	438	443	-5	-1.1	83	84	-1	-1.2	393	389	4	1.0	245	251	-6	-2.4
1921	37	53	-16	-30.2	475	470	5	1.1	101	101	0	0.0	477	474	3	0.6	302	301	1	0.3
1922	34	36	-2	-5.6	390	394	-4	-1.0	82	82	0	0.0	391	390	1	0.3	562	567	-5	-0.9
1923	35	35	0	0.0	431	434	-3	-0.7	70	70	0	0.0	488	492	-4	-0.8	364	370	-6	-1.6
1924	33	28	5	17.9	337	342	-5	-1.5	160	156	4	2.6	642	642	0	0.0	336	247	89	36.0
1925	35	31	4	12.9	562	411	151	36.7	230	154	76	49.4	499	491	8	1.6	497	354	143	40.4
1926	36	29	7	24.1	636	408	228	55.9	119	110	9	8.2	568	563	5	0.9	772	495	277	56.0
1927	9	10	-1	-10.0	441	455	-14	-3.1	95	90	5	5.6	531	551	-20	-3.6	450	443	7	1.6
1928	10	16	-6	-37.5	455	417	38	9.1	90	99	-9	-9.1	551	309	242	78.3	482	650	-168	-25.8
1929	16	16	0	0.0	386	386	0	0.0	74	74	0	0.0	364	364	0	0.0	606	606	0	0.0
1930	55	56	-1	-1.8	331	400	-69	-17.3	58	62	-4	-6.5	330	411	-81	-19.7	527	753	-226	-30.0
Total	335	347	-12	-3.5	4,882	4,560	322	7.1	1,162	1,082	80	7.4	5,234	5,076	158	3.1	5,143	5,037	106	2.1

Kasuya and Miyashita (1988) stated their belief that 'significant under-reporting' had occurred in the postwar Japanese coastal sperm whaling operations although they did not have documentary evidence.

Sex ratio in the catch

Questions over the sex ratio of the catches from the Japanese coastal sperm whale fishery were first raised by Gosho (1979), the international observer at the Japanese land stations. He reported a female catch percentage of 67.1% in the 140 animals he observed. He noted that this was very high when compared with the reported value of 19.4% ($n = 1{,}740$) for the entire 1978 season. However, his sample, despite including some animals from each of the five land stations operating in that season and throughout most (20 October 1978 to 1 April 1979) of the season (September 1978 to March 1979), represented only 8% of the total catch, thus precluding any firm conclusions being reached.

More recently, Kasuya and Miyazaki (1997) compared data collected by scientists from the WRI in seven seasons (1959-1965) with corresponding statistics from the Japan Whaling Association (JWA). The latter were the basis for the government statistics reported to the BIWS. At that time, national regulations did not allocate catch limits by gender. The authors found that the percentage of females in the WRI sample was around 67% ($n = 5{,}287$) whereas it was only about 52% ($n = 13{,}185$) in the JWA statistics. Earlier analyses (Kasuya and Miyashita, 1988; Kasuya, 1991) found a similar pattern but used smaller data sets.

Catches of sperm whales by small-type whalers

Balcomb and Goebel (1977) reported that the owner of a small-type whaling company taking Baird's beaked whales believed that published records for that species were too high and that this 'may be due to the inclusion of other species in the records'. Statistics for Baird's beaked whales were presented for the 1965-1975 seasons. Kasuya (1995) reported that a past custom of Baird's beaked whale hunters was to report a catch of several sperm whales as one Baird's beaked whale. His belief was that, unless such a misallocation of species occurred, companies could not have continued reporting an annual take of 100-300 Baird's beaked whales for nearly 22 years (1950-1971) from an apparently small stock of the species (Miyashita, 1986; Miyashita and Kato, 1993). The rationale for this misallocation is unknown. It is unlikely to have occurred for product conversion reasons as it would require several Baird's whales to equal the products of a single sperm whale.

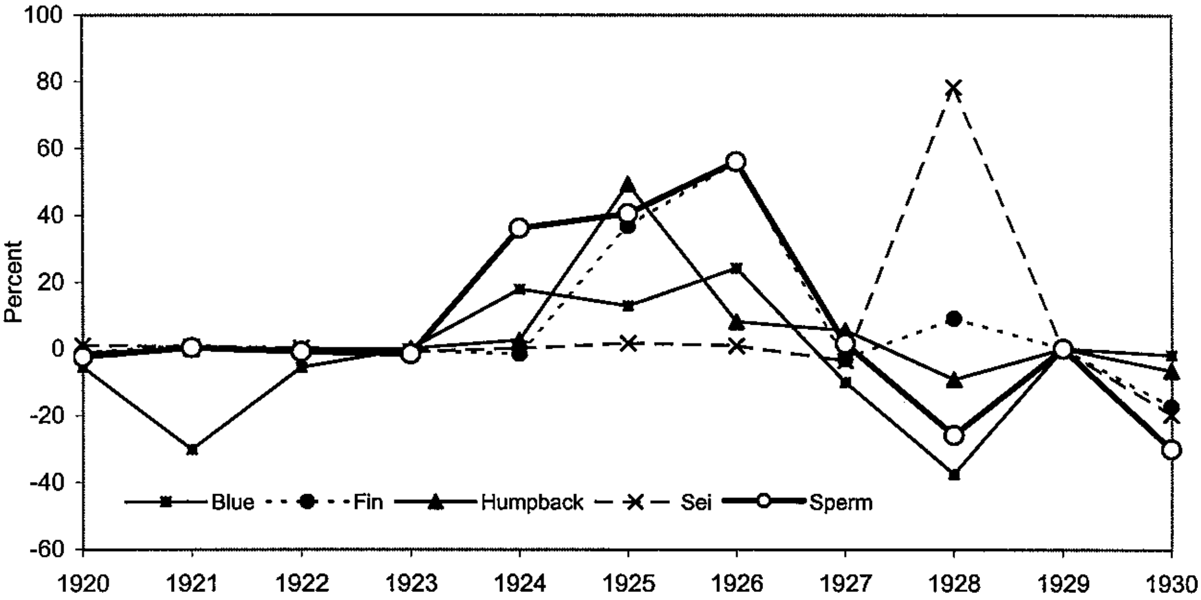

Fig. 2. Annual percentage of over- or under-reporting by species (see text).

An alternative explanation is that the aim was to hide illegal catches of sperm whales.

Kasuya and Miyazaki (1997) reported that a gunner from a small-type whaling company had stated that the company had illegally killed 50-100 sperm whales per year until the middle of the 1970s. The total extent of any illegal sperm whale catches by small-type whalers (around 10 vessels since the 1960s) is unknown.

Length data

Certain authors, including Allen (1980) and Cooke *et al.* (1983b), examining statistics from the North Pacific sperm whale fishery, observed a knife edge distribution of body lengths near the minimum size limit, and questioned the accuracy of these statistics. This distribution of body length implies that either: (1) the gunners were extremely good at estimating lengths at sea; (2) whales near but below the minimum size limit were 'stretched' (Best, 1989) or discarded (see below); or (3) all length data were fabricated.

Discarding of small animals

Watase (1995) reported the existence of some pelagic operations where the number of whales killed exceeded the processing capacity of the whaling vessel, and where smaller whales were later discarded before towing to the factory ship. This may reflect the high level of inspection on the factory ships. The likelihood of such a situation arising in coastal whaling is lower, given the generally lower level of inspection (see below).

Whales accompanied by calves

International whaling regulations prohibit the taking of whales accompanied by calves (e.g. see Donovan, 1992). Evidence to suggest that this regulation was sometimes broken can be found by examining the mammary glands to determine whether the animal was lactating[2]. For the 1983/84 coastal season, Kasuya (1986) reported discrepancies between the proportions of the various reproductive classes reported by the industry when compared to those he obtained directly. In particular, the proportion of lactating females was higher for his data. He suggested that this might reflect the ability of biologists to collect more accurate data than non-biologists, a feature also reported by Best (1984).

MATERIALS AND METHODS

Information collected by scientists, 1959-65

Data and biological samples were collected by scientists from the WRI (including the author) working at the land stations of five Japanese whaling companies under a contract with the Japanese Fisheries Agency, during the whaling seasons 1959-1965. The aim of the programme was to maximise sample size, geographical coverage and species of whale caught. Full coverage was impossible given that the number of scientists was less than the number of whaling stations. It is not clear how a particular whaling station was selected for sampling if several stations nearby were also processing their catches at the same time. Tables 2-4 (pp. 112-13) summarise information on the monthly number of sperm whales by sex examined by WRI scientists[3] (Whales Research Institute, 1961-1966) and the corresponding figures from the JWA (1961-1966) for the Sanriku (Pacific coasts, 38°-41°N) and Hokkaido (Pacific coasts, 42°-44°N) regions (detailed information is given in the Appendix Tables 1 and 2). Further disaggregation of the data is not possible because under the terms of the agreement with the industry, the names of companies or land stations were not recorded. Similar data are available for other species but are not considered in this paper. The WRI statistics are cited after correction of some simple typing errors. The analysis has been restricted to those months where the WRI sample represents ≥20% of the JWA sample and where the reported JWA catch is ≥40 whales, with some allowance if either of these criteria is fully satisfied. Although a somewhat arbitrary choice, it is an attempt to restrict the analysis to those months where one might expect the WRI sample to be reasonably representative. Data for the 1959 season (Whales Research Institute, 1960) are of only limited use because they are not available by month and region.

'A-log' data

The A-log data (Table 5, p. 113, and Appendix Table 3) are a daily summary of the catcher boat operations of a single whaling company (referred to here as Company A) recorded by a gunner during his employment. The log appears to cover all the catcher boats of the company that operated in one specific region (where he worked as a gunner), and includes the recorded noon positions of catcher boats and other data (e.g. whale species and the number of whales sighted and taken). Although A-log also contains records of a small number of vessels from other whaling companies, these data were not used in the present study.

The log covers the three seasons 1959-1961; these were the first three years that Japan set a national quota for the land-based sperm whale fishery. The land station used was only identified for catches off Oshima (Appendix Table 3), but these data are not considered further here as the catch of sperm whales in the region was insignificant. It was impossible to determine from the noon positions of catcher boats in the Sanriku and Hokkaido regions which land stations had been used, as most of the five whaling companies (including Company A) had stations in both regions and the whaling ground was situated at an equal distance from them both. Thus, the catches off Sanriku and Hokkaido have been combined as a single unit (Sanriku/Hokkaido) for this paper (Table 5). The number of land stations that have processed sperm whales (Table 5) is three in Sanriku (Kamaishi, Onagawa and Osawa) and two in Hokkaido (Kiritappu and Kushiro).

The tables also include the corresponding values from Company A from the JWA (1960-1962). Not all of the A-log data are suitable for comparative purposes as the author was not always present for complete months. Records for 'incomplete' (<90%) months have been excluded from Table 5 and the analysis. The last month of a season when operations ceased as soon as the catch limit had been reached is included. In principle, one can assume that the A-log data will under-represent true catches; as such they are of potential value in identifying under-reporting errors by the industry.

'B-log'data

'B-log' data are from the records of Company B and should thus provide the true data for sperm whales processed at the Taiji whaling station (Table 6, p. 114) during the two seasons (25 January-14 March 1984, and 24 December 1984-31 March 1985) for which data are available.

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[2] The discovery of a lactating whale in the catch does not necessarily mean that the whale was accompanied by a calf at the time of capture.

[3] Data from the 1959 season (Whales Research Institute, 1960) are not used since it is not available by month and region.

Table 2

Summary of the information given in Appendix 1, tables 1 and 2 showing the percentage of females in the WRI sample (% F (WRI)), the total reported catch given by the JWA (Total) and the total WRI sample size expressed as a percentage of the total JWA value (% WRI). Only months where % WRI ≥ 20 and Total ≥ 40 are shown (see text). **Bold** type indicates JWA figures that are exceeded in the sample taken by the scientists.

Sex	Month	1960	1961	1962	1963	1964	1965	Total	F (%)	P(%)*
Sanriku										
% F (WRI)	Jun.	85.7	66.7	70.0	73.3	0	75.8	65.8	65.8	<0.1
Total	Jun.	99	139	36	54	48	59	435	40.9	
% WRI	Jun.	21.2	34.5	27.8	55.6	33.3	55.9	36.3		
% F (WRI)	Jul.		64.0	50.0	62.1	30.8	56.0	54.1	54.1	<0.1
Total	Jul.		51	43	69	40	198	450	33.6	
% WRI	Jul.		49.0	65.1	95.7	65.0	46.0	53.8		
% F (WRI)	Aug.	55.3	73.0	74.1	66.7	29.3	49.3	58.2	58.2	1-0.1
Total	Aug.	107	282	87	171	237	326	1210	50.7	
	Aug.	71.0	13.1	**124.1**	61.4	24.5	42.3	43.1		
% WRI	Sep.	65.7		80.6	56.3		58.6	64.1	64.1	>90
Total	Sep.	170		216	312		236	1425	64.2	
% WRI	Sep.	61.8		16.7	15.4		29.7	18.2		
% F (WRI)	Oct.	84.0			62.5	71.7	75.9	72.7	72.7	50-30
Total	Oct.	38			97	111	206	553	61.7	
% WRI	Oct.	65.8			41.2	41.4	26.2	29.8		
% F (WRI)	Nov.	76.2		78.9				76.8	76.8	<0.1
Total	Nov.	40		79				335	51.6	
% WRI	Nov.	**157.5**		24.1				24.5		
Hokkaido										
% F (WRI)	Jul.		78				53.1	58.9	58.9	<0.1
Total	Jul.		208				73	574	39.5	
% WRI	Jul.		24.0				43.8	16.6		
% F (WRI)	Aug.	39.6	70.1		54.5	21.6		50.3	50.3	<0.1
Total	Aug.	253	297		112	140	66	1023	40.7	
% WRI	Aug.	79.8	59.6		39.3	26.4	27.3	48.4		
% F (WRI)	Sep.	73.8	71.8	76.6	69.3	69.9	72.5	72.9	72.9	<0.1
Total	Sep.	825	548	373	308	483	171	2708	59.3	
% WRI	Sep.	68.4	71.2	71.0	32.8	37.9	80.7	60.6		
% F (WRI)	Oct.	76	80.4	76.9	71.9	78		76.9	76.9	<0.1
Total	Oct.	176	80	395	161	188		1237	61.7	
% WRI	Oct.	56.8	**351.3**	52.7	**106.2**	48.4		70.1		
% F (WRI)	Nov.			81.4				78.5	78.5	<0.1
Total	Nov.			165				475	52	
% WRI	Nov.			26.1				19.6		

* Probability at which two sets of sex ratio data (WRI and JWA) represent a common population (chi-square test).

The total number of sperm whales and their body lengths given in B-log are identical to those reported to the government. However, the author of B-log has cast some doubt on the body lengths included therein as well as suggesting that there were a number of sperm whales processed that were not recorded in the actual log. For the purposes of this paper therefore, only the data on gender in B-log are considered reliable.

Inspection and observation

Any consideration of the reliability of the data referred to above must refer to:

(1) any national and international regulations in force at the time;
(2) any national inspection schemes or international observer schemes in force at the time.

Table 7 (p. 115) summarises the available information for the three data sets considered.

Ohsumi (1980) briefly reviewed the regulations affecting North Pacific sperm whales. A minimum length limit was the first regulatory measure applied to the Japanese sperm whale fishery. It came into effect in June 1938 and prohibited the take of animals less than 9.9m (30ft) in length for land based operations and less than 10.6m (35ft) for pelagic operations (Omura *et al.*, 1942). Although the size limits themselves were altered several times (e.g. the size limit for coastal operations was increased to 35ft (10.6m) in November 1945 (Maeda and Teraoka, 1952)), they continued until the sperm whale fishery closed in March 1988. A Japanese national catch limit for the coastal sperm whale fishery was established in 1959 (at 2,100 individuals per season) and changed several times (including no limits at all in 1967 and 1968) until international limits were set. These first came about as part of an agreement reached by the IWC Commissioners of the North Pacific whaling countries (pelagic operations came under control in 1970 and coastal operation in 1971). In 1972, catch limits were included in the Schedule of the IWC for both coastal and pelagic operations. Catch limits by gender began in 1973 and led to a decrease in catches of females.

Table 3

Summary of information from WRI and JWA pooled over months.

	1960	1961	1962	1963	1964	1965	Total
Sanriku							
M	99	47	56	107	90	160	559
F	199	92	145	185	58	226	905
Total (WRI)	298	139	201	292	148	386	1,464
Total (JWA)	572	851	538	839	810	1,173	4,783
% WRI	52.1	16.3	37.4	34.8	18.3	32.9	30.6
F % (WRI)	66.8	66.2	72.1	63.4	39.2	58.5	61.8
F % (JWA)	38.1	51	60.6	62.3	59.3	47.9	53.2
P(%)*	<0.1	<0.1	1-0.1	80-70	<0.1	1-0.1	<0.1
Hokkaido							
M	304	240	130	102	105	76	957
F	574	698	411	224	207	128	2,242
Total (WRI)	878	938	541	326	312	204	3,199
Total (JWA)	1,472	1,194	1,142	874	989	627	6,298
% WRI	59.6	78.6	47.4	37.3	31.5	32.5	50.8
F % (WRI)	65.4	74.4	76	68.7	66.3	62.7	70.1
F % (JWA)	59.3	56.4	65.1	49.3	37.5	39.8	52.9
P(%)*	1-0.1	<0.1	<0.1	<0.1	<0.1	<0.1	<0.1

*See footnote to Table 2.

RESULTS

Total catch numbers, 1960-1966

Information from WRI data (Tables 2 and 3)

Given the logistical constraints, it is clear that the number of whales examined by WRI scientists must be smaller than numbers of whales processed in the region, or at most equal to them. Clearly, it is not possible for the scientific sample to exceed the total number of whales processed, unless there was incorrect reporting by the companies. Examination of Appendix Tables 1 and 2 reveals that in some months and regions, the WRI sample was greater than the reported catch. The total sperm whale catch in those five months was 386 sperm whales in the JWA statistics while the WRI scientists recorded 663 whales (157 males and 506 females). Assuming that the WRI values are the true figures, then the JWA values represented only 58% of the catch for those months.

There are clearly problems with the data for those months and areas, at least before 1964, and this gives rise to some concern about the overall reliability of the total catch numbers. Several land stations and companies operated at that time, but given the level of disaggregation of the data, it is not possible to determine if the errors can be directly linked to all or a few of these.

Table 5

Summary of A-log and JWA data for those months for which A-log is believed to cover >90% of total (see text) for Sanriku and Hokkaido.

	Baleen				Sperm			
	A-log	JWA	Diff	%	A-log	JWA	Diff	%
1959								
May	82	78	-4	-4.9	30	38	8	26.7
Jul.	55	63	8	14.5	50	57	7	14.0
Aug	18	23	5	27.8	310	358	48	15.5
Sep.	21	40	19	90.5	249	231	-18	-7.2
Oct.	34	45	11	32.4	123	101	-22	-17.9
Nov.	0	0	0		45	19	-26	-57.8
Total	210	249	39	18.6	807	804	-3	-0.4
1960								
Sep.	7	12	5	71.4	416	443	27	6.5
Oct.	7	7	0	0.0	164	75	-89	-54.3
Total	14	19	5	35.7	580	518	-62	-10.7
1961								
Jun.	73	81	8	11.0	35	33	-2	-5.7
Sep.	18	12	-6	-33.3	293	270	-23	-7.8
Oct.	1	1	0	0.0	125	36	-89	-71.2
Nov.	0	0	0		134	27	-107	-79.9
Total	92	94	2	2.2	587	366	-221	-37.6
1959-61								
Total	316	362	46	14.6	1,974	1,688	-286	-14.5

Information from A-log

Table 5 shows reasonably good correlation (±10) between the A-log and JWA data for most months for baleen whales. Where the values were not identical, in all but two cases, the JWA values were slightly higher. The total catch was 316 baleen whales (A-log) and 362 whales (JWA) for these selected months. Table 5 also summarises the WRI and JWA catch data for sperm whales. There were two instances where the JWA data were higher than the A-log data, three instances where they were similar (±10) and seven instances where they were considerably lower. Lower values occurred later in the season, with the degree of apparent under-reporting (expressed as a percentage of the A-log values) increasing from September onwards and from 1959-1961.

The lower values for A-log can probably be attributed to the use of some months with less than 100% coverage, or to some missed vessel records by the gunner. There are a number of possible causes for the higher values in A-log, including: recording errors by the gunner; carry over of catch records to the subsequent month (e.g. sperm whales taken in March 1960 or a day before the season opened seemed to be processed in April); or under-reporting by the company.

Table 4

Summary of information from WRI and JWA pooled over region and years for Sanriku and Hokkaido.

	Apr.	May	Jun.	Jul.	Aug.	Sep.	Oct.	Nov.	Total
WRI									
M	0	19	62	150	464	537	245	39	1,516
F	0	17	104	187	553	1,363	787	136	3,147
Total	0	36	166	337	1,017	1,900	1,032	175	4,663
F%	-	-	62.7	55.5	54.4	71.7	76.3	77.7	67.5
JWA									
M	101	190	378	646	1,203	1,612	686	390	5,206
F	31	171	220	378	1,030	2,521	1,104	420	5,875
Total	132	361	598	1,024	2,233	4,133	1,790	810	11,081
F%	23.5	47.4	36.8	36.9	46.1	61	61.7	51.9	53
% WRI	0	10.0	27.8	32.9	45.5	46.0	57.7	21.6	42.1
P(%)*	-	>90	<0.1	<0.1	<0.1	<0.1	<0.1	<0.1	<0.1

*See footnote to Table 2.

Table 6

Body length composition constructed from individual records in B-log, indicating manipulation of gender of sperm whales at Taiji whaling station during 1984 and 1985 seasons. M: male, F*: female reported as male, F: female reported as female.

Body length	I-III,1984				XII,84-III,85				Total			
(feet)	M	F*	F	Total	M	F*	F	Total	M	F*	F	Total
31	6	6	2	14	12	2	3	17	18	8	5	31
32	5	3	8	7	6	2	15	12	9	2	23	
33	3	5	4	12	13	7	7	27	16	12	11	39
34	6	3	3	12	4	1	3	8	10	4	6	20
35	5	3	3	11	12	6	1	19	17	9	4	30
36	6	2	3	11	7	2	3	12	13	4	6	23
37	3	2	1	6	2	1	5	8	5	3	6	14
38	2	1		3	10	3	1	14	12	4	1	17
39	4		2	6	4		2	6	8	2	2	12
40		1		1	7			7	7	1		8
41	1	1		2	5	1		6	6	2		8
42		1		1	1		1	1	1		2	
43				2			2	2			2	
44				3			3	3			3	
55				1			1	1			1	
61	1			1				1				1
Total	42	28	18	88	90	31	25	146	132	59	43	234
True F%	52.3				38.4				43.6			
Rep. F%	20.5				17.1				18.4			-

Table 7

Summary of regulations and inspection pertinent to the data sets examined in this paper.

Year (s)	Catch limit	Total (JWA figures)	Length limits		National inspection	International observation
1959	2100	2104	Min. length	35ft (10.6m)	Partial	No
1960	2100	2107		10.6m	Partial	No
1961	2100	2101		10.6m	Partial	No
1962	1800	1685		10.6m	Partial	No
1963	1800	1714		10.6m	Partial	No
1964	1800	1800		10.6m	Partial	No
1965	1800	1800		10.6m	Partial	No
1984	400 males*	400	Min: 30ft (9.0m); Max: 45ft (13.6m) March-June incl.		**	8.4% of all sperm whale landings were observed.
1985	400 males*	400	As above		**	

* Although the catch limit for females was zero, a bycatch of not more than 11.5% females (i.e.46) was allowed in recognition of the difficulty in identifying the sex of animals at sea.

** To supplement insufficient coverage by national inspectors, local personnel were allocated the task of observing flensing. They visited the land stations at the invitation of the station masters.

Whilst the first two reasons may be sufficient to explain the differences for baleen whales, it seems clear that for the large differences seen for sperm whales, under-reporting was occurring. One interpretation of the A-log data is that Company A: (1) correctly reported baleen whales throughout most of the period; (2) correctly reported catches of sperm whale in early months; and (3) under-reported[4] sperm whales in the later part of the season. The magnitude of under-reporting appears to increase as a season progresses.

Table 8 represents an attempt to develop a 'corrected' catch series based on the A-log data. If one assumes that the need for under-reporting did not occur until the latter part of the season (September-November), and that the A-log values are correct, then in 1959 the under-reporting for the latter 3-month period is 66 whales (15.8% of A-log), in 1960 it is 83 (13.5%) and in 1961 it is 219 (39.6%). If one wishes to approximate this to the whole season, one approach is to assume that the JWA data are correct data for the May-August period (this is not inconsistent with the available data). Under this assumption the percentage under-reporting for the 1959 season is 7.5%, for 1960 is 8.4% and for 1961 is 21.4%.

Although this assumes that the A-log values are correct, they are in fact underestimates of the true catch to an unknown extent (for example around 10-15% for the pooled baleen whale data discussed above).

Percent females in the catch

Information from WRI data (Tables 2 and 3)

Table 2 presents the WRI and JWA data on the percentage of females in the catch by month and by year, as well as the percentage of the reported JWA total catch observed by the

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[4] The purpose of this paper is to examine the reliability of the available statistics, not to apportion blame. However, for the purposes of determining how much uncertainty one needs to take into account in any catch history dataset, it is worth noting that a senior staff member of a whaling company, who was unaware of the identity of Company A, had agreed that some under-reporting of total catches had occurred in the past. He had suggested the names of three companies who he believed might be the worst offenders; these did not include Company A.

Table 8

Reconstruction of the sperm whale catch data for company A based on the assumptions given in the text for Sanriku and Hokkaido.

Year/month	A-log	JWA	Difference	% under
1959				
May	38	38		
Jun.	7	7		
Jul.	57	57		
Aug.	358	358		
Sep.	249	231	-18	-7.2
Oct.	123	101	-22	-17.9
Nov.	45	19	-26	-57.8
Total (Sep.-Nov.)	417	351	-66	-15.8
Total (all months)	877	811	-66	-7.5
1960				
Apr.	18	18		
May	23	23		
Jun.	51	51		
Jul.	116	116		
Aug.	165	165		
Sep.	416	443	27	6.5
Oct.	164	75	-89	-54.3
Nov.	34	13	-21	-61.8
Total (Sep.-Nov.)	614	531	-83	-13.5
Total (all months)	987	909	-83	-8.4
1961				
Apr.	6	6		
May	37	37		
Jun.	33	33		
Jul.	132	132		
Aug.	261	261		
Sep.	293	270	-23	-7.8
Oct.	125	36	-89	-71.2
Nov.	134	27	-107	-79.9
Total (Sep.-Nov.)	552	333	-219	-39.7
Total (all months)	1,021	802	-219	-21.4

WRI scientists, for those cases where the WRI sample represents over 20% of the JWA reported total, or otherwise where the JWA (Total) is well above 40 individuals. In terms of annual data, apart from the Sanriku region in 1961 and 1964, WRI scientists observed over 30% of the reported catch (Table 3). Fig. 3 plots the annual WRI and JWA percentages for both regions. Although the differences vary annually and by region, in all but the year 1964 for Sanriku (when the sample size was less than 20%), the percentage females was either very similar (e.g. 1963 for Sanriku) or significantly higher for the WRI data. It is interesting to note that for Sanriku the agreement between the JWA and WRI values improves over the 6-year period, whereas almost the opposite is true for Hokkaido. The proportion of females in the 1959 season is 63.1% ($n = 582$) in the WRI sample, while it is 56.2% ($n = 2{,}104$) in the JWA statistics. Thus, inclusion of the 1959 season does not alter the disparity in sex ratio between the two sources.

In terms of monthly data, the WRI coverage was generally reasonable (>20%, total catch *ca* 40+) for the months of June, July, August and October for Sanriku, and August to October for Hokkaido. These data (WRI) are plotted by year in Figs 4 and 5. Inspection of these figures reveals that for both locations, the percentage of females within a month can vary considerably by year (e.g. Hokkaido-August, from 21.6-70.1%), although the range, particularly for Hokkaido, is generally smaller towards the end of the season (September to November). This will relate to some degree to greater sample sizes in September ($n = 171$-825) and October ($n = 80$-395) than in August ($n = 66$-297) in Hokkaido. The WRI sample suggests some monthly changes in female proportion, which is lower in July and August compared with September-October and perhaps June (Figs 4 and 5, overleaf, and Table 4).

The WRI sample is likely to give a less biased sex ratio of sperm whales processed by Japanese coastal whaling in 1959-1969. However, given the variability apparent within and between the regions of Hokkaido and Sanriku using the WRI data, it is not clear how they are representative of the entire catch, or if it is reasonable to pool these data in an attempt to derive a correction factor or a set of monthly correction factors for the JWA series that includes seasons not covered by WRI samples. A more appropriate response might be to note that there is considerable doubt over the reliability of the sex ratio data, noting that for the 1960-65 period the percentage of females was consistently under-estimated. If one does pool the monthly data over years, in some months the difference might be over 25% (Table 4).

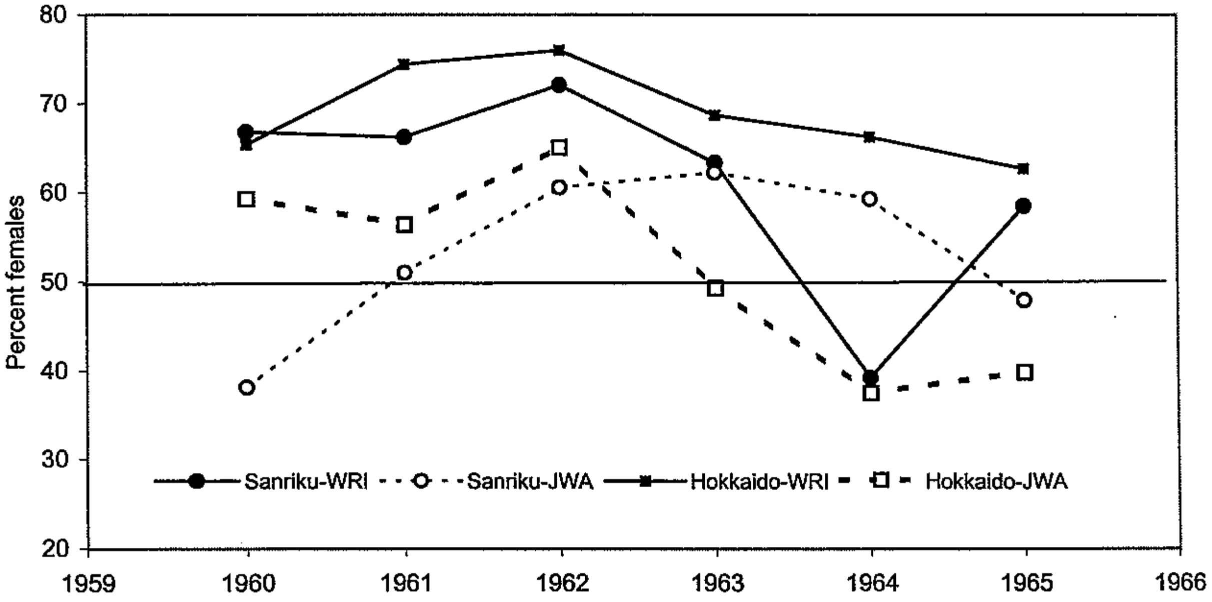

Fig. 3. Percentage of females reported in the WRI and JWA series for Sanriku and Hokkaido by year.

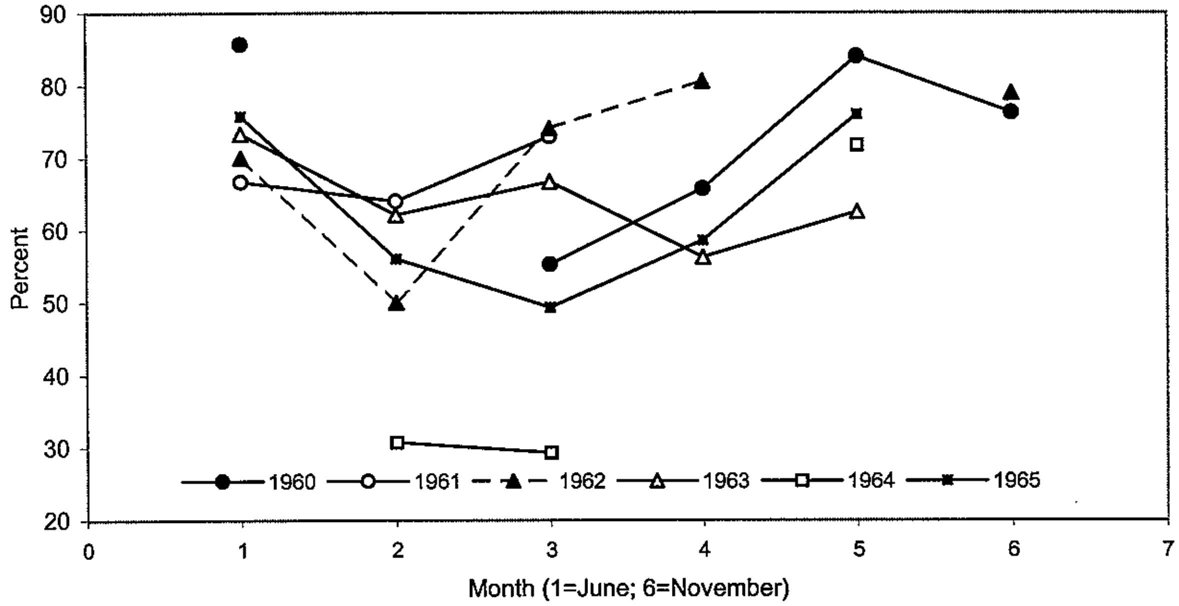

Fig. 4. Percentage of females in the WRI samples for Sanriku by month.

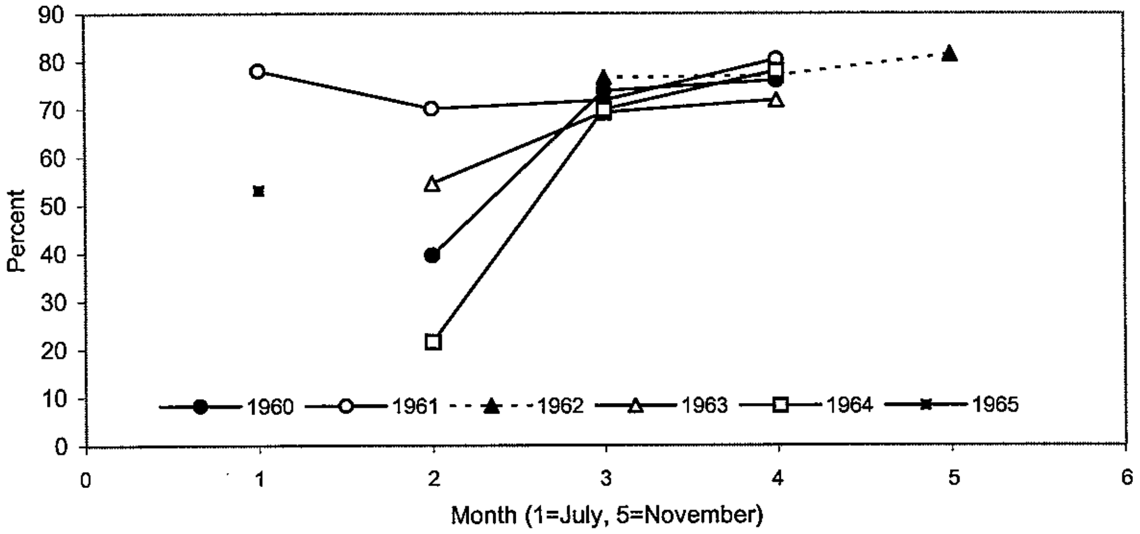

Fig. 5. Percentage of females in the WRI samples for Hokkaido by month.

Information from the B-log

At the Taiji land station, Company B (B-log) recorded a total catch of 234 sperm whales (132 males and 102 females) in the two whaling seasons 1984 and 1985 (Table 6, Fig. 6). The absence of sperm whales smaller than 31ft (9.3m) probably relates to the minimum size limit at the time (30ft). Best (1989) had noted a similar phenomenon for South African data. It is not possible to determine whether such a length distribution is a result of highly efficient size selection by gunners, 'stretching' of whales by the company, or discarding of smaller animals before towing them to the land station (see above). However, it seems unlikely that there would be a true peak at 31ft (31 whales representing 13% of individuals listed in the B-log) with no whales below that body length.

Assuming the validity of the B-log data, then all 132 males were correctly reported as males, while only 43 females out of 102 were reported with the correct gender, thus the true percentage of females in the catch (43.6%) was reported by the company as only 18.4%. Although still greater than the 11.5% allowed for the total catch, this value excludes data for the Ayukawa station for which there are no independent data.

DISCUSSION

The present paper is not the first to examine the reliability of catch data submitted to the Bureau of International Whaling Statistics. For example, Best (1989) made a number of observations on the reliability of the BIWS data based on his experiences of both pelagic and coastal whaling. Several of his concerns are echoed here.

Total catches

The first documented instance of differences between the 'official' statistics and those of biologists are those given in Tønnesen and Johnsen (1982) for the 1920-1930 period. However, the analysis of the data in this paper reveals little pattern: over-reporting as well as under-reporting was

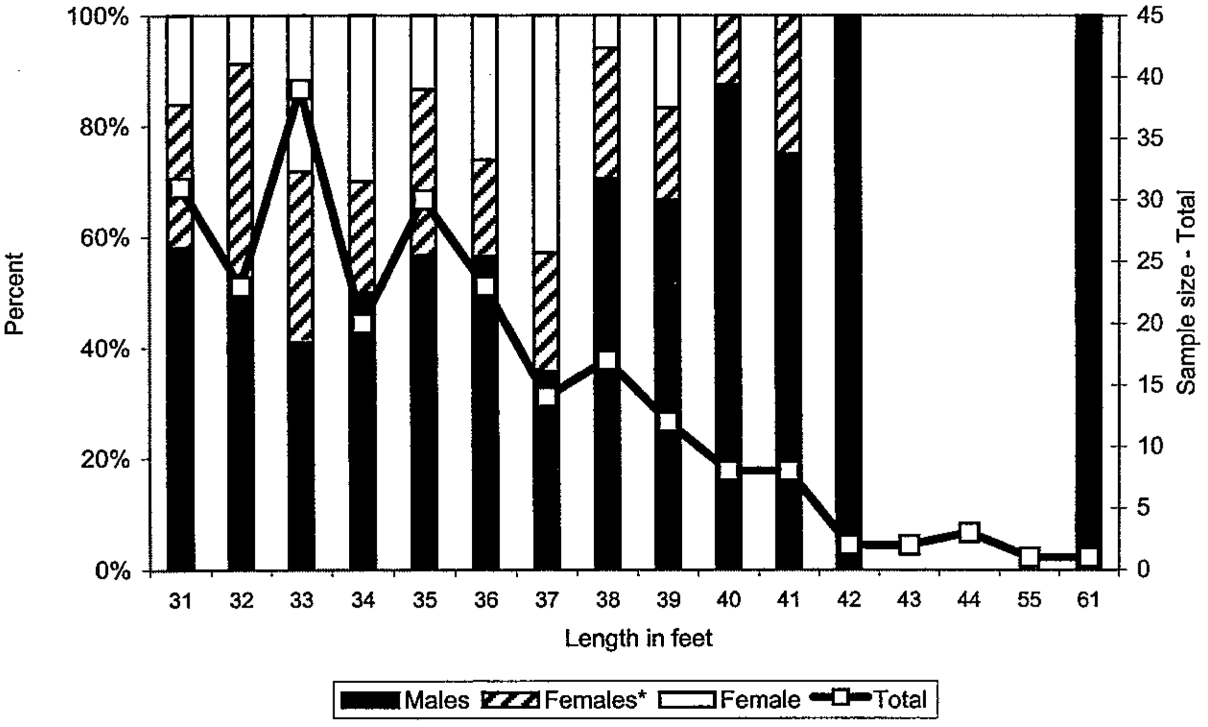

Fig. 6. Percentages of males, females and females reported as males using the data from B-log. Total sample size is also shown.

common and the reason for the disagreement between the WRI and BIWS data is unclear. At that time, there were no regulations controlling the number of whales taken (Omura *et al.*, 1942). Some local governors taxed land stations in their administrative area based on the number of whales processed (e.g. Ayukawa Village: N. Kimura pers. comm.) but whilst one might interpret this as an incentive to under-report the catch it does not explain over-reporting. It may be that investigation of the original data used by Omura can help to resolve this question.

The WRI data for the 1959-65 period also revealed some instances of under-reporting of catches, as did the A-log data for the period 1959-61. In four of the five instances in the WRI data, the confirmed under-reporting occurred late in the season (October in 1961 and 1963, November in 1960 and 1961). The A-log data revealed an increasing trend in under-reporting as the season progressed (Tables 5 and 8). Catch limits were first introduced in 1959 and it is not difficult to speculate why a company might increasingly under-report catches during a season when catch limits are in operation: for example it would enable catching to continue for an entire season, even after completion of the quota; and it might reflect a decline in inspector coverage in the later part of a season due to budgetary or other logistical constraints. It may be possible to address the latter at least by further inspection of records detailing the national inspection programme.

Interestingly, the A-log data do not preclude the possibility of over-reporting, especially in the case of baleen whales (Table 5). Over-reporting also occurred in the 1920-30 period (Fig. 2). It is more difficult to speculate why this should happen.

There were no catch limits or minimum size limits in force in the 1920-30 period and no baleen whale catch limits in the 1959-61 period. It is not obvious, therefore, why under-reporting should occur. Although there is no direct evidence to support this, one might perhaps speculate that a company might wish to hide its fishing grounds from competitors or to reduce its tax payments.

H. Omura (pers. comm.) knew of a custom in Japanese coastal whaling before World War II to classify small whales as 'unlisted' and exclude them from the catch statistics, rendering these unreliable to an unknown extent. Length regulations were first introduced to the coastal sperm whale fishery in June 1938 (Omura *et al.*, 1942). It is unknown whether 'unlisting' was a result of this regulation, due to size limits or whether there were some other reasons.

While working for the National Research Institute of Far Seas Fisheries of the Japanese Fisheries Agency, the author had an opportunity to examine library records of individual sperm whales processed by the coastal fishery. Some of the whales had a hand written note of '*bangai*' (i.e. unlisted) in red ink. Investigation of these records should help to clarify this issue.

Percentage of females in the catch

The Japanese coastal sperm whaling grounds covered the entire Japanese Pacific coast (25-45°N) (Ohsumi, 1981). Although information on stock identity is equivocal, the most recent hypothesis, which considers evidence from historical changes in the fishing grounds, the movement of marked whales and monthly changes in blood type composition (Kasuya and Miyashita, 1988) is that Japanese coastal waters include nursery schools (i.e. females, calves, immature males) from two putative populations, each breeding to the north and south of the Kuroshio/Oyashio front, and that the two stocks alternate seasonally off Sanriku (38°-41°N) and Hokkaido (42°-43°N) regions following the seasonal shift of the front.

Nursing schools from the northwestern North Pacific stock, which lack ju-2 positive individuals, summer mainly in northern waters east of the Kuril Islands and Kamchatka Peninsula (44°-55°N). In autumn, their range moves south and reaches 36°N. Thus, off Kushiro and Akkeshi (*ca.* 43°N) on the east coast of Hokkaido, the proportion of ju-2 positive individuals in a whaling sample declined from 53% (August/September) to 14% (October/November).

Wintering nursing schools were confirmed by a whaler (Shino, 1932) off Akkeshi (*ca.* 43°N) in January-March 1932 and at *ca.* 36°N by research whaling (Ohsumi and Satake, 1977) in January and February 1976. Nursing schools from the southwestern North Pacific stock, which are characterised by a high proportion of ju-2 positive individuals (>53%), winter in the western North Pacific south of 35°N, but their summer range extends north to the east coast of Hokkaido. Adult males apparently segregate, after the breeding season, to the north of the nursing schools (Kasuya and Miyashita, 1988). This explains the high female proportion in the catch off Sanriku/Hokkaido throughout the year with this ratio even possibly increasing in the winter months. Sperm whales are sparse in the southwestern North Pacific (10-25°N) as observed in Townsend (1935) and Miyashita *et al.* (1996).

If the industry was allowed to operate without regulations or self imposed length selectivity, one would expect a high proportion of females and animals <30ft of both sexes in the catch whatever the month. Thus the high female proportions found in the various non-JWA records are not particularly surprising. The introduction of catch limits by sex in 1977 and of a maximum percentage of females of 11.5% from 1979 might provide an incentive for an under-reporting of females, either by not reporting them at all or by mis-classifying females as males. The former approach would also result in an under-reporting of the total catch. For example, in order to maintain consistency between total catch numbers and production statistics, several small whales could have been converted into a larger whale.

What is surprising, is the extent of apparent under-reporting of females in the 1959-65 JWA statistics relative to the WRI sample. At that time, catch limits were not set by sex. However, a catch of large numbers of females might have invited suspicion of violation of the minimum size limit at the time (35ft), so this might have been one incentive to under-report them. The variability by month and the lack of any apparent pattern might suggest that the companies were not bothering to record sex information accurately rather than deliberately under-reporting. The situation was clearly somewhat different for the B-log data (1984 and 1985) when catch limits were in force by sex.

Detection of incorrect reporting

Although not strictly a scientific matter, an understanding of the social situations that surround fishing operations is critically important for the management of fishery resources. It would be remiss not to comment on the fact that three groups of people should perhaps have been in a position to detect any mis-reporting by the industry, but apparently did not report it: scientists; national inspectors; international observers. During the five year period (1961-1966) when the author worked for WRI as a scientist, although aware of the possibly low reliability of the sperm whale statistics, conclusive evidence was hard to accumulate from partial samples of multiple land stations. However, the availability of such evidence might not necessarily have resulted in prompt disclosure due to social constraints. Further discussion on the matter is available in Kasuya (1999).

From the scientists' perspective, two factors are relevant. The first is that the WRI scientists did publish their sample sizes, even though they did not personally comment on the differences with the official statistics. It should also be noted that the companies imposed a condition that the names of companies and land stations could not be included, only the geographical area (e.g. Sanriku or Hokkaido), making precise comparison of data considerably more difficult. The second and perhaps most important factor, is also applicable to inspectors and observers and relates to the fact that the number of personnel was insufficient for all stations to be continuously monitored throughout the season.

The fact the inspectors/observers were not assigned to each land station but that a single inspector/observer must cover several stations meant that it was at least possible for companies to choose to land whales at land stations without inspection. For example, the international observer at the Japanese land stations commented that the national inspection for sperm whales in coastal operations was as little as 7-10% (Gosho, 1979). Table 7 illustrates whaling regulations and availability of inspectors/observers to the whaling operation. Falsification may have been easier for the coastal fishery than for pelagic operations, since government inspectors were only present at the former for a small period of each fishing season.

CONCLUSION

The above analyses, even though they cover only a relatively short time series, clearly cast doubt on the reliability, particularly for post-World War II operations, of some of the BIWS data for the Japanese coastal sperm whale fishery in terms of total catches, length distribution and sex ratio. The data reveal that the degree of unreliability appears to differ considerably by month and year, and perhaps between companies.

The assessment of whale stocks requires information on historic catch levels. Where accurate data are not available, then it is important that the uncertainty in the data is incorporated into the analyses. This paper has begun the process of attempting to quantify the levels of uncertainty that may be present. However, further work is required to better determine this and perhaps to try and construct a corrected series.

A number of areas for future work are apparent:

(1) examine the additional data collected by the WRI to further elucidate the true age composition and sex ratio of catch by region, months and years, and to compare this with the equivalent JWA data - if it is possible, a comparison of JWA data and WRI data at a finer level might prove instructive - for example, one might expect the companies' data to be more rigorous on days when a biologist (or national inspector) was present;
(2) examine existing, but unanalysed, records of whaling operations (including small-type whaling operations), such as those kept in government laboratories and whaling companies;
(3) examine the prevailing legal and economic aspects of coastal sperm whaling in more detail, to try and determine any rationale for possible incorrect reporting;
(4) try to trace any private records that might have been kept by people involved in past operations.

Finally, it is important that this exercise is seen as a way to improve knowledge of the status of sperm whale stocks and not as an attempt to assign blame to individuals. Whaling is certainly not the only industry where companies have attempted to avoid national and international regulations and sometimes succeeded in avoiding detection. What is important is to use our best efforts to try to determine levels of reliability for past data and to learn from the past and ensure that inspection of any future operations is at a level which makes avoidance of regulations impossible.

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APPENDIX

Appendix Table 1

Sanriku Region, percentage of females and sample size for data collected by WRI scientists compared with JWA statistics. JWA figures that are exceeded in the sample taken by the scientists are in **bold.**

Item	1960	1961	1962	1963	1964	1965	Total	F (%)
April								
Males	0	0	0	0	0	0	0	
Females	0	0	0	0	0	0	0	
Total (WRI)	0	0	0	0	0	0	0	
Total (JWA)	50	20	1	4	11	1	87	28.7
May								
Males	2	12	0	3	2	0	19	
Females	0	17	0	0	0	0	17	
Total (WRI)	2	29	0	3	2	0	36	47.2
% F (WRI)	0	58.6	-	0	0	-	47.2	
Total (JWA)	19	120	9	96	38	6	288	50.7
% WRI	10.5	24.2	0.0	3.1	5.3	0.0	12.5	
June								
Males	3	16	3	8	16	8	54	
Females	18	32	7	22	0	25	104	
Total (WRI)	21	48	10	30	16	33	158	65.8
% F (WRI)	85.7	66.7	70.0	73.3	0	75.8	65.8	
Total (JWA)	99	139	36	54	48	59	435	40.9
% WRI	21.2	34.5	27.8	55.6	33.3	55.9	36.3	
July								
Males	5	9	14	25	18	40	111	
Females	1	16	14	41	8	51	131	
Total (WRI)	6	25	28	66	26	91	242	54.1
% F (WRI)	16.7	64.0	50.0	62.1	30.8	56.0	54.1	
Total (JWA)	49	51	43	69	40	198	450	33.6
% WRI	12.2	49.0	65.1	95.7	65.0	46.0	53.8	
August								
Males	34	10	28	35	41	70	218	
Females	42	27	80	70	17	68	304	
Total (WRI)	76	37	108	105	58	138	522	58.2
% F (WRI)	55.3	73.0	74.1	66.7	29.3	49.3	58.2	
Total (JWA)	107	282	87	171	237	326	1,210	50.7
% WRI	71.0	13.1	**124.1**	61.4	24.5	42.3	43.1	
September								
Males	36	0	7	21	0	29	93	
Females	69	0	29	27	0	41	166	
Total (WRI)	105	0	36	48	0	70	259	64.1
% F (WRI)	65.7	-	80.6	56.3	-	58.6	64.1	
Total (JWA)	170	166	216	312	325	236	1,425	64.2
% WRI	61.8	0.0	16.7	15.4	0.0	29.7	18.2	
October								
Males	4	0	0	15	13	13	45	
Females	21	0	0	25	33	41	120	
Total (WRI)	25	0	0	40	46	54	165	72.7
% F (WRI)	84.0	-	-	62.5	71.7	75.9	72.7	
Total (JWA)	38	34	67	97	111	206	553	61.7
% WRI	65.8	0.0	0.0	41.2	41.4	26.2	29.8	
November								
Males	15	0	4	0	0	0	19	
Females	48	0	15	0	0	0	63	
Total (WRI)	63	0	19	0	0	0	82	76.8
% F (WRI)	76.2	-	78.9	-	-	-	76.8	
Total (JWA)	40	39	79	36	0	141	335	51.6
%WRI	**157.5**	0.0	24.1	0.0	0.0	0.0	24.5	
Total								
Males	99	47	56	107	90	160	559	
Females	199	92	145	185	58	226	905	
Total (WRI)	298	139	201	292	148	386	1,464	61.8
Total (JWA)	572	851	538	839	810	1,173	4,783	53.2
% WRI	52.1	16.3	37.4	34.8	18.3	32.9	30.6	
F % (WRI)	66.8	66.2	72.1	63.4	39.2	58.5	61.8	
F % (JWA)	38.1	51	60.6	62.3	59.3	47.9	53.2	

Appendix Table 2

Hokkaido Region, percentage of females and sample size for data collected by WRI scientists compared with JWA statistics JWA figures that are exceeded by the sample taken by the scientists are in **bold**.

Item	1960	1961	1962	1963	1964	1965	Total	F (%)
April								
Males	0	0	0	0	0	0	0	
Females	0	0	0	0	0	0	0	
Total (WRI)	0	0	0	0	0	0	0	
Total (JWA)	1	10	6	21	2	5	45	13.3
May								
Males	0	0	0	0	0	0	0	
Females	0	0	0	0	0	0	0	
Total (WRI)	0	0	0	0	0	0	0	
Total (JWA)	42	2	17	8	3	1	73	34.2
June								
Males	0	0	8	0	0	0	8	
Females	0	0	0	0	0	0	0	
Total (WRI)	0	0	0	0	0	0	0	
Total (JWA)	8	31	23	48	30	23	163	25.8
July								
Males	10	11	0	2	1	15	39	
Females	0	39	0	0	0	17	56	
Total (WRI)	10	50	0	2	1	32	95	58.9
% F (WRI)	0	78	-	0	0	53.1	58.9	
Total (JWA)	158	208	8	37	90	73	574	39.5
% WRI	6.3	24.0	0.0	5.4	1.1	43.8	16.6	
August								
Males	122	53	4	20	29	18	246	
Females	80	124	13	24	8	0	249	
Total (WRI)	202	177	17	44	37	18	495	50.3
% F (WRI)	39.6	70.1	76.5	54.5	21.6	0	50.3	
Total (JWA)	253	297	155	112	140	66	1,023	40.7
% WRI	79.8	59.6	11.0	39.3	26.4	27.3	48.4	
September								
Males	148	110	62	31	55	38	444	
Females	416	280	203	70	128	100	1,197	
Total (WRI)	564	390	265	101	183	138	1,641	72.9
% F (WRI)	73.8	71.8	76.6	69.3	69.9	72.5	72.9	
Total (JWA)	825	548	373	308	483	171	2,708	59.3
% WRI	68.4	71.2	71.0	32.8	37.9	80.7	60.6	
October								
Males	24	55	48	48	20	5	200	
Females	76	226	160	123	71	11	667	
Total (WRI)	100	281	208	171	91	16	867	76.9
%F (WRI)	76.0	80.4	76.9	71.9	78.0	68.8	76.9	
Total (JWA)	176	80	395	161	188	237	1,237	61.7
% WRI	56.8	**351.3**	52.7	**106.2**	48.4	6.8	70.1	
November								
Males	0	11	8	1	0	0	20	
Females	2	29	35	7	0	0	73	
Total (WRI)	2	40	43	8	0	0	93	78.5
% F (WRI)	100	72.5	81.4	87.5	-	-	78.5	
Total (JWA)	9	18	165	179	53	51	475	52
% WRI	22.2	**222.2**	26.1	4.5			19.6	
Total								
Males	304	240	130	102	105	76	957	
Females	574	698	411	224	207	128	2,242	
Total (WRI)	878	938	541	326	312	204	3,199	70.1
Total (JWA)	1,472	1,194	1,142	874	989	627	6,298	52.9
% WRI	59.6	78.6	47.4	37.3	31.5	32.5	50.8	
F % (WRI)	65.4	74.4	76	68.7	66.3	62.7	70.1	
F % (JWA)	59.3	56.4	65.1	49.3	37.5	39.8	52.9	

Appendix Table 3

Comparison of A-log and JWA statistics (in parentheses).

	No. captured				Listed in A-log	
Month	Sperm	'Sei'	Fin	Blue	Day	Vessels
1959 Land station/Region: Oshima						
Apr.	25 (25)	0 (0)	0 (0)	0 (0)	1-25	2
May	(4)	(2)	(0)	(0)		
June	0 (0)	48 (70)	0 (0)	0 (0)	5-23	4
July	(1)	(70)	(0)	(0)		
Aug.	(6)	(6)	(0)	(0)		
Total[1]	25 (36)	48 (148)	0 (0)	0 (0)		
1959 Region: Sanriku/Hokkaido						
May	30 (38)	79 (74)	3 (4)	0 (0)	1-31	8
June	10 (7)	56 (113)	0 (1)	1 (1)	1-10, 23-30	7
July	50 (57)	51 (58)	4 (5)	0 (0)	1-31	5
Aug.	310 (358)	18 (23)	0 (0)	0 (0)	1-26	9
Sep.	249 (231)	21 (37)	0 (3)	0 (0)	1-29	10
Oct.	123 (101)	31 (43)	1 (2)	2 (0)	1-31	12
Nov.	45 (19)	0 (0)	0 (0)	0 (0)	1-7	4
Total[1]	817 (811)	256 (348)	8 (15)	3 (1)		
1960 Region: Sanriku/Hokkaido						
Mar.	10 (0)	0 (0)	0 (0)	0 (0)	30-31	1
Apr.	8 (18)	0 (0)	0 (1)	0 (0)	2-24	6
May	22 (23)	30 (43)	1 (2)	0 (0)	9-31	8
June	0 (51)	4 (80)	0 (0)	0 (0)	1-2	4
July	(116)	(39)	(4)	(0)		
Aug.	19 (165)	5 (17)	0 (0)	0 (0)	19-29	8
Sep.	416 (443)	7 (12)	0 (0)	0 (0)	1-30	9
Oct.	164 (75)	7 (7)	0 (0)	0 (0)	3-31	7
Nov.	34 (13)	0 (0)	0 (0)	0 (0)	7-22	4
Total[1]	673 (904)	53 (198)	1 (7)	0 (0)		
1961 Region: Sanriku/Hokkaido						
Apr.	6 (6)	0 (0)	0 (0)	0 (0)	17-20	2
May	31 (37)	39 (43)	0 (0)	0 (0)	6-30	10
June	35 (33)	72 (80)	0 (0)	1 (1)	1-27	9
July	(132)	(83)	(7)	(0)		
Aug.	122 (261)	4 (17)	0 (2)	0 (0)	22-31	9
Sep.	293 (270)	18 (12)	0 (0)	0 (0)	1-30	9
Oct.	125 (36)	1 (1)	0 (0)	0 (0)	2-31	4
Nov.	134 (27)	0 (0)	0 (0)	0 (0)	1-30	4
Total[1]	746 (802)	134 (236)	0 (9)	1 (1)		

[1] Two corresponding figures in the total are not directly comparable, because A-log is incomplete in some months.