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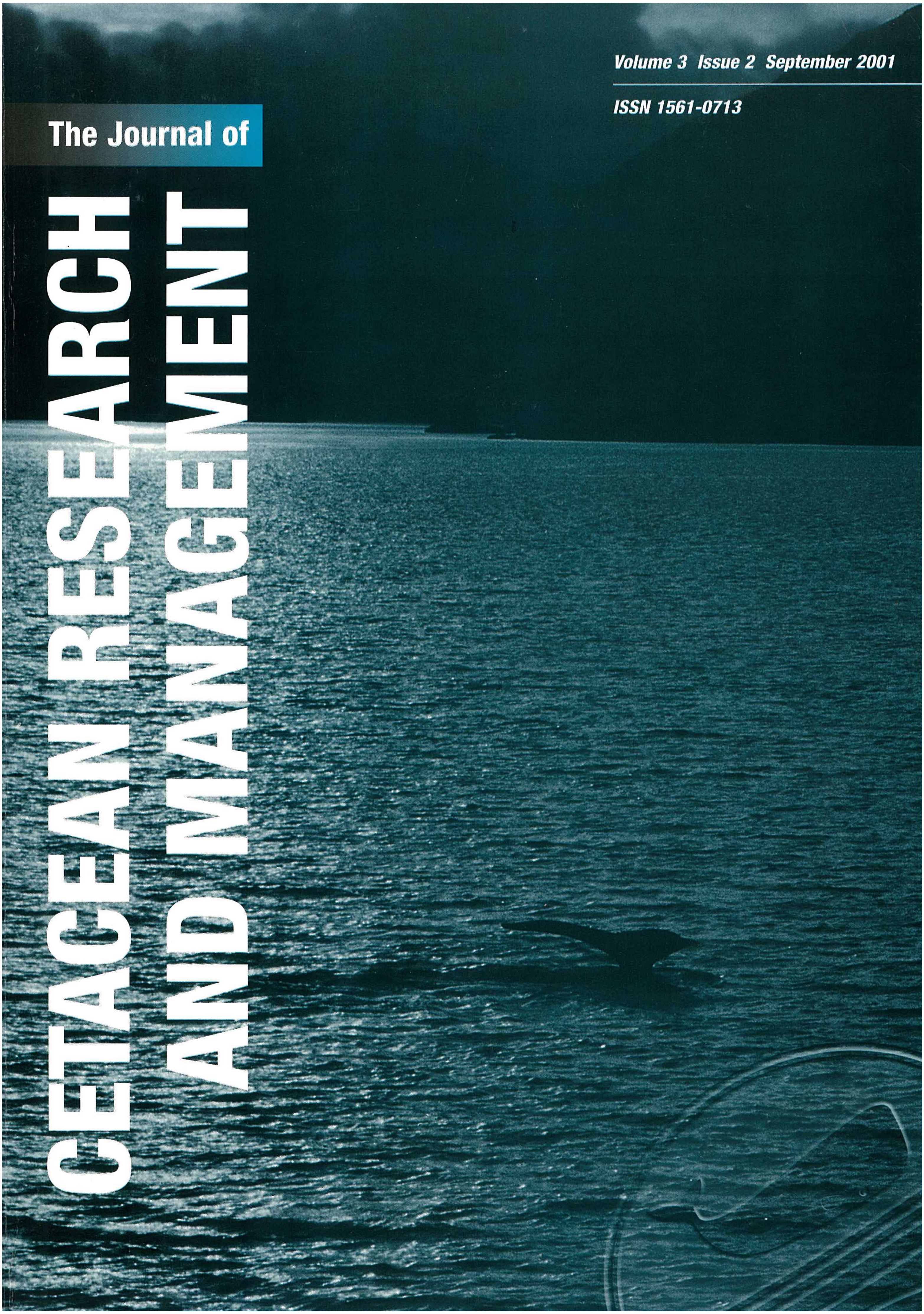

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Editorial

This issue of the Journal follows the 2001 meeting of the International Whaling Commission held in Hammersmith, London. Details of the Commission meeting will be published in the next *Annual Report of the International Whaling Commission.* The full report of the Scientific Committee will be published as *J. Cetacean Res. Manage.* 4 (Suppl.) in spring 2002. However, it seems timely to provide a short summary of the work of the Scientific Committee that updates the summary provided in Donovan (2000).

REVISED MANAGEMENT PROCEDURE

After the adoption of the moratorium on commercial whaling in 1982, the Committee spent over eight years developing the Revised Management Procedure (RMP) for baleen whales (IWC, 1999b). In brief, the RMP is a generic management procedure designed to estimate safe catch limits for commercial whaling. This was adopted some time ago by the Commission (IWC, 1993). However, the Commission has stated that it will not set catch limits for commercial whaling for any stocks until it has agreed and adopted a complete Revised Management Scheme (RMS). The RMS will also include a number of non-scientific matters, including inspection and enforcement. This is the subject of a considerable amount of discussion within the Commission, which has established an 'Expert Drafting Group' to work on this issue and report back to the Commission at its next Annual Meeting to be held in Shimonoseki, Japan in May 2002.

Implementation Simulation Trials

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

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

The Committee discussed the general question of how best to ensure that the process of carrying out *Implementations* (or *Implementation Reviews*) is efficient and prompt, whilst taking into account the available information. To achieve this it agreed that they should be conducted at discrete intervals, using the data available at one point in time. The whole process should be completed in two consecutive meetings of the Committee.

North Pacific common minke whales

At the 2001 meeting, the Committee's work concentrated on *Implementation Simulation Trials* for North Pacific minke whales. For North Pacific minke whales, the major factors being considered relate to stock identity and levels of anthropogenic removals other than direct whaling, such as bycatches in fishing gear. The Committee received new information on stock structure at the 2001 meeting. It recognised that this and other new information meant that some revision to the trial structure was necessary. The Committee agreed a timetable for its work on this implementation and will aim to recommend to the Commission one variant of the RMP at the 2002 meeting, irrespective of any further data forthcoming in the interim - this will constitute the end of the present *Implementation.* Any new information will be considered at the next *Implementation Review.*

North Pacific Bryde's whales

The Committee is in the process of developing initial *Implementation Simulation Trials* for western North Pacific Bryde's whales. In particular, it agreed that next year it will review the reliability of catch statistics and the need to incorporate any uncertainty about such statistics in the trial structure.

North Atlantic common minke whales

The Committee also began to plan for an *Implementation Review* of North Atlantic minke whales, which will take place at the Shimonoseki meeting in 2002. Amongst the new information to be considered will be new abundance estimates based on surveys carried out since 1995.

Bycatches of large whales

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

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

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

The latter potentially represents a new way of estimating bycatches. The Committee agreed that although genetic methods based on market samples may not be the primary approach to estimating bycatch, they could provide useful supplementary data that could not be obtained in another way. The use of market samples to provide absolute estimates should not be ruled out but would require further developments in sampling design with input from experts outside the Committee with detailed knowledge of market sampling issues. The Committee will consider bycatch issues further next year.

DEVELOPMENT OF AN ABORIGINAL WHALING MANAGEMENT PROCEDURE

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

At the 2001 meeting, the Committee made considerable progress with respect to the Bering-Chukchi-Beaufort Seas stock of bowhead whales. It has narrowed down the choice of a *Catch Limit Algorithm* for bowhead whales to two excellent candidates. Work will continue intersessionally on gray whales. If this progress is maintained, the Committee hopes to be able to present a formal recommendation to the Commission on all scientific aspects of a management scheme for bowhead and gray whales at the 2002 meeting. The situation for the Greenlandic fisheries for fin and minke whales is less promising. A considerable amount of research, especially concerning stock identity, is required and to this end the Committee has developed a research programme.

ASSESSMENT OF STOCKS SUBJECT TO ABORIGINAL SUBSISTENCE WHALING

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

At the 2002 meeting, the Committee reiterated its previous management advice for all of the stocks considered and made a number of research recommendations. The Committee welcomed the preliminary results of a successful census of bowhead whales carried out in 2001. A full evaluation will be carried out next year. The Committee further considered the 1999-2000 episode of increased gray whale strandings and sightings of emaciated individuals. It agreed that this should be considered as a stochastic event whose magnitude may have been exacerbated by the possibility that the population was at or close to its carrying capacity. Next year, the Committee will be carrying out in-depth assessments of both the Bering-Chuckchi-Beaufort Seas stock of bowhead whales and the eastern stock of gray whales.

A catch of a bowhead whale in August 2000 (by Canada, a non-IWC nation) was reported from the Hudson Bay – Foxe Basin stock. The Committee has expressed concern about the status of this stock (and the Baffin Bay – Davis Strait stock) in the past. Given the low estimated stock size and the lack of information on appropriate methods to manage small populations, the Committee urged caution in the setting of any catch limits for this population and recommended that priority be given to research to: (1) obtain improved abundance estimates; and (2) pursue modelling efforts for use in the management of small populations.

COMPREHENSIVE ASSESSMENT OF WHALE STOCKS

Antarctic minke whales

The Committee has carried out annual surveys in the Antarctic (south of 60°S) since the late 1970s. The last agreed estimates for each of the six management areas for minke whales (see Donovan, 1991) were for the period 1982/83 to 1989/90 (IWC, 1991). At the 2000 meeting, the Committee agreed that whilst these represented the best estimates for the years surveyed, they were no longer appropriate as estimates of current abundance. An initial crude analysis of available recent data had suggested that current estimates may be appreciably lower than the previous estimates.

At the 2001 meeting, considerable time was spent considering Antarctic minke whales with a view to obtaining final estimates of abundance and considering any trend in these. This included a review of data sources and analytical methodology. After considering many of the factors affecting abundance estimates, there is still evidence of a decline in the abundance estimates, although it is not clear how this reflects any actual change in minke abundance (and see the paper by Branch and Butterworth in this volume). Three hypotheses that might explain these results were identified:

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

Given the management implications of this, the Committee is giving high priority to work on this issue both intersessionally and during the 2002 meeting.

The 'Comprehensive Assessment' of whale stocks

The development of the concept of the 'Comprehensive Assessment' is reviewed in Donovan (1989). It can be considered as an in-depth evaluation of the status of all whale stocks in the light of management objectives and procedures; this would include the examination of current stock size, recent population trends, carrying capacity and productivity. Clearly, it is not possible to 'comprehensively assess' all whale stocks simultaneously, and the Committee has been working in an objective manner towards this, initially concentrating on stocks that have recently or are presently being subject to either commercial or aboriginal subsistence whaling.

Southern Hemisphere blue whales

The Committee is reviewing the current status of Southern Hemisphere blue whales. An important part of this work is to try to develop methods to identify pygmy blue whales from 'true' blue whales at sea (IWC, 1999). The Committee agreed on a number of issues that need to be resolved before it is in a position to carry out an assessment.

Southern Hemisphere humpback whales

Considerable progress has been made in recent years in working towards an assessment of humpback whales. Attention has focussed both on data from historic whaling operations and on newly acquired photo-identification, biopsy and sightings data. The Committee made a number of research recommendations to further progress towards an assessment.

North Atlantic humpback whales

At the 2001 meeting, priority was given to the Comprehensive Assessment of North Atlantic humpback whales. The Committee recognised the important contribution the international YoNAH (Years of the North Atlantic Humpback) project made to the assessment. This project combined photo-identification and molecular genetic techniques to collect as many photographs and skin biopsies as possible in four sampling periods over a wide geographical range during a period of two years (1992-1993). The principal objectives of the study were to increase understanding of: (a) abundance - both regionally and in total; (b) population genetic structure; (c) population spatial structure including rates of exchange among feeding grounds; and (d) reproductive behaviour and vital rates.

In reviewing population structure, the Committee concluded that North Atlantic humpback whales are characterised by relatively discrete feeding substocks, with strong site fidelity by individuals. This latter factor also influences movement patterns within feeding grounds.

There is clear evidence for at least two breeding stocks in the North Atlantic. Whales from the western North Atlantic breed primarily in the West Indies, as do some whales that feed in the central North Atlantic. However where other central North Atlantic animals and those from the Barents Sea breed is unknown

The only breeding ground, other than the West Indies, known from historical and contemporary data is the Cape Verde Islands, but to date there is no direct evidence to support the idea that this is a breeding ground used by central and eastern North Atlantic animals. There may be a separate breeding population in the Norwegian Sea (as suggested in the late 1920s) and the possibility that there are three separate breeding stocks in the North Atlantic cannot be ruled out.

The Committee reviewed a number of population estimates for the feeding and breeding grounds and agreed on a workplan to complete the Comprehensive Assessment at next year's meeting.

North Atlantic right whales

The Committee has paid particular attention to the status of the North Atlantic right whale in recent years (e.g. see the recently published special issue of the Journal – *Right whales: worldwide status*). The Committee is extremely concerned about this population, which, whilst probably the only potentially viable population of this species, is in serious danger. By any management criteria applied by the IWC in terms of either commercial whaling or aboriginal subsistence whaling, there should be no direct anthropogenic removals from this stock.

It is a matter of absolute urgency that every effort be made to reduce anthropogenic mortality in this population to zero. This is perhaps the only way in which its chances of survival can be directly improved. There is no need to wait for further research before implementing any currently available management actions that can reduce anthropogenic mortalities.

The Committee made a number of research and management recommendations concerning this stock.

STOCK IDENTITY

Of general concern to the assessment of any cetaceans is the question of stock identity and examination of this concept in the context of management plays an important role in much of the Committee's work, whether in the context of the RMP, AWMP or general conservation and management. In recognition of this, the Committee has established a Working Group to review theoretical and practical aspects of the stock concept in a management context. At the 2001 meeting, the Committee considered *inter alia:* terminology; stock structure in humpback whales; a range of analytical and statistical issues; the use of archetypes; and the combination of genetic and non-genetic information on stock identity.

Although humpback whale stock structure is complex, some general patterns do emerge. Most humpback whales migrate between low and high latitudes to feed and breed, showing strong site fidelity to individual feeding and breeding grounds. However, humpback whales from a single breeding ground often use various different feeding grounds; and humpbacks on a single feeding ground often come from various different breeding grounds. Good understanding has been reached only through major research effort on both feeding and breeding grounds. Based on the review, the Committee emphasised the need to consider humpback whale management within ocean basins on a case-by-case basis. In particular, consideration should be given to managing on the basis of feeding grounds as well as breeding grounds.

The Committee made considerable progress in discussing the complex issue of the way to define stocks for harvested populations.

EFFECTS OF ENVIRONMENTAL CHANGE ON CETACEANS

There is an increasing awareness that whales should not be considered in isolation but as part of the marine environment; detrimental changes to their habitat may pose a serious threat to whale stocks. The Committee has examined this issue in the context of the RMP and agreed that the RMP adequately addresses such concerns. However, it has also emphasised that the species most vulnerable to environmental threats might well be those reduced to levels at which the RMP, even if applied, would result in zero catches (IWC, 1994). Over a period of several years, the Committee has developed two multi-national, multi-disciplinary research proposals. One of these, POLLUTION 2000+ (Reijnders *et al.*, 1999) has two aims: to determine whether predictive and quantitative relationships exist between biomarkers (of exposure to and/or effect of PCBs) and PCB levels in certain tissues; and to validate/calibrate sampling and analytical techniques. The other, SOWER 2000 (IWC, 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.

At the 2001 meeting, the Committee's primary topic concerned pollutant issues, especially related to POLLUTION 2000+. It also considered progress on the SOWER 2000 programme, particularly with respect to future collaboration with Southern Ocean GLOBEC and preliminary results from last year's collaboration with CCAMLR. There was considerable discussion of the development of a report for the Commission that would provide an overview of regional environmental concerns and how best this might be achieved. Plans for intersessional workshops on habitat degradation and competition between cetaceans and fisheries were developed further. The Committee also considered the issues of (1) how to link environmental measures and cetacean demography and (2) health effects from the consumption of cetacean products.

SMALL CETACEANS

Despite disagreement within the Commission over the management responsibilities of the IWC with respect to small cetaceans, it has been agreed that the Scientific Committee can study and provide advice on them. As part of this programme, the Committee has reviewed the biology and status of a number of species and carried out major reviews of significant directed and incidental catches of small cetaceans (Bjørge *et al.*, 1994).

At the 2001 meeting, the Committee considered the status of Dall's porpoises (*Phocoenoides dalli*) off Japan. For reasons documented in the Committee's report, the Government of Japan had decided not to participate in this review.

Dall's porpoises have been subdivided into two subspecies: *P.d. truei* and *P.d. dalli*, primarily on the basis of colour patterns. From a variety of genetic and other evidence, the Committee identified at least eleven stocks. Of these, a *dalli*-type stock that breeds in the northern Okhotsk Sea, a *truei*-type stock that winters off the Pacific coast of Japan and breeds in the central Okhotsk Sea and at least one other stock are taken in the Japanese hand-harpoon fishery. Dall's porpoises are also taken incidentally in a Japanese fishery in the EEZ of the Russian Federation. Large numbers of this species have been taken in other fisheries in these and adjacent waters in the past (e.g. Bjørge e*t al.*, 1994) and this may continue. The Committee reviewed available information on the catches up to 1999 in conjunction with looking at the latest population estimates (IWC 1992). The Committee repeated the extreme concern it had previously expressed over these stocks and made a number of research and management-related recommendations.

The Committee also reviewed progress on previous recommendations it had made, particularly those concerning the critically endangered baiji (*Lipotes vexillifer*) and vaquita (*Phocoena sinus*). Unfortunately, no new information was received on the baiji this year and the Committee has requested that information be provided next year. The Committee was informed of a new, integrated framework being developed to implement the recovery plan for the vaquita, and welcomed this new approach. It reiterated its endorsement of the primary conclusion of CIRVA (International Committee for the Recovery of the Vaquita) – that to ensure the future survival of the vaquita it will be necessary to eliminate all bycatches as rapidly as possible.

Finally, the Committee considered the results of a modelling exercise carried out in response to a recommendation of the joint IWC/ASCOBANS working group on the harbour porpoise. The Committee welcomed the approach and suggested further development work.

SCIENTIFIC ASPECTS OF WHALEWATCHING

In 2000, the Committee had identified a number of areas for further research on possible long-term effects of whalewatching on whales and a number of possible data types that could be collected from whalewatching operations to assist in assessing their impact. The Committee developed this further at the 2001 meeting and will continue to work on data collection issues in the intersessional period.

The Committee also reviewed papers containing information on noise from whalewatching vessels and aircraft, and any potential effects this might have on cetaceans. It recommended that such work continues and new information will be considered at next year's meeting.

The Committee continued to consider national guidelines for whalewatching from a number of countries as well as papers examining their effectiveness. It received new information on dolphin feeding programmes in Australia and the USA and reconfirmed its view that programmes involving the feeding of wild cetaceans should be prohibited. Similarly, the Committee agreed that there are potential problems with 'swim-with' programmes for wild cetaceans and it will consider this issue further.

REVIEW AND COMMENT ON SCIENTIFIC PERMITS ISSUED FOR SCIENTIFIC RESEARCH

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

Much discussion at the 2000 meeting had centred on a proposal for a new programme (JARPN II) that involves taking 100 common minke whales, 50 Bryde's whales and 10 sperm whales each year. The stated goal was to obtain information to contribute to the conservation and sustainable use of marine living resources in the western North Pacific. It includes sub-projects on: feeding ecology; stock structure; and environmental effects on cetaceans and the marine ecosystem. There had been considerable disagreement within the Committee over most aspects of this research programme, including objectives, methodology, sample sizes, likelihood of success, effect on stocks and the amount and quality of data that could be obtained using non-lethal research techniques. This year, the Committee received preliminary results from the first year of the programme but again there was considerable disagreement over the value of the programme.

The Committee also briefly considered the continuing programme on Antarctic minke whales that was last extensively reviewed in 1997 (IWC, 1998). Discussions on how best to assess the effects of scientific permit catches on stocks are continuing.

WHALE SANCTUARIES

The Committee had been asked to comment on the scientific aspects of the proposal submitted by Brazil to the Commission last year to create a Sanctuary for great whales in the South Atlantic.

The Committee referred to a number of general arguments both in favour of and against sanctuary proposals but was unable to reach a consensus view on the need for a Sanctuary in this region.

G.P. Donovan
Editor

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Investigations of an Aboriginal Whaling Management Procedure using Adaptive Kalman Filtering

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ABSTRACT

The feasibilty of using Kalman Filter methods as the basis for an Aboriginal Whaling Management Procedure is explored in this paper. Adaptive Kalman Filters are used to obtain estimates of the stock size and posterior probability distributions for MSY rate (*MSYR*) and the pre-exploitation stock size *K*. A set of catch control laws is then used on these estimates of stock size, which together with the posterior distributions of the various combinations of *MSYR* and *K*, gives a cumulative distribution function for the strike limit. The eventual strike limit is then determined as a pre-specified percentile of this distribution. The procedure is tested on some *Evaluation Trials* set by the Standing Working Group on Aboriginal Whaling Management Procedures of the International Whaling Commission (IWC) Scientific Committee. The estimation of a bias factor was considered and results are presented.

KEYWORDS: WHALING-ABORIGINAL; MANAGEMENT PROCEDURE; KALMAN FILTER

INTRODUCTION

The Kalman Filter is widely used in the engineering sciences to obtain estimates of the state of a stochastic dynamical system with noisy observations, i.e. a system with both ‘process noise’ and ‘observation noise’. Kalman Filtering techniques have been applied to estimation problems in fisheries management with some success (e.g. Gudmundsson, 1994; Reed and Simons, 1996) to estimate stock sizes and population parameters using effort data and catch-at-age data. It would therefore seem feasible to apply these techniques to estimate the status of whale stocks. The equations used to describe the population dynamics of whales and the relation between the true stock size and observations thereof can be written in a form which lends itself to state estimation via Kalman Filters. Such estimation schemes together with appropriate catch control laws might then form the basis of an Aboriginal Whaling Management Procedure (AWMP). The potential AWMP described here uses the so-called Adaptive Kalman Filter (AKF) to obtain estimates for the present stock size N_t - conditional on fixed values of *MSYR* (MSY-rate), pre-exploitation population size *K* and bias factor *B* - together with posterior probability distribution for N_t and *(MSYR, K, B)* for each point in a three-dimensional grid of discrete values of these three parameters. Associated with each *(MSYR, K, B)* in the grid, there is a corresponding catch control law. A sequence of catch limits with associated probabilities is thereby obtained and hence a cumulative distribution function for the catch limit can be constructed. Fixing a percentile of this distribution then determines the actual catch limit. This method is therefore a combination of Kalman Filtering techniques and Bayesian methodology.

Fishery type 2 as defined in IWC (2000a) represents cases where substantial information exists. An example of such a fishery is the Bering-Chukchi-Beaufort (B-C-B) Seas stock of bowhead whales *(Balaena mysticetus)*. A series of abundance observations exists for this stock and observations will probably continue to be available at regular intervals. An AWMP proposed for a type 2 fishery must undergo a series of simulation trials. These have been designed by the Scientific Committee of the IWC and are given in IWC (2000b). The trials are conditioned on the data for the B-C-B bowhead stock, i.e. on the history of catches, past stock estimates and parameter values. The AWMP proposed here is fairly general and should be applicable to a range of stocks, but the specifications - including model equations and some parameter values - refer to an application to the B-C-B stock.

The next section is a brief review of the ideas underlying the discrete Kalman Filter. For further details, see for example Brown and Hwang (1997) or Gershenfeld (1999). A general framework is then formulated so that these methods can be applied to the case of a whale stock with abundance observations, followed by a fully specified model applicable to the B-C-B stock, for which results for a set of the AWMP simulation trials are presented. Finally, the results of some sensitivity tests are presented and discussed.

A BRIEF REVIEW OF KALMAN FILTERING TECHNIQUES

The Kalman Filter

The Kalman filter is designed to give an estimate of the state of a system:

$$x_{t+1} = F_t x_t + u_t \tag{1}$$

$$z_t = H_t x_t + v_t \tag{2}$$

where

x_t is the state of the system at time *t* (*n*-vector);
z_t is the observation of the system at time *t* (*m*-vector);
u_t is Gaussian white noise, $u_t \sim N(0,Q_t)$ (*n*-vector);
v_t is Gaussian white noise, $v_t \sim N(0,R_t)$ (*m*-vector); and
F, H are *nxn* and *mxn* matrices, respectively.

It is assumed that the process noise u_t and the observation noise v_t are uncorrelated. To start the estimation process, an estimate of the state at $t = 0$ needs to be specified, together with the corresponding error covariance matrix. The estimate of the state at time *t*, using data up to *t*-1 is denoted by $x_{t|t-1}$ and is known as the prior estimate of x_t. The corrsponding error covariance matrix at time *t* is:

$$P_{t|t-1} = E((x_t - x_{t|t-1})(x_t - x_{t|t-1})^T)$$

where *T* denotes transpose. When a new observation z_t becomes available, the estimate $x_{t|t-1}$ is updated according to:

$$x_{t|t} = x_{t|t-1}+\mathrm{K}_t(z_t-H_t x_{t|t-1}) \tag{3}$$

which is the posterior estimate of x_t i.e. the estimate of the state at time *t* using data up to *t*. Here K_t is known as the Kalman gain at time *t*. Note that the term in brackets on the right hand side is the difference between the actual observation and the predicted observation at time *t*. Thus a large difference between the actual and predicted observations will give a large modification in the state estimate and a small difference results in a correspondingly small modification. The Kalman gain is given by:

$$K_t = P_{t|t-1}\mathrm{H}_t^{\mathrm{T}}(H_t P_{t|t-1}\mathrm{H}_t^{\mathrm{T}}+R_t)^{-1} \tag{4}$$

The error covariance matrix $P_{t|t-1}$ is updated by:

$$P_{t|t} = (I-K_t H_t)P_{t|t-1} \tag{5}$$

Note that $P_{t|t}$ is the error covariance matrix associated with the updated (posterior) estimate of the state at time *t*.

Finally, new prior estimators of the state and the error matrix at *t* + 1, are obtained by:

$$x_{t+1|t} = F_t x_{t|t} \tag{6}$$

$$\mathrm{P}_{t+1|t} = F_t P_{t|t} F_t^{T}+Q_t \tag{7}$$

The Kalman gain at time *t*+1 can then be calculated and hence the posterior estimate of the state at *t*+1 and so on.

Equations (3) to (7) comprise the recursive equations for the discrete Kalman Filter. The particular form of the gain K_t given by equation (4) minimises value of trace($P_{t|t}$), i.e the mean square estimation error. The Kalman Filter is therefore the optimal linear estimator for systems with linear observations and dynamics. Note that the gain decreases with increasing observation variance *R*, and increases with increasing state variance *Q*. The effect of the observations on the updated state estimate will therefore depend on the relative values of state noise and measurement noise.

The Extended Kalman Filter (EKF)

The estimation procedure described above applies to linear systems. In order to obtain a linear estimator of the form given by Equation (3) for the non-linear system,

$$x_{t+1} = f(x_t,t) + u_t \tag{8}$$

$$z_t = h(x_t,t) + v_t \tag{9}$$

some approximations are required. Assuming that the prior estimate of the state at time *t*, $x_{t|t-1}$, is available, the function *h(x,t)* is linearised about that estimate giving the Jacobian matrix:

$$H_t = \left[\frac{\partial h}{\partial x}\right]_{x=x_{t|t-1}} \tag{10}$$

This H_t is then used in Equation (4) for the Kalman gain. The expression for updating the state estimate is:

$$x_{t|t} = x_{t|t\text{-}1} + K_t(z_t-h(x_{t|t\text{-}1},t)) \tag{11}$$

The error matrix is updated using Equation (5) with H_t given by Equation (10). The prior estimate of the state at *t*+1 is obtained by:

$$x_{t+1|t} = f(x_{t|t},t) \tag{12}$$

and finally, the forward projection of the error matrix via Equation (7) is carried out using the linearisation of *f(x,t)* about the posterior estimate of x_t at time *t*, i.e.

$$F_t = \left[\frac{\partial f}{\partial x}\right]_{x=x_{t|t}} \tag{13}$$

Equations (11) and (12), together with (4), (5) and (7) with *F* and *H* given by Equations (10) and (13) are the recursive equations for the Extended Kalman Filter.

The Adaptive Kalman Filter (AKF)

Unknown parameters in the system equations can be treated as system variables to be estimated. Alternatively, Bayesian methodology can be combined with Kalman Filters to obtain a posterior probability distribution of the unknown parameters. Assume that a vector of parameters, *A*, is unknown. A set of extended Kalman Filters is constructed, one for each value of *A* in a discrete set *{A*$\{A_i{:}i = 1,\ldots,l\}$. A prior distribution, $p(A_i)$, for *A* is given, and each time a new observation becomes available, a posterior distribution, $p(A_i|Z_t)$, where Z_t is the set of observations up to and including time *t*, is updated. This is done as follows:

$$p\,(A_i \mid Z_t) = \frac{p(Z_t \mid A_i)p(A_i)}{p(Z_t)} \tag{14}$$

where the conditional distribution $p(Z_t|A_i)$, is given by (assuming a scalar output for simplicity, i.e. $m = 1$, and dropping the index on *A* for convenience of notation),

$$p\,(Z_t \mid A) = \frac{1}{(2\pi)^{1/2}(H_t P_{t|t-1} H_t^T + R_t)^{1/2}} \exp\left(-\frac{(z_t - h(x_{t|t-1},t))^2}{2(H_t P_{t|t-1} H_t^T + R_t)}\right) p(Z_{t-1} \mid A) \tag{15}$$

where H_t, $x_{t|t\text{-}1}$, $P_{t|t\text{-}1}$ and R_t may depend on A_i and are obtained by the Extended Kalman Filter method. Note that a ‘small’ prediction error $z_t\text{-}h(x_{t|t\text{-}1},t)$, gives a ‘high’ value of $p(Z_t|A_i)$. Finally, $p(Z_t)$ is calculated by:

$$p\;(Z_t) = \sum_{i=1}^{\ell} p(Z_t \mid A_i)p(A_i)$$

GENERAL MODEL FORMULATION

It is assumed that the population dynamics and observations are governed by the following equations:

$$N_{t+1} = \left(S(N_t - C_t) + (1-S)\left(1 + A\left(1 - \left(\frac{N_t}{K}\right)^z\right)\right)N_t\right)e^{u_t} \tag{16}$$

$$N_t^{obs} = e_t^{v} N_t \tag{17}$$

where N_t is the total population of animals 1 year and older (1+) in year *t*; C_t is the catch in year *t* and u_t and v_t are normal random variables with zero mean and variances Q_t and R_t, respectively. This is the well-known Pella-Tomlinson (P-T) model with the parameters: annual survival rate *S*; pre-exploitation population size (carrying capacity) *K*; and the resilience parameter *A*, which is related to *MSYR* by $MSYR = A(1\text{-}S)/S(z/(z+1))$. Note that this is a simplification of the usual P-T models since there is no delay in the dynamics. Note also that the process noise enters by simply multiplying the usual P-T function by a lognormal random variable. This assumption might be questioned, but it enables the dynamics to be written in the required form – as specified in the previous section - by a logarithmic transformation. It should be pointed out that the assumption of normality is not strictly necessary since non-Gaussian assumptions can be accommodated within the extended Kalman Filter.

The state variable is defined to be $x = ln(N)$ and the observation $z = ln(N^{obs})$. The state and observation equations become:

$$x_{t+1} = f(x_t) + u_t$$
$$z_{\mathrm{t}} = x_t + v_t$$

where

$$f(x_t) = \ln\left(S(e^{x_t} - C_t) + (1-S)\left(1 + A\left(1 - \left(\frac{e^{x_t}}{K}\right)^z\right)\right)e^{x_t} \right) \qquad (18)$$

The numbers (note that the model is one-dimensional), F_t and H_t used in calculating the Kalman gain and updating the error covariance matrix P (which is simply a scalar variance now) are:

$$F_t = \frac{\partial f}{\partial x}(x) = \frac{S\cdot e^x + (1-S)\cdot e^x\left(1 + A\left(1 - \left(\frac{e^x}{K}\right)^z\right) - A\cdot z\cdot\left(\frac{e^x}{K}\right)^z\right)}{S(e^x - C_t) + (1-S)\left(1 + A\left(1 - \left(\frac{e^x}{K}\right)^z\right)\right)e^x} \qquad (19)$$

where the linearisation is about the point $x = x_{t|t}$ and $H_t = 1$.

The possibility of biased observations can be addressed by replacing $z_t = ln(N_t^{obs})$ with $z_t = ln(N_t^{obs})\text{-ln}(B)$, corresponding to the observation model $N_t^{obs} = BN_te^{v_t}$, where B is the bias factor.

Adaptive Kalman Filtering can be applied to this model by fixing some of the parameters, i.e. z and S and letting the resilience parameter A (or alternatively, the *MSYR*), the carrying capacity K, and the bias factor B, range over a sequence of discrete values. This gives a three dimensional grid of values (A_i,K_j,B_k) i = 1,2,…,I; j = 1,2,…,J; k = 1,2,…,K, with IJK different sets of these parameter values. To each parameter set there corresponds an extended Kalman Filter and a catch control law is associated with each filter. Whenever a new observation becomes available, the stock estimate, $x_{t|t-1}(A_i,K_j,B_k)$, and the posterior probability distribution, $p(A_i,K_j,B_k|Z_t)$, are updated for each of the IJK parameter sets, (A_i,K_j,B_k) as described in the previous section. Applying a catch control law corresponding to each parameter set (A_i,K_j,B_k), to $x_{t|t}(A_i,K_j,B_k)$, a total of IJK catch limits, $C(x_{t|t}(A_i,K_j,B_k);(A_i,K_j,B_k))$ are obtained, together with the associated posterior probability distribution $p(A_i,K_j,B_k|Z_t)$, i = 1,2,…,I; j = 1,2,…,J; k = 1,2,…,K. Arranging $C(x_{t|t}(A_i,K_j,B_k);(A_i,K_j,B_k))$ in an increasing sequence, the associated probability distribution makes it possible to construct the cumulative distribution function $F(C)$ for the catch limit. Once a percentile γ of this distribution is fixed, the eventual catch limit can be determined by solving:

$$F(C_t) = p(C < C_t) = \gamma \qquad (20)$$

for C_t. This percentile will be used as the tuning parameter for the procedure. The procedure is illustrated schematically in Fig. 1.

Specification of the Base Case Model and results

The general model described in the previous section needs to be specified further if it is to be applied to a specific stock. What will be termed the Base Case Model is an application

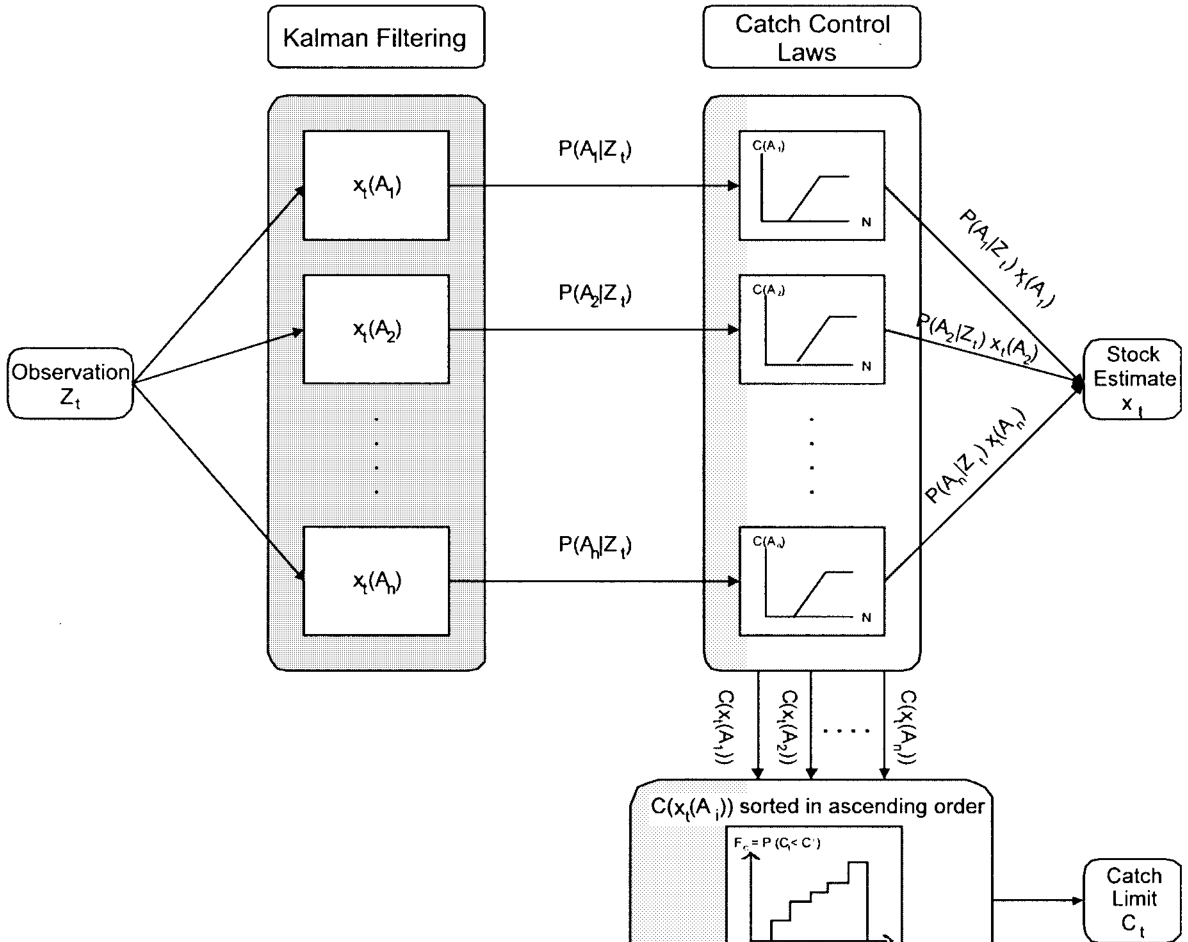

Fig. 1. An overview of the algorithm for setting catch limits.

to the B-C-B stock of bowhead whales and is defined as follows. The two parameters which are kept fixed, S and z, will be set at 0.99 and 2.39 respectively (this value of z corresponds to an *MSY*-level (*MSYL*) of 0.6). The carrying capacity K, ranges from 10,000 to 23,000 in increments of 100 and the values of the resilience parameter A correspond to *MSYR* of 1%, 2%, 3% and 4%. The possibility of bias is not considered in the Base Case Model. There are therefore 131 values of K and four values of *MSYR*, giving a total of 524 filters. It is assumed that the stock is at carrying capacity in 1848 when commercial whaling began. The filters are therefore started in that year, with initial conditions $x_0 = K$ and $P_0 = 0$ (note that there is no initial variance since K is pre-specified in each filter). The state x is projected forward by the equation:

$$x_{t+1} = f(x_t) \tag{21}$$

where $f(x_t)$ is given by Equation (18) and not updated until 1978 when the first observation becomes available. On the other hand, the variance P is projected forward every year by:

$$P_{t+1} = F_t P_t F_t^T + Q_t = (F_t)^2 P_t + Q_t \tag{22}$$

where F_t is given by Equation (19). Note that F_t is a scalar since the model is one-dimensional. The variables x and P are updated by Equations (3) and (5) respectively, whenever a new observation becomes available. There are 10 historical abundance observations between 1978 and 1993, and in the simulation trials, the management procedure will be given abundance observations in 2002, 2004 and then every five years. To each observation there is an associated estimate of the coefficient of variation (*CV*). The variance of the measurement noise v_t, is given by:

$$R_t = Var(v_t) = \ln\left(1 + CV(N_t^{obs})^2\right)$$

In order to get an estimate of the variance of the process noise Q, some simulations were carried out using a simplified population model. The survey estimates were generated using a Pella-Tomlinson model without age-structure and without demographic stochasticity, but with noisy observations where the noise was as specified in IWC (2000a). Q was chosen so as to roughly minimise prediction error in a small subset of simulation trials, which gave $Q = 10^{-3}$. Note that a high value of Q will give a high Kalman gain and hence the filter will tend to follow the individual observations, which is not a desirable feature. The sensitivity to the value of Q is investigated in the following section.

There is no prior information on the values of the parameters A and K. The prior distribution for each parameter set (A_i, K_j), i = 1,2,3,4; j = 1,2,…,131, is therefore assumed to be discrete uniform on the specified grid and the first update is in 1978 when the first observation becomes available. Let us first consider the results when the filters are applied to the historical data, i.e. up to 1993 (they will be continued past 1993 in the simulation trials discussed below). Fig. 2 shows the posterior probabilities in 1993, i.e. $p(K|Z_{1993})$, for the four values of *MSYR*. It is clear that although the mode is at 3% *MSYR*, the 1% *MSYR* has the greatest probability mass. This is to be expected since the population trajectory is less sensitive to the initial value, K, when the *MSYR* is low and there is therefore a wider range of K-values which 'agree' with the historical abundance data. Initially all K values are considered to be equally likely. Thus, although the mode of the 1% curve is lower than the 2% and 3% curves, the support of the probability density function is much wider, giving a higher marginal probability when integrating over all K-values. Fig. 3 shows the evolution of this marginal probability mass function from 1978 to 1993, i.e. *p(MSYR)*. Before 1978 the four *MSY*-rates all have the probability 0.25, but by 1993 *p(MSYR)* are 62%, 28%, 9% and 1% for *MSYR* of 1%, 2%, 3% and 4% respectively. These numbers are in fact the integrals under the four curves in Fig. 2.

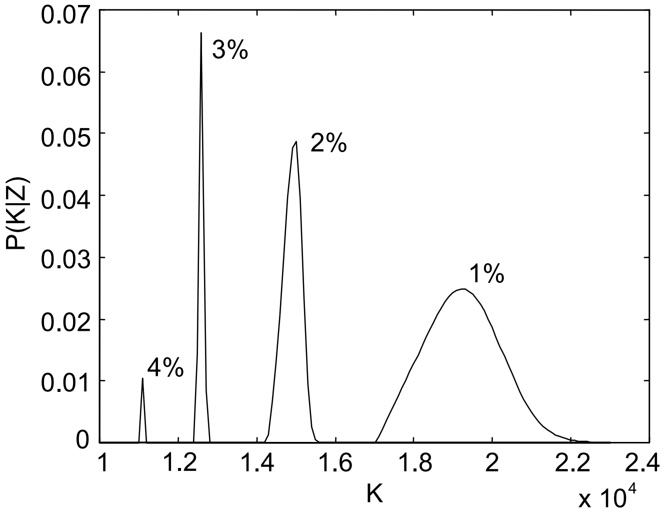

Fig. 2. The posterior probability distribution $p(K|Z_{1993})$ for four values of MSYR.

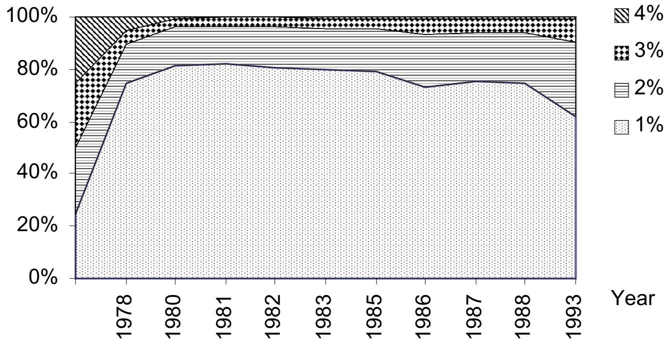

Fig. 3. The evolution of the marginal probability mass function $p(MSYR|Z_t)$ between 1978 and 1993 for four values of MSYR.

The only thing remaining to be specified in the management procedure are the catch control laws corresponding to each filter. The 'H' strike limit rule as defined in IWC (2000a) will be used. This rule gives a strike limit in year t by:

$$H_t = \min\left(Need_t, \begin{cases} 0 & if \quad N_t < 2000 \\ 0.8RY_t & if \quad 2000 \le N_t < MSYL \\ 0.9MSY & if \quad N_t > MSYL \end{cases} \right)$$

where $Need_t$ is the prespecified level of aboriginal need in year t and RY_t is the replacement yield. All parameters refer to the 1+ component of the population (i.e. the total number of animals one year and older). Finally, a maximum of 20% change in strike limits between years is imposed.

An illustration of the AKF-method will now be given by running it on a small subset of the trials defined in IWC (2000b). The main specifications of the trials are given in Table 1, but further details are found in IWC (2000b). The results are given in Table 2. The tuning parameter γ was chosen such that the median final depletion in trial BE01 was approximately 0.78, which is the final depletion when the H-rule with perfect information is applied (in accord with the

Table 1

A subset of trials used to test the AKF method. Initial need is set to 67 in all trials. The Historical survey bias in trials BE09 and BE12 increases linearly in the period 1978-1993 between the values given.

Trial no.	MSYR$_{1+}$	MSYL$_{1+}$	Final need	Historical survey bias	Future survey bias	Survey CV (true, estimated)
BE01	0.025	0.6	201	1	1	0.25, 0.25
BE03	0.025	0.6	201	1	1.5	0.25, 0.25
BE04	0.025	0.6	201	1	0.67	0.25, 0.25
BE06	0.025	0.4	201	1	1	0.25, 0.25
BE07	0.025	0.8	201	1	1	0.25, 0.25
BE09	0.01	0.6	201	0.67→1	1	0.25, 0.25
BE10	0.04	0.8	201	1	1	0.25, 0.25
BE12	0.01	0.6	134	1→1.5	1.5	0.25, 0.10

Table 2

Results of the AKF method for selected trials. The median, the 5th and 95th percentiles are shown for final depletion (D1), lowest depletion (D2), need satisfaction (N9) and the average annual variation (N10).

	D1			D2			N9			N10		
	5th	Median	95th	5th	Median	95th	5th	Median	95th	5th	Median	95th
BE01	0.763	0.777	0.885	0.656	0.711	0.748	0.771	0.985	1.000	0.039	0.051	0.098
BE03	0.791	0.795	0.799	0.656	0.711	0.748	0.970	0.971	0.972	0.039	0.039	0.040
BE04	0.915	0.921	0.929	0.656	0.711	0.748	0.585	0.626	0.657	0.034	0.047	0.064
BE06	0.269	0.451	0.602	0.269	0.407	0.476	0.613	0.702	0.971	0.035	0.058	0.126
BE07	0.931	0.934	0.948	0.717	0.797	0.844	0.965	0.999	1.000	0.039	0.051	0.061
BE09	0.331	0.443	0.593	0.331	0.428	0.509	0.678	0.843	1.000	0.043	0.071	0.134
BE10	0.957	0.967	0.987	0.956	0.960	0.977	0.708	0.973	1.000	0.039	0.056	0.127
BE12	0.210	0.286	0.351	0.210	0.286	0.343	0.776	0.849	0.989	0.045	0.070	0.104

recommendation of the IWC Scientific Committee). Only a few key statistics are given: final depletion (D1), lowest depletion (D2), need satisfaction (N9) and the average annual variation (N10). These statistics are fully defined in IWC (2000a). The results will not be discussed in any great detail here. Suffice it to say that the stock is under-utilised in trial BE04 and over-exploited in trials BE09 and BE12. These results and the possible causes will be discussed in the final section of this paper.

When the AKFs are continued past 1993, the estimated stock trajectories and the further evolution of the posterior probabilities will not only vary between trials but also between each of the 100 simulations comprising each trial. One realisation of trial BE01 is selected here to illustrate the future evolution of *p(MSYR)*. This is shown in Fig. 4. There is a general downward trend in the posterior probability of the 1% *MSYR* and a corresponding upward trend for the 2% and 3% *MSYR* for this particular realisation. Fig. 5 shows the true population trajectory, the estimated trajectory and the actual observations for the same realisation. Note that the estimate of the state *x* (i.e. the logarithm of the stock size) is the sum of the stock estimates coming from each filter, weighted by the posterior probabilities $p(A_i,K_j|Z_t)$, as illustrated in Fig. 1. The estimated trajectory follows the actual trajectory fairly well, in spite of a wide scattering in the observations.

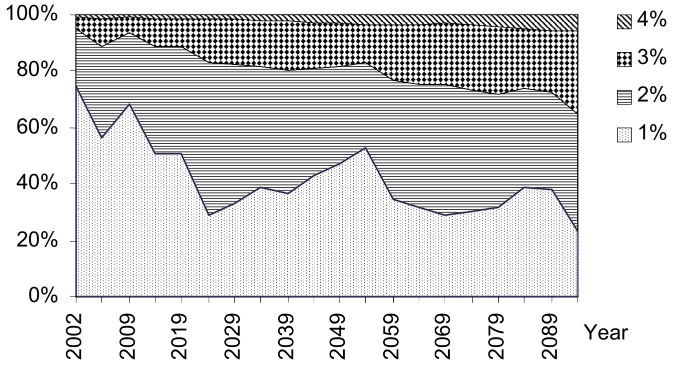

Fig. 4. The evolution of the marginal probabilty mass function $p(MSYR|Z_t)$ over the 100-year management period for one realisation of trial BE01.

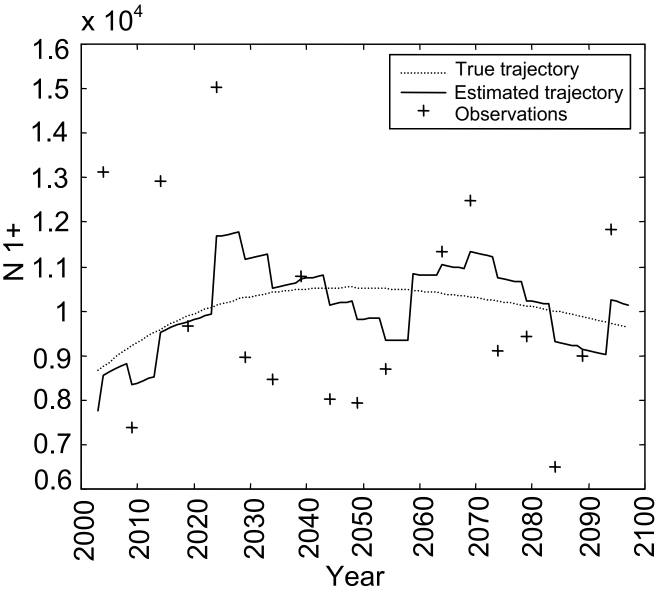

Fig. 5. The true population trajectory, the observations and the estimated trajectory using the Base Case version of the AKF method for one realisation of trial BE01.

SENSITIVITY TESTS

In order to investigate how sensitive the procedure is to the various features which specify the Base Case Model, a few of those specifications were varied.

Firstly, the effect of a finer *MSYR* grid was investigated by letting *MSYR* range from 0.5% to 4% with a step size of 0.5%, giving a total of 8 × 131 = 1,048 filters. Fig. 6 shows the posterior probability distribution $p(K|Z_{1993})$. The mode is now at for 3.5% *MSYR*, but the greatest mass is at 0.5% and 1%. The evolution of the marginal probability mass function $p(MSYR|Z_t)$ between 1978 and 1993 shows more or less the same pattern as the Base Case Model, except for the difference in resolution. This AKF model, was then tested on the same set of simulation trials as the Base Case Model. The value of the tuning parameter γ was chosen so that the median final depletion in trial BE01 was the same as for the Base Case Model. It turned out that the differences were minimal; the median values were more or less unchanged, but the spread was slightly higher in some trials and lower in others. In view of the small differences between the two versions, there appears to be no reason to change the specification of the Base Case Model by taking a finer *MSYR* resolution.

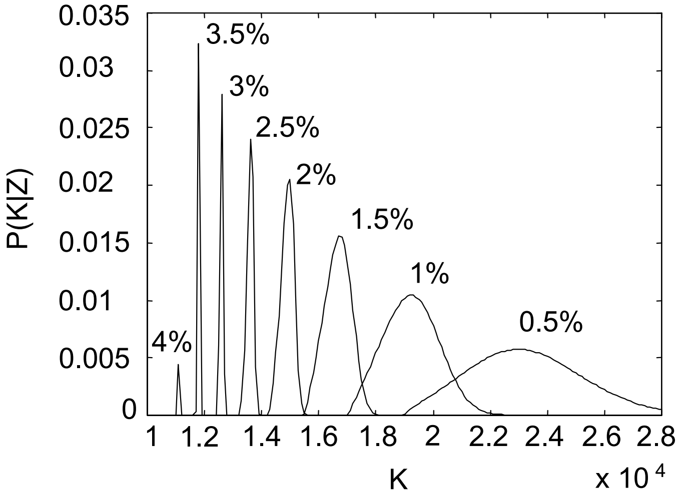

Fig. 6. The posterior probability distributions $p(K|Z_{1993})$, for eight values of MSYR.

Secondly, the effect of varying the process variance Q was examined. The value used in the Base Case Model is 10^{-3}, and here the values, 10^{-2}, 10^{-3}, 10^{-4}, 10^{-5} were used. Note that a large value of Q, means that the filter will place a relatively greater weight on the observations and thus the filters tend to follow the observed values more closely, leading to greater fluctuations. This is illustrated in Fig. 7 which shows the same realisation as Fig. 5, but with $Q = 0.01$. Fig. 8 shows the posterior probabilities, $p(MSYR|Z_{1993})$, demonstrating how the $MSYR$ = 1% filters get a larger share as Q increases. Fig. 9 shows need satisfaction (N9) as a function of Q for trials BE01 and BE09. The results in the former trial are not very sensitive to Q, but a high or a low Q value deplete the stock even further than the Base Case Model in BE09. These results do not provide justification for changing the value of the process variance used in the Base Case Model.

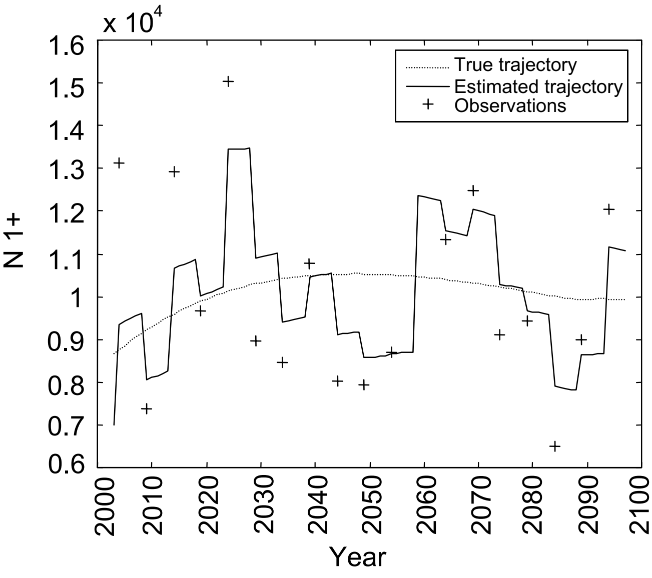

Fig. 7. The true population trajectory, the observations and the estimated trajectory using the AKF method with process variance equal to 0.01 for one realisation of trial BE01.

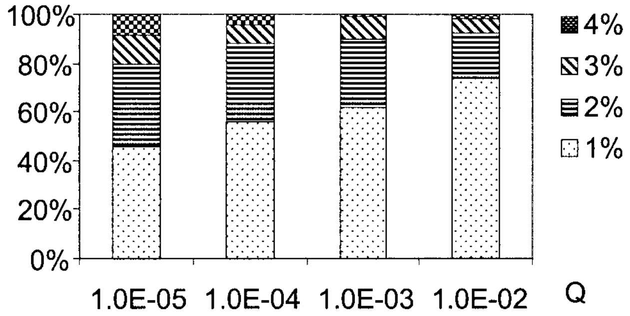

Fig. 8. The marginal probabilty mass function $p(MSYR|Z_{1993})$ for four different values of the process variance Q.

Finally, the possibility of detecting a bias was considered. A three-dimensional grid of filters was used; that is filters with a bias factor of 0.67, 1.0 or 1.5 were included, which gave a total of 4 × 3 × 131 = 1,572 filters. This version of the AKF-method was then applied to trials BE01, BE03 and BE04, which are trials with bias factors of 1.0, 1.5 and 0.67 respectively. A slight modification was made to the trials in that it was assumed that the historical observations were also biased; that is the historical observations were multiplied by the bias factor relevant to that trial and those numbers were then provided to the management procedure. This was done for reasons of consistency, since it is unlikely that future observations are biased when past ones are not. This change does in fact make the trials 'harder' since the jump in the bias factor helps in identifying a bias case. The results are shown in Fig. 10. Note that need was almost fully satisfied in BE01 and BE03 with the Base Case Model (but with the 5th percentile rather low in the former), but there was considerable under-utilisation in BE04. The results in trial BE01 for the version with bias filters are better than for the Base Case version since the median need is almost the same, but the 5th percentile is much higher; trial BE03 results are almost unchanged, but there is great improvement in BE04 where nearly full need satisfaction is achieved as opposed to only 63% for the Base Case Model. This particular grid of filters only includes cases with a constant bias and the possibility that the bias may be changing through time is not considered. This scenario is addressed in trials BE09 and BE12 where it is assumed that the bias in the historical (1978-1993) observations increased. The AKF with bias filters performs worse than the Base Case Model in trial BE09 where the stock is more heavily depleted (Fig.10c). The marginal posterior probabilities for the 12 combinations of *MSYR* and bias factor after the 100-year management period are shown in Fig. 11 for one realisation of BE01 and BE03. It is clear that those probabilities are highest for the correct bias factor. These results are therefore very

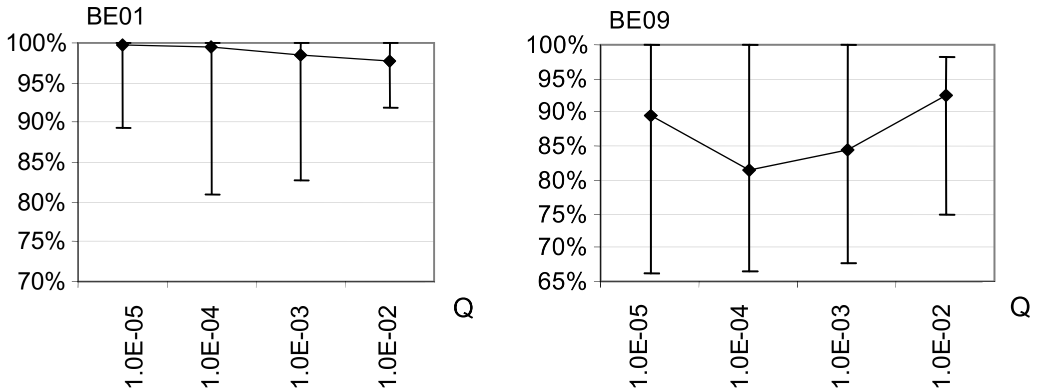

Fig. 9. Comparison of need satisfaction (N9) in trials BE01 and BE09 for four different values of the process variance *Q*.

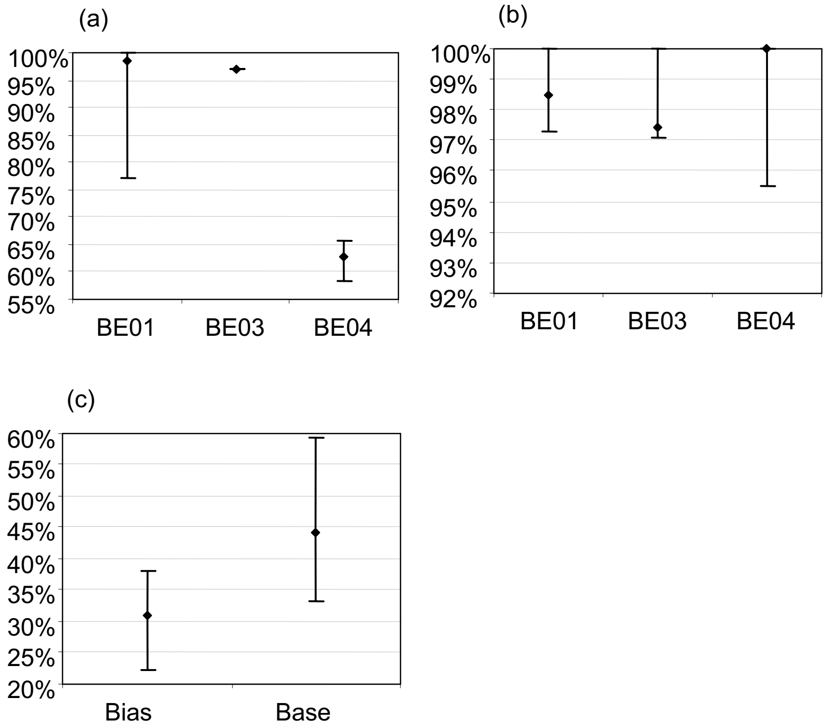

Fig. 10. Need satisfaction (N9) in trials BE01, BE03 and BE04 for the Base Case Model (a) and the version with bias filters (b). Final depletion (D1) in trial BE09 for Base Case Model and the bias filter version (c). Note the different scales on the vertical axis in (a) and (b).

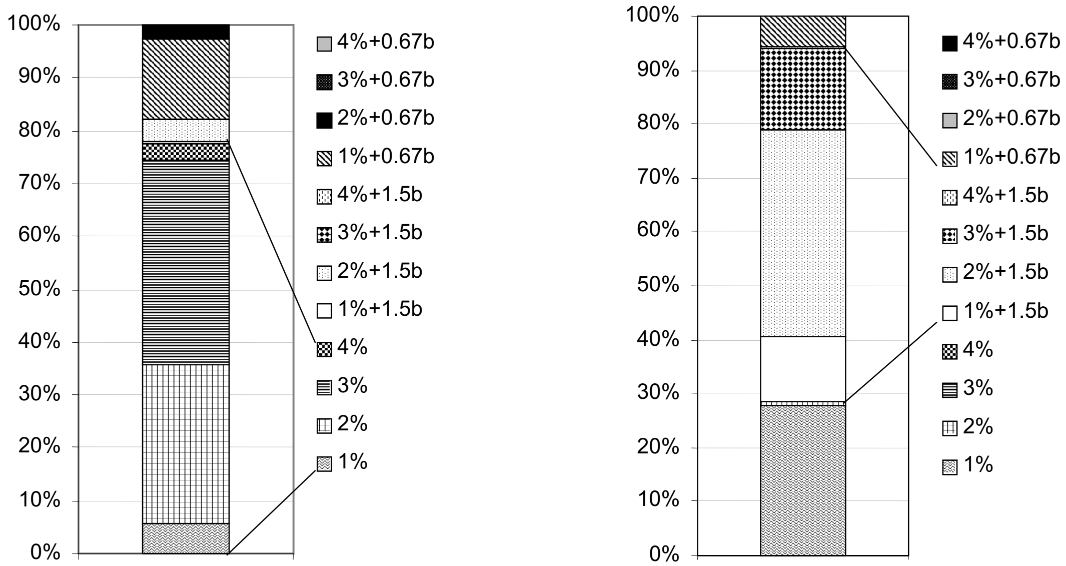

Fig. 11. One realisation of the marginal probabilty mass function $p(MSYR|Z_t)$ after 100 years of management for BE01 (left panel) and BE03 (right panel).

promising and give some cause for optimism that a bias in the data may in fact be correctly identified by the AKF-method.

DISCUSSION

The results of the set of trials presented in Table 2 show adequate or good performance in all except BE04 (low need satisfaction), BE09 and BE12 (too much depletion). Note that the final depletion in BE06 is quite acceptable since the *MSYL* is 0.4. The poor need satisfaction in BE04 is due to the fact that abundance observations are downwards biased by a factor 0.67. The performance in this trial can be greatly improved by including a bias factor in the set of filters (cf. Fig. 10). Trial BE12 is inherently difficult: low *MSYR*, positively biased observations and underestimated CVs. In fact, it may not be possible for a management procedure to perform adequately in this trial and simultaneously attain an acceptable level of need satisfaction in the other trials. Trial BE09 is a low *MSYR* trial, but it should be possible get a reasonable performance by the AKF-method. The 1% *MSYR* has the largest share of the posterior probability $p(MSYR|Z_{1993})$, about 62%. This fraction will generally decrease over the 100-year management period, albeit rather slowly. It would therefore seem that the strike limit is set more or less in accordance with the $MSYR = 1\%$ case. However, the particular tuning chosen requires a tuning parameter $\gamma = 0.75$. Thus, γ is larger than $p(MSYR = 0.01)$ which means that the eventual strike limit will be somewhat higher than appropriate for the 1% case. It may therefore be worthwhile to explore other tunings.

The sensitivity tests carried out in this paper provide no reasons for changing the Base Case version of the AKF-method, except possibly to add the third dimension to the grid of filters, i.e. to include bias filters. The preliminary results in this direction are promising and this possibility is worth investigating further. However, including filters with constant bias may lead to a deterioration in performance in scenarios where the bias is changing with time as illustrated in Fig. 10c. An obvious way of attempting to address this problem is to add filters with a changing bias and this may be worth exploring further. However, one must be careful not to let the set of filters mimic too closely the trial set. Some separation between the two sets must be maintained. Introducing a filter to correspond to each trial goes against the philosophy behind the process of developing a management procedure. Ideally, the trial details should not be known to the persons developing the management procedure.

The value of the process variance used in the AKF-method is not based on any knowledge of whale population dynamics. Rather, Q is to be regarded as a parameter, which should be set with improved trial performance in mind. It should however, be borne in mind that the Kalman Filter gives less weight to the model and more weight to the observations when Q is large. The filter may therefore disregard the model more or less; it can not distinguish between the different *MSY*-rates for example, and the strike limit is therefore set on the basis of observations alone. This may be the main explanation for the behaviour in Fig. 9. The need satisfaction in BE01 decreases with Q, but increases in BE09. The former is a 2.5% and the latter a 1% *MSYR* trial. The filters are less able to discriminate between 1% and 2.5% as Q increases and the catch levels in the two trials will therefore approach each other.

Some preliminary investigations of the sensitivity of the results to the population model used in the filters have been made using different models, for example a model with delay in the dynamics, (Dereksdóttir and Magnússon, 2000) and a model that finds the K that best fits the historical data for pre-specified values of *MSYR*, thus giving pairs of $[MSYR,K]$, and thereby a one-dimensional grid of filters. The results of those tests were not dramatically different from the ones presented here, but performance was not improved in general. It should also be noted that the model of the stock dynamics used in the AKF-method is not the same as that used to generate the data in the trials. The method is nevertheless fairly successful in tracking the actual trajectory (an example is given in Fig. 5). Other variations of the AKF-method were also investigated, but this will not be discussed here. Suffices to say, that the model presented here as the Base Case Model gave the best overall performance of all the different versions tried, except possibly for the version of the AKF-method with bias filters. Exploring this version further is a future task. Other tasks for the future, are to explore whether performance can be improved by amending the catch control laws and to look at the sensitivity of the results to the values of the fixed parameters z and S.

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Historical occurrence and distribution of humpback whales in the eastern and southern Caribbean Sea, based on data from American whaling logbooks

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ABSTRACT

The best-known present-day wintering areas for the North Atlantic population of humpback whales (*Megaptera novaeangliae*) are in the northern West Indies, notably off the island of Hispaniola. However, it is known that in the nineteenth century American whalers hunted humpbacks in the Windward Islands (primarily from Guadeloupe southwards), along the coast of Trinidad, in the Gulf of Paria and westwards along the Venezuelan coast. To investigate the historical distribution and occurrence of humpback whales, data were extracted from nineteenth century American whaling logbooks and journals covering 48 voyages by 29 vessels to the West Indies from 1823-1889. Humpback whale records in these documents came from a geographical area that encompassed Haiti to the coast of Venezuela. Of 807 records in which whales were mentioned (as sightings, strikes or catches), the largest number was from the Windward Islands and Venezuela, especially St Vincent and the Grenadines (319 records covering an estimated 958 humpbacks), Guadeloupe (190 records, 592 humpbacks), Dominica/Martinique/St Lucia (74 records, 193 humpbacks) and Venezuela (64 records, 216 humpbacks). These totals should be regarded only as approximate indicators of the relative abundance of whales since the effort involved cannot be meaningfully quantified. Similarly, effort-uncorrected data suggest that the peak months for humpback whales in the Windward Islands were February, March and April. Few sightings were recorded off the Dominican Republic after March, but this may reflect a lack of effort there in April and May. However, humpbacks apparently were abundant in the Windwards in April and even May, which is not the case in the major present-day wintering areas off Hispaniola. With one notable exception, there is little evidence in the logbooks and journals that humpbacks were taken on a more than casual basis in waters off Hispaniola, where the major aggregations are found today; possible explanations for the marked contrast in present versus historical distribution are discussed. The highly seasonal visitation of the West Indies by the American nineteenth-century whalers precludes a meaningful investigation of the possibility that some humpbacks from the Southern Hemisphere migrated to the Caribbean Sea in the austral winter.

KEYWORDS: HUMPBACK WHALE; WHALING–HISTORICAL; CARIBBEAN SEA; WEST INDIES; DISTRIBUTION

INTRODUCTION

Most of the North Atlantic population of humpback whales (*Megaptera novaeangliae*) is today believed to overwinter in the West Indies region (Winn *et al.*, 1975; Katona and Beard, 1990). When the whales are in these warm tropical waters, calving and mating take place, but little feeding occurs. Whaling data compiled by Townsend (1935), Mitchell and Reeves (1983) and Price (1985) indicate that humpbacks were taken by American whalers during the nineteenth and early twentieth centuries primarily in the Windward Islands region from Guadeloupe south to the coast of Venezuela. In contrast, most of the recent research effort directed at overwintering humpbacks has been focussed in the northern part of the Antillean chain, with the greatest concentrations of whales found on banks north of the Greater Antilles. The greatest concentrations of humpbacks are found today off the northern coast of the Dominican Republic (on Silver Bank and Navidad Bank, and in Samana Bay). To the east of this region (from Puerto Rico to the Windwards), whale densities are at least one order of magnitude lower (Mattila and Clapham, 1989; Mattila *et al.*, 1994).

Improved understanding of the stock origin and status (current versus historical abundance) of humpbacks in the eastern and southern Caribbean Sea is needed for the IWC's Comprehensive Assessment of humpbacks in the North Atlantic and for planning field work in the Caribbean region. The study by Mitchell and Reeves (1983) was intended primarily as a reconstruction of the humpback's catch history; it was not among those authors' priorities to specify the precise dates and positions of kills or sightings. The primary objective of the present study was to establish where and when the sailing-vessel whalers encountered humpbacks in the eastern and southern Caribbean region. The unpublished data presented here are from whaling records and refer only to years well before the late 1920s, by which time American pelagic whaling in the North Atlantic had ended (Hegarty, 1959) and shore whaling for humpbacks was no longer practised in the Caribbean region except on the island of Bequia (Adams, 1971; Mitchell and Reeves, 1983). A map showing the places referred to in the text is given as Fig. 1.

MATERIALS AND METHODS

Identifying the logbook/journal sample

Mitchell and Reeves (1983) tabulated humpback catch data from logbooks or journals covering some 80 American whaling voyages. They selected documents to maximise the probability of finding evidence of humpback whaling in the West Indies. Their sample was taken from two major collections: Providence Public Library (PPL) and Old Dartmouth Historical Society (ODHS). In a later, similar study targeted at North Atlantic right whales (*Eubalaena glacialis*), Reeves and Mitchell (1986) examined the logbooks or journals from an additional 50 voyages to North Atlantic whaling grounds, including documents from six other major North American collections. Although their focus on right whales meant that Reeves and Mitchell (1986) did not consistently extract data on humpback observations,

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Fig. 1. Map of study area.

their study identified additional approaches to obtaining such data. Some collections have their own indices which include ports of call mentioned in logbooks and journals. This provides an efficient way of identifying promising manuscripts in the collection (i.e. by checking for voyages that called at Caribbean destinations). The Dennis Wood Abstracts at the New Bedford Free Public Library (NBFPL) contain valuable data on the itineraries and production (oil and baleen on board at various stages of a voyage) for some 3,500 American whaling voyages (cited herein as: Wood, no date, MS). Sherman *et al.* (1986), in a comprehensive inventory of logbooks and journals in public collections, provide a means of determining whether a document covering a particular voyage was available as of the mid-1980s. This volume is particularly useful because it is indexed by port, master and keeper, sailing year, ground(s) visited and document repository.

For the present study, the documents previously checked by Mitchell and Reeves (1983) and Reeves and Mitchell (1986) were subsampled. Initially, voyages were selected that were already known or suspected to have whaled for humpbacks in the eastern or southern Caribbean. The characteristics described by Mitchell and Reeves (1983) were then used to identify additional voyages likely to have included a period of whaling for humpbacks in this region. The most promising voyages were those by smaller vessels (brigs and schooners of less than about 140 tons) sailing from Provincetown and a few other minor ports (e.g. Westport, Mattapoissett, Fairhaven, Edgartown and Boston) and indicating a ‘North Atlantic’ or ‘Atlantic’ destination. A late autumn or early winter departure (e.g. November to January) and a return to home port by the following late summer or autumn were considered especially favourable, although it was not unusual for a vessel to visit the West Indies and to whale for humpbacks in the second winter of a multi-year cruise.

Clark (1887) describes a typical humpbacking itinerary for a Provincetown whaler, on the authority of Captain Atwood. The vessel would sail in mid to late January and go directly to the West Indies. It would cruise for humpbacks near one or more of the islands between Tobago (11°20’N, 60°27’W) and Marie-Galante, Guadeloupe (15°52’N, 61°18’W) until late April or early May. From the West Indies most vessels headed for the Western, Charleston or Hatteras Ground in pursuit of sperm whales (*Physeter macrocephalus*), returning to Provincetown in September.

In many instances the foregoing considerations were supplemented with information on itineraries, ports of call and oil returns (intermediate or final) from Wood (no date, MS). Although final returns for most voyages are given by Starbuck (1878) or Hegarty (1959), these are generally expressed only in barrels of sperm oil, barrels of whale oil and pounds of bone (i.e. whalebone, or baleen). In contrast, Wood (no date, MS) frequently specifies whether the whale oil was from blackfish (pilot whales, *Globicephala* spp.) or humpbacks. However, his references to blackfish oil were not always found to be reliable. For example, his abstract of the 1857-59 cruise of the barque *N.D. Chase* of Beverly makes it clear that several right whales were taken on the Cintra Bay Ground off West Africa (also confirmed by Reeves and Mitchell (1986, table 4) on the basis of information in another vessel’s logbook). In his summary at the end of the abstract, Wood indicates a return of 575 barrels of ‘blackfish’ oil alongside 6,000 pounds of bone (no mention of ‘whale’ oil in the summary). This is a rather egregious example of an inconsistency that arises often in the Wood material. On a few occasions Wood mentions humpbacking explicitly as an activity reported for a particular voyage. Inclusion of ‘bone’ (baleen) in the returns listed by Starbuck, Hegarty or Wood usually means that one or more right whales were taken and thus that at least some of the whale oil (or ‘blackfish’ oil; see above) listed was from right whales rather than humpbacks or blackfish.

Data recording

Data were recorded onto two types of data sheet: (1) for information on the voyage as a whole, including the vessel specifications, itinerary, time spent on the humpback grounds and other vessels seen there; and (2) for details of humpback observations. Very few documents were read in their entirety. As a rule, it was determined by rapid scanning whether and when the vessel reached the West Indies. From that point until the vessel departed the region, daily entries were checked for references to humpbacks. Most logbook or journal writers made clear the distinction between humpbacks and other whales although in some instances the reader had to infer the identity of the whales. Pilot whales were always called ‘blackfish’. When sperm whales were seen or chased on the humpback grounds, the writer seems invariably to have specified them as such. ‘Finbacks’ mentioned in this region could have been fin whales (*Balaenoptera physalus*), sei whales (*B. borealis*) or Bryde’s whales (*B. edeni*) (cf. Mead, 1977).

The whalemen who kept logbooks or journals present the reader with an often bewildering array of place names; this makes the work of determining where the vessel was at any given time painstaking at best and exasperating at worst. Legibility of the manuscripts is highly variable and so is the level of detail provided by the writers. In some instances landmarks are very precise, referring to a rock, islet or farm (i.e. plantation or estate). On other occasions nothing is provided beyond the name of the island. Frequently reference is made to the site where the vessel anchored for the night, and it is either stated or implied that the intervals between anchorings were spent cruising, with a lookout kept for whales. At times the vessel would remain anchored while the boats were lowered to chase whales in nearby waters. More often than not, the reader is told approximately where a whale was towed for processing and can only infer that it was therefore taken within a few miles of that site.

Data management

A computer database was established with two components. The first was a summary of each voyage, and included information on vessel name, voyage number (a reference number that was assigned by us), port and date of sailing, ground(s) worked, and notes about the legibility, usefulness or other characteristics of the log. The second component contained a summary of all relevant records from each log, including vessel and voyage number, record type (see below), date, location and (where relevant) number of whales seen, struck or killed. Record types examined here were categorised as either 'whale' (information about sightings of, or attempts to kill, whales), or 'no whales' (records in which a log explicitly refers to the absence of whales in a particular location). Other information about where the vessel was on a particular day, and records which mention shipments of whale oil, processing of whales, reports of other vessels and other miscellaneous items not related to whale sightings *per se* were included in the database but are not discussed further here. Reports of 'lowering for whales' or of whales seen but lacking any indication of how many whales were present, were recorded but not used in this analysis.

Records of whales were further broken down into five categories: 'taken number' (a specific number of whales reported as killed and secured); 'taken barrels' (records in which the number of whales taken is expressed in terms of oil yield, in barrels); 'struck' (whales chased and struck with a harpoon but not killed, or killed but not secured); 'seen number' (a specific number of whales reported as sighted but not struck); and 'seen category' (records in which sightings of whales are not associated with a number but rather with some descriptive term, e.g. 'few', 'many').

With regard to the latter category, the various descriptive terms found in the logs were grouped for simplicity as follows: 'many' = *many, a school, plenty, great number, a pod, a gam*; 'several' = *a number, several, some, more, saw humpbacks, chased humpbacks*; and 'few' = *few*. For the purpose of analysis, an 'average' number was assigned to each of these categories, as follows: 'many' equalled ten whales, 'several' equalled four whales and 'few' equalled two whales. It is recognised that these choices are arbitrary, and results are presented with that caveat.

Location information associated with whale reports fell into two categories. In many cases, an exact location (such as a bay or a latitude and longitude) was given; in the database, these were termed 'certain' locations. In other cases, an exact location was not given but a general location could be inferred from preceding or subsequent log entries; in the database, these are termed 'inferred' locations. Cases in which a lack of information precluded assignment of even an inferred location were treated as 'no location'. Major geographic names used in this report are defined in Appendix 1.

RESULTS

Summary of the data

The data described here came from a total of 48 voyages to the West Indies by 29 vessels. The earliest cruise occurred in 1823, the latest in 1889. Ports of departure for these voyages were: Beverly, Massachusetts (1 voyage); Boston, Massachusetts (1); Dartmouth, Massachusetts (2); Fairhaven, Massachusetts (1); New Bedford, Massachusetts (6); Provincetown, Massachusetts (26); Rochester, Massachusetts (3); and Westport, Massachusetts (5). The port was uncertain for three voyages (two of them by a vessel known to have made six other voyages, all from Provincetown). A total of 850 records was used in the analysis. This included 807 records of whales and 43 records of 'no whales' (Table 1).

Table 1

Summary of records relating to humpback whales for all West Indies locations. 'Dominican Republic' includes all records relating to Mona Passage. 'Coast of Venezuela' excludes the Gulf of Paria. Regions for which there was no mention in the logbooks of the presence (or absence) of humpback whales were ignored.

Region	Whales	No whales	Total
St Martin to Montserrat	16	3	19
Barbados	3	0	3
Caribbean Sea (Aves Is.)	1	0	1
Dominica, Martinique, St Lucia	74	2	76
Dominican Republic	68	2	70
Gulf of Paria	24	6	30
Guadeloupe	190	5	195
Haiti	1	0	1
Puerto Rico	8	2	10
St Vincent and the Grenadines	319	18	337
Trinidad and Tobago	39	3	42
Coast of Venezuela	64	2	66
Total	807	43	850

The study area was divided somewhat arbitrarily into 12 regions. This division was not intended to provide a grid of equal-sized regions, but rather to distinguish the major whaling grounds geographically. The 12 regions are listed in Table 1, with a summary of the number of records available for each. Some logbooks mention other regions (Anguilla to the Virgin Islands, Cuba, Jamaica and the Turks and Caicos) but provide no information on the presence (or absence) of humpback whales there, and thus were ignored. By far the largest number of records (337) came from St Vincent and the Grenadines. Other regions with numerous records included Guadeloupe (195), Dominica/Martinique/St Lucia (76) and the coast of Venezuela (66, with an additional 30 from the Gulf of Paria).

Records of humpback whales

The number of records ('whale' and 'no whale') are summarised by month in Table 2. The great majority of humpback whale observations were reported in February, March and April: 679 (85.1%) of the 798 whale records are from these three months. Nine additional whale records had no month indicated.

Table 2

Summary of West Indies whale-related records by month. There were no records for the months of July to November. Nine records (all concerning whales) for which no month was specified are excluded.

Month	Whale records	'No whales' records
January	43	8
February	168	13
March	278	9
April	233	11
May	74	1
June	2	0
December	0	1
Total	798	43

Records of humpback whales are summarised by region in Table 3, together with estimates of the total numbers of whales represented. These estimates involve assumptions

Table 3

Summary of records of humpback whales, for all West Indies locations, and estimates of total numbers represented by these records. Areas for which no whale records were found were omitted. Whales were either reported as an exact number of animals (either *Taken*, *Struck* or *Seen*), or by various terms which are grouped here as *Few*, *Several* and *Many*. For the purpose of estimating whale numbers, the following values were assigned to the latter three categories: *Few* = 2, *Several* = 4, *Many* = 10. The resulting numbers are given in the *Whales* column under each of the three categories; the previous column (*Recs* = records) shows the number of records found for each category (in *italics*, since these are not included in the *Total Whales* column at the end). See text for other definitions.

		Humpback whales reported									
	Total whale	Number of whales			'Few'		'Several'		'Many'		
Region	records	Taken	Struck	Seen	*Recs*	Whales	*Recs*	Whales	*Recs*	Whales	Total whales
St Martin to Montserrat	16	0	1	22	*0*	0	*3*	12	*0*	0	35
Barbados	3	0	0	3	*0*	0	*1*	4	*0*	0	7
Caribbean Sea (Aves Is.)	1	0	0	0	*0*	0	*1*	4	*0*	0	4
Dominica, Martinique, St Lucia	74	20	20	71	*1*	2	*15*	60	*2*	20	193
Dominican Republic	68	15	5	63	*0*	0	*21*	84	*0*	0	167
Gulf of Paria	24	2	2	11	*0*	0	*7*	28	*6*	60	103
Guadeloupe	190	72	15	83	*21*	42	*80*	320	*6*	60	592
Haiti	1	0	0	0	*0*	0	*1*	4	*0*	0	4
Puerto Rico	8	1	0	3	*0*	0	*4*	16	*0*	0	20
St Vincent and the Grenadines	319	102	57	141	*1*	2	*139*	556	*10*	100	958
Trinidad and Tobago	39	4	5	10	*2*	4	*23*	92	*3*	30	145
Coast of Venezuela	64	13	18	21	*0*	0	*26*	104	*6*	60	216
Total	807	229	123	428	*25*	50	*321*	1,284	*33*	330	2,444

regarding the number of whales represented by terms such as 'few' or 'many ' (see above); given this, as well as probable inaccuracies in reporting, the estimates should be treated as no more than crude approximations. That said, they probably provide reasonably valid indications of the relative abundance of whales and/or effort in each of the regions concerned. Of the estimated 2,444 humpback whales represented in the records, the largest numbers were reported from St Vincent and the Grenadines (estimated total 958, or 39.2%); followed by Guadeloupe (592 whales, 24.2%); the coast of Venezuela (216 whales, and an additional 103 from the Gulf of Paria, 13.1% combined); Dominica/Martinique/ St Lucia (193 whales, 7.9%); the Dominican Republic (167 whales, 6.8%); and Trinidad and Tobago (145 whales, 5.9%). As noted below, more than a third of the estimated number of whales for the Dominican Republic (65 or 38.9%) come from the logbook of a single voyage, that of the *Cicero* in 1872.

The relative numbers of humpback whales in each region for the months of January through May are shown in Fig. 2 (with regions arranged from north to south). Peak numbers appear to have occurred somewhat earlier to the south (February or March off Trinidad, Venezuela and in the Gulf of Paria) and later to the north (March and April in the area from Guadeloupe to St Vincent and the Grenadines). Once again, however, it is stressed that these records cannot be corrected for effort and thus only crudely reflect the occurrence and movements of humpback whales.

The 43 records in which the absence of humpback whales was explicitly noted are broken down by region and month in Table 4. It is difficult to interpret these 'no whale' records. The absence of whales would likely be recorded in the logbook only on days when sighting conditions were acceptable and there was some search effort, although it cannot be assumed that the whalers' thresholds of 'acceptable' sighting conditions and the quality of their search effort were in any sense standardised. While it may be reasonable to conclude that whales were not present in the immediate vicinity of the vessel on these 'no whale' days, the very fact that the whalemen were searching for them

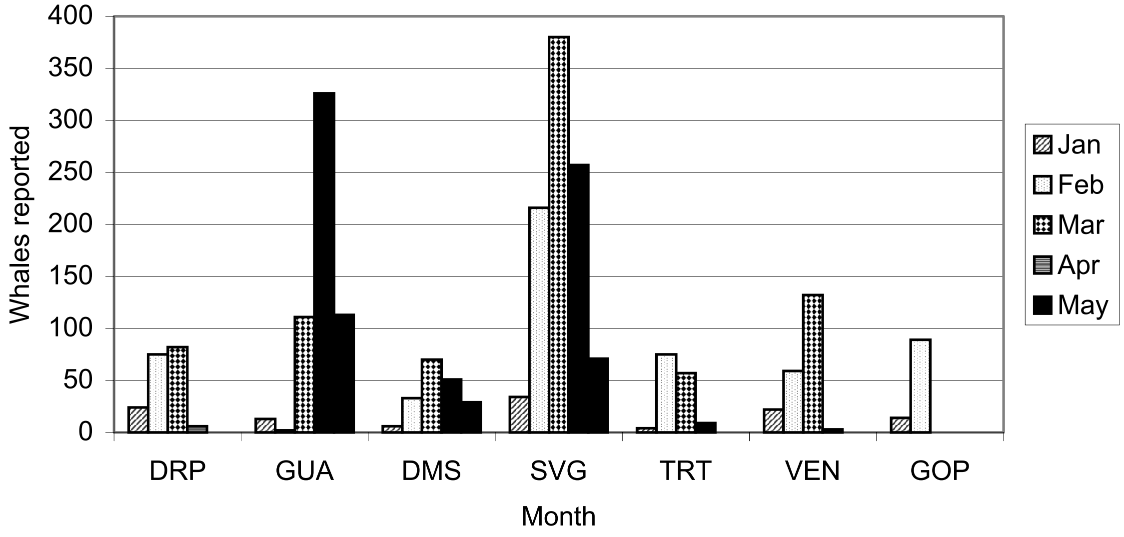

Fig. 2. Estimated numbers of humpback whales observed (sightings, strikes and kills) by month and region. The regions are arranged from north to south, with abbreviations as follows: *DRP* Dominican Republic and Puerto Rico, *GUA* Guadeloupe, *DMS* Dominica/Martinique/St Lucia, *SVG* St Vincent and the Grenadines, *TRT* Trinidad and Tobago, *VEN* coast of Venezuela and *GOP* Gulf of Paria.

implies an expectation of finding humpbacks in the area, and this expectation may have arisen from empirical knowledge concerning whale distribution and movements. No further consideration of the 'no whale' records was judged appropriate.

Table 4

Summary of records, by region and month, in which the absence of humpback whales was explicitly stated.

Region	Records of 'no whales' Jan.	Feb.	Mar.	Apr.	May	Dec.	Total
St Martin to Montserrat				3			3
Dominica, Martinique, St Lucia	1	1					2
Dominican Republic			2				2
Gulf of Paria	3	3					6
Guadeloupe	1			3	1		5
Puerto Rico		2					2
St Vincent and the Grenadines	3	3	6	5		1	18
Trinidad and Tobago		2	1				3
Coast of Venezuela		2					2
Total	8	13	9	11	1	1	43

Narrative of results by area

A detailed narrative of results for each area is given below. The results are presented in geographical order starting in the north and working south. The evidence is summarised for humpback whales and whaling in the vicinity of each major island or island group.

Greater Antilles

A puzzling feature of the logbook records is how little effort seems to have been devoted to pursuing humpbacks in areas of the Greater Antilles where they are known to be abundant today. The brig *Annawan* of Rochester (1836-37, MS) cruised along the southern coast of Puerto Rico ('Porto Rico') during the last week of February and first few days of March 1837, clearly in pursuit of sperm whales and blackfish. No attempt was made to catch humpbacks even though one was seen on 20 February at 17°17'N and more off Isla Caja de Muertos ('Deadman's Chest') on 2 March. This lack of interest in humpbacks is particularly striking because the *Annawan* had made dedicated searches for them earlier in the season around St Vincent, Bequia and Trinidad. Two years later the brig *Solon* of Rochester (1838-39, MS) also encountered humpbacks off the south side of Puerto Rico on 10 and 15 March but ignored them. Similarly, on 12 April 1843 the schooner *Esquimaux* of Provincetown (1843, MS) lowered the boats to close on a 'breach' in Mona Passage[1] only to discover that the whale was a humpback, at which point the chase was abandoned and the crew's attention redirected to the search for blackfish.

The brig *Medford* (1849, MS) of Provincetown was in Mona Passage for approximately the first three weeks of March 1849. Humpbacks were reported as being seen several times, including a cow and calf on 6 March, and the boats were lowered for humpbacks once (17 March). Most lowerings were for blackfish. By early April the *Medford* was whaling elsewhere to the west and north (calling at Port au Prince Bay and at Watling and Mayaguana islands in the Bahamas, for example), clearly in search of sperm whales and blackfish. Two years later the *Medford* (1850-51, MS) again visited Mona Passage, this time from 17 February to 7 March. Occasionally within sight of as many as eight other whaling ships, the *Medford* cruised daily for humpbacks and blackfish between Isla Mona and Cabo Rojo ('Cape Roxo'). Humpbacks were seen on at least seven days. Although the boats were lowered to chase them several times, no humpbacks were struck. On 7 March, while the vessel was heading west around Hispaniola, humpbacks were seen off Isla Saona.

In the late 1860s several vessels devoted considerable effort to catching humpbacks in Mona Passage. The schooner *Winged Racer* of Provincetown (1867, MS) sailed directly to Mona Passage ('Mooner Passage') and began chasing humpbacks there on 14 February. By the second week of April, when the *Winged Racer* relocated to Samana Bay (on the northeastern coast of the Dominican Republic), five humpbacks had been secured. At least one other vessel had been seen whaling in the Passage in mid-March (schooner *Watchman*). The next year the *Winged Racer* (1868, MS) returned to the same area and hunted humpbacks in company with the *Ellen Rizpah* of Provincetown from early February through March. At least two humpbacks were taken, and one was struck and lost.

There is circumstantial evidence that several other vessels might have taken humpbacks off Puerto Rico. The brig *Imogene* of Provincetown was in the same area as the *Solon* in March 1839 with 125bbl of humpback oil on board (*Solon* 1838-39, MS; also noted in Wood, no date, MS). The schooner *Harmony* of Nantucket was on the Bahama Banks in June 1837 with 200bbl of humpback oil on board, having been seen off the west end of Puerto Rico in early May (Wood, no date, MS). The barque *Richard Henry* of Rochester was off Puerto Rico on 30 March 1843 with 40bbl of humpback oil on board, having been reported less than three months earlier at La Blanquilla ('Blanco') with only sperm oil on board (Wood, no date, MS). The barque *Parker Cook* of Provincetown was reported off the southwestern coast of Puerto Rico on 20 January 1848 with 200bbl of sperm oil on board and then off Santo Domingo ten days later with 200bbl of sperm and 20bbl of humpback oil (Wood, no date, MS). The brig *Ellen Rodman* of New Bedford was off Puerto Rico in mid-February 1847 with two whales, apparently humpbacks judging by the oil returns (70bbl humpback oil) (Wood, no date, MS). The schooner *Oread* of Provincetown sailed on 1 January 1861 and was off Saona Island, Santo Domingo, on 10 March with 100bbl of humpback oil on board (Wood, no date, MS). It is important to note that it was not unusual for voyages to the Grenadines for humpbacks to end in April or May, with the vessel stopping at Dominica or St Eustatius to transship oil and refit, then head to Hispaniola, Puerto Rico or the Bahamas to hunt sperm whales *en route* northwards.

With one notable exception (see below), humpbacking in Samana Bay ('Sam Bay', 'Samba' etc.) on the northeastern coast of Hispaniola was desultory. The brig *Mexico* of Westport (1823-24, MS) cruised there from about 13 January to early March 1824 and reported seeing humpbacks on only one occasion (24 February); no attempt was made to take them. The *Annawan* (1836-37, MS) was in the bay hunting sperm whales and blackfish during the first two weeks of March 1837 but reported no humpbacks. The schooner *Walter Irving* (1856-57, MS) of Provincetown, having spent a month and a half chasing humpbacks in the Cape Verde Islands, arrived in Samana Bay on 24 March

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[1] Mona Passage lies between the west coast of Puerto Rico and the eastern end of Hispaniola. Because locations were usually not specific, and for the sake of simplicity, all whale records mentioning Mona Passage were assigned to the 'Dominican Republic' region.

1857. The boats were lowered for humpbacks twice (24 March and 1 April), but it is clear that sperm whales and blackfish were the primary prey, and by 10 April the vessel was 'running down' the south side of Cuba and headed for the sperm whale grounds in the Gulf of Mexico. In 1891 the schooner *Golden City* of New Bedford (1889-91, MS) took a cow/calf pair of humpbacks on 25 March while whaling in Samana Bay for sperm whales and blackfish. A year earlier, on 24 February 1890, the schooner's boats had been lowered in Samana Bay for two humpbacks, 'thinking it was Sperm Whales'.

Although the above would suggest that humpbacks were not plentiful in Samana Bay, the log of the barque *Cicero* of New Bedford (1871-73, MS) tells a rather different story. The *Cicero* cruised widely in the North Atlantic in the early winter of 1871-72, briefly visiting Madeira, Cintra Bay on the west coast of Africa, and the Cape Verde Islands before arriving in Dominica in the second week of January. During the following two weeks, the vessel worked northwards, chasing humpbacks off the northern end of Guadeloupe (12 January) and in Mona Passage (25 January) before stopping in Samana Bay on 26 January. For the next two and a half months, the *Cicero* devoted full attention to humpbacking in Samana. At least 10 humpbacks were taken or struck, including cows with calves on 20 February and 18 and 27 March. Wood (no date, MS) reports the *Cicero* as having been in Samana Bay on 24 February 1872 with 135bbl of humpback oil on board from the 'last cruise' (by this time, three had been taken and processed in Samana). It was next reported on 6 April 1872 , landing 290bbl of humpback oil and 1,300lb of bone in Samana Bay for shipment (Wood, no date, MS). No more humpbacks were taken after that date although one was struck and lost in Samana Bay on 10 April (*Cicero*, 1871-73, MS). Overall, the *Cicero* accounts for 65, or 38.9%, of the estimated 167 humpback whales taken, struck or seen off the Dominican Republic (Table 3).

Leeward Islands

Little evidence was found of whaling in the northern Leeward Islands. In 1878, towards the end of a humpbacking season that began in late February in Tobago and ranged northwards along the island chain to Guadeloupe through mid-April, the Provincetown schooner *Rising Sun* (1875-83, MS) was off the northern end of St Christopher (St Kitts) when a cow and calf were seen on 16 April. From 18-20 April the vessel cruised for humpbacks off St Martin, chasing cow-calf pairs twice. The following winter the *Rising Sun* made another brief and desultory effort at whaling in this area from 4-18 April. Humpbacks (including cow-calf pairs) were sighted and chased in the vicinity of Barbuda; St John's and Five Island harbours, Antigua; St Martin; and St Barthélemy ('St Barts') (*Rising Sun,* 1875-83, MS). Several humpbacks (also 'finbacks') were seen in the area between Antigua, Redonda and Montserrat on 7-8 January (*Annawan*, 1836-37, MS).

The island of Sint Eustatius (often called 'St Eustatia' by the whalers) was a regular port of call for American whalers, particularly as they sailed northwards in the spring from the Lesser Antilles to Puerto Rico, Hispaniola or the Bahamas. Although the vessels seem not to have spent more than a few days there at a time, humpbacks were seen and occasionally taken (e.g. a cow/calf pair chased on 28 May 1886; *D.A. Small*, 1886-88, MS).

Humpback whaling in the southern Leeward Islands began at least as early as the late 1820s (e.g. *Industry*, 1828-29, MS). Most activity was centred around the small island of Marie-Galante (adjacent to Guadeloupe), with the vessels working mainly in the area bounded in the west by Basse-Terre and Les Saintes ('the Saints') and in the east by Îles de la Petite Terre ('Peter Terry Island'). The *Rising Sun* (1875-83, MS) spent six winter seasons whaling near Marie-Galante in the period 1875-83. In all of these seasons other Provincetown vessels were there as well. The journal kept by the *Rising Sun*'s master documents a minimum of 20 vessel-seasons of humpbacking at Marie-Galante by other Provincetown schooners in 1875-77, 1880 and 1883. The *Rising Sun* alone accounted for at least 34 killed humpbacks in these five seasons, and at least 11 more taken by other vessels are reported in the *Rising Sun* master's journal. Judging by whale oil returns and itineraries of the other vessels (from Hegarty, 1959), at least 50 additional humpbacks were killed in the same area in the five seasons concerned. In April 1880, when the Provincetown schooner *Agate* took a humpback off Marie-Galante, the crew saved the baleen ('bone') as well as boiling the blubber (*Rising Sun*, 1875-83, MS). This practice of keeping the baleen of humpbacks was exceptional, although there was some demand for it during at least the 1860s and 1870s (Mitchell and Reeves, 1983). In each of the three seasons 1886, 1887 and 1888 the brig *D.A. Small* of Provincetown (1886-88, MS) whaled at Marie-Galante for at least part of the period 21 March-20 May, accounting for at least eight cow-calf pairs and four other humpbacks killed (including those taken by other vessels but mentioned in the *Small* logbook).

It is clear from the *Rising Sun* master's journal that humpbacks, including cow-calf pairs, were still present near Marie-Galante in mid to late May. Indeed, in 1882 the last sighting of the season was at Îles de la Petite Terre on 6 June (*Rising Sun*, 1875-83, MS). The decision each year to stop whaling and head north seems to have been made for reasons other than the abandonment of Guadeloupe waters by humpbacks. The *Agate* (1872, MS) also reported late-season success near Marie-Galante. While *en route* northwards from a season's humpbacking in the Grenadines, the *Agate* took a calf at Marie-Galante on 25 May and a cow on 28 May and chased a cow-calf pair on 1 June. Similarly the *D.A. Small* (1886-88, MS) continued chasing humpbacks, including cows and calves, into mid-May in 1886 and 1887.

It was unusual for vessels that were humpbacking in the Lesser Antilles to see and chase sperm whales on the humpback grounds. However, this happened at least occasionally at Marie-Galante. For example, on 15 May 1875 the *Rising Sun*'s crew took a 49bbl sperm whale and struck another of similar size while whaling for humpbacks off St Louis (on the western side of Marie-Galante). The next year, on 3 April, the *Rising Sun* and four other vessels chased a school of sperm whales somewhere between St Louis and Îles de la Petite Terre. The *Gracie M. Parker* secured a sperm whale, while on the same day the *Rising Sun*'s crew killed (and lost) one of several humpbacks seen (*Rising Sun*, 1875-83, MS).

Certain New England schooners, most of them from New Bedford, were involved in the late 1870s-1880s in near-shore right whaling off the southeastern United States (Reeves and Mitchell, 1986; 1988). The *Rising Sun* (1875-83, MS) sailed from Provincetown on 12 November 1879 and headed initially for the Charleston Ground (29-32°N, 74-77°W; Clark, 1887, p.8) in pursuit of sperm whales. On 5 January 1880, the *Rising Sun* anchored at St Simon, South Carolina, and the next day the boats were lowered to search for right whales. The crew worked along the coast to Brunswick, Georgia, for a month, with no whales sighted. On 4 February the *Rising Sun* sailed for

Marie-Galante, where humpbacking began on 26 February and continued until 15 May. The following winter, the *Rising Sun* made a special (completely unsuccessful) two month cruise (26 February-29 April 1881) for right whales, concentrating effort along the Outer Banks of North Carolina. Two other schooners, the *Bloomer* of Provincetown and the *Lottie E. Cook* of New Bedford, were also there (*Rising Sun,* 1875-83, MS) as were the schooners *E.H. Hatfield* and *Emma Jane* of Edgartown (Reeves and Mitchell, 1988). The next two winters the *Rising Sun* sailed in early March directly for Marie-Galante to humpback (*Rising Sun,* 1875-83, MS). Although 'finbacks' were reported occasionally while the whalers were searching for right whales on the near-shore Southeast US Coast Ground, no references to humpbacks were found there.

Humpbacks were seen occasionally by vessels visiting Dominica but it does not appear that this was a major destination for humpbacking. In the last week of February 1859, the schooner *Washington* of Edgartown (1858-59, MS) and bark *Orray Taft* of New Bedford took humpbacks in a Dominican bay (probably Prince Rupert Bay) but the season was short (21 February-9 March) and the effort seemingly desultory. On 3 May 1869, while the *Nellie S. Putnam* (1868-69, MS) was anchored in Prince Rupert Bay, the crew interrupted their painting of the ship to chase a humpback cow-calf pair that passed close by. Two days later, as the vessel was leaving Dominica for Guadeloupe, a cow and calf were taken. On some occasions, it was impossible to determine whether a sighting or take was on the Guadeloupe or Dominica side of the channel between the two islands. The brig *Industry* of Westport (1828-29, MS) took a humpback in Dominica Passage on 7 February 1828 during what was primarily a cruise for sperm whales. In fact, the crew interrupted their processing of the humpback on 8 February to chase a school of sperm whales. On the following day the *Industry* was cruising for humpback and sperm whales near Martinique.

Martinique

Martinique is often mentioned in logbooks and journals (sometimes as 'Martinico') but mainly just as a landmark as the vessel cruised past it. No evidence was found that the American whalers used Martinique as a base of operations for humpbacking, although whalers based in St Lucia hunted humpbacks in the channel separating the two islands (see below).

A passing comment in the logbook of the schooner *E.H. Hatfield* (1867-68, MS) refers to 'plenty of Humpbacks' in the channel between Dominica and Martinique on 3 May 1867. However, no effort was made to chase them. The *Industry* (see above) struck a humpback off Martinique on 10 February 1828.

St Lucia

Lindeman (1880; see True, 1904, p.61) claimed that one or two American vessels whaled for humpbacks along the western and southern coasts of St Lucia during the 1870s between March and July. Judging by our logbook sample, St Lucia was visited regularly by humpback whalers from New England during the 1880s. However, no evidence was found that they saw or took humpbacks there as late in the season as July; nor was any evidence found of humpback whaling off the southern coast of the island.

A detailed record of whaling activities is provided in the logbook of the schooner *Franklin* (1885-87, MS) of New Bedford. The *Franklin* stopped for two days at Dominica for provisions (23-25 January 1886), then proceeded directly to Castries on the northwestern coast of St Lucia. From the last few days of January until 3 May the crew followed a daily routine of cruising for humpbacks between the northern half of St Lucia and the southern coast of Martinique, with anchorages including Castries, Soufrière, Cul de Sac Bay, Gros Islet ('Gross let') and Pigeon Island. Humpbacks were seen on at least 47 days; at least seven were secured and three struck and lost. Cow-calf pairs were reported on 9, 16, 24 and 28 March; 3, 10, 21, 26 and 29 April; and 1 and 3 May. At least one other Provincetown vessel, the brig *D.A. Small,* was whaling at St Lucia that season.

Although few details are given about localities in its logbook, the New Bedford schooner *Union* (1882-83, MS) spent two consecutive winter/spring seasons humpbacking in St Lucia. The first season spanned 23 February-early May 1882 (first humpback taken 24 February, last taken 27 April); the second, 6 February-17 May 1883 (first humpbacks seen 6 February, last taken 10 May). Cow-calf pairs were reported on 2 and 27 April. At least four other New England vessels were present, apparently also humpbacking, during the 1883 season.

A report that the schooner *Sarah E. Lewis* of Boston was at St Lucia on 24 February 1866 and then at Bermuda three months later with 100bbl of humpback oil (Wood, no date, MS) suggests that there was some humpbacking around St Lucia that season.

Barbados

Considering the regularity with which the shore whalers at Barbados took humpbacks, it is surprising that so few pelagic whalers seem to have humpbacked there other than opportunistically. Barbados was a major port of call for the American whaling fleet, but most of the whalemen's activity there involved business transactions on shore rather than active whaling. Mitchell and Reeves (1983) summarised the evidence of shore whaling in Barbados from 1869-1913. Shore whaling reportedly began at Speightstown early in 1867, when one cow-calf pair was taken prior to 24 April (Anon., 1867). The following year a large female was taken in mid-May (Anon., 1868).

The whaling operation established by A. Archer in 1869 was based on the central part of the leeward side of the island (Archer, 1881; also see Lindeman, 1880; True, 1904, p.61). It was the practice during the whaling season to launch four whaleboats every weekday, two going north and two south from the station. The humpbacks normally arrived in January and left by June. Although the daily whaling regimen did not begin until March, the boats were kept ready before then and whales were often taken opportunistically in January and February. According to Archer (1881), 'In the month of March they begin to arrive pretty plentifully, and the cows then begin to calve or bring in their young calves with them to feed close in shore in smooth water'. The cows and calves apparently were taken with relative ease except when accompanied by a 'bull'. In Archer's experience this companion whale 'kept watch' and made the cow and calf more difficult to approach. Archer makes the following comment but unfortunately fails to elaborate: 'It is very interesting to see the whales at feed in the shallow and clear water, and to notice the manner in which the mother protects her offspring, and the way it suckles her'.

Takes by the American pelagic whalers included: a 24bbl whale (one of a pair) by the barque *Messenger* of Salem in March 1859 in Carlisle Bay (Anon., 1859; Wood, no date, MS); a 55bbl whale by the barque *Willis* 'in port' sometime between 12-21 May 1863 (Wood, no date, MS; also *Whalemen*'s *Shipping List* as cited by Mitchell and Reeves, 1983); one in 1864 (*Whalemen*'s *Shipping List* 22(16): 21 June 1864; see Mitchell and Reeves, 1983, p.192); and a 70bbl whale by the *Willis* 'while at anchor' sometime in June 1866 (before the 21st) (Wood, no date, MS; also *Whalemen*'s *Shipping List* 24(18): 3 July 1866; see Mitchell and Reeves, 1983, p.192). In addition, two humpbacks were seen at Barbados on 10 February 1840 (*Two Sisters*, 1839-40, MS); 'several' were seen on 26 January 1853 as the barque *Solon* 'sailed outside' from Bridgetown (*Solon*, 1852-53, MS); the *Willis*'s boats chased humpbacks 'a dozen times' off Barbados without success in February-April 1858 (Mitchell and Reeves, 1983); one was struck but lost by the crew of the *A.R. Tucker* while at anchor in Barbados in May 1863 (Mitchell and Reeves, 1983); and one was seen from the *Mattapoissett* (1862-64, MS) while anchored in Bridgetown harbour on 12 February 1864.

St Vincent and Bequia

This area was a fairly popular destination for humpbacking from at least as early as the 1830s and through the 1880s. Among the best records from the logbook sample is that of the schooner *Nellie S. Putnam* (1867-68, MS) of Provincetown, which arrived at St Vincent on 25 January 1868 and remained in the Grenadines for the next four months. The daily routine between 7 February-26 April was to cruise in the inter-island channels and occasionally in Friendship Bay (Bequia) and the upper bay of Mustique. Humpbacks seem to have been present almost continuously during this time but the *Putnam* secured none and managed only to strike three (several were taken by other vessels). Cow-calf pairs were not seen until the *Putnam* made a brief sojourn in the Canouan-Mayreau-Union area to the south (see below) between 27 April and 3 May. A pair was sighted near Canouan on 2 May. Upon returning to Bequia a second cow-calf pair was chased off Paget ('Packet') Farm on 4 May. The humpback season ended for the *Putnam* in mid-May (*Nellie S. Putnam*, 1867-68, MS). The Provincetown schooner *J. Taylor* spent the winter seasons of 1866 (*ca* 15 March-19 May) and 1867 humpbacking between Bequia and Mustique, and at least three other Provincetown schooners (*C.H. Cook, A.H. Brown* and *Watchman*) did the same in 1866 (*J. Taylor*, 1866-67, MS). The barque *Mattapoissett* of Westport (1862-64, MS) spent about a month humpbacking at Bequia ('Beckque') at the end of a multi-year voyage. Four schooners were already present when the *Mattapoissett* arrived on 18 February 1864. The barque obtained only one humpback in spite of repeated efforts to catch others. The barque *Leonidas* of New Bedford (1864-65, MS) spent the entire period 23 February-2 May 1865 humpbacking in the area bounded by Paget Farm, Friendship Bay, Baliceaux ('Balaso'), Petit Nevis ('Pettaneaves') and Mustique, taking one cow humpback (yielding 1,323 gallons of oil, or about 42bbl), striking at least two calves and striking but losing an additional three humpbacks. At least four Provincetown schooners were also present and presumably humpbacking in this area.

Adams (1971) provides a detailed description of the shore-based whaling operations at Bequia, including a chart of the main whaling grounds (also reproduced in Adams, 1975). Most of the whales were taken within a 10-15 n.mile (16-24km) radius of the shore stations at Friendship, Pt Hillary, Semple Cay and Petit Nevis (Adams, 1971: his Map 5). Adams indicates that the whalers generally worked to the windward so that they would receive assistance from the trade winds in towing killed whales ashore. This, according to Adams, explains why the hunting grounds lay as they did mainly to the east of Bequia, embracing Mustique, Battowia and Baliceaux, and occasionally reaching all the way to Argyle on the southeastern coast of St Vincent. The heavy seas made it difficult to spot whales from the whaleboats, especially in January and February, so shore-based lookouts with flashing mirrors were often used to direct the boat crews onto whales (Adams, 1971).

A few humpbacks were seen each year by whalemen (i.e. the pilot whale fishermen) along the lee shore of St Vincent during the 1960s (Caldwell *et al.*, 1971) but we have no evidence that humpbacks have been hunted there in recent times.

Grenadines South from Bequia

Lindeman's (1880; see True, 1904, p.61) reference to whaling in 'the Grenada Ids.' in spring and early summer may apply to anywhere from St Vincent south to Grenada. He claimed that 500-800bbl of oil were secured from humpbacks annually in this region. At an average yield of 25bbl per whale (Mitchell and Reeves, 1983) this would imply a secured catch of 20-32 whales per year.

A series of logbooks from the schooner *Agate* of Provincetown (1869-70, 1871, 1872, MSS) contain detailed records of humpbacking in the Grenadines south of Bequia. Much success at finding humpbacks was reported off the southwestern coast of Grenada (Saint George's to Calivigny Island, with anchorages including Anse aux Pines, Point Saline, Grande Anse and Glover Island) from 12 March-7 April 1869 and again from 9 February-24 March 1870 and 14 April-18 May 1870. In these two seasons the *Agate* secured 13 humpbacks and struck/lost five. Cow-calf pairs were reported off Anse aux Pines on 18 and 30 March. In the following two winters the *Agate* worked primarily in the chain north of Grenada around Mayreau ('Mirou', 'Myro' etc.), Union and Carriacou ('Curracaouia', 'Caricou' etc.) with anchorages including Frigate Island, Chatham Bay, Hillsborough, Harborville and L'Esterre ('Lestere'), and with occasional forays to Sail Rock. The *Agate* took 20 humpbacks in the two seasons, and of those, at least 15 were members of cow-calf pairs. Humpbacks were seen regularly between late February and mid-May. The proportion of cow-calf pairs mentioned in the logbooks is exceptionally high, particularly for the 1871 and 1872 seasons in the middle Grenadines. Judging by reports in the *Agate* logbooks (and corresponding whale oil returns in Starbuck, 1878), much of the Provincetown fleet humpbacked, with considerable success, in these same Grenadine waters from 1869-72. The schooner *Clara L. Sparks* of Provincetown (1879-80, MS), along with at least four other New England schooners, seems to have whaled in this area from about 10 March-9 April 1880. In 1886 the *D.A. Small* (1886-88, MS) spent a month (20 February-17 March) humpbacking at Carriacou and Union before relocating to Marie-Galante for the rest of the season.

Another itinerary, based somewhat farther north, was followed by the schooner *Arthur Clifford* of Provincetown in five consecutive winters (*Arthur Clifford*, 1866, 1867, 1867-68, 1868-69, 1869-70, MSS). The seasons were all within the period from mid-January to early or mid-May and the *Clifford* cruised primarily between Bequia and Union. Mayreau and Canouan ('Kanawan' etc.) were the centres of whaling operations in all five seasons but humpbacks were also observed consistently around Bequia and Union. Between late January and late April 1870, the *Clifford* secured 9 humpbacks, most of them at Mayreau; the *Clifford* logbook records an additional 16 taken and 7 struck and lost, of which 14 and 4, respectively, were at Mayreau, by the four other Provincetown vessels whaling there that season. Of all the humpbacks mentioned in the five *Clifford* logbooks as having been taken or struck in the Bequia-Union corridor (whether by the *Clifford* or another vessel), at least 55% (36 of 66) were members of cow-calf pairs. In addition, several 'bulls' were struck or taken, and many of the whales seen and chased but not struck were described as cow-calf pairs or cow-calf-bull groups. When the *Rising Sun* (1875-83, MS) took a small calf on 18 March 1878, they towed it to Canouan 'and sold him to parties on shore'. Although rarely mentioned in the logbooks and journals, such sales may have been common in view of the local demand for fresh meat on the Caribbean islands (cf. Adams, 1994).

The Provincetown schooner *Nellie S. Putnam* (1868-69, MS) followed a similar itinerary to the *Clifford*'s in the winter of 1868-69. The *Putnam* arrived at Union Island on 23 December and began cruising daily for whales. Nothing was seen until 13 January when the first three humpbacks were seen and chased. From then until about 20 April humpbacks and blackfish were chased regularly, mainly at Mayreau and Union but also occasionally off Bequia and Kingstown (St Vincent). The *Putnam* took six and struck but lost four humpbacks in the Grenadines that season. Four additional New England schooners (including the *Clifford*, see above) were humpbacking on the same grounds.

Tobago, Trinidad and Coast of Venezuela

Clark (1887) cites the vicinity of Trinidad and the Gulf of Paria (often given as 'Para'), specifically waters between 10-11°N and 61-63°W, as among 'the most noted places for hunting humpbacks in the North Atlantic'. Voyages to this area seem to have been undertaken with the sole and explicit purpose of catching humpbacks. The earliest voyage to the area by an American whaler in the logbook sample was in 1837 and the latest in 1871. However, other evidence shows that a few earlier voyages took place, and also that shore-based whaling for humpbacks in northern Trinidad began some time in the 1820s (Reeves *et al.*, 2001).

The logbook of the barque *Solon* (1852-53, MS) provides evidence that at least a few American vessels continued to visit the Gulf of Paria and Dragon's Mouth (the northern entrance to the Gulf between Trinidad and the Paria Peninsula) in search of humpbacks through mid-century (see Reeves *et al.*, 2001). After touring the Gulf from 28 January to late February 1853, the vessel worked west along the Caribbean side of the Paria Peninsula on 26 February and 'saw plenty of whales outside some going into the Bay [Gulf of Paria]'. A small humpback (which proved to be 'very fat') was taken on 27 February as the vessel steered towards Isla de Margarita and the carcass was towed to Isla Coche ('Coache', 'Cotche') for processing. On 3 March, as the *Solon* approached Isla Cubagua, the logbook records that there were 'plenty of whales round'. After anchoring off the south coast of Isla de Margarita on 4 March, the *Solon* found humpbacks to be plentiful in all directions, but the sea was too rough for whaling and the ship steered for Cumana. Several days were spent negotiating with authorities about the payment of duties to whale in the Gulf of Cariaco ('Carriarca'). Finally, on 11 March the vessel proceeded east into the Gulf, coming to anchor on the south side about 25 n.miles east of Cumana. Humpbacks were moving into and out of this gulf, and the *Solon* remained there until 23 March. Although two whales were struck on 17 March, none were secured. On 21 March, a whaleboat was purchased for the *Solon* from Captain Heath of the brig *September* of Boston; this ship was apparently also humpbacking in the Gulf of Cariaco (*Solon*, 1852-53, MS). The *September* was reported at Cumana on 18 April with 50bbl of sperm oil on board and had 120bbl of sperm and 150bbl of humpback oil upon arrival in Boston 18 June 1853 (Wood, no date, MS). A humpback was struck by the *Solon*'s crew on 10 April somewhere between Isla de Margarita and Cumana. Three days later the vessel headed to Blanquilla and resumed the hunt for sperm whales and blackfish, having had an eventful but unproductive season humpbacking off Trinidad and Venezuela (*Solon*, 1852-53, MS).

The brig *Star Castle* of Fairhaven (1867-68, MS) sailed west from the Cape Verdes in January 1868, calling at St Eustatius and Guadeloupe, then heading directly from St Eustatius towards the coast of Venezuela on 4 February. Two humpbacks were seen 10 n.miles offshore of Bahía de Margarita ('Margriter Bay') on 6 February and the boats were lowered on 7 February to chase humpbacks in the Gulf of Cariaco ('Corraco'). After looking for humpbacks in the Gulf, the vessel relocated to Isla de Margarita ('Magerate Island') on 13-14 February, then steered south and came to anchor at Isla Piritu on 18 February. Humpbacks were chased regularly through the rest of the month, with three taken (including a cow-calf pair) and two more struck but lost between 27 February-4 March. On 7 March the *Star Castle* was 'beeting up to Gulf [of Cariaco]' and five more humpbacks were taken between 9-21 March. On 26-28 March the vessel was anchored at Isla Borracha ('Berracer'). A cow-calf pair was struck (only the cow secured) on 29 March, and on 2 April the *Star Castle* came to anchor at Santa Fe for water. The 6 April logbook entry states, 'take our Departure from Humpback ground bound to Northwd', with 160bbl of humpback oil on board.

The schooner *Thriver* of Boston (1870-71, MS) spent at least three months in 1871 (7 January-9 April) humpbacking in an area centred on Cumana. It has been impossible to identify some of the places mentioned as landmarks in the logbook. In general, however, it appears that the *Thriver* sailed directly from Dominica to Isla Piritu ('Purata'), arriving on 25 December 1870. For a week, daily cruises were made to look for whales and the vessel returned to anchor at the island each night. The vessel re-located to Cumana on 6 January, and the first humpbacks were chased the next day in Cumana Bay. From then onwards, the *Thriver* cruised back and forth, throughout the Gulf of Cariaco, offshore to Isla Cubagua and Isla de Margarita and along the mainland coast to Guanta and Isla Piritu. Humpbacks were seen, chased and occasionally struck in all of these areas. A cow and calf were chased near Isla Piritu on 5 March. There is no suggestion that the season was over when the logbook abruptly stops on 9 April with the vessel moving west from the head of the Gulf of Cariaco.

The schooners *George J. Jones* of Fairhaven and *Eleanor B. Conwell* of Provincetown were whaling in the same region that winter *(Thriver*, 1870-71, MS) and the *Jones* secured 140bbl of humpback oil (Wood, no date, MS). The *Jones* is also known to have been at Trinidad in February and March 1867 (Wood, no date, MS). The *Thriver* seems to have followed a similar itinerary in 1866 (arrived at Barbados 4 January; at Curaçao 6 May with 100bbl of humpback oil) and 1867 (at Piritu in February with 80bbl of humpback oil; at Curaçao 26 April with 160bbl of oil) (Wood, no date, MS).

An entirely different type of itinerary was followed by the schooner *Rainbow* of Dartmouth (1866-67, MS), which sailed in mid-December 1866, spent about a month at Bermuda undergoing repairs, then proceeded directly to the southern coast of Trinidad in search of humpbacks. The *Rainbow* came to anchor at Galeota Point on 8 February, finding the schooner *George J. Jones* of Fairhaven already there. For the next two months the *Rainbow* (and apparently also the *Jones*) cruised almost daily along the coast between Galeota Point and Erin Bay ('Herron Bay'), frequently calling at Moruga, with humpbacks seen or chased on most fair-weather days. Cow-calf pairs were chased on 23 February and on 1, 13 and 27 March. Four humpbacks were taken, another was killed but lost and two more were struck (none of these totals include calves that were struck in order to capture their mothers). Humpbacks were still being sighted through the first week of April when the *Rainbow* departed northwards. The next year the *Rainbow* visited the same grounds in early February but made no attempt to catch humpbacks (*Rainbow*, 1867-68, MS). Several 1868 logbook entries refer to 'pods' or 'shoals' of 'bull humpbacks', and the entry for 7 February states: 'Saw plenty humpbacks ... but ... no cows and calves'.

The schooner *William Martin* of Orleans was off Trinidad sometime between 9 February-1 March 1857, probably humpbacking. This North Atlantic cruise had some unusual features, judging by notes in Wood (no date, MS). After sailing from Orleans the day after Christmas 1856 the schooner was at Dominica on 27 January, having taken one right whale (neither the locality of the take nor the oil production is given). The *Martin* was next reported on Grenada Bank, 9 February, with 25bbl of whale oil (presumably the yield from the right whale); then off Trinidad, no date, with 120bbl of whale oil (presumably some of it from humpbacks); and at Grenada on 1 April with 110bbl whale oil. In the same winter the schooner *Delaware* of Edgartown was reported at Trinidad in January with no oil on board. The vessel later capsized in a squall south of Puerto Rico (Wood, no date, MS).

DISCUSSION

Historical and present distribution

In January and February of 1972/73 Winn *et al.* (1975) surveyed what they presumed was the entire range of humpback whales in the West Indies. This assumption was apparently based on Townsend's (1935) plotted catch positions of nineteenth-century American whalers. Their conclusion that they covered the main areas of the species' winter distribution is generally supported by the findings here, except that they did not enter the Gulf of Paria, visit the southern coast of Trinidad or travel farther west than about 63°W on the Venezuelan coast.

As Winn *et al.* (1975) observed, the relatively small numbers of whales seen and heard in the 'Lower Chain' compared with the 'Upper Chain' to the north was the reverse of what would be expected on the basis of Townsend's (1935) historical catch data. This conclusion is borne out by the whaling logbook data summarised here, which often show an abundance of humpbacks in the eastern and southeastern Caribbean, but relatively few off the islands of the Greater Antilles (notably Hispaniola).

Subsequent surveys of much of the West Indies have generally confirmed Winn *et al.*'s (1975) concept of the present distribution of humpback whales in this region. As noted previously, Silver and Navidad Banks off the northern coast of the Dominican Republic today host large numbers (probably thousands) of humpbacks (Balcomb and Nichols, 1982; Whitehead and Moore, 1982; Mattila *et al.*, 1989). Local abundance at nearby Samana Bay is quite large but approximately an order of magnitude lower than on Silver and Navidad Banks (Mattila *et al.*, 1994), and humpbacks occur in relatively small numbers from Mona Passage through the various island waters to the east (Mattila and Clapham, 1989).

A recent research cruise described by Swartz *et al.* (in press) has provided the most comprehensive coverage to date of the eastern and southeastern Caribbean region, and represents the first systematic survey of this area since that summarised by Winn *et al.* (1975). The Swartz *et al.* (in press) survey, conducted between 16 February and 29 March 2000, covered most of the Lesser Antilles, Trinidad, Tobago, the Gulf of Paria and much of the coast of Venezuela as far west as Islas Los Roques (at about 67°W). Using sonobuoys deployed throughout the study area, 75 acoustic detections of singing humpback whales were obtained from approximately 350 hours of monitoring. In contrast, there were only 30 visual sightings of 46 humpbacks (including three calves), with most of these detected first acoustically (only nine humpback whales were found by visual observation without prior acoustic detection).

In sharp contrast to these recent observations, the whaling data reviewed for this paper demonstrate that humpbacks were formerly common throughout the Lesser Antilles, along the Caribbean coast of Venezuela, in the Gulf of Paria and along the southern coast of Trinidad during January through May. It is emphasised that the records reviewed here represent only part of the historical picture, given that many logbooks and journals from this period of whaling have not survived or are otherwise unavailable for study. That the ultimate cause of the relative scarcity of humpback whales in this region today is the overexploitation to which they were subject in the nineteenth and early twentieth centuries is difficult to question. Whaling in this region continued into the early part of the twentieth century, culminating in a Norwegian shore-based whaling operation from the island of Grenada in 1925/26 (Mitchell and Reeves, 1983; Romero and Hayford, 2000); the collapse of this fishery after two years of substantial catches likely reflects the severe depletion of the local population of humpbacks. However, the failure of humpback whales to recover or to recolonise the eastern and southeastern Caribbean in significant numbers since the cessation of commercial whaling in 1926 is curious.

Winn *et al.* (1975) offered two possible explanations for the difference between former and current humpback whale distributions in the West Indies: (1) that the timing of their survey in the Lower Chain may have been too early, ahead of the main influx of whales; and (2) that the ongoing hunt at Bequia (which was taking zero to six animals per year at the time) may have 'kept the population suppressed, due to the fact that only females and calves are caught'. Other possibilities are that: (1) the catch positions from American whaleships (Townsend, 1935; this study) are unrepresentative of the nineteenth-century distribution and relative abundance of humpbacks in different parts of the West Indies; (2) the relatively few animals found in the southeastern Caribbean today are the descendants of a distinct population that was overexploited historically, either locally or also in high latitudes (Mitchell and Reeves, 1983); or (3) the winter distribution of North Atlantic humpbacks has changed since the nineteenth century.

Of these explanations, the first cannot be excluded but seems unlikely. Although the timing of the most recent dedicated survey of the region (Swartz *et al.*, in press) did not extend beyond late March, the peak of observations from the whaling data were in March for St Vincent and the Grenadines as well as for Venezuela, and in February for the Gulf of Paria (Fig. 2). The contention that the hunt at Bequia might have suppressed the population is not tenable in view of the small catch (presently two whales per annum) and the known resilience of humpback whale populations elsewhere (Clapham *et al.*, 1999). The possibility that positions noted from whaling manuscripts by Townsend (1935) and by the present study are unrepresentative of contemporary distribution cannot be ruled out, but beyond noting the marked contrast in numbers of whales from the eastern versus northern Caribbean, this issue cannot be addressed further. The fourth explanation (that the region hosts a population separate from that found in the major modern breeding areas to the north) seems unlikely in light of recent photo-identification data (Stevick *et al.*, 1999).

With regard to the final hypothesis, Clapham and Hatch (2000) suggested that the difference in historical and current distributions of humpback whales was probably real, and had its origin in a characteristic of the mating system of this species. Specifically, they suggested that there is likely to be only one major aggregating point in any humpback whale breeding range and, following the overexploitation of the nineteenth century, this focal point shifted to the northern West Indies. Further consideration of this idea is beyond the scope of this paper, but it may be the most parsimonious explanation in light of current knowledge.

Although the data presented here certainly strengthen the argument that humpback whales were not historically abundant in their present major wintering areas off Hispaniola, we do not consider this question to be closed. The experience of the *Cicero* at Samana Bay in 1872 notwithstanding, if the large numbers of humpbacks found today off Hispaniola had been present there in the nineteenth century, it is hard to imagine whalers failing to find or exploit them. However, too little is known about the possible economic, logistical and other factors that might have influenced the whalers' itineraries and search effort, so it is premature to draw definitive conclusions.

Other issues

Observations of cow-calf pairs and cow-calf-bull groups were recorded regularly in the whaling manuscripts of voyages to the Grenadines and Trinidad-Venezuela coasts. Those records, together with published accounts of whaling in Barbados (Archer, 1881) and the Grenadines (Fenger, 1913), demonstrate that these areas served as calving, nursing and probably mating grounds in the past. The positions where humpback songs were recorded during 1969-77 (Winn and Winn, 1978), and during the 2000 survey (Swartz *et al.*, in press) suggest that mating, if not also calving and the nurturing of calves, still occurs throughout much of the historic range.

No evidence was found that the whalers sailed farther westwards along the Spanish Main than approximately longitude 65°30'W, although the offshore island La Blanquilla (often called 'Blanca' or 'Blanco'; not to be confused with the small island of Branco in the northwestern Cape Verde Islands) was a frequent landmark and stopover site for sperm whale and blackfish hunting cruises. Although such occurrences may have been exceptional, humpbacks were sometimes seen at La Blanquilla (e.g. some on 7 January 1891, many on 28 January 1891 – *Golden City*, 1889-91, MS). The recent sightings of solitary humpbacks in January and February near the coast of Curaçao (Debrot and Barros, 1994) demonstrate that the total Northern Hemisphere winter range of humpbacks today extends at least as far west as latitude 69°W in the southern Caribbean. In addition, the logbook of the *E.B. Conwell* (1890-92, MS) of New Bedford records a sighting of a 'large school of humpbacks' at 12°15'N, 65°00'W on 22 January 1891; this position is northwest of La Blanquilla and approximately midway between Grenada and Bonaire. Movements by humpbacks across deep water within the eastern Caribbean region (e.g. the Grenada and Tobago basins) can be inferred from these sightings, as well as others at Barbados (see above) and west of Dominica (e.g. 11 February 1892 at 16°06'N, 62°59'W and 13 February 1892 at 16°08'N, 65°36'W - *E.B. Conwell*, 1890-92, MS). Humpbacks were also seen well offshore to the east of Trinidad ('plenty' on 9-10 February 1868 at 9°23'-9°56'N, 59°20'-59°46'W – *Rainbow*, 1867-68, MS) and at least occasionally far to the east of Barbados (e.g. 28 February 1868 at 12°55'N, 53°10'W – *Rainbow*, 1867-68, MS).

The suggestion by Acevedo and Smultea (1995) that Southern and Northern Hemisphere humpbacks use the same wintering grounds along the Pacific coast of Costa Rica (six months out of phase) raises the possibility that a similar situation exists in the southeastern Caribbean Sea. The possibility that humpbacks from the South Atlantic at least occasionally visit the southern or eastern Caribbean during the boreal summer cannot be ruled out. However, the historical data indicate that American whalers visited this area primarily during the boreal winter, so they had few opportunities to observe and report humpbacks there during the season when Southern Hemisphere animals would be expected to appear. In effect, the highly seasonal character of the 'sighting effort' in the present study precludes any evaluation of the possibility that Southern Hemisphere humpbacks occurred in the study area during the austral winter.

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KEY: KWM = Kendall Whaling Museum, Sharon, MA, USA; PPL = Providence Public Library, Providence, RI, USA; NBFPL = New Bedford Free Public Library, New Bedford, MA, USA; ODHS = Old Dartmouth Historical Society, New Bedford, MA, USA.

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Rising Sun. Journal of T. Taylor aboard the schooner *Rising Sun* of Provincetown, T.S. Taylor, Master. 27 March 1875-12 September 1883. [Phillips Library, Peabody Essex Museum, Salem, Massachusetts]

Solon. Logbook of the brig *Solon* of Rochester, -- Hammond, Master. 6 June 1838-15 April 1839. [KWM]

Solon. Logbook of the barque *Solon* of Westport, Joseph E. Smith, Master. 10 July 1852-15 October 1853. [ODHS]

Star Castle. Logbook of the brig *Star Castle* of Fairhaven, Henry Clay, Master. 1 October 1867-19 July 1868. [PPL]

Thriver. Logbook of the schooner *Thriver* of Boston, S.D. Pierce (or Capt. Soper), Master. 28 November 1870-9 April 1871 (last entry while vessel still off Venezuela coast). [ODHS]

Two Sisters. Logbook of the brig *Two Sisters* of Rochester, --Hammond, Master. 30 July 1839-24 March 1840. [KWM]

Union. Logbook of the schooner *Union* of New Bedford, J.B. Foster, Master. 30 January 1882-16 September 1883. [ODHS]

Walter Irving. Logbook of the schooner *Walter Irving* of Provincetown, -- Holmes, Master. 18 November 1856-7 October 1857 (Starbuck 1878 gives return date as January 1858). [PPL]

Washington. Logbook of the schooner *Washington* of Edgartown, Brazilla Fisher, Master, 20 May 1858-11 August 1859. [KWM]

Wood, D. No date. Abstracts of whaling voyages [1835-75]. 5 vols. [NBFPL]

Winged Racer. Logbook of the schooner *Winged Racer* of Provincetown, Xenophen Rich, Master, 30 January-31 July 1867. [ODHS]

Winged Racer. Logbook of the schooner *Winged Racer* of Provincetown, Xenophen Rich, Master, 24 January-6 September 1868. [ODHS]

Appendix 1

TOPONYMY (BASED ON ‘WEST INDIES AND CENTRAL AMERICA’, SUPPLEMENT TO *NATIONAL GEOGRAPHIC*, FEBRUARY 1981, PAGE 224A, VOL. 159, NO. 2; EXCEPT WHERE NOTED OTHERWISE).

Greater Antilles: the island chain from Cuba in the west to Puerto Rico and the Virgin Islands in the east.

Leeward Islands: the island chain from Dominica in the south to Anguilla and Sint Eustatius in the north.

Lesser Antilles: the north-south-oriented Windward and Leeward Islands in the east, and the east-west-oriented chain of islands off the Venezuelan coast in the south (Aruba eastward).

Lower Chain: defined by Winn *et al.* (1975:502) as Martinique and all islands to the south (including Trinidad and Tobago).

Spanish Main: formerly the northeast coast of South America, between the Orinoco River and the isthmus of Panama, and the adjoining part of the Caribbean Sea (*Century Dictionary*, 1904).

Upper Chain: defined by Winn *et al.* (1975:502) as areas north of Martinique to Hispaniola and the Grand Turks, including Mouchoir Bank.

Windward Islands: the island chain from Grenada in the south to Martinique in the north.

Application of photogrammetric methods for locating and tracking cetacean movements at sea

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ABSTRACT

Accurate measurements of the locations of surfacing cetaceans are important data for behavioural studies and sightings surveys. A system for tracking cetacean movements based on photogrammetric analysis of digital images has been developed and tested at sea. Radial distances from the ship to surfacing whales were calculated from video images by measuring the angle of dip between the whale and the horizon. Bearings were either measured from still images of reference points on the ship, from a magnetic bearing compass or from the bearing ring of stand-mounted binoculars. The system uses readily available equipment and can be operated by one person. Calibration tests were conducted to assess the accuracy of the system. Errors in distance measurement increased approximately linearly with distance. Under typical survey conditions, from a large vessel with an eye height of 18m, distances to whales could be measured with a root mean square error of 3.5%. A model was developed to enable corrections to be made for atmospheric refraction. This has implications for other studies using reticle binoculars. If refraction is not corrected then distance estimates will be negatively biased. Field trials of the system were conducted from several different types and sizes of vessel during studies of a number of different species. Results of these trials demonstrated that the system is a practical tool for fine-scale tracking of cetacean movements and could also be used on line transect surveys. The limitations of the system are the need for a clear horizon and difficulties, for some species, in obtaining suitable quality images of all surfacings. There is also a moderate overhead in increased analysis time. Advances in digital imaging technology are likely to solve many of the image quality problems in the future.

KEYWORDS: PHOTOGRAMMETRY; SURVEY-VESSEL; MOVEMENTS

INTRODUCTION

The aim of this work was to develop a practical system using readily available equipment that would enable the location of a surfacing cetacean to be accurately determined from a moving vessel. Determining locations has applications for both behavioural studies involving tracking of animal movements and also for line transect analyses that rely on knowing the location of sightings relative to the survey vessel. Tracking of whale movements close to shore is frequently achieved by using theodolites from fixed observation positions on land. This relies on the instrument being precisely aligned at a known fixed location, which is clearly impossible on a moving vessel. A commonly used alternative at sea is to use the horizon as a reference point enabling the distance to an object to be determined by the angle of dip from the horizon to the object, measured from a platform of known height. One way of measuring this angle is to use reticle binoculars that superimpose a visual scale on the image (e.g. Thompson and Hiby, 1985). However, accurate readings from reticle binoculars to a cetacean that only surfaces briefly are difficult to obtain and become increasingly so as vessel motion increases. Use of a video camera can overcome these problems by allowing measurements to be taken from still images captured at the optimum moment in the surfacing sequence. One of the difficulties in interpreting data from instantaneous measurements of distance in the field, whether made by eyeball or reticle binoculars, is that it is impossible to estimate the accuracy of the distances. Although calibration experiments can be performed on test targets where the distance can be measured by other means, these are not necessarily representative of the problems faced in estimating distance to a cetacean. An advantage of the video system is that measurements can be made to real targets which allows the accuracy of such a system to be reliably assessed.

Although photogrammetric methods have been used in several studies to measure distance (Gordon, 1990; 1994; 2001; Best *et al.*, 1996) and electronic instruments do exist for measuring bearing, these methods have not yet become a standard feature of general survey design. Routine use of such methods would enable a much more complete and accurate record of the raw data in line transect surveys to be collected, greatly increasing the precision and repeatability of possible analyses. In addition to accurate locations, video methods can provide precise timing of events such as blows or surfacings. Detailed behavioural observations can also be recorded as a verbal commentary. The combination of accurate time and position makes identification of duplicate sightings from independent observation platforms during line transect surveys more reliable. Accurate tracking during surveys may also allow factors such as animal movements in response to the survey vessel to be investigated.

Accurate measurement of location is also important for many behavioural studies. In particular, studies investigating response to disturbance often utilise data on swim speed and direction. Additional information can also be collected with video, including distribution of animals within pods (DeNardo *et al.*, 2001), body size (Gordon, 1990) and the properties of visual cues such as the height and duration of a blow.

The main limitation of these methods is the need for a clear horizon (or a shoreline at a known distance). This could present a problem in some areas. However, accurate distances to even a proportion of sightings would be of value in line transect surveys and use of the video system does not interfere with estimation of distance by other means. The other key limitation of the system is in the maximum

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distance at which cetaceans are detectable on video images due to image quality. The rapid pace of development of digital imaging technology makes it likely that digital devices will have a higher acuity than the human eye in the near future.

METHODS

To fix the target animal's location using these methods, three items of data are required: (1) the vessel's position at the time the image was taken; (2) the distance to the animal; and (3) its absolute bearing from the observer. The position of the vessel at the time an image was captured can be readily obtained by logging the ship's location from a Global Positioning System (GPS) at frequent (every few seconds) intervals.

Theoretical background to distance measurement

The general formulae for calculating distance between a vessel and an object at the sea surface, based on the angle of dip between the whale and the horizon, measured from a platform of known height, are given in Gordon (1990) and Lerczak and Hobbs (1998).

Suppose h is the observation height, is the angle between the horizontal (perpendicular to a line to the centre of the Earth) at the observer and the horizon, and θ is the observed angle between the whale and the horizon.

Let $\psi = \frac{\pi}{2} - \theta - \varphi$. Then the distance d to the object of interest is given by:

$$d = (R_E + h)Cos\psi - \sqrt{(R_E + h)^2 Cos^2\psi - (R_E + h)^2 + R_E{}^2} \quad (1)$$

where R_E is the radius of the Earth (6,356,766m).

This formula assumes that light travels in a straight line between the object and observer and ignores refraction. Light rays from objects at the sea surface pass through an atmosphere of decreasing density and are thus refracted downwards. This means that the observed angle of dip to the horizon (the angle between the horizontal and the horizon) is less than the true angle. The observed angle of dip to the object of interest will also be less than the true angle. However, the light from the horizon will be refracted more than the light from the object resulting in the measured angle between the object and the horizon being greater than the true angle. If this is not corrected, distance measurements will be negatively biased.

The standard correction used by mariners for the angle σ (in radians) between the horizontal and the horizon, for the height h measured in metres, is given by Burton (1974) as:

$$\sigma = 0.02933 \frac{\pi}{180} \sqrt{h} \quad (2)$$

For the purposes of whale length measurement, Gordon (1990) used this standard correction for the effect of refraction between the horizon and the observer. A correction for refraction between the observer and whale was not necessary in that study because the distances to whales were only of the order of a few hundred metres.

Predicting the path of a light ray between an object at the sea surface and an observer at height h requires knowledge of the properties of the atmosphere through which the ray passes. For the purposes of estimating refraction, the atmosphere can be modelled as a set of fixed spherical shells concentric with the Earth. The temperature distribution can then be specified by values at the layer boundaries with a linear gradient in between. For shipboard observations of objects at the sea surface between the ship and the horizon, with an eye height of less than 30m, it is realistic to model the atmosphere as a single layer with a constant temperature gradient. The ray paths within a layer can be approximated by a parabolic arc using rectangular coordinates where x is tangential to the Earth's surface and z is perpendicular (Lehn, 1983). Using this coordinate system, the arc of a ray can be represented by:

$$z = \frac{-x^2}{2r} + x \tan\phi + h \quad (3)$$

where:

r is the radius of curvature of the ray;
ϕ is the ray-elevation angle (the angle between the ray direction and the horizontal) at its starting point;
h is the height of the observer's eye above sea level.

Rees (1990) demonstrates that for a horizontally stratified medium, the second derivative of the ray path d^2z/dx^2 is a function only of z and not of ϕ. Further, for rays from whales or the horizon which are close to horizontal (i.e. ϕ is very small) the radius of curvature can be expressed as $1/\mathrm{r} \approx \mathrm{d}^2 z/dx^2$ and this will also be approximately independent of the ray parameter ϕ. Hence, if the radius of curvature can be estimated for the atmospheric conditions when an observation is made, this can be used to estimate the total angle through which light has been refracted between an object and the observer. A correction (α) to the angle measured between the horizon and the object can then be applied to compensate for refraction.

This simple model for calculating refraction is shown in Fig. 1. V represents the observer at height h above sea level and W represents the object of interest at the sea surface at a distance x_w from the observation position. The lower layer of the atmosphere including the observer is assumed to have a constant temperature gradient from T_0 to T_1. The path of the ray from W to V is represented by the circular arc of radius r, centre A, passing through W and V. The correction α, relative to the direct path WV is the angle $W\hat{V}B$ which is equal to $W\hat{A}V$ / 2. Now $W\hat{A}V \approx x_w / r$, giving:

$$\alpha \approx X_w / 2r \quad (4)$$

Lehn (1983) showed that the radius of curvature of the light rays can be derived from the temperature gradient by:

$$\frac{1}{r} = \frac{\varepsilon\rho}{(1+\varepsilon\rho)T}\left(\frac{dT}{dz} + g\beta\right) \quad (5)$$

where:
Atmospheric density ρ can be expressed in terms of pressure p and absolute temperature T by

$$\rho = \frac{p\beta}{T} \quad (6)$$

β = 0.00348 (the reciprocal of the specific gas constant);
ε = 0.000226 (from the refractive index of air);
g = 9.81 (the gravitational constant).

For the special case of a ray from the horizon, the angle of dip ϕ_h between the horizontal and the horizon at an observation height h is given by:

$$\phi_h = \tan^{-1}\left(\sqrt{2h(\frac{1}{R_E} - \frac{1}{r})}\right) \quad (7)$$

where R_E is the radius of the Earth.

In some instances (e.g. to check if the true horizon is visible when land can be seen in the background) it is also

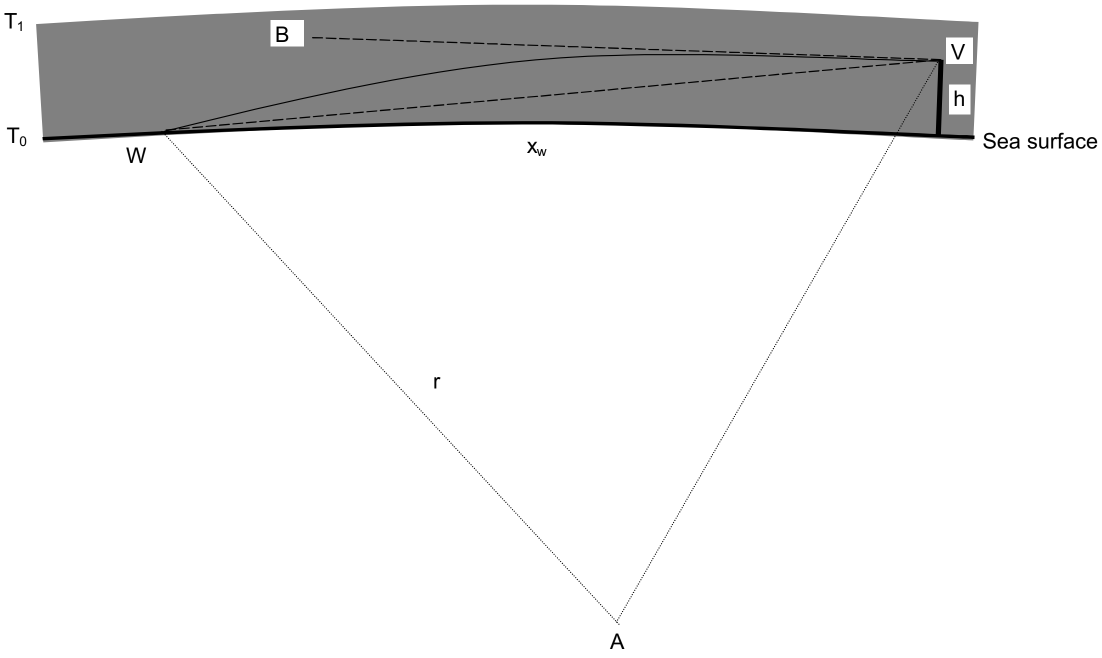

Fig. 1. Cross-section view of surface layer of atmosphere, showing path of light from object to observer (see text). Shaded area represents the lower layer of atmosphere assumed to have a constant temperature gradient from T_0 to T_1. *V* is the location of the observer's eye; W is the object of interest at the sea surface; *A* is the centre of the arc of radius *r* passing through *W* and *V*; *VB* is the tangent to the Earth's surface at *V*; h = height of observer above sea level; x_w = distance to whale along Earth's surface; r = radius of curvature of light ray.

useful to know the distance to the horizon x_h from a particular observation height. Lehn (1983) gives this as:

$$x_h = \left(\frac{1}{R_E} - \frac{1}{r}\right)^{-1} \tan\phi_h \qquad (8)$$

For an atmospheric pressure of 1,000mB, a surface temperature of 289.6K (16.4 °C) and a temperature gradient of –6.5K/km, values of ϕ_h calculated using Equation (7) are equivalent to the standard correction given in nautical tables (Equation 2). For the US standard atmosphere (Fleagle and Businger, 1980) with a pressure of 1,013mB, a temperature of 288.15K and a temperature gradient of –6.5K/km, values of ϕ_h calculated using Equation (7) are within 0.02% those calculated using Equation (2).

The differences using formulae such as given by Lerczak and Hobbs (1998) which ignore refraction are shown in Fig. 2 for three different air temperatures (curves A-C). In all cases, distances calculated ignoring refraction are negatively biased. Although it is straightforward to measure both the temperature and the atmospheric pressure, the temperature gradient may need to be assumed. Within the range of the majority of conditions encountered at sea, the effects of changes in atmospheric temperature profiles on the correction needed to account for refraction are relatively minor compared to ignoring refraction completely. An extreme condition, which is sometimes observed at sea, is when the images of objects such as ships or distant land appear inverted above the horizon. This is known as 'superior mirage' and occurs when there is a strong temperature inversion at 10m or so above a roughly isothermal layer at sea level. The effect of refraction may be more difficult to predict under these conditions but the error caused by using the standard atmosphere model are nevertheless likely to be relatively small compared to ignoring refraction completely. This is illustrated by curve 'D' of Fig. 2.

For the purposes of the calibration tests, calculations were performed using this model for refraction with measured temperature and pressure values but assuming a standard temperature gradient of −6.5K/km. Distances were also calculated for comparison purposes making no correction for refraction.

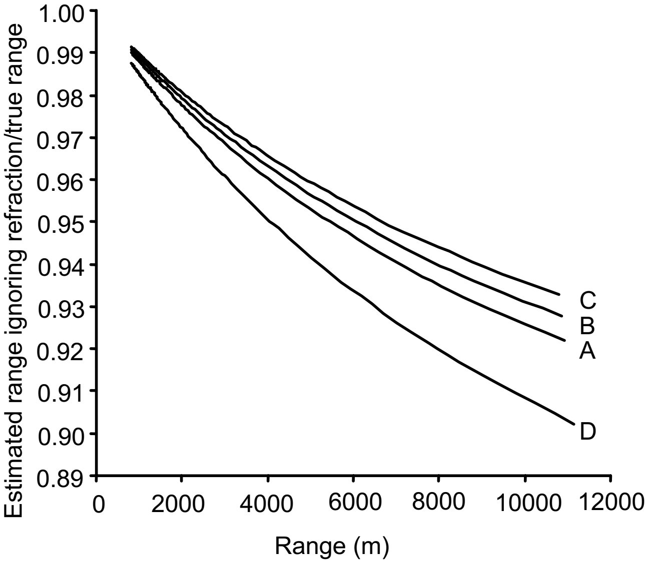

Fig. 2. Ratio of estimated distance ignoring refraction to true distance for three atmospheric profiles. A = Air temp. 0ºC, Surface pressure 1,000mB, Temperature gradient −6.5ºC/km. B = Air temp. 10ºC, Surface pressure 1,000mB, Temperature gradient −6.5ºC/km. C = Air temp. 20ºC, Surface pressure 1,000mB, Temperature gradient −6.5ºC/km. D = Air temp. 0ºC, Surface pressure 1,000mB, Temperature gradient 0ºC/km.

Practical techniques for obtaining images for distance measurement

The utility of the video system is clearly dependent on the practicalities of obtaining suitable images from which the appropriate measurements can be taken. It will usually be easier to see an animal than to film it, and so an important consideration in designing the system was to maximise the likelihood of obtaining images once an animal had been sighted. The probability of obtaining a distance and bearing will vary with species, distance and the method being used to detect the animals. The standard line transect assumption is that the perpendicular distances of the locations where animals or groups are first seen are used to model the detection function. Hence, it is also important to be able to locate a whale as soon as it is detected.

The situation is most straightforward in cases where observers exclusively use binoculars to search for animals, either to make primary sightings (e.g. IDCR/SOWER surveys) or to sight animals well ahead of the survey vessel and track them through the field of view of the primary observers (e.g. Borchers *et al.*, 1998). In these cases, it is likely that, with a good commentary to help interpretation, most animals that are seen for more than one surfacing will be detectable on video. There will always be some delay in starting the video recorder, especially if tape has to be wound around recording heads. One solution would be to video continuously and then analyse the sections of tape when sightings were made. Another option currently being developed is to use a computer-based recording system incorporating a buffer. This would enable video to be stored for a set time period prior to the observer pressing a button.

Observers scanning with binoculars need to be able to operate the video camera without taking their eyes off the sighting. This requires the camera to be mounted so that it is always aligned with the field of view of the binoculars. Separate systems were developed for hand-held 7 × 50 and for tripod-mounted 25 × 150 binoculars[1]. A *CANON MV1* digital camcorder was used in both cases. The main feature of the *MV1* which made it suitable for this work was the progressive scan facility, which allowed both interlaced fields (essentially alternate lines of data which make up the video image) to be captured simultaneously. This effectively doubled the vertical resolution of the camera compared to capturing each interleaved field 1/50s apart. The focus was set to infinity for all measurements. This ensures a fixed focal length of lens and also prevents problems encountered with most auto-focus systems that do not focus efficiently on images at sea because of the lack of contrast. Shutter speeds were set as fast as conditions would allow, and were typically less than 1/1,000s.

Design of hand-held frame

A rigid frame was built to hold 7 × 50 binoculars, video camera and digital still camera (Fig. 3). The frame was designed to allow scanning with binoculars for long periods of time with minimum fatigue but also to allow complete freedom of movement. The centre of gravity of the frame was centred over the observer's shoulder so that the weight was borne on the shoulder and hands were used for steadying purposes and operating the controls. A monopod attached to the frame by a thick rubber universal joint was also used under certain conditions to take some of the weight. A digital still camera was mounted on a strut projecting forwards under the binoculars and pointed vertically downwards at reference lines marked on the deck that were used for the measurement of bearings (see below). A microphone input to allow a verbal commentary on the video sound track was mounted on the frame beneath the binoculars such that it was close to the observer's mouth and also protected from wind noise. The timing of events was recorded to the nearest second by the built-in clock in the video.

Variants of the frame described have been tested at sea from a number of vessels during studies of several different cetacean species. The final version of the system described here has been used to track the movements of right whales in the Bay of Fundy from *Song of the Whale*, a 14m research vessel, during the past three field seasons. It was also used from the British Antarctic Survey vessel *James Clark Ross* during a survey around South Georgia in 1999/2000 and during the IWC/CCAMLR survey in 2000, both as a survey tool and for tracking whale movements during a small-scale study.

For the IWC/CCAMLR survey, the camera was operated on full zoom with a 72.8mm focal length giving an image size of 3.76° horizontally and 2.70° vertically. Although this is considerably less than the horizontal field of view of 7° of the Fujinon 7 × 50 binoculars, this was not a problem in practice, due to the natural tendency of the observer to place the object of interest in the centre of the image. The choice of field of view also depends on the minimum distance at which measurements are likely to be required. For a given

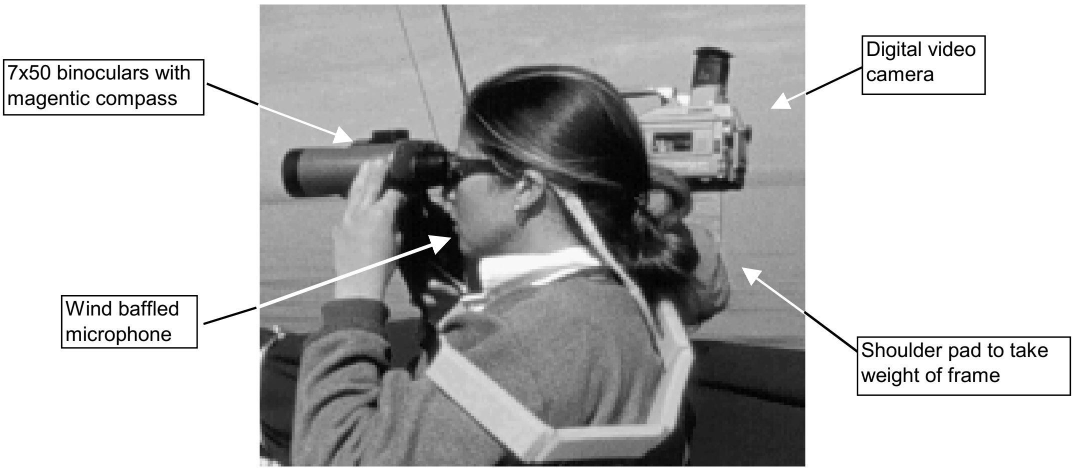

Fig. 3. Use of rigid frame to hold video camera and 7 × 50 binoculars. A downward pointing digital still camera (not shown here) was also attached below the binoculars for taking bearings relative to reference points on deck.

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[1] After completion of this paper the authors were made aware that Tim Gerrodette (Southwest Fisheries Science Center, La Jolla, California, US) had attempted a similar video system for range finding in 1992. *Cohu* monochrome video cameras with telephoto lenses were mounted on top of 25x binoculars with the fields of view aligned, and observers captured individual frames by pushing a button when the animals were in view. However, the researchers concluded that the acuity of the video equipment available at that time was not adequate to make the technique practical.

field of view this minimum distance will be approximately proportional to the observation height. For example, the 2.70° vertical field of view limited the closest range at which distances could be measured to around 400m from an 18.3m high platform.

During right whale (*Eubalaena australis*) tracking studies, the vessel followed the subjects, so maximising the range of detection was not an important consideration. The focal length of the lens was set to give a vertical field of view equivalent to the 7 × 50 binoculars (7°). Increasing the field of view allows distances to be measured to closer whales but limits the maximum range of detection and could result in some loss of accuracy at greater distances. It is quite possible to change the focal length of the lens during a tracking sequence provided that images of a calibration object at known distance are obtained each time it is changed.

Mounting video on 25 × 150 'Big Eye' binoculars

The large size and solid support stands of these binoculars make it relatively easy to attach a camcorder to them without affecting their normal functionality. A robust pan and tilt tripod head was bolted to a rigid support and this was attached to the lens barrels using hose clips. A quick release shoe in the tripod head, which allows cameras to be removed and replaced without needing realignment, was useful. A 72.8mm lens and 2x tele-converter was used. This gave a field of view of 2.66° horizontally and 1.91° vertically. Mounted on top of big-eye binoculars, the video camera was some 25cm above the observer's height of eye and quite inaccessible. This resulted in some practical difficulties in assuring that the camera was aligned and was correctly configured and functioning. A useful addition, which was available on one cruise, was a video monitor allowing the operator to check camera alignment. A system with a separate video camera on top of the binoculars and a video recorder or computer capture device at deck level would be advantageous. 'Big eye' stand-mounted video was used by JG on three days during a NMFS Gulf of Maine/Bay of Fundy harbour porpoise abundance survey, Cruise No. AJ 99-02, in July 1999. This survey was conducted from the 30m research vessel *Abel-J* with a lens height of 8.4m above sea level. The system was also used from the NOAA ship *Gordon Gunter* (length 68m, camera height 14.2m) during an inter-agency cruise in July 2000 to study sperm whales in the Gulf of Mexico.

Measurement of bearings

If the vessel is constructed from non-magnetic material then a magnetic sighting compass can provide bearings directly with a good level of accuracy. These are built-in to some suitable models of binoculars. Steel vessels distort the earth's magnetic field to an extent that varies with location on the boat, and also with the vessel's heading. This makes the use of magnetic sightings compasses unreliable on such platforms so that indirect methods of determining bearing are needed. Two pieces of information are required: (1) the vessel's heading; and (2) the bearing to the target relative to the ship. Vessel heading will be provided (usually in computer readable format) by a gyro-compass on most large vessels. On smaller boats the net movement over ground of the vessel provided by a GPS navigator may have to be used. However, there are two potential sources of error. In a cross-current, the vessel's heading through the water will be different from the direction of movement over the ground provided by the GPS. Secondly, the 'heading' provided by a GPS represents the net movements between fixes and small heading changes in between these will not be represented. For a vessel attempting to steer a straight course, variation in heading will tend to be greater the smaller the vessel. A high quality gyro-compass attached to the camera and binoculars could give the best results but these tend to be heavy and expensive and we have not attempted to incorporate these into hand-held equipment.

Powerful binoculars, such as 'Big Eyes' need to be supported and they are usually firmly mounted in a good viewing position on an adjustable stand incorporating some degree of vibration isolation. 'Big Eye' stands also incorporate a ring showing relative bearing. When using video techniques with 'Big Eyes', relative bearings were read, to the nearest degree, from the bearing ring on the stand and this was spoken onto the voice track of the tape. It should be relatively easy to improve this system by measuring and recording bearing automatically (a wind direction sensor with computer readable output could be adapted for this purpose for example). The continuous stream of bearing data that this would provide could also be used to investigate observer scanning patterns.

There are disadvantages to using smaller binoculars on rigid stands. The human body is very efficient at motion compensation and a rigid stand does not allow flexible movement to compensate for the pitch and roll of the vessel. In addition, the observer is also unable to move position to get a better view of a sighting or move around to reduce fatigue. Thus, a system that allowed as much freedom of movement as possible was developed. This involved putting reference marks on the deck in the form of lines running fore and aft and taking a photograph using a downward-pointing digital still camera every time a bearing was required. The camera also recorded the time to the nearest second. The reference marks should extend over a sufficiently large area of deck to provide coverage wherever the observer is likely to stand.

Analysis to obtain distances and bearings

The first stage of analysis was usually to view the video sequences and use simple event recording software to log events from the verbal commentary. Individual frames or sequences of video were then captured using commercially available digital video capture cards and software, and stored on the computer so that the best quality image in any surfacing sequence could be selected. A dedicated software program written in *Microsoft* Visual Basic was used to analyse these images. The software was designed to reduce the number of keystrokes required in processing each image and to write the data to a database. For each sequence this involved making the appropriate measurements of the size of the calibration target then using the mouse to click on the sea surface at the object of interest and two points on the horizon. Analysis of digital still images to determine relative bearing was performed using another Visual Basic program. Bearing and ship's heading data were related to distance measurements by their time stamp.

Calibration tests

A number of different calibration tests have been performed to investigate the accuracy of the system from different platform heights under different conditions. The tests reported here are from a 14m auxiliary powered sailing vessel, *Song of the Whale*, in coastal waters (Bay of Fundy, Canada) giving an eye height of 4m, and from a 99m long oceanographic vessel (*James Clark Ross*) in the Southern Ocean with an eye height of 18.3m. Bearings from the *Song of the Whale* which is constructed of fibreglass, could be measured using the magnetic compass, whereas on *James Clark Ross* bearings were measured relative to the ship using the digital still camera.

Tracking from small vessel using magnetic bearings

The calibration tests from *Song of the Whale* were performed with either a buoy in the water or a small inflatable boat with a radar reflector. Distances were obtained using LEICA GEOVID 7 × 42 BD infrared binoculars which have a specified accuracy of ±2m, or by radar. Distances using the infrared binoculars could be obtained easily up to 2-300m. At distances of 3-600m it became more difficult to get a good reflection from the target resulting in fewer data points. The radar was used for all distances greater than 600m. Observations using the radar involved the boat approaching the target at a steady rate. A simple linear regression of distance against time was applied to the individual radar distance measurements. This reduced the effects of errors in individual measurements and allowed interpolation between measurements.

No systematic tests were conducted to assess the accuracy of bearings derived from compass binoculars in the field but this is a system that has been used for many years for navigation of small craft. From a steady platform it is reasonable to expect such bearings to be within ±1° and from small craft under moderate conditions bearings within ±3° are usually achieved. For this analysis, bearing errors were assumed to be normally distributed with a mean of 0 and a standard deviation of 2°. Over the distances at which right whales were observed (mean of 360m) this contributed to a root mean square (RMS) error of 13m in distance from true position. This makes errors in bearing a relatively minor component of location error compared to errors in distance from a small vessel with a low observation height.

The accuracy of the positions obtained from the GPS receiver was assessed from position readings at a fixed location close to the study area. The overall RMS error in distance from true position was 31.2m. The RMS error in distance between pairs of locations taken five minutes apart was 41.0m. These GPS positions were obtained at a time when the accuracy of the system had been deliberately down-graded. The removal of selected availability will improve the accuracy of standard GPS receivers considerably. Accuracy of within a few metres would be possible using a differential GPS system in areas where this is available.

During the study of whale response to vessels, it was sometimes possible to use a combination of the video system and laser range-finding binoculars to continue data collection even when no horizon was visible. This was achieved by using the range-finding binoculars to obtain distances to vessels which were close enough to the whale that both were in the field of view of the camera. The vessel at known distance could then be used as a reference for analysis of video images (e.g. DeNardo *et al.*, 2001). The range-finding binoculars could be used to obtain distances to vessels, which presented a large reflective target, at up to 1,000m. However, distances to right whales could only be obtained using the laser binoculars when the whales were closer than 2-300m.

Tracking from large vessel using photogrammetric bearing

In order to test the accuracy of positions derived from the *James Clark Ross* using photogrammetric measurements of both distance and bearing, small icebergs or 'growlers' were tracked from ahead of the vessel until the closest point of approach when they came abeam. Using the position measured at the closest point of approach as the estimate of true location, the errors for the positions measured at greater distances were estimated. This effectively gives an upper bound on the error since any motion of the ice due to wind or currents would be counted as measurement error. In some cases when the ship was in areas with large amounts of ice, frequent course changes were required. Although the reading from the gyro-compass was recorded every time a bearing was taken, it was found that the errors on the bearing measurements were rather greater when the ship did not steam a straight track for the duration of the tracking experiment. The ship's position was recorded to a high degree of accuracy using multiple differential GPS receivers.

RESULTS

Accuracy of distances

Distance measurements from large oceanographic vessel

Fig. 4 shows the overall distribution of errors in distance measured from the *James Clark Ross* including the corrections for refraction. These are approximately normal with mean of –3m ($\sigma^2 = 11$). Thus, the mean was not significantly different from 0, suggesting no evidence of overall bias in the distance measurements.

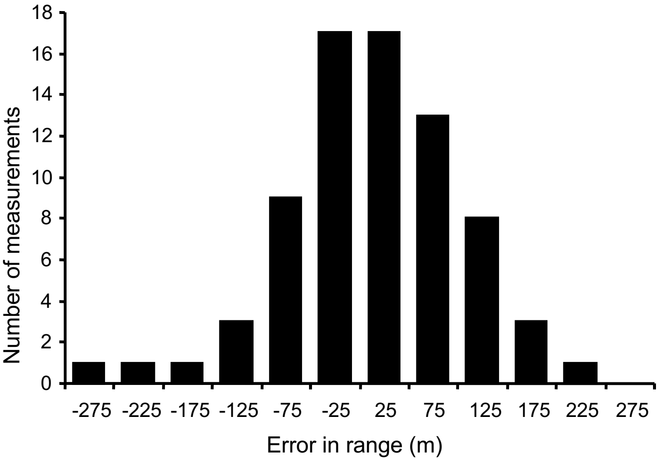

Fig. 4. Distribution of errors in distance from 'growler' tracks. Hand-held frame. 18m eye height.

If refraction was ignored, then the mean error was minus 98m ($\sigma^2 = 31$) suggesting a bias over the distances for which calibration tests were conducted. This resulted in a mean error of –5.1%. This bias will increase with increasing distance. The observed mean bias of –5.1% from the calibration tests agrees well with the values predicted by the refraction model of –6.8% at 8km, –4.0% at 5km and –2.2% at 2km. The simple model for refraction used in this study would appear to give good results but the method may still be susceptible to errors due to refraction in unusual atmospheric conditions such as strong temperature inversion.

Fig. 5 shows the overall RMS error taken from data from seven different tracking experiments with wind speeds in the range 5-13ms^{-1} (Beaufort 3-6) and estimated swell heights in the range 1-3m (i.e. typical survey conditions). The RMS error is approximately linear with distance with relationship RMS error = 0.033 distance. This gave an approximate 95% confidence interval for distance estimates of +6.5%.

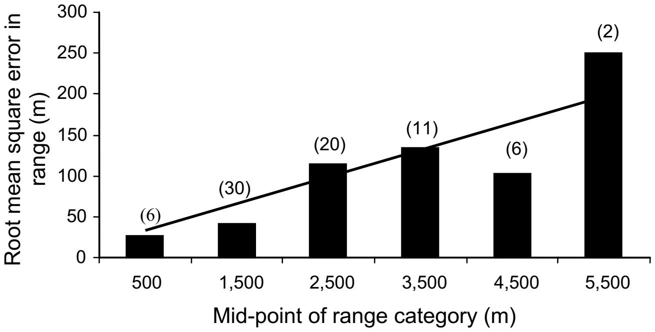

Fig. 5. Mean RMS error in distance estimates to 'growlers' for different distance categories (numbers in brackets indicate sample sizes). Hand held frame, 18m eye height.

Distance measurements from small research vessel

Fig. 6 shows data collected from the deck of *Song of the Whale* with an eye height of 4m. Whale location data can clearly only be collected at closer distances from smaller vessels with lower vantage points and the majority of data were collected within 500m of the whale. In this case the approximate relationship between RMS distance error and distance was RMS error = 0.08 distance. This gave an approximate 95% confidence interval for distance estimates of +16%.

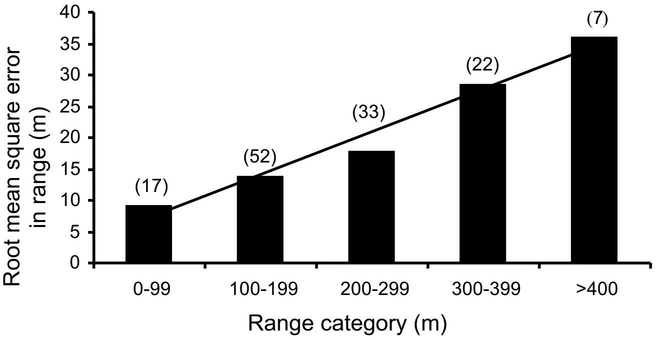

Fig. 6. Combined RMS error for different distance categories from calibration experiments. Hand-held frame. Data from *Song of the Whale* with an eye height of 4m. Numbers in brackets indicate sample sizes.

These two calibration tests from very different vessel types and platform heights give an indication of the range of accuracy that can be achieved. The main controlling factors on distance error will be platform height and the effects of waves and swell. These results are consistent with Gordon (2001) who found that errors in distance were approximately inversely proportional to platform height and lower from larger more stable vessels.

Accuracy of photogrammetric bearings

For fixed targets with the vessel moored alongside a quay, the RMS error in bearing measurement was 0.37° and this error should be considered as the limit to the accuracy of the system in terms of measuring bearing relative to the ship. The RMS error in bearing measurements at sea ranged from 0.6-1.7° for tracks where the ship made no course alterations, and the overall RMS error was 1.21°. For tracks during which the ship altered course, RMS errors were as high as 3.2°. This was most likely due to timing errors between obtaining correct gyro-compass readings and bearing measurements but the cause of these errors was not identifiable. For the ship steaming in a straight line, the mean RMS variation in gyro-compass readings was 0.5° with swell height and orientation being the main factor affecting the variation in heading. These results suggest that the current system achieved close to the maximum accuracy that can be achieved from a moving vessel at sea.

Practical use of the system to track cetaceans

Examples of the use of the system for tracking whales are given in Figs 7-10. These examples illustrate the type of data that can be obtained tracking right whales from a small vessel (Fig. 7) and humpback whales from a large vessel (Fig. 8). Fig. 7 shows an example of the track of a right whale over a period of four hours during which time it was approached several times by whalewatching vessels.

Fig. 8 shows the track of a group of three humpback whales that were followed from the *James Clark Ross* during an experimental small-scale study during the IWC/CCAMLR survey. The boxes around each position represent the standard deviation of the errors in distance and bearing derived from the calibration tests. The numbers in boxes refer to the time in minutes from the start of the tracking sequence with dotted lines linking the position of the vessel with the corresponding whale location. The plot illustrates the change in accuracy of the whale locations with distance from the vessel. One of the proposed components of the SOWER 2000 programme included small-scale studies to relate krill distribution to whale movements. This short experiment showed that the video system could be a useful tool for such work in that it would allow accurate mapping of the whale movements in relation to concentrated krill patches located by the ship's echo-sounders.

The tracking data shown in Figs 7 and 10 were collected when the vessels were manoeuvring to follow the whales. This meant that the whales remained well within distances at which they could be easily detected on video images. Successful tracking studies have also been conducted in this way with minke whales. Sperm whales also proved easy to locate and track using the 'Big Eye' mounted system in the Gulf of Mexico.

Use of system for line transect survey

The requirements for tracking whales during sightings surveys are more demanding because of the need to determine the location of the initial sighting. Fig. 10 shows an example of tracking a group of fin whales under survey conditions. In this case the first location obtained was within a few seconds of the initial detection by the observer. However, there were situations in which whales could not be detected on video at the same distance that they could be seen by visual observers and also occasions where the initial surfacing sequence was not captured. The maximum distances of detection of different species that have been made using the hand-held and 'Big Eye' systems are given in Table 1. These do not necessarily represent the maximum under optimum conditions but do give an idea of the likely effective distance under good conditions. In general, it appeared that the distance at which measurements could be made from the video using a lens equivalent to the field of view of the 7 × 50 binoculars were roughly the same as the distance at which whales could be detected with the naked eye.

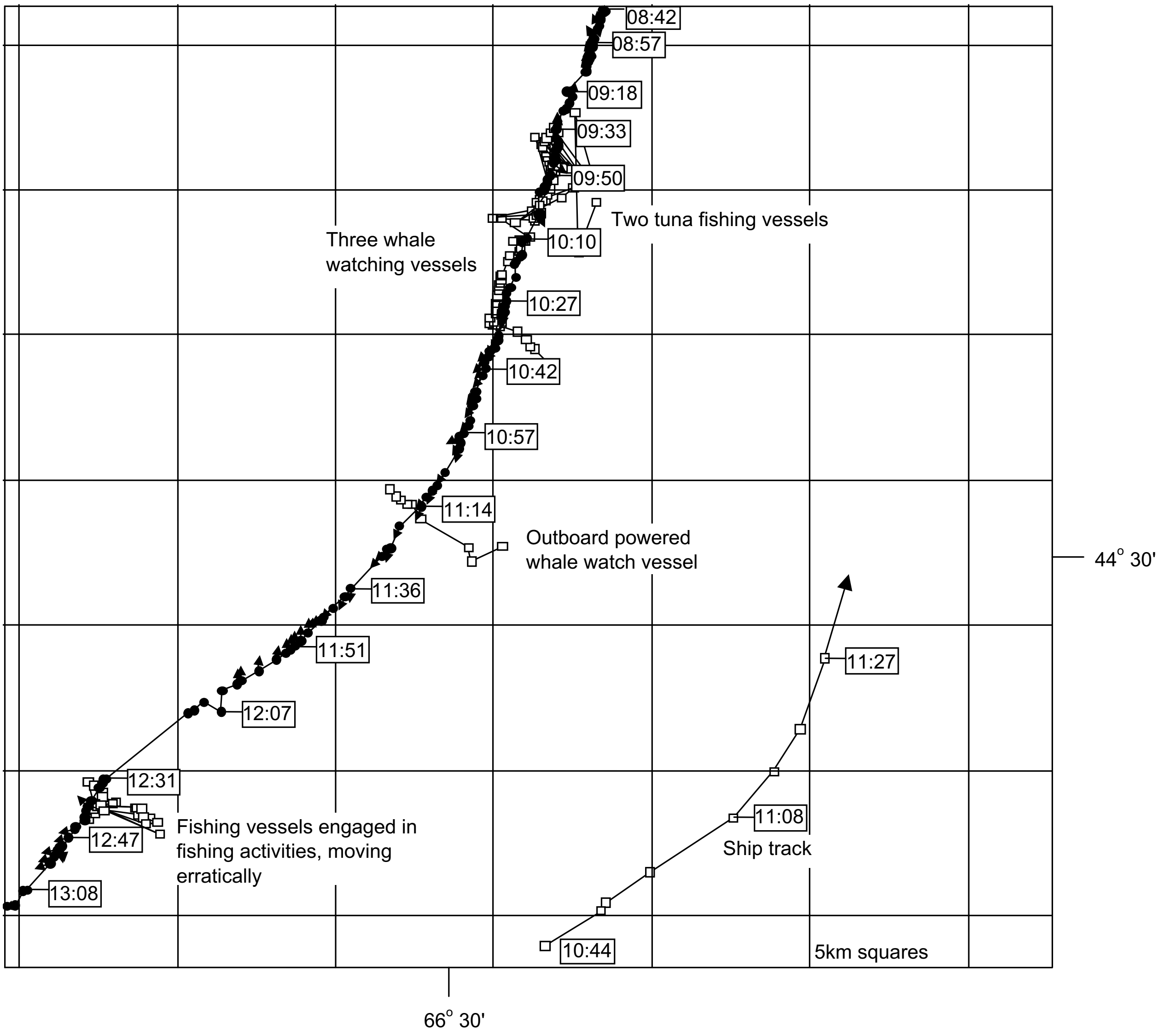

Fig. 7. Track of right whale and other vessels in the Bay of Fundy. Tracked from *Song of the Whale*.

The tests of the system during the IWC/CCAMLR survey were not part of the primary data collection tasks of relaying reticle and angle board readings to a data recorder via a hand-held radio (Reilly *et al.*, 2000). The observer's other duties meant that it was not possible to evaluate the proportion of encounters for which distances would have been successfully obtained by video had this been the primary method of data collection. In practice, use of the video system was found not to interfere with the collection of other data.

During the 1999 NMFS harbour porpoise abundance cruise, video was used to locate animals beyond the view of the primary sightings team and track them as the boat moved past them; this exercise was a feasibility trial and the video data did not contribute to the final abundance analysis. This provided suitable data for mark-recapture line transect methods (e.g. Borchers *et al.*, 1998). Data were only collected in good sighting conditions with a sea state of less than three. It was found that, provided a good commentary was spoken onto the tape, the cues of distant porpoises could be identified on the tape and accurate measurements made. These were often very small features on the captured image and without the benefit of a commentary they could not have been identified as porpoises with any confidence. Fig. 9 shows some of the tracks obtained during this exercise. Although porpoises were the focus of this survey, several other species were also sighted and the maximum distances for these are shown in Table 1.

DISCUSSION

Under suitable conditions, the system described here allows whales to be located and tracked from vessels at sea, with a measurable degree of accuracy, using standard, readily available equipment. As with the use of reticle binoculars, the method described relies on a clear horizon to enable distances to be measured. Nevertheless, the system offers considerable advantages over methods that rely solely on observer estimates of distance. The methods described are by no means the only way of making such measurements and the capability of systems will undoubtedly improve with the rapid development of digital imaging technology. However, we believe that the results obtained are sufficiently encouraging for there to be no reason to wait for improved technology before incorporating this level of instrumentation into standard survey design. Many researchers are understandably reluctant to adopt new survey methodologies if these complicate comparison with previous datasets. This system merely provides the data that existing methods require but with a higher degree of accuracy. Further, the

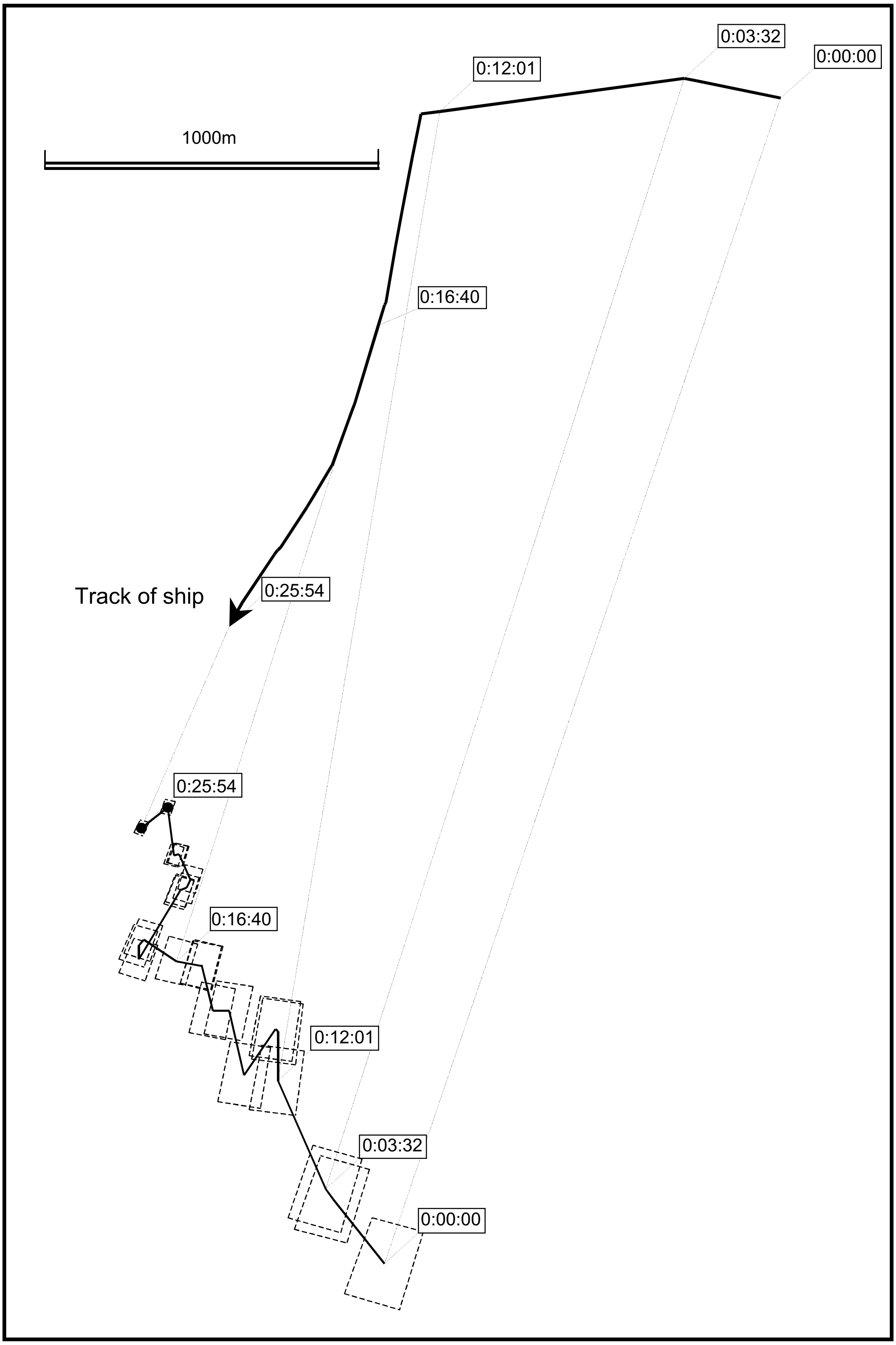

Fig. 8. Track of humpback whale group during small scale study in Southern Ocean. Dotted lines link ship's position at a particular time to whale location at the same time. The boxes around each position represent the standard deviation of the errors in distance and bearing derived from the calibration tests. Tracked from *James Clark Ross.*

experimental use of the system during the IWC/CCAMLR survey demonstrated that it could be used by an observer who was additionally collecting data visually using an angle-board and reticle binoculars.

For sightings surveys, the ranges at which the radial distance of the initial detection can be measured will clearly be an issue for the utility of the system. It is difficult to establish the distances at which detections are made visually but cannot be measured because they are not detected on the video image. However, it is inevitable that depending on weather conditions and the species being studied, the video system will only provide distances for a certain proportion of the initial sightings made during a survey. The focal length of the lens used with the 7 × 50 binoculars provided a

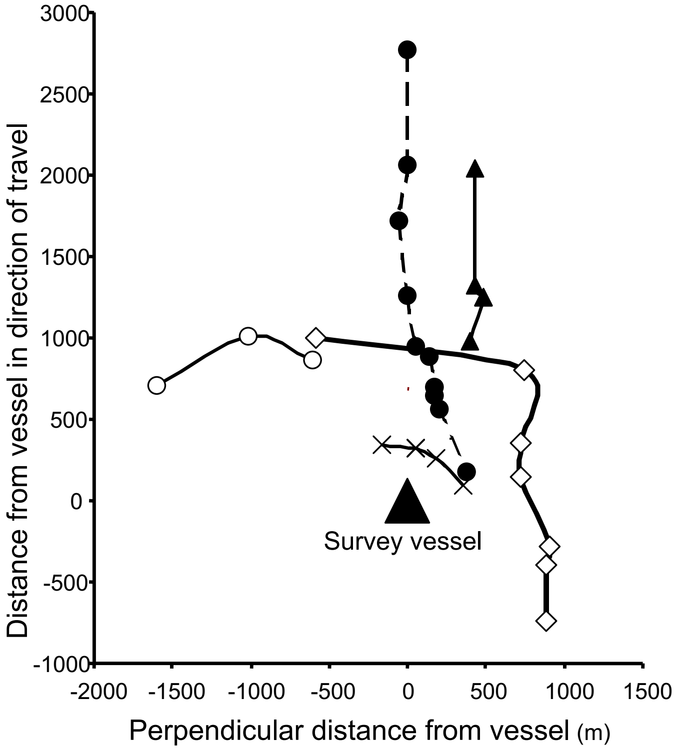

Fig. 9. Tracks of harbour porpoises, from *Abel-J* using video camera mounted on ‘Big Eye’ binoculars. Porpoise locations are shown relative to the survey vessel with different symbols representing different encounters.

vertical resolution of 3.5 pixels per minute of arc. This is theoretically better than the typical one cone per minute of arc in the human eye (Spillman and Werner, 1990). However, the performance of the human eye is enhanced by hyper-acuity (the ability to resolve objects subtending angles smaller than the theoretical resolution). The enhanced performance of the human eye relative to the current video system is offset by the fact that the observer needs sufficient visual cues to determine that the sighted object is in fact a surfacing cetacean whereas distance measurement just requires that the sighting can be located on the video image. It is likely that within the next few years, digital imaging technology will have advanced sufficiently that the quality of image obtained can match that of the human eye for an equivalent field of view. The use of computer based systems to store video data will also enable images to be stored prior to the observer responding to the sighting. This will ensure that initial surfacings are not missed because of delays in operating the equipment.

These techniques are particularly appropriate for survey methods that require tracking of whales subsequent to the initial detection. These methods frequently require additional personnel to act as data recorders as well as the observers. This adds to the expense, and the number of berths required on the survey vessel may also be a limiting factor. There are also practical problems and the potential for error when observers have to relay data to a second person. The video system allows the complete dataset to be recorded without observers taking their eyes from the binoculars. For behavioural studies, the fine scale data on movements and behaviour from a large number of animals that this technique can provide is complimentary to sparser, coarse-scale data from only a few individuals from VHF and satellite telemetry, and may also assist with interpretation of these data.

An unavoidable overhead of the video system is the time required for analysis. However, for some surveys the difficulties of accounting for measurement error have necessitated considerable additional analysis effort (e.g. IWC, 1997). The specially written software reduces the number of keystrokes required for analysis of video images to a minimum and writes the data into a database automatically. On average, for a number of different operators and a number of different sequences, it took about two hours to analyse each hour of video. On a survey with a high sighting rate, such as the Gulf of Maine porpoise survey, around one hour of video was collected each day. The additional analysis time can be offset against the time required to analyse datasets using visual estimates that are subject to a much greater degree of estimation error. The effort and financial expenditure expended in any ship-based sightings survey is likely to more then justify these small overheads if they contribute to a significant increase in the quality of the survey’s primary data.

During the process of testing the video system, the use of laser binoculars to measure distance to cetaceans was evaluated. In theory, laser-based devices have a number of potential advantages over the video system. There is no need for a clear horizon or an elevated viewing platform and instant readings can be obtained. However, obtaining a reading from a surfacing cetacean requires considerable skill and distances appeared to be limited to a few hundred metres

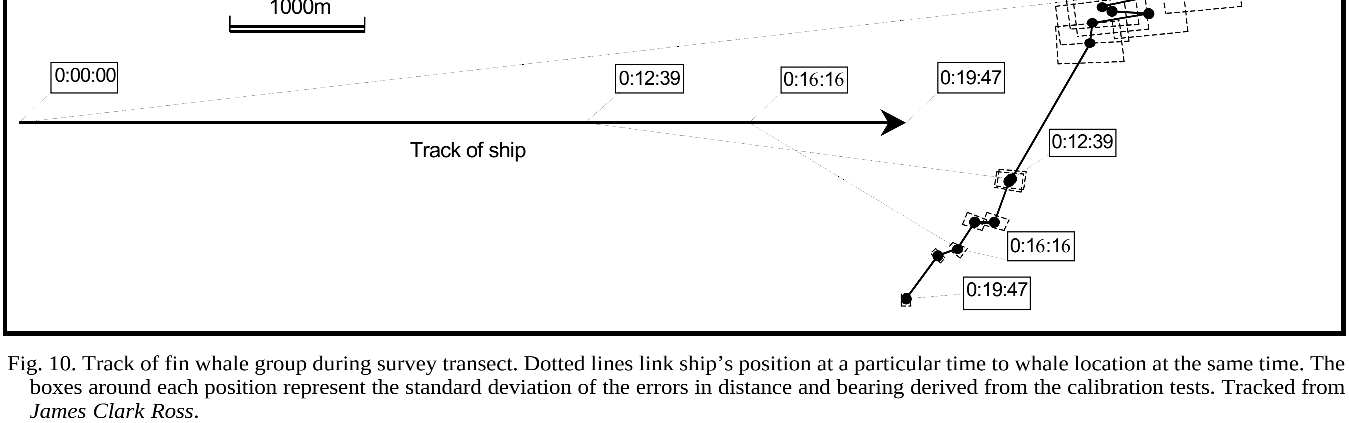

Fig. 10. Track of fin whale group during survey transect. Dotted lines link ship’s position at a particular time to whale location at the same time. The boxes around each position represent the standard deviation of the errors in distance and bearing derived from the calibration tests. Tracked from *James Clark Ross*.

Table 1

Maximum distances at which most visual cues from different species were measured under optimum sighting conditions.

		Maximum distance (km)	
Species	Cue	Shoulder mount system (2.7^{o} vertical field of view)	'Big Eye' system (1.8^{o} vertical field of view)
North Atlantic minke	Body	1.3	3.7
Southern bottlenose whale	Body	1.5	
Harbour porpoise	Body		2.8
White-sided dolphin	Splash		2.5
Southern right	Blow	3.3	
Killer whale	Blow	2.6	
Fin whale	Blow	8.8	7.9
Humpback whale	Blow	6.9	
Sei whale	Blow	3.5	
Sperm whale	Blow	3.9	8.0

even for large whales. There is also considerable scope for obtaining precise readings from false targets and these errors would be very difficult to quantify.

The model used to predict refraction has implications for other surveys that rely on measurements of distance using reticle binoculars. If refraction is not allowed for, then distances will be negatively biased, resulting in a positive bias in abundance estimates. Although the effects of refraction are relatively small in relation to the likely errors in reticle readings, there is nevertheless the possibility of a consistent bias of several percent depending on the distances at which most observations are made.

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Southern Hemisphere minke whales: standardised abundance estimates from the 1978/79 to 1997/98 IDCR-SOWER surveys

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ABSTRACT

Minke whale abundance estimates, standardised by the use of consistent methodology throughout, are presented from the IWC/IDCR and SOWER Antarctic circumpolar sightings surveys for three circumpolar sets of cruises: 1978/79–1983/84, 1985/86–1990/91 and 1991/92–1997/98 (*still incomplete). The database estimation package DESS is used to obtain these standardised estimates. Two survey modes (closing and IO) are used in the surveys; IO mode is considered to provide less biased estimates. An updated estimate for the conversion factor from closing to 'pseudo-passing' mode of $R = 0.826$ (CV = 0.089) is obtained. IO and 'pseudo-passing' estimates are then combined using inverse-variance weighting to give estimates of 608,000 (CV = 0.130), 766,000 (CV = 0.091) and 268,000* (CV = 0.093) for the three circumpolar sets of cruises. These cruises have covered approximately 65%, 81% and 68% of the ice-free area south of 60°S. As estimates of abundance for Southern Hemisphere minke whales, these are negatively biased because some areas inside the pack ice cannot be surveyed, not all whales migrate into the area south of 60°S, the assumption is made that all whales on the trackline are sighted, and minke whale sightings for which species identification is uncertain ('like minkes') are omitted. The three circumpolar estimates are extrapolated simply to account for the different areas covered in the sets of surveys, and also for the increasing proportion of 'like-minke' sightings over time. The results suggest that for comparable areas the abundance estimates for the third circumpolar set of cruises are 55% (closing mode only) and 45% (IO mode only) of those for the second set, but that the first and second set estimates are within 15% of each other. The decrease in abundance between the second and third sets is statistically significant at the 5% level. Possible reasons for this estimated decline are discussed, related both to factors that might render the estimates non-comparable, and to population dynamics effects that could have led to a real decline. Further attention should be given, in particular, to the most appropriate method for estimation of mean school size for these surveys.

KEYWORDS: ANTARCTIC MINKE WHALE; SOUTHERN HEMISPHERE; ANTARCTIC; ABUNDANCE ESTIMATE; SURVEY-VESSEL

INTRODUCTION

There has been some recent controversy over the current status of Antarctic minke whales (*Balaenoptera bonaerensis*). The best source of data to address this issue is the series of 22 consecutive annual surveys conducted almost exclusively south of 60°S between 1978/79 and 1999/2000. The first 18 surveys fell under the IWC's IDCR programmes (International Decade of Cetacean Research) and the last four under its SOWER circumpolar programme (Southern Ocean Whale and Ecosystem Research). These surveys may be divided into three circumpolar sets of cruises: 1978/79–1983/84, 1985/86–1990/91 and 1991/92–1999/2000 (incomplete). The 1984/85 cruise was devoted mainly to experiments, and is normally excluded from abundance analyses (e.g. Brown and Butterworth, 1999). The data are at present encoded and validated as far as the 1997/98 cruise, and are contained in a database package DESS (IWC Database-Estimation System Software v 3.0 - Strindberg and Burt, 2000), which automates the process of extraction and abundance estimation. This paper is deliberately restricted to estimation procedure options available in DESS, in part to ensure that the results presented are readily replicable.

Abundance estimates for minke whales have previously been calculated for each survey separately - most recently by Burt and Stahl (2000) for the 1997/98 cruise. However, the original data were thoroughly re-checked when they were being entered in DESS in recent years, resulting in minor changes to the sightings and effort data and to the areas of the open ocean regions associated with the survey strata. Furthermore several aspects of the estimation process adopted by the IWC Scientific Committee have changed over the period of the assessments (as summarised in Appendix 1). The most recent change was to the mean school size ($\bar{s}$) estimation method from the 1995/96 survey onwards (Burt and Borchers, 1997). The effective search half-width (w) has been estimated by fitting a hazard-rate function to the perpendicular distance (y) distribution data from the 1985/86 survey onwards (Butterworth and Silberbauer, 1987). In general, estimates of $\bar{s}$ and w have been calculated on a stratum- and vessel-specific basis, but in certain cases small sample size forces some pooling. The pooling rationale was *ad hoc* in the earlier assessments, but from the 1993/94 survey (Borchers and Burt, 1996) onwards, Akaike's Information Criterion was used (AIC, Akaike, 1973). A contouring method was used to convert daily density estimates into abundance for the surveys from 1978/79 to 1982/83 (e.g. Best and Butterworth, 1980) before it was supplanted by the current approach of treating segments of search effort as random and independent samples within pre-defined strata.

These changes in the assessment methodology have resulted in a growing incomparability between earlier and more recent abundance estimates. Butterworth *et al.* (1987 - see also IWC, 1988, Appendix 7) revised the estimates from the 1978/79 to 1983/84 cruises, fitting the hazard-rate function for w and also stratifying the areas surveyed. Haw corrected and extended that series to the 1988/89 survey, to provide the estimates used for the 1990 Comprehensive

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Assessment of Southern Hemisphere minke whales (IWC, 1991, p.117). These were marginally further corrected in Haw (1993b). The Comprehensive Assessment selected the most recent cruise at that time in each of the six Antarctic Management Areas (see Fig. 1 and Donovan, 1991) to provide the best individual estimates of minke whale abundance. These estimates sum to the widely quoted circumpolar estimate of 760,000 (CV = 0.098) for Southern Hemisphere minke whales. This figure was considered at that time (IWC, 1991, pp.120-21, 130) to be representative of abundance in the mid-1980s, but is no longer regarded as an appropriate estimate of current abundance (IWC, 2001, p.31). Accordingly, an updated set of estimates is timely, especially given that the IWC Scientific Committee is planning a thorough review of minke whale abundance estimates commencing in 2001. This paper therefore presents revised estimates of abundance from each survey between 1978/79 and 1997/98, using methodology available in DESS applied consistently throughout this time period.

METHODS

The methodology outlined in Burt and Stahl (2000) (referred to here as the 'standard methodology' or 'standard analyses'), together with their notation, is followed here as far as possible for obtaining abundance estimates from each survey. Points of departure are expanded upon below where appropriate. This standard methodology is essentially that adopted by the IWC Scientific Committee in 1992 (IWC, 1983, p.106), except for the subsequent procedure adopted for mean school size estimation (see Appendix 1).

Survey modes and activity codes

Searching on the surveys is restricted to Beaufort states of 5 or less. The searching speed was originally 12 knots, but was reduced in 1987/88 to 11.5 knots in order to assist in fuel efficiency and reduce vibration. Further details of the survey procedures (and experiments) on the first ten cruises are summarised in Joyce *et al.* (1988); for later years, such details can be found in the annual cruise reports (e.g. Ensor *et al.*, 1998 for the 1997/98 survey).

Survey effort is divided into closing mode and IO (independent observer) mode. The first circumpolar set of surveys was conducted in closing mode only, i.e. when a school is sighted, the vessel suspends primary searching effort, turns[1] off the trackline and closes with the sighting. This mode enables better species identification and school size estimation. Later surveys (from 1984/85) alternated between closing and IO mode. In IO mode, the vessel continues steaming along the trackline after a sighting, with observers in the barrel and the IO (independent observer) platform[2] (both located on the main mast) maintaining full search effort while those on the upper bridge concentrate on tracking and identifying the sighting. IO mode was introduced because of concern about possible biases introduced into density estimation by the closing mode procedure: for example, upward bias through deviations from the trackline drawing the vessel into preferentially higher density areas, downward bias from neglect of 'secondary sightings' while the vessel closed off primary effort on an original sighting, and the many end effects that arise from frequently switching on and off primary search effort to close with sightings. IO mode was intended as the standard, with closing mode retained because of the unreliability[3] of school size estimation and species identification in IO mode (many of the sightings are not approached closely in this mode).

A number of activity codes are used to distinguish between different aspects of these main modes. The following codes are used for closing mode and IO mode in these analyses (*denotes those used in the 'standard analyses'). More details of the different codes can be found in Strindberg and Burt (2000); a summary of the amount of primary search effort under each code in each survey is given in Branch and Butterworth (2001, table 4).

Closing mode
BA*: Ice navigation during closing mode reduces the effective search effort.
BC*: Searching on the trackline.
BR*: Returning to the trackline after closing with a sighting.
SE*: Closing mode, no distinction between BC and BR.
BB: Closing with independent observer tracking (1987/88 survey only).

IO mode
BI*: Ice navigation in passing mode reduces the effective search effort.
BO*: Passing mode with independent observer in position (i.e. standard IO mode).
BU: Cue counting from the bridge during BO mode (1986/87 survey only).
BQ: Passing with independent observer tracking (1987/88 survey only).

Excluded activity codes
BP: Passing mode with no independent observer.
BH: High density of schools in IO mode causes difficulty in discriminating between schools.
BL: High density of schools in closing mode causes difficulty in discriminating between schools.

In the first six surveys, closing mode search effort data were always recorded under the SE code - for the later surveys this was split into BC and BR to distinguish between these two components. Almost all of the effort recorded by vessel *Shonan Maru 2* in 1986/87 was under the BU code, which is included here since the manner in which cue counting was conducted did not compromise the normal collection of sightings data. The codes BB and BQ were used only in 1987/88, where they comprised 20% of closing mode and 44% of IO mode effort respectively, so that their exclusion would compromise the representative nature of the remaining data for that survey.

In practice, no effort during closing mode survey was recorded as BL. In IO mode, the recorded school sighting rate under BH is some six times the average over the other

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[1] In some of these earlier cruises, the turn was delayed until the angle between the sighting and trackline became larger, to better estimate perpendicular distance from the trackline, but this practice was later discontinued as it increased the chance of losing track of sightings.

[2] The additional observer in the IO platform in this mode was introduced to provide data for the estimation of $g(0)$, the probability that a school on the trackline is sighted (e.g. Butterworth and Borchers, 1988). The observers in the standard barrel and the IO platform are kept unaware of each others sightings.

[3] This unreliability was confirmed by 'SSII' experiments, which indicated school size estimation in passing/IO mode to be negatively biased by about one third (IWC, 1987, p.70).

codes for this mode, but since only 0.2% of the total IO effort is specified as BH, neglect thereof does not introduce any substantial bias.

Only sightings of schools comprised entirely of minke whales are used for the analyses of this paper[4]. Sightings and search effort are included only if they were recorded inside the survey region, during primary search effort, and outside periods when experiments were conducted.

Survey vessels

Up to four vessels were used in the earlier cruises. Most of the sightings data have come from the *Shonan Maru* and *Shonan Maru 2* (SM1 and SM2) which have been used in every survey since 1981/82. The *Kyo Maru 27* (K27) was used in five surveys to 1986/87, the *Toshi Maru 11* (T11) in the second and third surveys, and the *Toshi Maru 16* and *18* (T16 and T18) in the first survey only. During the 1980/81 to 1986/87 cruises, the *Vdumchivy 34* (V34) or the *Vderzhanny 36* (V36) was used predominantly to map the ice edge and for marking, so their sightings and effort data are excluded, as for previous analyses.

Species codes

The recommendations of Branch and Ensor (2001) regarding interpretation of the various species codes used for minke whales have been incorporated into DESS 3.0. Thus over 1978/79-1996/97, minke whales were recorded as code 04, and 'like minke' whales as code 39. From the 1993/94 survey, code 74 was introduced for dwarf minke whales, following recognition that this sub-species could be present in the region covered by these surveys. Dwarf minke whales have not yet been formally named, but are closer to ordinary minke whales (*Balaenoptera acutorostrata*) than to Antarctic minke whales (*B. bonaerensis*) in several respects (e.g. Best, 1985; Kato and Fujise, 2000). To distinguish whether identification was uncertain at the species or sub-species level, further codes were introduced for the 1997/98 survey. For that survey, codes 04, 90, 91 and 92 are taken to be minke whales, and code 39 is considered to be 'like minke'[5]. Estimates in this paper referring to 'minke whales' are put forward as estimates for Antarctic minke whales, although it is possible that these estimates include a very small proportion of dwarf minke whales (Kato and Fujise, 2000). Only two sightings of dwarf minke whales have been recorded in the survey regions since a code for this sub-species was introduced in 1993/94. However, it can be difficult to distinguish dwarf minke whales from Antarctic minke whales, particularly for distant sightings made in IO mode (P. Best, pers. comm.).

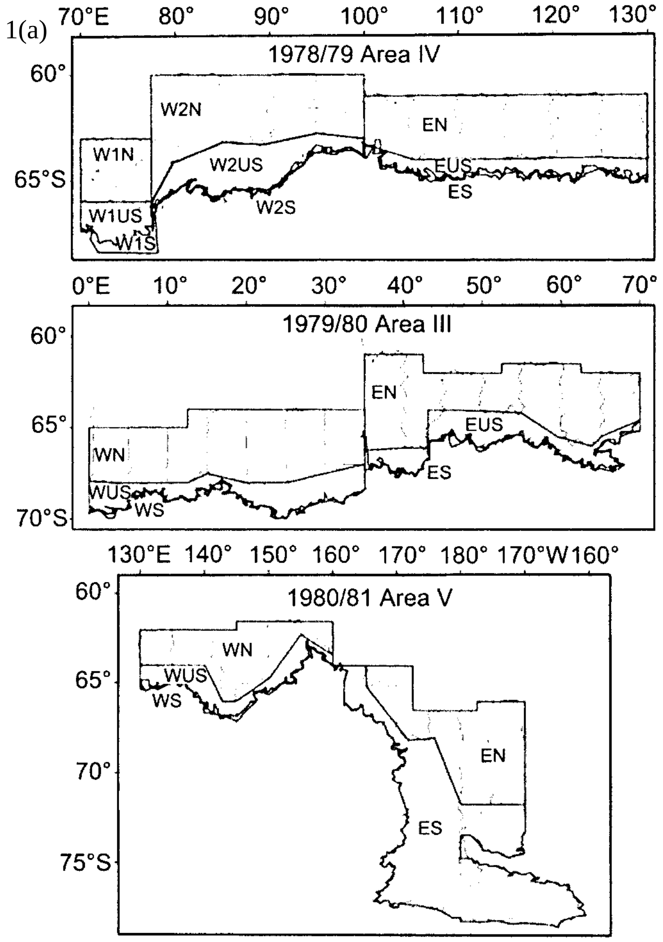

Fig. 1a. Strata surveyed in each year from 1978/79 to 1980/81. The southern boundary for each survey was the ice edge. Bold lines indicate the stratum boundaries, whilst cruise tracks are indicated by lighter lines. Only primary search effort (closing mode and IO mode data are combined) is indicated; gaps in the cruise tracks indicate off-primary-effort steaming (e.g. because of poor weather conditions). The 'US' strata in the early surveys were unsurveyed regions between the south ('S') and north ('N') strata.

Note that Figs 1b–f are given on the following two pages.

Strata and cruise tracks

When these IDCR surveys were first planned in 1978, mark-recapture methods were conceived as the primary basis to estimate abundance, with sightings playing a secondary role only. This required marking as many whales as possible, so that the effort of one of the two survey vessels was concentrated close to the ice-edge where the greatest minke whale densities were expected. This changed from the 1983/84 cruise for two reasons: (1) minke whale abundance turned out to be considerably larger than anticipated when the programme was planned such that the resultant low number of recaptures gave estimates with notably worse precision than had been expected from these surveys; (2) the decision taken in 1982 to impose a moratorium on commercial whaling three years thereafter removed the basis to obtain recaptures. As a result, sightings became the primary data source to estimate abundance.

The areas surveyed by each cruise are outlined in Figs 1a-f, together with the tracklines followed while on primary effort. It is immediately obvious that the survey design for most of the first circumpolar set of surveys (Figs 1a-b) differed from that in later cruises. In the first five of these

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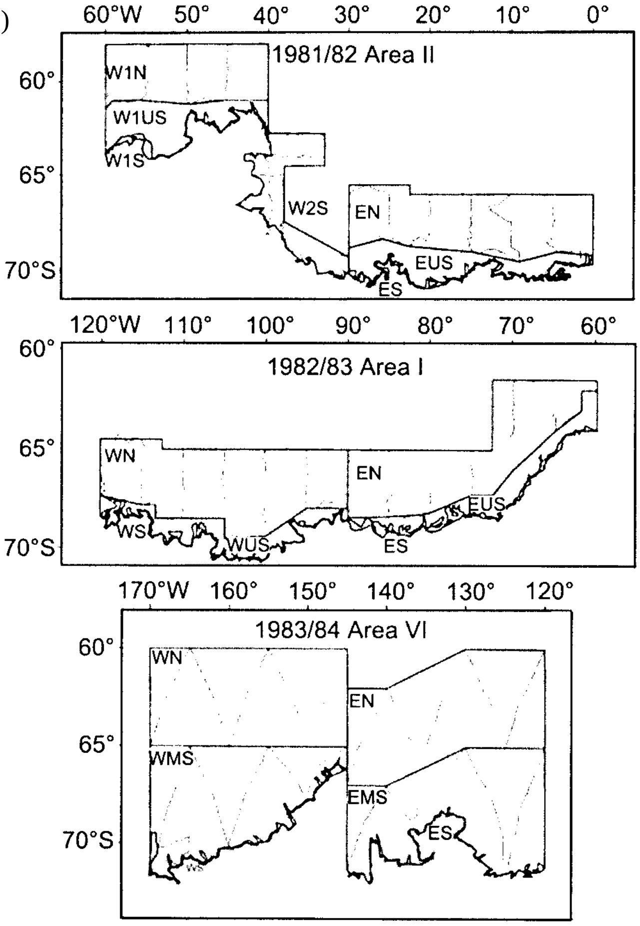
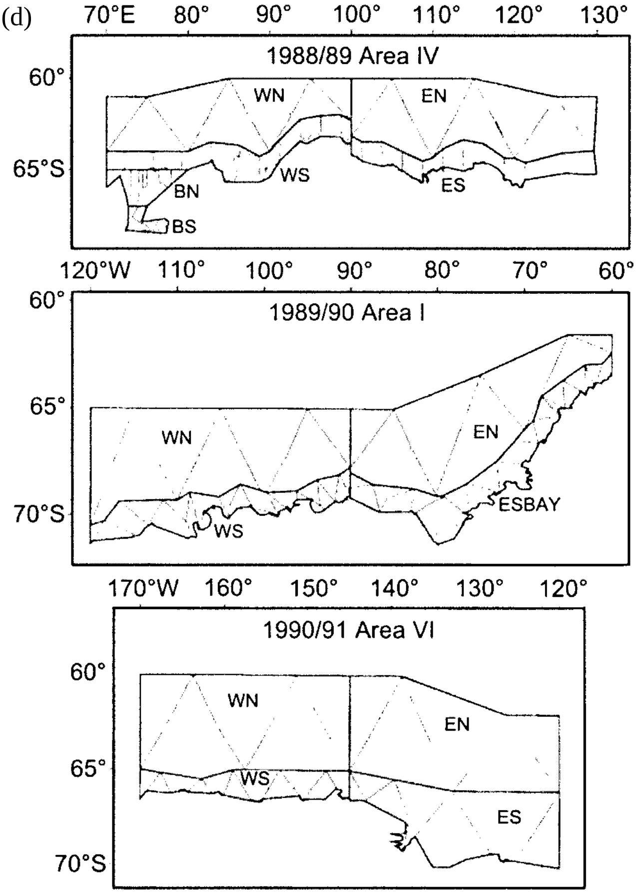
[4] Since 1993/94, schools of more than one species have been recorded using different sighting forms for each species, so that such 'mixed' schools are included in these analyses. Prior to that date they are excluded, as has been past analysis practice; this represented less than 0.5% of schools of minke whales only (see Branch and Butterworth, 2001, table 3), so alternative choices here would hardly impact final estimates.

[5] In the 1997/98 survey, the codes in DESS 3.0 are: 04: definitely Antarctic minke; 39: like minke: probably a minke, but not certain; 74: definitely dwarf minke; 90: definitely minke and probably dwarf minke, but not certain; 91: definitely minke, but unsure whether Antarctic or dwarf; 92: definitely minke and probably Antarctic minke, but not certain.

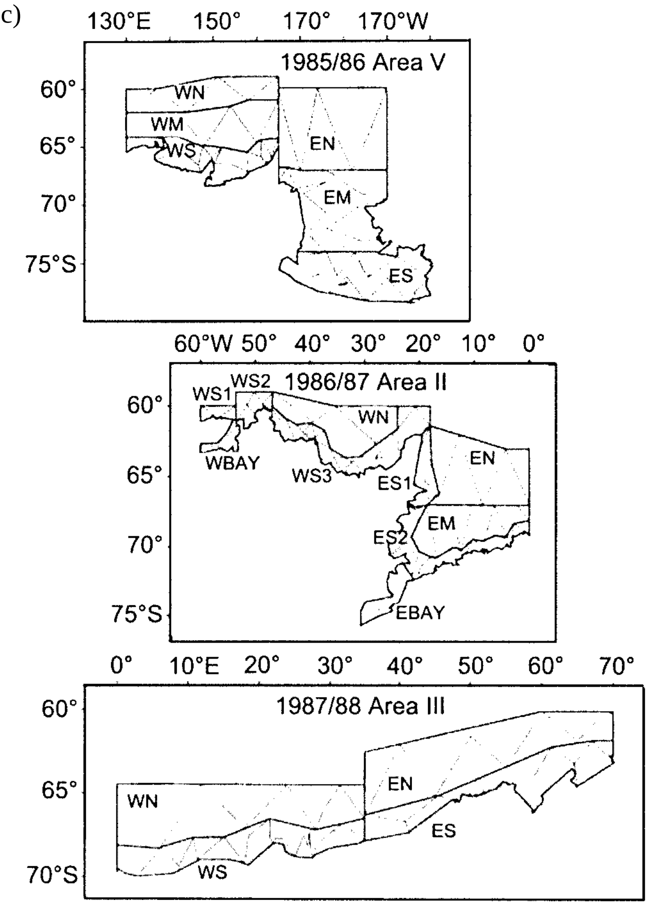
1(b)



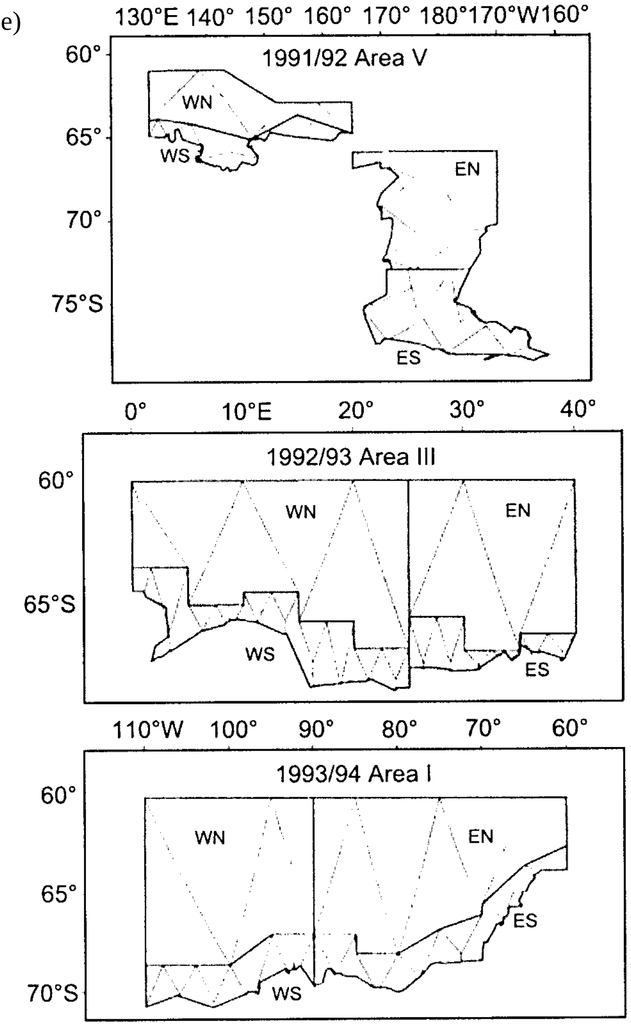
1(d)



1(c)



1(e)



Figs 1b to 1e. Strata surveyed in years 1981/82 to 1993/94. Details as for Fig. 1a.

1(f)

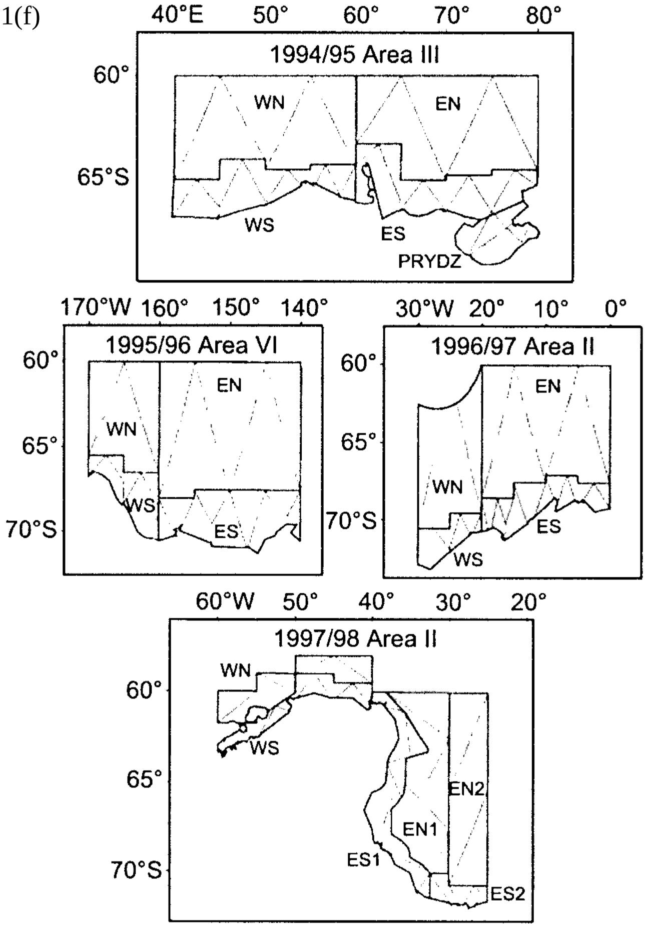


Fig. 1f. Strata surveyed in years 1994/95 to 1997/98. Details as for Fig. 1a. Note that the circular 'bite' missing from the WN stratum in 1996/97 falls within the EEZ of the South Georgia and South Sandwich Islands.

early cruises, one vessel followed the ice-edge[6] closely (the 'S' strata), while another vessel alternated between latitudinal and longitudinal legs (the 'N' strata), typically 60 n.miles or more north of the pack ice. An unsurveyed area ('US') generally remained between the 'S' and 'N' strata. The 'S' strata were considered to cover an area twice that between the ice-edge and the vessel's trackline. In 1987, the IWC Scientific Committee decided to assign the average density of whales in the 'S' and 'N' strata to this unsurveyed area, thus effectively adding half the area of each 'US' stratum to the area of the corresponding 'S' and 'N' strata (IWC, 1988, pp.77-8). This approach was considered reasonable based on 'density gradient' experiments conducted in 1980/81 and 1981/82 to check the rate of minke whale density fall off away from the ice-edge (Butterworth *et al.*, 1982; 1984a). These suggested that averaging the density estimates in this manner would not introduce substantial bias in the abundance estimates. Typically (see Figs 1a-f) the 'S' strata for the second and third circumpolar sets of cruises cover comparable latitudinal ranges to the 'S' and 'US' strata combined for the first five cruises. These later cruises thus contain further information about the pattern of minke whale density with distance from the ice-edge in the 'US' regions, which could be used to refine this 1987 decision.

There are two exceptions to this general pattern in the first six cruises. First, the 1980/81 ES stratum and the 1981/82 W2S stratum are not divided into 'S' and 'US' portions since there was some search effort in the centre of each of these areas. Secondly, for the 1983/84 survey, the data from the vessel following the ice edge are not used in the standard DESS stratification (for convenience) since the middle vessel covered the entire region south of the 'N' strata (i.e. the WMS and EMS strata are included, but the WS and ES strata are omitted, in abundance estimation). In addition, in the 1983/84 cruise, vessels off the ice edge followed the zigzag cruise-track design that was to be used in subsequent cruises.

The second and third sets of circumpolar cruises followed a zigzag cruise-track design within each stratum (Figs 1c-f)[7]. The survey region was typically divided into four strata: WN, WS, EN and ES. Exceptions occur when there are bays in the south strata (e.g. the Ross Sea in Area V).

There are differences in the latitudinal coverage of the survey regions (Figs 2a-c). In the first and second circumpolar sets of cruises, coverage between the ice edge and 60°S was not complete (except for Area V in 1985/86). In contrast, in the third circumpolar set of cruises, the entire area south of 60°S was always surveyed (except for Area V in 1991/92). The three sets of surveys reflect coverage of roughly 65%, 81% and 68% of the open ocean area south of 60°S respectively; the last figure reflects the incomplete nature of the third circumpolar set of cruises as at 1997/98. This raises problems of comparability between abundance estimates from the three different sets of cruises, as discussed later.

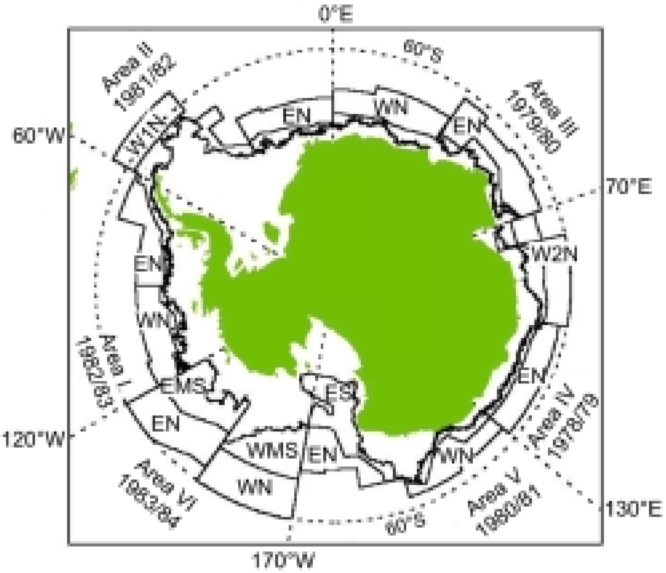


Fig. 2a. The area surveyed by the first circumpolar cruise.

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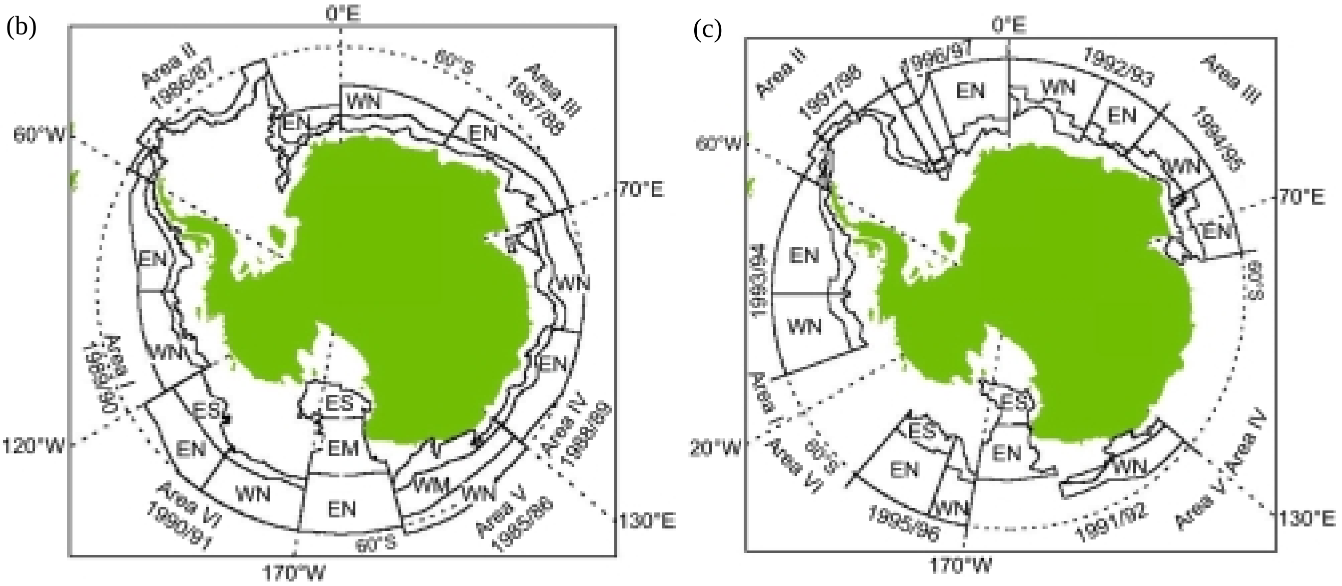
[6] The 'ice-edge' is generally the edge of the pack ice. In the first two circumpolar sets of surveys, the ice-edge was determined by dedicated vessels, but the JIC satellite system was used to map the ice-edge in later cruises. There are often large areas of open water inside the ice-edge which are not accessible to the survey vessels, but would be suitable habitat for minke whales.

[7] Although the cruise tracks shown in Figs 1c-f may seem to reflect similar designs, there was in fact an underlying change effected from the 1992/93 cruise. Between 1984/85 and 1991/92, the track design algorithm used as the cruise proceeded was developed to enable subsequent abundance computation using a Horvitz-Thompson estimator approach. This required the ability to separately estimate the probability of sighting each school (e.g. Cooke, 1987). Later, however, with the prospect of abundance estimates being required for 5° longitude sectors to relate to the *Small Areas* adopted by the IWC Scientific Committee for the Revised Management Procedure (IWC, 1994b), the track design was changed to give more representative coverage of the 5° sectors.



Figs 2b-c. The areas surveyed on the second and third (up to 1997/98) circumpolar cruises.

In addition to differences in cruise track design and in the areal coverage of the surveys, there were also some changes in the timing of the surveys (Fig. 3). In particular, as recommended by the Scientific Committee (IWC, 1994c), the surveys from 1994/95 onwards started about 2-3 weeks later than all the earlier surveys, in order to improve the chances of the ice edge receding before the start of the survey, and thus ease the task of cruise track design (Ensor *et al.*, 1995).

Duplicate and triplicate sightings

In IO mode, duplicate and even triplicate sightings are a common occurrence. The same school may be sighted from the IO platform, from the barrel or from the upper bridge. Each pair/triplet is assigned a probability status (‘definite’, ‘possible’, or ‘remote’) that the same school has been sighted. In the standard analyses (and in this paper), only one sighting from each pair/triplet in the ‘definite’ duplicates is retained when estimating abundance. Normally, the sighting

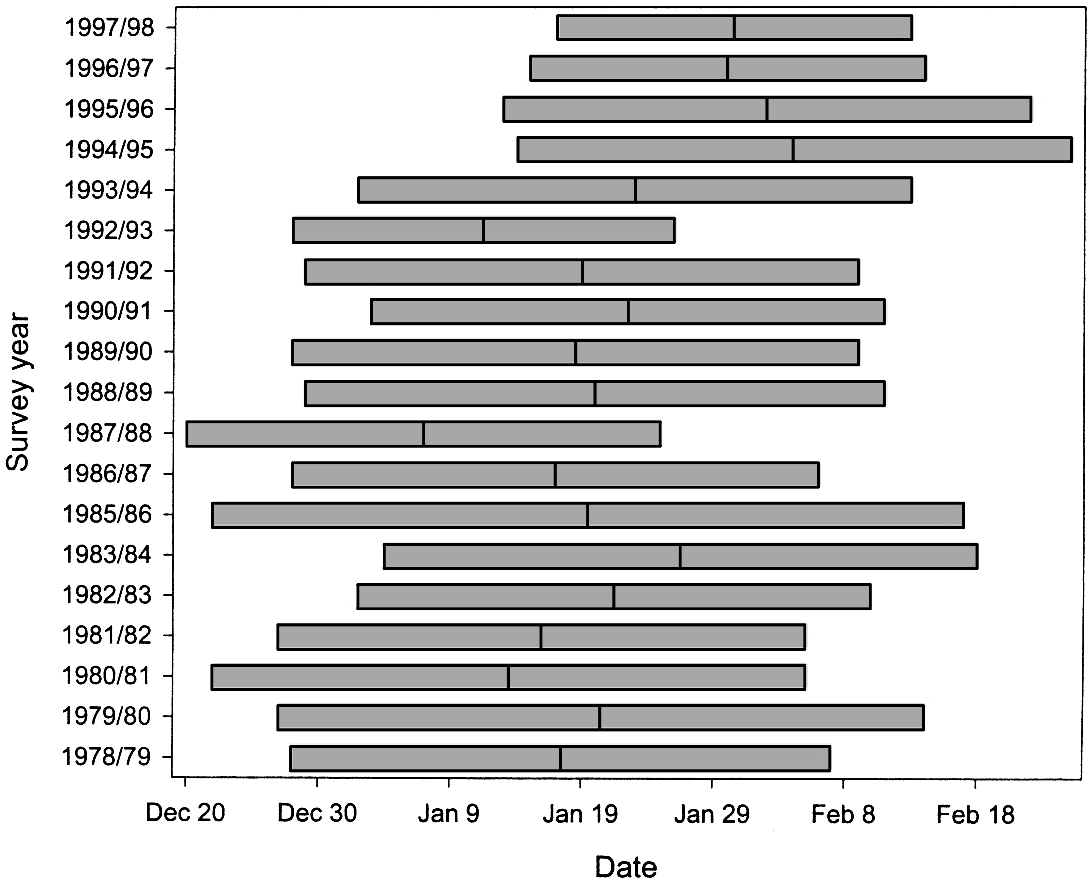


Fig. 3. Start and end dates of each survey, with the mid-point of the survey indicated by a solid line.

made first in time is the one retained, although data from this sighting may be combined with a school size estimate or species identification from one of the other sightings in the pair/triplet (Strindberg and Burt, 2000). 'Possible' and 'remote' duplicates/triplicates are treated as separate schools.

ABUNDANCE ESTIMATION

The basic equation used for abundance estimation is:

$$P = \frac{A \cdot \bar{s} \cdot n}{2 \cdot w_s \cdot L} \qquad (1)$$

where:

P = uncorrected abundance (assumes all schools on the trackline are sighted and makes no correction for random school movement)
A = open ocean area of stratum
$\bar{s}$ = mean school size
n = number of schools sighted during primary search mode
w_s = effective search half-width for schools, equal to the inverse of the detection function intercept $f(0)$
L = search effort (distance steamed in primary search mode).

The CV for P is calculated as follows[8]:

$$[CV(P)]^2 = \left[CV\left(\frac{n}{L}\right)\right]^2 + [CV(\bar{s})]^2 + \left[CV\left(\frac{1}{w_s}\right)\right]^2 \qquad (2)$$

Strictly this formula is correct only in the limit of very small CVs. It is applied here as its use has been standard practice in the past analyses of these surveys, and it is the formula built into DESS. Although it is generally a reasonable approximation, larger CVs reported for abundance estimates in this paper are consequently slightly negatively biased.

The transect is the sampling unit used to estimate the variance of the sighting rate (*n/L*), with transects defined by a waypoint file which records instances of changes in mode and major changes in course[9]. For the first five surveys, however, for which the cruise track design does not readily admit such an interpretation, the sampling unit adopted was a survey day. The variance estimate is effort weighted[10], i.e. if survey in the stratum consisted of $i = 1, 2 \ldots k$ units of length l_i and with n_i schools sighted, then:

$$\mathrm{var}\left(\frac{n}{L}\right) = \frac{1}{k-1} \sum_{i=1}^{k} \frac{\ell_i}{L} \left(\frac{n_i}{\ell_i} - \frac{n}{L}\right)^2 \qquad (3)$$

where

$$n = \sum_{i=1}^{k} n_i \quad \text{and} \quad L = \sum_{i=1}^{k} \ell_i$$

Confirmed and unconfirmed school sizes

School size is 'confirmed' if the number of whales in a school is determined reliably, as assessed by observers on the vessels who take account of the time for which the school was observable. Furthermore, during data validation for the earlier (1978/79 to 1987/88) surveys, the condition was imposed that minke school size could only be classified as 'confirmed' if the school was closed to within 0.3 n.miles. This restriction was relaxed for the later surveys although on average 86% of all confirmed sightings were still approached to within 0.3 n.miles. Thus school size confirmation is usually achieved in closing, but seldom in IO mode. For convenience, in the text following, a sighting for which school size is confirmed is referred to as a 'confirmed sighting'.

Number of schools sighted

The radial distance and angle data associated with each sighting are smeared using Method II of Buckland and Anganuzzi (1988), which uses the sightings data themselves to estimate the extent of rounding by observers to favoured distance and angle values. A sighting at radial distance r and angle to the trackline θ is smeared over radial distance $[r(1\text{-}s), r(1+s)]$ and angular $[\theta\text{-}\phi, \theta+\phi]$ ranges[11]. These definitions of s and ϕ are as used in DESS but differ from s and ϕ as defined in Fig. 2 of Buckland and Anganuzzi (1988): $s_{\mathrm{BA}} = r(1+s_{\mathrm{DESS}})$ and $\phi_{\mathrm{BA}} = 2\phi_{\mathrm{DESS}}$. After smearing, the perpendicular distance distribution is truncated at 1.5 nmi, which overall excludes slightly more than 5% of the minke school sightings. The number of schools sighted after truncation and smearing is denoted n_s, and this includes both confirmed and unconfirmed sightings. Population estimates are calculated with n_s substituted for n in equation 1.

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[8] Equation 2 makes no allowance for uncertainty in stratum area *A*, which arises because of difficulties in demarcating the position of the ice-edge (which can change quite rapidly during the period of the surveys). The only quantitative analysis reported on this matter is that by Butterworth and Silberbauer (1987) for the 1985/86 cruise in Area V. This found that the most conservative and most generous specifications of the ice-edge led to differences of only ~1-2% in the total minke whale abundance estimate for the Area. Such differences are dwarfed by the typical sizes of the other contributors to CV(*P*). The conclusion by Butterworth and Silberbauer (1987) at that time that uncertainties about ice-edge definition did not therefore seem to be a serious concern for estimates of abundance is likely the reason for the absence of any further attention to this issue.

[9] For the longer transects in the N strata, during which survey mode might change between closing and IO on more than one occasion, the mode alternation procedure was effected to ensure a balanced design if these full transects were treated as single sampling units for variance estimation. DESS, however, does not have this combination capability, so that every change in survey mode or major change in course is taken to define the start of an additional sampling unit for variance estimation purposes.

[10] In cases where k is too small to allow reliable estimation of variance in this manner (taken as $k < 5$), neighbouring strata (j) are pooled to estimate an overall sighting rate $S = \sum_j n_j / \sum_j L_j$ with CV(S) being estimated by application of equation 3. The sighting rate CV for an individual stratum j, CV(S_j), is then estimated by $\sqrt{\sum_p L_p / L_j}\,$CV($S$), i.e. a Poisson-like variance structure is assumed.

[11] While angles between the direction to the whale school when first sighted and the vessel trackline have always been based on observers' estimates (though with the assistance of angle boards which were first introduced for the 1983/84 survey), the practice used to provide radial distance measures has changed over time. Originally these distance estimates were based upon the product of vessel speed and the time taken to close with the sighting after the whales were first sighted and the vessel deviated from the trackline. Observer estimates of such distances upon first sighting were originally mistrusted as too subjective. However, the use of graticuled binoculars with distance scales (based upon the angle between the sighting and the horizon), together with satisfactory results from annual 'estimated distance' experiments that were first introduced on the 1981/82 cruise, enhanced confidence in these estimates. In 1986 use of observer estimates of radial distance became standard, particularly because for IO mode the other approach required specification of the time the vessel came abeam of the school sighted, and this proved difficult to judge for a transitory target (Butterworth, 1986). The 'estimated distance' experiment (conducted on every cruise since 1981/82 for each vessel) involves

Effective search half-width

The smeared and truncated sightings of schools are grouped into intervals (or ‘bins’) of 0.1 n.miles to estimate the detection function intercept, $f(0)$, where $f(y)$ is the probability density function for the sightings distribution in relation to perpendicular distance from the trackline (y). Both confirmed and unconfirmed sightings are included in this estimation process. The hazard rate model (accepted by the Scientific Committee [IWC, 1988, p.77] based on Buckland [1987a]), defined by the following equation, is fitted to these data:

$$\begin{aligned} f(y) &= f(0)\,g(y) \\ &= f(0)\left[1-\exp\left(-\left[\frac{y}{a}\right]^{-b}\right)\right] \end{aligned} \tag{4}$$

where: $g(y)$ is the probability that a school at a perpendicular distance y from the trackline will be sighted, and a, b are parameters estimated in the fitting process, subject to the constraints[12]:

$a \geq 0.0001$ n.miles
$b \geq 1$.

The analyses conducted here make the ‘standard analyses’ assumption that all schools on the trackline are seen, and hence that $g(0) = 1$[13].

The effective search half-width is then given by:

$$w_s = \frac{1}{f(0)} \tag{5}$$

Mean school size $\bar{s}$

Mean school size is based on confirmed schools sighted during closing mode only, because of the low number of confirmed sightings in IO mode. In some instances, there is evidence of observed school sizes (s) tending to increase with perpendicular sighting distance y, reflecting a faster drop with y in the probability of sighting smaller schools. DESS compares the results of two methods for estimating mean school size: the actual mean for schools sighted within the truncation distance, and the regression estimate for $y = 0$ of a $\ell n\ s$ vs. $g(y)$ regression (the method proposed by Buckland *et al.*, 1993), with the latter used if the regression is significant at the 15% level and has a slope in the direction expected. Estimates of mean school size ($\bar{s}$ in equation 1) obtained in this manner are denoted $E[s_{sc}]$. The basis for use of 15%, rather than the usual 5% criterion, is discussed by Buckland *et al.* (1993, p.75-6). Essentially it is to lessen the risk of biased estimates of abundance and negatively biased estimates of variance in situations of low sample size and hence low power to detect trends with $g(y)$. In one instance, the 1983/84 cruise stratum EN, the regression method obtains $E[s_{sc}] = 0.71$ (CV = 0.202). As a mean school size less than unity is not plausible, this has been replaced by the actual mean school size for that stratum.

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

Due to small sample sizes in some strata, it is necessary to pool strata in order to estimate w_s and $E[s_{sc}]$. In the standard analyses, AIC is used as a basis to determine the level of pooling. On the surface, AIC appears to provide a convenient and statistically defensible basis for determining how to best pool across strata within a survey. AIC values were therefore calculated for each survey for the following pooling combinations: all strata pooled, all strata separate, strata surveyed by the same vessel pooled, north and south strata pooled separately, and east and west strata pooled separately. However, a number of problems, as listed below, were encountered in using AIC as the basis for choice between these options.

(1) The standard analyses compute AIC values based upon w_s estimation, which uses both confirmed and unconfirmed sightings. However, estimates of $E[s_{sc}]$ use confirmed sightings only, so there is no guarantee that this approach will leave enough sightings to determine $E[s_{sc}]$ reliably.

(2) Separate estimates of w_s (and hence AIC values) are obtained for closing and for IO mode analyses. In the interests of simplicity, data for the two modes on the same survey should be pooled in the same way, but for eight of the 13 surveys concerned, the recommended pooling option on the basis of AIC values is different for closing and IO modes.

Footnote 11 continued from previous page
comparing observer estimates of the distance and angle to a radar-reflecting buoy with radar readings (Butterworth *et al.*, 1984a). If bias (statistically significant at the 5% level) is detected in observer estimates, these estimates are corrected by the bias factor estimated before perpendicular distances y are computed. Originally the variance of the observations in these experiments about the radar readings was used to specify the extent of smearing. However, concerns arose that this approach might produce smearing factor estimates that were too low, because of the greater ease of reliably estimating distance and particularly angle to a continuously visible target (the buoy) compared to a transient whale cue (usually a blow). Smearing of angles has a much greater effect than that of distances on abundance estimates, especially because of observations recorded as $\theta = 0$ (hence $y = 0$), the proportion of which was quite large for the earlier cruises. This led to the Buckland-Anganuzzi approach being preferred. Allowing only for rounding to estimate the extent of smearing in this approach would be of concern if the actual observation errors greatly exceeded the extent of rounding. However, comparison of smearing factors estimated from the ‘estimated distance’ experiment, as calculated for the 1983/84 (Butterworth *et al.*, 1984b) and for the 1984/85 cruises (Butterworth and McQuaid, 1985), with those from the Buckland-Anganuzzi approach (see Fig. 5) indicates rough similarity.

[12] Analyses pre-dating DESS specified $a \geq 0.1$ n.miles and $b \geq 2$ (IWC, 1988, p.77). The constraint for b above does not, however, reflect a change. Earlier convention, e.g. Buckland (1987b), in the Scientific Committee was to write the power in equation 4 as $1\text{-}b$. More recently, however, the DISTANCE package used in DESS has adopted the convention of Buckland *et al.* (1993) of writing this power as $-b$.

[13] Historically, over the period 1981 to 1983, the Scientific Committee used results of analyses of variable speed and parallel ship experiments to select $g(0)$ values that were less than 1 in computing minke whale abundance estimates (see, for example, Butterworth *et al.*, 1982; 1984a and Joyce *et al.*, 1988 for more details of these experiments and their analysis). However, at the 1984 Scientific Committee meeting, methodological questions about these approaches were raised, and in the absence then of their resolution, the Committee effectively decided to set $g(0) = 1$ (linked to the use of the negative exponential form for the detection function $g(y)$). Despite considerable efforts to obtain a satisfactory estimate of $g(0)$ from these experiments and from IO mode duplicate sightings data over the next six years, problems in interpreting the data continued (see, e.g., IWC, 1988, p.78; IWC, 1989, p.72-3). In the absence of any agreed estimate of $g(0)$, use of the value $g(0) = 1$ was continued for abundance estimation purposes. Finally, during the 1990 Comprehensive Assessment of Southern Hemisphere minke whales, the results of a review (Butterworth, 1991) of estimates of $g(0)$ for the barrel from IO survey data were noted, together with the fact that applying these to sightings from the barrel alone yielded density estimates not much different from these based on sightings from all platforms linked to the assumption $g(0) = 1$ (IWC, 1991, p.116). This was followed by agreement to continue use of the value $g(0) = 1$, a decision reconfirmed two years later (IWC, 1993, p.106).

(3) AIC can be applied only to model fits to the unsmeared perpendicular distance data, since its computation requires independence of the grouped data in each of the 0.1 n.miles bins chosen to fit the *f*(*y*) model. However, for the actual abundance estimation, the detection function is applied to bins of smeared data, which are not independent so that the AIC values computed are not really applicable. This could be a problem for the early surveys in particular, for which the unsmeared data (although not necessarily the smeared data) frequently show large peaks close to the trackline that the hazard rate function has difficulty fitting, thus perhaps unduly penalising the associated AIC value.

(4) When actually applying the AIC criterion, some further problems immediately become apparent. For example, in 1988/89 the minimum AIC value for closing mode is obtained when all the strata are separate. Yet for IO mode, one stratum (SM2, WN) has only one sighting, so that some pooling is essential. In most of the early surveys, there are certainly sufficient sightings to render stratum-specific estimation viable, but the AIC values always indicate some pooling. An extreme example occurs in 1982/83, where the smallest number of sightings in any stratum is 64, yet the AIC criterion suggests pooling all the strata. This runs counter to the view that pooling should be kept to a minimum, because of the possibility that the true values of w_s and $\bar{s}$ did indeed differ among the strata concerned.

Based on these considerations, the consistent use of AIC throughout the time series as a basis to select between pooling options does not seem reasonable. In these analyses therefore, the following rules for pooling have been applied.

(i) If there are more than a total of 15 confirmed and unconfirmed sightings in each stratum, do not pool. This criterion is satisfied for the 1978/79–1985/86 and 1989/90 surveys, for which all w_s and $E[s_{sc}]$ estimates used are stratum-specific.

(ii) If there are too few sightings in either IO or closing mode to meet the criterion in (i), then pool all strata that were surveyed by the same vessel. When applied to the remaining surveys, nearly all such 'super-strata' contain more than 15 sightings.

(iii) Two cases are not covered by the criteria above. In 1978/79, the strata surveyed by T16 are pooled by combining north and south strata, but the strata surveyed by T18 include sufficient sightings to remain separate. In 1981/82, the perpendicular distance distribution of the sightings data for W1N stratum was anomalous and poorly fitted by the detection function; the strata surveyed by SM1 were therefore pooled, but those surveyed by SM2 remain separate.

The choice of a total of 15 sightings in a stratum as the minimum required to avoid pooling is somewhat *ad hoc*. It is based primarily on the considerations that a lesser number would likely create difficulties in fitting the two-parameter hazard rate function reliably and would also compromise the procedure used to estimate stratum-specific smearing parameters. On the other hand, a number not much larger than 15 would have substantially increased the extent of pooling.

Averaging where strata were surveyed by two vessels

Occasionally, two vessels surveyed the same stratum. In such cases, the two density estimates are combined using an effort-weighted average.

Factors applied to the uncorrected abundance estimate

Two multiplicative correction factors are applied to the abundance estimates in the standard analyses. The correction factor *m* makes allowance for random whale movement, and the factor *h* for schools on the trackline that were missed. The standard analyses assume $h = 1.0$, i.e. that the probability of detection on the trackline is one, and that $m = 0.985$, with both assumed to be known exactly (i.e. $\text{CV} = 0$). The latter value is based on Koopman's (1956) model of a fixed detection radius within which every school is definitely seen. It results from an average whale swimming to vessel surveying speed ratio of 3 knots : 12 knots = 0.25 (Best and Butterworth, 1980; IWC, 1983, p.95). In the analyses of this paper, neither *m* nor *h* are taken into account; *m* has been neglected because the model previously used to estimate this is simplistic and the quantitative effect in any case rather small. The abundance estimates of this paper are accordingly termed 'uncorrected'.

Combining IO and closing mode abundance estimates

IO mode survey involves greater search effort because of the additional observer in the IO platform (Haw, 1991b), so that the assumption that all schools on the trackline are seen is likely to introduce less bias than for closing mode survey. Furthermore, closing mode involves other potential biases as discussed earlier. The IO-based abundance estimates are therefore taken as the standard. Under the standard methodology, the closing mode estimates (P_{closing}) are therefore converted to 'pseudo-passing' estimates (P_{pseudo}) by dividing them by a calibration factor *R*, which reflects the ratio of minke whale school density estimates in closing mode compared to IO mode:

$$P_{\text{pseudo}} = P_{\text{closing}} / R \tag{6}$$

$$CV(P_{\text{pseudo}}) = \sqrt{\left[CV(P_{\text{closing}})\right]^2 + \left[CV(R)\right]^2} \tag{7}$$

The IO mode and the pseudo-passing mode estimates are then combined by taking an inverse-variance weighted average, to obtain the final abundance estimate (P_{average}):

$$a = \frac{\text{var}(P_{\text{IO}})}{\text{var}(P_{\text{pseudo}}) + \text{var}(P_{\text{IO}})}$$

$$b = \frac{\text{var}(P_{\text{pseudo}})}{\text{var}(P_{\text{pseudo}}) + \text{var}(P_{\text{IO}})}$$

$$P_{\text{average}} = a \cdot P_{\text{pseudo}} + b \cdot P_{\text{IO}} \tag{8}$$

$$CV(P_{\text{average}}) = \frac{\sqrt{a^2 \cdot \text{var}(P_{\text{pseudo}}) + b^2 \cdot \text{var}(P_{\text{IO}})}}{P_{\text{average}}} \tag{9}$$

In the interests of simplicity, this does not take into account the covariance between the pseudo-passing and IO estimates that occurs because they use common estimates of mean school size. The variances given for the combined estimates are therefore slightly negatively biased.

Updated estimate of R

The standard analyses use $R = 0.751$ ($\text{CV} = 0.152$), obtained by Haw (1991b) from the 1985/86-1988/89 surveys. Burt and Stahl (2000) obtain an estimate for *R* of 0.893 ($\text{CV} = 0.109$) from the more recent 1989/90-1997/98 surveys only, but they continue to use the older value of *R* in combining closing and IO estimates[14]. However, both these estimates for R are problematic because they are not based on consistent estimates of density from the two modes over all the surveys. The consistent estimates obtained in this study therefore provide a convenient opportunity to update R.

An estimate (assumed to be lognormally distributed) of the density of schools:

$$D_s = \frac{n_s}{2 \cdot w_s \cdot L} \tag{10}$$

can be obtained for each stratum surveyed from 1985/86 onwards for both closing and IO mode, and hence an estimate of R provided for each of those strata. Two strata were excluded from this process because one of the school density estimates was zero. The equations in Borchers and Butterworth (1990) were used to calculate an inverse-variance weighted average of the individual estimates of R from each stratum:

$$\overline{\ln R} = \sum_i V_i \ln R_i$$

$$\text{var}\left(\overline{\ln R}\right) = 1 / \sum_i \left[\text{se}\left(\ln R_i\right)\right]^{-2} \tag{11}$$

$$R = \exp\left(\overline{\ln R} + \text{var}\left(\overline{\ln R}\right) / 2\right)$$

$$\text{se}(R) = \sqrt{\left[\exp\left\{\text{var}\left(\overline{\ln R}\right)\right\} - 1\right]} R$$

where $V_i = \left[\text{se}\left(\ln R_i\right)\right]^{-2} / \sum_j \left[\text{se}\left(\ln R_j\right)\right]^{-2}$

$$CV(R_i) = \sqrt{CV(D_{i\,\text{closing}})^2 + CV(D_{i\,\text{IO}})^2}$$

$$\text{se}(\ln R_i) = \sqrt{\ln[CV(R_i)^2 + 1]}$$

Where strata had been pooled for the estimation of w_s and $E[s_{sc}]$, the sightings rates were also combined (to compute school density and hence R) according to the 'super-stratum' method of Haw (1991b) that was subsequently adopted by the Scientific Committee (IWC, 1991, p.117). In this method n_s/L and an estimate of $CV(n_s/L)$ are provided separately for each stratum by DESS. Given further common w_s and $E[s_{sc}]$ estimates over strata $i = 1 \ldots m$, which are to be combined into a 'super-stratum' for which R is to be estimated, the area of each stratum as a proportion of that of the 'super-stratum' is first calculated:

$$W_i = \frac{A_i}{\sum_{j=1}^{m} A_j} \tag{12}$$

The average density of minke whale schools in the 'super-stratum' for the survey mode under consideration is then estimated using an area-weighted average of the sighting rate:

$$\overline{D} = \frac{1}{2\hat{w}_s} \sum_{j=1}^{m} W_j \cdot \left(\frac{n}{L}\right)_j$$

$$CV\left(\overline{D}\right) = \sqrt{\left[CV\left(\frac{1}{\hat{w}_s}\right)\right]^2 + \frac{\sum_{i=1}^{m} W_i^2 \left(\frac{n}{L}\right)_i^2 \cdot \left[CV\left(\frac{n}{L}\right)_i\right]^2}{\left[\sum_{i=1}^{m} W_i \cdot \left(\frac{n}{L}\right)_i\right]^2}} \tag{13}$$

The impact of 'like minke' sightings

More sightings have been recorded as 'like minke' in the third circumpolar set than in the second set of surveys, whereas almost no such sightings were recorded in the first circumpolar set. This difference does not arise only from the introduction of IO mode after the first circumpolar set of surveys. Although 'like minke' sightings are more frequent in IO than closing mode, there has also been an increase in the proportion recorded in closing mode since the first circumpolar set was completed (Fig. 3). This suggests a change in species-classification over time (possibly resulting from the use of topmen with increasingly less identification experience from whaling operations as the surveys progressed). This change would probably confound comparisons of results from the three sets of surveys that are based on minke sightings only. Uncorrected abundance estimates are therefore also calculated with 'like minke' sightings included, to investigate the influence of this factor.

Comparing abundance estimates for the different circumpolar sets of surveys

A great deal of interest has been expressed in determining trends in abundance, particularly for minke whales, from the IDCR-SOWER circumpolar surveys. However, problems arise because of non-comparability of areal coverage between the circumpolar sets of surveys. These are of two kinds: first, most surveys in the first two circumpolar sets did not completely cover the full latitudinal range to 60°S; secondly, the third circumpolar set of cruises has not yet completed a full circuit of the Antarctic - the longitudinal ranges of 140°W-110°W and 80°E-130°E have yet to be surveyed (Figs 2a-c).

Previous attempts to compare abundance estimates for the same region from surveys in different years (e.g. Punt *et al.*, 1997) have been based upon scaling estimates down to a 'common northern boundary', so that abundance contributions from northerly areas not surveyed by all the cruises under comparison are not taken into account. However, as the number of cruises has increased, this approach is proving problematic as the highly variable nature of the ice-edge from year to year has led to instances where sections of the ice-edge for one cruise were north of the northernmost area surveyed in another (i.e. no common area for such sectors).

Pending the development of more sophisticated approaches to obtain comparable estimates of abundance over time in these circumstances, a simpler approach has been pursued here to allow initial comparisons to be made. The unsurveyed northern areas are assumed to have the same density of whales as the northern surveyed strata in each survey (Tables 5a-c), in order to extrapolate all abundance estimates to a common area south of 60°S[15]. In some cases,

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[14] Burt and Stahl (2000) reports $R = 0.832$ (CV = 0.0953), but these authors have revised this figure on rechecking their computations (M.L. Burt, pers. comm.).

[15] This assumption probably introduces some positive bias into the resultant estimates, as minke whale density tends to decrease with movement north away from the ice-edge. In turn, this could bias estimates of trend in abundance, as the sizes of the unsurveyed areas tend to decrease over time.

the surveys covered areas north of this range, in which case the abundance estimates from the northern strata are scaled down proportionately. Abundance estimates from each Management Area not as yet fully covered during the third circumpolar set of cruises are decreased according to the fraction of the area of each stratum that falls outside the longitudinal range covered to date by the third set[16].

The areas of the unsurveyed regions (and those surveyed north of 60°S) were obtained from table 3b of Butterworth *et al.* (1994) for 1978/79–1990/91. *MapInfo* 5.5 (which is incorporated into DESS) was used to obtain the corresponding areas for the remaining surveys and to re-check the original values. *MapInfo* was also used to calculate the areas needed to evaluate proportional coverage by the third circumpolar set of cruises.

The effects of increasing proportions of 'like species' sightings in the later surveys must also be taken into account when comparing abundance estimates across the circumpolar sets of surveys. The proportional increase (or decrease) in abundance estimates when 'like minke' sightings are included (obtained as described above) is therefore used to modify the corresponding extrapolated estimates above, to investigate this source of bias.

RESULTS

Abundance estimates

Revised abundance estimates, and the values of the parameters used to compute these estimates in the consistent manner described above, are presented for closing mode (Table 1a-c) and IO mode (Tables 1d-e). Plots showing the fit of the hazard rate function to the perpendicular distance distributions for the sightings data are given in Figs 4a-c, and show no obvious indications of model mis-specification. There is no obvious trend towards distributions with sharper peaks near the trackline in the earlier years, as is evident when estimated detection functions for some other species are examined (Branch and Butterworth, 2001). The smearing parameters are markedly higher at the start of the first circumpolar set of cruises than for the two later sets (Fig. 5). The decrease in smearing parameters over time relates to the introduction of angle boards and graticuled binoculars, with a consequent improvement in the precision of the recorded angles and distances.

Sensitivity to duplicate identification

Uncertainties about duplicate identification affect only the abundance estimates for IO mode. If instead of the 'standard analyses' practice of considering only 'definite' duplicate pairs/triplets as single sightings, the 'probable' duplicates are also treated in this manner, the number of sightings in IO mode in the second and third circumpolar sets of surveys decrease by 1.6% and 1.2% respectively, and the corresponding abundance estimates decrease by 0.2% and 1.0%.

Tables 1a-e, Figs 4a-c and Fig. 5 occur on the following 9 pages.
Text continues on p. 163

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[16] DESS has the capability of computing abundance estimates based only upon the sightings and effort within a user-defined new stratum. This option could have been used here in place of area-based pro-ratio, but the latter was preferred as this paper is based upon the more straightforward features of DESS, for simplicity.

Table 1a

Abundance estimates of minke whales obtained from closing mode data for the first circumpolar set of cruises (1978/79 to 1983/84) - CPI. Strata with the same number in the 'Ave' column were surveyed by two vessels and the resulting abundance estimates were combined using an effort-weighted average. The symbols used here and in subsequent Tables denote the following:

A - stratum area (n.miles^2);

N_L - number of transects;

n_s - number of schools sighted (primary effort), after smearing and truncation at a perpendicular distance of 1.5 n.miles;

L - primary search effort (n.miles);

w_s - effective search half-width for schools (n.miles);

$E[s_{sc}]$ - estimated mean school size (based on schools with confirmed school size in closing mode only);

D_w - density of whales (per n.miles^2);

P - uncorrected abundance estimate.

The complete longitudinal extent of the Management Area (I-VI) associated with each cruise, as indicated in this and subsequent Tables, was covered unless an asterisk is appended to the Area number.

Year	Vessel	Stratum	A	N_L	n_s	L	n_s/L	CV	w_s	CV	$E[s_{sc}]$	CV	D_w	CV	P	CV	Ave	Total	CV
1978/79 (IV)	T16	EN	156,766	18	68.0	2,155.5	0.032	0.321	0.295	0.137	2.75	0.113	0.1473	36.6	23,099	0.366			
		W1N	39,256	2	9.0	222.2	0.018	0.784					0.1891	80.4	7,423	0.804	1		
		W2N	153,914	3	5.0	384.7	0.013	0.298					0.0607	34.7	9,337	0.347	2		
		W1S	20,389	5	56.0	200.6	0.279	0.187	0.374	0.190	2.81	0.086	1.0511	28.0	21,430	0.280			
		W2S	29,600	12	83.3	1,073.3	0.078	0.141					0.2923	25.1	8,653	0.251	3		
	T18	ES	27,571	16	167.0	1,436.6	0.116	0.160	0.393	0.181	5.89	0.105	0.8710	26.3	24,014	0.263			
		W1N	39,256	6	35.6	685.3	0.052	0.266	0.238	0.341	2.36	0.167	0.2572	46.4	10,096	0.464	1		
		W2N	153,914	11	25.8	1,212.5	0.021	0.363	0.530	0.223	2.05	0.131	0.0412	44.6	6,343	0.446	2		
		W2S	29,600	4	40.8	393.4	0.104	0.222	0.314	0.357	1.85	0.124	0.3057	43.8	9,048	0.438	3	93,808	0.147
1979/80 (III)	K27	ES	41,772	20	166.3	1,346.5	0.124	0.194	0.254	0.257	2.43	0.088	0.5905	33.4	24,668	0.334			
		WN	200,724	16	53.0	2,014.9	0.026	0.249	0.261	0.336	2.36	0.127	0.1193	43.7	23,950	0.437			
	T11	EN	217,865	20	56.4	2,636.7	0.021	0.188	0.263	0.516	3.23	0.123	0.1314	56.3	28,627	0.563			
		WS	33,619	19	138.2	968.2	0.143	0.211	0.303	0.214	3.15	0.080	0.7420	31.1	24,944	0.311		102,188	0.218
1980/81 (V)	K27	EN	208,159	14	77.7	877.3	0.089	0.141	0.331	0.378	1.87	0.093	0.2506	41.4	52,172	0.414			
		ES	98,766	5	54.1	439.6	0.123	0.376	0.480	0.371	3.36	0.216	0.4296	57.1	42,425	0.571	4		
		WS	34,164	17	74.0	698.1	0.106	0.240	0.262	0.366	3.41	0.114	0.6898	45.2	23,568	0.452			
	T11	ES	98,766	21	293.1	2,133.3	0.137	0.244	0.531	0.153	2.87	0.222	0.3704	36.3	36,578	0.363	4		
		WN	139,191	15	43.6	1,151.6	0.038	0.439	0.324	0.512	2.49	0.220	0.1454	70.9	20,244	0.709		133,560	0.228
1981/82 (II)	SM1	ES	29,633	18	169.4	1,162.9	0.146	0.174	0.515	0.136	2.08	0.059	0.2938	22.8	8,705	0.228			
		W1N	135,504	10	18.7	1,064.9	0.018	0.691					0.0361	70.0	4,885	0.700			
		W2S	52,096	10	76.0	920.6	0.083	0.317					0.1671	35.0	8,704	0.350	5		
	SM2	EN	145,063	17	54.9	1,748.8	0.031	0.331	0.428	0.389	1.63	0.100	0.0596	52.0	8,647	0.520			
		W1S	35,725	9	30.9	872.2	0.035	0.318	0.359	0.571	2.70	0.140	0.1333	66.8	4,763	0.668			
		W2S	52,096	12	94.7	812.4	0.117	0.189	0.501	0.276	2.12	0.089	0.2468	34.6	12,856	0.346	5	37,649	0.202
1982/83 (I)	SM1	ES	33,050	15	114.6	928.0	0.123	0.214	0.396	0.280	2.57	0.071	0.4005	36.0	13,235	0.360			
		WN	163,926	15	62.7	1,426.1	0.044	0.217	0.804	0.162	1.63	0.106	0.0445	29.1	7,288	0.291			
	SM2	EN	149,433	17	84.3	1,054.4	0.080	0.303	0.862	0.137	3.55	0.114	0.1646	35.2	24,598	0.352			
		WS	25,596	19	314.5	1,414.8	0.222	0.176	0.615	0.098	1.66	0.043	0.3004	20.6	7,688	0.206		52,808	0.194
1983/84 (VI)	K27	EMS	158,893	5	47.4	1,094.4	0.043	0.394	0.422	0.229	1.52	0.136	0.0778	47.6	12,355	0.476			
		WN	207,721	5	49.9	875.6	0.057	0.142	0.489	0.191	2.11	0.127	0.1229	27.0	25,536	0.270			
	SM1	EN	202,108	5	19.0	911.6	0.021	0.584	0.328	0.533	2.27	0.238	0.0722	82.6	14,593	0.826			
	SM2	WMS	156,457	5	69.8	1,309.0	0.053	0.187	0.309	0.236	2.22	0.140	0.1914	33.2	29,939	0.332		82,423	0.261

Table 1b

Abundance estimates of minke whales obtained from closing mode data for the second circumpolar set of cruises (1985/86 to 1990/91) - CPII.

Year	Vessel	Stratum	A	N_L	n_s	L	n_s/L	CV	w_s	CV	$E[s_{sc}]$	CV	D_w	CV	P	CV	Ave	Total	CV
1985/86 (V)	K27	EN	279,611	8	38.0	865.3	0.044	0.413	0.362	0.260	3.20	0.222	0.1942	53.7	54,314	0.537			
		WS	104,814	14	44.6	767.6	0.058	0.248	0.625	0.140	3.55	0.216	0.1647	35.8	17,267	0.358			
	SM1	EM	165,912	10	96.3	735.0	0.131	0.255	0.605	0.152	2.69	0.143	0.2907	33.0	48,238	0.330			
		WM	166,349	4	27.5	354.0	0.078	0.498	0.458	0.355	1.91	0.196	0.1624	64.2	27,007	0.642			
	SM2	ES	107,717	11	137.5	763.4	0.180	0.189	0.479	0.150	3.33	0.113	0.6272	26.6	67,562	0.266			
		WN	139,065	5	19.0	566.7	0.034	0.516	0.304	0.297	1.93	0.184	0.1063	62.4	14,787	0.624		229,175	0.188
1986/87 (II)	K27	ES1	23,142	3	7.0	179.0	0.039	0.548	0.369	0.173	2.82	0.113	0.1492	58.5	3,453	0.585			
		WS1	10,270	2	11.0	81.8	0.134	0.275					0.5130	34.4	5,268	0.344			
		WS2	21,143	2	3.0	111.0	0.027	0.121					0.1031	23.9	2,180	0.239	6		
		WS3	79,605	8	41.0	544.4	0.075	0.510					0.2873	55.0	22,869	0.550	7		
		EN	124,057	4	62.4	538.2	0.116	0.342					0.4422	40.0	54,864	0.400			
	SM1	EBAY	15,242	3	13.0	106.4	0.122	0.382	0.551	0.293	2.23	0.122	0.2466	49.7	3,758	0.497			
		ES2	44,975	13	42.6	565.8	0.075	0.301					0.1520	43.8	6,834	0.438			
		WBAY	11,505	2	18.6	92.2	0.202	0.741					0.4079	80.6	4,693	0.806			
		WN	95,361	4	3.0	315.6	0.010	0.444					0.0192	54.6	1,829	0.546			
	SM2	EM	69,908	3	33.7	473.0	0.071	0.307	0.526	0.144	1.92	0.109	0.1298	35.6	9,073	0.356			
		WS2	21,143	1	1.0	82.8	0.012	1.000					0.0220	101.6	465	1.016	6		
		WS3	79,605	5	21.0	239.4	0.088	0.415					0.1596	45.2	12,706	0.452	7	110,984	0.249
1987/88 (III)	SM1	ES	87,677	7	8.0	454.9	0.018	1.038	0.280	0.785	5.31	0.275	0.1668	133.0	14,625	1.330			
		WN	148,821	6	10.7	450.4	0.024	0.928					0.2252	125.4	33,513	1.254			
	SM2	EN	168,881	7	3.0	540.7	0.006	0.416	0.336	0.379	4.00	0.282	0.0330	63.0	5,571	0.630			
		WS	74,351	12	59.7	623.5	0.096	0.429					0.5694	63.8	42,334	0.638		96,043	0.631
1988/89 (IV)	SM1	BS	6,520	1	14.0	87.4	0.160	0.267	0.237	0.625	2.44	0.094	0.8276	68.6	5,396	0.686			
		EN	181,166	6	7.0	498.8	0.014	0.333					0.0725	71.4	13,137	0.714			
		WS	58,693	5	22.9	237.8	0.096	0.324					0.4976	71.0	29,204	0.710			
	SM2	BN	17,486	6	7.0	231.0	0.030	0.719	0.550	0.247	4.26	0.198	0.1174	78.5	2,053	0.785			
		ES	52,441	5	26.9	310.3	0.087	0.339					0.3362	46.3	17,630	0.463			
		WN	156,617	6	13.0	701.9	0.019	0.761					0.0718	82.4	11,239	0.824		78,660	0.445
1989/90 (I)	SM1	ESB	62,594	11	23.7	587.9	0.040	0.324	0.450	0.419	1.79	0.144	0.0803	54.9	5,026	0.549			
		WN	168,761	7	26.6	560.4	0.047	0.292	0.510	0.264	2.25	0.249	0.1044	46.5	17,621	0.465			
	SM2	EN	153,029	7	36.4	679.7	0.054	0.263	0.221	0.570	1.77	0.122	0.2136	64.0	32,687	0.640			
		WS	45,128	15	64.0	602.2	0.106	0.201	0.573	0.132	2.67	0.094	0.2481	25.8	11,195	0.258		66,529	0.343
1990/91 (VI)	SM1	EN	191,954	3	6.5	193.0	0.034	0.458	0.413	0.835	2.50	0.191	0.1025	97.2	19,676	0.972			
		WS	45,414	5	5.8	304.1	0.019	0.438					0.0582	96.2	2,642	0.962			
	SM2	ES	108,268	5	40.0	476.6	0.084	0.281	0.536	0.170	2.92	0.182	0.2287	37.5	24,758	0.375			
		WN	211,788	5	5.0	479.7	0.010	0.232					0.0284	34.0	6,016	0.340		53,091	0.445

Table 1c

Abundance estimates of minke whales obtained from closing mode data for the as-yet incomplete third circumpolar set of cruises (1991/92 to 1997/98) - CPIII.

Year	Vessel	Stratum	A	N_L	n_s	L	n_s/L	CV	w_s	CV	$E[s_{sc}]$	CV	D_w	CV	P	CV	Ave	Total	CV
1991/92 (V)	SM1	EN	165,429	9	76.3	434.0	0.176	0.210	0.486	0.224	2.54	0.096	0.4594	32.1	76,005	0.321			
		WS	58,643	10	11.7	278.1	0.042	0.354					0.1103	42.9	6,468	0.429			
	SM2	ES	82,039	11	48.5	645.7	0.075	0.303	0.419	0.406	1.41	0.097	0.1264	51.6	10,366	0.516			
		WN	137,734	5	3.0	345.0	0.009	0.348					0.0146	54.4	2,017	0.544		94,855	0.279
1992/93 (III*)	SM1	ES	23,207	10	7.5	380.2	0.020	0.452	0.189	0.907	1.67	0.214	0.0869	103.6	2,017	1.036			
		WN	210,035	8	9.0	648.9	0.014	0.235					0.0613	96.1	12,882	0.961	8		
		WS	61,527	1	2.0	67.1	0.030	0.707					0.1317	117.0	8,105	1.170	9		
	SM2	EN	150,547	4	6.0	498.2	0.012	0.391	0.526	0.206	1.44	0.077	0.0165	44.8	2,477	0.448			
		WS	61,527	15	78.9	812.3	0.097	0.317					0.1326	38.6	8,161	0.386	9		
		WN	210,035	1	0.0	134.2	0.000	-					0.0000	-	0	-	8	23,322	0.564
1993/94 (I*)	SM1	WS	50,596	11	25.5	501.7	0.051	0.276	0.439	0.427	1.51	0.130	0.0878	52.5	4,441	0.525			
		EN	293,196	11	4.0	819.4	0.005	0.981					0.0084	107.8	2,468	1.078			
	SM2	WN	251,735	8	17.0	583.8	0.029	0.313	0.430	0.343	1.63	0.154	0.0553	48.9	13,914	0.489			
		ES	72,249	10	33.9	457.2	0.074	0.241					0.1408	44.7	10,170	0.447		30,993	0.359
1994/95 (III*+IV*)	SM1	WS	51,938	12	15.6	414.3	0.038	0.337	0.482	0.444	2.56	0.198	0.1003	59.1	5,208	0.591			
		EN	146,681	7	5.0	523.8	0.010	0.396					0.0254	62.7	3,726	0.627			
	SM2	WN	148,803	7	3.0	463.8	0.006	0.850	0.335	0.327	1.87	0.110	0.0181	91.7	2,689	0.917			
		ES	60,046	9	19.9	439.7	0.045	0.540					0.1262	64.1	7,577	0.641			
		PRYD	21,096	4	18.0	210.7	0.085	0.255					0.2386	42.9	5,034	0.429		24,234	0.359
1995/96 (VI*)	SM1	WS	34,051	10	25.8	403.3	0.064	0.299	0.925	0.104	2.33	0.094	0.0804	33.0	2,736	0.330			
		EN	242,073	10	27.5	490.8	0.056	0.369					0.0703	39.5	17,029	0.395			
	SM2	WN	97,945	4	6.0	246.6	0.024	0.775	0.499	0.249	1.76	0.131	0.0429	82.5	4,200	0.825			
		ES	72,349	9	31.7	506.7	0.063	0.290					0.1104	40.4	7,984	0.404		31,950	0.272
1996/97 (II*)	SM1	ES	67,072	20	26.4	563.6	0.047	0.383	0.835	0.269	1.72	0.117	0.0484	48.3	3,245	0.483			
		WN	113,687	5	8.0	262.3	0.030	0.331					0.0314	44.2	3,575	0.442			
	SM2	EN	241,928	15	14.0	588.2	0.024	0.541	0.306	0.372	2.06	0.104	0.0802	66.5	19,396	0.665			
		WS	23,028	7	6.0	154.5	0.039	0.844					0.1308	92.8	3,012	0.928		29,228	0.482
1997/98 (II*)	SM1	WS	32,620	7	2.0	187.0	0.011	0.751	0.612	0.355	1.79	0.126	0.0157	84.0	511	0.840			
		EN1	84,726	6	9.0	236.0	0.038	0.600					0.0558	70.8	4,730	0.708			
		ES2	10,451	4	28.9	83.5	0.346	0.235					0.5069	44.4	5,298	0.444			
		EN2	44,064	2	9.0	114.3	0.079	0.619					0.1153	72.5	5,079	0.725			
	SM2	WN	52,135	4	1.0	240.1	0.004	1.050	0.881	0.175	1.81	0.136	0.0043	107.3	223	1.073			
		ES1	47,036	8	24.0	356.3	0.067	0.697					0.0689	73.2	3,243	0.732			
		EN2	35,949	2	9.0	160.0	0.056	0.562					0.0577	60.4	2,074	0.604		21,158	0.373

Table 1d

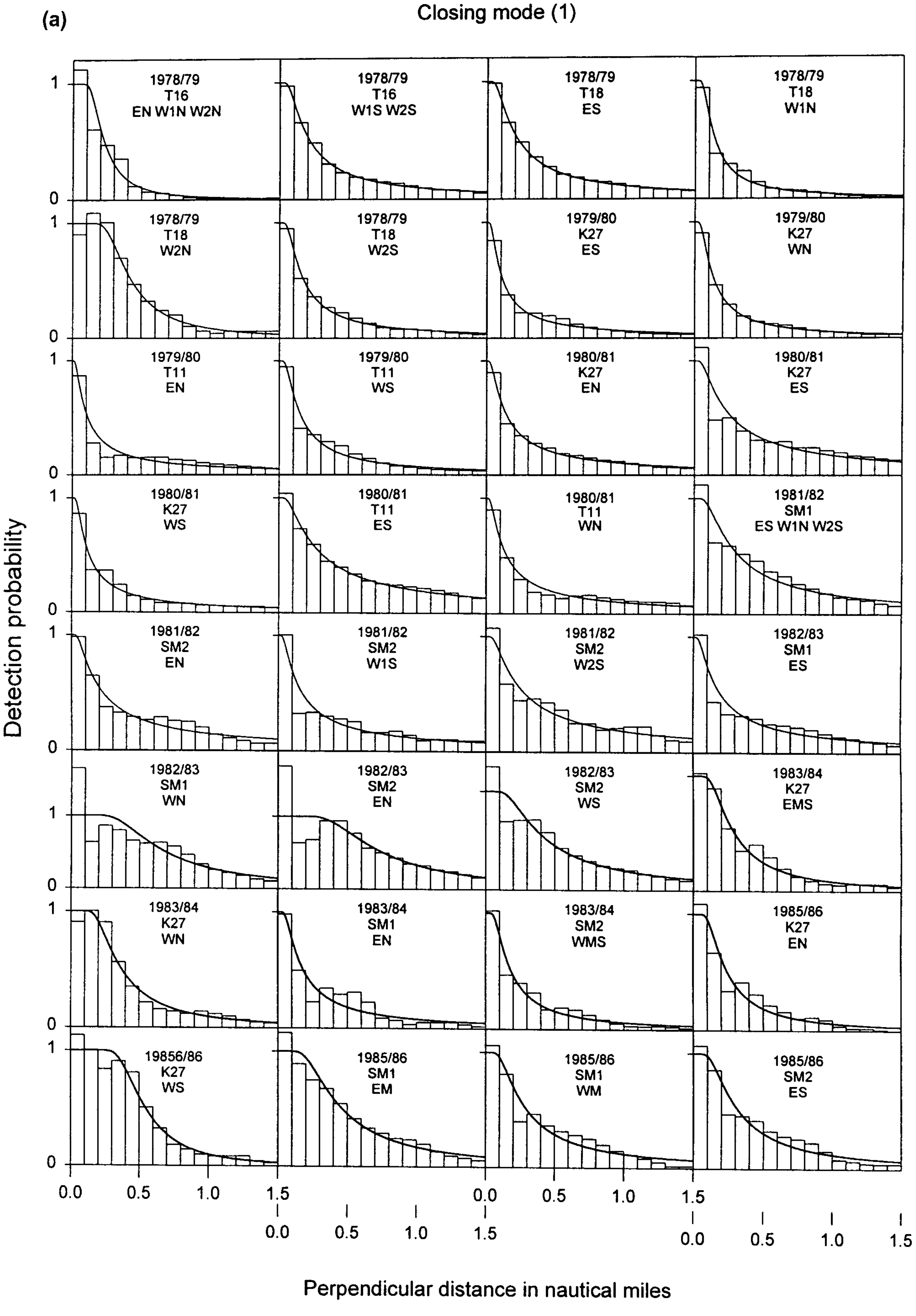
Abundance estimates of minke whales obtained from IO mode data for the second circumpolar set of cruises (1985/86 to 1990/91) - CPII.

Year	Vessel	Stratum	A	N_L	n_s	L	n_s/L	CV	w_s	CV	$E[s_{sc}]$	CV	D_w	P	CV	Ave	Total	CV
1985/86	K27	EN	279,611	8	69.3	884.4	0.078	0.325	0.702	0.157	3.20	0.222	0.1786	49,939	0.424			
(V)		WS	104,814	13	109.4	662.0	0.165	0.147	0.812	0.214	3.55	0.216	0.3615	37,886	0.338			
	SM1	EM	165,912	10	155.5	1,063.5	0.146	0.347	0.742	0.096	2.69	0.143	0.2648	43,937	0.388			
		WM	166,349	4	42.4	492.0	0.086	0.593	0.355	0.273	1.91	0.196	0.2319	38,583	0.682			
	SM2	ES	107,717	8	178.3	739.2	0.241	0.276	0.426	0.109	3.33	0.113	0.9431	101,590	0.317			
		WN	139,065	3	44.0	386.8	0.114	0.379	0.310	0.230	1.93	0.184	0.3543	49,273	0.480		321,207	0.176
1986/87	K27	ES1	23,142	5	25.0	348.6	0.072	0.526	0.367	0.177	2.82	0.113	0.2752	6,368	0.567			
(II)		WS1	10,270	2	10.0	103.7	0.096	0.384					0.3701	3,801	0.438			
		WS2	21,143	2	4.0	128.7	0.031	1.087					0.1192	2,521	1.107	6		
		WS3	79,605	7	42.4	470.4	0.090	0.251					0.3458	27,527	0.327	7		
		EN	124,057	3	47.5	427.7	0.111	0.448					0.4266	52,920	0.495			
	SM1	EBAY	15,242	4	35.8	125.8	0.284	0.367	0.663	0.188	2.23	0.122	0.4773	7,275	0.430			
		ES2	44,975	16	100.5	722.0	0.139	0.246					0.2335	10,501	0.333			
		WBAY	11,505	1	28.3	74.2	0.382	0.188					0.6404	7,368	0.645			
		WN	95,361	2	0.0	201.0	0.000	0.000					0.0000	0	0.000			
	SM2	EM	69,908	3	72.5	447.0	0.162	0.265	0.571	0.194	1.87	0.107	0.2662	18,612	0.346			
		WS2	21,143	2	2.0	151.8	0.013	0.346					0.0216	457	0.411	6		
		WS3	79,605	8	44.8	449.8	0.100	0.395					0.1634	13,010	0.453	7	128,680	0.244
1987/88	SM1	ES	87,677	8	30.7	660.1	0.046	0.512	0.514	0.280	5.31	0.275	0.2401	21,047	0.645			
(III)		WN	148,821	7	25.6	365.1	0.070	0.356					0.3623	53,914	0.530			
	SM2	EN	168,881	7	9.0	546.1	0.016	0.394	0.566	0.123	4.00	0.282	0.0583	9,840	0.500			
		WS	74,351	9	142.9	617.9	0.231	0.142					0.8177	60,799	0.339		145,600	0.300
1988/89	SM1	BS	6,520	3	48.6	144.5	0.336	0.765	0.503	0.284	2.44	0.094	0.8178	5,332	0.821			
(IV)		EN	181,166	6	17.0	617.5	0.028	0.247					0.0669	12,129	0.388			
		WS	58,693	5	23.0	245.7	0.094	0.320					0.2276	13,360	0.438			
	SM2	BN	17,486	9	24.1	396.8	0.061	0.251	0.966	0.162	4.26	0.198	0.1337	2,337	0.358			
		ES	52,441	4	43.6	244.0	0.179	0.262					0.3942	20,674	0.366			
		WN	156,617	6	1.0	730.0	0.001	1.115					0.0030	473	1.144		54,305	0.257
1989/90	SM1	ESB	62,594	13	65.7	793.1	0.083	0.466	0.838	0.139	1.79	0.144	0.0886	5,545	0.507			
(I)		WN	168,761	6	30.8	606.7	0.051	0.325	0.916	0.349	2.25	0.249	0.0623	10,522	0.537			
	SM2	EN	153,029	7	45.0	750.2	0.060	0.257	0.419	0.175	1.76	0.122	0.1262	19,318	0.334			
		WS	45,128	15	184.3	830.9	0.222	0.229	0.519	0.152	2.67	0.094	0.5713	25,783	0.291		61,169	0.192
1990/91	SM1	EN	191,954	4	22.0	473.6	0.046	0.635	0.706	0.151	2.50	0.191	0.0822	15,782	0.680			
(VI)		WS	45,414	9	36.8	645.9	0.057	0.226					0.1009	4,581	0.332			
	SM2	ES	108,268	4	19.0	476.3	0.040	0.516	0.388	0.295	2.92	0.182	0.1499	16,233	0.622			
		WN	211,788	4	12.0	563.7	0.021	0.389					0.0800	16,945	0.521		53,541	0.360

Table 1e

Abundance estimates of minke whales obtained from IO mode data for the as-yet incomplete third circumpolar set of cruises (1991/92 to 1997/98) - CPIII.

Year	Vessel	Stratum	A	N_L	n_s	L	n_s/L	CV	w_s	CV	$E[s_{sc}]$	CV	D_w	P	CV	Ave	Total	CV
1991/92 (V)	SM1	EN	165,429	8	114.6	574.8	0.199	0.230	0.812	0.097	2.54	0.096	0.3120	51,619	0.268			
		WS	58,643	5	122.8	456.4	0.269	0.457					0.4211	24,692	0.477			
	SM2	ES	82,039	10	77.0	687.5	0.112	0.417	0.588	0.151	1.41	0.097	0.1345	11,038	0.454			
		WN	137,734	4	10.0	310.3	0.032	0.691					0.0387	5,335	0.714		92,684	0.221
1992/93 (III*)	SM1	ES	23,207	11	16.9	408.8	0.041	0.341	1.003	0.136	1.67	0.214	0.0345	802	0.425			
		WN	210,035	7	32.0	755.6	0.042	0.444					0.0353	7,412	0.511	8		
		WS	61,527	2	3.0	75.8	0.040	0.050					0.0330	2,029	0.259	9		
	SM2	EN	150,547	5	12.0	603.0	0.020	0.483	0.534	0.164	1.44	0.077	0.0268	4,033	0.516			
		WS	61,527	14	148.9	905.4	0.164	0.215					0.2214	13,620	0.281	9		
		WN	210,035	0	0.0	0.0	-	-					0.0000	0	-	8	24,970	0.239
1993/94 (I*)	SM1	WS	50,596	12	52.0	566.6	0.092	0.216	0.387	0.144	1.51	0.130	0.1793	9,071	0.290			
		EN	293,196	11	11.0	762.5	0.014	0.642					0.0282	8,264	0.671			
	SM2	WN	251,735	8	8.0	550.2	0.015	0.267	0.502	0.166	1.63	0.154	0.0236	5,949	0.350			
		ES	72,249	10	72.2	598.1	0.121	0.363					0.1962	14,175	0.428		37,459	0.257
1994/95 (III*+IV*)	SM1	WS	51,938	11	35.0	496.4	0.071	0.375	0.765	0.122	2.56	0.198	0.1181	6,136	0.441			
		EN	146,681	8	20.0	630.7	0.032	0.514					0.0531	7,793	0.564			
	SM2	WN	148,803	7	15.3	457.9	0.033	0.416	0.693	0.110	1.87	0.110	0.0451	6,716	0.445			
		ES	60,046	8	37.0	459.5	0.080	0.432					0.1086	6,520	0.459			
		PRYD	21,096	4	40.0	203.5	0.197	0.296					0.2653	5,597	0.335		32,761	0.234
1995/96 (VI*)	SM1	WS	34,051	9	10.0	335.6	0.030	0.574	0.662	0.175	2.33	0.094	0.0524	1,783	0.608			
		EN	242,073	11	20.9	554.6	0.038	0.375					0.0663	16,055	0.424			
	SM2	WN	97,945	5	10.9	281.8	0.039	0.255	0.414	0.389	1.76	0.131	0.0823	8,058	0.483			
		ES	72,349	10	40.6	561.8	0.072	0.258					0.1533	11,093	0.485		36,988	0.301
1996/97 (II*)	SM1	ES	67,072	18	30.7	665.6	0.046	0.428	0.637	0.188	1.72	0.117	0.0624	4,186	0.482			
		WN	113,687	5	8.0	201.6	0.040	0.626					0.0537	6,104	0.664			
	SM2	EN	241,928	17	14.0	672.2	0.021	0.221	0.468	0.257	2.06	0.104	0.0459	11,106	0.355			
		WS	23,028	8	25.0	230.0	0.109	0.229					0.2396	5,517	0.360		26,913	0.268
1997/98 (II*)	SM1	WS	32,620	10	2.0	303.2	0.007	0.916	0.878	0.159	1.79	0.126	0.0067	219	0.939			
		EN1	84,726	6	6.7	345.1	0.020	0.419					0.0199	1,687	0.465			
		ES2	10,451	5	11.5	142.8	0.080	1.320					0.0819	856	1.335			
		EN2	44,064	2	2.0	87.8	0.023	0.954					0.0232	1,023	0.975			
	SM2	WN	52,135	4	6.0	253.3	0.024	0.434	0.672	0.128	1.81	0.136	0.0319	1,661	0.473			
		ES1	47,036	8	37.0	385.1	0.096	0.659					0.1292	6,078	0.685			
		EN2	35,949	2	5.0	170.8	0.029	0.600					0.0394	1,416	0.629		12,939	0.375



Figs 4a-c. Hazard rate model for the detection function fitted to the number of schools as a function of the perpendicular distance from the trackline. The number of schools is smeared and then grouped into 0.1 n.miles perpendicular distance intervals, with truncation at 1.5 n.miles. Some strata are pooled as discussed in the text. Graphs are provided for all detection functions estimated under closing mode (Figs 2a-b) and IO mode (Fig. 2c).

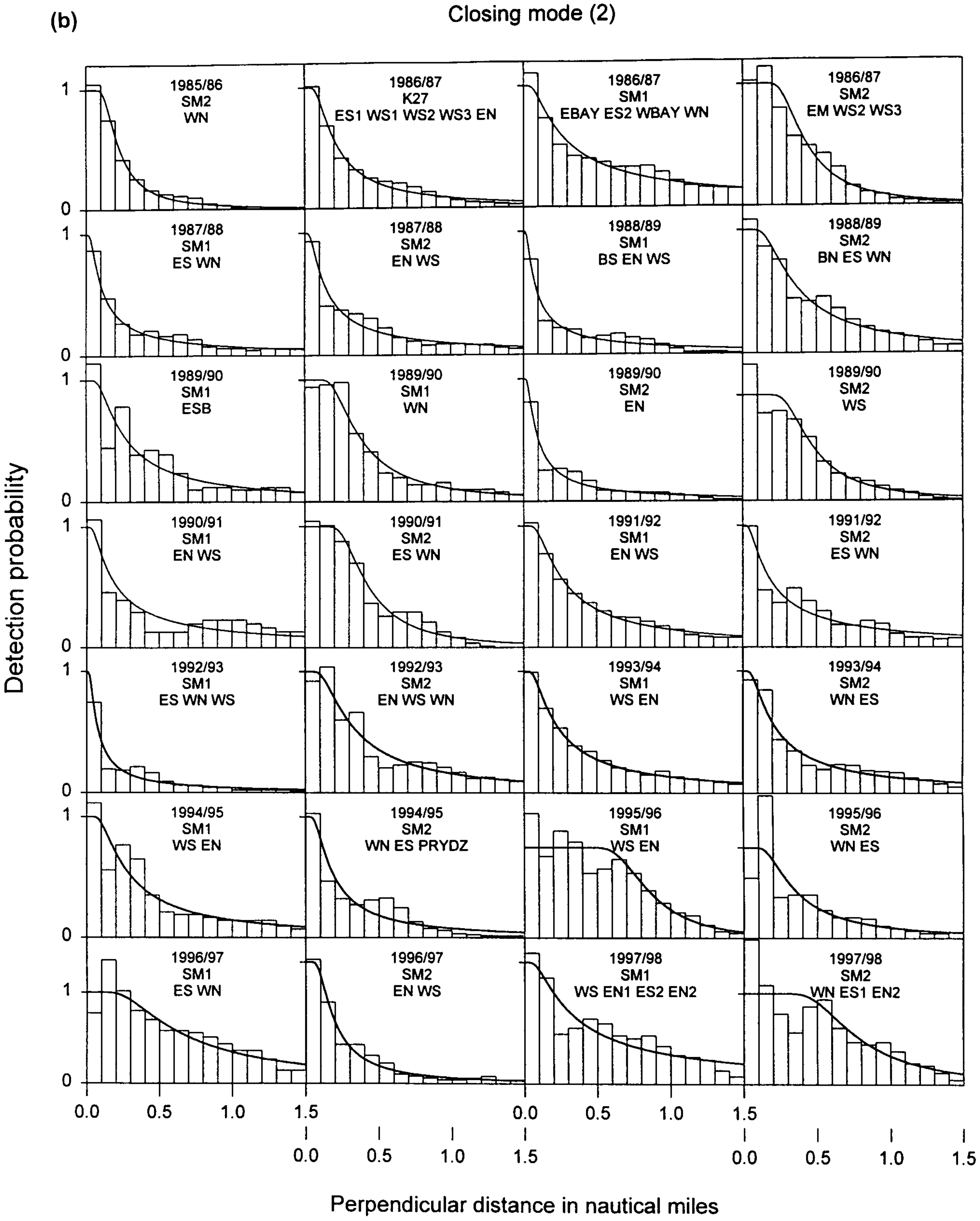

(b)
Closing mode (2)
1985/86 SM2 WN
1986/87 K27 ES1 WS1 WS2 WS3 EN
1986/87 SM1 EBAY ES2 WBAY WN
1986/87 SM2 EM WS2 WS3
1987/88 SM1 ES WN
1987/88 SM2 EN WS
1988/89 SM1 BS EN WS
1988/89 SM2 BN ES WN
1989/90 SM1 ESB
1989/90 SM1 WN
1989/90 SM2 EN
1989/90 SM2 WS
1990/91 SM1 EN WS
1990/91 SM2 ES WN
1991/92 SM1 EN WS
1991/92 SM2 ES WN
1992/93 SM1 ES WN WS
1992/93 SM2 EN WS WN
1993/94 SM1 WS EN
1993/94 SM2 WN ES
1994/95 SM1 WS EN
1994/95 SM2 WN ES PRYDZ
1995/96 SM1 WS EN
1995/96 SM2 WN ES
1996/97 SM1 ES WN
1996/97 SM2 EN WS
1997/98 SM1 WS EN1 ES2 EN2
1997/98 SM2 WN ES1 EN2
Detection probability
0
1
0.0
0.5
1.0
1.5
Perpendicular distance in nautical miles

Fig 4b.

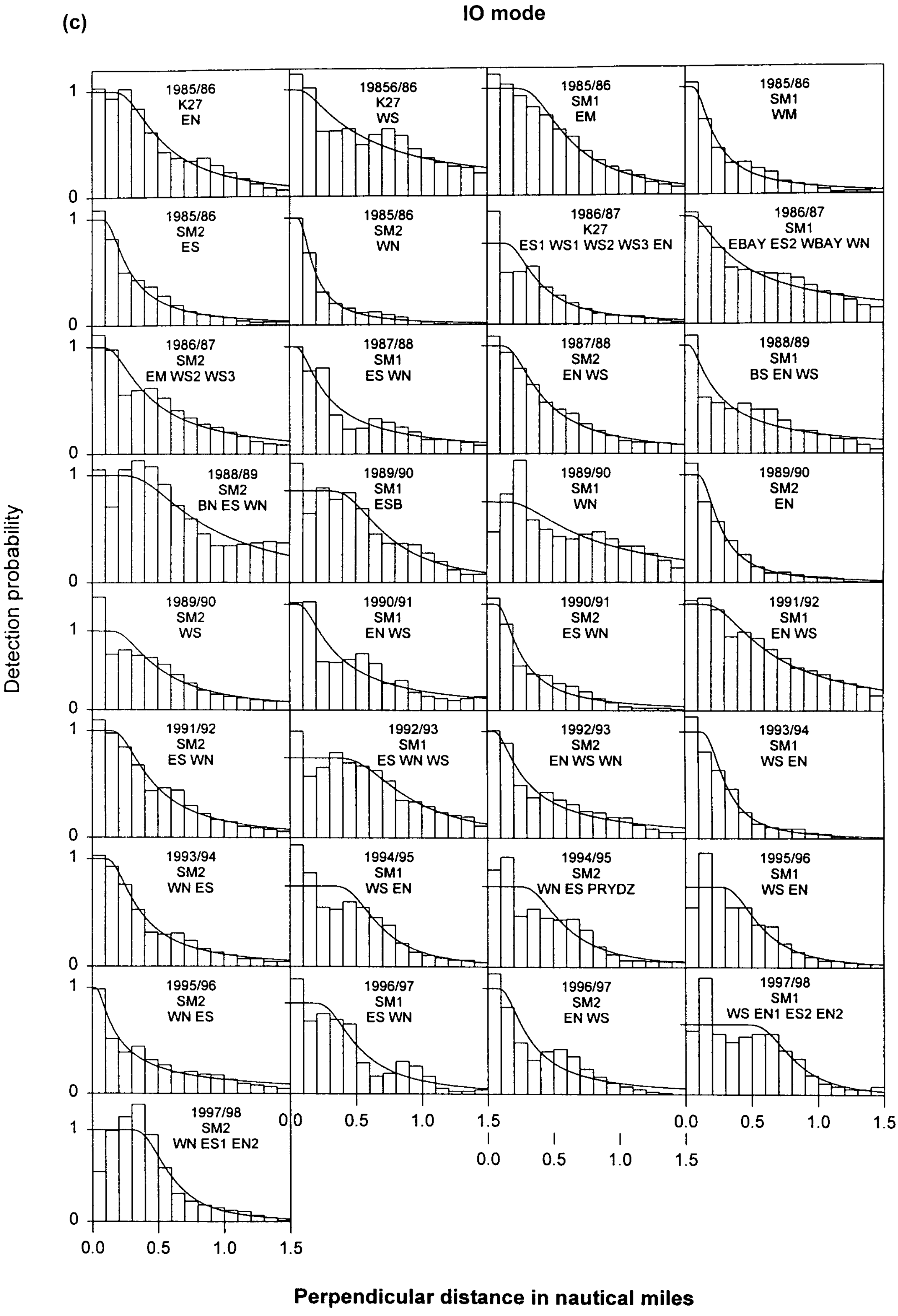
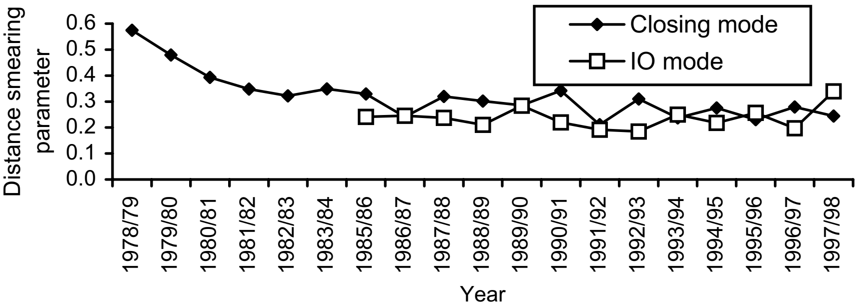

(c)
IO mode
Detection probability
1
0
1985/86
K27
EN
19856/86
K27
WS
1985/86
SM1
EM
1985/86
SM1
WM
1985/86
SM2
ES
1985/86
SM2
WN
1986/87
K27
ES1 WS1 WS2 WS3 EN
1986/87
SM1
EBAY ES2 WBAY WN
1986/87
SM2
EM WS2 WS3
1987/88
SM1
ES WN
1987/88
SM2
EN WS
1988/89
SM1
BS EN WS
1988/89
SM2
BN ES WN
1989/90
SM1
ESB
1989/90
SM1
WN
1989/90
SM2
EN
1989/90
SM2
WS
1990/91
SM1
EN WS
1990/91
SM2
ES WN
1991/92
SM1
EN WS
1991/92
SM2
ES WN
1992/93
SM1
ES WN WS
1992/93
SM2
EN WS WN
1993/94
SM1
WS EN
1993/94
SM2
WN ES
1994/95
SM1
WS EN
1994/95
SM2
WN ES PRYDZ
1995/96
SM1
WS EN
1995/96
SM2
WN ES
1996/97
SM1
ES WN
1996/97
SM2
EN WS
1997/98
SM1
WS EN1 ES2 EN2
1997/98
SM2
WN ES1 EN2
0.0
0.5
1.0
1.5
Perpendicular distance in nautical miles

Fig 4c.

Table 2

Updating the value of *R*, the ratio between the estimated density of minke schools (D_s) obtained during closing mode and during IO mode. Individual estimates of *R* are shown for each of the 'super-strata' used in obtaining the overall value.

			Closing mode		IO mode			
Year	Vessel	Strata	D_s	CV	D_s	CV	*R*	CV
1985/86	K27	EN	0.061	0.488	0.056	0.361	1.088	0.607
		WS	0.046	0.285	0.102	0.260	0.456	0.385
	SM1	EM	0.108	0.297	0.099	0.360	1.098	0.467
		WM	0.085	0.612	0.121	0.653	0.699	0.894
	SM2	ES	0.188	0.241	0.283	0.296	0.665	0.382
		WN	0.055	0.595	0.184	0.444	0.300	0.742
1986/87	K27	ES1 WS1 WS2 WS3 EN	0.122	0.305	0.128	0.323	0.952	0.444
	SM1	EBAY ES2 WBAY WN	0.046	0.388	0.068	0.245	0.680	0.459
	SM2	EM WS2 WS3	0.068	0.305	0.100	0.295	0.678	0.424
1987/88	SM1	ES WN	0.038	1.064	0.060	0.406	0.642	1.139
	SM2	EN WS	0.049	0.538	0.073	0.182	0.678	0.568
1988/89	SM1	BS EN WS	0.079	0.663	0.051	0.356	1.549	0.752
	SM2	BN ES WN	0.032	0.421	0.024	0.284	1.316	0.508
1989/90	SM1	ESB	0.045	0.530	0.049	0.486	0.906	0.719
		WN	0.047	0.394	0.028	0.476	1.678	0.618
	SM2	EN	0.121	0.628	0.072	0.311	1.690	0.701
		WS	0.093	0.240	0.214	0.275	0.434	0.366
1990/91	SM1	EN WS	0.037	0.929	0.034	0.518	1.091	1.063
	SM2	ES WN	0.033	0.286	0.036	0.436	0.928	0.522
1991/92	SM1	EN WS	0.145	0.297	0.134	0.236	1.080	0.379
	SM2	ES WN	0.040	0.482	0.053	0.391	0.757	0.620
1992/93	SM1	ES WN WS	0.047	0.951	0.021	0.350	2.248	1.013
	SM2	EN WS WN	0.018	0.331	0.029	0.258	0.603	0.420
1993/94	SM1	WS EN	0.013	0.580	0.033	0.356	0.398	0.681
	SM2	WN ES	0.046	0.401	0.038	0.315	1.197	0.510
1994/95	SM1	WS EN	0.018	0.513	0.027	0.353	0.641	0.623
	SM2	WN ES PRYDZ	0.036	0.456	0.044	0.253	0.813	0.522
1995/96	SM1	WS EN	0.031	0.337	0.028	0.384	1.110	0.511
	SM2	WN ES	0.041	0.412	0.064	0.430	0.636	0.595
1996/97	SM1	ES WN	0.022	0.368	0.033	0.451	0.662	0.582
	SM2	EN WS	0.041	0.609	0.030	0.306	1.348	0.681
1997/98	SM1	WS EN1 ES2 EN2	0.051	0.454	0.012	0.467	4.126	0.652
	SM2	WN ES1 EN2	0.023	0.493	0.037	0.472	0.606	0.683
All strata combined							0.826	0.089



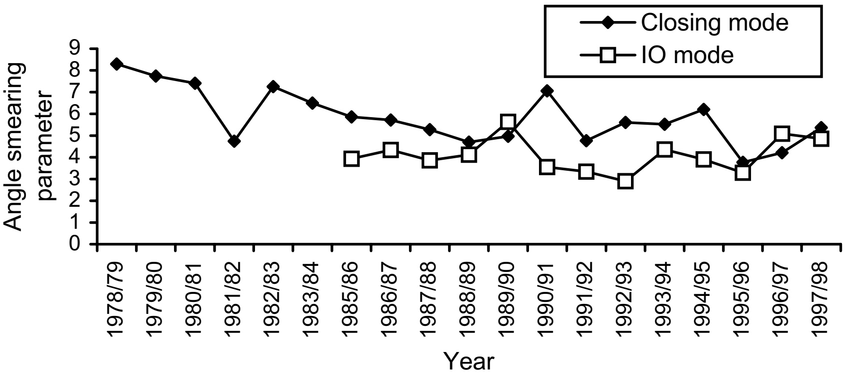


Fig. 5. The radial distance (*s*) and angle (ϕ) smearing factors used in estimating effective search half-width w_S. The mean value is plotted for each year separately for closing and IO mode. These factors are defined as follows: a sighting at radial distance *r* and angle to the trackline θ is smeared over radial distance [*r*(1-*s*), *r*(1+*s*)] and angular [θ-ϕ, θ+ϕ] ranges.

Updated estimate of R

The individual values of *R* for the ‘super-strata’ are given in Table 2. In 20 of the 33 ‘super-strata’, the closing mode school density estimate is lower than that for IO mode. The overall inverse-variance weighted estimate of *R* is 0.826 (CV = 0.089).

Combined passing and closing mode estimates

The combined closing and IO mode estimates are contained in Table 3 where they are compared to previously published results. For the 1978/79 to 1988/89 surveys, these are listed in Haw (1993b); for the 1989/90 to 1997/98 cruises, they may be found respectively in Haw (1991a), Haw (1993a), Borchers (1993), Borchers and Cameron (1995), Borchers and Burt (1996), Burt and Borchers (1996), Burt and Borchers (1997), Burt and Borchers (1999) and Burt and Stahl (2000), except that an error in Burt and Stahl (2000) (in their estimates for minke and undetermined minke whales: codes 4 and 91) has been corrected.

[*Text continues overleaf*]

Table 3

Summary of abundance estimates for each survey obtained in this paper (‘Revised’) and those published in previous papers (‘Previous’). Pseudo-passing estimates for the ‘Revised’ estimates are calculated by dividing the closing mode estimate by $R = 0.826$ (CV = 0.089). See main text (footnotes 17 and 18) for details of procedures used to obtain circumpolar estimates and their variances. The ‘Previous’ estimates used $R = 0.751$ (CV = 0.152) and were corrected for random whale movement by a multiplicative factor $m = 0.985$. *The third circumpolar set is incomplete. ‘Previous’ estimates are taken from Haw (1993a) for 1978/79 to 1988/89 and from individual assessment papers for the remaining years (see text).

	Closing mode		IO mode		Pseudo-passing		Inverse-var. weighted	
Year	Total	CV	Total	CV	Total	CV	Total	CV
Revised								
1978/79	93,808	0.147			113,569	0.172	113,569	0.172
1979/80	102,188	0.218			123,714	0.235	123,714	0.235
1980/81	133,560	0.228			161,695	0.245	161,695	0.245
1981/82	37,649	0.202			45,580	0.221	45,580	0.221
1982/83	52,808	0.194			63,932	0.213	63,932	0.213
1983/84	82,423	0.261			99,786	0.276	99,786	0.276
1985/86	229,175	0.188	321,207	0.176	277,452	0.208	299,793	0.135
1986/87	110,984	0.249	128,680	0.244	134,363	0.264	131,177	0.180
1987/88	96,043	0.631	145,600	0.300	116,275	0.637	138,022	0.273
1988/89	78,660	0.445	54,305	0.257	95,230	0.454	58,170	0.228
1989/90	66,529	0.343	61,169	0.192	80,544	0.354	63,972	0.170
1990/91	53,091	0.445	53,541	0.360	64,275	0.454	56,807	0.283
1991/92	94,855	0.279	92,684	0.221	114,837	0.293	98,682	0.177
1992/93	23,322	0.564	24,970	0.239	28,235	0.571	25,363	0.220
1993/94	30,993	0.359	37,459	0.257	37,522	0.370	37,479	0.211
1994/95	24,234	0.359	32,761	0.234	29,339	0.370	31,620	0.198
1995/96	31,950	0.272	36,988	0.301	38,680	0.286	37,839	0.207
1996/97	29,228	0.482	26,913	0.268	35,385	0.490	28,158	0.236
1997/98	21,291	0.373	12,939	0.375	25,776	0.383	15,434	0.282
CPI	502,436	0.094			608,276	0.130	608,276	0.130
CPII	634,482	0.146	764,502	0.108	768,138	0.171	765,529	0.091
CPIII*	251,805	0.149	257,479	0.109	304,849	0.174	267,881	0.093
Previous								
1978/79	72,867	0.156			97,027	0.218	97,027	0.218
1979/80	61,272	0.188			81,587	0.242	81,587	0.242
1980/81	133,382	0.216			177,606	0.264	177,606	0.264
1981/82	35,760	0.203			47,617	0.254	47,617	0.254
1982/83	55,050	0.203			73,302	0.254	73,302	0.254
1983/84	81,077	0.243			107,959	0.287	107,959	0.287
1985/86	211,150	0.174	303,284	0.172	281,158	0.231	294,610	0.138
1986/87	92,114	0.206	121,549	0.285	122,655	0.256	122,156	0.190
1987/88	51,820	0.521	102,984	0.309	69,001	0.543	88,735	0.273
1988/89	64,403	0.343	68,570	0.349	85,756	0.375	74,692	0.257
1989/90	53,236	0.258	49,592	0.197	70,887	0.299	53,314	0.166
1990/91	47,995	0.399	51,718	0.391	63,908	0.427	56,039	0.290
1991/92	78,461	0.263	87,145	0.250	104,475	0.304	92,709	0.194
1992/93	11,715	0.306	15,583	0.193	15,599	0.341	15,587	0.168
1993/94	19,076	0.335	27,505	0.271	25,401	0.368	26,687	0.218
1994/95	15,649	0.342	28,100	0.246	20,838	0.374	24,905	0.208
1995/96	31,690	0.287	35,861	0.304	42,197	0.325	38,317	0.223
1996/97	28,790	0.482	26,719	0.271	38,336	0.505	28,143	0.241
1997/98	22,258	0.365	12,056	0.346	29,638	0.395	14,033	0.280
CPI	439,408	0.093			585,097	0.178	585,097	0.178
CPII	520,718	0.113	697,697	0.111	693,366	0.190	696,579	0.096
CPIII*	203,571	0.142	225,817	0.122	271,067	0.208	234,538	0.106

The estimates of abundance from the three circumpolar sets of cruises are 608,000 (CV = 0.130), 766,000 (CV = 0.091) and 268,000 (CV = 0.093) respectively[17,18]. These appear to be very similar to the circumpolar abundances obtained by summing previous estimates of 585,000 (CV = 0.178), 697,000 (CV = 0.096) and 235,000 (CV = 0.106). However, these previous estimates incorporated a correction factor m for random whale movement of 0.985, and also used Haw's (1991b) estimate of $R = 0.751$. When the updated estimate of $R = 0.826$ is applied to these previous circumpolar abundance estimates, and the adjustment factor m is omitted, they decrease to 540,000 (CV = 0.128), 680,000 (CV = 0.088) and 236,000 (CV = 0.099), somewhat lower than the revised estimates in all three cases.

Inclusion of 'like minke' sightings

Including 'like minke' sightings in the analyses has no effect on the estimates from the first circumpolar set of surveys (Table 4, Fig. 6). For closing mode, although the mean increase in sightings changes from 0% to 9% to 15% across the three circumpolar sets, the overall impact on abundance estimates is only slight, amounting to a mean increase of 6% for the second set and only 0.3% for the third circumpolar set

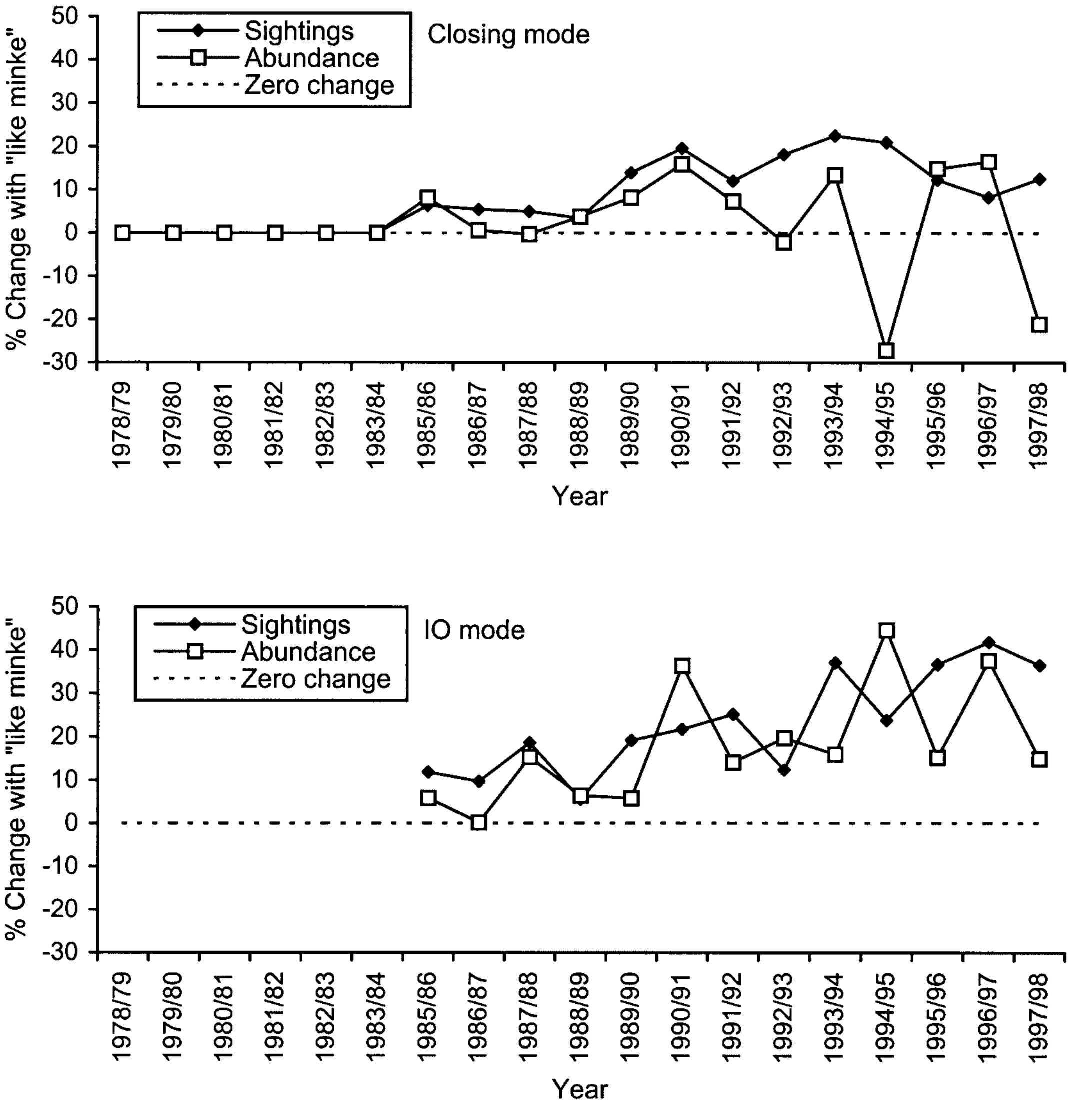


Fig. 6. Percentage changes in the number of sightings and in the uncorrected abundance estimates when 'like minke' sightings are included.

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[17] The circumpolar estimates and their CVs in Table 3 were obtained by simply adding the estimates and variances for the individual surveys. Note, however, that in Table 3 and subsequent Tables which list 'Pseudo-passing' abundance estimates, the associated CVs for circumpolar estimates take account of the fact that a common estimate of R has been applied to all surveys. Furthermore, inverse-variance weighted circumpolar estimates (and their CVs) are derived by combining the associated circumpolar IO and 'Pseudo-passing' estimates. Consequently these inverse-variance weighted circumpolar estimates differ slightly from the sum of such estimates for the constituent areas. As the constituent surveys were not synoptic, but took place over a period of years, this procedure could lead to negatively biased estimates of the CVs for the circumpolar estimates. This is because of the effect of 'additional variance' arising from factors other than the sampling variability upon which the CV estimates for the constituent surveys are based. For example, one source of such additional variance could be a changed distribution of minke whales, on a scale similar to that of the individual survey coverage, from one year to the next. However, computations of the magnitude of this additional variance at the Management Area level (that typically covered by these individual surveys) by the procedure of Punt *et al.* (1997) gives a point estimate of zero (see footnote 24 of Butterworth *et al.*, 1999). Thus this potential source of bias in these CV estimates does not seem likely to be particularly large.

[18] The 1996/97 and 1997/98 cruises both covered the longitudinal range 30°-25°W. The abundance summations for the third circumpolar set of surveys use the whole estimate for 1997/98 survey, which surveyed this region more intensively. Contributions to the summations from strata for the 1996/97 survey are pro-rated down in proportion to the fraction of their areas inside the 30°-25°W region.

of surveys. In fact, for four of the thirteen surveys from 1985/86, the closing mode estimate decreases when 'like minke' sightings are included. For IO mode, the mean increases in sightings are 14% and 31% for the second and third circumpolar sets, and abundance estimates increase for every survey when 'like minke' sightings are included. This translates into abundance estimate increases of 12% and 23% for these two circumpolar sets of surveys.

Comparable abundance estimates from the circumpolar sets of surveys

The values of the factors used to provide comparable abundance estimates are given in Table 5a-c. Portions of the strata surveyed were north of 60°S for all Area II cruises, and for the 1985/86 cruise in Area V (see Figs 1a-f). The inverse-variance weighted estimates (Table 6) are 729,000 (CV = 0.150), 824,000 (CV = 0.117) and 359,000 (CV = 0.108) for the three circumpolar sets of surveys, when excluding longitude ranges yet to be covered in the third set from the first two. If only the first two circumpolar sets are considered, which both cover the complete circumpolar longitudinal range, the inverse-variance weighted estimates are 813,000 (CV = 0.142) and 955,000 (CV = 0.106) respectively.

After further adjustments to allow for the change in proportions of 'like minke' sightings over time, the comparable estimates for closing mode are 602,000 (CV = 0.121), 700,000 (CV = 0.205) and 384,000 (CV = 0.185) respectively (Table 7). These adjustments are made by applying factors for the proportional change in abundance when 'like species' are included ('% change (*P*)' in Table 4) to the extrapolated abundance estimates of Table 6 separately for each year and survey mode, and then summing over the surveys comprising each circumpolar set. The corresponding values for IO mode for the second and third circumpolar sets are 900,000 (CV = 0.139) and 404,000 (CV = 0.123). Pooling these estimates across modes as before would require re-computation of the calibration factor *R*, because of the differing impact of including 'like minke' sightings on closing and IO mode abundance estimates over time. If the 'minke plus like-minke' combination is assumed to reflect a more stable classification over time than 'minke' only, then such a re-computed *R* would be a more reliable estimate for this calibration factor.

Table 4

The impact of including 'like minke' sightings in the abundance estimates. The number of schools sighted in primary search mode during surveys is indicated, together with the number of sightings when 'like minkes' are included (n_{like}). The uncorrected abundance estimates for each survey are shown for both closing and IO mode. Sightings are smeared and truncated at a perpendicular distance of 1.5 n.miles. *The third circumpolar set is incomplete.

	Number of sightings			Uncorrected abundance				
Year	n	n_{like}	% change (n)	P	CV	P_{like}	CV	% change (P)
Closing mode								
1978/79	490.5	490.5	0.0	93,808	0.147	93,808	0.147	0.0
1979/80	413.9	413.9	0.0	102,188	0.218	102,188	0.218	0.0
1980/81	542.5	542.5	0.0	133,560	0.228	133,560	0.228	0.0
1981/82	444.6	444.6	0.0	37,649	0.202	37,649	0.202	0.0
1982/83	576.1	576.1	0.0	52,808	0.194	52,808	0.194	0.0
1983/84	186.1	186.1	0.0	82,423	0.261	82,423	0.261	0.0
1985/86	362.9	385.7	6.3	229,175	0.188	247,686	0.182	8.1
1986/87	257.3	271.2	5.4	110,984	0.249	111,642	0.241	0.6
1987/88	81.4	85.4	4.9	96,043	0.631	95,760	0.621	-0.3
1988/89	90.8	93.9	3.4	78,660	0.445	81,607	0.421	3.7
1989/90	150.7	171.7	13.9	66,529	0.343	71,982	0.364	8.2
1990/91	57.3	68.5	19.5	53,091	0.445	61,553	0.423	15.9
1991/92	139.5	156.3	12.0	94,855	0.279	101,793	0.276	7.3
1992/93	103.4	122.2	18.2	23,322	0.564	22,826	0.347	-2.1
1993/94	80.4	98.5	22.5	30,993	0.359	35,161	0.343	13.4
1994/95	61.5	74.4	21.0	24,234	0.359	17,650	0.285	-27.2
1995/96	91.0	102.2	12.3	31,950	0.272	36,707	0.264	14.9
1996/97	54.4	58.9	8.3	29,228	0.482	34,068	0.455	16.6
1997/98	82.9	93.3	12.5	21,158	0.373	16,696	0.256	-21.1
CPI	2,653.7	2,653.7	0.0	502,436	0.094	502,436	0.094	0.0
CPII	1,000.4	1,076.4	8.9	634,482	0.146	670,230	0.140	6.0
CPIII*	613.1	705.8	15.3	251,805	0.149	260,027	0.142	0.3
IO mode								
1985/86	598.1	668.7	11.8	321,207	0.176	339,947	0.176	5.8
1986/87	412.9	452.8	9.7	128,680	0.244	128,878	0.213	0.2
1987/88	207.9	246.5	18.6	145,600	0.300	167,806	0.320	15.3
1988/89	157.3	166.0	5.5	54,305	0.257	57,775	0.253	6.4
1989/90	325.7	387.9	19.1	61,169	0.192	64,715	0.192	5.8
1990/91	90.8	110.5	21.7	53,541	0.360	72,985	0.313	36.3
1991/92	325.6	407.5	25.2	92,684	0.221	105,704	0.215	14.0
1992/93	212.8	239.0	12.3	24,970	0.239	29,878	0.236	19.7
1993/94	143.2	196.3	37.1	37,459	0.257	43,418	0.253	15.9
1994/95	147.3	182.3	23.8	32,761	0.234	47,385	0.226	44.6
1995/96	82.4	112.6	36.7	36,988	0.301	42,613	0.223	15.2
1996/97	77.7	110.2	41.8	26,913	0.268	37,017	0.291	37.5
1997/98	70.2	95.8	36.5	12,939	0.375	14,862	0.307	14.9
CPII	1,792.7	2,032.4	14.4	764,502	0.108	832,106	0.108	11.6
CPIII*	1,059.2	1,343.7	30.5	257,479	0.109	311,520	0.102	23.1

Text continues on p. 168

Table 5a-b

Values of factors used to obtain comparable abundance estimates for each circumpolar set of surveys for closing mode. Areas are given in n.miles^2. To extrapolate the abundance estimates to 60°S, the density of whales in each unsurveyed area between a northern stratum and 60°S is assumed to be the same as that in the associated northern stratum. If a stratum extends north of 60°S, the associated abundance estimate is proportionately decreased. The fraction of each stratum area that lies within the area covered by the incomplete third circumpolar set of cruises is calculated, and the abundance estimate for the stratum multiplied by that fraction. The final result ('Total') comprises estimates of the uncorrected abundance south of 60°S in regions that correspond to those covered in the third circumpolar set of cruises to 1997/98. Note that for the WN and WS strata in 1996/97, the stratum areas have been reduced (as recorded in the 'Area overlap' column) to adjust for the fact that parts of these strata were re-surveyed in 1997/98.

(a) Comparable closing mode estimates CPI.

Year	Stratum	*P*	CV	Area surveyed	Area unsurveyed	Area N of 60°S	Area overlap	*P* (S of 60°S)	Fraction in 3rd set	*P* (fraction in 3rd set)	Total	CV
1978/79	W1N	9,442	0.405	39,256	38,645			18,736	1.00	18,736		
	EN	23,099	0.366	156,766	53,181			30,935	0.00	0		
	W2N	7,064	0.323	153,914				7,064	0.15	1,039		
	W1S	21,430	0.280	20,389				21,430	1.00	21,430		
	W2S	8,759	0.218	29,600				8,759	0.06	496		
	ES	24,014	0.263	27,571				24,014	0.00	0	41,701	0.232
1979/80	WN	23,950	0.437	200,724	255,938			54,488	1.00	54,488		
	EN	28,627	0.563	217,865	100,763			41,867	1.00	41,867		
	Other	49,612	0.228	75,391				49,612	1.00	49,612	145,967	0.242
1980/81	WN	20,244	0.709	139,191	91,934			33,615	1.00	33,615		
	EN	52,172	0.414	208,159	263,267			118,156	1.00	118,156		
	Other	61,145	0.260	132,930				61,145	1.00	61,145	212,916	0.266
1981/82	W1N	4,885	0.700	135,504	100,005	74,162		5,817	1.00	5,817		
	EN	8,647	0.520	145,063	288,507			25,843	1.00	25,843		
	Other	24,118	0.190	117,454				24,118	1.00	24,118	55,778	0.265
1982/83	WN	7,288	0.291	163,926	243,506			18,114	0.68	12,400		
	EN	24,598	0.352	149,433	178,386			53,962	1.00	53,962		
	WS	7,688	0.206	25,596				7,688	0.67	5,128		
	ES	13,235	0.360	33,050				13,235	1.00	13,235	84,725	0.235
1983/84	EN	14,593	0.826	202,108	35,088			17,126	0.19	3,286		
	WN	25,536	0.270	207,721				25,536	1.00	25,536		
	WMS	29,939	0.332	156,457				29,939	1.00	29,939		
	EMS	12,355	0.476	158,893				12,355	0.17	2,057	60,818	0.204

(b) Comparable closing mode estimates CPII and CPIII.

Year	Stratum	*P*	CV	Area surveyed	Area unsurveyed	Area N of 60°S	Area overlap	*P* (S of 60°S)	Fraction in 3rd set	*P* (fraction in 3rd set)	Total	CV
1985/86	WN	14,787	0.624	139,065		38,305		10,714	1.00	10,714		
	Other	214,388	0.196	824,403				214,388	1.00	214,388	225,102	0.189
1986/87	WS2	1,447	0.249	21,143		11,992		626	1.00	626		
	WN	1,829	0.546	95,361		10,596		1,626	1.00	1,626		
	EN	54,864	0.400	124,057	74,341			87,741	1.00	87,741		
	Other	52,844	0.211	254,647				52,844	1.00	52,844	142,837	0.258
1987/88	WN	33,513	1.254	148,821	263,930			92,947	1.00	92,947		
	EN	5,571	0.630	168,881	54,823			7,379	1.00	7,379		
	Other	56,959	0.584	162,028				56,959	1.00	56,959	157286	0.771
1988/89	WN	11,239	0.824	156,617	17,772			12,514	0.33	4,169		
	EN	13,137	0.714	181,166	17,772			14,426	0.00	0		
	BS	5,396	0.686	6,520				5,396	1.00	5,396		
	WS	29,204	0.710	58,693				29,204	0.26	7,692		
	BN	2,053	0.785	17,486				2,053	1.00	2,053		
	ES	17,630	0.463	156,617				17,630	0.00	0	19,311	0.394
1989/90	WN	17,621	0.465	168,761	249,265			43,648	0.62	27,183		
	EN	32,687	0.640	153,029	167,243			68,410	1.00	68,410		
	WS	11,195	0.258	45,128				11,195	0.64	7,176		
	ESBAY	5,026	0.549	62,594				5,026	1.00	5,026	107,795	0.424
1990/91	EN	19,676	0.972	191,954	43,706			24,156	0.23	5,435		
	WS	2,642	0.962	45,414				2,642	1.00	2,642		
	ES	24,758	0.375	108,268				24,758	0.11	2,627		
	WN	6,016	0.340	211,788				6,016	1.00	6,016	16,721	0.376
1991/92	WN	2,017	0.544	137,734	120,700			3,785	1.00	3,785		
	EN	76,005	0.321	165,429	247,210			189,584	1.00	189,584		
	Other	16,834	0.358	140,682				16,834	1.00	16,834	210,202	0.291
1992/93	All	23,322	0.564	445,316				23,322	1.00	23,322	23,322	0.564
1993/94	All	30,993	0.359	667,776				30,993	1.00	30,993	30,993	0.359

cont...

Table 5b continued.

Year	Stratum	*P*	CV	Area surveyed	Area unsurveyed	Area N of 60°S	Area overlap	*P* (S of 60°S)	Fraction in 3rd set	*P* (fraction in 3rd set)	Total	CV
1994/95	All	24,234	0.359	428,564				24,234	1.00	24,234	24,234	0.359
1995/96	All	31,950	0.272	446,418				31,950	1.00	31,950	31,950	0.272
1996/97	WN	3,575	0.442	113,687	14,510		55,590	2,283	1.00	2,283		
	WS	3,012	0.928	23,028			17,740	692	1.00	692		
	Other	22,641	0.574	309,000				22,641	1.00	22,641	25,616	0.509
1997/98	WN	223	1.073	52,135		32,722		83	1.00	83		
	WS	511	0.840	32,620		14,040		291	1.00	291		
	Other	20,424	0.300	222,226				20,424	1.00	20,424	20,798	0.295

Table 5c

Values of factors used to obtain comparable biomass estimates for the 2nd and 3rd circumpolar sets of surveys in IO mode, developed as for Tables 5a-b.

(c) Comparable IO mode CPII and CPIII.

Year	Stratum	*P*	CV	Area surveyed	Area unsurveyed	Area N of 60°S	Area overlap	*P* (S of 60°S)	Fraction in 3rd set	*P* (fraction in 3rd set)	Total	CV
1985/86	WN	49,939	0.424	139,065		38,305		36,183	1.00	36,183	307,451	0.178
	Other	271,268	0.193	824,403				271,268	1.00	271,268		
1986/87	WS2	1,404	0.915	21,143		11,992		608	1.00	608	159,596	0.284
	WN	0	0.000	95,361		10,596		0	1.00	0		
	EN	52,920	0.495	124,057	74,341			84,633	1.00	84,633		
	Other	74,355	0.233	254,647				74,355	1.00	74,355		
1987/88	WN	53,914	0.530	148,821	263,930			149,528	1.00	149,528	244,408	0.352
	EN	9,840	0.500	168,881	54,823			13,035	1.00	13,035		
	Other	81,846	0.400	162,028				81,846	1.00	81,846		
1988/89	WN	473	1.144	156,617	17,772			527	0.33	176	11,364	0.415
	EN	12,129	0.388	181,166	17,772			13,319	0.00	0		
	BS	5,332	0.821	6,520				5,332	1.00	5,332		
	WS	13,360	0.438	58,693				13,360	0.26	3,519		
	BN	2,337	0.358	17,486				2,337	1.00	2,337		
	ES	20,674	0.366	156,617				20,674	0.00	0		
1989/90	WN	10,522	0.537	168,761	249,265			26,063	0.62	16,232	78,736	0.216
	EN	19,318	0.334	153,029	167,243			40,431	1.00	40,431		
	WS	25,783	0.291	45,128				25,783	0.64	16,528		
	ESBAY	5,545	0.507	62,594				5,545	1.00	5,545		
1990/91	EN	15,782	0.680	191,954	43,706			19,376	0.23	4,360	27,608	0.344
	WS	4,581	0.332	45,414				4,581	1.00	4,581		
	ES	16,233	0.622	108,268				16,233	0.11	1,723		
	WN	16,945	0.521	211,788				16,945	1.00	16,945		
1991/92	WN	5,335	0.714	137,734	120,700			10,011	1.00	10,011	174,496	0.218
	EN	51,619	0.268	165,429	247,210			128,756	1.00	128,756		
	Other	35,730	0.410	140,682				35,730	1.00	35,730		
1992/93	All	24,970	0.239	445,316				24,970	1.00	24,970	24,970	0.239
1993/94	All	37,459	0.257	667,776				37,459	1.00	37,459	37,459	0.257
1994/95	All	32,761	0.234	428,564				32,761	1.00	32,761	32,761	0.234
1995/96	All	36,988	0.301	446,418				36,988	1.00	36,988	36,988	0.301
1996/97	WN	6,104	0.664	113,687	14,510		55,590	3,898	1.00	3,898	20,457	0.303
	WS	5,517	0.360	23,028			17,740	1,267	1.00	1,267		
	Other	15,292	0.367	309,000				15,292	1.00	15,292		
1997/98	WN	1,661	0.473	52,135		32,722		619	1.00	619	11,802	0.406
	WS	219	0.939	32,620		14,040		125	1.00	125		
	Other	11,059	0.433	222,226				11,059	1.00	11,059		

Table 6

Comparable abundance estimates for each circumpolar set of surveys, extrapolated to 60°S. The estimates do not cover the entire circumpolar range but are restricted to the longitudinal range covered in the third circumpolar set of surveys.

Same areas	Closing mode		IO mode		Pseudo-passing		Inverse-var. weighted	
Year	Total	CV	Total	CV	Total	CV	Total	CV
1978/79	41,701	0.232			50,485	0.248	50,485	0.248
1979/80	145,967	0.242			176,715	0.258	176,715	0.258
1980/81	212,916	0.266			257,767	0.281	257,767	0.281
1981/82	55,778	0.265			67,528	0.279	67,528	0.279
1982/83	84,725	0.235			102,572	0.252	102,572	0.252
1983/84	60,818	0.204			73,629	0.223	73,629	0.223
1985/86	225,102	0.189	307,451	0.178	272,521	0.209	290,724	0.136
1986/87	142,837	0.258	159,596	0.284	172,926	0.273	166,000	0.197
1987/88	157,286	0.771	244,408	0.352	190,419	0.776	230,755	0.322
1988/89	19,311	0.394	11,364	0.415	23,379	0.404	13,764	0.307
1989/90	107,795	0.424	78,736	0.216	130,503	0.433	83,038	0.196
1990/91	16,721	0.376	27,608	0.344	20,243	0.386	23,220	0.260
1991/92	210,202	0.291	174,496	0.218	254,482	0.304	190,081	0.180
1992/93	23,322	0.564	24,970	0.239	28,235	0.571	25,363	0.220
1993/94	30,993	0.359	37,459	0.257	37,522	0.370	37,479	0.211
1994/95	24,234	0.359	32,761	0.234	29,339	0.370	31,620	0.198
1995/96	31,950	0.272	36,988	0.301	38,680	0.286	37,839	0.207
1996/97	25,616	0.509	20,457	0.303	31,012	0.517	21,828	0.265
1997/98	20,798	0.295	11,802	0.406	25,179	0.308	15,506	0.263
CPI	601,905	0.121			728,698	0.150	728,698	0.150
CPII	669,052	0.212	829,163	0.137	809,990	0.230	823,976	0.117
CPIII*	367,115	0.181	338,933	0.126	444,449	0.201	358,504	0.108

With ‘like minkes’ included, for closing mode the comparable estimate of abundance for the third circumpolar set of cruises is 55% of that in the second set, whereas for IO mode the corresponding estimate is just 45%. The closing mode estimates for the first and second circumpolar sets of surveys are quite similar.

DISCUSSION

Comparison with previous estimates

The revised abundance estimates of this paper are similar to previously published estimates for most cruises, for both closing and IO modes (Table 4). There are three main reasons for differences.

(i) Corrections to the recorded data. Data are thoroughly re-checked when incorporated into DESS. Many of the minor differences in values for the components of the abundance estimation formula (e.g. stratum area A, search effort L, number of sightings n_s) can be traced to this thorough revision process. The appendices in Strindberg and Burt (2000) provide an exhaustive guide to all changes made to the data they received (which comprised the data recorded on the survey vessels, as modified in validation exercises carried out by the IWC Secretariat for the 1986/87 cruise onwards, and at the University of Cape Town for the earlier cruises).

(ii) The mean school size estimation method changed from the 1995/96 assessment. The updated method is used throughout in this paper, and often gives quite different estimates for the mean school sizes in surveys before 1995/96. In some previous assessments (e.g. those for 1991/92, 1993/94 and 1994/95), the estimated mean school size for some strata was less than one, a major reason for the methodological change made for the 1995/96 analysis.

(iii) Changes in pooling. Previous assessments made pooling decisions on either an *ad hoc* basis, or by using the AIC criterion. For many of the cruises, the pooling selected for this paper is different from that for the corresponding previous assessment. Since pooling affects estimates of both mean school size ($\bar{s}$) and search half-width (w_s), the changes in pooling explain a number of the differences between the previous and revised abundance estimates.

A brief summary of reasons (in order of importance) for such differences is given below for each cruise where the difference exceeds 25% for either closing or IO mode.

1978/79: higher $\bar{s}$ in the ES stratum, increase in sightings due to corrected data (Strindberg and Burt, 2000, appendix T)
1979/80: higher $\bar{s}$
1987/88: higher $\bar{s}$, smaller w_s in closing mode (the results of different pooling)
1992/93: higher $\bar{s}$, lower w_s (the results of different pooling)
1993/94: higher $\bar{s}$
1994/95: different pooling.

For all nine cases (for either closing or IO mode) for which the differences in abundance estimates exceeded 25%, the revised estimate is higher than the previous estimate. In most of these cases the increase can be ascribed to a larger estimate of mean school size obtained using the new method of regressing against $g(y)$. This raises concerns about the impact of the change in this methodology on the abundance estimates. In DESS, if there is a significant (at the 15% level) relationship between perpendicular distance y and school size, the regression method is used; otherwise, the mean school size within a perpendicular distance of 1.5 n.miles is adopted. This approach can result in a marked change in the estimate of $\bar{s}$ with only minor changes to the recorded data. Since obtaining a significant regression depends heavily on sample size, $\bar{s}$ is invariably set to this mean size for strata with small numbers of sightings, while those with larger numbers of sightings apply the regression method, which produces smaller $\bar{s}$ estimates. Further investigation of the most appropriate method to use to estimate mean school size is needed.

Table 7

Comparable abundance estimates with ‘like minke’ frequencies taken into account. The average abundance increase for each survey if ‘like minkes’ are included (‘% change P’ column in Table 4) is applied to the estimates in Table 6.

Closing mode		% Change	Closing (include like)	
Year	Total	Include like	Total	CV
1978/79	41,701	0.0	41,701	0.232
1979/80	145,967	0.0	145,967	0.242
1980/81	212,916	0.0	212,916	0.266
1981/82	55,778	0.0	55,778	0.265
1982/83	84,725	0.0	84,725	0.235
1983/84	60,818	0.0	60,818	0.204
1985/86	225,102	8.1	243,284	0.189
1986/87	142,837	0.6	143,684	0.258
1987/88	157,286	-0.3	156,823	0.770
1988/89	19,311	3.7	20,034	0.394
1989/90	107,795	8.2	116,631	0.424
1990/91	16,721	15.9	19,386	0.376
1991/92	210,202	7.3	225,577	0.291
1992/93	23,322	-2.1	22,826	0.564
1993/94	30,993	13.4	35,161	0.359
1994/95	24,234	-27.2	17,650	0.359
1995/96	31,950	14.9	36,707	0.272
1996/97	25,616	16.6	29,858	0.509
1997/98	20,798	-21.1	16,412	0.295
First circumpolar set of surveys			601,905	0.121
Second circumpolar set of surveys			699,841	0.205
Third circumpolar set of surveys			384,191	0.185

IO mode		% Change	IO (include like)	
Year	Total	Include like	Total	CV
1985/86	307,451	5.8	325,389	0.178
1986/87	159,596	0.2	159,841	0.284
1987/88	244,408	15.3	281,684	0.352
1988/89	11,364	6.4	12,090	0.415
1989/90	78,736	5.8	83,301	0.216
1990/91	27,608	36.3	37,634	0.344
1991/92	174,496	14.0	199,009	0.218
1992/93	24,970	19.7	29,878	0.239
1993/94	37,459	15.9	43,418	0.257
1994/95	32,761	44.6	47,385	0.234
1995/96	36,988	15.2	42,613	0.301
1996/97	20,457	37.5	28,137	0.303
1997/98	11,802	14.9	13,556	0.406
Second circumpolar set of surveys			899,939	0.139
Third circumpolar set of surveys			403,995	0.123

Updating the value of the calibration factor R

Previous intent was that the estimate of the closing/IO mode calibration factor *R* would be updated annually as further data became available. This, however, has not been done, and a fully updated estimate of *R* is now long overdue. The updated estimate of $R = 0.826$ ($CV = 0.089$) is somewhat higher than the previous estimate: $R = 0.751$ ($CV = 0.152$) (Haw, 1991b; 1985/86 to 1988/89 surveys). The changing proportions of ‘like minke’ sightings over time (different for closing and IO mode, Table 4) suggest that changes in classification practice may have led to changes over time in the closing/IO mode density estimate ratio, hence rendering global averaging to estimate *R* a questionable procedure.

Combined passing and closing estimates

The final inverse-variance weighted abundance estimates (see Table 3) for the areas covered in the surveys (i.e. no extrapolation) are 608,000 ($CV = 0.130$) for the first circumpolar set, 766,000 ($CV = 0.091$) for the second, and 268,000 ($CV = 0.093$) for the incomplete third set. As estimates of total Southern Hemisphere minke whale abundance, these are negatively biased for reasons that include the following.

(i) The surveys cover (most of) the area between 60°S and the ice edge. However, as has been emphasised in the cruise reports (e.g. IWC, 2000), there are often large areas of open water (polynyas) within the pack ice that are inaccessible to the survey vessels. Naito (1982) reports observations of minke whales made in summer from an ice-breaker vessel operating inside the pack ice. Minke whales are found in highest densities in and around the pack ice, so that large numbers may be missed in surveys of some parts of the Antarctic where polynyas occur.

(ii) The analyses assume that no schools on the trackline are missed. In principle, the extent of this bias can be determined from the duplicate sightings data recorded under IO mode, but attempts to date to estimate this bias from these data are probably substantially positively biased because of unmodelled heterogeneity (Ashbridge *et al.*, 1998).

(iii) The numbers south of 60°S constitute only part of the total abundance of minke whales in the Southern Hemisphere, because a proportion of the whales (particularly the younger animals) do not migrate as far south as 60°S. The relative under-representation of younger animals has in the past been argued from the relatively high proportion of takeable minke whales (>8.2m) reported in the IDCR sightings surveys, but has since been more reliably demonstrated by the lower selectivities estimated for animals below about seven years of age from analyses of age composition data provided by the JARPA programme (Butterworth *et al.*, 1999). Japanese sighting vessel (JSV) sighting rate information for lower latitudes at the same time of the year as the IDCR-SOWER surveys does indicate minke whales (a proportion of which would be dwarf minke whales) north of 60°S, but in relatively low densities, such as would add only some 10% to the abundance estimates for the area south of 60°S (Borchers *et al.*, 1990).

(iv) A number of sightings are recorded as ‘like minke’, ‘whale’ or even ‘cetacean’. It is probable that some of these sightings (especially ‘like minke’) were actually minke whales, but these are not included in the baseline estimates quoted above. Furthermore, the proportion of these unassigned sightings has increased in the later surveys (Table 4, Fig. 6; Branch and Butterworth, 2001, table 1). If the ‘like minke’ sightings are included in the analyses, closing mode estimates increase on average by only 6% and 0.3% for the second and third circumpolar sets of surveys, but IO mode estimates increase by rather more substantial amounts of 12% and 23% respectively. Sightings recorded under more general codes than ‘like minke’ which were, in reality, minke whales seem unlikely to constitute a major source of potential further negative bias in abundance estimates because the number of such sightings (for which the species was not identified) is relatively low.

Comparability among circumpolar sets of cruises

Last year (IWC, 2001), initial rough extrapolations of the incomplete third circumpolar set of surveys led to a point estimate of abundance that was considered ‘appreciably lower’ than the total of the previously agreed (IWC, 1991) point estimates by Area. This paper has made proportional coverage adjustments and also accounted for the increase in the proportion of ‘like minke’ sightings in the later surveys in a manner that provides estimates that are more defensible (in the context of making temporal comparisons) than those presented last year. The resultant estimates for comparable areas for the three sets of circumpolar surveys (Table 7) are in the ratio 0.86 : 1.00 : 0.55 for closing mode and 1.00 : 0.45 for IO mode. The associated CVs indicate that the drop between the second and third sets of surveys is of borderline significance at the 5% level for the closing mode estimates, but definitely significant for the IO mode estimates.

These comparisons suggest a notable decrease in minke whale abundance between the mid-1980s and mid-1990s. It is important to try to determine whether this reflects a true decrease rather than a failure above to take all necessary factors into account in attempting to produce comparable abundance estimates. Three reasons that the latter might be the case are:

(1) decreased sighting efficiency, as younger less experienced observers were introduced onto the vessels during the later surveys[19], which could have led to a decrease in $g(0)$ over time[20];
(2) a changed minke whale distribution pattern, such that a considerably smaller proportion of the population has been present in the area surveyed during the third circumpolar set of surveys than the second;
(3) a change in the timing of the surveys, so that the surveys no longer span the peak of minke whale abundance in the Southern Ocean.

The increased sighting rates for some other species in the IDCR/SOWER surveys over the same period (Branch and Butterworth, 2001) do not provide immediate support for the possibility that decreased sighting efficiency could be playing a major role, but quantitative analysis of this effect would be of interest.

The second possibility does not seem supported by past analyses of the JSV data (as discussed above), which do not suggest a large component of the population north of 60°S during the months the surveys are conducted. Both a very large density of minke whales, and a substantial increase in the area within the pack ice that is accessible to these whales, would be needed to explain the extent of the decrease in the abundance estimates above. It might be that minke whale distribution patterns have changed since the time of the JSV surveys, with a smaller proportion now migrating to the Southern Ocean. This could be in response to possible changes in the abundance of their primary food source, krill, which Loeb *et al.* (1997) report to have shown a declining trend (based upon trawl surveys) in the Elephant Island region off the Antarctic Peninsula area (i.e. in the neighbourhood of the boundary between Areas I and II) over the 1976-1996 period. They suggest that this may be linked to a longer trend, since the 1940s, of warming and associated decreased sea-ice cover in this region. However, the two synoptic acoustic surveys of krill that have taken place over a rather larger part of this region in 1981 and 2000 reflect an increase in krill abundance (SC-CAMLR, 2000).

Since 1994/95, the surveys have started some 2-3 weeks later than in earlier years, so that a greater proportion of these later surveys has taken place in February. From data from Japanese surveys south of 50°S (including IDCR surveys) from 1976/77 to 1987/88, Kasamatsu *et al.* (1996) reported a decrease in minke whale sighting rates of about 50% from late January to late February. Analyses by Free (1983, plot 18) similarly show a decrease of about the same size in commercial minke whale catch rates from their peak in January to February. Thus some of the decrease in abundance estimates for the last four (though not the earlier three) surveys of the third circumpolar set analysed here may arise from their lesser coverage of the period of peak minke abundance off Antarctica.

To the extent that the decrease in abundance is real, it must reflect some combination of an increased mortality rate and a decreased birth rate (where birth rate is considered to be a product of pregnancy rate and natural survival over the first few years of life).

(i) Large recent fishing mortality hardly seems a plausible candidate for the first of these possibilities. The combined effect of the research catches of some 400 minke whales per year taken since the 1987/88 season is more than an order of magnitude too small to explain this reduction in abundance. An increase in natural mortality rate could be postulated, but there is no independent evidence for this.

(ii) There is some evidence pointing to a decrease in the birth rate. Analyses of minke whale catch-at-age data for Areas IV and V by Butterworth *et al.* (1999) indicate a recruitment trend for both Areas that first increases over the 1950s and 1960s, but then drops again from about 1970. This would lead to a lower overall abundance in due course.

Butterworth and Punt (1999, table 4a) fit a variant of the Baleen II population model which allows for time trends in minke whale carrying capacity to these recruitment estimates for Area IV. Their results suggest a total minke whale abundance for this Area which drops by about 40% from a maximum in the early 1970s to a minimum in the late 1980s, and is relatively steady during the 1990s. This decrease in abundance results from the combined effect of the commercial catches of the 1970s and early 1980s, supercompensation[21] and a recent decrease in carrying capacity[22].

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[19] During the second circumpolar set of surveys, every topman had participated in at least 10 previous sighting survey cruises. However, from the 1992/93 cruises onwards, about 40% of the topmen had previous experience from less than six earlier surveys (K. Matsuoka, pers. comm.).

[20] Even without this consideration, comparability of abundance estimates over time could be compromised if the assumption of the standard methodology that $g(0)$ is constant over time and equal to one is invalid. Existing analyses do not rule out this possibility. There has, however, been a tendency to suspect that $g(0)$ is close to 1 for minke whales on these surveys, so that any change in $g(0)$ could not be that large. This has been based on the high intensity of searching effort in IO mode (which is the standard for abundance estimates), with two observers in the barrel, one in the IO platform, and at least one dedicated observer on the upper bridge. Given vessel searching speeds (11-12 knots), and typical minke whale blow rates (48 per hour, Ward, 1988) and radial distances at first sighting ($\sim$1.5 n.miles, e.g. Butterworth and Best, 1982, table 8), there are a fair number of opportunities (typically six) to sight a minke whale on the trackline. Attempts to estimate $g(0)$ from duplicate sightings data recorded in IO mode (Butterworth and Borchers, 1988; Butterworth, 1991; Ashbridge *et al.*, 1998) have seemed to support the contention that $g(0)$ (for all platforms combined) must be close to 1, but such inferences are not conclusive because the methods used likely give substantially positively biased estimates of $g(0)$ as a result of unmodelled heterogeneity. Furthermore, consideration of the estimated detection functions (Fig. 3) and estimates of effective search half-width (w_s, Table 1) does not suggest any obvious reason to suspect marked trends in $g(0)$ over time. Average w_s values for IO mode for the second and third circumpolar sets of cruises scarcely differ. For closing mode, such averages are similar for the first and second circumpolar sets of cruises, increasing by about 20% for the third. Closing mode detection functions are typically narrower than those for IO mode (average w_s about 20% less), but any relationship which that difference might have to a possible lower $g(0)$ value for closing mode is taken into account through the closing/IO mode calibration factor R.

[21] The phenomenon of a sufficiently high level of density-dependence coming into play as a population approaches (and possibly also overshoots) its carrying capacity level, that recruitment in absolute terms falls as the mature component of the population increases further.

Point estimates of abundance for Area IV in Table 3, which decrease notably although not significantly (at the 5% level) between the 1978/79 and 1988/89 cruises, are compatible with the results from this model. However, the results of this paper point to a decrease of minke abundance in a combination of the other Antarctic Areas that occurs a little later - roughly speaking between the mid-1980s and mid-1990s. Further modelling studies would be needed to ascertain to what extent this later response might be explained by the differing commercial catch histories in those Areas and slight temporal shifts in patterns of change in carrying capacity.

These changes in recruitment in absolute terms are likely associated with changes in *per capita* recruitment, which must in turn be linked to changes in the value of some vital parameter, for example a modified pregnancy rate or age at first parturition[23]. Detection of such changes in sampled animals at the times and in the directions predicted by population model fits to catch-at-age data would add weight to conclusions about overall trends in minke whale abundance based upon the IDCR-SOWER survey data alone.

Priority areas for future research

In terms of baseline methodology, the most important aspect highlighted by these analyses is that the regression method used from the 1995/96 cruise onwards for school size estimation makes larger differences to the abundance estimates from some earlier cruises than might have been anticipated. More attention to the most appropriate method for mean school size estimation is clearly warranted. Furthermore, consideration would be desirable as to whether the algorithm adopted here to determine the level of pooling used for effective search half-width and mean school size estimation could be improved.

The potential to quantify a number of factors that bias abundance estimates (generally downwards) also merits attention. The more important of these raise the following issues:

(1) how best to deal with ‘like minke’ sightings, particularly since the proportions recorded have changed over time;
(2) how best to evaluate a closing/IO mode calibration factor R for combining abundance estimates from these two survey modes, given possible confounding effects introduced by the ‘like minke’ classification changes over time, as indicated above; adjustments might also be made for the probable dependence of R on whale density, if the data prove sufficient to allow this to be estimated with adequate precision;
(3) the need to investigate the potential for using duplicate sighting information from IO mode to provide estimates for $g(0)$; and
(4) estimating the proportion of the population not covered by the survey because of animals within the pack-ice and north of 60°S.

Finally, methods are needed to improve upon the simple extrapolation approach that was used here to compare abundance estimates from surveys of the same region with different spatial coverages.

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[22] The model requires an increase in minke whale carrying capacity over the middle decades of the 20th century to explain the initial increasing trend in recruitment. This is a plausible consequence of the decrease of populations of other large baleen whales during those middle decades as a result of over-exploitation. A subsequent reduction in this carrying capacity could arise from some combination of the effects of the partial recovery of the larger Antarctic baleen whales under protection, increases in other competing predators (such as crabeater seals), and changes in the physical environment (IWC, 1997a).

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Appendix 1

SUMMARY OF HISTORICAL CHANGES TO THE ‘STANDARD METHODOLOGY’

Effective search half-widths for schools (w_s)

1979: Negative exponential model, but over time adjustments for truncation and smearing were introduced.

1986: Radial distances used to calculate perpendicular distance from the trackline based upon observer estimates of these distances at first sighting, in place of a vessel speed multiplied by closure time basis (Butterworth, 1986).

1987: Hazard rate model with truncation at a perpendicular distance of 1.5 n.miles and smearing as per method II of Buckland and Anganuzzi (1988) (adopted: IWC, 1988, p.77).

Mean school size estimation ($\bar{s}$)

1979: Weighted linear regression of $\bar{s}$ against perpendicular distance y out to $y = 1.0$ n.miles (Best and Butterworth, 1980), to obtain an estimate of the intercept at $y = 0$; if the regression slope was negative, the actual average school size out to $y = 1.0$ n.miles was used.

1987: Estimated by the ratio of whale density estimates to school density estimates, where the former were computed by fitting the $f(y)$ model to school sightings, with each sighting replicated by the estimated number of whales in the school (Butterworth, 1988) (adopted: IWC, 1988, p.77).

1997: Regression of $\bar{s}$ against estimated f(y), provided statistically significant at the 15% level, otherwise actual average school size out to $y = 1.5$ n.miles (Burt and Borchers, 1997) (re *de facto* adoption see IWC, 1994a, p.105; IWC, 1997b, p.130; IWC, 1998, p.144 and evaluation by Borchers, 1994).

Stratification considerations

1979: Contouring of daily density estimates to obtain abundance estimates (e.g. Best and Butterworth, 1980).

1983: Stratum densities estimated from effort-weighted averages of sighting rates from transects treated as independent (1984, pp.80, 92-3).

1983/84: Cruise track design modified to facilitate stratum-based abundance estimation (see Fig. 1).

1987: Definitions of strata finalised (IWC, 1988, pp.77-8).

1992: Stratification and related options for abundance estimation for RMP adopted (IWC, 1993, p.106).

1992/93: Cruise track design modified to link with RMP *Small Area* specifications (see footnote 7).

Satellite tracking of minke whales (*Balaenoptera acutorostrata*) off the coast of northern Norway

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ABSTRACT

Two minke whales were tagged with satellite-linked radio transmitters off the coast of northern Norway in order to obtain data on daily locations, movements and swimming speed. One whale was tagged in September 1994, south of Lofoten at the entrance to the Vestfjorden, and one whale was tagged in August 1999 just north of Vesterålen. The whale tagged in 1994 was successfully tracked for 31 days (located 1.5 times/day on average). The whale tagged in 1999 was successfully tracked for 19 days (located 3.0 times/day on average), although the first locations were not obtained until 18 days after the instrumentation. The whale tagged in 1994 travelled between two apparent feeding areas on the west coast of northern Norway: one in the mouth of Vestfjorden and the other along the continental slope north of Vesterålen. The whale tagged in 1999 moved to an area inside Vestfjorden and remained there until early September, after which it began a southward movement out of Vestfjorden offshore to the edge of the continental shelf. Both whales were presumably feeding on herring (*Clupea harengus*), which is particularly abundant in these waters at this time of year. The two minke whales travelled 78 and 79 km/day when distances between all positions were used, and 66 and 53 km/day when the daily average positions (all qualities) were used. Both calculations illustrate that minke whales can move considerable distances on a daily basis.

KEYWORDS: MINKE WHALE; SATELLITE TRACKING; TELEMETRY; MOVEMENTS

INTRODUCTION

Information on the stock identity and seasonal segregation of North Atlantic minke whales (*Balaenoptera acutorostrata*) is fundamental to the development of sustainable harvest regimes. Observations and catch data show that minke whales are widely dispersed in the northeastern Atlantic during the summer (Horwood, 1990; Øien, 1990) but virtually nothing is known about the movements, site fidelity and dispersal patterns of minke whales in this area. Swimming speeds (vertical and horizontal speeds combined) have been measured directly for four minke whales for up to 24hrs (Folkow and Blix, 1991) although no information exists on daily movement rates.

Satellite telemetry is a powerful tool for collecting data on migration, winter distribution and key behavioural and physiological parameters for several cetacean species (e.g. Dietz *et al.*, 2001; Heide-Jørgensen *et al.*, 2001a). The insights obtained from free-ranging and undisturbed animals are substantial. The purpose of this study was to examine the feasibility of satellite tracking minke whales and to determine the seasonal movement patterns along the coast of northern Norway.

MATERIALS AND METHODS

Minke whale tagged in 1994

In September 1994, a minke whale was tagged off northern Norway using a 68kg *Panzer* crossbow (*Barnett Inc.*, Wolverhampton, UK). The tag was launched from the vessel M/S *Jan Bjørn*, a 15m whaler. The satellite transmitter was a *Telonics* ST-10 RF-unit (*Telonics*, Arizona, USA) connected to a microprocessor and cast in epoxy by *Wildlife Computers* (Redmond, Washington, USA). The transmitter (4.1 × 11.2 × 2.2cm, 230g) was programmed to transmit for two 5hr periods per day (03:00-08:00 and 15:00-20:00 GMT) with a repetition interval of 40 seconds. The transmitter, attached to an anchor via a stainless steel wire, was equipped with a saltwater switch ensuring that transmissions only took place when the tag was above the surface. The anchor consisted of a 15cm long stainless steel needle (Ø = 0.35cm) with thin stainless steel barbs attached near the tip. The needle and barbs were rinsed in ethyl alcohol and smeared with antibiotic cream (basimycin) before deployment, in order to reduce the risk of infection. The anchor was designed to penetrate the whale’s blubber layer and fasten within the underlying muscle layer. A polycarbonate stop ring (Ø = 4.0cm) prevented the anchor from penetrating deeper than 15cm into the whale. The crossbow arrow carrying the transmitter was attached to a monofilament nylon line, which allowed for easy retrieval if the transmitter missed the whale.

Minke whale tagged in 1999

In August 1999, a minke whale was tagged from the vessel K/V *Thorsteinson* with the Air Rocket Transmitter System (ARTS, specifically developed for remote deployment of satellite tags on baleen whales). The ARTS consists of a modified gun-shaped pneumatic line thrower that launches a rocket, containing the transmitter, which is equipped with tail feathers (Heide-Jørgensen *et al.*, 2001b). The rocket is designed to float, in case of misses. The ARTS was initially calibrated to a shooting distance of 20m at a pressure of 20 bar, using rockets of similar weight and length as those containing satellite transmitters. Test shooting showed that the ARTS was accurate to a distance of 50m. The transmitter was deployed on the whale from a distance of 15m, using a pressure of 15 bar. The cylindrical transmitter (22 × 2.5cm, 200g) was a modified *Telonics* ST-15 RF-unit with a 3cm steel dart with sharp edge. It was equipped with a stop plate

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(Ø = 3.8cm) that only allowed half of the transmitter to be buried into the blubber. The transmitter had a repetition interval of 45s, was not duty cycled, but was equipped with a saltwater switch, which only allowed transmissions when the whale was at the surface.

Analyses

Data on positions of the whales were retrieved from the Service Argos Data and Collection System. Service Argos operates with different location quality classes (LC) with decreasing precision in the following order: 3, 2, 1, 0, A and B. The LC 0, A and B are based on less than three successive uplinks and have no estimated location accuracy; LC 1, 2 and 3 have a presumed accuracy of < 1km (Fancy *et al.*, 1988; CLS/Service Argos, 1989). To reduce the noise introduced by the low-precision of the poor quality positions, a daily mean position (using all location qualities) was calculated to plot the movements of the whales in ESRI ArcView® and to calculate horizontal swimming speed.

RESULTS

Minke whale tagged in 1994

The minke whale tagged south of Lofoten (67°38'N, 13°21'E) on 5 September 1994 had an estimated body mass of about four tonnes and length of 7m. The tag penetrated the skin near the dorsal midline of the whale, about 1.5m in front of the dorsal fin. This position ensured that the antenna was exposed for approximately two seconds during each surfacing, allowing for successful transmissions. The tag was active for 31 days, during which 234 transmissions were received (on average 7.5 successful uplinks per day). This resulted in a total of 46 locations, or 1.5 locations per day. Locations were obtained on 71% of the days. Out of six possible location classes (A, B, 0, 1, 2 and 3), 0 was the best quality obtained. Most locations (68%) were of B quality (Table 1).

Table 1

The frequency distribution of locations belonging to four location classes (LC), as obtained from two satellite-linked radio transmitters that were deployed on minke whales in 1994 and 1999.

LC	1994 Percentage distribution *n*=46	1999 Percentage distribution *n*=58
0	4	0
A	28	17
B	68	83

The minke whale stayed in the outer Vestfjorden area for 10 days, later moving to the continental slope, and then moving 320km northeast in 52hrs. The whale then stayed off the coast of Vesterålen for about nine days, moving back and forth, along the continental slope. On September 27, the whale swam back to the Lofoten area, and stayed in the mouth of Vestfjorden for eight days until contact was lost on 5 October.

During the tracking period (5 September-5 October) the whale travelled 2,336km (straight line distance between all locations), corresponding to a daily average of 78km (SD = 48km, range 6.8-277km), or 3.2km/hr. As transmissions were not received at regular intervals, an average daily position was calculated for each day based on all transmissions received within that 24hr period. The 23 average daily positions gave a minimum travel distance of 1,450km in total and an average horizontal speed of 66km/day (SD = 64km, range 19.8-277.1) or 2.7km/hr.

Minke whale tagged in 1999

On 2 August 1999, a tag was deployed on a small minke whale, with an estimated body length of 5m, just north of Vesterålen (69°31'N, 15°52'E). The tag penetrated the skin in front of the dorsal fin, on the left dorso-lateral side of the whale. The rocket that accompanied the transmitter when the tag was launched did not instantly separate from the transmitter. No transmissions were received for 16 days and no locations were obtained until 18 days after instrumentation. The delayed release of the rocket may explain why transmissions were not initially received from the whale. A total of 407 transmissions, starting on day 16 after tagging, were received over the course of 19 days with transmissions. This resulted in a total of 58 locations, or 3.0 locations per day. Locations were obtained on 79% of the days. Out of six possible location classes, LC A was the best quality obtained. Most locations (83%) were of B quality (Table 1).

Eighteen days after tagging off the north coast of Vesterålen the whale had moved inshore to Vestfjorden, where it made localised movements in coastal waters until the end of the month (Fig. 1). In early September it started a southward movement along the coast, first inshore and later offshore out to the continental shelf edge where contact was lost on 8 September.

During the tracking period (20 August-8 September), the whale apparently travelled 1,530km at an average horizontal speed of 79km/day (SD = 22, range 2.4-87.3km) or 3.3km/hr. Sixteen average daily positions were calculated for days where locations were received from this whale. Using these data, the whale was found to have travelled at least 739km in total, at an average horizontal speed of 53km/day (SD = 27km, range 13.8-89.8) or 2.2km/hr.

DISCUSSION

The two minke whales stayed in the Vestfjorden and Vesterålen areas for more than a month in late summer and early autumn, indicating a preference for this area. The whale that was instrumented in August 1999 first utilised an inshore habitat in the Vestfjorden area and later moved south off the continental shelf. This pattern differs from that of the minke whale instrumented in September 1994, which first moved north to the Vesterålen area, and then returned south to the same area where it was tagged. This whale was still inshore in early October. Nevertheless, both whales explored habitats in the Vesterålen and Vestfjorden areas in August and September.

Minke whales that are found in Vestfjorden in early September could be either animals migrating south from feeding grounds in the far north or whales that are part of an aggregation that spends the summer in the Vestfjorden and Vesterålen areas (cf. Jonsgård, 1951). The northward trip of the minke whale in 1994 from the Vestfjorden area to the continental slope and back to Vestfjorden shows that whales are not necessarily limited to Vestfjorden - movements of their prey probably dictate their local occurrence. Since the whales have a preference for Vestfjorden and Vesterålen, they are probably feeding in these areas.

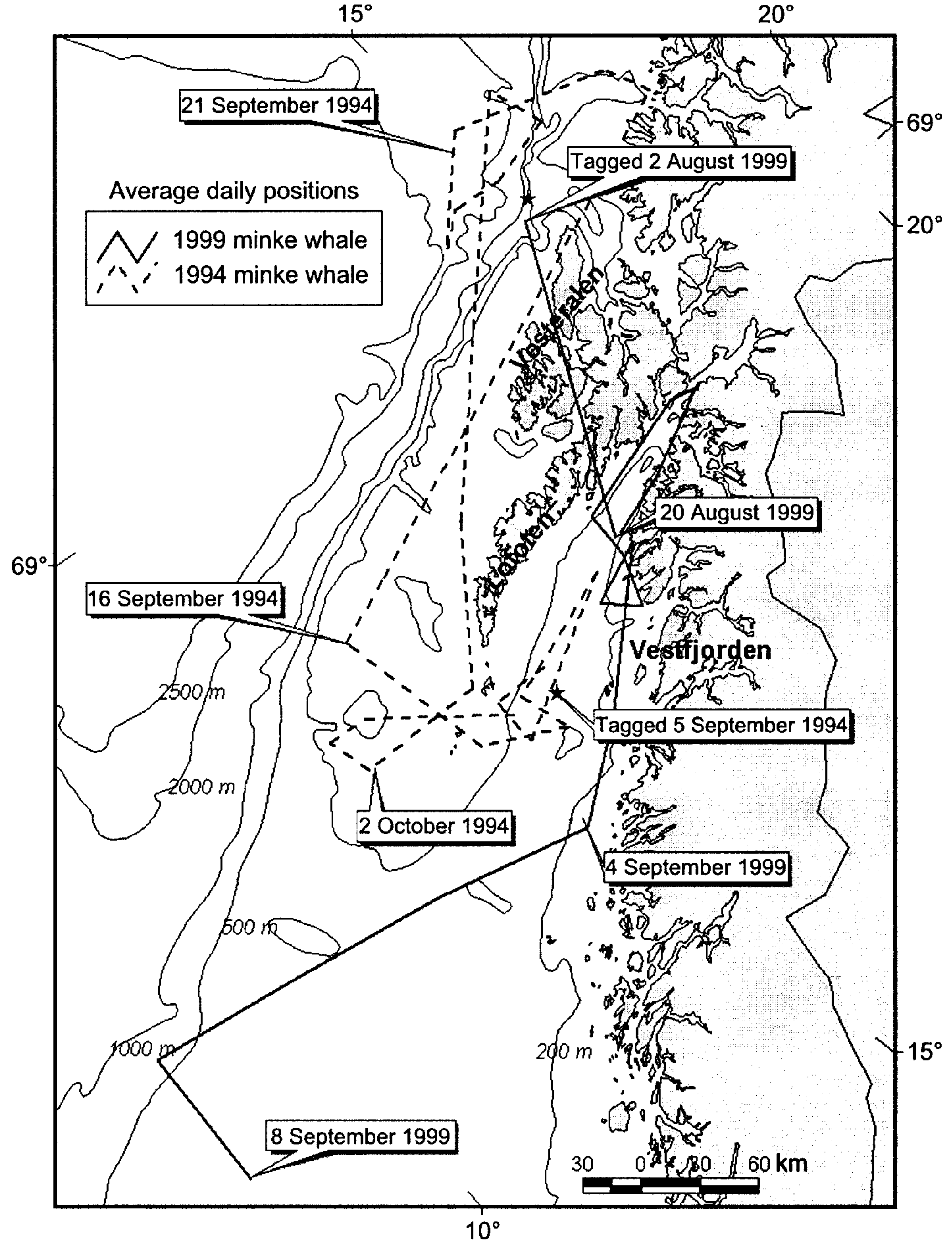

Fig. 1. Movements of two minke whales that were tagged with satellite-linked radio transmitters in 1994 and 1999. Dashed line: whale tagged on 5 September 1994. Solid line: whale tagged on 2 August 1994. Both whales were tagged off the coast of northern Norway, and were tracked for 31 days and 38 days, respectively.

The assumption that the Vestfjorden and Vesterålen areas are important feeding grounds for minke whales in August-September is supported by observations on the distribution of whales relative to herring (*Clupea harengus*), an important prey item of minke whales (e.g. Nordøy and Blix, 1992; Haug *et al.*, 1996). Lydersen *et al.* (1991) found that stomachs of 15 minke whales collected between 3 and 18 August 1988 in the Lofoten and Vesterålen areas all contained herring, which constituted an average of 92% of the total prey volume. Ten out of 15 stomachs analysed in that study were 100% full of herring.

The spawning stock of herring is reported to migrate east in early September from summer feeding grounds in the Norwegian Sea to the coast of Lofoten/Vesterålen, to spend the winter in the Vestfjorden-area (Anon., 1993; 1994). In September 1994, between 7 and 20 minke whales were observed on a daily basis in this area (Nordøy, pers. obs.). The presence of large shoals of herring at depths of 30-100m (concurrent with minke whale sightings) was confirmed by use of an echo sounder installed in the vessel (Folkow and Nordøy, pers. obs.). This same area is considered to be productive by the commercial herring fishery, which conducted intensive herring fishing in early September in 1994. Between September and December 1993, this fishery landed about 200,000 tonnes representing most of the 1993 quota of Norwegian spring-spawning herring in this region (Anon., 1994).

In 1994, the minke whale was in the Lofoten, Vesterålen and Vestfjorden areas at the peak abundance of herring. In 1999, the herring came close to the coast west of Lofoten in the last week of August and moved into Vestfjorden in the first two weeks of September (Institute of Marine Research *in litt.*). The herring catches peaked in Vestfjorden in mid-October but remained high until mid-December. However, in 1999 the minke whale passed through the area earlier in the season (mid-August) before the high abundance of herring in September. The minke whales tagged in 1994 and 1999 were in the herring concentration areas approximately one month apart. Although the temporal shift may be dictated by annual variations in fish occurrence, this is not supported by the information on herring abundance.

The horizontal speeds calculated for the two whales were fairly consistent for both distances between all positions and distances between average daily positions. Speeds calculated using all quality positions might be biased by the unknown error in the poor quality positions. Calculations based on an average daily position are negatively biased because this method only captures the large-scale movement of the whales. In any case, both the calculated speeds and the distances travelled by the whales show that minke whales undertake considerable movements over short time periods, and that their horizontal swimming speeds appear to be well within the most cost-effective range determined by Blix and Folkow (1995).

In conclusion, this study demonstrates that satellite-linked radio transmitters are useful tools for tracking the movements of individual minke whales. The use of this technique to reveal wintering locations of these mammals requires improvement in tag longevity.

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A note on common minke whale (*Balaenoptera acutorostrata*) diets in the Norwegian Sea and the North Sea

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ABSTRACT

Visual observations and quantitative samples of forestomach contents were made of minke whales caught in the Norwegian Sea (15 visual observations in 1999, 8 in 2000 and 1 stomach sample) and North Sea (15 visual observations and 7 stomach samples, all from 1999). Prey species were identified, and from the forestomach samples, each prey's relative contribution by weight to the diet was calculated. In the Norwegian Sea, the diet was dominated by Norwegian spring-spawning herring (100%). This was consistent with the large and dominant abundance of herring in the area. Observations and forestomach samples from the North Sea indicated a more varied diet, with sandeel (*Ammodytes spp.*) contributing 86.7% to the diet by weight, followed by mackerel (9.3%), whiting (2.4%), herring (1.1%) and Norway pout (0.5%). Haddock was observed in one stomach, but was not found in any of the samples. Sandeel occurred in all observed and four of the sampled stomachs. The domination of pelagic species in the diet strongly indicates pelagic feeding behaviour in both areas.

KEYWORDS: COMMON MINKE WHALE; ECOSYSTEM; FEEDING GROUNDS; FISH; FOOD/PREY

INTRODUCTION

The common minke whale (*Balaenoptera acutorostrata*) is both in numbers (Schweder *et al.*, 1997) and biomass one of the largest marine mammal populations in the ecosystems of the eastern North Atlantic. In the 19th century, minke whales in Norwegian waters were described as herring predators (Sars, 1897) and ichthyophagous (Greig, 1894). Later studies by Jonsgård (1951) and Haug *et al.* (1995) revealed that North Atlantic minke whales were rather euryphagous.

There have been few formal studies of the diet of this species in the North Atlantic. Larsen and Kapel (1981) made *ad hoc* observations of the regurgitated stomach contents of seven whales caught west of Greenland in 1979. Only two prey items were observed: krill in two stomachs and sandeel (*Ammodytes* spp.) in five stomachs. When observing at whaling stations on the Canadian east coast in 1948 and 1951-61, Sergeant (1963) recorded seven prey items in the stomach contents. The dominant prey was capelin (*Mallotus villosus*) occurring in 85% of stomachs sampled. Cod (*Gadus morhua*), herring (*Clupea harengus*), salmon (*Salmo salar*), and several species including squids, euphausiids and copepods constituted the rest.

The only quantitative analyses of diet in the North Atlantic are available from the Barents Sea and along the coast of Northern Norway (Haug *et al.*, 1995; 1996; Lindstrøm *et al.*, 1999). These studies showed large variations in relation to area, season and year. Along the coast of Norway, fish predominated, with herring being the major component. Gadoid fish predominated in the central Barents Sea. In the areas further to the north (around Bear Island and Spitzbergen), krill (*Thysanoessa* spp.) and capelin characterised the diet (Haug *et al.*, 1996). This study also indicated a preference for the pelagic fish species capelin and herring over other prey items.

In recent years, emphasis has been given to an ecosystem approach to fisheries management. However, *inter alia* this requires considerable knowledge of the ecological significance of large predator populations. Both total consumption and the consumption of the individual prey populations are therefore of interest. Based on recent information on minke whale abundance (Schweder *et al.*, 1997) and diet, Folkow *et al.* (2000) presented an estimate of the total annual prey consumption of minke whales in the northeast Atlantic waters. The consumption by prey species was presented for the Barents Sea and off the coast of North Norway. However, they had no information on prey species for the North Sea.

This paper presents information on the diet of minke whales in the North Sea and the Norwegian Sea, two important feeding areas for North Atlantic minke whales for which information is lacking. The observed diets are discussed in light of the differences between the North Sea and Norwegian Sea ecosystems.

MATERIALS AND METHODS

The stomach contents of minke whales were recorded or sampled by personnel from the Institute of Marine Research (Bergen) onboard commercial whale catchers in the central North Sea and Norwegian Sea in June and July of 1999 and 2000. Catch positions are shown in Fig 1. As the study was based on a commercial operation, the sampled animals may not be representative of animals in the broad areas of the North and Norwegian Seas.

Stomach contents from 46 whales were examined, 22 from the North Sea and 24 from the Norwegian Sea. Stomach contents of 38 whales (15 North Sea, 23 Norwegian Sea) were determined by visual observation of ruptured forestomachs or from regurgitated stomach content, whilst for eight whales (7 North Sea, 1 Norwegian Sea), the contents of the forestomach were sampled and total volume measured. In the sampled stomachs, forestomach contents were separated from stomach fluids using a 1mm sieve. A 5 litre sample of the remaining content was frozen at –23 °C and later analysed at the Institute of Marine Research. From this sub-sample, prey was identified to genera or species based on morphology of whole prey, or from otoliths and bones of digested prey. Each prey group was weighed, and when possible, individuals were counted and their length

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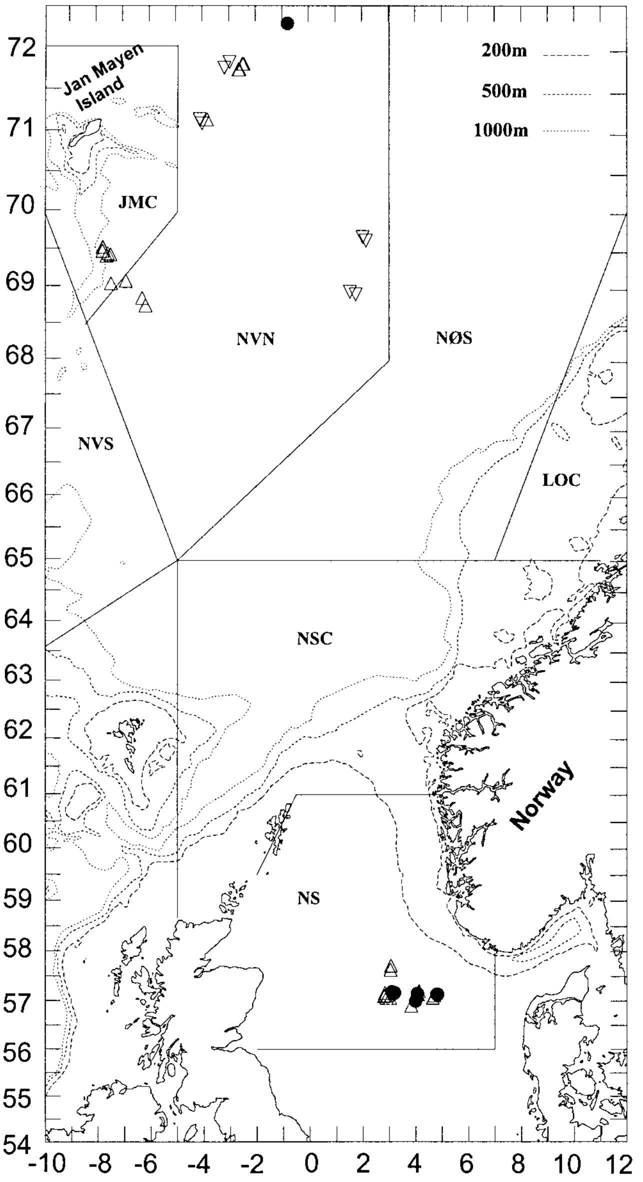

Fig. 1. Survey blocks for which individual abundance estimates of minke whales had been estimated in 1995 with catch positions of investigated minke whales from the Norwegian Sea and North Sea. Positions where visual observations of stomach content were made are marked by △ for the whales sampled in 1999 ($n = 30$) and ▽ for whales sampled in 2000 ($n = 8$). Positions where samples of the stomach content was taken is marked by ● ($n = 8$).

measured. Prey were allocated to age groups either by estimating the age from the otoliths, e.g. Norway pout (*Trisopterus esmarkii*), or by using ICES length-at-age tables (ICES, 1999) to calculate the age, e.g. for herring, sandeel, whiting (*Merlangius merlangus*) and mackerel (*Scomber scombrus*). For each prey species the relative and absolute contribution to diet by weight was estimated. In addition the weight of the total stomach content was calculated by multiplying the weight of the 5 litre sample with the measured volume of the stomach content.

RESULTS

Norwegian Sea

The only prey observed in the stomach contents of the 24 minke whales caught in the Norwegian Sea in 1999 and 2000 was adult (> 29cm) herring (Table 1); herring length in 2000 ranged between 34 and 40cm. These observations were supported by the findings in the single sampled whale where herring was the only species recorded in the analysed stomach sample (Table 2). The total weight of stomach contents of the sampled whale was 39.9kg.

Table 1

Area, date, catch position and visually observed stomach content of minke whales (*Balaenoptera acutorostrata*) caught in the Norwegian Sea (1999 and 2000) and North Sea (1999).

Area	Date	Catch position	Stomach content
Norwegian Sea 1999	30 May	68°46’N, 6°12’W	Herring (adult)
	31 May	68°52’N, 6°20’W	Herring (adult)
	01 June	69°06’N, 6°57’W	Herring (adult)
	01 June	69°04’N, 7°31’W	Herring (adult)
	04 June	69°27’N, 7°32’W	Herring (adult)
	04 June	69°28’N, 7°38’W	Herring (adult)
	04 June	69°26’N, 7°41’W	Herring (adult)
	05 June	69°33’N, 7°50’W	Herring (adult)
	05 June	69°30’N, 7°58’W	Herring (adult)
	05 June	69°33’N, 7°49’W	Herring (adult)
	15 June	71°10’N, 3°53’W	Herring (adult)
	19 June	71°46’N, 2°40’W	Herring (adult)
	20 June	71°46’N, 2°42’W	Herring (adult)
	20 June	71°50’N, 2°33’W	Herring (adult)
	20 June	71°50’N, 2°30’W	Herring (adult)
Norwegian Sea 2000	09 June	68°55’N, 1°44’E	Herring (34-40cm)
	09 June	68°57’N, 1°31’E	Herring (34-40cm)
	12 June	69°41’N, 2°00’E	Herring (34-40cm)
	12 June	69°38’N, 2°07’E	Herring (34-40cm)
	17 June	71°10’N, 4°10’W	Herring (34-40cm)
	17 June	71°07’N, 4°04’E	Herring (34-40cm)
	18 June	71°47’N, 3°14’E	Herring (34-40cm)
	18 June	71°51’N, 3°02’W	Herring (34-40cm)
North Sea 1999	17 June	57°38’N, 3°03’E	Sand eel
	12 June	57°43’N, 3°04’E	Sand eel
	13 June	56°54’N, 3°50’E	Sand eel, haddock, mackerel
	14 June	57°10’N, 2°50’E	Sand eel
	15 June	57°07’N, 2°56’E	Sand eel
	15 June	57°06’N, 2°48’E	Sand eel
	16 June	57°07’N, 2°51’E	Sand eel, herring
	18 June	57°04’N, 3°02’E	Sand eel
	18 June	57°04’N, 2°54’E	Sand eel
	08 July	57°07’N, 4°43’E	Sand eel
	08 July	57°04’N, 4°39’E	Sand eel
	08 July	57°12’N, 4°08’E	Sand eel
	09 July	57°08’N, 4°06’E	Sand eel
	10 July	57°08’N, 4°06’E	Sand eel
	10 July	57°09’N, 4°03’E	Sand eel

North Sea

The visual observations made in the North Sea in 1999 indicated a more mixed diet in this area, dominated by sandeel. Sandeel was recorded from all 15 stomachs observed. Additional prey was observed in two of these: herring in one stomach, and haddock (*Melanogrammus aeglefinus)* and mackerel in the other (Table 1). In the sampled stomachs, sandeel was by far the most common prey species, constituting 86.7% by weight (Table 2, Fig. 2). Sandeel, mackerel and herring comprised 97.1% of the total weight of stomach content by weight. Gadoid fish (whiting and Norway pout) constituted the rest (2.9%). None of the seven sampled stomachs were empty, but the total weight of the stomach contents (excluding liquid) varied from 1.7kg to 110.9kg. In all but one sampled stomach, only one prey species was found. This stomach contained a mix of sandeel (93.2% by weight) and herring (6.8%). The degree of

Table 2

Date, catch position and fore-stomach content of minke whales from the Norwegian Sea and North Sea in 1999. All weights are in kg.

					Composition of samples							
					Herring		Sand eel		Whiting		Norway pout	Mackerel
No.	Date	Position	Sample weight	Calc. total weight	Weight	No.	Weight	No.	Weight	No.	Weight	Weight
Norwegian Sea												
17	23 June	72°18'N, 0°51'W	4.156	39.9	4.156							
North Sea												
19	11 July	57°0'N, 4°0'E	4.856	64.1			4.856					
23	11 July	57°9'N, 4°4'E	3.715	54.2	0.25	10	3.456	1,728				
29	18 July	57°8'N, 5°50'E	0.071	110.9			0.071	50				
30	18 July	57°9'N, 4°48'E	3.363	71.3			3.363					
33	29 July	57°11'N, 3°6'E	4.046	8.1					4.046	14		
34	30 July	57°10'N, 3°12'E	2.124	1.7							1.77	
35	30 July	57°9'N, 3°10'E	3.886	31.9								3.886

Parasitic nematoda (*Anasakis spp.)* were found in stomach no. 23 and 34. These were separated from the rest of the content and their weight subtracted from the calculated weight of the stomach content.

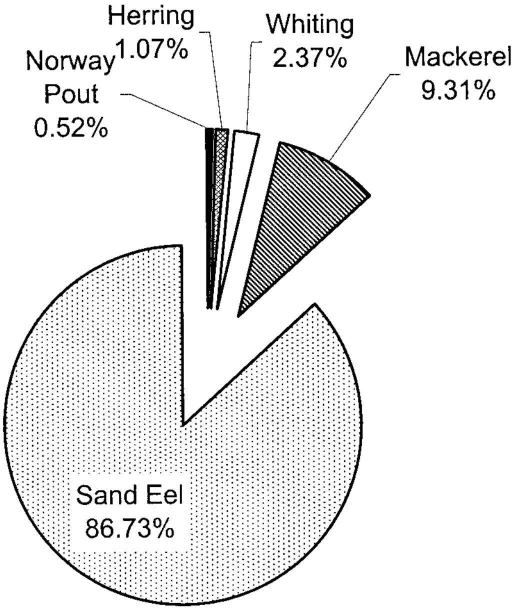

Fig. 2. Forestomach content compositions of North Sea minke whales ($n = 7$) presented as relative contribution by calculated weight.

digestion in the stomachs (and hence time since feeding) varied; only two stomachs (nos 23 and 29) had undigested prey (sandeel). Based on otoliths found and length measurements of whole prey, all sandeels were 0-1 years, the whiting were 3-4 years, the Norway pout 0-1 years and the mackerel over 3 years. The observed prey age distribution suggested that a large component of the minke whale diet in the central North Sea consisted of young fish. No herring otoliths or whole herring were found, and the age of this prey could therefore not be estimated.

DISCUSSION

The dietary data in this study are based on both quantitative stomach samples and *ad hoc* observations of stomach contents. As might be expected, more prey species were recorded from properly sampled stomachs. As such, the records from the sampled stomach contents are probably more reliable although the sample size is small.

The results indicate that herring was the only prey species for minke whales feeding in the western Norwegian Sea in June-July. This is the main feeding area of the Norwegian spring spawning herring stock, which was estimated at 6,400,000 tonnes in the actual area in 1999 (Holst *et al.*, 1999a) and somewhat less in 2000 (Holst *et al.*, 2000). The size of the herring observed and sampled from the whale stomachs was in agreement with the known size of herring in the area during June-July (Nøttestad *et al.*, 1999). This is further substantiated by age and length distributions from research trawl catches made by the Institute of Marine Research in the sampling area in May and August 1999 which found herring of the 1990, 1991 and 1992 year classes, measuring approximately 31-35cm (Holst *et al.*, 1999a).

By late July, the herring migrate to the east towards the Norwegian coast for the wintering areas in the Lofoten archipelago (Nøttestad *et al.*, 1999). At this time they probably become available as prey for the near-shore portion of the Northeastern Atlantic minke whale population prior to their southward migration in the autumn (Jonsgård, 1951).

During the 1970s and early 1980s, Norwegian spring spawning herring was effectively removed as an important minke whale prey in the western Norwegian Sea, following an almost total collapse of the herring stock in the late 1960s. This may have forced minke whales to feed on less preferred prey species, or caused profound changes in distribution of foraging minke whales. Apart from herring, blue whiting (*Micromesitius poutassou*) (Holst *et al.*, 1999a), lumpsucker (*Cyclopterus lumpus*) (Holst, 1993) and post-smolt salmon (Holst *et al.*, 1999b; Holm *et al.*, 2000) feed in these areas during summer. However, their biomass was probably many orders of magnitude less than the current herring biomass. In addition, blue whiting, being meso-pelagic (200-500m) are probably less available to minke whales than the schooling, pelagic herring, which is found from 0-450m depth in the Norwegian Sea during summer (Vilhjálmsson *et al.*, 1997). Therefore, it seems reasonable that the western Norwegian Sea feeding areas were sub-optimal during the 1970s and 1980s when compared with today.

In the North Sea, minke whales had a more a mixed diet, although sandeel dominated in both observed and sampled stomachs. Field observations made by on-board observers of daytime minke whale feeding behaviour in the area indicated feeding in sandeel schools close to the surface. Sandeels hide in the sediments during night and migrate to the surface during daytime to feed (Helfman, 1993). Mackerel, the second most frequently occurring prey species, has pelagic distribution close to the sea surface during summer (Iversen and Skagen, 1989). Whiting, the third most frequently occurring prey species, is known to feed on sandeels (Pedersen, 1999), and may have been caught by minke whales targeting sandeels. These findings support a hypothesis that pelagic foraging is important for minke whales in relatively shallow continental shelf waters. However, the finding of haddock in one stomach shows that demersal foraging does occur in North Sea minke whales. Both cod and haddock are described as demersal predators on sandeel (Adlerstein *et al.*, 1998).

Similar indications of a pelagic feeding behaviour in continental shelf waters have been found in other areas, e.g. the Barents Sea (Haug *et al.*, 1996). Fewer prey species were found in the diet in the present study than in the studies of the Barents Sea minke whales (Haug *et al.*, 1995; 1996), but the latter study covered a much larger geographic area and spanned four months, while the present study was more limited in geographic range and time. Neither euphausiids nor any other crustaceans were recorded in any of the stomach samples. This is in contrast to the Barents Sea where euphausiids have been shown to constitute up to 45% of the diet (Lindstrøm *et al.*, 1999). Euphausiids have also been shown to be the main constituent of the Antarctic minke whale (*Balaenoptera bonaerensis*) diet in the Antarctic (Ichii and Kato, 1991).

Given the commercial nature of the operations, the sampling locations were aggregated, particularly in the North Sea. Since the samples were taken from a limited area, they probably do not represent the diet for the entire North Sea minke whale feeding grounds. Haug *et al.* (1996) showed that the minke whale diet varies dramatically between areas and seasons in the Barents Sea. In the western Norwegian Sea, prey occurrence is less spatially variable suggesting less variability in minke whale diet between areas. It is possible that the diet observed from the Norwegian Sea samples is more likely to represent the diet of a wider part of the Norwegian Sea ecosystem. However, further samples from the waters north of Jan Mayen Island and north of the polar front may alter this impression.

Although the results presented here are only based on small sample sizes and thus may not be wholly representative of the summer diet of minke whales in the Norwegian and North Seas, they suggest interesting differences in the diet in the two areas. These differences probably reflect differences in the fish fauna of the two ecosystems rather than different minke whale prey preferences. The Norwegian Sea pelagic ecosystem is characterised by few but abundant species where herring is the dominant plankton feeding fish. The North Sea ecosystem comprises a fish community with less dominance by one or a few fish species and a more complex trophic structure.

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Biology and conservation of the franciscana (*Pontoporia blainvillei*) in the north of Rio de Janeiro State, Brazil

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ABSTRACT

This paper describes the interactions of the franciscana (*Pontoporia blainvillei*) with fisheries in the north of Rio de Janeiro State (21^{0}18'S-22^{0}25'S) and presents new information on its biology. A total of 181 dolphins were caught in gillnet fisheries in northern Rio de Janeiro from 1986-1999. The annual catch per unit effort (CPUE) values varied from 0.2-1.8 dolphins per gillnet fishing effort. Incidental captures were recorded throughout the year, usually less than 10 n.miles from shore, in depths less than 30m and in surface-set gillnets. There was no difference in the proportion of sexes (1 male:1.1 females). Males ranged from 66-130.0cm and 0-5 years and females from 74-147.5cm and 0-9 years. The predicted asymptotic length (using the Gompertz model) was 121.9cm for males and 145.6cm for females. Calving occurs throughout the year, with no seasonal pattern. Females attain sexual maturity at 3 years and 130.0cm in length and males at 2 years and 115.0cm. Individuals up to the age of three years represented 74% of the dolphins captured. Franciscana preferentially feed on the teleosts *Stellifer* sp., *Anchoa filifera*, *Pellona harroweri* and *Isopisthus parvipinnis*, measuring up to 10cm of length, and on the cephalopods *Loligo sanpaulensis* and *L. plei*. No internal parasites were observed. The barnacle *Xenobalanus globicipitis* was recorded on only one individual. Sightings were recorded in all seasons and 90% of them were obtained up to 5 n.miles from shore, in waters up to 15m deep. Around 70% of groups sighted consisted of up to five dolphins. Estimates of the population size and continuous gillnet fleet monitoring are required to conserve franciscana in the northern limit of its distribution range. The differences in the somatic, reproductive and genetic patterns of franciscana represent important aspects that may be used as evidence to best define their stocks. These variations may reflect the reduction of gene flow between populations, the allocation of resources between growth and reproduction and/or the influence of environmental features, such as water temperature and food availability.

KEYWORDS: FRANCISCANA; BIOLOGY; CONSERVATION; SOUTH ATLANTIC; BRAZIL

INTRODUCTION

The franciscana, *Pontoporia blainvillei* (Gervais and D'Orbigny, 1844), is restricted to the coastal Atlantic waters of South America from Itaúnas (~18°S), southeastern Brazil to Nuevo Gulf (~42°S), Argentina (Siciliano, 1994; Crespo *et al.*, 1998). The preferred habitat of the species is the upper continental shelf, within 30 n.miles from the coastline or depths of up to 30m (Praderi *et al.*, 1989).

Stock identity

Pinedo (1991) proposed at least two different forms of franciscana based on osteological differences: one found to the north (smaller animals) and the other to the south (larger animals) of Santa Catarina State (~29°S). Ramos *et al.* (2000a) presented data on age and growth of individuals from Rio de Janeiro State (~22°S) and found asymptotic lengths smaller than those found by Kasuya and Brownell (1979) for franciscanas from Uruguay (~34°S). This corroborates the study of Pinedo (1991) regarding the existence of at least two different phenotypic forms. Further, Ramos *et al.* (2000b) presented data on growth of franciscana collected in São Paulo State (~24°S) and found that they were smaller than individuals from Rio de Janeiro State (~22°S). Thus the existing morpholgical data support the existence of more than two stocks.

Secchi *et al.* (1998) analysed the mtDNA from 10 franciscanas of each of the geographic forms proposed by Pinedo (1991). Samples from Rio de Janeiro and Rio Grande do Sul States (~33°S) provided genetic evidence for at least two genetic populations. Recent studies on mtDNA analyses for franciscanas from Uruguay and Argentina were conducted by Lázaro and Lessa (2000) and Hamilton *et al.* (2000). These studies made comparisons with the results published by Secchi *et al.* (1998) and suggested the existence of one genetic population involving dolphins from Rio Grande do Sul State, Uruguay and Argentina. No haplotypes from these locations were shared with dolphins from Rio de Janeiro State, corroborating the hypothesis of at least two genetically distinct populations of franciscana. In addition, Zanelatto and Valsecchi (2000) presented preliminary results on the analysis of the mtDNA obtained from franciscanas collected in Paraná State (~25°S), an intermediate area between Rio Grande do Sul and Rio de Janeiro States. These results were also compared with those published by Secchi *et al.* (1998) and suggest that individuals from Paraná State are more similar to those from Rio Grande do Sul than to those from Rio de Janeiro State.

Fishery interactions

The franciscana has been affected by fisheries along its distributional range (e.g. Praderi *et al.*, 1989; Corcuera *et al.*, 1994; Pinedo, 1994; Siciliano, 1994; Secchi *et al.*, 1997). The assessment of the coastal fisheries impacts on franciscana populations and knowledge of its life history are essential for conservation and management (IWC, 1994).

The objective of this paper is to describe the interactions of the franciscana with fisheries and present new information on its biology in northern Rio de Janeiro, Brazil.

MATERIALS AND METHODS

Study area

The State of Rio de Janeiro has the third longest coastline (636km) in Brazil and is the third largest fish producer (Di Beneditto *et al.*, 1998). The geographic limits to its northern coast are Barra do Itabapoana (21°18'S) and Macaé (22°25'S) and the Paraíba do Sul River (the major river run off of Rio de Janeiro) is located in this area (Muehe and Valentini, 1998). The area offshore northern Rio de Janeiro is known as Campos Basin (Fig. 1), where the shelf break is located from 40-60 n.miles from the coastline (Petrobras, 1993).

Gillnets are the only fishing gear responsible for incidental mortality of small cetaceans in northern Rio de Janeiro (Di Beneditto *et al.*, 1998) and Atafona (21°35'S) is the most representative harbour in terms of gillnet fishing effort.

Interactions with fisheries

Fishing effort

Fishing effort was calculated through monthly interviews with the master of each gillnet boat based in Atafona village. Information requested included: (1) gillnet dimensions; and (2) days of active fishing operations.

The gillnet fishing effort presented by Di Beneditto *et al.* (1998) for the same region and the effort calculated in this study were used to calculate annual catch per unit effort (CPUE) values for franciscanas in northern Rio de Janeiro.

Bycatches

Information on franciscana interactions with fisheries was collected through weekly interviews with fishermen on board each gillnet boat based in Atafona village. The following information was targeted when collecting data on franciscana mortality: (1) mortality area (distance from the coastline and depth); (2) gillnet position in the sea; (3) seasonality of occurrence; and (4) utilisation of the incidentally captured dolphins. The seasons were grouped into spring-summer (October to March) and autumn-winter (April to September) with high and low temperatures and rain, respectively.

Biological information

Growth and reproductive parameters of the franciscana in northern Rio de Janeiro were initially analysed by Ramos *et al.* (2000a) and they have been revised and updated in the present study. The total sample ($n = 117$) consisted of the 93 specimens analysed previously by Ramos *et al.* (2000a) between 1989 and 1998, 20 specimens collected between 1986 and 1988 (Museum of the Universidade de São Paulo – MUZUSP) and 4 specimens collected recently by the authors. Methodology followed that in Ramos *et al.* (2000a).

Length

The body length of all individuals, including foetuses, was measured along the longitudinal axis of the body from the tip of the upper jaw to the notch of the flukes (Norris, 1961).

Age

Age was estimated by counting the number of growth layers groups (GLGs - IWC, 1980) in the dentine and cementum. The previously described franciscana GLG pattern (Pinedo and Hohn, 2000; Ramos *et al.*, 2000a) was adopted, i.e. one complete dentinal GLG comprising one narrow, unstained layer and one stained broad layer; a fine darker layer demarcated the unstained layer of subsequent GLGs. In the cementum, one complete GLG comprised one narrow stained layer and one wide weakly stained layer. The method of obtaining decalcified thin and stained sections of the teeth followed the recommendations of Hohn *et al.* (1989) and IWC (1980). Foetal age was extrapolated through a combination of length at birth of 71cm, gestation period of 10.5 months and prenatal growth rate of 0.25cm/day

Growth

Growth was determined by fitting a non-linear Gompertz model to length-at-age data (Zullinger *et al.*, 1984) using *Curve Expert* 1.3 for Windows.

Maturity

Females with at least one corpus on the external surface of the ovary, pregnant (judged by the presence of foetus) or lactating (judged by the presence of milk in the mammary glands) were considered sexually mature. Males with sperm in the epididymis were considered sexually active (although see below). Individuals showing all epiphyses fused to vertebra were considered physically mature (Perrin and Reilly, 1984; Pinedo, 1995).

Feeding

Stomach contents of 89 franciscanas were analysed in order to investigate feeding habits. Undigested prey were measured and weighed. Teleost otoliths and cephalopods beaks were used to identify, quantify and estimate the length and weight of the prey species. Crustaceans were quantified and identified by the rostrum or telson and it was not possible to estimate their length and weight. The Index of Relative Importance (IRI; Pinkas *et al.*, 1971) was calculated to

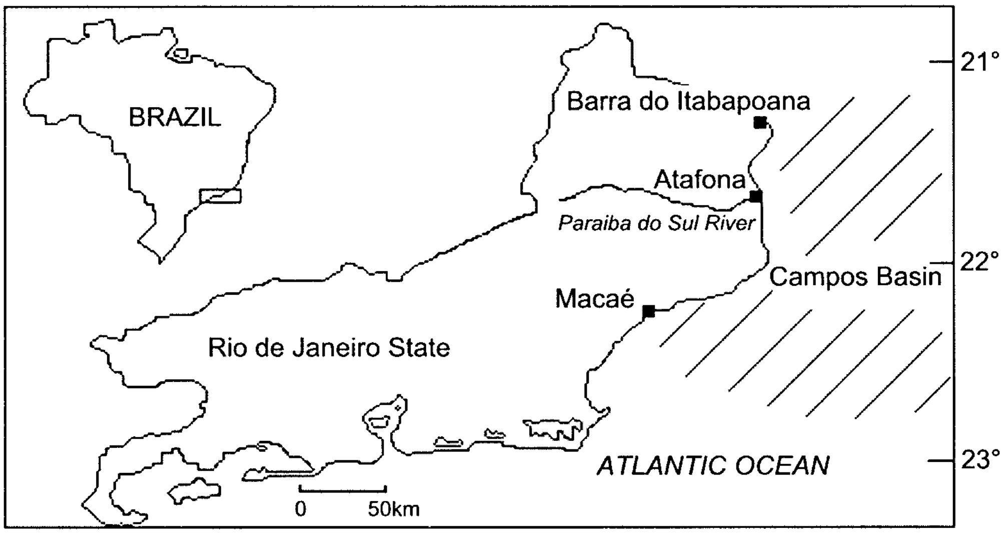

Fig. 1. Map of Rio de Janeiro State, indicating the geographic limits of the northern coast (Barra do Itabapoana and Macaé), Atafona village and Campos Basin area.

determine representative prey species; teleosts and cephalopods were considered as independent prey to reduce under or overestimation of their importance (Clarke, 1986).

Epizoics and parasites

The external body surface of 97 individuals and the internal organs (stomach, heart, lungs, kidneys and gonads) of 48 individuals were macroscopically examined in order to determine the presence of epizoics and parasites, respectively. The prevalence of infestation was calculated according to Bush *et al.* (1997).

Distribution and relative abundance

Three methods were used to obtain information on the distribution and abundance of franciscana: (1) nine boat cruises were carried out between Atafona and Macaé; (2) observations were made from a fixed platform in Atafona; and (3) sightings information provided by fishermen who operated along the Campos Basin was compiled. The cruises were conducted from a local fishing boat, and occurred monthly between April and December 1993 with each trip lasting 2-3 days. Transects were parallel to the coastline and located between 0.5 and 3.0 n.miles from the coast, in waters ranging from 5-12m deep. The fixed platform in Atafona was located on the beach, 1km away from the Paraíba do Sul River mouth and 20m away from the surf-zone. Observations took place from July 1994 to October 1997 and the sightings effort ranged from 12-24 days each month, totalling 796 days. Information on sightings [(1) group size; (2) sighting area (distance from the coastline and depth); and (3) seasonality of occurrence] was also obtained from 60 fishermen through monthly interviews. These fishermen represented 10% of the total fishermen based in Atafona village and they contributed sightings data between January 1995 and December 1998.

RESULTS AND DISCUSSION

Interactions with fisheries

Fishing gear

The gillnet locally called *caída* is the most commonly used in the study area (Fig. 2). Its position in the sea is determined by wind conditions and/or target species. If the wind is from the northeast, the net is usually surface-set, while with southwest or southerly winds it is bottom-set. The *caída* comprises approximately 20-22 panels and the total length of each net is 2.2-2.4km. Each panel is 110m long and has 25 small rounded floats (8cm in diameter) attached to the upper frameline and 24 200g leads in the lower frameline. When the net is set near the sea bottom, a stone of 8×8×8cm is attached to every eight leads, totalling three stones per panel. There are floats of 30×24×24cm for every six panels. The *caída* net stretched mesh size is 14cm, selecting species ranging from 40-80cm in length. Sharks (*Carcharhinus acronotus*, *C. plumbeus*, *C. brevipina*, *C. limbatus*, *Rhizoprionodon porosus*) and sciaenids (*Micropogonias furnieri*, *Cynoscion* sp.) are the main target species. Boats using the *caída* net operate along the Campos Basin from 1-40 n.miles offshore, in depths ranging from 6-70m. The fishing ground is usually defined by the target species (Di Beneditto *et al.*, 1998).

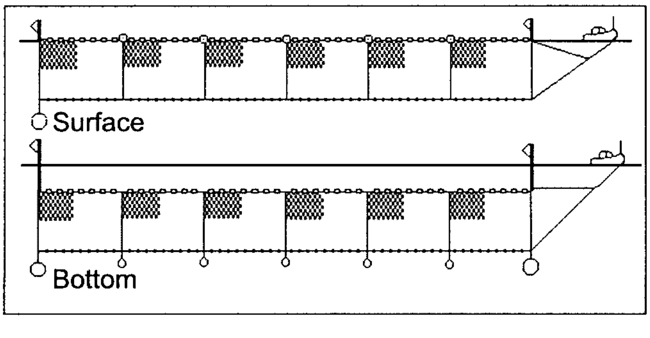

Fig. 2. Scheme of the surface and bottom-set gillnet used in northern Rio de Janeiro, locally called *caída*.

Effort

Data on the gillnet fishery in northern Rio de Janeiro were analysed by Di Beneditto *et al.* (1998) from 1987-88 and from 1990-1996. During the period mentioned above, approximately 60 boats used gillnets and their fishing area encompassed the Campos Basin. The authors estimated that the total gillnet fishing effort in each year was around 12,000km of net.

Since 1997, the number of gillnet boats operating along the Campos Basin has decreased to 50 boats. From this it has been assumed that the effort decreased by 19% and the total gillnet fishing effort in each year was around 9,700km of net, from 1997-1999.

Franciscana catches

The first record of franciscana in northern Rio de Janeiro was in June 1986, when three individuals were incidentally captured (Lodi *et al.*, 1987). From June 1987 to May 1988, Lodi and Capistrano (1990) monitored the gillnet fishery in Atafona village and recorded the entanglement of 20 franciscanas. From June 1988 to August 1989, the fishery was not monitored, but the incidental capture of two franciscanas was recorded (Di Beneditto *et al.*, 1990). In the subsequent years (September 1989 to December 1999), the gillnet operation was continuously monitored and 156 dolphins were recorded. A total of 181 dolphins were caught in gillnet fisheries in northern Rio de Janeiro from 1986-1999.

According to the interviews with fishermen, almost 75% of the incidental captures in northern Rio de Janeiro occurred within 10 n.miles from shore and in depths shallower than 30m. Although the gillnet fishery can operate up to 40 n.miles away from the coastline, this information suggests that the impact on the franciscana is greater when the fishery occurs closer to the coast. This has also been found in other areas, e.g. southern Brazil, Uruguay and Argentina (Praderi *et al.*, 1989; Corcuera *et al.*, 1994; Secchi *et al.*, 1997).

Around 55% of the captures occurred in surface-set nets while 29% were observed in bottom-set nets. It was not possible to obtain information on the position of the net for 16% of the captures. The predominance of captures in surface-set nets may be biased due to the prevailing local wind conditions, since the northeast wind is predominant in the study area (Martin *et al.*, 1998). Unfortunately, data on the relative fishing effort for surface and bottom-set gillnets are not available.

The capture data suggest that there is no seasonal variation in the occurrence of franciscana off northern Rio de Janeiro (52% in spring-summer and 48% in autumn-winter).

Blubber of incidentally captured franciscanas were used as shark bait in the longline fishery. Each individual provided around 30-40 pieces of bait, measuring 8×12cm. Since 1995, this fishery has become uncommon in the study area. However, franciscana was never a target of the fishery and its usage as bait was occasional, following incidental capture.

CPUE analysis

In this study, the CPUE analysis considered the incidental capture of 166 franciscanas that occurred from 1987-88 and from 1990-1999. Until 1996 the annual fishing effort used in the CPUE analysis was 12,000km of net (Di Beneditto *et al.*, 1998), and from 1997-1999 the annual effort used was 9,700km of net.

The annual CPUE values varied from 0.2-1.8 dolphins per gillnet fishing effort, and the changes in the catch recorded in 1994 and 1999 are probably random or due to uncontrolled variables (Fig. 3). The CPUE values in northern Rio de Janeiro are lower when compared to other areas, e.g. southern Brazil (~ 31° - 32°S) (Secchi *et al.*, 1997), Uruguay (~ 34° - 35°S) (Crespo *et al.*, 1986) and Argentina (~ 36°-41°S) (Corcuera *et al.*, 2000).

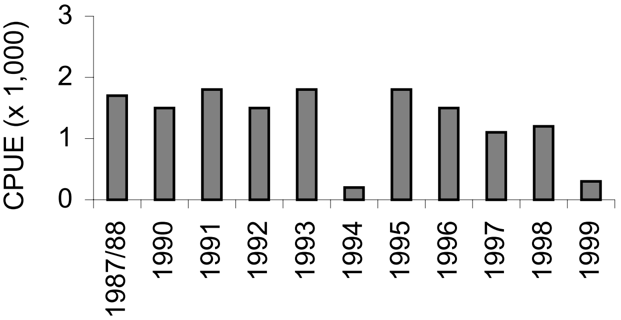

Fig. 3. Catch per unit of effort (CPUE x1,000) of franciscanas in northern Rio de Janeiro from 1987-1988 and from 1990-1999.

Biological information

Age, length and growth

No difference was observed in the ratio of males and females of franciscana (sex ratio 1:1.1), suggesting that there is no sexual segregation of the species in the area. The age ranged from two months to five years for males ($n = 62$) and zero (newborn) to nine years for females ($n = 57$). The oldest known female is 21 years (Pinedo, 1994) and male is 16 years (Kasuya and Brownell, 1979).

Males and females up to three years old represented 74% of the captures. Similar age structures have been observed for incidentally killed franciscanas in southern Brazil (50% - Pinedo, 1994; 81.3% - Ott, 1997), Argentina (64% - Corcuera *et al.*, 1994) and Uruguay (77.5% - Kasuya and Brownell, 1979). The age structure of the populations affected by the fisheries indicates a capture bias towards juveniles.

Franciscanas ranged in length from 66.0-130.0cm for males ($n = 62$) and from 74.0-147.5cm for females ($n = 57$). Length distributions (Fig. 4) were unimodal for males and bell-shaped for females. The largest male (130cm) and female (147.5cm) captured off Rio de Janeiro were substantially smaller than those taken in more southern areas. The largest male and female from Uruguay were 147cm and 171cm long, respectively (Kasuya and Brownell, 1979). In southern Brazil, the largest male and female were 152.0cm and 177.0cm, respectively (Pinedo, 1995).

Growth curves fitted to length-at-age data by a Gompertz model are presented in Fig. 5 and the estimated growth parameters are given in Table 1. The estimated asymptotic length of males was 121.9cm and that of females was 145.6cm. Although these values may represent further evidence of phenotypic differences, caution should be exercised given the under-representation of old animals in this sample.

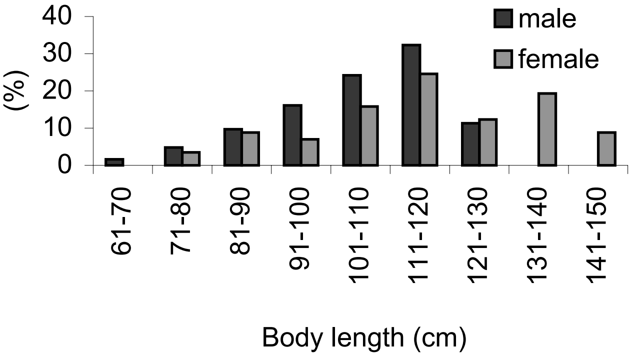

Fig. 4. Length distribution of males ($n = 62$) and females ($n = 57$) of franciscana incidentally captured in northern Rio de Janeiro.

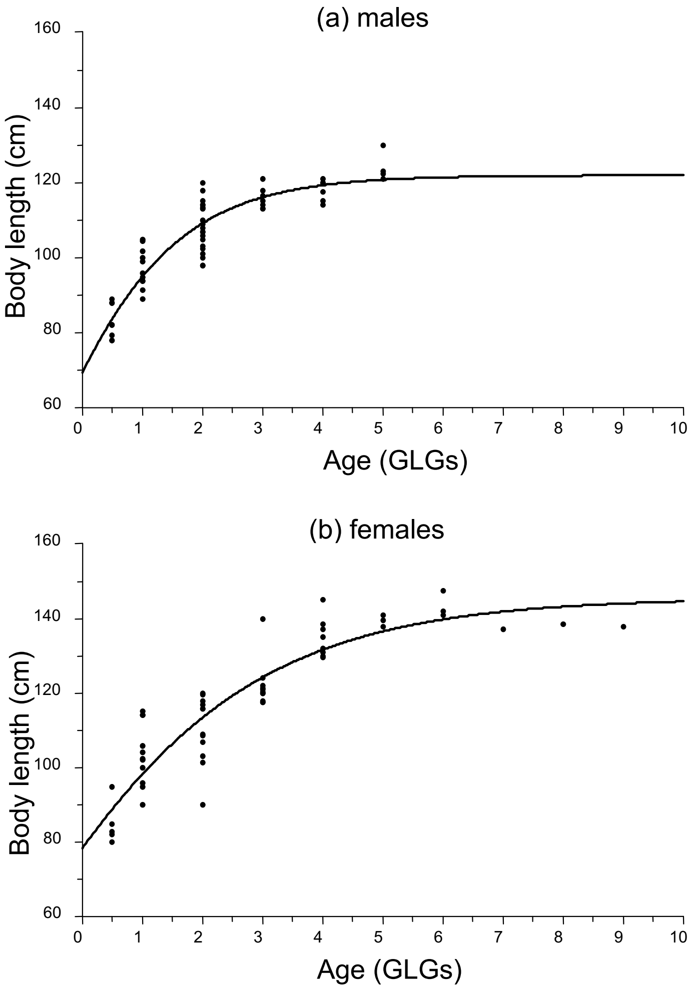

Fig. 5. Length-at-age data of 60 males (curve a) and 57 females (curve b) of franciscana incidentally captured in northern Rio de Janeiro. The solid line represents the predicted growth trajectory from the Gompertz model.

The lengths of the nine foetuses ranged from 8.5-65.5cm and the estimated range of ages was 1.3-9.7 months. Body length of new-born (0 GLG) and calves (0.5 GLG) varied between 66.0 and 85.0cm. The limited information available suggests that calving may occur throughout the year and that seasonal breeding does not occur in northern Rio de Janeiro. This differs from the seasonal timing of births proposed for franciscanas from southern Brazil and Uruguay, which show

Table 1

Growth parameter values from the Gompertz growth model fitted to length-at-age data of franciscana incidentally captured in northern Rio de Janeiro State.

Sex	*n*	Age range (years)	Body length range (cm)	Asymptotic length (cm)	Correction factor	Growth rate constant	Correlation coefficient (r)
Male	60	0-5	66.0-130.0	121.9	-0.5764	0.815	0.93
Female	57	0-9	74.0-147.5	145.6	-0.4825	0.453	0.92

parturition occurring in the spring from September to December (Harrison *et al.*, 1981; Brownell, 1984; Pinedo *et al.*, 1989).

The youngest mature females were three years old. The length of mature females ranged from 130.0-147.5cm. Of the 15 mature females, 6 were pregnant, 4 lactating and 2 pregnant and lactating. Due to the testis size, it was not possible to observe macroscopically the sperm in the epididymis. Ramos *et al*. (2000a) had examined the relationship between the length of the testis and body length in the study area. They observed an increase in testis size when individuals attained approximately 115cm in length and reached the age of two. These results suggest that females attain sexual maturity at three years and about 130cm long and males at two years and about 115cm long.

Individuals from northern Rio de Janeiro reached sexual maturity at ages 2-3 years to that estimated for animals from Uruguay 2.7-3.0 years but at somewhat smaller lengths than those from Uruguay where males were about 130cm and females about 140cm (Kasuya and Brownell, 1979; Harrison *et al.*, 1981; Brownell, 1984).

Physical maturity was observed in males from 120-121cm in length (average of 120.5cm) and from 3-5 years. Whereas in females, the length and age varied from 138-147.5cm (average of 140.6 cm) and from 3-9 years old. The length at physical maturity was smaller than observed for animals from Uruguay (133.3cm for males and 150cm for females - Kasuya and Brownell, 1979).

Feeding

Eighty-five out of 89 dolphins examined contained food remains. The youngest specimen with contents in the stomach was a 79cm two-month old male, suggesting that it was already ingesting solid food.

Teleosts were recorded in 95% of the stomachs. Twenty species from six families were identified (Table 2). The number of species in each stomach varied from one to nine. All species are neritic and 55% of them are associated with estuarine areas (Menezes and Figueiredo, 1980). The franciscana appears to feed preferentially on *Stellifer* sp., *Anchoa filifera, Pellona harroweri* and *Isopisthus parvipinnis*. Backcalculation of prey lengths indicate that franciscana feed on individuals of up to 10cm in length. Observed feeding habits in other areas also reveal a preference for juveniles or small sized teleosts (Pinedo *et al.*, 1989; Ott, 1994; Bassoi, 1997).

Cephalopods were recorded in 66% of the stomachs. Loliginidae species *Loligo sanpaulensis*, *Loligo plei* and *Lolliguncula brevis*, were identified. The number of species in each stomach varied from one to three and the average

Table 2

Prey species of franciscana in northern Rio de Janeiro State.

	Density (per stomach)		Size (cm)		Biomass (g) (per stomach)		
Species	Range	Mean ± SD	Range	Mean ± SD	Range	Mean ± SD	IRI
Teleosts							
Stellifer sp.	1-148	23.2 ± 33.8	1.8-5.1	2.9 ± 0.6	0.2-102.7	12.4 ± 19.0	1,629.3
Anchoa filifera	1-129	10.3 ± 22.0	4.0-7.6	6.1 ± 0.9	1.1-245.6	28.9 ± 50.4	1,368.4
Pellona harroweri	1-93	12.3 ± 20.8	2.0-9.6	4.3 ± 2.1	0.2-200.8	21.7 ± 40.6	1,137.2
Isopisthus parvipinnis	1-78	10.9 ± 17.9	1.7-8.4	5.0 ± 1.7	0.1-103.2	18.2 ± 24.8	1,029.3
Cynoscion jamaicensis	1-122	12.6 ± 26.9	2.8-13.8	4.5 ± 2.4	1.3-78.4	14.1 ± 20.4	429.8
Chirocentrodon bleekerianus	1-40	12.6 ± 11.8	5.6-8.7	7.3 ± 0.9	3.4-205.8	51.8 ± 52.6	408.5
Stellifer brasiliensis	1-29	6.7 ± 7.9	2.2-5.6	3.2 ± 0.8	0.5-29.3	6.4 ± 7.5	249.7
Sardinella brasiliensis	1-32	14.4 ± 12.9	4.4-11.1	5.9 ± 2.1	6.0-211.6	106.1 ± 86.8	161.6
Peprilus paru	1-13	3.3 ± 4.3	2.7-8.1	5.5 ± 1.6	1.5-249.2	35.0 ± 70.0	112.5
Stellifer rastrifer	1-27	9.9 ± 9.7	1.5-5.9	3.7 ± 1.5	0.4-88.7	27.6 ± 30.4	53.5
Odontognathus mucronatus	1-13	4.0 ± 4.0	3.9-11.9	8.0 ± 3.1	0.6-100.2	22.2 ± 32.8	36.4
Micropogonis furnieri	2-10	4.2 ± 2.7	3.9-7.0	6.1 ± 1.1	0.8-28.1	8.8 ± 7.9	25.1
Trichiurus lepturus	1-3	1.4 ± 0.7	11.3-36.7	24.8 ± 8.8	1.6-43.1	10.3 ± 13.3	20.5
Ctenosciaena gracilicirrhus	1-4	2.0 ± 1.4	2.8-7.4	4.3 ± 1.6	0.8-57.0	11.2 ± 20.6	14.2
Anchoviella lepidentostole	1-26	14 ± 12.5	5.6-6.8	6.3 ± 0.6	3.6-105.7	47.4 ± 52.6	12.2
Paralonchurus brasiliensis	1-3	2.0 ± 0.8	1.3-5.6	3.6 ± 1.8	0.3-4.5	2.5 ± 1.7	3.6
Porichthys porossisimus	1-2	1.5 ± 0.7	5.5-6.4	6.0 ± 0.6	2.4-3.1	2.8 ± 0.5	0.5
Cynoscion virescens	-	-	2.2-2.4	3.0 ± 0.7	-	-	0.4
Larimus breviceps	-	-	-	4.5	-	-	0.1
Macrodon ancylodon	-	-	-	4.7	-	-	0.1
Cephalopods							
Loligo sanpaulensis	1-75	15.3 ± 18.8	2.3-11.1	5.4 ± 1.9	1.1-815.9	128.1 ± 187.0	6,382.6
Loligo plei	1-32	6.6 ± 7.2	7.9-23.0	15.0 ± 4.0	14.1-2,415.1	473.1 ± 593.9	3,007.2
Lolliguncula brevis	1-11	3.4 ± 2.8	3.9-7.5	5.2 ± 1.0	4.9-89.8	34.7 ± 28.1	340.3

mantle length from 5.2-15.0cm. These cephalopods are also neritic and *L. brevis* is also associated with estuarine areas (Roper *et al.*, 1984). The species *L. sanpaulensis* and *L. plei* were the most representative in the diet of franciscana (Table 2).

Crustaceans were recorded in only 25% of the stomachs, which suggests that they are of lesser importance in the diet of the franciscana. Two species, *Artemesia longinaris* and *Xyphopenaeus kroyeri*, were identified.

In southern Brazil (30°S-33°S), franciscanas feed mainly on the teleost *Cynoscion guatucupa* and the cephalopod *L. sanpaulensis* (Pinedo *et al.*, 1989; Ott, 1994; Bassoi, 1997). Differences in the diet along its distribution may reflect differences in prey availability and, possibly, abundance.

In northern Rio de Janeiro, the main prey species of the franciscana are abundant throughout the year in coastal areas (Haimovici *et al.*, 1989; Di Beneditto *et al.*, 1998). In general, they have low commercial value or are considered as bycatch species in the local fisheries. Even when the franciscana prey is commercially valuable (e.g. *I. parvipinnis, L. sanpaulensis* and *L. plei*), the fishery targets larger individuals than those consumed by the franciscana (Costa and Haimovici, 1990; Di Beneditto *et al.*, 1998). A comparison between the diet of the franciscana and another small cetacean species common in the region, the tucuxi (*Sotalia fluviatilis*), indicates that they are coexisting with a low competition level for the trophic resources (Di Beneditto, 2000).

Epizoics and parasites

In the present study, 97 franciscanas were externally examined. Only the epizoic, the barnacle *Xenobalanus globicipitis* attached to the caudal fin was recorded and then for only one individual (intensity = 1, prevalence = 1.03%, total length of the epizoic = 48.3mm). This species has also been recorded on the body of franciscanas along the Uruguayan coast (Pinedo *et al.*, 1989).

None of the 48 dolphins examined in this study had parasites in their internal organs. Santos *et al.* (1996) analysed the same internal organs of 42 franciscanas incidentally captured in northern Rio de Janeiro and discussed the absence of parasites in this region, comparing this with the high prevalence of parasites found in franciscanas from other areas (Raga *et al.*, 1994; Andrade *et al.*, 1995). These authors suggested that the non-occurrence of parasites in franciscanas in northern Rio de Janeiro is due to a lack of suitable intermediate hosts or the lack of parasitism in such intermediate hosts. The results in this study corroborate Santos *et al*. (1996) regarding the absence of parasites in franciscana in the study area.

Distribution and relative abundance

Forty sightings of franciscanas were recorded by all combined methods in northern Rio de Janeiro. Group sizes ranged from 1-15 dolphins. In general, groups were small and 70% of them were composed of five dolphins or less. Sightings were made in areas near the coast and 90% of the total were obtained up to 5 n.miles away, in waters up to 15m deep. The frequency of occurrence of franciscana was 52.5% in the spring-summer period and 47.5% in the autumn-winter period.

Sightings of this species are difficult to record due to their small body size, small group size and the absence of aerial behaviour (Jefferson *et al.*, 1993; Bordino *et al.*, 1999). Group sizes of franciscana sighted in northern Rio de Janeiro follows the same pattern noted in other areas (Pinedo, 1994; Crespo *et al.*, 1998; Bordino *et al.*, 1999).

In Argentina, franciscana sightings near the coastline are frequent during spring and summer. In winter, groups usually move away from the coast (Bordino *et al.*, 1999). This pattern was not observed in northern Rio de Janeiro, where sightings close to the coastline were recorded throughout the year. Lack of seasonal variation in movement patterns may be related to two non-excluding factors: water temperature and prey availability. Sea surface temperature in the region (ranging from 21°18'S to 22°00'S) does not change substantially throughout the year, varying from 20-24°C (Muehe and Valentini, 1998; Souza *et al.*, 1998). This region corresponds to the area where the sightings of franciscana have been frequently recorded off northern Rio de Janeiro. Temperature changes of the water surface within the range of this species may affect the seasonality of occurrence in certain areas. Unlike northern Rio de Janeiro, there is a marked variation in sea surface temperature in Argentina and a possible consequent movement pattern as proposed by Bordino *et al.* (1999).

In addition, there may be variation in the availability and/or movement of the prey preferably consumed by franciscana throughout its distribution area. In northern Rio de Janeiro, the franciscana prey species are resident teleost and cephalopod resources that are abundant year round. This may be also related to the lack of seasonal variation in the franciscana movement pattern in the study area.

CONCLUSIONS

Estimates of the population size and continuous gillnet fleet monitoring are required to conserve franciscana in the northern limit of its distribution range.

The differences in the somatic, reproductive and genetic patterns of franciscana represent important factors that may be used as evidence to define their stocks for management purposes. These variations can reflect the reduction of gene flow between populations, the allocation of resources between growth and reproduction and/or the influence of environmental features, such as water temperature and food availability.

Further research, especially in Rio de Janeiro and Rio Grande do Sul States, is necessary to better understand the biological and conservation aspects regarding the franciscana.

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Spatial and temporal structure of the western North Pacific minke whale distribution inferred from JARPN sightings data

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ABSTRACT

The density of minke whales (*Balaenoptera acutorostrata*) in the western North Pacific was examined using a generalized additive model in order to investigate the spatial and temporal distribution patterns. The data used were a subset of JARPN sightings data collected from 1994 to 1999. The process for estimating the density was divided into two parts: the detection process for the estimation of the effective search half-width; and the encounter process for the estimation of the encounter rate. Model selection was carried out using information criteria. The selected model for the detection process included 'sightability', a synthetic index of detectability, as a covariate, and for the encounter process included the interaction between latitude and longitude and the interaction between month and latitude. The trend surface of the transformed density predicted by each month revealed no clear gaps. The monthly transition of the density distribution also suggested the northward seasonal feeding migration of the minke whales.

KEYWORDS: COMMON MINKE WHALE; NORTH PACIFIC; INDEX OF ABUNDANCE; STOCK IDENTITY; MIGRATION

INTRODUCTION

The JARPN (Japanese Whale Research Program under Special Permit in the Western Part of North Pacific) programme was carried out from 1994-99 with the primary aim of determining the stock structure of the common minke whale (*Balaenoptera acutorostrata*) in the western North Pacific. The results of the programme were reviewed in February 2000 by the Scientific Committee of the International Whaling Commission (IWC, 2001). Although several papers presented to the review meeting suggested that there was no explicit evidence for multiple stocks of minke whales off Japan, it was pointed out that this conclusion might be due to the inappropriate pre-stratification of the western North Pacific (Martien and Taylor, 2000; Taylor, 2000; Taylor and Chivers, 2000). It was suggested that the examination of density distribution patterns might provide valuable information to determine the appropriate partition of the area. The IWC Scientific Committee recommended that the sightings data should be analysed using a multiple regression model such as a generalized linear model (GLM; McCullagh and Nelder, 1989) that includes the covariates of year, month, Beaufort Sea state and sea temperature (IWC, 2001). This paper examines the available sightings data using a multiple linear regression and a generalized additive model (GAM; Hastie and Tibshirani, 1990) to include several important covariates influencing the detection and encounters. It also examines the monthly distribution patterns.

MATERIALS AND METHODS

The data used were a subset of the JARPN sightings data presented in Matsuoka *et al*. (2000). Fig. 1 shows the sub-areas of the western North Pacific used by the IWC. This paper concentrates on the data available for sub-areas 7, 8 and 9, as the primary issue raised in IWC (2001) was whether more than one population exists in these three sub-areas or not. The pooled effort by 1° square is shown in Fig. 2. Most effort occurred in the northern part of the sub-areas whilst effort in the southern parts was sparse. The monthly plots of the tracklines surveyed are provided in Matsuoka *et al*. (2000).

The sightings data have been divided into two panels, one for detection (perpendicular distance, environmental conditions at detection such as the sea state) and the other for searching activities (effort, year, month, day, averaged environmental conditions such as the sea surface temperature for on-effort portions of the day). The density index was calculated through these two processes, one to estimate the effective search half-width and the other to estimate the encounter rate.

The detection process

The effective search half-width (including the effects of several covariates) is estimated by the following method of Beaver and Ramsey (1998) as described below.

(1) The perpendicular distance from the transect to the *i*th detected pod of whales is the detection distance, y_i. When a set of covariates, $x_i = (x_{i1},\ldots,x_{ip})$, is associated with the *i*th detected pod, it is assumed that the effective search half-width surveyed under condition x_i is w_i, where

$$\log(w_i) = \beta_0 + \sum_{j=1}^{p} \beta_j x_{ij}$$

The ordinary least squares regression of $\log(y_i)$ on the covariates provides unbiased estimates of the parameters $(\hat{\beta}_1,\ldots,\hat{\beta}_p)$;

(2) Determine average detectability conditions for the covariates, $\bar{x}_j$;

(3) Adjust all detection distances to the average conditions according to

$$\tilde{y}_i = y_i \times \exp\left(\sum_{j=1}^{p} \hat{\beta}_j (\bar{x}_j - x_{ij}) \right)$$

(4) Use the adjusted detection distances to select a semi-parametric estimator of the effective half-width,

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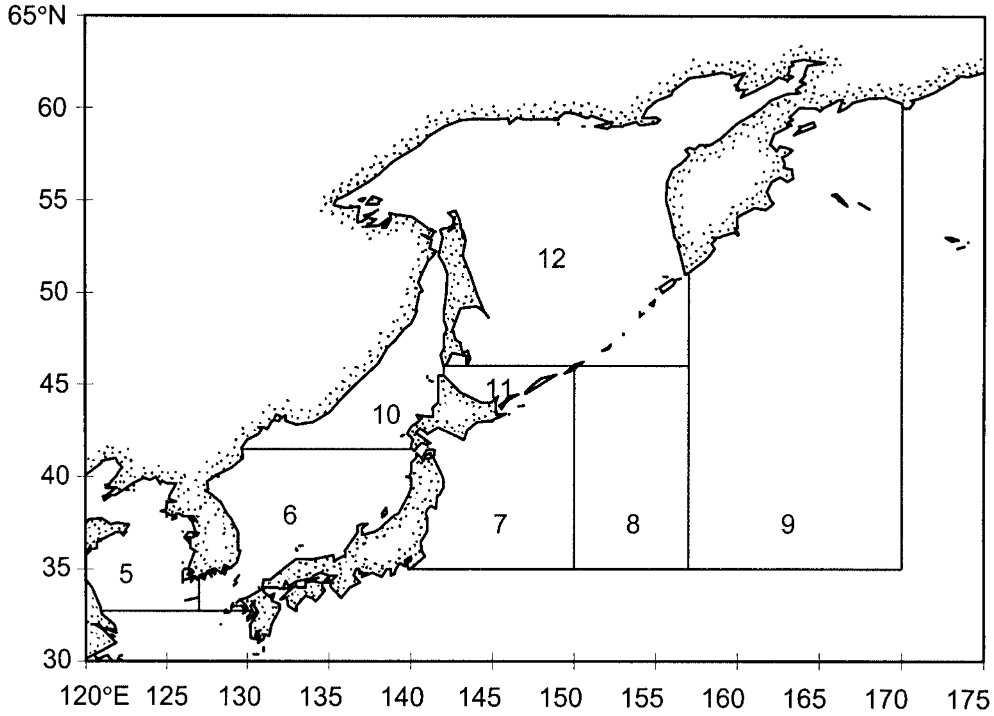


Fig. 1. Sub-areas for the western North Pacific minke whales.

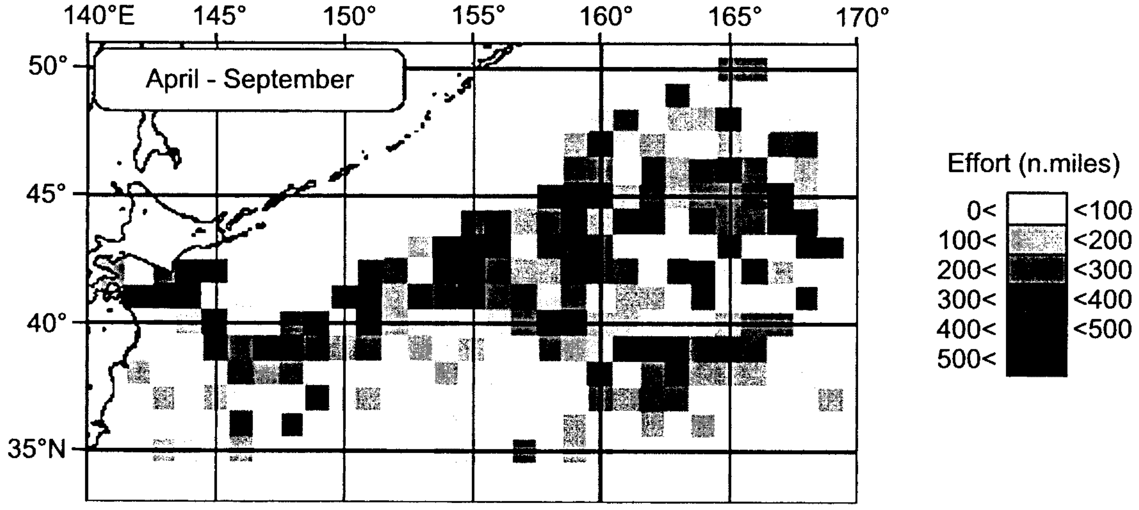


Fig. 2. Search efforts surveyed by JARPN from April to September in 1994-1999. The amount of effort in one degree square cell is divided into six categories with a unit of 100 n.miles.

$\hat{w}_0$, at average conditions. Program DISTANCE (Laake *et al.*, 1993) provides an estimate of effective half-width.

(5) Estimate the constant term with

$$\hat{\beta}_0 = \log(\hat{w}_0) - \sum_{j=1}^{p} \hat{\beta}_j \bar{x}_j$$

The model selection for multiple linear regression is made using the Bayesian Information Criterion (BIC; Swartz, 1978) assisted by Akaike's Information Criterion (AIC; Akaike, 1973). The BIC that approximates the logarithm of the Bayes factor in an approximate manner (Kass and Raftery, 1995) is given by

$$\hat{D} + \log_e(N)p$$

where D is the deviance residual, N is the number of observed pods, p is the number of parameters and 'hat' $(\hat{\cdot})$ denotes an estimate from fitting the model. D is the amount defined from the log-likelihood and is given by

$$D(\mu; y) = 2l\,(\mu^*; y) - 2l\,(\mu; y)$$

where y is the logarithm of the perpendicular detection distance, $\mu = E(y)$, $E(\,)$ is the expectation, l is a log-likelihood function and μ^* is the parameter estimate maximized under no limitation (Chambers and Hastie, 1992). The AIC is obtained by replacing $\log_e(N)$ in the BIC with 2.

The covariates considered are Air Temperature in degrees Celsius (*AT*), Sightability (*SA*) and Sea State (*SS*). The interaction between covariates is not considered for simplicity. *SA* is based on synthetic impression of average detectability reported by navigation officers, whilst *SS* is based on the height of waves. Thus, *SA* includes more information than *SS*, although it can be criticised for being subjective. In this paper, *SA* and *SS* are treated as categorical variables, whilst *AT* is treated as a continuous variable. The effect of school size is considered in the DISTANCE program (see Discussion).

The encounter process

The expected number of encounters, $E(n_k)$, on day k is first modelled as

$$E(n_k) = L_k \hat{w}_k \exp(f(Year) + f(Month) + lo(LAT, LONG, 1/h) + s(SST))$$

where n_k has a Poisson distribution and

L_k	effort on day k as an offset,
$\hat{w}_k$	effective search half-width for day k estimated from the above detection process as an offset,
Year	1994 to 1999,
Month	April to September,
LAT	latitude averaged from the period spent on-effort during a day,
LONG	longitude as above,
SST	sea surface temperature,
$f(\bullet)$	factor,
$lo(\bullet,\bullet, 1/h)$	locally-weighted running-line smoother with the span of $1/h$, i.e. the smoothing parameter for a loess fit. The span is the percentage of total data used to fit the local polynomial at each point,
$s(\bullet)$	spline smoother with the degree of freedom of 4.

The form of the above model is similar to that of Cumberworth *et al.* (1996). Covariates *Year* and *Month* enter the model as categorical variables, whilst other covariates enter the model as smoothed functions such that the single terms are fitted by spline functions and the pairwise terms by loess functions (Hastie and Tibshirani, 1990). The possibility of an annual trend is examined by treating *Year* as a linear term. The span ($1/h$) of loess functions for the first model is selected by using the minimisation of the BIC assisted by the AIC with the change of h shifted by 1. The BIC for the GAM is given by

$$\hat{D} + \log_e(M) p_e$$

where D is the deviance residual, M is the number of days, p_e is the effective number of parameters that is the sum of the degrees of freedom for parametric parts of the model and the equivalent degrees of freedom for non-parametric parts, and 'hat' $(\hat{\cdot})$ denotes an estimate from fitting the model (Hastie and Tibshirani, 1990; Chambers and Hastie, 1992). The number of degrees of freedom of spline functions is fixed at 4.

After the determination of the span ($1/h$), the existence of over-dispersion and the needed covariates are examined under a fixed value of h. The existence of over-dispersion is investigated by using hypothesis testing and the bootstrap method. The details for hypothesis testing are given below. The stepwise model selection based on the information criteria such as the AIC and the BIC for the GAM is also employed for the variable selection. If there is over-dispersion, the information criteria are modified based on principles of quasi-likelihood. The details are also given below.

After the final model selection, the sensitivity of h is examined by changing values of h and calculating the information criteria. All the analyses in this paper are carried out using the *S-Plus* program.

Examination of an overdispersed Poisson distribution

In order to examine whether the sampling variance exceeds the theoretical variance ($var(n) = E(n)$ for the Poisson model), the overdispersion parameter (c) was estimated from the Pearson chi-square statistics of the global model and its degrees of freedom,

$$\hat{c} = \chi^2 / df$$

where $\chi^2 = \sum_{i=1}^{n} \frac{(n_i - \hat{\mu}_i)^2}{V(\hat{\mu}_i)}$, $\mu_i = E(n_i)$ and $df = M - p_e$ (Burnham and Anderson, 1988). The global model is defined as the first model plus all the pairwise interactions:

$$\text{first model} + \sum lo(X_i, X_j)$$

where X_i is each covariate such as *Year* and *SST*.

To test whether $c = 1$ or $c > 1$, the bootstrap approach with resampling of the residuals can be used (Efron and Tibshirani, 1993). In this case, we use the Pearson residuals,

$$r_i^P = \frac{n_i - \hat{\mu}_i}{V(\hat{\mu}_i)^{1/2}}$$

as the resampling unit.

The overdispersion parameters for B generated bootstrap data are calculated respectively (c^{*b}). Then an approximate significance level (P) is calculated by

$$\hat{P} = \#\{c^{*b} < 1\} / B$$

The hypothesis $c = 1$ is considered rejected if $P < 0.05$ (one-sided test with 5% significance level) following the standard statistical convention.

If $c > 1$, model selection is carried out by using QAIC (Burnham and Anderson, 1988) and QBIC again. QAIC and the QBIC are given by

$$\text{QAIC} = \hat{D} / \hat{c} + 2p_e$$

$$\text{QBIC} = \hat{D} / \hat{c} + \log_e(M) p_e$$

RESULTS

The final covariate selected by both the BIC and the AIC was *SA* in the detection process. The estimated parameters and the estimated mean effective search half-width are shown in Table 1. The hazard rate key function with no adjustment parameters was used to model the detection function since this had the lowest AIC value of the available functions in the DISTANCE program. The influence of school size was not significant. The increase in sightability increased the effective search half-width.

Table 1

The estimates and the standard errors of the parameters for the detection process.

	Value	Standard Error	*t* value	Sample size
SA1	-1.660	0.145	-11.436	51
SA2	-1.733	-1.733	-15.046	81
SA3	-1.495	-1.495	-17.782	152
SA4	-1.432	-1.432	-14.220	106
SA5	-0.856	-0.856	-3.600	19
β_0	0.723			
The estimated mean effective search half-width				
w_0		0.452		

For the encounter rate, the span $1/h$ for loess functions selected by minimizing the BIC was 1/2 ($h = 2$), whilst the span for loess functions selected by minimising the AIC was 1/31. The latter value is unreasonably large and thus we used only the result from the BIC ($h = 2$).

The over-dispersion parameter observed for the global model was 1.470. The estimated significance level $\hat{P} = 0.0004$ was obtained from 10,000 bootstrap samples for the Pearson residuals of the global model. The 95% bootstrap confidence interval of the over-dispersion parameter was [1.195, 1.783]. Because $c > 1$, model selection was carried out using QBIC.

The selected model for the encounter rate with the estimated effective search half-width was given by

$$E(n_k) = L_k \hat{w}_k \exp(lo(LAT, LONG, 1/2) + lo(LAT, LONG, 1/2))$$

which had the lowest QBIC of the models considered (QBIC = 769.89). The covariates of the model that had the second lowest QBIC was *Year* + *lo*(*LAT*,*LONG*,1/2)+*lo*(*Month*, *LAT*,1/2) with *Year* as a linear term (QBIC = 771.59). A sensitivity test for *h* was carried out by changing the value of *h* incrementally and calculating the QBIC for the above final model. The model with $h = 2$ was still selected. The plots of residuals of the final model over each covariate showed no systematic trend.

The plots of smooth terms for the final model are shown in Fig. 3. The top plot is for the loess smoother for the interaction between latitude and longitude and the bottom plot for the loess smoother for the interaction between month and latitude. They indicate that the density in high latitudes is higher and the area with high density moves north as month changes.

The monthly densities in each 1° square were predicted from the final model. The monthly density indices in each cell were calculated by standardisation after the logarithm transformation:

$$\text{Density index} = \frac{\log_e(density(LAT, LONG, Month)) - \overline{\log_e(density(Month))}}{\sqrt{Var(\log_e(density(Month)))}}$$

where:

$$\overline{\log_e(density(Month))} = \frac{1}{L} \sum_{LAT,LONG} \log_e(density(LAT, LONG, Month))$$

$$Var(\log_e(density(Month))) = \frac{1}{L-1} \sum_{LAT,LONG} (\log_e(density(LAT, LONG, Month)) - \overline{\log_e(density(Month))})^2$$

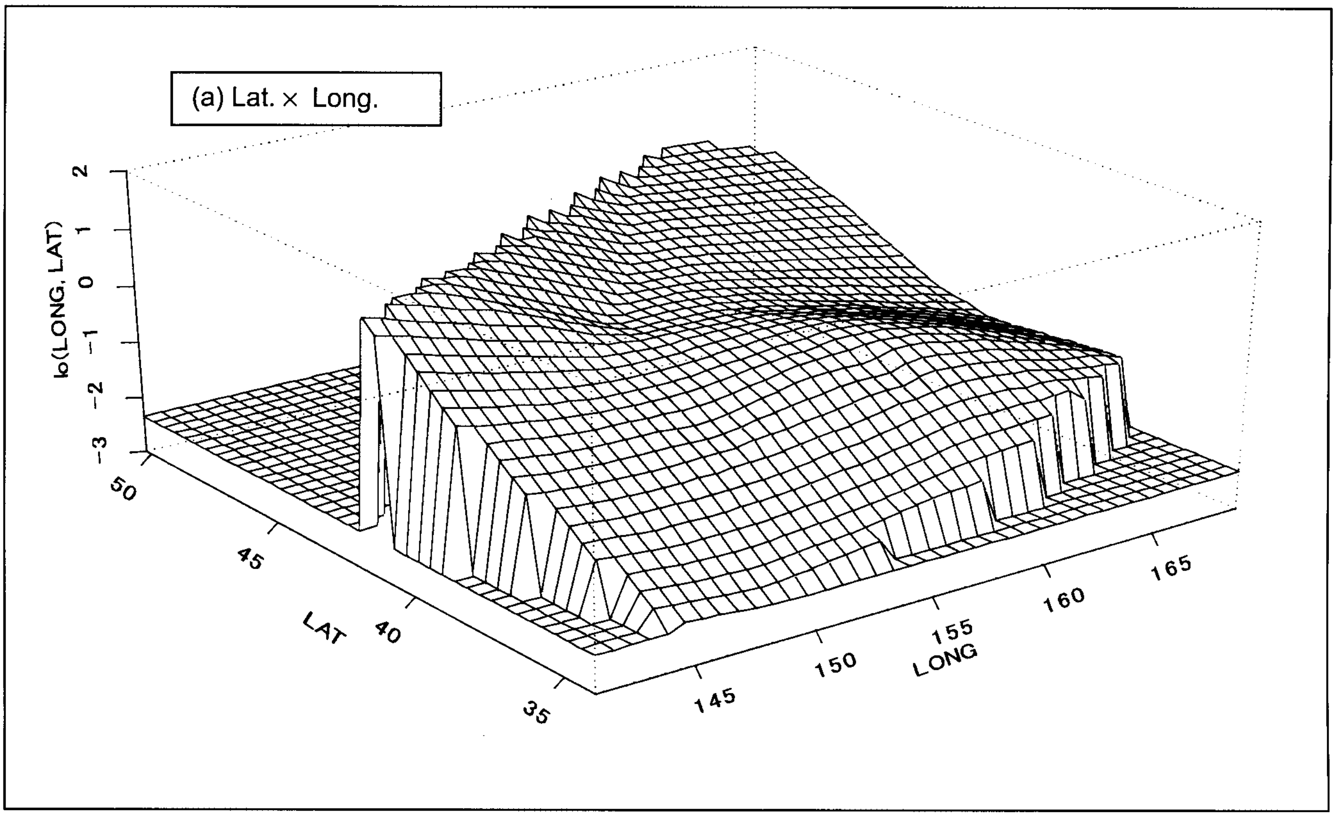
and *L* is the number of combination of *LAT* and *LONG* that is equal to the number of cells in gray- and black-coloured zone in Fig. 4. The trend surfaces of monthly-predicted density indices are shown in Fig. 3.

DISCUSSION

It is perhaps not surprising that only sightability remains in the model of detection process since sightability is the overall judgment for detectability made in the field and will represent a subjective integration of a number of factors including wave height, swell, wind speed, weather conditions etc. In this paper, the influence of school size was not considered as a covariate in the detection model because the resulting model cannot be used to estimate the density in regions where no whales were found if school size is treated as a covariate. Although Beaver and Ramsey (1998) recommended the method of Drummer and McDonald (1987), for simplicity, the adjustment contained in the DISTANCE program was used here. The appropriateness of this should be considered in a future study. However, it should be noted that in the present data set the school size was almost exclusively one (total number of detected schools = 422, total number of detected individuals = 443).

GAMs have been applied to obtain distribution patterns of density in several other areas (e.g. Palka, 1995; Hedley *et al.*, 1999). The GAM analysis in this paper results in a number of density distribution maps for western North Pacific minke whales. These reveal no conspicuous drops in the central part of the western North Pacific (Fig. 3 (a) and Fig. 4) i.e. they do not suggest a need to sub-divide this area of the North Pacific. However, this conclusion requires some qualification.

Model selection was carried out using the BIC (or QBIC), not the AIC values. AIC sometimes results in more parameters than BIC because AIC tends to overestimate the number of parameters needed (Kass and Raftery, 1995). In fact, the sensitivity test of the span of loess functions for the first model presented here showed that the BIC resulted in the model with the span of 0.5 whereas the AIC tended to suggest a much smaller value ($1/h = 0.032$). However, it cannot be ruled out that the result of the BIC is too conservative such that the selected span is too large to detect any true gaps in the study area. Other extended information criteria such as AIC_c (Burnham and Anderson, 1988) and CAIC (Bozdogan, 1987) were examined for selecting an appropriate *h* value. The result was that AIC_c selected $1/h = 0.05$ and CAIC selected $1/h = 0.5$. The former value is very small and would require considerably more data to reasonably apply such a complex model. Therefore, somewhat arbitrarily we produced plots such as those in Fig. 3 and Fig. 4 for the final model with values of $1/h$ of 0.25 and 0.125. These generally were similar to Figs 3 and 4 except that the increase in density from lower to higher latitudes lacked smoothness to some degree. However, we believe that model selection tools other than information criteria should be considered to look for the presence of gaps in distribution in any future study.



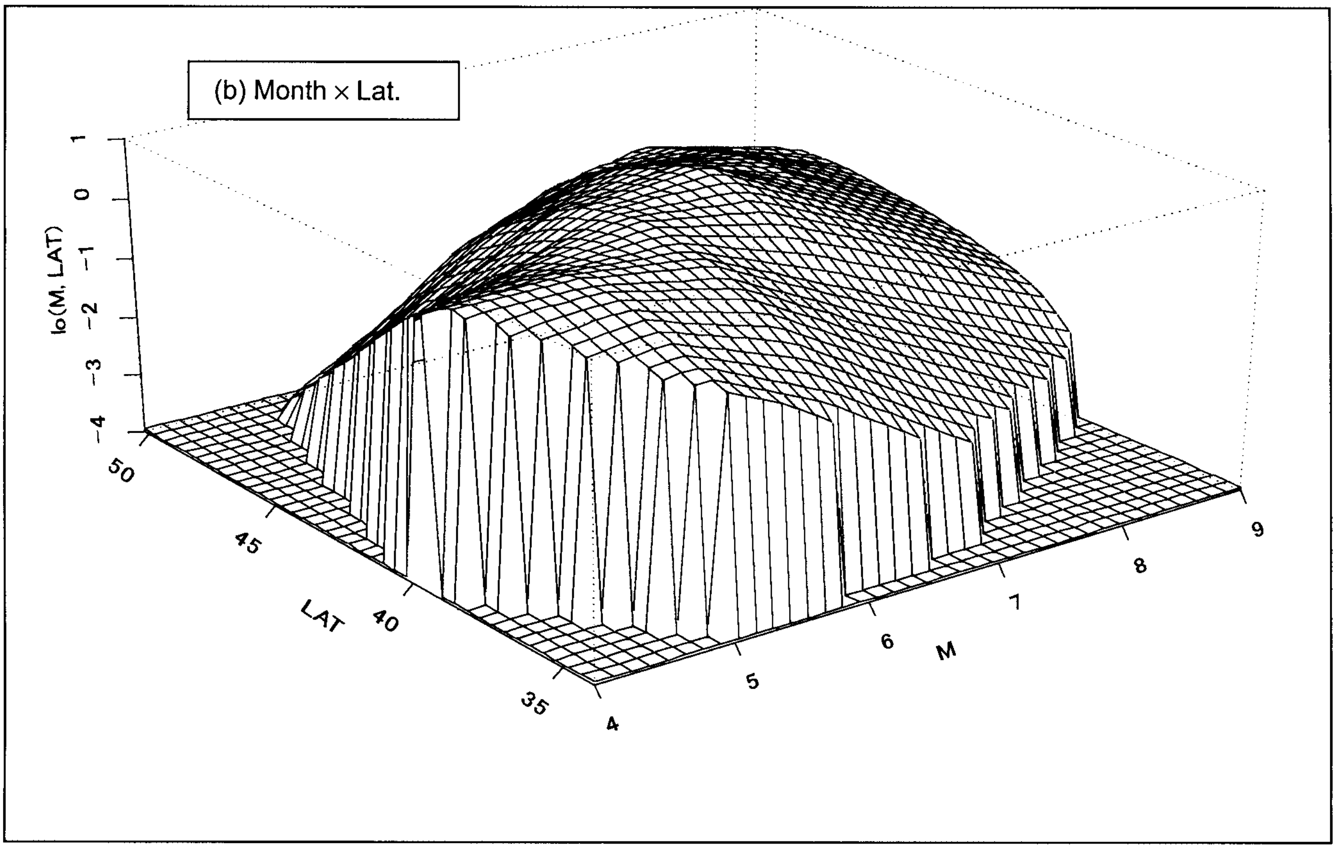


Fig. 3. Plots of fitted spline functions and perspective plots of fitted less smooth functions in the generalized additive model. The top plot is for latitude and longitude, and the bottom for month and latitude.

Fig. 3 (b) reveals some monthly variation in density with indices in high latitudes increasing whilst those in low latitude decreased as time passes. This result agrees with Hatanaka and Miyashita (1997). Fig. 4 shows these monthly changes in density more explicitly. In April, the peak in density indices occurs between 38°N-39°N and 154°E-160°E (Fig. 4 (a)), but this peak is not present in June and July (Fig. 4 (c) and (d)). However, there was clearly more effort in June and July than in April and May. In particular, the data for April are too patchy to be useful. It is

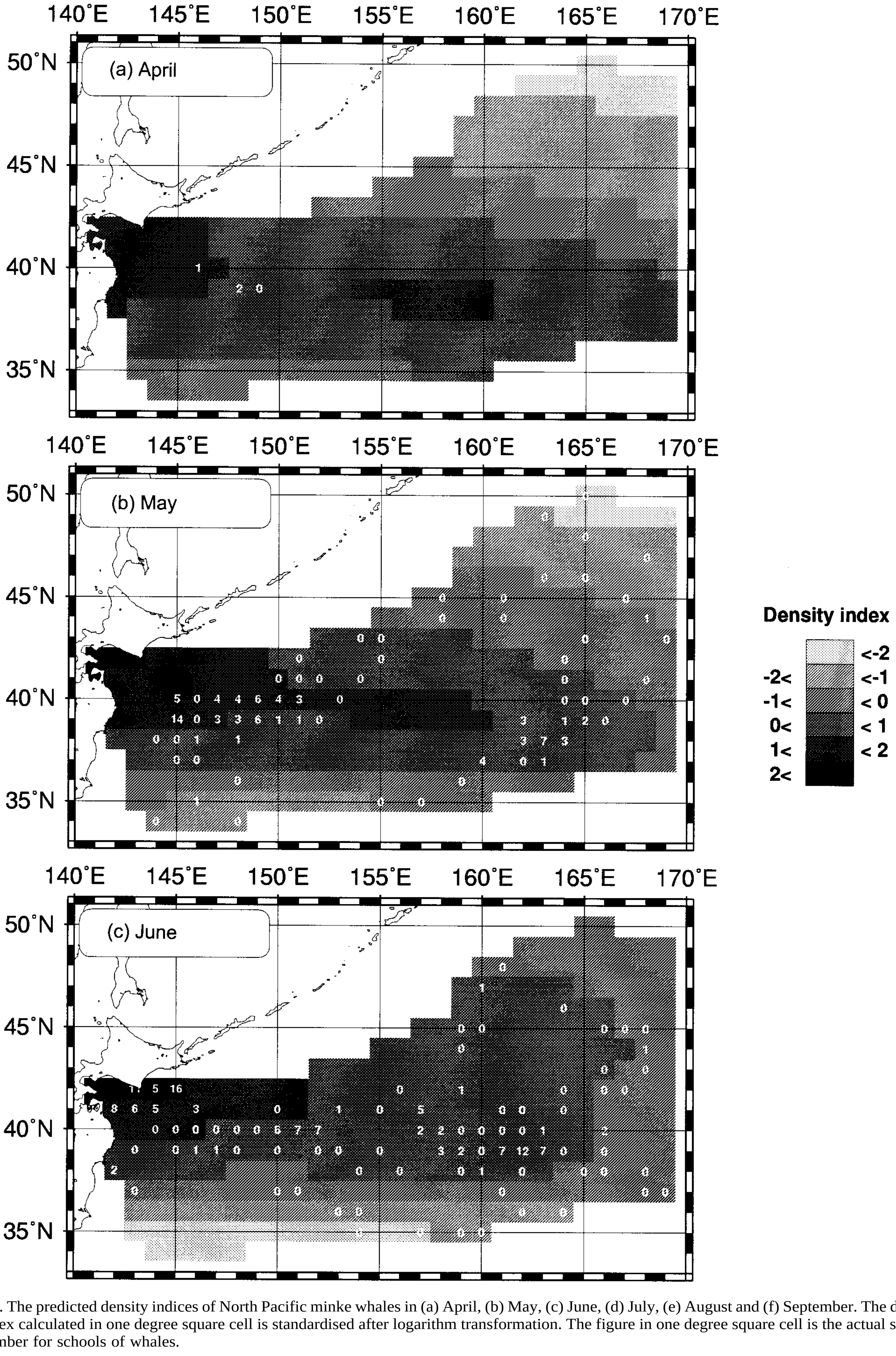


Fig. 4. The predicted density indices of North Pacific minke whales in (a) April, (b) May, (c) June, (d) July, (e) August and (f) September. The density index calculated in one degree square cell is standardised after logarithm transformation. The figure in one degree square cell is the actual sighted number for schools of whales.

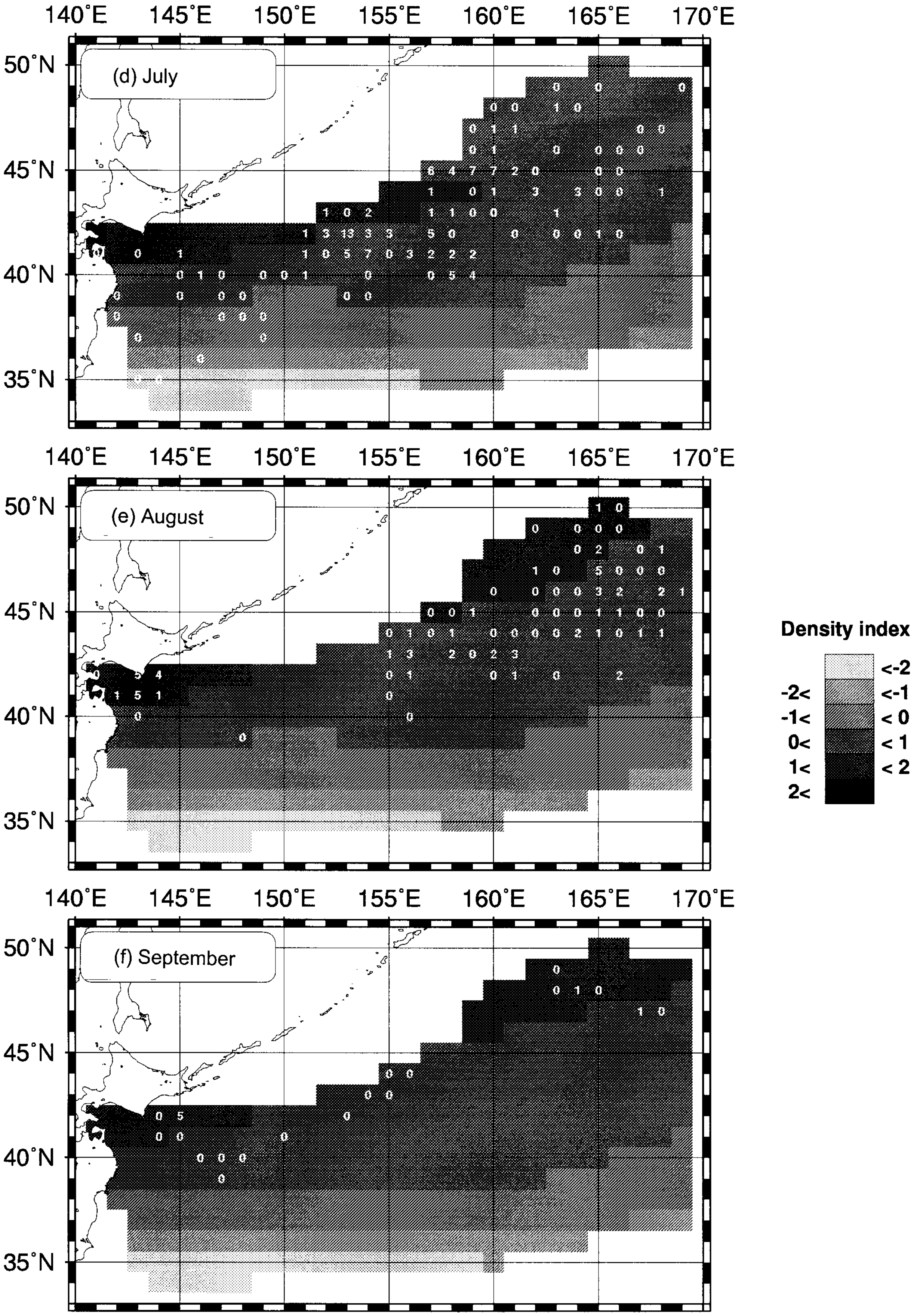


Fig. 4. (Continued).

also plausible that the high-density area in the western part of Fig. 4 reflects many sightings off the coast of Hokkaido which may reflect segregation of young whales (Hatanaka and Miyashita, 1997).

In conclusion, our analysis revealed no evidence to suggest a further division of the western North Pacific. However, in addition to the factors discussed above it is apparent that there was little effort to the south of the central part of the study area (Figs 2 and 4). Thus the density in that area is a result of extrapolation predicted from the model and this is important in reaching the conclusion. Future survey should try to increase sighting effort (and sightings) in this southern area.

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Factors affecting perpendicular sighting distances on shipboard line-transect surveys for cetaceans

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ABSTRACT

Factors that affect cetacean perpendicular sighting distances are investigated using a Generalised Additive Modelling (GAM) framework to analyse 8,203 sightings of 34 cetacean species seen on 200,000km of shipboard line-transect surveys in the eastern Pacific in 1986-96. Perpendicular sighting distance is modelled as a non-linear function of the following predictor variables: species; an *a priori* species grouping; the logarithm of group size; Beaufort sea state; presence of rain or fog; sighting cue; sun glare; geographic stratum; observer; ship; year; cruise; and, in 1991-96, visibility and swell height. Based on Akaike Information Criteria (AIC), the best model for 1986-96 included all variables except rain/fog code. For the 1991-96 data, swell height anomaly was also important and replaced ship and year in the best-fit model. For independent subsets of the data, GAM coefficients were highly correlated, indicating that many of the same factors were acting in different areas and at different times. Species and sighting methods (25x binoculars vs unaided eye) had the largest effects on perpendicular sighting distances. The *a priori* species groups captured much, but not all of the among-species differences. Two other species-related factors (group size and sighting cue) were also important in all models. Factors related to search conditions (Beaufort sea state and swell height anomaly) and to the searchers themselves (individual observer) were also important. We anticipate that this information on the relative magnitudes of factors affecting perpendicular sighting distance can be used to improve both design and analysis of line-transect data.

KEYWORDS: ABUNDANCE ESTIMATE; SURVEY-VESSEL; LINE-TRANSECT; MODELLING; PACIFIC OCEAN

INTRODUCTION

The distance between a detected group of animals and a transect line is commonly referred to as the perpendicular sighting distance and its measurement is critical to the estimation of animal density using line-transect survey methods. Distributions of perpendicular sighting distances are used to estimate effective strip width (*esw*), a critical line-transect parameter (Buckland *et al.*, 1993). Many factors can potentially affect the perpendicular distance at which any particular group of cetaceans is first seen from a ship at sea. These factors can be roughly categorised as: (1) search conditions (e.g. sea state, swell height, atmospheric conditions, sun glare, visual range, vessel characteristics, search method); (2) group characteristics (e.g. species, body size, group size, activity, diving behaviour, associated animals); (3) observer characteristics (e.g. training, experience, skill, motivation); and (4) chance factors (e.g. position and movement of the group relative to the trackline, coincidence of surfacing behaviour and an observer's field of view). Typically in line-transect analysis, researchers do not attempt to quantify all of these factors; rather, they fit a curve to the pooled distribution of perpendicular distances (for a species) and depend on 'pooling robustness' to allow them to make reliable estimates of animal density (Burnham *et al.*, 1980; Buckland *et al.*, 1993). However, there are limits to pooling robustness and explicit consideration of other factors can reduce bias and improve precision (Buckland *et al.*, 1993).

A number of methods have been used to explicitly incorporate factors that affect perpendicular sighting distance. Perhaps the simplest approach is post-stratification; this approach has been used with group size, sea state, geographic stratum, cloud cover and vessel (e.g. Barlow, 1988; 1995; Buckland *et al.*, 1993). Another approach is to include factors as covariates in estimating a detection function (e.g. Drummer and McDonald, 1987; Ramsey *et al.*, 1987; Borchers *et al.*, 1998) or as terms in a linear model used to scale a detection function (Beavers and Ramsey, 1998).

The opposite of stratification is pooling which has also been used to improve precision in line-transect abundance estimates. As sample sizes become small (typically less than 30-50), the precision of line-transect estimates declines markedly. Pooling similar samples can improve precision with an acceptable increase in potential bias. For example, if too few sightings are made of one species, the detection function for that species can be estimated by pooling with sightings of another species that would, based on size, behaviour, etc, be expected to have a similar detection function (e.g. Barlow, 1995; Jefferson, 1996). The degree to which data are pooled or stratified is a tradeoff between bias and precision (Burnham and Anderson, 1998).

Despite the many examples of large-scale ship line-transect studies for cetaceans, there have been few attempts to examine which factors are most important in determining perpendicular sighting distance. For example, it is not known whether differences in sighting distances between similar species are greater or less than the differences due to sea state or group size. Most studies lack an adequate sample size to stratify simultaneously by all of the factors that might be significant. Model selection by Akaike Information Criteria (AIC) or other objective criteria can also be hampered by insufficient data.

This paper analyses cetacean line-transect data that have been collected on SWFSC (Southwest Fisheries Science Center) marine mammal surveys from 1986-96 in the eastern Pacific Ocean (Wade and Gerrodette, 1993; Barlow, 1995; 1997; Barlow and Gerrodette, 1996). These surveys have covered 200,000km of transect. The resulting 8,203 sightings include at least 34 species ranging in habitat from the tropical Fraser's dolphin *(Lagenodelphis hosei)* to the cold temperate Dall's porpoise *(Phocoenoides dalli)* and in size from the diminutive vaquita (*Phocoena sinus)* to the grand blue whale (*Balaenoptera musculus)*. A generalised additive modelling (GAM) framework is used to fit perpendicular distance data from these surveys as a function of many potentially important factors. This large sample size allows examination of more factors than can normally be studied and provides sufficient statistical power to accurately determine the relative magnitudes of these factors. The generality of the results is tested by comparison of results for two large subsets of data.

METHODS

Field methods

Survey methods remained relatively constant throughout this 11-year study period (Kinzey *et al.*, 2000). Two National Oceanic and Atmospheric Administration (NOAA) ships were used in most years: the 52m *David Starr Jordan* and the 53m *McArthur*. On both ships, the observation height from the flying bridge deck was approximately 10m above the sea surface. The primary team consisted of two observers (port and starboard) searching through pedestal-mounted 25 × 150 *Fujinon* binoculars (typically from 10° on the opposite side of the bow to 90° on their side) and one centre observer searching by unaided eyes and (occasionally) 7 × 50 handheld binoculars. The centre observer was also responsible for recording search effort and sightings data. Observers rotated among these three observation stations for two hours and then had two hours off duty to rest. The vessels surveyed pre-determined transect lines at 10 knots during daylight hours (dawn to dusk). Typically when a marine mammal was sighted, the team went ‘off-effort’ and directed the ship towards the animal(s) to obtain species identity and group size estimates. Immediately after making a sighting (and before turning the ship), the bearing angle from the bow to the animal (or the approximate centre of a group of animals) was measured using a protractor at the base of the 25× binoculars and the distance to the animal (or group) was measured using ocular reticules (Barlow and Lee, 1994; Lerczak and Hobbs, 1998; Kinzey and Gerrodette, 2001).

Although some changes in protocol were implemented during this time period, these are not expected to affect line-transect data collection significantly. A conditionally independent observer position was used intermittently after 1991 to measure the fraction of animals missed by the primary team; however, the person in that position did not disclose sighting information until the animal(s) had passed abeam and had been clearly missed by the primary observer team. In 1991, computer-based data entry replaced a system based on paper forms. At this time, two additional data fields were added: swell height and visibility. In 1996, approximately one third of the effort was conducted in passing mode (not turning towards or approaching cetaceans for identification or enumeration) and a new data field was recorded to indicate survey mode. Recorded variables and transformed variable used in analyses are summarised in the Appendix.

Surveys were designed to cover different geographic areas in each year. The cruises in 1986-90 were designed to estimate the abundance and trends in abundance for all dolphin populations that are affected by tuna fishing in the eastern tropical Pacific. The survey in 1991 was designed to estimate the abundance of all cetaceans in waters off California. The surveys in 1992 and 1993 were designed to estimate the abundance of the central and northern stocks (respectively) of common dolphins *(Delphinus delphis*) in the eastern Pacific. The survey in 1996 was designed to estimate the abundance of all cetaceans in waters off California, Oregon and Washington. SWFSC survey efforts in 1994 and 1995 were not included in the analyses: the former because it sampled a novel environment (the foggy area south of the Aleutian Islands) that was not replicated in any other years and the latter because it was an experimental acoustic survey. Despite differing purposes, all sightings of cetaceans were recorded on all cruises. Approximately 200,000km of tracklines were searched (Fig. 1).

Analytical methods

Perpendicular sighting distance (*PDist*) was modelled in a Generalised Additive Model (GAM) framework (Hastie and Tibshirani, 1990) using SPLUS software. The full regression model can be expressed as:

$$\begin{aligned} E[1n(PDist + 0.5)] = {} & d[Species] + s[Beauf,n] \\ & + s[1n(TotSS),n] + d[Cue] + d[BinoCode] \\ + d[GeoStrata] & + d[Obsvr] + d[Rain / Fog] \\ & + s[SwelAnom,n] + s[Vis,n] \\ & + d[Glare] + d[Ship] + d[Year] \end{aligned}$$

where:

$E[y]$	denotes the expected value of the dependent variable y;
$d[x]$	denotes a separate parameter value for each discrete value of the variable x;
$s[x,n]$	denotes a spline fit to the continuous variable x with n degrees of freedom.

Variable names are as given in the Appendix. Residuals were modelled with a Gaussian distribution, and the identity link function was used (i.e. no link function). *PDist* (in km) was fitted as a transformed variable (*ln(PDist* + 0.5km)) to make deviations roughly symmetrical about the mean value and to construct a model of multiplicative effects on *PDist* (in exploratory analyses, values from 0.1km to 1.0km were added prior to log-transformation and the value of 0.5km was found empirically to work best). *TotSS* was log-transformed to provide greater resolution at low group sizes (where most of the data are clumped). *Beauf* is actually a ranked categorical variable, but was treated as an integer in this analysis. *SwelAnom* and *Vis* are continuous variables. All other independent variables are categorical. Sightings with more than one species were included multiple times (once for each species), but each observation was weighted by the inverse of the number of species present (weight = *1/n*, where *n* = the number of species).

Perpendicular distance models were fitted using step-wise model building based on AIC as implemented in the SPLUS procedure *step.gam*. Models of increasing complexity were built incrementally by testing the addition or deletion of each variable to the prior best model and repeating the process with the new best model. The best model was the one with the lowest AIC value, which effectively is a likelihood criterion penalised for additional parameters. Burnham and Anderson (1998) argue that model selection based on AIC results, on average, is the minimum loss of information. Continuous variables (*Beauf, SwelAnom, Vis* and *TotSS*) were smoothed using a spline-fitting algorithm with variable degrees of freedom. Once these variables were added to the model, each iteration of the step-wise model selection process tested the prior best model against versions of the model that included these variables with higher and lower degrees of smoothing. After the *step.gam* algorithm arrived at an optimal model, the procedure was restarted at that point with a new estimate of the Gaussian dispersion parameter.

Two variables (*Ship* and *Year)* are completely determined by another variable (*CruzNo*) and all could not be included in the same model. The initial stepwise fit was based on *Ship* and *Year*, and additional models were tested by substituting *CruzNo* for both variables. Similarly, *SppGroup* is determined by *Species* and both were not included in the

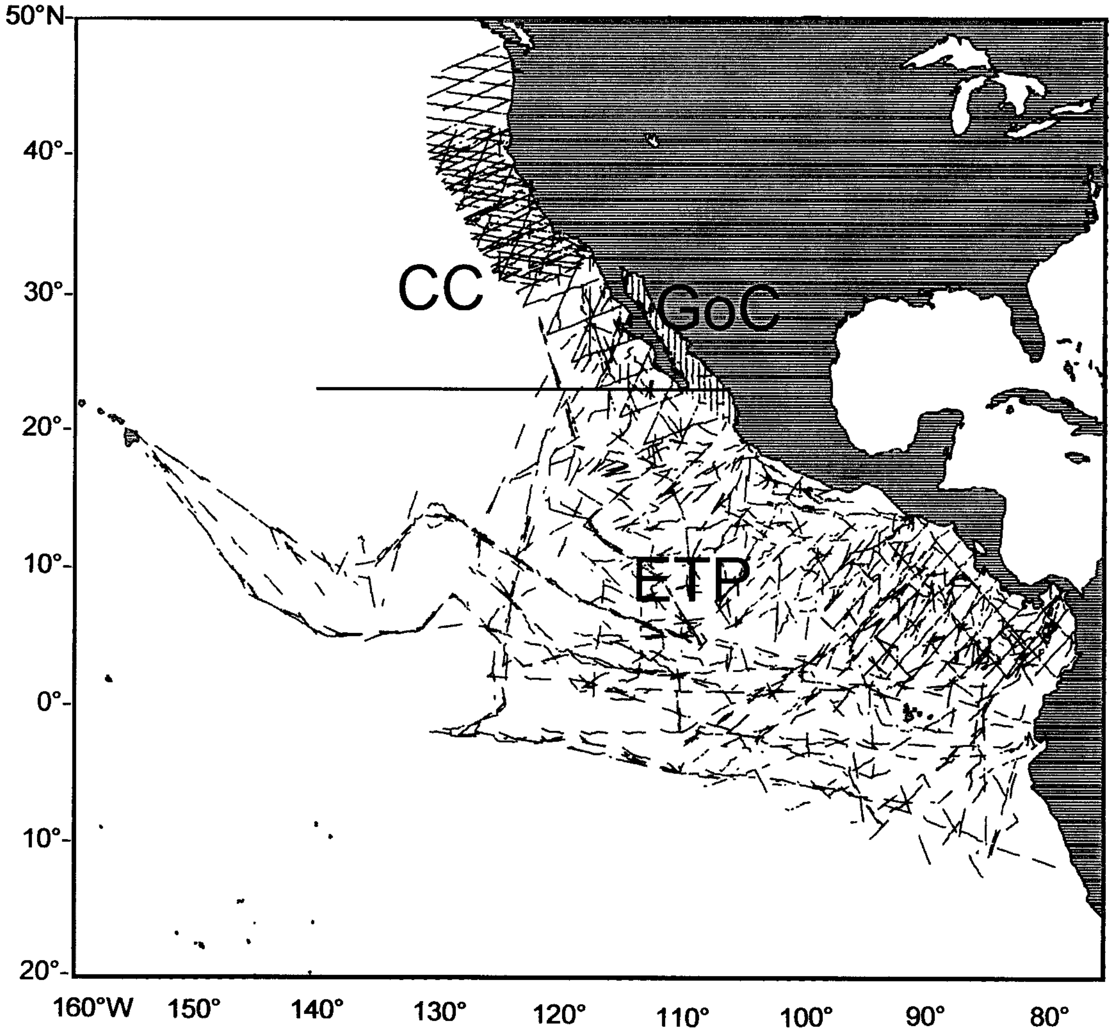

Fig. 1. Sightings used in this paper were made on approximately 200,000km of transect lines surveyed by the SWFSC from 1986-96 in the eastern Pacific Ocean. Three geographic strata are defined by the thick horizontal line at 23°N: the eastern tropical Pacific (ETP), Gulf of California (GoC) and California Current (CC).

same model. Many other strong correlations or associations are expected in the data, especially for *GeoStrata* (with *Year, Species, CruzNo*) and *Species* (with *Cue, Beauf* and *TotSS*).

Vis and *SwelHght* were added in 1991 and subsequent years. The stepwise model building was repeated using these variables (actually *Vis* and *SwelAnom*, see Appendix) and the 1991-96 subset of survey data.

To determine the robustness of GAM coefficients, models were fitted to two subsets of the data that did not overlap geographically: surveys in the eastern tropical Pacific stratum and surveys in the California Current stratum. Geographic stratification variables were excluded because there was no overlap. The sample size of overlapping observers was too small for meaningful comparison, so *Obsvr* was also excluded. Only those species with more than 15 sightings in each area were included. The resulting models fit to these independent subsets potentially included *Beauf, Ln(TotSS), Cue, BinoCode, Ship* and *Species*.

To evaluate various species groupings, the 1986-96 best-fit model based on all the *Species* was compared to two models with different species groups: the *a proiori* grouping (*SppGroup*) given in Table 1 and an *a posteriori* grouping which was based, in part, on the estimated GAM coefficients for each species.

RESULTS

1986-96 data

The step-wise sequence of forward model selection for the 1986-96 perpendicular distance data is given in Table 2. This ‘base model’ included *Ship* and *Year* (in place of *CruzNo*) and allowed either *Species* or *SppGroup* to be added (but not both). Based on minimising AIC, the best model included all variables except *Rain/Fog*. Of the continuous variables, *Beauf* and *Ln(TotSS)* were added as smoothed splines (df = 2 and 7, respectively). Models with AIC differences (ΔAIC) of 2.0 or less are generally considered to be worth further consideration (Burnham and Anderson, 1998) and it was found that a simpler model with almost equivalent explanatory power (ΔAIC = 0.5) could be formulated by excluding *Glare*, by including *Beauf* as a linear term and by

Table 1

Species groups, species codes, common and scientific names used in this paper, number of sightings and normalized GAM coefficients. Species group refers to a subjective classification of species (used first by Barlow, 1995) based on similarities in size, behaviour and other sighting characteristics (his category of 'cryptic species' was split into 'Porpoises' and '*Kogia* spp.'). Spotted and spinner dolphins were of special interest on the 1986-90 surveys and were typically recorded to subspecies or 'stocks'. GAM coefficients (normalised to zero mean) are from the 1986-96 best-fit model using *CruiseNo* in place of *Ship* and *Year.*

Code	Scientific name	Common name	No. sightings	GAM coefficient
Small delphinids				
02	*Stenella attenuata* (offshore)	Offshore pantropical spotted dolphin	741	-0.13
06	*Stenella attenuata graffmani*	Coastal pantropical spotted dolphin	46	0.06
90	*Stenella attenuata* (unid. subsp.)	Unidentified pantropical spotted dolphin	52	-0.01
03	*Stenella longirostris* (unid. subsp.)	Unidentified spinner dolphin	43	-0.04
10	*Stenella longirostris orientalis*	Eastern spinner dolphin	310	-0.20
11	*Stenella longirostris* hybrid	Whitebelly spinner dolphin	178	-0.17
05	*Delphinus* spp.	Unidentified common dolphin	67	-0.14
13	*Stenella coeruleoalba*	Striped dolphin	1,071	-0.03
15	*Steno bredanensis*	Rough-toothed dolphin	167	-0.22
16	*Delphinus capensis*	Long-beaked common dolphin	49	-0.25
17	*Delphinus delphis*	Short-beaked common dolphin	677	-0.14
22	*Lagenorhynchus obliquidens*	Pacific white-sided dolphin	52	-0.14
26	*Lagenodelphis hosei*	Fraser's dolphin	25	-0.14
27	*Lissodelphis borealis*	Northern right whale dolphin	40	-0.17
77	Unid. delphinoid	Unidentified dolphin or porpoise	1,239	0.47
Large delphinids				
18	*Tursiops truncatus*	Bottlenose dolphin	537	-0.14
21	*Grampus griseus*	Risso's dolphin	347	-0.17
31	*Peponocephala electra*	Melon-headed whale	16	-0.06
32	*Feresa attenuata*	Pygmy killer whale	31	-0.38
33	*Pseudorca crassidens*	False killer whale	38	-0.08
34	*Globicephala* spp.	Unidentified pilot whale	86	0.04
36	*Globicephala macrorhynchus*	Short-finned pilot whale	198	0.06
37	*Orcinus orca*	Killer whale	77	0.27
Porpoises				
40	*Phocoena phocoena*	Harbour porpoise	42	-0.41
41	*Phocoena sinus*	Vaquita	14	-0.53
44	*Phocoenoides dalli*	Dall's porpoise	285	-0.18
Kogia spp.				
80	*Kogia simus/breviceps*	Dwarf or pygmy sperm whale	141	-0.34
Small whales				
49	Ziphiid whale	Unidentified beaked whale	152	0.05
51	*Mesoplodon* spp.	Unidentified Mesoplodon	148	0.15
61	*Ziphius cavirostris*	Cuvier's beaked whale	135	-0.21
71	*Balaenoptera acutorostrata*	Minke whale	18	-0.11
78	Unid. small whale	Unidentified small whale	247	0.13
Large whales				
46	*Physeter macrocephalus*	Sperm whale	285	0.46
63	*Berardius bairdii*	Baird's beaked whale	12	0.00
74	*Balaenoptera physalus*	Fin whale	129	0.25
75	*Balaenoptera musculus*	Blue whale	217	0.28
76	*Megaptera novaeangliae*	Humpback whale	98	0.37
99	*Balaenoptera borealis/edeni*	Sei or Bryde's whale	157	0.05
70	Unid. rorqual	Unidentified rorqual	234	0.61
79	Unid. large whale	Unidentified large whale	184	0.58
98	Unid. whale	Unidentified whale	157	0.50
Other				
96	Unid. cetacean	Unidentified cetacean	154	0.02

reducing the spline fit of *Ln(TotSS)* to 4 degrees of freedom. A better fitting model was obtained using *CruzNo* in place of *Ship* and *Year* (ΔAIC = –7.7, Table 2).

The magnitude of the coefficients for each of the variables in the best model is illustrated in Fig. 2 (including the version that substitutes *CruzNo* for *Ship* and *Year*). The q-q plot for this last model (the cumulative distribution of residuals versus the expected normal cumulative distribution, Fig. 3) shows that residuals are symmetrically distributed and are approximately normal within +/–1 standard error, but that the tails of the distribution are shorter than expected for a normal distribution. The q-q plots were similar for all models.

1991-96 data

The initial stages of model building for 1991-96 (which includes two new variables: *SwelAnom* and *Vis*) was similar to the 1986-96 model (Table 3); however, *SwelAnom* and *Rain/Fog* were included and *Ship, Year* and *Glare* were excluded in the best-fit model. The best-fit model used spline fits for *Ln(TotSS)* and *SwelAnom* (df = 5 for both). A model with similar explanatory power (ΔAIC = 1.3) was obtained by using a spline with 4 degrees of freedom for *SwelAnom* (Table 3) and by eliminating *GeoStrata*. When *CruzNo* was added separately to the step-wise best-fit model, a modest improvement was seen in ability to model *PDist* (ΔAIC = –1.5). When *SwelAnom* was excluded from the model

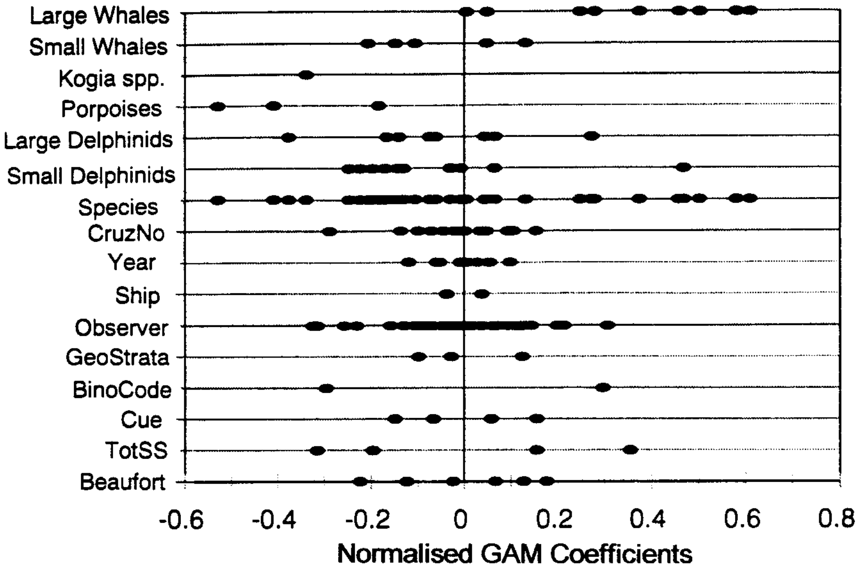

Fig. 2. GAM coefficients (normalised to a mean of zero within each factor) estimated for the best model fit to the 1986-96 sightings using *Ship* and *Year* (Table 1). GAM coefficients are also presented for the same model, substituting *CruzNo* for *Ship* and *Year*. *Species* coefficients were fit separately, but are also grouped by *SppGroup* for presentation here (these groups are not normalised). Coefficients for spline-fits to the continuous variables (*Beauf* and *TotSS*) were replaced with model fits at discrete values (Table 4).

Table 2

Sequential order in which variables were added to and/or deleted from the best GAM fit to 1986-96 data. For continuous variables, parentheses are used to indicate the degrees of freedom for spline smoothing used at that step in the model building. *SppGroup* was used as an alternate for *Species*. The dispersion parameter for modelling residuals was re-estimated and the algorithm was restarted after an optimal model had been found (dashed line); AIC values are not comparable above and below this line. The last three lines represent alternative models substituting *CruzNo* (for *Ship* and *Year*), and *a priori SppGroup* and *a posteriori SppGroup2* (for *Species*).

Model									AIC
BinoCode									4838.5
BinoCode +	*SppGroup*								4522.2
BinoCode +	*Species*								4392.6
BinoCode +	*Species* +	*Ln(TotSS)* (1)							4271.4
BinoCode +	*Species* +	*Ln(TotSS)* (1) +	*Beauf* (1)						4196.0
BinoCode +	*Species* +	*Ln(TotSS)* (1) +	*Beauf* (1) +	*Cue*					4143.3
BinoCode +	*Species* +	*Ln(TotSS)* (1) +	*Beauf* (1) +	*Cue* +	*Ship*				4128.2
BinoCode +	*Species* +	*Ln(TotSS)* (2) +	*Beauf* (1) +	*Cue* +	*Ship*				4119.2
BinoCode +	*Species* +	*Ln(TotSS)* (2) +	*Beauf* (1) +	*Cue* +	*Ship* + *Year*				4110.5
BinoCode +	*Species* +	*Ln(TotSS)* (3) +	*Beauf* (1) +	*Cue* +	*Ship* + *Year*				4106.6
BinoCode +	*Species* +	*Ln(TotSS)* (3) +	*Beauf* (1) +	*Cue* +	*Ship* + *Year* +	*Geostrata*			4104.9
BinoCode +	*Species* +	*Ln(TotSS)* (3) +	*Beauf* (1) +	*Cue* +	*Ship* + *Year* +	*Geostrata* +	*Obsvr*		4101.0
BinoCode +	*Species* +	*Ln(TotSS)* (4) +	*Beauf* (1) +	*Cue* +	*Ship* + *Year* +	*Geostrata* +	*Obsvr*		4099.5
BinoCode +	*Species* +	*Ln(TotSS)* (5) +	*Beauf* (1) +	*Cue* +	*Ship* + *Year* +	*Geostrata* +	*Obsvr*		4099.0
BinoCode +	*Species* +	*Ln(TotSS)* (6) +	*Beauf* (1) +	*Cue* +	*Ship* + *Year* +	*Geostrata* +	*Obsvr*		4098.7
BinoCode +	*Species* +	*Ln(TotSS)* (6) +	*Beauf* (2) +	Cue +	*Ship* + *Year* +	*Geostrata* +	*Obsvr*		4098.5
BinoCode +	*Species* +	*Ln(TotSS)* (6) +	*Beauf* (2) +	Cue +	*Ship* + *Year* +	*Geostrata* +	*Obsvr*		4069.8
BinoCode +	*Species* +	*Ln(TotSS)* (7) +	*Beauf* (2) +	*Cue* +	*Ship* + *Year* +	*Geostrata* +	*Obsvr*		4069.6
BinoCode +	*Species* +	*Ln(TotSS)* (7) +	*Beauf* (2) +	*Cue* +	*Ship* + *Year* +	*Geostrata* +	*Obsvr* +	*Glare*	4069.5
BinoCode +	*Species* +	*Ln(TotSS)* (7) +	*Beauf* (2) +	*Cue* +	*CruzNo* +	*Geostrata* +	*Obsvr* +	*Glare*	4061.8
BinoCode +	*SppGroup* +	*Ln(TotSS)* (7) +	*Beauf* (2) +	*Cue* +	*CruzNo* +	*Geostrata* +	*Obsvr* +	*Glare*	4279.0
BinoCode +	*SppGroup2* +	*Ln(TotSS)* (7) +	*Beauf* (2) +	*Cue* +	*CruzNo* +	*Geostrata* +	*Obsvr* +	*Glare*	4059.3

selection process, the resulting bestfit model did not include any different variables (ΔAIC = 10.1).

Geographic comparisons

GAM coefficients fitted to sightings data from the eastern tropical Pacific and from the California Current stratum (Table 4, Fig. 4) are correlated. The correlation is lower for coefficients associated with species-specific differences in mean perpendicular sighting distance ($r^2 = 0.49$) than for other coefficients ($r^2 = 0.83$). Correlations were calculated from the actual number of parameters estimated for each variable, which is one less than the number of normalised, dummy coefficients given in Table 4.

Species groups

The best-fit model based on all 42 *Species* (Table 1) and using *CruzNo* in place of *Ship* and *Year* (Table 2) was used as a standard for comparison to models with alternative species groupings. The *a priori* species grouping (*SppGroup*, Table 1) performed poorly relative to this

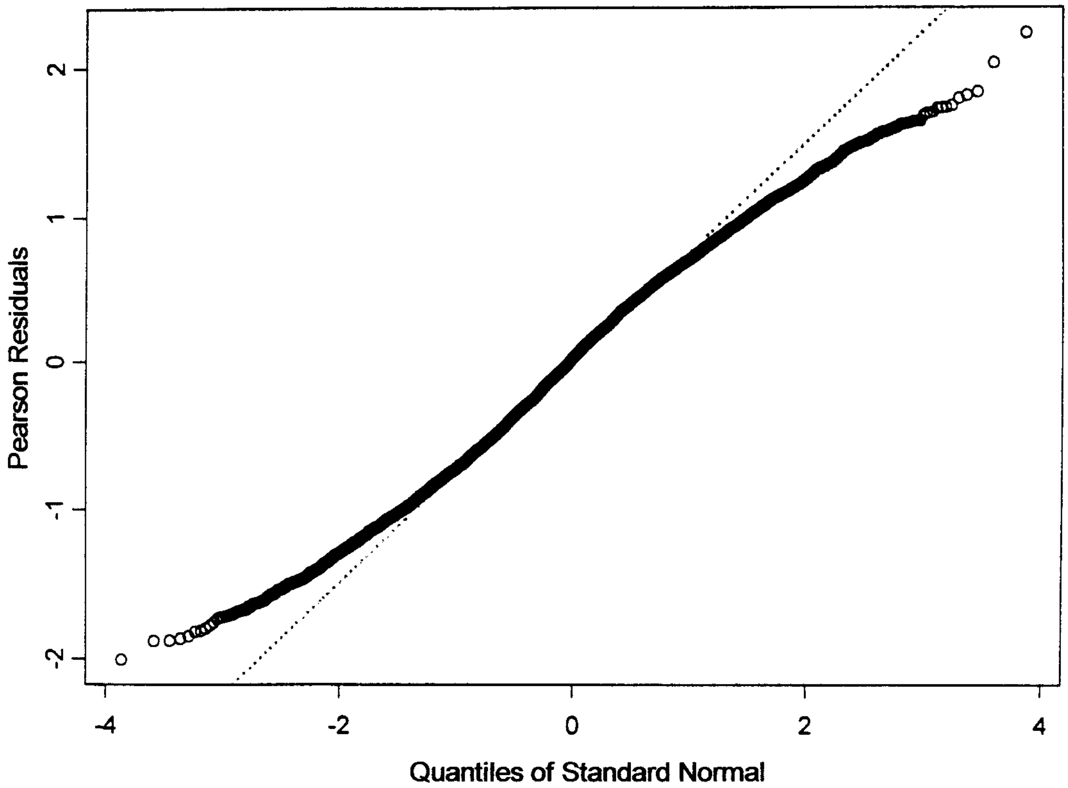

Fig. 3. A quantile (q-q) plot of residuals from one of the models developed here (open circles) compared to the expected quantiles from a standard normal distribution (dotted line). The model fits shown here are from the third to the last in Table 2, but q-q plots from all models were similar.

Table 3

Sequential order in which variables were added to and/or deleted from the best-fit GAM fit to 1991-96 data. For continuous variables, parentheses are used to indicate the order of spline smoothing used at that step in the model building. *SppGroup* was used as an alternate for *Species*. The dispersion parameter was re-estimated and the algorithm was restarted after an optimal model had been found (dashed line); AIC values are not comparable above and below this line.

Model									AIC
BinoCode									1828.6
BinoCode +	*SppGroup*								1696.5
BinoCode +	*SppGroup* +	*Ln(TotSS)* (1)							1665.3
BinoCode +	*Species* +	*Ln(TotSS)* (1)							1590.3
BinoCode +	*Species* +	*Ln(TotSS)* (1) +	*Beauf* (1)						1575.8
BinoCode +	*Species* +	*Ln(TotSS)* (1) +	*Beauf* (1) +	*Cue*					1557.7
BinoCode +	*Species* +	*Ln(TotSS)* (1) +	*Beauf* (1) +	*Cue* +	*SwelAnom* (1)				1544.6
BinoCode +	*Species* +	*Ln(TotSS)* (1) +	*Beauf* (1) +	*Cue* +	*SwelAnom* (1) +	*Rain/Fog*			1539.2
BinoCode +	*Species* +	*Ln(TotSS)* (2) +	*Beauf* (1) +	*Cue* +	*SwelAnom* (1) +	*Rain/Fog*			1536.1
BinoCode +	*Species* +	*Ln(TotSS)* (3) +	*Beauf* (1) +	*Cue* +	*SwelAnom* (1) +	*Rain/Fog*			1533.1
BinoCode +	*Species* +	*Ln(TotSS)* (4) +	*Beauf* (1) +	*Cue* +	*SwelAnom* (1) +	*Rain/Fog*			1531.9
BinoCode +	*Species* +	*Ln(TotSS)* (4) +	*Beauf* (1) +	*Cue* +	*SwelAnom* (2) +	*Rain/Fog*			1530.8
BinoCode +	*Species* +	*Ln(TotSS)* (4) +	*Beauf* (1) +	*Cue* +	*SwelAnom* (3) +	*Rain/Fog*			1529.5
BinoCode +	*Species* +	*Ln(TotSS)* (4) +	*Beauf* (1) +	*Cue* +	*SwelAnom* (4) +	*Rain/Fog*			1529.1
BinoCode +	*Species* +	*Ln(TotSS)* (5) +	*Beauf* (1) +	*Cue* +	*SwelAnom* (4) +	*Rain/Fog*			1529.0
BinoCode +	*Species* +	*Ln(TotSS)* (5) +	*Beauf* (1) +	Cue +	*SwelAnom* (4) +	*Rain/Fog*			1512.3
BinoCode +	*Species* +	*Ln(TotSS)* (5) +	*Beauf* (1) +	*Cue* +	*SwelAnom* (4) +	*Rain/Fog* +	*Obsvr*		1511.2
BinoCode +	*Species* +	*Ln(TotSS)* (5) +	*Beauf* (1) +	*Cue* +	*SwelAnom* (4) +	*Rain/Fog* +	*Obsvr* +	*GeoStrata*	1510.0
BinoCode +	*Species* +	*Ln(TotSS)* (5) +	*Beauf* (1) +	*Cue* +	*SwelAnom* (5) +	*Rain/Fog* +	*Obsvr* +	*GeoStrata*	1509.9

best-fit model (ΔAIC = 217.2, Table 2). Inspection of the GAM coefficients for *Species* (Table 1) indicated that the largest outliers within a *SppGroup* were the sightings that could not be assigned to a species with certainty (unidentified dolphin or porpoise, unidentified beaked whale, unidentified small whale, unidentified rorqual, unidentified large whale, unidentified whale and unidentified cetacean). A new, *a posteriori* species grouping (called *SppGroup2*) was created from the *a priori SppGroup* by keeping these unidentified categories separate (but combining unidentified rorquals and unidentified large whales because of similarities in their GAM coefficients). The identified categories of small delphinids and large delphinids were also combined based on similarities in their GAM coefficients. Based on GAM coefficients, Dall's porpoises were an outlier among the porpoise group, and sperm whales were an outlier among the large whales, so these species were given separate categories. Killer whales were an outlier among the large delphinids, so they were combined with large whales which had similar GAM

Table 4

Comparison of GAM coefficients (normalised to zero mean) estimated by fitting a model of perpendicular sighting distance to sighting data from two non-overlapping geographic strata: the eastern tropical Pacific (ETP) and the California Current (CC). Coefficients for spline-fits to the continuous variables (*Beauf* (d.f.=5) and *LnTotSS* (d.f.=4)) were replaced with model fits at discrete values representing the spread of typical values (*Beauf* = 1, 2, 3, 4 and 5 and *TotSS* = 1, 10, 100 and 1000). Because normalised, dummy coefficients are presented, the actual number of coefficients listed is one greater than the number of parameters estimated for each variable.

		GAM Coefficients	
Factors	Codes	ETP	CC
Intercept		0.456	0.565
Beauf	1	0.150	0.230
	2	0.120	0.170
	3	0.010	0.070
	4	- 0.070	- 0.120
	5	- 0.190	- 0.210
TotSS	1	- 0.130	- 0.320
	10	- 0.080	- 0.080
	100	0.200	0.380
	1000	0.490	0.500
Cue	Bird	0.180	- 0.030
	Splash	- 0.067	0.026
	Mammal	- 0.140	- 0.122
	Blow	0.026	0.126
BinoCode	25x	0.344	0.228
	eye/7x	- 0.344	- 0.228
Ship	DSJ	0.051	- 0.010
	MAC	- 0.051	0.010
Species	Striped dolphin	- 0.017	- 0.382
	Short-beaked common dolphin	- 0.080	- 0.449
	Bottlenose dolphin	- 0.193	- 0.169
	Risso's dolphin	- 0.233	- 0.233
	Killer whale	0.248	0.194
	Sperm whale	0.433	0.371
	Ziphiid whale	- 0.079	0.195
	Mesoplodon spp.	- 0.213	0.049
	Cuvier's beaked whale	- 0.256	- 0.299
	Blue whale	0.291	0.142
	Unidentified dolphin	0.443	0.156
	Unidentified small whale	0.033	0.144
	Unidentified large whale	0.526	0.514
	Kogia spp.	- 0.485	- 0.081

coefficients. Baird's beaked whales and sei/Bryde's whales shared similar GAM coefficients and were separated from the other large whales into a new category of medium sized whales. The resulting *a posteriori* species groups contained 13 categories (Table 5). A model based on this *a posteriori* species group was slightly better than the previous best-fit model using all *Species* (ΔAIC = –2.5, Table 2).

DISCUSSION

'All models are wrong, but some are useful' (Box, 1976).

The analyses presented here are based on perpendicular sightings distance although factors that affect effective strip width (*esw*), a line-transect parameter, are ultimately of greater interest. Mean perpendicular sighting distance is used here as a surrogate for *esw* in order to gain the power and versatility of the Generalised Additive Modelling framework. However, it should be noted that mean perpendicular distance is a sufficient surrogate for *esw* only for the simplest 1-parameter line-transect models (such as the half-normal or negative exponential). Nonetheless, *esw* will be closely related to mean perpendicular distance for any family of line-transect models. It seems probable that any factor that affects mean perpendicular sighting distance will also affect *esw*.

The modelling of perpendicular sighting distance was motivated by a desire to identify the most important factors to be included in future line-transect analyses. The best model for the 1986-96 data included most of the potential variables. This result is not entirely surprising given that the variables were recorded because they were thought to potentially affect the distance at which cetaceans can be seen. Nonetheless, no approach to modelling can guarantee that all of the included variables are truly important. Some of the factors that were included in the best model may just be correlated with causal factors (either other factors in the model or factors that were not recorded).

Based on reductions in AIC, the most important factors affecting mean perpendicular distance were, in order, method of searching (*BinoCode*), differences among species *(Species or SppGroup)*, group size (*ln(TotSS)*), sea state (*Beauf)*, and the cue that lead to the sighting *(Cue*) (Table 2). These factors are intuitive and have long been suspected to be the most important factors affecting *esw*, but this study represents the first empirical demonstration of their importance based on field data.

Species

Species-specific factors are clearly important in determining the perpendicular distance at which cetaceans can be seen. The range of GAM coefficients for different species is greater than the range for any other single factor (Fig. 2). *Species* entered the models second, after *BinoCode*. The *a priori* species groupings captured some, but not all of the among-species differences. Killer whales appear to be an outlier among large delphinids and are seen at greater perpendicular distances. Dall's porpoises are seen at greater distances than the other two species of porpoises. Sperm whales are seen at greater distances and both Bryde's and sei whales are seen at lesser distances than other members of the large whale group. The grouping of species to estimate line-transect detection functions is a valuable tool when dealing with small sample sizes and mixed-species aggregations (Barlow, 1995). Relatively minor adjustments to the species groups (e.g. including killer whales with large whales, combining the other large delphinids with small delphinids, separating Dall's porpoise from the other porpoises and creating new groups for the unidentified categories) resulted in a lower AIC value and hence a better fitting model of perpendicular sighting distance than the model which included all species. The success of these *a posteriori* groupings is somewhat artificial because the groupings were based, in part, on knowledge of GAM coefficients. Nonetheless, use of *a posteriori* species groupings from a GAM analysis may improve precision when estimating *esw* and abundance by line-transect methods.

The 'unidentified' species categories (e.g. unidentified dolphin, unidentified large whale, etc.) were clearly outliers in the species groups and were, on average, seen at greater perpendicular distances than the categories that could be identified to species. This result was not unexpected because animals that are seen further from the ship are less likely to be identified. Indeed, this dependence between the 'apparent' distribution of unidentified groups and distance from the trackline violates one of the primary assumptions of

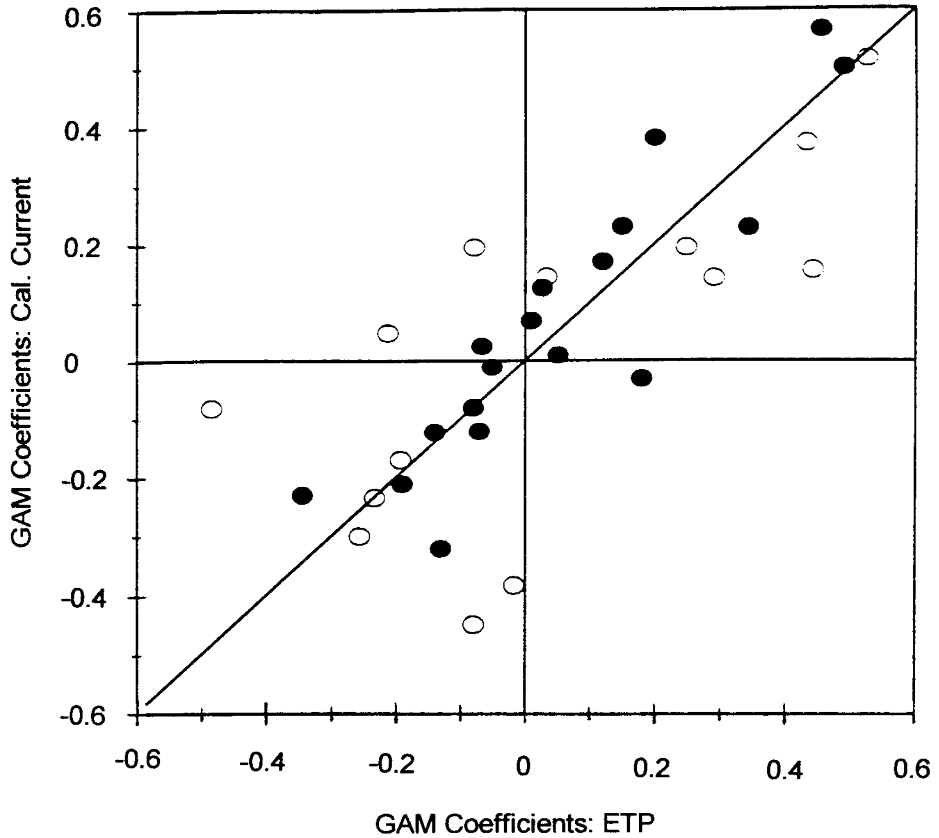

Fig. 4. Comparison of GAM coefficients (normalised to zero mean) estimated by fitting a model of perpendicular sighting distance to sighting data from two non-overlapping geographic strata: the eastern tropical Pacific (ETP) and the California Current. Coefficients for spline-fits to the continuous variables (*Beauf* with 5 degrees of freedom and *TotSS* with 4 degrees of freedom) were replaced with model fits at discrete values (Table 4). Species coefficients are given as open circles, and all others as closed circles. Diagonal lines represents 1:1 parity line. Because normalised, dummy coefficients are presented, the actual number of points plotted is one greater than the number of parameters estimated for each variable.

line-transect abundance estimation. Additional work is needed on appropriate methods for estimating the abundance of groups that cannot be identified to species.

Comparison of the species coefficients for the two non-overlapping data subsets (Table 4) shows two clear outliers: short-beaked common dolphins and striped dolphins. Both of these species were seen closer to the trackline in the California Current than in the eastern tropical Pacific. This difference could be related to behavioural differences between these areas. Common dolphins are much more likely to bow-ride and thus be attracted to ships off California compared to the eastern tropical Pacific. Striped dolphins seldom bow-ride but are frequently associated with bow-riding common dolphins off California; whereas, in the tropics, striped dolphins are wary of ships and are seldom associated with any other species.

Two of the other factors that most affect perpendicular sighting distance (*TotSS* and *Cue*) are also related to species. For fin whale and blue whales, group sizes are typically less than two, whereas for some of the small delphinids, group size may be in the hundreds or even thousands. The relationship between perpendicular sighting distance and the logarithm of total school size is a complicated non-linear function (Fig. 5) but shows a general increase in sighting distances with group size. *Cue* also varies between species, with the *cue* of 'blow' being most common for large whales and some large delphinids and the *cue* of 'splash' being seldom associated with vaquita or harbour porpoise. The *cues* of 'bird' and 'blow' are usually above the horizon and are conspicuous even when sighting conditions are poor; these two *cues* were seen at the greatest perpendicular distances (Fig. 5).

Other factors

Several factors other than species are important in determining perpendicular sighting distances in a predictable manner. *BinoCode* was added first to all models and perpendicular distances are obviously greater when observers search with 25x binoculars compared to naked eye and 7x binoculars (Table 4, Fig. 5). Beaufort sea state was also important and was negatively (and very nearly linearly) related to mean perpendicular distance (the only deviation from linearity appeared between the (rarely observed) Beaufort 0 and Beaufort 1) as seen in Fig. 5. This linear relationship implies that at each higher sea state, mean perpendicular distance (and hence sighting rate) is reduced by a constant proportional amount, as assumed by Beavers and Ramsey (1998).

Differences in sighting distances between individual observers were large and potentially very important. These differences are not unexpected, because sighting distances should be inversely related to sighting rates, and sighting rates sometimes differed among individuals by a factor of two (cf. Hill and Barlow, 1992; Table 5). Individual differences in sighting distances or sighting rates are, however, difficult to interpret because observers work in teams of three with a region of overlap in their search patterns. Groups are unavailable to one observer if they have

Table 5

A posteriori species groups. GAM coefficients (normalised to zero mean) are from Table 1.

Species group and common name	GAM coefficient	Species group and common name	GAM coefficient
Delphinids		**Dwarf and pygmy sperm whales**	
Offshore pantropical spotted dolphin	-0.13	Dwarf or pygmy sperm whale	-0.34
Coastal pantropical spotted dolphin	0.06		
Unid. pantropical spotted dolphin	-0.01	**Small whales**	
Unid. spinner dolphin	-0.04	Unid. Mesoplodon	-0.15
Eastern spinner dolphin	-0.20	Cuvier's beaked whale	-0.21
Whitebelly spinner dolphin	-0.17	Minke whale	-0.11
Unid. common dolphin	-0.14		
Striped dolphin	-0.03	**Unid. small whales**	
Rough-toothed dolphin	-0.22	Unid. beaked whale	0.05
Long-beaked common dolphin	-0.25	Unid. small whale	0.13
Short-beaked common dolphin	-0.14		
Pacific white-sided dolphin	-0.14	**Sperm whales**	
Fraser's dolphin	-0.14	Sperm whale	0.46
Northern right whale dolphin	-0.17		
Bottlenose dolphin	-0.14	**Large whales**	
Risso's dolphin	-0.17	Killer whale	0.27
Melon-headed whale	-0.06	Fin whale	0.25
Pygmy killer whale	-0.38	Blue whale	0.28
False killer whale	-0.08	Humpback whale	0.37
Unid. pilot whale	0.04		
Short-finned pilot whale	0.06	**Medium whales**	
		Baird's beaked whale	0.00
Unid. Delphinoid		Sei or Bryde's whale	0.05
Unid. dolphin or porpoise	0.47		
		Unid. large whales	
Harbour Porpoises		Unid. rorqual	0.61
Harbour porpoise	-0.41	Unid. large whale	0.58
Vaquita	- 0.53	Unid. whale	0.50
Dall's Porpoises		**Unid. cetacean**	
Dall's porpoise	-0.18	Unid. cetacean	0.02

been already seen by another observer. Given the methods, it would be difficult to adjust for individual differences between observers in line-transect abundance estimation. Early in the study, from 1986 to 1990, two teams of three observers were generally constant throughout a cruise, thus it would be possible to consider a line-transect analysis stratified by team. However, since 1991, an open rotation system was adopted and six teams could be defined for each cruise.

The least important factors in determining perpendicular sighting distances in these data are *Ship*, *Year* and *GeoStrata* (in that order, Fig. 2), which provides *post hoc* justification for pooling over these factors in past analyses (Wade and Gerrodette, 1993; Barlow and Gerrodette, 1996).

Interaction effects

Exploration of interaction effects between factors that affect perpendicular sightings distance have been deliberately avoided in this study. Given the large number of important factors, the number of potential interaction effects is enormous and some are certainly important. This exclusion of interaction effects is not intended to downplay their importance. However, the primary aim of the paper is to identify and concentrate on the first-order effects.

The most important interaction effects are probably those that include *Species* and other sighting conditions. Sea conditions (Beaufort and swell height) are more likely to obscure a small *Species* or one producing an inconspicuous *Cue*. *Glare* makes it more difficult to see animals, but backlighting makes blows easier to see. Group sizes span four orders of magnitude and often the ranges do not overlap between species. The effect of group size on perpendicular sighting distance is almost certainly different for different species. There are, however, so many *Species* that interaction effects will be difficult to tease out. Clearly from this analysis, species can be clustered in groups with similar sighting characteristics and these similarities are evident in the similarities between GAM coefficients of *species* within our *a priori* groups. The use of species groups is one possible approach to reduce the dimensionality of the problem and to allow future analyses of interaction effects.

Covariation and colinearity

Some variables included as linear terms were co-linear (i.e. correlated to one another). For example, *CruzNo* determined *Ship* and *Year* effects. In the best model, *Species* & *Cue* and *GeoStrat* & *CruzNo* were pairs of linear terms that would be expected to be correlated. A strong co-linearity may affect the ability to correctly estimate model parameters (Legendre and Legendre, 1998), which may be the ultimate use of the GAM analysis. If model parameters are to be directly used (such as in the Beavers and Ramsey (1998) approach to scaling detection functions), every effort should be made to minimise co-linearities. One useful approach (used here for Beaufort sea state and swell height) may be to express one variable as deviations from expected values based on the other.

Recommendations for design and analysis

The results presented here have implications for both the design and analysis of cetacean line-transect surveys. It is clear that there may be many factors that significantly affect perpendicular sighting distance. In designing surveys, researchers should ensure the accurate recording of as many of these variables as possible so that the information will be

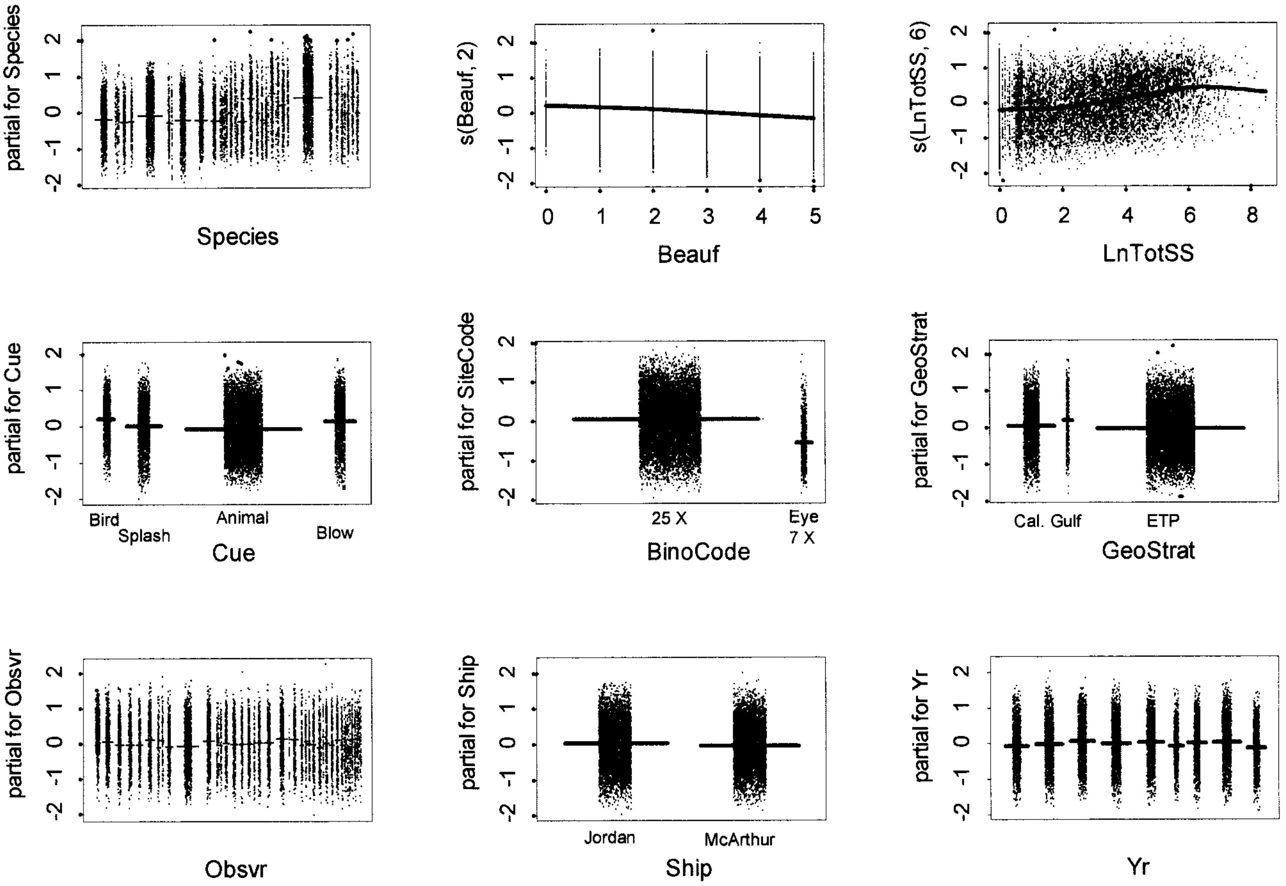

Fig. 5. Partial residuals for significant factors affecting perpendicular sighting distance on 1986-96 surveys based on a generalised additive model. Y-axes represent residual deviations from a model that include all factors other than the one represented on the x-axis. Positive residuals represent greater perpendicular distances from the trackline.

available for analysis. Most notably, Beaufort sea state is not a sufficient descriptor of sea surface conditions and additional important information is contained in swell height.

One encouraging finding, from the perspective of data analysis, is that the species that are similar in size and behaviour have similar mean perpendicular sighting distances (after accounting for other variables such as sighting conditions and group size). This is significant because it greatly increases the ability to estimate the abundance of rare species which might not, by themselves, be seen frequently enough to estimate a detection function. Abundance of these rare species can be estimated by pooling them with other more abundant species; however, this approach would require that other variables that affect perpendicular sighting distance, such as group size, are included as covariates or stratification criteria if the distributions of these variables differ among species.

Another important finding is the relative lack of differences in perpendicular sighting distances among years or between similar vessels (again, after controlling for other variables that do affect perpendicular sighting distance). This is significant because it justifies the pooling of sightings made on different surveys for the purpose of estimating a detection function. This approach is likely to greatly increase the precision of line-transect abundance estimates.

The analyses and results presented here represent a first step in uncovering the factors that most affect *esw* in cetacean line-transect surveys. Mean perpendicular sighting distance was used as a convenient surrogate for *esw* in order to gain the power and flexibility of GAM analysis. However, additional research is needed to extend these analyses to direct estimates of *esw*. Such work is ongoing at our laboratory.

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Surveys of this magnitude cannot be accomplished without the help of innumerable people. We thank the observers, cruise leaders, officers and crews for their years of dedicated work. The chief scientists and cruise coordinators included R. Holt, S. Sexton, K. Mangles, P.S. Hill and A. VonSaunder (also J.B. and T.G.). This manuscript was improved by reviews by M. Ferguson, K. Forney, S. Hedley, T. Schweder and one anonymous referee.

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APPENDIX

Recorded effort variables

Effort variables were recorded at the start of search effort and whenever sighting conditions changed. In addition to time, date, latitude and longitude, these include:

Beauf	Beaufort sea state is a categorical variable that is representative of wind speed as judged by eye based on the characteristics of the ocean's surface (Bowditch, 1975).
Rain/Fog	Rain/fog code is used to indicate the presence of rain, fog, haze, or both rain and fog within the primary search area (typically defined as within 3 n.miles from the ship in the two forward quadrants).
SwelHght	Swell height is an estimate of the height of the dominant swell in feet.
Vis	Visibility is the observers' estimate of the distance (in n.miles) at which a conspicuous cue could be seen if present.
CruzNo	Cruise number is a unique number assigned to each marine mammal survey cruise from the SWFSC. Each year's effort on each ship is given a different cruise number.

Recorded sighting variables

Sighting variables are recorded whenever a cetacean sighting is made. In addition to time, date, latitude and longitude, these include:

RDist	Radial (or line-of-sight) sighting distance is the estimated distance (in n.miles) between the ship and the cetacean(s). *RDist* was typically estimated using reticles in the oculars of the 7x or 25x binoculars but was occasionally estimated 'by eye' for sightings that were made without binoculars or were very close to the ship.
Angle	Sighting angle is the angular deviation of the group from the trackline.
Species	Species codes (Table 1) represent the lowest taxonomic group into which an animal could be classified based on observed field characteristics. For pantropical spotted dolphins and spinner dolphins, sightings were often classified into sub-species or distinct stocks (Perrin *et al.*, 1991; 1994). Some sightings could not be identified to species, in which case the species code represented the lowest taxonomic category for which identification was certain (e.g. *Kogia* spp., or unidentified rorqual). When more than one category of '*Species*' was present within a group, all appropriate species codes were listed with an estimate from each observer of the proportion of that species present in the group. Because a large fraction of *Kogia* spp. and *Mesoplodon* spp. sightings were identified only to genus, these genus categories were used in the analyses.
TotSS	Total school size was estimated as the weighted geometric mean of calibrated group size estimates (Barlow *et al.*, 1988) from all observers who made an estimate. Direct calibration factors for individual observers were

	based on aerial photographic counts of actual school size (Barlow *et al.*, 1998). Indirect calibration factors are based on comparisons with other, directly calibrated observers (Barlow, 1995).
Cue	Cue code represents the aspect of the sighting that first drew the observer's attention to the likely presence of a cetacean. These primarily included bird flocks, splashes, blows and the body of the animal itself.
BinoCode	Sighting code represents the method used by the observer who made the sighting: either 25x binoculars or naked eye/7x binoculars.
Obsvr	Each observer is assigned a unique number. Observer numbers have been assigned sequentially to each new observer and have been used consistently whenever this individual worked on our surveys.
VSun/HSun	Vertical and horizontal sun angles relative to the ship's bow were recorded to provide a measure of the potential effect of sun glare. Horizontal sun angle was recorded in integer bearings from 1 to 12 (based on a clock's face, with 12 o'clock being straight ahead, 3 o'clock being abeam on the starboard side, etc.). Vertical sun angle was recorded in 4 categories: 12 o'clock (directly overhead) to 3 o'clock (on the horizon).

Derived variables

GeoStrata	Geographic stratum represents one of three general areas where surveys were conducted (Fig. 1) and was derived from the recorded latitude and longitude. The areas included the Eastern Tropical Pacific (south of 23°N), the Gulf of California (north of 23°N and east of Baja California) and California Current (north of 23°N and west of Baja California).
SppGroup	Species group is a subjective *a priori* assignment of species into one of seven groups (small delphinids, large delphinids, small whales, large whales, porpoises, *Kogia* spp. and 'other'; Table 1) which are expected to have similar sighting characteristics.
Glare	Sun glare is a binary variable created from the vertical and horizontal sun positions and is used to indicate the presence of glare on the trackline. Based on at-sea experience, sun glare was assumed to be a potential problem if the horizontal sun angle was 11, 12 or 1 o'clock and the vertical sun angle was 2 or 3 o'clock or if the horizontal sun angle was 12 o'clock and the vertical sun angle was 1 o'clock.
PDist	Perpendicular sighting distance is the primary dependent variable in this analysis and was estimated from the radial sighting distance (*RDist*) and the angular deviation of the group from the trackline (*Angle*): *PDist* = *RDist* * sin*(Angle).*
SwelAnom	Swell height is correlated with Beaufort sea state ($r^2 = 0.166$), so the swell anomaly (the deviation of the swell height from that expected for a given Beaufort sea state) was used calculated from regression: *SwelAnom* = *SwelHght* –1.90 –(0.465**Beauf*).

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Cetacean sightings around the Republic of the Maldives, April 1998

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ABSTRACT

In April 1998, as part of a project to collect biopsy samples of putative pygmy blue whales (*Balaenoptera musculus brevicauda*) in the waters around the Republic of the Maldives, Indian Ocean, incidental sightings of cetaceans encountered were recorded. Using modified line-transect methods and handheld binoculars, a total of 267 sightings of 16 species of whales and dolphins were recorded during 20 at-sea days in the northeastern part of the atoll. Significant results include the following: (1) cetaceans were abundant and species diversity was high, including nearly every pantropical species of pelagic cetacean; (2) the spinner dolphin (*Stenella longirostris*) was by far the most common species encountered (56 sightings) and also had the largest mean school size (= 50.3 individuals); (3) blue whales were rare; only four individuals were sighted; (4) a large concentration of Bryde's whales (28 sightings in two days) was apparently feeding in nearshore waters; (5) this paper reports the first records for the Maldives of Cuvier's beaked whale *(Ziphius cavirostris),* Blainville's beaked whale *(Mesoplodon densirostris)* and the dwarf sperm whale (*Kogia sima*): the latter was particularly common (17 sightings); (6) the spotted dolphin *(Stenella attenuata)* was rare and almost always associated with yellowfin tuna (*Thunnus albacares*), spinner dolphin, or seabirds, as has been reported in the eastern Pacific and western Indian oceans.

KEYWORDS: FEEDING GROUNDS; INDIAN OCEAN; SANCTUARIES; INCIDENTAL SIGHTINGS; SURVEY-VESSEL; TAXONOMY; BIOPSY SAMPLING; PHOTO-ID; BLUE WHALE; BRYDE'S WHALE; PANTROPICAL SPOTTED DOLPHIN; SPINNER DOLPHIN

INTRODUCTION

The Republic of the Maldives in the central Indian Ocean consists of an archipelago of approximately 1,200 islands in a series of atolls which straddle the equator from 7°N to 1°S (Fig. 1). These islands are of interest to cetologists for several reasons. First, relatively little is known about the cetaceans of the region; there have been no systematic at-sea surveys for cetaceans in the area, and apart from occasional stranding reports (e.g. Anderson *et al.*, 1999), there is little to indicate which species are present and their relative abundance. This lack of information is significant, as the Maldives are located within the Indian Ocean Sanctuary, established in 1979 (IWC, 1980, p.27) to encourage conservation and research of cetaceans in the area (Anon., 1981).

Secondly, populations of large whales here are of special interest, as they are potentially recovering from commercial exploitation; this situation provides an opportunity to monitor this process. In particular, this area may be critical to the recovery of north Indian Ocean blue whales (*Balaenoptera musculus*), as there is evidence that a resident population occurs in the Sri Lanka/Maldives area (Alling *et al.*, 1991; Ballance and Pitman, 1998). Soviet whalers took 1,294 blue whales from the Arabian Sea during 1963-67 (Mikhalev, 1996) and presumably severely depleted the population because there have been relatively few sightings reported since then. Based on catch data, Mikhalev (1996) recognised four areas of concentration within the western tropical Indian Ocean but the only recent sightings come from the Sri Lanka/Maldives area (Alling *et al.*, 1991; Ballance and Pitman, 1998). The taxonomic status of this population is unclear. Both Alling *et al.* (1991) and Mikhalev (1996) suggested that these were pygmy blue whales (*Balaenoptera musculus brevicauda*). However, because north Indian Ocean blue whales are geographically isolated from known populations of *Balaenoptera musculus brevicauda* farther south, and because a blue whale stranded at Sondip in the Bay of Bengal, India, was described as a separate species (*Balaenoptera indica*; Blyth, 1859; see Rice, 1998 for discussion of type locality), the taxonomic status of the northwestern Indian Ocean blue whale populations remains unresolved (Brownell and Donahue, 1994; Rice, 1998).

Finally, there is substantial interest among Maldivians in understanding and protecting their natural resources, including cetaceans. There is no evidence that large whales were ever hunted here and the only directed take of dolphins (as bait in the fishery for tiger sharks, *Galeocerdo cuvier*) ceased in the early 1960s (Anderson *et al.*, 1999). Today, the capture of cetaceans is banned under Maldivian law (Anderson *et al.*, 1999). Thus, research here, in cooperation with local scientists and resource managers, will encourage maintenance of programmes focused on the biology and conservation of whales and dolphins.

With this in mind, the primary objective of the survey described here was to investigate the status of blue whales around the Maldives and to collect biopsy samples for molecular genetic analysis. A secondary objective was to record occurrence and relative abundance of other cetacean species in the area. Although relatively few blue whales were encountered, considerable information on the status of other cetacean species in the Maldives was collected.

METHODS

The survey was conducted aboard an 18m motor vessel from 2-21 April 1998 (20 days). Effort was designed to maximise chances of encountering blue whales. Thus, tracklines covered primarily the northeastern part of the archipelago,

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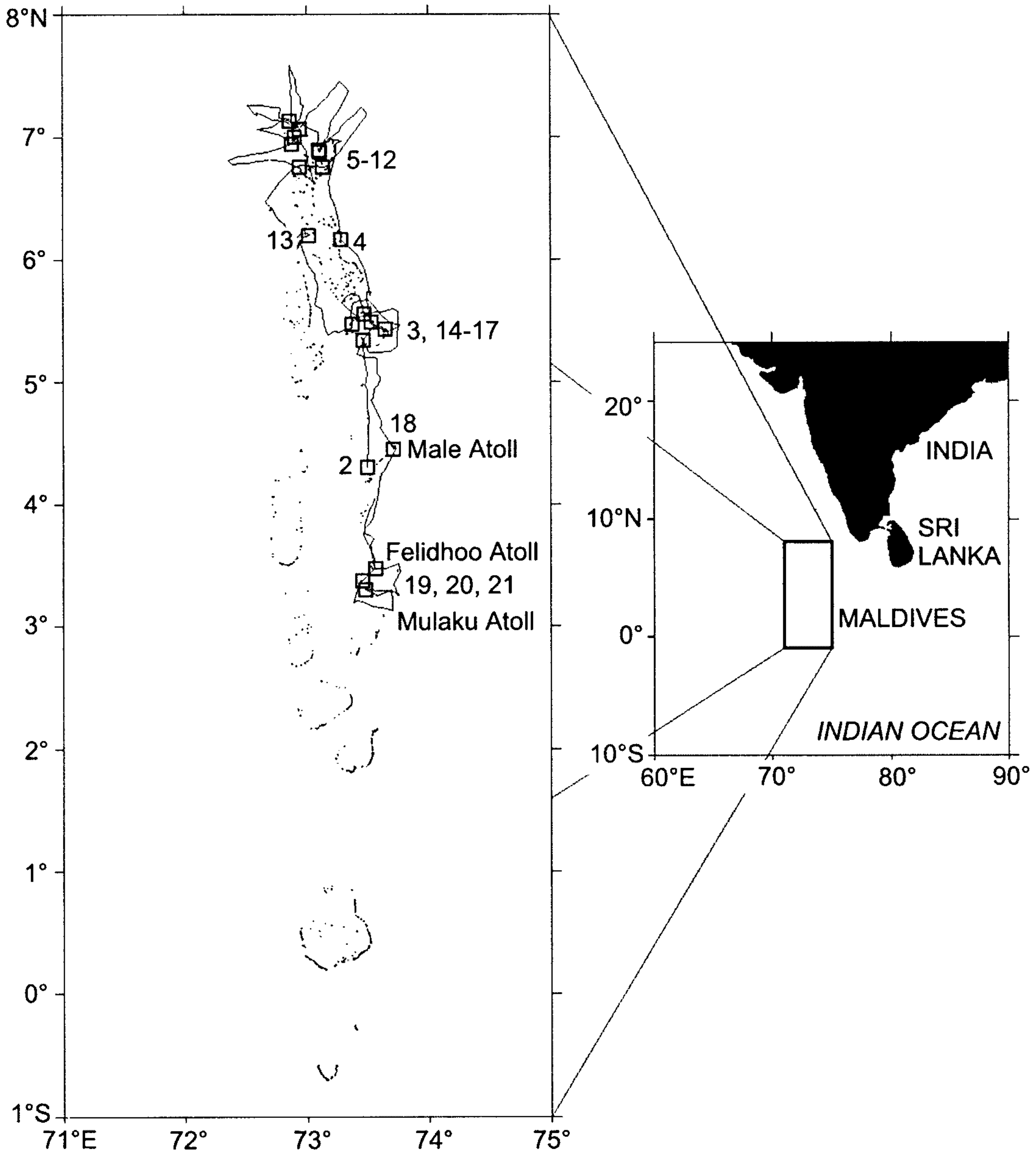

Fig. 1. Map of the Republic of the Maldives and survey effort. Islands can be seen as dots; they outline a series of north-south oriented atolls. Small squares along the trackline represent locations for start of effort on each day. Numbers correspond to dates in April of 1998 where survey effort was focused.

near where this species had been previously encountered (Ballance and Pitman, 1998) and effort was spent almost entirely in deep waters outside atolls (Fig. 1). With the exception of survey in the far north, effort occurred within 50km of the nearest island.

Data were collected using line transect methods (Buckland *et al.*, 1993), modified slightly as follows. Between two and six persons maintained visual watch during all daylight hours, weather permitting, from a platform approximately 4m above the water. Vessel speed was approximately 11km/h (six knots). Observers used handheld binoculars or unaided eye to scan for cetaceans. Every hour, or when conditions changed, vessel position (using a handheld GPS), Beaufort sea state and sighting conditions (excellent, good or fair) were recorded.

When a cetacean sighting was made, vessel position and the estimated distance (nautical miles) and angle to the sighting were recorded, then the vessel was turned and the school approached in order to obtain species identification, estimate school size and make notes on behaviour. For selected species, several types of additional data were collected. Skin biopsy samples were obtained using a crossbow with floating darts fired from the bow of the vessel or from a 3m inflatable launch. All biopsy samples are held at Southwest Fisheries Science Center (contact L.T. Ballance). Selected species were photographed for individual identification purposes, using handheld 35mm cameras and telephoto lenses. Photographs are maintained at Marine Research Centre (contact R. C. Anderson). Acoustic recordings of vocalisations were made using an ITC 1032 hydrophone (flat response from 1Hz to 32kHz and sensitivity of -192dB re 1V/μPa; preamplifier sensitivity of -130dB re 1V/μPa) on 30m of cable and connected to a Digital Audio Tape Recorder. Recordings are held at Alaska Fisheries Science Center/National Marine Mammal Laboratory (contact K. Stafford).

RESULTS AND DISCUSSION

Survey effort totalled 155.5h (mean = 7.8h/d, SE±0.4) and covered approximately 1,700 linear km on effort. Observation conditions were almost always good to excellent. Seventy-nine percent (122.7h) of on-effort time was during Beaufort 0-3; 20% (30.7h) during Beaufort 4, and 1% (2.1h) during Beaufort 5.

Cetaceans were abundant. A total of 267 sightings were recorded, 233 of which were on effort. The mean number of sightings per day was 11.8 (SE±1.5, range 0-21) and the mean encounter rate for the entire survey was 13.6 sightings per 100 linear km.

The cetacean community was also diverse, representing a minimum of 16 species: 2 rorquals, the sperm whale (*Physeter macrocephalus*), the dwarf sperm whale (*Kogia sima*), 2 beaked whales and 10 tropical delphinids (Table 1). With perhaps only the exception of the blue whale, these species comprise the typical tropical cetacean community throughout the world (Mullin *et al.*, 1992; Wade and Gerrodette, 1992; Ballance and Pitman, 1998). Although this survey reports the first records in Maldivian waters for Cuvier's beaked whale (*Ziphius cavirostris*, *cf.* Heyning, 1989), Blainville's beaked whale (*Mesoplodon densirostris*, *cf.* Mead, 1989) and *Kogia sima* (*cf.* Caldwell and Caldwell, 1989), all three are pantropical; their occurrence here is not unexpected. The only pantropical cetacean species that were not sighted during the survey were the melon-headed (*Peponocephala electra*) and killer whale (*Orcinus orca*). Both have been observed around the Maldives (R.C. Anderson, unpublished notes) and there are stranding records for each (Dawbin *et al.*, 1970; Pilleri and Gihr, 1974; Anderson, 1990; Leatherwood *et al.*, 1991; Anderson *et al.*, 1999).

Selected species accounts

Blue whale (Balaenoptera musculus)

This species was rarely encountered. Only four sightings were recorded, all of single individuals (Table 2). Biopsy samples from three individuals were collected and acoustic recordings of three animals were attempted. Subsequent analysis indicated that none were vocalising. It was not possible to confirm the sub-specific identity of any of these four individuals from field observations, and results of genetic analysis of biopsy samples have, to date, been inconclusive (Richard LeDuc, pers. comm.). However, at least two animals had a notably broad head and wide rostrum, indicating that they may have been pygmy blue whales. One of these individuals appeared very thin; the dorsal processes of the vertebral column were clearly visible projecting along the back anterior to the dorsal fin and the lack of tissue lateral to the column resulted in a hollowed-out appearance.

Three of the four animals sighted were diving, each in a localised area, fluking each time. Dive durations (Table 2) are comparable to those recorded from blue whales off Peru with similar behaviour (Donovan, 1984). Although this

Table 1

Species recorded during on-effort periods, listed in decreasing order of number of sightings.

Species	No. of sightings	School Size			Comments
		Mean	SE	Range	
Spinner Dolphin *Stenella longirostris*	56	50.3	10.1	8-400	6 biopsy samples (4 schools); calves present (min 3 schools); associated with birds and/or tuna (1 school)
Bottlenose Dolphin *Tursiops truncatus*	24	6.9	1.3	1-25	2 biopsy samples; calves present (2 schools)
Dwarf Sperm Whale *Kogia sima*	17	1.6	0.2	1-4	Calves present (3 sightings); includes 2 sightings identified as *Kogia* sp.
Unidentified Rorqual	16	1.4	0.2	1-3	Most probably Bryde's whales
Risso's Dolphin *Grampus griseus*	16	9.9	2.1	2-35	Calves present (2 schools)
Short-finned Pilot Whale *Globicephala macrorhynchus*	15	14.5	2.4	4-35	6 biopsy samples (3 schools); identification photographs (7 schools); calves present (2 schools); includes 3 sightings identified as *Globicephala* sp.
Bryde's Whale *Balaenoptera edeni*	12	3.2	1.4	1-15	8 biopsy samples (4 schools); identification photographs (4 schools); acoustic recordings (4 schools)
Striped Dolphin *Stenella coeruleoalba*	9	39.3	8.1	4-90	4 biopsy samples (3 schools); calves present (1 school)
Unidentified Beaked Whale	6	2.3	0.2	2-3	
Spotted Dolphin *Stenella attenuata*	5	50.0	11.6	15-75	3 biopsy samples (3 schools); associated with birds and/or tuna (4 schools)
Blue Whale *Balaenoptera musculus*	4	1.0	0	-	3 biopsy samples (3 sightings); identification photographs (4 animals)
Sperm Whale *Physeter macrocephalus*	3	15.7	8.1	2-30	Identification photographs (2 schools)
Cuvier's Beaked Whale *Ziphius cavirostris*	2	1.5	0.5	1-2	
Blainville's Beaked Whale *Mesoplodon densirostris*	2	2.5	0.5	2-3	
Mesoplodon sp.	2	2.5	0.5	2-3	
Pygmy Killer Whale *Feresa attenuata*	2	22.5	7.5	15-30	1 biopsy sample; calves present (1 school)
Rough-toothed Dolphin *Steno bredanensis*	2	30	10	20-40	1 biopsy sample; calves present (1 school)
False Killer Whale *Pseudorca crassidens*	1	50	-	-	1 biopsy sample
Fraser's Dolphin *Lagenodelphis hosei*	1	40	-	-	3 biopsy samples

pattern can be indicative of feeding, no other feeding indicators such as defecation were observed. One of these individuals appeared very thin; the dorsal processes of the vertebral column were clearly visible projecting along the back anterior to the dorsal fin.

It had been suspected that blue whales would be more frequently encountered. Anderson *et al.* (1999), concluded from strandings in the Maldives that blue whales are most abundant there during January to April. Alling *et al.* (1991) identified a minimum of 35 individuals around Sri Lanka using photographic identification techniques; some of these animals were resighted in different years. Ballance and Pitman (1998) sighted 13 blue whales and 2 unidentified large rorquals that were probably also blue whales in the Eight Degree Channel north of the Maldives during two separate transits in April 1995. A group of 4-5 blue whales was sighted in deep water west of the Maldives in April, 1983 (Leatherwood *et al.*, 1984). A strong El Niño event was recorded worldwide during 1998. In Maldivian waters that year, there were significant increases in sea surface temperature, widespread coral bleaching and coral mortality (R.C. Anderson, unpublished notes). Further monitoring is needed to determine the status of blue whales around the Maldives, spatial and temporal variation in distribution and abundance and to what extent these patterns are affected by interannual variation in oceanographic conditions and irregular, periodic events such as El Niño.

Table 2

Sighting information for blue whales. (Each sighting represents a single whale.)

Date	Latitude	Longitude	Mean ± SE dive time (min)
3 April 1998	5°43.8'N	73°29.4'E	13.9 ± 0.8 (n = 6)
14 April 1998	5°30.1'N	73°39.8'E	7.7 ± 0.7 (n = 14)
16 April 1998	5°15.1'N	73°41.8'E	6.3 ± 0.2 (n = 10)
17 April 1998	5°0.3'N	73°36.0'E	-

Bryde's whale (Balaenoptera edeni)

A dense concentration of this species was encountered in the waters between Felidhoo and Mulaku atolls on 19-20 April (Fig. 1, Table 3). During this time a total of 141.9 linear km was surveyed. Mean encounter rate of Bryde's whales and unidentified rorquals (all of which were probable Bryde's whales) was slightly more than one animal per linear km (mean = 1.2, SE ± 61.6) with a high of 4.5 animals per linear km on one segment. Three-quarters of all our sightings on these two days (28 sightings from a total of 37) were of Bryde's whales or unidentified rorquals.

These whales were diving regularly and not obviously travelling. Although defecation was not observed, it is believed they were feeding. Two whales appeared thin, with the dorsal processes of the vertebral column visible along the back, but most appeared healthy. No calves were sighted in the area.

The taxonomic status of Bryde's whales in the Indian Ocean is unclear. Rice (1998) has concluded that a small form that typically occurs in coastal and shelf waters of the eastern Indian Ocean, the Sunda Shelf and the western Pacific, is referable to *B. edeni*. A larger form is typically found in tropical and warm temperate waters around the world; its description fits *B. brydei*. The animals recorded here are of probably the second, larger form. Genetic analyses of the biopsy samples collected (Richard LeDuc, pers. comm.), as well as catch data records from this area (Y.A. Mikhalev, pers. comm.) support this conclusion. However, because the holotype of *B. edeni* has not been confirmed to be the smaller form, the nominal species name (*B. edeni*) is retained here.

Little is known about the abundance of Bryde's whales in the northwestern Indian Ocean. Between 1963 and 1967 Soviet whaling operations killed 848 in three main areas: the Gulf of Aden, waters around the Seychelles, and near the Maldives (Mikhalev, 1997). The data from this survey indicate that some localised areas around the Maldives may represent important feeding areas for this species. Topographic features, including island archipelagos, are known to be sites of increased productivity due to topographically-induced oceanographic processes which concentrate planktonic prey, with consequent effects on upper trophic levels (e.g. Alldredge and Hamner, 1980; Hamner and Hauri, 1981; Wolanski and Hamner, 1988; Schneider, 1991). Such an effect may have been witnessed here.

Table 3

Sighting information for Bryde's whales.

Date	Latitude	Longitude	Number of animals
7 April 1998	6°53.3'N	72°59.8'E	1
9 April 1998	7°11.0'N	72°34.7'E	1
19 April 1998	3°17.3'N	73°43.4'E	2
19 April 1998	3°21.0'N	73°42.8'E	1
19 April 1998	3°18.2'N	73°31.5'E	1
19 April 1998	3°15.4'N	73°43.4'E	15
20 April 1998	3°15.4'N	73°35.1'E	1
20 April 1998	3°16.4'N	73°30.4'E	12
20 April 1998	3°9.2'N	73°36.2'E	1
20 April 1998	3°17.8'N	73°41.7'E	1
20 April 1998	3°15.4'N	73°35.2'E	1
20 April 1998	3°12.7'N	73°24.3'E	1

Spinner dolphin (Stenella longirostris)

This was by far the most abundant and most frequently sighted species, and the cetacean with the largest mean school size (Table 1). Spinner dolphins were often sighted early in the morning entering atoll lagoons and late in the evening exiting from them. A similar behaviour pattern has been described for this species in Hawaii, except that there, dolphins enter bays of high islands to spend the night (Norris and Dohl, 1980).

The spinner dolphin was also the most abundant species seen in a survey of the pelagic western tropical Indian Ocean (Ballance and Pitman, 1998), where school size was significantly higher ($\bar{x} = 169.8$ dolphins) and diurnal behaviour patterns were different. Recent research has identified significant genetic differences between inshore and offshore populations of what were once considered closely related, or conspecific, to the extent that, for example, offshore populations of cetaceans in different ocean basins may be more closely related than populations in adjacent nearshore waters (e.g. Rosel *et al.*, 1994; Curry and Smith, 1997; Rice, 1998). It is clear that reef-inhabiting spinner dolphins will be subjected to different selective regimes than oceanic populations and character divergence including aspects of behaviour and ecology is to be expected (e.g. Perrin and Gilpatrick, 1994). This may represent an incipient speciation process; molecular genetic studies would be useful in determining the extent of this divergence.

Spotted dolphin (Stenella attenuata)

All sightings of this species were associated with large yellowfin tuna (*Thunnus albacares*, 80% of sightings) or spinner dolphins (40% of sightings). Half of the assemblages with tuna attracted seabirds; one also contained spinner dolphins. Seabirds frequently associate with tuna in the Maldives and local fishermen use flocks to locate tuna, which they capture with hook and line (Anderson, 1996). The association between dolphins and tuna here is restricted to large yellowfin tuna and is much less commonly reported (Anderson and Shaan, 1998). This as-yet-unexplained association between spotted dolphins and yellowfin tuna is a regular feature in the eastern tropical Pacific (Perrin and Hohn, 1994) and is also known to occur in the western tropical Indian Ocean (Ballance and Pitman, 1998).

CONCLUSIONS

Abundance and diversity of cetaceans around the Maldives were remarkable. In a four-month survey of the western tropical Indian Ocean that covered 9,784 linear km, Ballance and Pitman (1998) recorded 589 sightings comprising a minimum of 21 species. The present study represents only 22% of the survey time and 17% of the survey distance reported in Ballance and Pitman (1998); it also represents 45% of the sightings and 76% of the species recorded during the larger spatial and temporal scale survey.

It is well known that habitat diversity is directly correlated with species diversity. The Maldives, with their 1,200 islands, provide a wide variety of cetacean habitat types within a small geographic area, ranging from sheltered lagoons within atolls to deep waters adjacent to the islands. The monsoon adds another layer of complexity with upstream and downstream eddies affecting productivity, and shifting spatially with season. The archipelago extends for almost 1,000 linear km. Given the limited survey coverage here, the Maldives appear to have extensive cetacean resources.

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