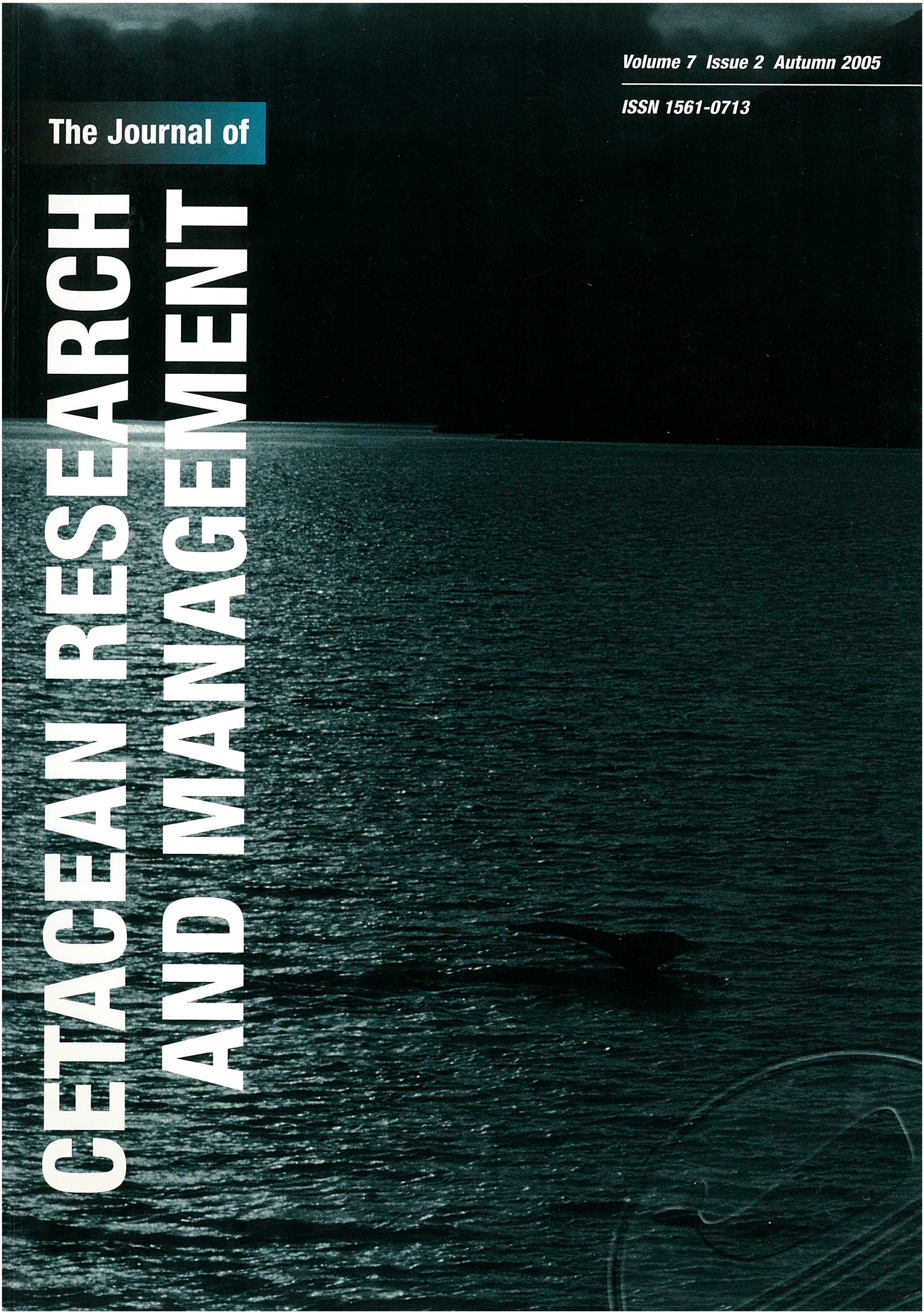
Volume 7 Issue 2 Autumn 2005

ISSN 1561-0713

The Journal of
CETACEAN RESEARCH AND MANAGEMENT



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Editorial

This issue of the Journal follows the 2005 meeting of the International Whaling Commission held in Ulsan, Korea. Details of the Commission meeting will be published in the next *Annual Report of the International Whaling Commission.* The full report of the Scientific Committee will be published in spring 2006 as *J. Cetacean Res. Manage*. 8 (Suppl.). However, as is now traditional, here follows a short summary of the work of the Scientific Committee at the recent annual meeting.

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 of baleen whales. 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) which will include a number of non-scientific matters, including inspection and enforcement. The RMS has been the subject of a considerable amount of discussion within the Commission. The Commission had received a proposal by the Chair of the Commission for an RMS package of measures that he believed was a fair and balanced approach to move to the rapid completion of the RMS. Although this was not accepted as a package by the Commission, there will be a special meeting of the Commission's RMS Working Group during the period leading up to the 2006 meeting in St. Kitts and Nevis.

Implementation Simulation Trials

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

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

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

North Pacific Bryde's whales

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

North Atlantic fin whales

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

Bycatches of large whales

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

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

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

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

(1) to review available methods that have been used to provide estimates of large cetacean bycatches via market samples, including a consideration of their associated confidence intervals in the context of the RMP; and
(2) to provide advice as to whether market-sampling-based methods can be used to reliably estimate bycatch for use in addressing the Commissions objectives regarding total removals over time and, if so, the requirements for such methods.

The Committee agreed that market sampling provided potentially useful methods to supplement bycatch reporting schemes and agreed to a proposal for a follow-up workshop to investigate this further. It also agreed that any such bycatch estimates obtained from market surveys would be improved considerably if carried out in conjunction with the use of data from DNA registers on whales entering the market. Whilst recognising the political sensitivity of market-related issues in an IWC context, the Committee respectfully requested relevant governments to consider a collaborative effort to investigate these methods as a potentially valuable source of information for management and use in the RMP.

Other work to further explore improved bycatch estimation methods for the two approaches noted above is continuing. Improved data reporting for bycatches was also recommended.

REGIONAL WORKSHOPS TO ADDRESS CETACEAN BYCATCH ISSUES

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

In some areas, considerable advances have been made in the assessment and mitigation of cetacean bycatch since the pioneering IWC La Jolla Workshop held in 1990 (Perrin *et al.*, 1994). In other areas, however, little progress has been made and, as a result, a growing number of cetacean species (both large and small) face critical conservation problems as a result of fisheries bycatch. Rather than holding another large generic workshop, it was agreed that given the case- and area-specific nature of the problem, a series of broad-based regional workshops would be more effective, focusing on regions where bycatch problems:

(1) have been given priority by the Scientific Committee as part of its normal review process; and
(2) are not already being addressed.

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

DEVELOPMENT OF AN ABORIGINAL WHALING MANAGEMENT PROCEDURE

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

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

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

ASSESSMENT OF STOCKS SUBJECT TO ABORIGINAL SUBSISTENCE WHALING

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

The present catch limits had been set up to the 2002 season and so at the 2002 meeting, the Committee had to provide management advice for all of the stocks considered. The Commission sets catch limits based on the scientific advice and a 'need' statement from the countries involved.

Eastern gray whales

In 2002, the primary assessment carried out was for the eastern gray whale population (Issue 1 of volume 4 of the *Journal* was devoted to gray whale papers). New information on abundance, distribution, catches and ecology was presented. The population is believed to be close to carrying capacity. The Committee agreed that an annual take of up to 463 whales was acceptable; based on the submitted need statement, the Commission set a total for the 2003-6 seasons of 620 with a maximum of 140 in any one year. The Committee confirmed this advice this year.

Bering-Chukchi-Beaufort Seas stock of bowhead whales

In addition to the work on the *Bowhead SLA*, the Committee has also been examining the status of the Bering-Chukchi-Beaufort Seas stock of bowhead whales. New information in 2002 included a preliminary abundance estimate for 2001 of 9,860 (95%CI 7,700-12,600) giving a rate of increase between 1978 and 2002 of 3.3% (95%CI 2%, 4.7). This year the Committee undertook an in-depth assessment at the 2004 meeting. The primary focus of the in-depth assessment was: (a) the data required for the *Bowhead SLA*; and (b) examining whether the present situation is within the tested parameter space for that *SLA*. The latter effort will include consideration of such issues as stock identity and biological parameters.

The discussions of uncertainty over stock structure issues made it clear that these must form a major component of the forthcoming *Implementation Review*. This *Implementation Review* will begin at the 2006 annual meeting and in particular will examine the robustness of the *Bowhead SLA* with respect to plausible stock hypotheses via simulation trials. If shown to be necessary, this may result in changes to the *Bowhead SLA*. Management advice will be provided at the 2007 meeting based on the best science then available. In providing advice at this meeting, the Committee noted:

(1) the continuing increase in the abundance estimates derived from the census under the recent catch limits and record high calf counts;
(2) the spatio-temporal distribution and opportunistic nature of the hunt and the low numbers of whales struck annually in St. Lawrence Island and Chukotka; and
(3) the development of an extensive research programme that will address questions of stock structure and allow the formulation of one or more plausible stock structure hypotheses.

Given this, the Committee agreed that the *Bowhead SLA* remains the most appropriate tool for providing management advice for this harvest, at least in the short-term. The results of its application at the 2004 meeting showed that no change is needed to the current block quota for 2003-2007. Discussions in 2005 focussed on progress being made in stock structure studies and preparation for the 2007 assessment. A timeline for this work was agreed and the first intersessional workshop will take place in or around March 2006.

Minke and fin whales off West Greenland

In 2002, at the Commission, the same catch limits as previously in force were agreed for the 2003-6 period, i.e. West Greenland minke whales – an annual limit of up to 175 strikes; East Greenland minke whales – an annual catch of up to 12 animals; West Greenland fin whales – an annual catch of up to 19 whales. The Committee had been unable to provide scientific advice on safe catch limits at that time and had stressed that its inability to provide any advice on safe catch limits was a matter of great concern.

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

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

Humpback whales off St Vincent and the Grenadines

In 2002, after considerable debate in the Commission, a catch of up to 20 whales for the period 2003-7 was agreed (the Scientific Committee must review this in 2005). This year, the Committee received positive confirmation that eastern Caribbean humpbacks are part of the West Indies breeding population (abundance in 1992/93 – 11,570, 95%CI 10,100-13,200) and agreed that the catch limit set by the Commission would not harm the stock.

HISTORIC ABUNDANCE ESTIMATION, GENETIC METHODS.

In 2004, in the light of the genetic modelling paper by Roman and Palumbi (2002), the Committee had considered the general methodological issue of estimating *K* and/or pre-exploitation population size in the context of the Committee's assessment work. As a result of its discussions, the Committee agreed that such genetic methods have the potential to be one of a suite of tools that can be used to examine pre-exploitation abundance but that there are a number of limitations and uncertainties that must be considered when examining such data in a present-day management context. The Committee had agreed that the estimates of historic abundance provided in Roman and Palumbi (2002) for the initial pre-whaling population sizes of humpback, fin and common minke whales in the North Atlantic have considerably more uncertainty than reported, and can not be considered reliable estimates of immediate pre-whaling population size. Particularly important in this regard is the mismatch between the time-period to which genetic estimates apply (i.e. the time period is difficult to determine and extremely wide) and the population sizes of whales immediately prior to exploitation. It also agreed that the paper provides no information to suggest that changes are required in either the RMP or AWMP approaches to management.

The Committee had identified further work necessary to assess whether genetically-based estimates of 'initial' abundance can provide useful information for the management of cetaceans and received a progress report on this work at the 2005 meeting.

STOCK IDENTITY

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

A specialist Workshop to examine the use of simulation testing to assess the performance of methods to identify population structure was held in January 2003 (see IWC, 2004c). The Workshop developed a suitable simulation framework to allow evaluation of genetic methods used in inferring population structure both in general terms (the issue is of great relevance to conservation and management outside the IWC) and from a specifically IWC viewpoint (particularly in an RMP/AWMP context).

This is a complex project that must proceed in an iterative fashion. Great progress has been made on the most challenging module, i.e. the development and validation of a program to simulate realistic genetic datasets and the Committee has agreed to hold an intersessional workshop to build on this and begin the testing of some existing methods. This will take place at the University of Potsdam in Spring 2006. Preliminary testing of various methods under certain simple scenarios will begin during the intersessional period.

COMPREHENSIVE ASSESSMENT OF WHALE STOCKS

The 'Comprehensive Assessment' of whale stocks

The development of the concept of the 'Comprehensive Assessment' is reviewed in Donovan (1990). 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 iterative manner towards this, initially concentrating on stocks that have recently or are presently being subject to either commercial or aboriginal subsistence whaling. Some of these stocks have already been discussed in the sections on the RMP and AWMP.

Antarctic minke whales

The Committee has carried out annual surveys in the Antarctic (south of 60°S) since the late 1970s. The last agreed estimates for each of the six management Areas for minke whales (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 analysis of available recent data had suggested that current estimates might be appreciably lower than the previous estimates (e.g. see Branch and Butterworth, 2001).

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

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

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

Southern Hemisphere blue whales

The Committee is beginning the process of reviewing the status of Southern Hemisphere blue whales. An important part of this work is to try to develop methods to identify pygmy blue whales from 'true' blue whales at sea (IWC, 1999a) and progress is being made on this. Work on genetic and acoustic differentiation techniques is continuing and there is considerable progress with morphological methods. Last year, the Committee reviewed a paper by Branch *et al.* (2004) and agreed that this research supported the conclusions that, (1) on average, the Antarctic blue whale population is increasing at a mean rate of 7.3% per annum (1.4–11.6%); (2) had an estimated circumpolar population size of 1,700 (860–2900) in 1996; and (3) that this population is still severely depleted with the 1996 population estimate estimated to be at 0.7% (0.3–1.3%) of the estimated pre-exploitation level.

The Committee has agreed on a number of issues that need to be resolved before it is in a position to carry out an assessment, and progress was made at the 2005 meeting with a view to beginning the assessment process in 2006.

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. Considerable progress has been made in this work and the Committee has agreed that it should give high priority to completing the assessment at the 2006 meeting. To this end, an intersessional workshop will be held in Hobart, Australia in early 2006.

North Atlantic right whales

The Committee has paid particular attention to the status of the North Atlantic right whale in the western North Atlantic in recent years (e.g. see Best *et al.*, 2001). The Committee is extremely concerned about this population, which, whilst probably the only potentially viable population of this species, is in serious danger (*ca* 300 animals). By any management criteria applied by the IWC in terms of either commercial whaling or aboriginal subsistence whaling, there should be no direct anthropogenic removals from this stock.

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

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

Western North Pacific gray whales

This is one of the most endangered populations of great whales in the world. It numbers less than 100 animals (see the paper by Weller *et al.*, 2002) and there are a number of proposed oil and gas-related projects in and near its only known feeding ground. The Committee held a Workshop in October 2002 to review this further. The Workshop report was published in IWC (2004b). Overall, the Workshop agreed with the conclusions of previous reviews on western gray whales. Specifically, that the population is very small, and suffers from a low number of reproductive females, low calf survival, male-biased sex ratio, dependence upon a restricted feeding area and apparent nutritional stress (as reflected in a large number of skinny whales). Other major potential concerns include behavioural reactions to noise (notably in light of increasing industrial activity in the area) and the threat of an oil spill off Sakhalin which could cover all or part of the Piltun area and thus potentially exclude animals from this feeding ground. The Workshop had noted that assessments of the potential impact of any single threat to the survival and reproduction of western gray whales were insufficient and had strongly recommended that risk assessments consider cumulative impact of multiple threats (from both natural and anthropogenic sources).

This year, the Committee welcomed and supported the report (Reeves *et al.*, 2005) and recommendations of the independent scientific review panel (ISRP) that had included five members of the IWC Scientific Committee (Brownell, Cooke, Donovan, Moore and Reeves). It commended SEIC (the Sakhalin Energy Investment Corporation) for requesting this review and IUCN for facilitating the process. Despite some difficulties, it believes that this process represented an important step forward for western gray whale conservation.

The Committee strongly supported efforts to build upon this in the future and to develop a framework for collaborative research, monitoring and mitigation efforts between oil companies, independent experts, national programmes and authorities and the IWC and other intergovernmental organisations. It particularly urged that other companies in the area co-operate with this process.

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

EFFECTS OF ENVIRONMENTAL CHANGE ON CETACEANS

There is an increasing awareness that whales should not be considered in isolation but as part of the marine environment; detrimental changes to their habitat may pose a serious threat to whale stocks. The Committee has examined this issue in the context of the RMP and agreed that the RMP adequately addresses such concerns. However, it has also emphasised that the species most vulnerable to environmental threats might well be those reduced to levels at which the RMP, even if applied, would result in zero catches (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) is to examine the influence of temporal and spatial variability in the physical and biological Antarctic environment on the distribution, abundance and migration of whales. Progress reports on both of these programmes were considered at the 2005 meeting.

The Committee received the report of the intersessional Workshop on Habitat Degradation that took place in November 2004 at the University of Siena, Italy. The Committee stressed the importance of undertaking work relating habitat conditions to cetacean status in the context of conservation and management. It recognised that this is a particularly complex area of study, requiring both theoretical developments in modelling approaches and a commitment to long-term interdisciplinary data collection programmes.

Utilisation of the framework developed at the Workshop will require a much longer-term view to be taken by management and research bodies, although it will eventually result in major improvements in advice to resource managers for conservation and management of cetaceans with respect to predicting the effects of habitat degradation and the effects of many anthropogenic activities, as well as the development of appropriate mitigation measures. The Workshop noted that the continuation of the present *ad hoc* and usually insufficient processes (such as 'Environmental Impact Assessments' based on short-term limited datasets) is unsatisfactory.

The Committee also stressed the value of long-term monitoring of both cetaceans and key aspects of their habitat at appropriate temporal and geographical scales. Baseline data on natural variability in cetacean populations and their habitat are a prerequisite to determining whether anthropogenic changes in the habitat are important to the conservation of cetacean species. Obtaining suitable information on the biotic and abiotic features of habitat will require interdisciplinary efforts and cooperation; spatial modelling approaches are particularly valuable in integrating data on cetacean distribution and abundance with data on their habitat. There is also a need to better understand the feeding and reproductive behaviour of cetaceans, and especially the relationship of cetacean distribution with their prey.

At the 2005 meeting, a symposium entitled 'High Latitude Sea Ice Environments: Effects on Cetacean Abundance, Distribution and Ecology' was held to review information on sea ice environments in the Arctic and Antarctic, and to develop means of incorporating sea ice and similar data into analyses and models used by the Scientific Committee in its work. The symposium identified a number of high priority intersessional projects targeted at issues in both the Arctic and Antarctic. Two Arctic projects were proposed, one focussing on retrospective analyses of sea ice conditions, and the other investigating health status and variability in sea ice. Antarctic projects proposed focussed on issues related to Antarctic minke whale distribution and abundance and sea ice. Finally, the Committee recommended co-operation with two initiatives: Integrated Analysis of Circumpolar Ecosystem Dynamics (ICCED) and the International Polar Year (IPY).

There will be a two-day workshop in advance of the 2006 Annual Meeting to assess the potential for seismic surveys to impact cetaceans.

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).

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

The priority topic for the 2005 meeting was the status of the finless porpoise (*Neophocaena phocaenoides*), of which three sub-species are recognised. Finless porpoises may exhibit multiple populations over relatively small distances (e.g. off Japan), with the result that there may be numerous small and vulnerable populations along their coastal range. No large scale commercial hunts for this species have been recorded, although small scale local hunting may occur. However, incidental mortality is probably substantial throughout the species' range but there is generally little or no bycatch monitoring of these fisheries. Given the limited information on the size of their source populations it is difficult to quantify the population level impacts. The species is in no immediate danger of extinction, but some populations for which the status has been assessed (such as in the Inland Sea of Japan) are apparently declining. A number or recommendations were made to improve knowledge of population abundance, threats and status.

The Committee also reviewed progress on previous recommendations it had made, particularly those concerning the critically endangered baiji and vaquita. The Committee noted that the prospects for the baiji remain extremely poor. It noted that an international Workshop on the Conservation of the Baiji and Yangtze Finless Porpoise took place in late 2004 in Wuhan, China. The Committee did not discuss the pros and cons of *ex-situ* versus *in-situ* approaches but agreed with the conclusion of the workshop that any captured dolphins should be temporarily monitored in a holding-pen prior to their release. It also stressed that the recommendation for a range-wide baiji survey should be implemented as a matter of urgency and any capture efforts be targeted on the most threatened areas while concomitant *in situ* conservation work should be pursued in areas ostensibly subject to lower levels of risk.

The Committee has followed with considerable interest progress on conservation of the highly endangered vaquita (*Phocoena sinus*); several members of the Committee also serve on the International Committee for the Recovery of the Vaquita (CIRVA). This year the Committee was pleased to hear that it had been agreed to declare the highest vaquita concentration area as a refuge for this species.

The Committee has had considerable involvement in the assessment of the harbour porpoise in the North Atlantic and has worked closely with ASCOBANS in the formulation of conservation programmes. Last year the Committee reviewed and endorsed plans for the project Small Cetaceans of the European Atlantic and North Sea, or SCANS-II, which has three primary objectives: to update estimates of abundance from the original SCANS survey area and to obtain estimates for previously unsurveyed areas; to develop a management framework for assessing the impact of bycatches and setting safe bycatch limits; and to develop methods for monitoring small cetacean populations during periods between major decadal surveys. The Committee looked forward to receiving further information on the progress of SCANS-II and raised the possibility of a joint IWC-ASCOBANS workshop.

The Committee also reiterated previous advice concerning the need to minimise or eliminate anthropogenic direct removals or threats to habitat of the humpback dolphin, Irrawaddy dolphin and the Ganges river dolphin.

The Committee agreed to update the present IWC list of recognised species of cetaceans as follows:

(i) Bahamonde's beaked whale (*Mesoplodon bahamondi*) (change to *M. traversii*, recognise common name spade-toothed whale).
(ii) Perrin's beaked whale (*M. perrini*) (recognise species).

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

SCIENTIFIC ASPECTS OF WHALEWATCHING

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 2005 meeting. Last year the Committee endorsed the recommendations of the Workshop on the Science for Sustainable Whalewatching held in Cape Town in March 2004. This year the Committee received a number of papers detailing progress on those recommendations as well as reviewing: whalewatching guidelines and regulations; and new information on dolphin feeding and 'swim-with' programmes. It was also agreed that next year the Committee should review opportunistic sources of cetacean data (including from whalewatching operations) of potential value to the work of the Scientific Committee.

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.

Two continuing permits were discussed this year. JARPNII is a long-term research programme primarily aimed at feeding ecology in the context of contributing to the 'conservation and sustainable use of marine living resources in the western North Pacific, especially within Japan's EEZ.' The programme involves the taking of 150 minke whales, 50 Bryde's whales, 50 sei whales and 10 sperm whales in the western North Pacific. A proposed permit by Iceland, primarily for feeding ecology studies for 100 common minke whales, 100 fin whales and 50 sei whales in each of two years was presented two years ago; the government had only given a permit for 25 common minke whales from Iceland in 2004. Again, as in the past, different views on the value of this research were expressed in the Scientific Committee.

The major discussions this year centred on a new proposal by Japan (JARPA II). The previous JARPA programme was an 18 year programme that finished last year. The complete programme will be reviewed by the IWC Scientific Committee in 2006, when all of the data and analyses become available. The stated objectives of the new long-term research programme proposal are: (1) monitoring of the Antarctic ecosystem; (2) modelling competition among whale species and developing future management objectives; (3) elucidation of temporal and spatial changes in stock structure; and (4) improving the management procedure for the Antarctic minke whale stocks.

The proposed catches for the full programme are: 850 (with 10% allowance) Antarctic minke whales, 50 humpback whales (not to begin for two years) and 50 fin whales (10 in the first two years). There was considerable disagreement over the value of this research both within the Scientific Committee and the Commission. A Resolution was passed (30 votes to 27 votes with 1 abstention) by the Commission that strongly urges the Government of Japan to withdraw its JARPA II proposal or to revise it so that any information needed to meet the stated objectives of the proposal is obtained using non-lethal means. Japan withdrew a proposed resolution in favour of the research programmes.

As in previous years, there was severe disagreement within the Committee regarding advice that should be provided on a number of issues, including: the relevance of the proposed research to management, appropriate sample sizes and applicability of alternate (non-lethal) research methods.

The Committee continued preparations for a full review of the JARPA programme when the complete set of results is available following the completion of the 16-year programme in 2006.

WHALE SANCTUARIES

Last year, when reviewing the Southern Ocean Sanctuary, the Committee endorsed a number of recommendations that were to be implemented generically to the review of sanctuary proposals.

(1) The purpose(s) of IWC Sanctuaries should be better articulated through a set of refined overall objectives (e.g., preserving species biodiversity; promoting recovery of depleted stocks; increasing whaling yield). In particular, the relationships between the RMP and the Sanctuary programme should be articulated.
(2) Appropriate performance measures both for Sanctuaries in general, and the SOS in particular, should be developed. These performance measures should link the refined objectives of the SOS with monitoring programmes in the field.
(3) Systematic inventory and research programmes should be established or further developed so as to build the required information base for a Sanctuary management plan and subsequent monitoring programmes.
(4) A Sanctuary management plan should clearly outline the broad strategies and specific actions needed to achieve Sanctuary objectives.
(5) A monitoring strategy that measures progress toward achieving the Sanctuary objectives should be developed and subsequently implemented. A key component of this monitoring strategy would be the development of tangible indicators to monitor progress. (6) Review criteria that reflect the goals and objectives of the Sanctuary (as described above) should be established.
(7) The Sanctuary management plan should be refined periodically to account for ecological, oceanographic and possible other changes in an adaptive fashion (IWC, 2005, p.50).

This year, the Committee received a request to review a proposal for a South Atlantic Sanctuary, a modified version of a proposal it had reviewed several times in the past. As in previous reviews, there was disagreement within the Committee over whether such a Sanctuary was justified scientifically. The Committee agreed that the information presented in IWC (2004a) remained a reasonable summary of the two primary viewpoints of the Scientific Committee regarding this proposal relative to the most recent guidance from the Commission, although some additional information was produced by those in favour of and those against the Sanctuary.

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Editor

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Erratum: Page 33 of the previous issue (*Journal of Cetacean Research and Management* 7(1)), title should have read '*Balaena*' not '*Balaenoptera*'.

J. CETACEAN RES. MANAGE. 7(2):85–95, 2005

Application of a *Strike Limit Algorithm* based on adaptive Kalman filtering to the eastern North Pacific stock of gray whales

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ABSTRACT

The application of a *Strike Limit Algorithm* (*SLA*) based on Adaptive Kalman Filtering techniques to the eastern North Pacific (ENP) stock of gray whales is described. This *SLA* is a modification of an earlier one which was designed for the Bering-Chukchi-Beaufort Seas stock of bowhead whales. Extended Kalman filters are used to estimate the present stock size and posterior probability distributions for Maximum Sustainable Yield (*MSY*) and *MSY*-rate (*MSYR*). A catch control law selected from a one-parameter family of such rules is then used on the conditional estimates of stock size. These conditional strike limits together with the posterior distributions of the various combinations of *MSYR* and *MSY*, give a cumulative distribution function for the strike limit. The eventual strike limit is then determined as a pre-specified percentile of this distribution. The *SLA* can be tuned to varying degrees of risk by the choice of internal model parameters – so-called tuning parameters. The procedure is tested based on a set of trials specified by the IWC Scientific Committee Standing Working Group on Aboriginal Whaling Management Procedures, designed to test the performance of potential *SLA*s for the ENP gray whale stock.

KEYWORDS: WHALING-ABORIGINAL; MANAGEMENT; GRAY WHALES; MODELLING; MSY RATE

INTRODUCTION

Aboriginal whaling refers to subsistence hunting of large whales by native communities. In the context of aboriginal subsistence whaling a fishery type 2 as defined in IWC (2000) is a case where a substantial amount of information exists about the stock in question. An example of such a fishery is the aboriginal harvesting of the eastern North Pacific (ENP) stock of gray whales (*Eschrictius robustus*). This stock has been studied extensively (e.g. Buckland and Breiwick, 2002; Butterworth *et al.*, 2002a; b; Wade, 2002; Witting, 2003; Punt *et al.*, 2004); stock identity is unambiguous, a series of abundance observations exists (from 1968) and estimates of various parameters are available. However, despite this good information it has not been possible to reconcile the catch history with the observed population increase in recent years using a simple density dependent population model (IWC, 1993). Various adjustments have been proposed in order to address this problem, see for example Butterworth *et al.* (2002b) and Witting (2003). This paper addresses the problem of determining strike limits for this stock such that the nutritional and cultural needs of the hunting communities (as recognised by the IWC) are satisfied without endangering the stock.

The term *Strike Limit Algorithm* (*SLA*) is used in connection with aboriginal whaling. An *SLA* is an input-output rule or algorithm where a data series – usually abundance data —is input into the algorithm which produces as output the total number of whales which can be struck in any one year or block of years. An *SLA* based on Adaptive Kalman Filtering (AKF) applied to the Bering-Chukchi-Beaufort Seas (BCB) stock of bowhead whales *(Balaena mysticetus*) has been presented earlier (Dereksdóttir and Magnússon, 2001; 2003). This *SLA* is fairly general and is applicable with suitable modifications to a range of type 2 fisheries. This paper describes in detail the Adaptive Kalman Filtering *SLA* – hereafter referred to by the acronym AKF-*SLA* – applied to the eastern North Pacific stock of gray whales. This *SLA* forms one of the two component *SLA*s that make up the gray whale *SLA* – known by the acronym GUP, which stands for ‘Grand Unified Procedure’ – recommended by the Scientific Committee of the International Whaling Commission (IWC, 2005) and subsequently adopted by the Commission. The other component is the Johnston-Butterworth *SLA*, which uses a penalised likelihood method (see IWC, 2005 for a technical description). The strike limit produced by the GUP is the arithmetic average of the strike limits produced by each of the component *SLA*s.

The next section describes the AKF-*SLA*, starting with a general description of the basic principles, followed by a detailed mathematical description of the various components, which make up the *SLA*. Finally, some results of testing the performance of the procedure on a set of simulation trials specified by the Standing Working Group on Aboriginal Whaling Management Procedure (IWC, 2005) are given, together with some explorations of its flexibility.

THE ADAPTIVE KALMAN FILTER *STRIKE LIMIT ALGORITHM* (AKF-*SLA*)

General description

The state estimation part of the AKF-*SLA* applies the techniques of the Kalman filter (Kalman, 1960), which is a mathematical tool to obtain estimates of the state of stochastic dynamic systems with noisy observations, i.e. systems with both ‘process noise’ and ‘observation noise’. In the case of a linear system, the estimate obtained is optimal in the sense that the mean square estimation error is minimised. In order to apply Kalman filtering methods, a mathematical model of the dynamics and the relationship between the observations and the true state – i.e. the abundance in this case – is required. The way the Kalman filter works is that the most recent state estimate is projected forward in time (a prediction) until a new observation becomes available. The prediction is then compared to the observation and the state estimate corrected. The correction or update is proportional to the difference between the prediction and the observation. A large difference results in a large correction and a small difference results in a correspondingly small update in the estimate. The proportionality constant, known as the Kalman gain, depends on the magnitude of the measurement noise and the noise in the dynamics. If the measurement noise is large and the level of confidence in the observation therefore low, the gain is small, thus giving a small correction in the model prediction. On the other hand, if the measurement noise is small relative to the process noise and the level of confidence therefore high, the gain will be high and the update thus large. The two extremes are to follow the observation exactly (corresponding to zero observation noise) or to ignore the observation completely and use only the model to obtain the state estimate (corresponding to infinite observation noise). The updated estimate of the state is then projected forward in time until a new observation is made. In the Kalman filtering application presented here, the state of the system is the size of the stock and the observations are the census estimates of the stock size.

The underlying model used in the *SLA* based on AKF is a simple population dynamics model, together with a linear model for the relationship between observed stock size and true stock size. The model contains both process noise and observation noise which are taken to be Gaussian and additive after a log transformation of the variables.

The stock dynamics model and the observation model contain a number of unknown parameters. In the basic application of the AKF-*SLA* to gray whales, two of the parameters, i.e. Maximum Sustainable Yield Level (*MSYL*) and annual survival rate *S* are fixed. The remaining two parameters, i.e. *MSY*-rate (*MSYR*) and *MSY* are estimated by Bayesian methods in conjunction with the Kalman filtering estimation scheme as described below in detail. Each of the two parameters ranges over a sequence of discrete values giving a two-dimensional grid of parameter values. A prior probability distribution is given to the parameter combinations in the grid and a Kalman filter is associated with each combination. Other choices for the parameter grid are possible in variants of the AKF-*SLA*; for example a bias filter can be added giving a three-dimensional parameter grid (see Dereksdóttir and Magnússon (2001) for an application to the BCB stock of bowhead whales).

The probability associated with each parameter combination in the grid is updated by Bayesian methods each time a new survey estimate becomes available. The estimate of the state associated with each of the combinations is updated at the same time by the corresponding Kalman filter. Thus, for each (*MSYR, MSY*) combination in the grid, there corresponds a posterior probability for this particular combination and an estimate of the state (i.e. stock size) conditional on this particular parameter combination. This combination of Kalman filtering and Bayesian methodology is known as AKF. The overall estimate of the present state (stock size) is then obtained by summing all the stock estimates corresponding to the different parameter combinations, weighted by the respective probabilities. This overall stock estimate is not used in the *SLA* described here.

The AKF method therefore comprises a set of Kalman filters – one filter for each parameter combination in the grid. The state estimates and the posterior probabilities associated with each point in the parameter grid and with the corresponding stock estimate are then updated every time a new survey estimate becomes available.

A catch control law selected from a one-parameter family of such rules is then used on the conditional estimates of stock size. These conditional strike limits together with the posterior distributions of the various combinations of *MSYR* and *MSY*, give a cumulative distribution function for the strike limit. The eventual strike limit is then determined as a pre-specified percentile of this distribution.

The AKF-*SLA*: mathematical description

The Kalman Filter

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

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

$$N_t^{obs} = N_t e^{v_t} \tag{2}$$

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 parameters: annual survival rate *S*, pre-exploitation population size (carrying capacity) N_∞ and the resilience parameter *A*, which is related to *MSYR* by $MSYR=A(1\text{-}S)/(S(z(z+1)))$. The exponent *z* in equation (1) determines the *MSYL* according to $MSYL = (z+1)^{-1/z} N_\infty$. This model is a simplification of the usual P-T models since no delay in the dynamics is incorporated.

The state variable is defined to be $x=\ln(N)$ and the observation $y = \ln(N^{obs})$. The state and observation equations can therefore be written in the form:

$$x_{t+1} = f(x_t) + u_t \tag{3}$$

$$y_t = x_t + v_t \tag{4}$$

where:

$$f(x_t) = \ln\left(S(e^{x_t} - C_t) + (1-S)\left(1 + A\left(1 - \left(\frac{e^{x_t}}{N_\infty}\right)^z\right)\right) e^{x_t} \right) \tag{5}$$

The state of the system is estimated by the Extended Kalman Filter (the equation describing the dynamics is non-linear and hence the EKF – in which non-linear functions are linearised – must be used). In order to apply the Kalman filtering method a linearisation of *f(x)* is required:

$$F_t = \frac{\partial f}{\partial x}(x) = \frac{S \cdot e^x + (1-S)\, e^x \left(\begin{array}{l} 1 + A\left(1 - \left(\frac{e^x}{N_\infty}\right)^z\right) \\ -A \cdot z \left(\frac{e^x}{N_\infty}\right)^z \end{array} \right)}{S(e^x - C_t) + (1-S)\left(1 + A\left(1 - \left(\frac{e^x}{N_\infty}\right)^z\right)\right) e^x} \tag{6}$$

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 corresponding variance at time *t* is:

$$P_{t|t-1} = E((x_t - x_{t|t-1})^2) \tag{7}$$

When a new observation y_t becomes available, the estimate $x_{t|t-1}$ is updated according to:

$$x_{t|t} = x_{t|t-1} + K_t(y_t - x_{t|t-1}) \tag{8}$$

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*. 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:

$$K_t = P_{t|t-1}(P_{t|t-1} + r_t)^{-1} \tag{9}$$

The variance $P_{t|t-1}$ is updated by:

$$P_{t|t} = (1 - K_t)P_{t|t-1} \tag{10}$$

$P_{t|t}$ is the variance associated with the updated (posterior) estimate of the state at time *t*.

Finally, new prior estimators of the state and the variance at $t+1$, are obtained by the forward projection equations:

$$x_{t+1|t} = f(x_{t|t}) \tag{11}$$

$$P_{t+1|t} = F_t P_{t|t} F_t^T + q_t \tag{12}$$

where F_t is given by equation (6) and the linearisation is about the point $x=x_{t|t}$. 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.

Initial values for x_0 and P_0 (the state with an associated variance) are required to start the filter. The natural starting value is the pre-exploitation stock size N_∞, provided the catch history is fully known and the stock dynamics can be described by a standard density dependent model. This approach is adopted in the BCB bowhead version of the AKF-*SLA* (Dereksdóttir and Magnússon, 2003). However, neither of these conditions are fullfilled for the ENP gray whale stock so this does not work here. Since the first gray whale abundance estimate was in 1968 it would seem natural to start the filters in that year. However, this entails that all trajectories pass through the value of the 1968 estimate (i.e. 12,921), which might be regarded as an unreasonable constraint since this estimate is no more correct than subsequent ones. One way to avoid forcing the trajectories through the 1968 estimate is to start the filters earlier and either use this earlier starting value as an additional parameter to be estimated or simply start at an arbitrary value with some associated variance.

We have selected 1930 as the starting year for the filters. The initial condition for the Kalman filters is therefore a stock estimate for 1930 together with an associated coefficient of variation (*CV*). However, since no abundance estimate from 1930 exists, the starting value and the associated variance can be freely chosen and used as tuning parameters. The 1930 population size is normalised by the carrying capacity N_∞, i.e. the 1930 population size N_{1930} is defined by a tuning parameter, α, where $N_{1930} = \alpha N_\infty = (MSY/(0.6MSYR))$ with an associated *CV*, P_0, which is also used as a tuning parameter. The first update is made in 1968 when the first abundance estimate becomes available.

Bayesian estimation of model parameters

Equation (1) contains four unknown parameters, *S, A, z,* and N_∞. Two of those, *z* and *S* are fixed at 2.39 (corresponding to the standard choice of $MSYL = 0.6\ N_\infty$) and 0.97 (this value lies well within the likelihood range obtained in Butterworth *et al.* (2002b) and in Wade (2002)), respectively and the others – i.e. the resilience parameter *A* and the carrying capacity N_∞ – estimated by Bayesian methods, or rather, the equivalent parameters *MSYR* and $MSY=MSYR\cdot 0.6\ N_\infty$ are estimated. The reason for estimating *MSYR* and *MSY* rather than *MSYR* and N_∞ is that the latter two parameters are usually highly negatively correlated. Each of the two parameters range over a sequence of discrete values giving a 2-dimensional grid of ($MSYR_i$,MSY_j), *i*=1,..., *I*; *j*=1,..., *J* values. To each of the *IJ* pairs there corresponds an extended Kalman filter. In the ENP gray whale version the (*MSYR, MSY*) parameter grid is made up of *MSYR* values 1%, 2%,..., 5% and 6% and *MSY* ranging from 100 to 2176 in increments of 12, i.e. 6 values of *MSYR* and 174 values of *MSY*, giving a total of 1,044 parameter combinations and the same number of filters. A few words about the range and the increments in the grid selected are appropriate here. Obviously, the number of filters should be kept low for computational reasons. That being said, there are two criteria to consider: the range of values should be sufficiently large for parameter values outside the range to have negligible probability; and the grid fine enough for the calculated probability distribution functions to be reasonably smooth and without 'gaps'. This question will be addressed below, but we note that the range of *MSYR* values in Butterworth *et al.* (2002b) and Wade (2002) is within the 1-6% range used here. Furthermore, those authors consider a carrying capacity greater than 60,000-70,000 to be unlikely. A maximum value of 60,000 for carrying capacity and 6% for *MSYR* gives (assuming *MSY*=0.6), *MSY*=0.6×60,000×0.006=2160 which is very close to the maximum *MSY* value in the grid. However, the ultimate test of the size and fineness of the grid lies in the calculated posterior distributions, which will be presented below. Since there is no prior information on the values of the parameters *MSYR* and *MSY*, the prior distribution for the parameter set ($MSYR_i$, MSY_j), *i*=1,2, .., *I*; *j*=1,2, …, *J*, is assumed to be discrete uniform on the specified grid. This probability distribution is updated every time a new census estimate becomes available.

Whenever a new observation becomes available, the conditional stock estimate $x_{t|t-1}$ ($MSYR_i$, MSY_j), is updated as described above and the posterior probability distribution $p(MSYR_i,\ MSY_j|Y_t)$ is updated for each of the pairs of parameters by Bayesian methodology. Here Y_t is the set of observations up to and including time *t*. The probability distribution is updated as follows.

Let κ denote the vector of parameters (*MSYR*,*MSY*). There are *IJ* possible values of κ corresponding to the *IJ* pairs ($MSYR_i$, MSY_j). A prior distribution, $p(\kappa_k)$ for the vector κ is given and each time a new observation becomes available, a posterior distribution, $p(\kappa_k|Y_{t=1})$ is updated according to:

$$p(\kappa_k \mid Y_t) = \frac{p(Y_t \mid \kappa_k)p(\kappa_k)}{p(Y_t)} \tag{13}$$

where the conditional distribution $p(Y_t|\kappa_k)$ is given by the recursive formula:

$$p(Y_t \mid \kappa_k) = \frac{1}{(2\pi)^{1/2}(P_{t|t-1}+r_t)^{1/2}} \exp\left(-\frac{(y_t - x_{t|t-1})^2}{2(P_{t|t-1}+r_t)}\right) p(Y_{t-1} \mid \kappa_k) \tag{14}$$

where $x_{t|t-1}$, and $P_{t|t-1}$ depend on κ_k and are obtained by the Extended Kalman Filter method. A 'small' prediction error $y_t - x_{t|t-1}$, gives a 'high' value of $p(Y_t|\kappa_k)$. Finally, $p(Y_t)$ is calculated by:

$$p(Y_t) = \sum_{k=1}^{IJ} p(Y_t \mid \kappa_k) p(\kappa_k)\,. \tag{15}$$

To each abundance observation there is an associated estimate of the *CV*. The variance of the measurement noise ν_t is given by:

$$r_t = Var(v_t) = \ln(1 + CV(N_t^{obs})^2) \tag{16}$$

The estimate of *CV*, CV_{est}, in (16) is probably an underestimate of the true *CV* of the abundance estimate. The historical observations of the abundance of gray whales with the given *CV* are not compatible with a standard density dependent population model and a constant CV_{add} is therefore added to all *CV* – estimates (historical and future) provided to the *SLA*. This value is treated as a tuning parameter.

This scheme described here for updating the state estimate and the conditional probability distribution associated with the parameter values is the AKF.

Catch Control Law

Applying a catch control law corresponding to each of the *IJ* pairs of (*MSYR,MSY*) to $x_{t|t-1}$ ($MSYR_i$,MSY_j) a sequence of *IJ* strike limits is obtained, together with the associated posterior probability distribution $p(MSYR_i,MSY_j|Y_t)$, i=1,2,…, I; j=1,..., J. Arranging all the *IJ* strike limits in an increasing sequence, the associated probability distribution makes it possible to construct the cumulative distribution function $F(C)$ for the strike limit. Once a percentile γ of this distribution is set, a provisional strike limit is determined by solving:

$$F(C_t) = p(C < C_t) = \gamma \tag{17}$$

for C_t. A one-parameter family of catch control laws is used. If the stock size *N* is less than *MSYL*, then the conditional strike limit is determined by the rule $C=\rho RY$, relating catch and replacement yield (*RY*) as calculated from equation (1), and by $C=\rho MSY$ if *N* is greater than *MSYL*. The multiplier ρ is a function of the conditional estimate of the stock size (i.e. conditional on *MSYR* and *MSY*) and is chosen from a family of continuous piecewise linear functions. This family is parameterised by β, the ρ-value at 0.5*MSYL*. The multiplier ρ depends on *N* as follows:

$$\rho = \begin{cases} 0 & N < 2000 \\ \dfrac{\beta}{(0.5MSYL - 2000)}(N - 2000) & 2000 < N < 0.5MSYL \\ \dfrac{(0.8-\beta)}{0.4MSYL}(N - 0.5MSYL) + \beta & 0.5MSYL < N < 0.9MSYL \\ \dfrac{N - 0.9MSYL}{MSYL} + 0.8 & 0.9MSYL < N < MSYL \\ 0.9 & MSYL < N \end{cases} \tag{18}$$

The parameter β is a measure of the steepness of the catch control law (Fig. 1) and is used as a tuning parameter. A strike limit is then set as:

$$SL_t = \min\left(C_t, Need_t\right) \tag{19}$$

where $Need_t$ is the pre-specified level of aboriginal need in year *t*. All components refer to the 1+ component of the population, i.e. the total number of animals one year and older.

A so-called 'Snap to Need' feature is incorporated whereby the strike limit is increased to need if the provisional strike limit resulting from the *SLA* exceeds 95% of need, and finally, a maximum of 20% change in strike limits between years is imposed. The strike limit is set for 5-year blocks at a time.

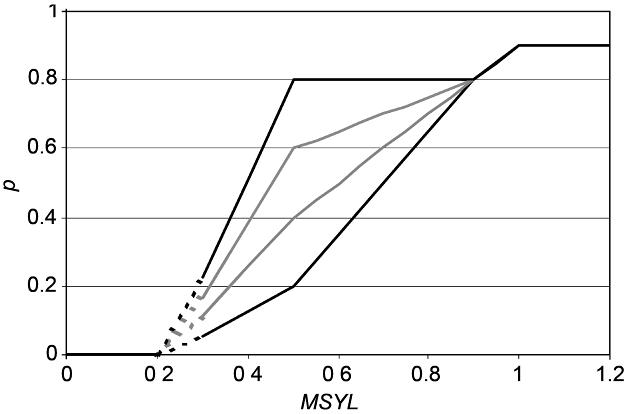

Fig. 1. A family of continuous piecewise linear catch control laws with β = 0.2, 0.4, 0.6 and 0.8. The parameter ρ is the fraction of replacement yield resulting from the catch control law, i.e. $C = \rho RY$.

RESULTS

A set of simulation trials – where each trial consists of 100 replicates simulated stochastically over a 100 year management period, starting in 2003 – for evaluating the performance of *SLA*s for the ENP gray whale stock have been developed; for a full description of all the trials see IWC (2005). The trials are conditioned on data for this stock, i.e. on the partial history of catches, past stock estimates, and parameter values. However, as mentioned above, this stock poses a problem since it is not possible to reconcile the catch history with the observed population increase in recent years (since 1968) using a simple density dependent population model (IWC, 1993). This problem is bypassed in the simulation trials by starting the population projections in 1930 – assuming a stable age distribution and ignoring the earlier catch history – rather than with a pre-exploitation stock size. The population rate of increase in 1930 is selected such that if the population dynamics model is projected from 1930 to 1968, the size of the 1+ component of the population in 1968 (the year of the first census) equals a pre-specified value, P_{1968}, selected from a probability distribution. Trials were also conducted with a so-called inertia model (Witting, 2003; IWC, 2004), which is quite different from the simple density dependent model. The performance of the various candidate *SLA*s was evaluated from a set of calculated performance statistics, designed to capture how well aboriginal need is satisfied, the risk to the stock as well as the stability of strike limits. For a full definition of all the performance statistics, see IWC (2003).

The criteria underlying the final choice of the variant and the tuning of the *SLA*, are of course the trial results, but we will also look briefly at the ability of the algorithm to detect the true *MSYR* value and to estimate the true stock size. We only present the Depletion and Need satisfaction statistics of a few key trials, GE01, GE04, GE10, GE16 and GE45 (Table 1). Note that need is set at 150 for 2003 and generally increases linearly over the management period to the value given in the column headed 'Final need'. Depletion is defined as the size of the population as a fraction of the carrying capacity and need satisfaction is the number of whales which can be struck as a fraction of the pre-specified aboriginal need. The present gray whale evaluation trials do not really pose a challenge to *SLA*s with a couple of exceptions. Need can be fully satisfied in most cases without depleting the stock unduly. The only exceptions are trials GE04 (high *MSYR* and negatively biased future observations) where need is not satisfied in spite of the stock being well above *MSY* level, GE16 (time varying bias on the historical observations, low *MSYR* and high need) and GE45 (time varying bias on the historical observations, low *MSYR* and the stock crashes in 1999/2000) where the stock may end up too depleted.

Tuning parameters and sensitivity

The gray whale version of the AKF-*SLA* contains the following tuning parameters:

(1) β: Height of the breakpoint at 0.5*MSYL* in the catch control law;
(2) γ: Percentile in the cumulative distribution function for the nominal catch limit;
(3) α: Stock size in 1930 as a fraction of carrying capacity N_∞, i.e. $N_{1930} = \alpha N_\infty$;
(4) P_0: Variance associated with N_{1930};
(5) CV_{add}: Additional variance added to the *CV* given to the *SLA*.

The variance in process error is not used in the tuning process, but is fixed at q=0.001 (corresponding to a *CV* of 3.2%). The values of all these tuning parameters were selected subjectively, rather than by attempting to optimise some function of the trial results. Tests show that the trial results are not sensitive to the value of β and this parameter was therefore fixed at 0.7 throughout. The cumulative distribution function for the nominal catch limit is shown in Fig. 2 for β=0.7. This function is 'nice and smooth' without the step function behaviour which occurred occasionally in the application of the AKF-*SLA* to the BCB stock of bowhead whales (Dereksdóttir and Magnússon, 2003). The results deteriorated as P_0 was increased and this parameter was therefore fixed at zero.

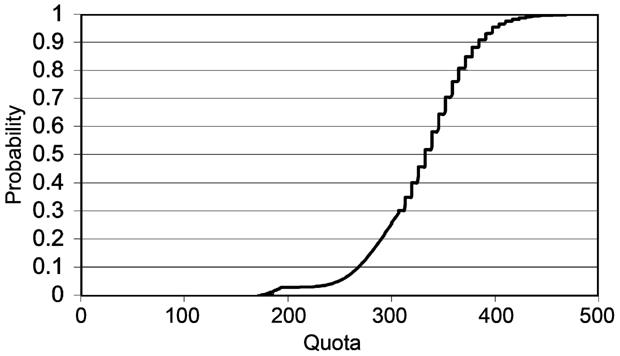

Fig. 2. The cumulative distribution function for the strike limit at the beginning of management (2003) for a set of (*MSYR, MSY*) filters.

Since the historical abundance estimates fluctuate rather wildly, in fact too much if the estimated *CV* is to be believed, it was considered necessary to increase this *CV* estimate to limit the consequent *SLA* fluctuations. However, the value of CV_{add} should not be set so high that the future observations are more or less ignored. In an attempt to achieve some balance between these two conflicting objectives, values of CV_{add}=0.10 and 0.15 were (subjectively) selected. Fig. 3 shows – for one simulation of trial GE16 – how the estimated trajectory tracks the observations more closely for small values of CV_{add}. The reason for the slight 'kink' in the true trajectory 1992-93 is that there was no hunting in those two years. There is considerable discrepancy between the true and estimated trajectories in the early part of the historical period 1968-2003. The estimated trajectory follows the observations, which are well below the true trajectory to begin with. The reason lies in the negative bias in the historical observations, which changes from 0.5 to 1.0 from 1968 to 2003. The agreement between the true and estimated trajectories from 2003 onwards is quite good.

The impact of the 1930 parameter α with values of 0.20, 0.25 and 0.30 together with the above two values of CV_{add} (0.10 and 0.15) and values of γ in the range 0.3-0.8 was investigated for two of the key trials GE16 and GE04 by plotting simultaneously the points for depletion statistic in the former and the need statistic in the latter (Fig. 4). Obviously, the further to the right (better depletion in GE16) and higher up (higher need satisfaction in GE04) the points lie, the better. Thus, a triple (α, CV_{add}, γ) of the three tuning

Table 1

Specifications for a few key gray whale evaluation trials for which results are reported.

Trial	Description	$MSYR_{1+}$	$MSYL_{1+}$	Final need	Survey freq.	Historical survey bias	Future survey bias
GE01	Base case	3.5%	0.6	340	10	1	1
GE04	Future negative bias	3.5%	0.6	340	5	1	1→0.5 in yr 25
GE10	$MSYR_{1+}$ = 5.5%	5.5%	0.6	340	10	1	1
GE16	$MSYR_{1+}$ = 1.5%; high need	1.5%	0.6	530	10	0.5 -> 1	1
GE45	GE16+40% die in 99/00	1.5%	0.6	340	10	0.5 -> 1	1

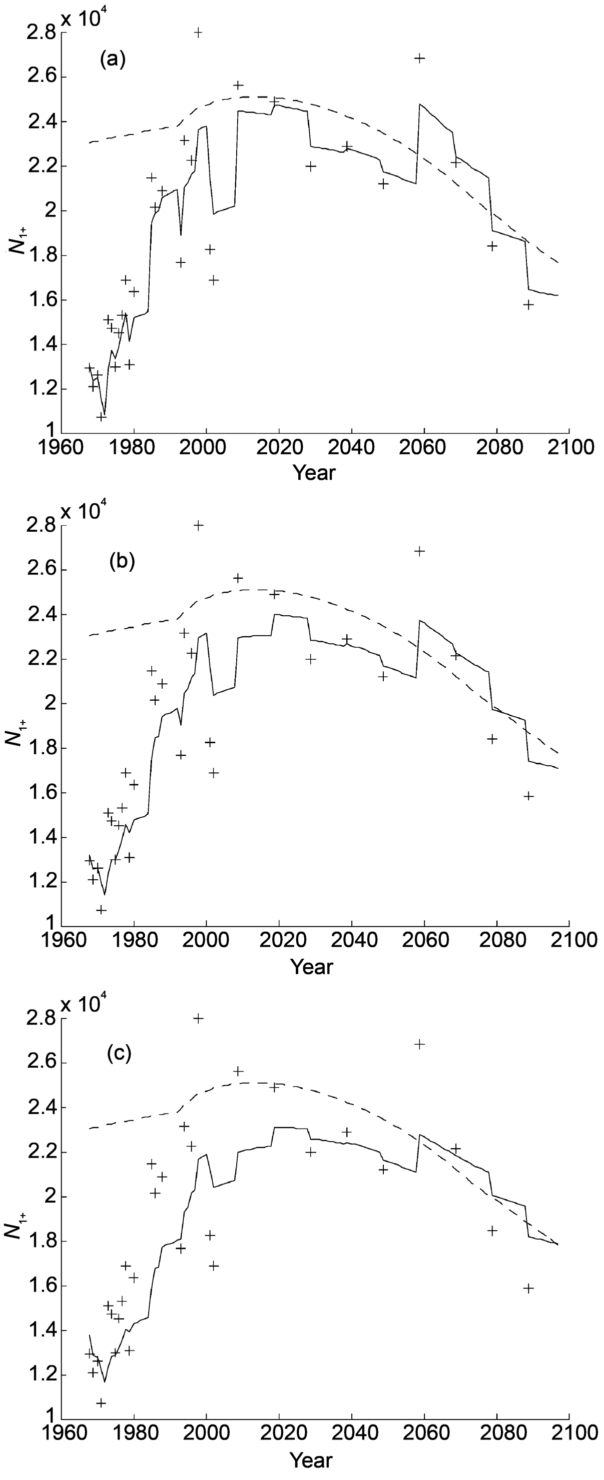

Fig. 3. Estimated and true stock trajectories from 1968 to 2100, along with observations for one simulation of trial GE16. In figure (a) CV_{add}=0, (b) CV_{add}=0.1 and (c) CV_{add}=0.2.

parameters, giving a point in the Depletion-Need plane lying both to the right and higher than a point corresponding to a different triple is clearly preferable since performance is better on both statistics.

Since the goal is to maximise both the depletion and need satisfaction statistics the most desirable tuning will provide results in the upper right hand corner of the figure. Two features are apparent in this figure. Firstly, tunings with CV_{add}=0.15 generally outperform CV_{add}=0.10 for values of γ within the range 0.3-0.8, since the curves corresponding to

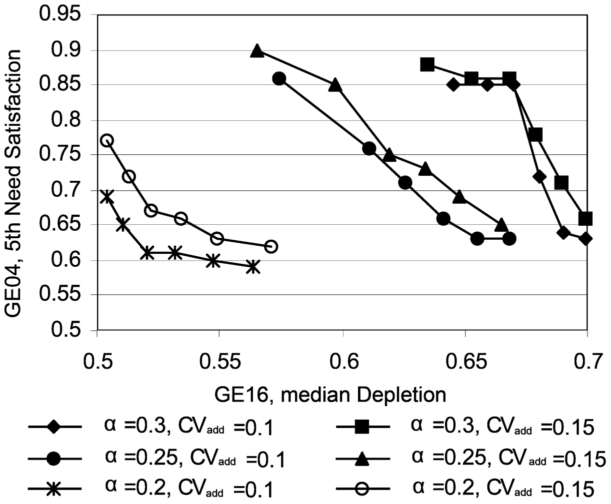

Fig. 4. 5th percentile Need satisfaction in GE04 and median Depletion in GE16 for three values of α and two values of CV_{add}. To construct each line γ ranges from 0.3 to 0.8 in increments of 0.1 and decreases from left to right for each pair of α and CV_{add}.

the former lie completely to the right and above the latter for fixed α-values in all cases; thus an increase in CV_{add} with a fixed α will move the point in the Depletion-Need plane up and to the right (some adjustment of γ may be required to maintain supremacy). However, the difference between CV_{add}=0.10 and CV_{add}=0.15 decreases as α and γ are increased and moreover the ability to detect sudden changes in stock size, such as in trial GE45, diminishes with increased CV_{add}. To obtain a good balance a value of 0.11 was selected for CV_{add}. Secondly, increasing improves performance since the curves move up and to the right for a fixed , except that there is a slight drop in need satisfaction between α-values 0.25 and 0.3 for the highest γ-value (0.8) since the top of the curve is lower for α=0.30. It would appear from Fig. 4 that α should be taken to be as high as possible, but need satisfaction in other trials starts to deteriorate with α=0.30. Thus, a version with α set to 0.25 was selected throughout.

We only present here the results of the tuning referred to as the D-M2 tuning in IWC (2005). This specific tuning of the AKF-*SLA* is one of two components in the GUP procedure. The values of the tuning parameters were set as follows:

$$\beta=0.7;\ \gamma=0.8;\ \alpha=0.25;\ P_0=0;\ CV_{add}=0.11.$$

The depletion and need satisfaction results for this tuning are given in Table 2 for the five selected trials. A complete set of trial results for the gray whale AKF-*SLA* with this tuning and for a higher tuning also are given in IWC (2005).

Table 2

Results for a few key gray whale evaluation trials of the D-M2 tuning of the AKF-*SLA*.

	D1: Final 1+ Depletion			N9: Need Satisfaction		
	5%	Med	96%	5%	Med	96%
GE01	0.854	0.885	0.911	1	1	1
GE04	0.881	0.898	0.922	0.86	0.99	1
GE10	0.902	0.914	0.924	1	1	1
GE16	0.425	0.548	0.695	0.92	0.94	0.96
GE45	0.369	0.498	0.574	0.92	0.94	0.95

Sensitivity to S, the survival rate was investigated by looking at values 0.95, 0.96, …, 0.99. There was very little difference in the trial results, except in trial GE16, when depletion improves slightly with higher values of S (Table 3). The value used in the algorithm (S=0.97) is somewhat arbitrary, but is similar to that estimated by Wade (2002).

Table 3

Results for trial GE16 using five different values for survival rate, *S*.

	D1: Final 1+ Depletion			N9: Need Satisfaction		
S	5%	Med	96%	5%	Med	96%
0.95	0.411	0.536	0.694	0.93	0.95	0.96
0.96	0.419	0.539	0.694	0.92	0.94	0.96
0.97	0.425	0.548	0.695	0.92	0.94	0.96
0.98	0.430	0.555	0.696	0.92	0.94	0.96
0.99	0.433	0.561	0.696	0.92	0.93	0.96

Sensitivity to q, the size of the process error was also investigated. Reducing q means that greater confidence is placed in the model and the effects of the observations are consequently down-weighted and *vice versa*. The main effect on the trial results of varying q was that the depletion improved in the 1.5% *MSYR* trials (GE16 and GE45) as q was reduced. This appears counter-intuitive at first, especially for GE45, where the stock crashes at the start of management, since a lower q-value will make the algorithm less responsive to the observations and hence slower to react to the population crash (Fig. 5 (a-c)). However, the reason is clear from the *MSYR* charts in Fig. 5 (d-f) showing the time evolution of the median, 5th and 95th percentiles from the 100 replicates of estimated *MSYR* (i.e. the expected value obtained from the posterior distribution): with a low q-value (i.e. high confidence in the model), the trajectory does not follow the rather steep rise exhibited in the biased historical observations as closely as with a higher q and the estimated *MSYR* is therefore lower, resulting in lower strike limits. It is worth noting from Fig. 5b that the algorithm with the selected q-value (0.001) is responding reasonably well to the population crash. It was therefore felt that this value of q strikes a reasonable balance between the model and observations.

Estimation of MSYR

Fig. 6 shows the time evolution of the probability distribution for *MSYR* between 1968 and 2002 (i.e. that based on the historical observations) and Fig. 7 shows the posterior probability distribution in 2002 for *MSYR* and *MSY*. Note that the probabilities of the *MSYR* values illustrated in Fig. 6 and those given in each column in Fig. 7 are the marginal probabilities, obtained by integrating over the *MSY* values (shown on the horizontal axis in Fig. 7). Based on the historical observations nearly all the posterior probability mass in 2002 is concentrated at *MSYR* 2% and 3%. It is worth pointing out that the probabilities for *MSYR* of 1% and 6% are practically zero as are probabilities for *MSY* higher than 1000. This confirms that the selected range of the parameter grid is sufficiently wide.

Fig. 8 shows the time evolution of the median, 5th and 95th percentiles from the 100 replicates of estimated *MSYR* over the subsequent 100 years for the five key trials GE01, GE04, GE10, GE16 and GE45. The *MSYR* estimate at the beginning of management is 2.5%. For GE01, which is a 3.5% trial the median *MSYR* declines to approximately 2.0%; for GE04, another 3.5% trial, but with a negative future bias, the medium *MSYR* rises slightly initially but levels off slightly above 2.5%; for the 5.5% trial GE10, the median *MSYR* stays level at 2.5% and for the 1.5% trials, GE16 and GE45 the median declines slightly to somewhere between 2.0 and 2.5%. It is evident that the algorithm is not particularly successful in picking up the true *MSYR* value.

Bias filters

The observations in some of the trials are biased (see Table 1). We carried out some explorations into the possibility of using filters with a bias, i.e. modifying the observation equation (2) as follows:

$$N_t^{obs} = B_t N_t e^{v_t}$$

where B is a possibly time-varying bias factor. We first added filters with a time-increasing historical bias, as in trials GE16 and GE45, but no future bias, thus using *MSYR* values 1%, 2%, …, 6% with and without a historical bias and thereby doubling the number of filters. This did not improve the depletion results in the two aforementioned trials, quite the contrary (in fact, median depletion went down to 0.454 and 0.428 in GE16 and GE45 respectively), the reason being that the bias filters with high *MSYR* values end up with most of the posterior probability mass in 2002, thus leading to higher future strike limits. Judging from the posterior values, it would thus appear that the best fit to the historical data with a simple density dependent model is for (time-increasing) biased observations and high *MSYR* values (median value 4.7% in 2002). We also looked at bias filters with a future bias as in GE04; i.e. added filters with a time-decreasing (1-0.5) and time-increasing (1-1.5) bias in the first 25 years of management, thus tripling the number of filters. This did not improve the results and will not be discussed further here. Additionally the use of future biases can be questioned since the possible scenarios are innumerable and one might be tempted to imitate the trials in order to improve performance. The conclusion is therefore that the addition of bias filters to the present version of the AKF-*SLA* is not a desirable option.

DISCUSSION

The present AKF-*SLA* for the ENP stock of gray whales has evolved from the version designed for the BCB stock of bowhead whales (Dereksdóttir and Magnússon, 2003). There are however a number of differences, of which the most notable are summarised below.

(1) The bowhead whale version uses a grid in the (*MSYR*, N_∞) parameter space, whereas the gray whale version uses an (*MSYR*, *MSY*) grid for the reason given above (i.e. the high negative correlation between *MSYR* and N_∞).

(2) The filters in the bowhead whale version were started in 1848 since it was assumed that the stock was at carrying capacity at that time. The variance associated with N_∞ was set to zero since (*MSYR*, N_∞) are simply points in the parameter grid which are given posterior probability values by the Bayesian methods described above, as abundance observations become available. The first update is made in 1978, the year of the first bowhead

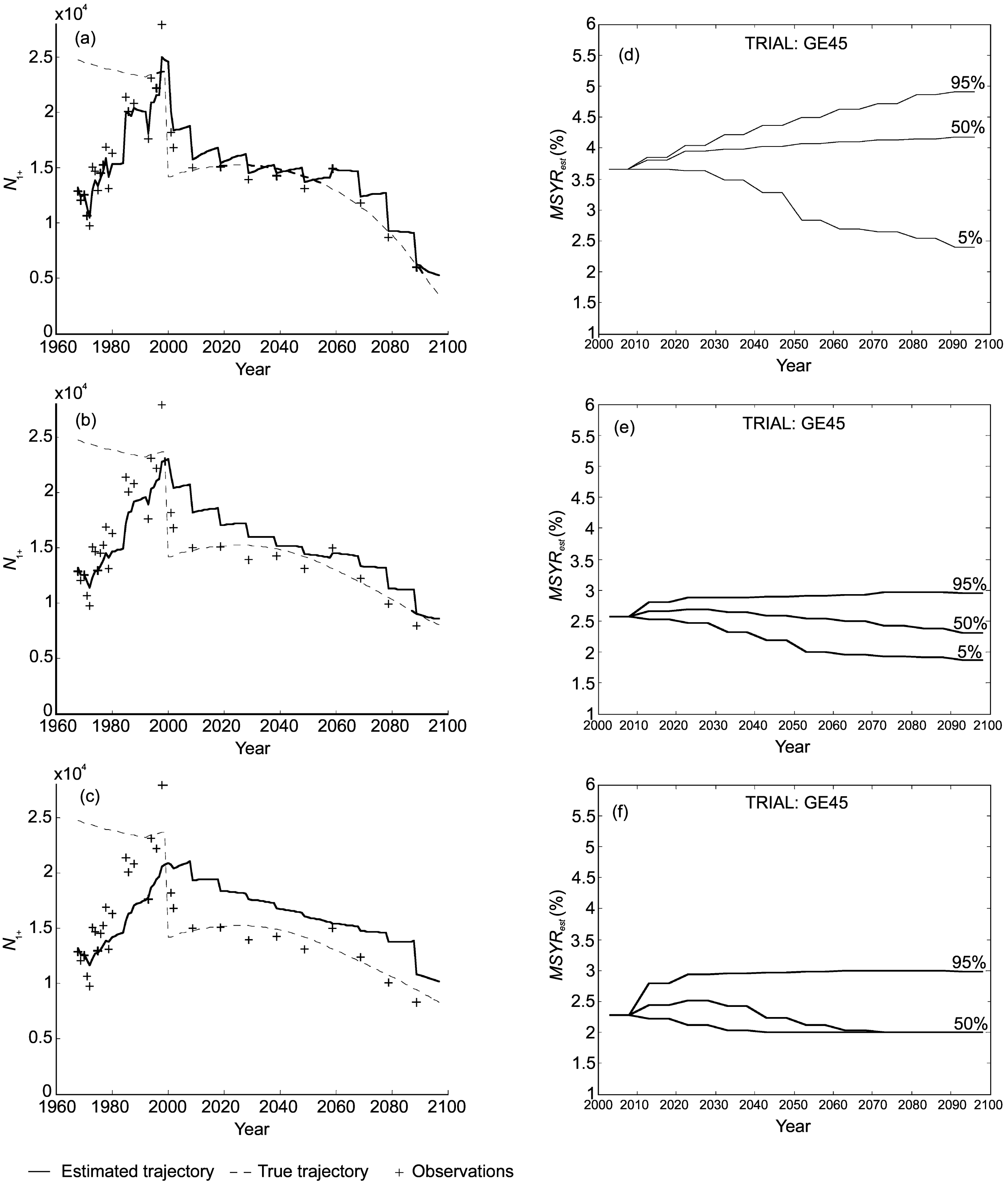

Fig. 5. Estimated and true stock trajectories from 1968 to 2100, along with observations for one simulation of trial GE45 are shown in the left column for three different values of q_t. In the column on the right the median, 5th and 95th percentiles for estimated *MSYR* are shown for the same three values of q_t. In figures (a) and (d) q_t=0.01, (b) and (e) q_t=0.001 and (c) and (f) q_t=0.0001.

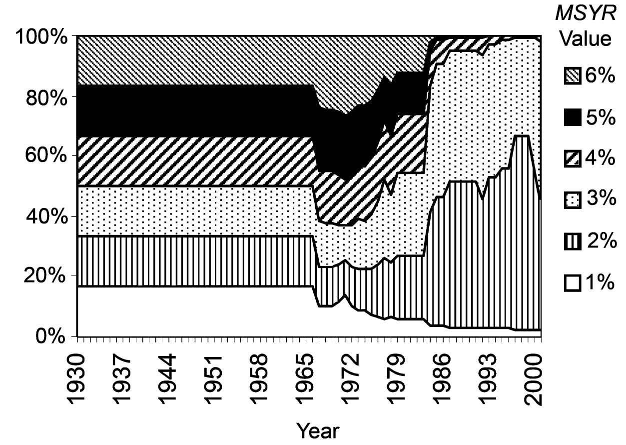

Fig. 6. The time evolution of the marginal probability distribution for each group of *MSYR* filters from 1930 to 2002.

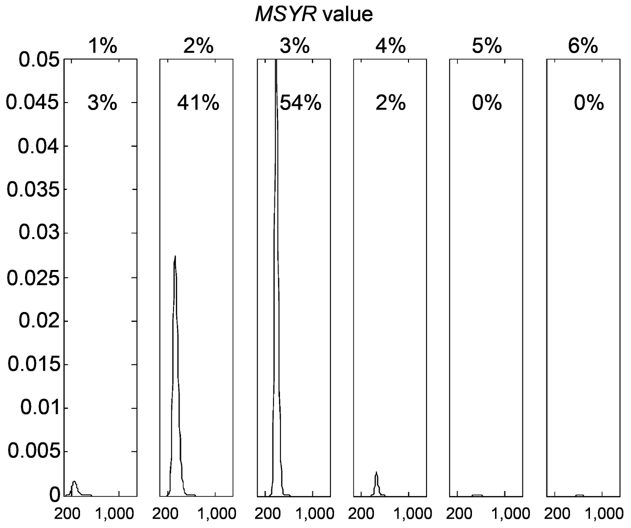

Fig. 7. The posterior probability distribution for *MSYR* and *MSY* in 2002 at the beginning of management. The numbers in each column are the probabilities of the six *MSYR* values.

abundance estimate. In the gray whale *SLA* it is not possible to start at a given year under the assumption that the stock is in its pristine state at that time for reasons given above. The first gray whale abundance estimate is from 1968, but to avoid forcing all trajectories through this estimate, the set of filters was started somewhat earlier, i.e. in 1930. Instead of using the 1930 population size as the starting value, the population is normalised by the carrying capacity N_∞, i.e. the 1930 population size N_{1930} is defined by a tuning parameter α, where $N_{1930} = \alpha N_\infty = \alpha(MSY/(0.6MYSR))$ with an associated *CV*, P_0, which is also used as a tuning parameter. The first update is made in 1968.

(3) The total number of filters in the bowhead whale version is 917 (7 *MSYR* values: 1%, 1.5%, 2%,…,4% and 131 values of N_∞ (from 10,000 to 23,000 in increments of 100). The number of filters in the gray whale version is slightly higher, 1,044. This is mainly due to the larger parameter range in the latter version. Note that the *MSYR* grid is coarser for the gray whales. This is mainly for computational reasons and the relative smoothness of the cumulative distribution function shown in Fig. 2 confirms that the grid is sufficiently fine.

(4) The estimated *CV*s in the abundance estimate, CV_{est}, provided to the *SLA* are used unchanged in the bowhead version. However, the historical observations of the abundance of gray whales with the provided *CV*s are not compatible with a standard density dependent population model. This *CV* is therefore likely to be an underestimate of the true *CV* in the abundance estimate. A constant CV_{add} is therefore added to all *CV* estimates (historical and future) provided to the *SLA*. This value is treated as a tuning parameter.

(5) The tuning in the bowhead *SLA* is two dimensional, the two parameters being β, the steepness of the catch control law, and γ, the percentile in the cumulative distribution function for the conditional strike limits. The tuning of the gray whale *SLA* is more flexible, with three additional tuning parameters (see the results section).

This list indicates how the AKF-*SLA* could be modified to apply to other aboriginal type 2 fisheries, i.e. changing the parameter grid, using different starting conditions for the set of filters, changing the tuning parameters, etc.

It is clear from Fig. 8 that the algorithm is not particularly successful in obtaining an estimate of *MSYR*. There is little difference between the *MSYR* estimates for GE01, GE10 and GE16, which are trials with *MSYR*, 3.5%, 5.5% and 1.5% respectively and the estimates change very little during the management period. This is to some extent due to the addition of CV_{add} but also due to the time-increasing bias in GE04 and GE16. However, it would also appear (at least by looking at one replicate in each of the trials GE16 and GE45 and also confirmed in other replicates) that the algorithm is tracking the true trajectory reasonably well and responding to the observations, but not unduly because of the (fairly) high value of CV_{add} (Fig. 3).

In addition to the percentile γ, α – the stock in 1930 as a fraction of N_∞ – is the parameter to which the trial results are most sensitive (Fig. 4). The reason is that the estimate of *MSYR* in 2003 decreases as α increases making the algorithm more conservative. It is interesting however, that depletion in trial GE16 and need satisfaction in trial GE04 both increase with increasing α.

Other variants of the AKF-*SLA* were also investigated. Firstly, a variant where N_{1930} is used as a tuning parameter instead of α. Secondly, variants where N_{1930} (or α) is treated as the third parameter in a 3-dimensional grid of filters (*MSYR*,*MSY*, N_{1930}). These changes did not lead to any improvements on the trial results obtained by the version described above.

ACKNOWLEDGEMENTS

The development of this *SLA* has benefitted greatly from extensive discussions in the IWC Scientific Committee Standing Working Group on Aboriginal Whaling Management Procedures. The input from the group has been invaluable, which we gratefully acknowledge. We would also like to thank Andre Punt for a very thorough review of the manuscript and suggestions for improvements, as well as another anonymous reviewer. We also wish to thank Cherry Allison for all her work in setting up and running the trials. Finally, we thank the IWC for a contribution from the Developers' Fund.

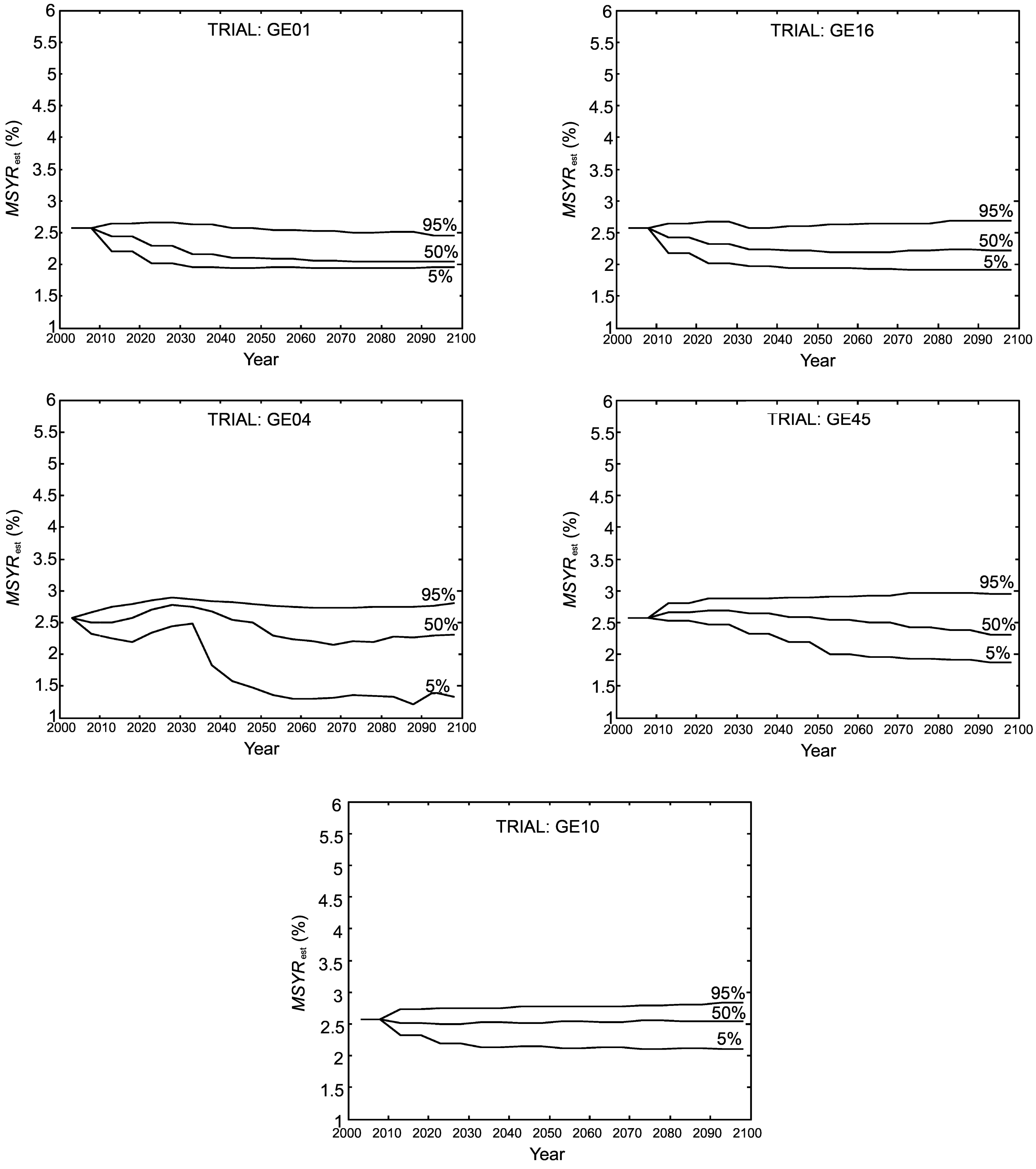

Fig. 8. Estimated *MSYR* results. The median, 5th and 95th percentiles of estimated *MSYR* for five key trials for the D-M2 tuning.

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Date Received: February 2005
Date Accepted: May 2005

J. CETACEAN RES. MANAGE. 7(2):97–106, 2005

An improved method for line transect sampling in Antarctic minke whale surveys

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ABSTRACT

The series of abundance estimates for Antarctic minke whales obtained using standard line transect methods from IWC/SOWER surveys imply drastic (and probably unrealistic) changes in true abundance. One possible factor is that the detection probability on the trackline, $g(0)$, may have decreased with the introduction of inexperienced observers in the most recent surveys. Additionally, mean observed school size may have decreased in the third circumpolar survey in comparison with the second survey. This paper introduces an extended and generalised hazard probability model without the assumption that $g(0)=1$ to estimate true school size distribution in the population. The proposed method uses a survey design that combines the use of both passing mode with independent observers and closing mode in which the vessel turns off the trackline and closes with the sighting for confirmation of school size and species. The abundance estimate is based on the Horvitz-Thompson estimator in an unequal detectability sampling scheme. The method is applied to the IDCR/SOWER dataset of Antarctic minke whales for illustrative purposes.

KEYWORDS: ANTARCTIC MINKE WHALE; ABUNDANCE ESTIMATE; $g(0)$; SCHOOL SIZE; SURVEY-VESSEL; SOWER; MODELLING

INTRODUCTION

The abundance of whales and dolphins in an area are frequently estimated using distance-based line transect sampling (e.g. Buckland *et al.*, 1993; IWC, 2005a; b; c). Put simply, this entails usually an observer following a pre-determined line, searching for animals on and near to that line and measuring the distances and angles to each detected animal. One of the important assumptions in conventional line transect sampling is that all animals on the line are detected without failure, i.e. the probability of seeing an animal if it occurs on the trackline, commonly called $g(0)$, is equal to 1. However, the diving behaviour of cetaceans can lead to this assumption being violated, even if they occur on (or below) the trackline. Double-platform line transect surveys are often conducted to try to resolve this problem (Cooke, 1997; Schweder *et al.*, 1997; Skaug and Schweder, 1999). Such surveys enable collection of data for estimating the probability of missing animals, i.e. duplicate sightings from independent observers.

The International Decade of Cetacean Research – Southern Ocean Whale and Ecosystem Research (IDCR/SOWER) surveys have been conducted annually in the Antarctic since the late 1970s (Branch and Butterworth, 2001). The main purpose of these surveys has been to collect sightings data to estimate the abundance of Antarctic minke whales (*Balaenoptera bonaerensis*). Sightings data from these surveys consist of three circumpolar sets of cruises: 1978/79-1983/84, 1985/86-1990/91 and 1991/92-2003/2004. The survey effort of IDCR/SOWER surveys is divided into closing and passing modes. In closing mode, when a school of whales is detected, the vessel turns off the trackline and closes with the sighting to confirm the school size and species. Survey data in 'closing mode' may cause some bias in school density, but gives more accurate information on school size (Branch and Butterworth, 2001). 'Passing' mode represents double-platform line transect sightings with independent observers. Data collected under passing mode contain valuable information about $g(0)$. However, since a vessel is not allowed to leave the trackline for confirmation of school size and species identification of detected animals, school size (and sometimes species identification) estimated from many of the schools detected in passing mode may be unreliable.

The abundance estimates of Antarctic minke whales have been estimated by conventional line transect methods with $g(0)=1$ (Branch and Butterworth, 2001). The abundance estimates for the third circumpolar survey obtained from IDCR/SOWER data showed a dramatic decrease compared with the second circumpolar survey. Branch and Butterworth (2001) reported that the abundance estimates for the third circumpolar survey are 45% (passing mode only) and 55% (closing mode only) of those for the second circumpolar survey. Although the third circumpolar survey data are not fully analysed, a substantial decrease in estimates from the third circumpolar survey on the basis of standard line transect methods (Buckland *et al.*, 1993; Branch and Butterworth, 2001) is obvious, although whether such drastic declines in true abundance are real is the subject of considerable work; the Scientific Committee of the International Whaling Commission (IWC) has listed a number of possible causes that might result in the change in estimates (IWC, 2002). Two proposed causes for the decline are changes in the detection probability on the trackline and changes in the distribution of school size. The focal point of this paper is how to estimate changes of $g(0)$ and school size distribution.

A new efficient method for estimating the abundance of diving animals from double-platform line transect survey data was recently developed by Okamura *et al.* (2003). This method concentrated on the estimation of $g(0)$ based on double-platform line transect sampling, but ignored the problem of possible downward bias of school size estimates in passing mode. As noted above, the size of detected

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schools is rarely confirmed in passing mode, and the observed mean school size in passing mode is generally less than that of closing mode. This paper considers the question of the removal of bias induced by unconfirmed school size under passing mode.

MATERIALS AND METHODS

Data requirements

This method requires: the perpendicular and forward distances of sightings; on-board determination of whether each detection is either a single sighting, a simultaneous sighting or delayed duplicate sighting (see below); school size estimates; and the confirmation status (i.e. how certain the observers are that the estimate is good) of school size for each sighting under both passing and closing mode. The simultaneous duplicate sighting represents detection of the same animal at the same time by multiple platforms and the delayed duplicate sighting represents detection of the same animal at different times by multiple platforms. For illustrative purposes, this method has been applied to the 1989/90 IDCR data, although these do not completely satisfy the above data requirements. Necessary data processing for the IDCR data is described after the explanation of the model.

Likelihood function

A hazard probability model is used to estimate the detection function and $g(0)$, of which a detailed description is given in Appendix 1. In IDCR/SOWER passing mode, sightings from an incompletely independent platform (IIP) on an upper bridge of a vessel account for a large proportion of the total (Okamura *et al.*, 2003). Therefore, two independent platforms (A: top barrel and B: independent observer (IO) booth) and an incompletely independent platform (C: upper bridge) are considered. Sightings made by completely independent platforms (CIP) on the top barrel and the IO booth of a vessel are immediately communicated to the IIP on the upper bridge. Hence, duplicate sightings by the IIP could never be classed as delayed duplicates after detection by the CIP, although duplicates by the CIP may have been delayed after detection by the IIP. Therefore, the output from the initial sighting is categorised according to 11 types of detection (u); A, B, C, $A \times B$, $A \rightarrow B$, $B \rightarrow A$, $C \rightarrow A$, $C \rightarrow B$, $C \rightarrow A \times B$, $C \rightarrow A \rightarrow B$, and $C \rightarrow B \rightarrow A$, where for instance $A \times B$ and $A \rightarrow B$ denote simultaneous and delayed duplicates between A and B, respectively. The detection probability in passing mode is then written as $p_1(x, y, u|s)$ where x is perpendicular distance, y is the forward distance, u is the type of detection, and s is the true size of the detected school. Dependency of school size is modelled using the equation like $\log(\sigma) = a_0 + a_1 \log(s)$, where σ is a parameter of detection probability function. Closing mode has two sighting platforms, a top barrel, A and an upper bridge, C of a vessel. These two platforms are completely dependent, i.e. one platform immediately knows of any detection by another platform. The type of detection in closing mode simply becomes the combination of the top barrel and upper bridge, $A \cup C$, and the detection probability in closing mode is then written as $p_2(x, y, A \cup C|s)$. For all platforms, measurement error in distances is not considered here.

As would be expected, the proportion of unconfirmed school sizes in passing mode was much higher than that in closing mode during the 1989/90 IDCR survey (see Table 1). Mean unconfirmed school size tends to be lower than mean confirmed school size, possibly due to overlooking part of a school. This leads to an underestimate of abundance when only passing mode school size data are used, if the difference between confirmed and unconfirmed school size is not taken into account. Both passing and closing mode data can be used simultaneously to estimate the true probability distribution of school size in the population. The assumption here is that confirmed school size reflects the probability distribution of true school size, given it is detected, while unconfirmed school size is biased to some degree.

Buckland *et al.* (1993) and Borchers (1999) suggested using a probability distribution of school size to correct for the size bias of detected schools; if large schools are detected at greater distances than small schools, mean school size will be biased upwards. Antarctic minke whale surveys have a more complicated structure of school size bias due to the 'confirmation' process. A probability distribution of 'unconfirmed' school size conditioned on unobserved true school size is used here. Since confirmation status is also a stochastic event, it is treated probabilistically. The mathematical details are given in Appendix 2.

Putting the above-mentioned hazard probability model (Appendix 1) and correction method for mis-estimation of school size (Appendix 2) together, the log-likelihood function for sighting distance (x, y), type of detection (u), observed school size (z), confirmation status (c), and survey mode (t) is given by:

$$\log(L) = \sum_{t=1}^{2}\sum_{i=1}^{n_t}(c_i \log\{p_t(x_i, y_i, u_i \mid z_i)d_t(z_i)\pi(z_i)\}$$
$$+(1-c_i)\log[\sum_{s=z_i}^{\infty} p_t(x_i, y_i, u_i \mid s)\rho(z_i \mid s)\{1-d_t(s)\}\pi(s)] \qquad (1)$$
$$-\log\{\sum_{s=1}^{\infty} esw_t(s)\pi(s)\})$$

where:

n_t is the sample size under each mode;
$p_1 = p_1(x_i, y_i, u_i|s)$, a detection probability in passing mode and is altered following the type of detection, p_2 is equal to

$$p_2(x, y, A \cup C \mid s) = \frac{\lambda}{v} Q_{A\cup C}(x, y)$$
$$\exp\left\{-\frac{\lambda}{v}\int_y^{\infty} Q_{A\cup C}(x, y)dy\right\}$$

which is a detection probability in closing mode;

esw_1 and esw_2 are effective search half-widths in passing and closing mode, respectively (Appendix 1);

$\pi(s)$ is the probability distribution of true school size;

$\rho(z|s)$ is the probability distribution of observed school size given the animals are detected and unconfirmed;

$d(z)$ represents the probability that the animals with school size z are confirmed (Appendix 2).

Parameters are then estimated by maximising the log-likelihood, $\log(L)$. When $c_i = 1$ (all i) and $d_t(z) \equiv 1$, the log-likelihood function corresponds to those of Buckland *et al.* (1993) and Borchers (1999). When $d_t(z) = d_t$, the log-likelihood function is equal to the log-likelihood function conditioned on the confirmation status.

The density estimator of animals based on the Horvitz-Thompson estimator (Horvitz and Thompson, 1952) is then given by:

$$\hat{D} = \frac{1}{2L}\sum_{i=1}^{n_1} \frac{\{\hat{\phi}_0(1-\hat{\phi}_1)/\hat{\phi}_1\}+1}{\sum_{s=1}^{\infty} e\hat{s}w_1(s)\hat{\pi}(s)} \tag{2}$$

where L is total survey distance, and the numerator is derived from $\phi_1 = \phi_0/\{\phi_0 + E(s) - 1\}$ using the parameters of a negative binomial distribution (Appendix 2). Note that the parameters in relation to $\rho(z|s)$ and $d(s)$ are nuisance parameters and not used in density estimation. Only passing mode data were used in density estimation, since density estimation under closing mode causes additional biases, such as an upward bias through deviations from the trackline and a downward bias from neglect of secondary sightings (Branch and Butterworth, 2001).

The abundance estimator is given by $\hat{P} = a{\cdot}\hat{D}$, given the area size a. An estimator for the unconditional asymptotic variance of $\hat{P}$, as in Okamura *et al.* (2003), is then:

$$\hat{\mathrm{var}}(\hat{P}) = \left[\left\{\frac{dP(\underline{\theta})}{d\underline{\theta}}\right\}^T I(\underline{\theta})^{-1}\frac{dP(\underline{\theta})}{d\underline{\theta}}\right]_{\underline{\theta}=\hat{\underline{\theta}}} + \frac{a^2}{J-1}\sum_{j=1}^{J}\frac{l_j}{L}(\hat{D}_j - \hat{D})^2 \tag{3}$$

where $\underline{\theta}$ is a vector of parameters in (1), $I(\underline{\theta})$ is the Fisher information matrix obtained from the log-likelihood function that is often substituted by the Hessian matrix, and l_j ($j = 1, \ldots, J$; $\Sigma\ l_j = L$) is a replicate line. If there is no sighting in replicate line l_j, $\hat{D}j$ is defined as being equal to 0. Although abundance estimates by stratum are required, duplicate data are sparse in each stratum so that $g(0)$ estimation tends to be biased. Therefore, estimates of the detection function, effective search half-width and school size distribution are obtained by pooling detection distance data and school size data across strata. Assuming that effective search half-width and mean school size are common to all strata, the abundance estimate and its variance for the whole area are given by:

$$\hat{P}_{all} = \sum_h a_h\hat{D}_h \tag{4}$$

$$\hat{\mathrm{var}}(\hat{P}_{all}) = \left[\left\{\frac{dP_{all}(\underline{\theta})}{d\underline{\theta}}\right\}^T I(\underline{\theta})^{-1}\frac{dP_{all}(\underline{\theta})}{d\underline{\theta}}\right]_{\underline{\theta}=\hat{\underline{\theta}}} + \sum_h \frac{a_h^2}{J_h-1}\sum_{j=1}^{J_h}\frac{l_{j,h}}{L_h}(\hat{D}_{j,h} - \hat{D}_h)^2 \tag{5}$$

where the subscript h is index of stratum.

Application of the proposed model to IDCR/SOWER data

The 1989/90 IDCR/SOWER data were used to investigate the reliability of the method developed above (see Table 1). The 1989/90 data generally correspond to those collected from IWC Management Area I (between 60°W and 120°W; see Donovan, 1991). Area I has a relatively stable ice-edge so it seemed appropriate to concentrate the problem on the estimation of $g(0)$ and school size, without the additional confounding factor of a changing ice-edge.

The detection by observers other than independent observers was re-coded as detection by incompletely independent observers so that sightings were not distinguished between an upper bridge and other incompletely independent platforms such as the bridge. The method requires a sufficient number of duplicates, so sighting data pooled across strata were used to estimate effective search half-width and school size distribution. Duplicates recorded as ‘possible’ as well as ‘definite’ were used as duplicates for acquiring sufficient sample size for $g(0)$ estimation. Inclusion of ‘possible’ duplicates should have little effect on outcomes in this example because the number of possible duplicates is only 3 out of 89. Although the model requires a clear distinction between simultaneous and delayed duplicates, the independent observer data under passing mode of IDCR/SOWER surveys have no such distinction at present. Therefore, for the purposes of this study it was provisionally assumed that duplicate data with a difference between sighting times less than 20 seconds were simultaneous duplicates. If the time between sightings was more than 20 seconds, it was assumed that they were delayed duplicates with a difference of sighting (radial) distances and sighting angles as the auxiliary information. For duplicates and triplicates, school size was not always confirmed by all platforms. It was assumed that a school confirmed by at least one platform was confirmed, and the observed school size was used. When different platforms had different unconfirmed school size estimates for duplicates and triplicates, the school size estimate from the initial observer was used. Observations without confirmation status were considered unconfirmed.

For simplicity, only school size was considered as a covariate in this paper. Other possible covariates might be the difference in platform and weather conditions. The logarithm of school size s was linked with the parameters as follows:

$\log(\sigma) = a_{10} + a_{11}\log(s)$;
$\log(\tau) = a_{20} + a_{21}\log(s)$;
$\mathrm{logit}(\mu) = a_{30} + a_{31}\log(s)$;
$\log(\lambda) = a_{40} + a_{41}\log(s)$;
$\mathrm{logit}(b) = a_{50} + a_{51}\log(s)$;
$\mathrm{logit}(d_1) = a_{60} + a_{61}\log(s)$; and
$\mathrm{logit}(d_2) = a_{70} + a_{71}\log(s)$.

The number of estimated parameters was 18 including the parameters $\underline{\phi}$, γ_1 and γ_2. Formal model selection was not conducted. The sightings data that were detected behind the vessel and the delayed duplicates recorded by incompletely independent observers were discarded prior to any analyses.

Increasing forward distances were found in some duplicates, possibly due to measurement error. To avoid this problem, a method that focused on an initial forward distance by integrating over remaining forward distances in detection probability was adopted. Perpendicular and forward distance data were not truncated.

RESULTS

A summary of data used is shown in Table 1. Mean school size in closing mode is larger than mean school size in passing mode (P-value <0.001 by t-test). This indicates that school size in passing mode is probably underestimated due to missing part of the group. Both mean perpendicular and forward distances in passing mode are larger than those in closing mode. The difference in perpendicular distances is statistically significant (*P*-value = 0.002 by *t*-test), but the differences in forward distance are not (*P*-value = 0.114 by *t*-test). This probably reflects the greater number of observers in passing mode.

The estimated parameters are summarised in Table 2 and the results from the proposed model are shown in Table 3. Most often, a blow was the sighting cue for Antarctic minke whales. Estimated mean blowing rate, $\hat{\lambda}$, in 1989/90 was 33.9 blows per whale per hour, taking into account that vessel speed was constantly set at 11.5 knots. This value is less than the 48 blows per whale per hour from the experiment reported by Ward (1988). Since that experiment was conducted under excellent weather conditions, the lower estimate here may be due to variable weather conditions. Estimated $\hat{\mu}$, which is the level parameter of surfacing detection probability, was small. This reflects the fact that minke whales are likely to be missed because of their small blows and body size, even though they surface frequently.

The estimated $g(0)$ was 0.61 when it was averaged over school sizes (Table 2). The mean effective search half-width in 1989/90 was 0.36 (CV=0.15), which was less than the estimates from passing mode data (0.419-0.916) given by Branch and Butterworth (2001). As a result, the total population size (89,181, CV=0.187) estimated by this method was larger than the estimate (61,169, CV=0.192) of Branch and Butterworth (2001). The CV was slightly lower than that of Branch and Butterworth (2001) but because Branch and Butterworth (2001) provided stratified estimates, direct comparison is impossible. In addition, because their standard method only used information on perpendicular distance and confirmed school size under closing mode, their estimate may be less precise than that here. The values of $g(0)$ and effective search half-width for each school size are shown in Fig. 1.

Fig. 2 shows the fitted values predicted from the method with observed school size, distance and duplicate-categorical data. The predicted values appear to fit well with the observed data despite no truncation or smearing of the data (e.g. Buckland and Anganuzzi, 1988). Although the fit of school size distributions from passing mode/confirmed and closing mode/unconfirmed does not look good, this may reflect the low sample size. The sample size of sighting data in closing mode is 155, while the sample size in passing mode is 449. This difference may cause the discrepancy between observed and predicted distance distributions in closing mode because common parameters in detection function were assumed for passing and closing modes. Because the 1989/90 data had some 'bunching' at zero perpendicular distance, the plot of perpendicular distance did not show a 'shoulder' near the line. The method is not dependent directly on probability density at zero distance unlike the standard method (Buckland *et al.*, 1993) so that the result might be robust against the presence of a shoulder; but this requires further investigation in the future. The fit may be improved by taking into account suitable truncation, smearing, other forms of the detection function and additional covariates.

Table 2

Summary of estimated parameters in the detection function. The symbols used in this table are following the notation used in the text except where they were averaged using estimated school size distribution. $E(s)$ is estimated mean school size in the population.

	γ_1	γ_2	σ	τ	μ	λ/v	$\mu\lambda/v$	$g(0)$	*esw*	$E(s)$
Estimate	1.20	2.15	0.43	1.53	0.10	2.95	0.29	0.61	0.36	1.91
CV	0.12	0.09	0.15	0.06	0.31	0.41	0.17	0.11	0.15	0.08

Table 3

The abundance estimates of minke whales in the IDCR/SOWER 1989/1990 Area I surveys, along with estimated coefficients of variation (CV), where A is area size (n.miles^2), L is survey distance (n.miles), n_s is number of schools sighted, D_w is density of whales, and P is estimated population size. N, E, W and S in the name of stratum denote North, East, West and South of the corresponding area. B denotes 'Bay'.

Stratum	A	L	n_s	N_s/L	D_w	P	CV
EN	153,029	750.2	45	0.060	0.157	23,970	0.300
ESB	62,594	793.1	66	0.083	0.217	13,601	0.560
WN	168,761	606.7	32	0.053	0.138	23,245	0.328
WS	45,128	830.9	200	0.241	0.629	28,365	0.249
Total	429,512	2,981	343	0.115	0.208	89,181	0.187

Fig. 3 shows the expected number and proportion of confirmed individuals in schools recorded as unconfirmed, and the expected proportion of confirmed schools in passing and closing modes. These variables were plotted against school size because they were all modelled as functions of school size. The proportion of confirmed individuals in schools recorded as unconfirmed was about 0.4-0.7 for school sizes greater than 1. Substantial components of school sizes of about 5 are likely to be missed when they are recorded as 'unconfirmed'. The expected proportion of confirmed schools in passing and closing modes showed the

Table 1

Summary of 1989/90 IDCR/SOWER data.

	n	n_p	s_p	s_c	$P_{uc}(P)$	$P_{uc}(C)$	pd_p	fd_p	pd_c	fd_c	%dup
Estimate	498	343	1.85	2.84	0.95	0.14	0.50	1.18	0.37	1.06	25.4
CV	-	-	0.05	0.10	-	-	0.05	0.04	0.08	0.06	-

The symbols used in this table denote the following:

n = number of all schools sighted under passing mode and closing mode (no truncation/no smearing).

n_p = number of all schools sighted under passing mode only (no truncation/no smearing).

s_p = mean school size in passing mode.

s_c = mean school size in closing mode.

$P_{uc}(P)$ = proportion of unconfirmed school size in passing mode.

$P_{uc}(C)$ = proportion of unconfirmed school size in closing mode.

pd_p = mean perpendicular distance under passing mode.

fd_p = mean forward distance under passing mode.

pd_c = mean perpendicular distance under closing mode.

fd_c = mean forward distance under closing mode.

%dup = the percentage of duplicates, #dup./$n_{A \cup B \cup C}$ x 100.

opposite trend; the decreasing trend in passing mode perhaps seems counter-intuitive. However, it may reflect the fact that the judgment of confirmation in passing mode is dependent on the perpendicular distance to the school, rather than its size, because the survey vessel does not leave the trackline line. The fact that confirmation of closing mode is increasing with school size is convincing. The estimated proportion shows most sightings are confirmed in closing mode and most are unconfirmed in passing mode.

DISCUSSION

The method proposed in this paper enables us to estimate $g(0)$ and true school size distribution in the population. Furthermore, various covariates can be dealt with in the estimation process with flexibility. The diagnostic plots indicate the method is quite promising for the abundance estimation of Antarctic minke whales. The effective search half-width in the model is fundamentally based on the hazard probability model proposed in Okamura *et al.* (2003). Additionally, parameters of the true school size distribution can be estimated within the consistent estimation process proposed in this paper. The proposed model is easy to interpret and can be considered a likelihood-based model with random effects (Pawitan, 2001). It enables the use of various techniques based on a likelihood principle in a similar way to Schweder *et al.* (1997) and Skaug and Schweder (1999). The sensitivity of the proposed method will be investigated through extensive simulation study in the near future by the Scientific Committee of the IWC.

When mean unconfirmed school size is larger than mean confirmed school size, the true school size distribution cannot be estimated, due to the assumption constrained on the model. This assumption is quite reasonable, because observers usually tend to miss whales in schools detected at a distance from the vessel. Larger unconfirmed school sizes may occur under certain circumstances. For instance, Mori *et al.* (2002) reported that during the SSII experiments on the 1985/86 IDCR cruise ‘as observers began to realise that they were tending to appreciably underestimate school size at abeam time, their abeam estimates started to increase in an attempt to compensate, and the experiment was consequently suspended’. If records of school sizes estimated by observers before closure under closing mode exist, they can be incorporated into the likelihood function for closing mode, improving the precision of the estimates. If unusually large unconfirmed school sizes occur, the model will not provide correct estimates. To avoid such a problem in the future, it is important to instruct observers carefully about the definition of unconfirmed school size.

School size bias has been taken into account by regressing school size (or the logarithm of school size) on the detection function (Buckland *et al.*, 1993). Sometimes this produces unreasonable mean school sizes less than 1 (Branch and Butterworth, 2001). The present model consistently gives reasonable mean school size estimates, and statistically deals with the distribution of true school sizes in the population.

Selection between two models with the assumption of $g(0)=1$ and $g(0)<1$ can be carried out by likelihood ratio test and AIC (Akaike, 1973). Therefore, the model greatly extends the province to which the line transect method can be applied. We recommend line transect surveys that use passing mode with independent observers and closing mode alternately, for estimating unbiased abundance of diving animals such as Antarctic minke whales, or any other marine mammal with complicated school size structure and a

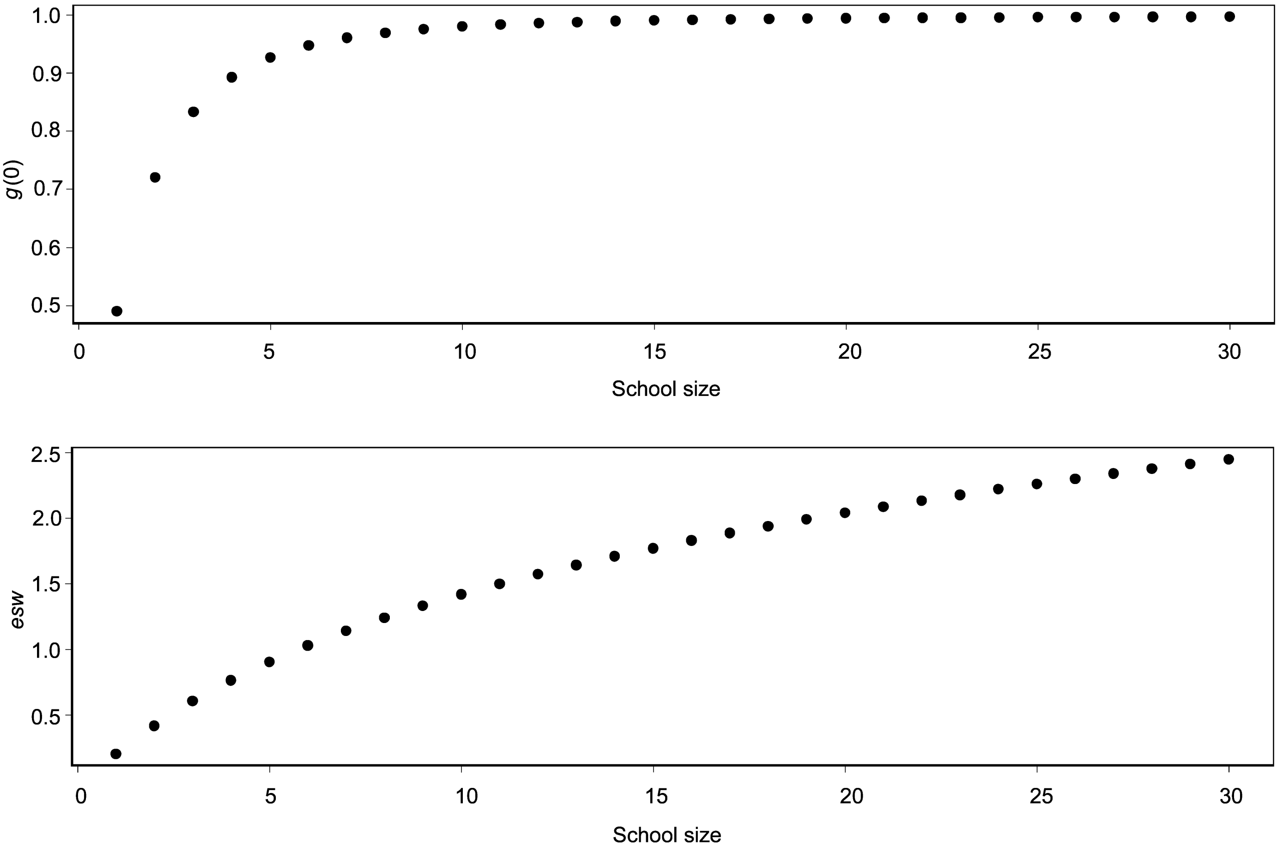

Fig. 1. Plots of the estimated $g(0)$ and effective search half-width (esw) against school size.

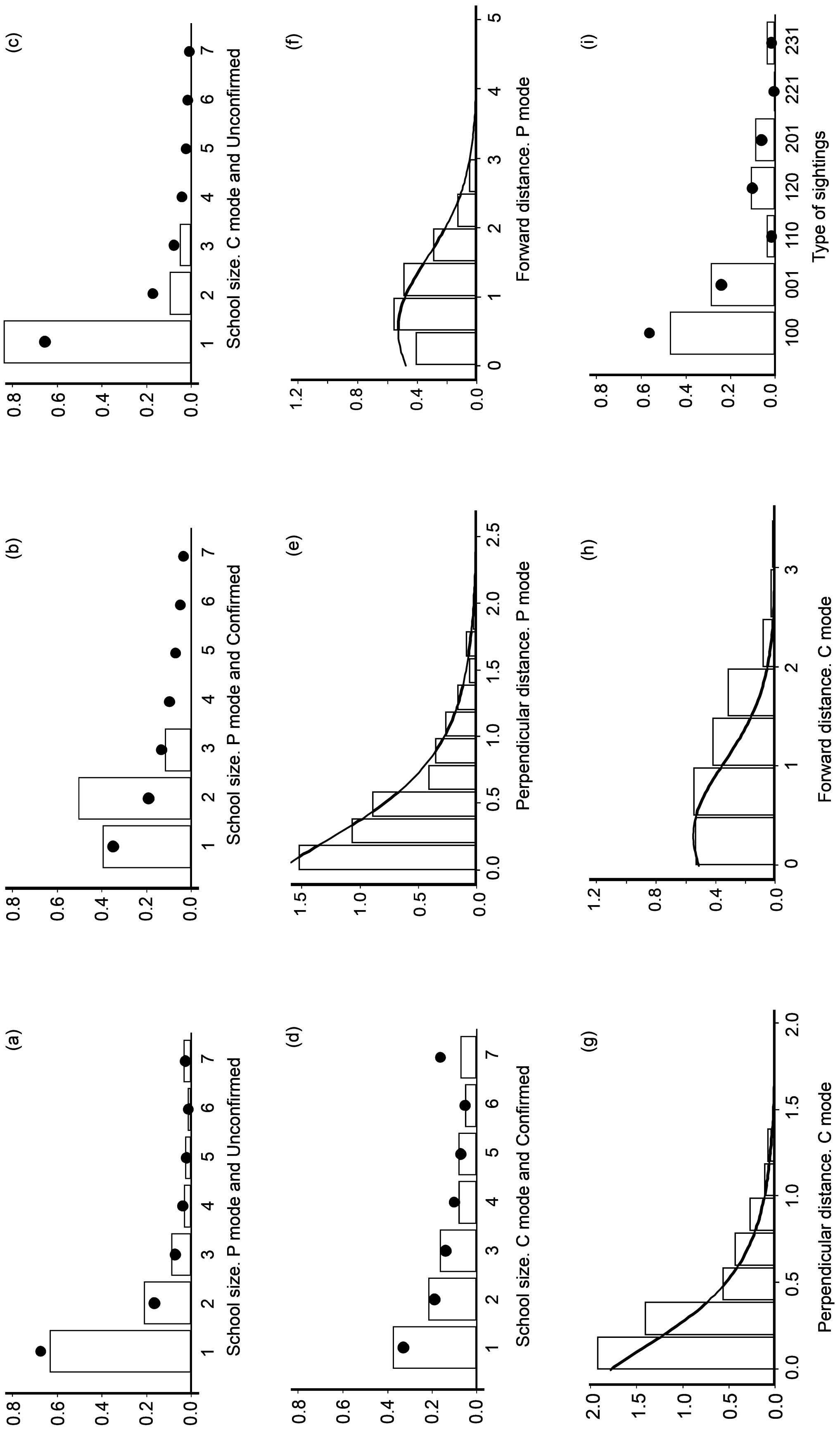

Fig. 2. The diagnostic plots for 1989/90 IDCR/SOWER data. Panels (a) to (d) show observed frequency of school size together with the model predicted frequency (●) under each survey mode and state of confirmation for observed school size. School sizes >6 were classed as size 7. Panels (e) to (h) show observed frequency of perpendicular and forward distance under each mode, with the model predicted frequency curves. Panel (g) shows frequency for the type of sightings, where 100 denotes a single detection by a CIP, 001 a single detection by a IIP, 110 a simultaneous duplicate, 120 $A \to B$ or $B \to A$, 201 $C \to A$ or $C \to B$, 221 $C \to A \times B$, and 231 $C \to A \to B$ or $C \to B \to A$. Frequency is scaled as a probability density, thus Σ the bar heights $\times$ bar widths =1.

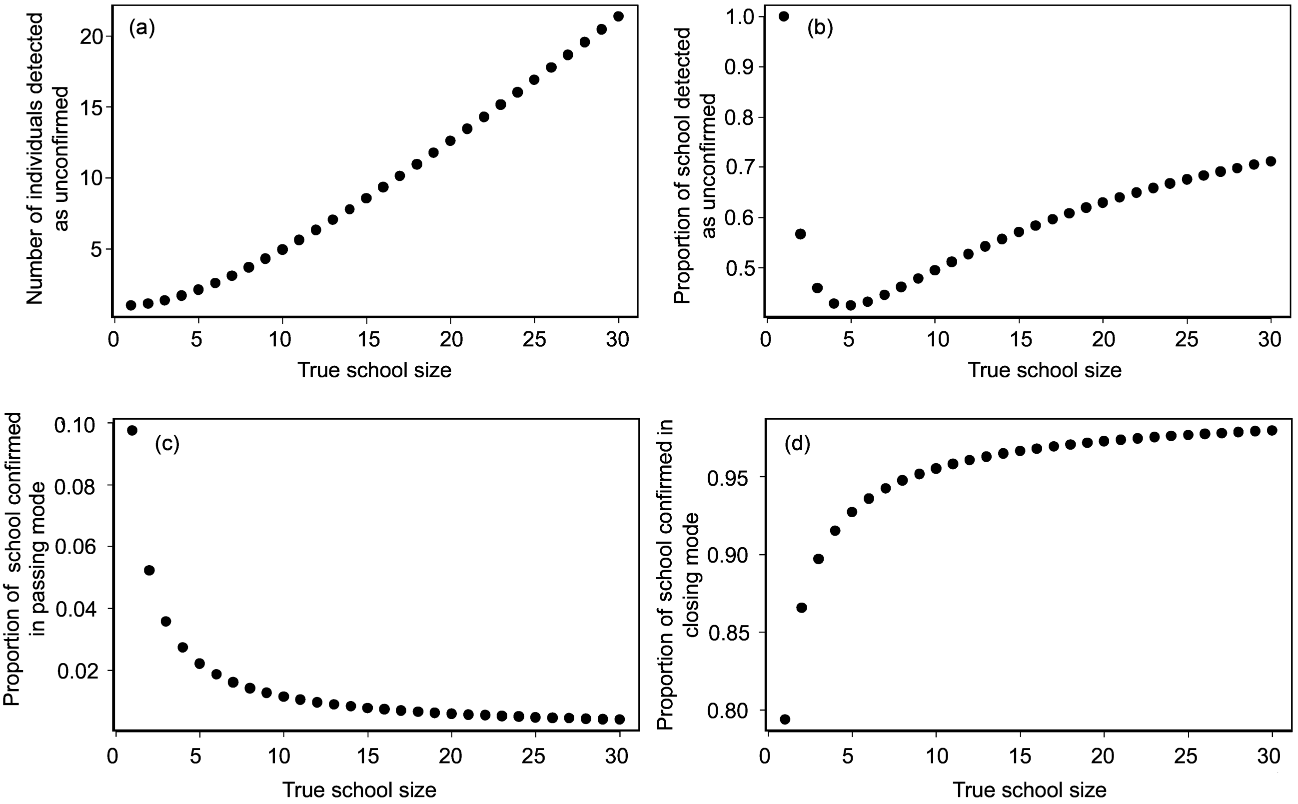

Fig. 3. Plots of the expected number of individuals (a) and proportions (b) confirmed in each school recorded as unconfirmed, and the expected proportion of each school confirmed in passing (c) and closing mode (d). All were plotted against true school size.

detection probability on the trackline of less than 1. It is essential to record sighting time and distance to whales as accurately as possible to correctly discriminate simultaneous and delayed duplicates after sighting surveys. The method proposed in this paper provides a basis for more refined methods for analysing such line transect sighting data. Since $g(0)$ and mean school size are closely related to each other (Cooke, 1985; Butterworth, 2002), the trend and abundance estimates in the population assessment can be miscalculated unless there is an appropriate allowance for bias in mean school size under passing mode. It is extremely important to obtain unbiased trends and abundance estimates for the proper conservation and management of marine resources.

ACKNOWLEDGMENTS

We thank K. Hiramatsu, D.S. Butterworth, K. Matsuoka, S.L. Hedley and M.V. Bravington for helpful discussions, and E. Ward and T. Branch for useful comments on an earlier manuscript. We also thank the officers and crew who participated in the IDCR/SOWER surveys. We are grateful for permission from the IWC office to use their data in this paper. Comments from two anonymous referees are greatly acknowledged.

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Date Received: April 2004
Date Accepted: September 2004

Appendix 1

HAZARD PROBABILITY MODEL

The hazard probability function $Q(x, y)$ is the conditional probability that a school of diving animals is detected by an observer on a sighting platform, given that it surfaced at a relative position (x, y) from a vessel and was not previously sighted by the observer, where x is the perpendicular distance, and y the forward distance in Cartesian co-ordinates. Because $Q(x, y)$ is a probability, $0 \leq Q(x, y) \leq 1$. The surfacing-diving pattern of a school of animals is modelled by a Poisson process. Then, the detection function is given by:

$$g(x) = 1 - \exp\{-(\lambda / v)\int_0^\infty Q(x, y)dy\} \qquad \text{(A1)}$$

where λ is surfacing intensity, and v is constant vessel speed (Butterworth, 1982; Cooke, 1997; Skaug and Schweder, 1999). The assumption of a Poisson process is probably robust for abundance estimation of animals with surfacing pattern such as minke whales (Cooke, 1997; Skaug and Schweder, 1999). In consideration of dependency of school size s on λ, we use the relationship, $\lambda = \lambda_1 e^{af(s)}$ where λ_1, is the surfacing intensity for a single animal and $f(s)$ is a function of school size s which has a value of 0 at $s = 1$.

The hazard probability function for a platform k ($k = A$ or B; observers are distinguished using the notation of $A, B, \ldots$ in this paper) is assumed to be:

$$Q_k(x, y) = \mu_k \exp\{-(x / \sigma_k)^{\gamma_1} - (y / \tau_k)^{\gamma_2}\} \qquad \text{(A2)}$$

where $0 < \mu_k < 1$, $\sigma_k > 0$, $\tau_k > 0$, $\gamma_1, \gamma_2 > 0$, μ_k is the level parameter of the hazard probability function, σ_k and τ_k are the scale parameters, and γ_1 and γ_2 are the shape parameters (Skaug and Schweder, 1999). The corresponding detection function from this hazard function is explicitly expressed as:

$$g_k(x) = 1 - \exp[-\lambda v^{-1} c_2^k \exp\{-(x / \sigma_k)^{\gamma_1}\}] \qquad \text{(A3)}$$

where $c_2^k = \tau_k \mu_k \gamma_2^{-1} \Gamma(\gamma_2^{-1})$, where Γ is the gamma function.

The probability density for the independent sighting data $\{(x_i, y_i, u_i), i = 1, \ldots, n\}$ is then given by:

$$\frac{p(x_i, y_i, u_i)}{esw_{A \cup B \cup C}} \qquad \text{(A4)}$$

where $p(x_i,y_i,u_i)$ is the detection probability given the initial sighting distance (x_i,y_i) and the pattern of detection u_i,

$esw_{A \cup B \cup C} = \int_0^\infty g_{A \cup B \cup C}(x)dx,$

$g_{A \cup B \cup C}(x) = 1 - \exp\{-(\lambda / v)\int_0^\infty Q_{A \cup B \cup C}(x, y)dy\},$

$Q_{A \cup B \cup C} = 1-(1-Q_A)(1-Q_B)(1-Q_C)$, $Q_{AB} = Q_A Q_B$,

$Q_{ABC} = Q_A Q_B Q_C$ and etc (Okamura *et al.*, 2003).

For instance, when all three platforms see a school of animals, say, first C, then A and then B, let y_1, y_2, y_3 ($y_1 > y_2 > y_3$) be forward distances of each initial sighting, the probability function is given by:

$$p(x, y_1, y_2, y_3, C \to A \to B) = \left(\frac{\lambda}{v}\right)^3 Q_B(x, y_3)\{Q_A(x, y_2) - Q_{AB}(x, y_2)\}\{Q_C(x, y_1) - Q_{CA}(x, y_1) - Q_{CB}(x, y_1) + Q_{ABC}(x, y_1)\}$$
$$\times \exp\left(-\frac{\lambda}{v}\left[\begin{array}{l}\int_{y_3}^\infty Q_B(x, y')dy' + \int_{y_2}^\infty \{Q_{A \cup B}(x, y') - Q_B(x, y')\}dy' \\ + \int_{y_1}^\infty \{Q_{A \cup B \cup C}(x, y') - Q_{A \cup B}(x, y')\}dy'\end{array}\right]\right). \qquad \text{(A5)}$$

Appendix 2

CORRECTION FOR UNDERESTIMATION OF SCHOOL SIZE

Let the probability distribution of true school sizes in the region be $\pi(s)$, $s = 1, 2, 3, \ldots$. This distribution applies to all the schools in the population whether they are detected or not. For instance, as in Borchers (1999), it can be assumed that the school sizes have the probability distribution:

$$\Pr(s) = \pi(s) = \frac{\Gamma(\phi_0 + s - 1)}{\Gamma(\phi_0)\Gamma(s)}(1-\phi_1)^{s-1}\phi_1^{\phi_0},\ \phi_0 > 0, \text{ and } 0 < \phi_1 < 1 \qquad \text{(B1)}$$

where ϕ_0 is allowed to be continuous for flexibility following Borchers (1999). It should be noted that (B1) is a negative binomial distribution for $s - 1$ if ϕ_0 is an integer.

Let I be the indicator variable of the detection, i.e.

$$I = \begin{cases} 1, & \text{if detected} \\ 0, & \text{if missed} \end{cases} \qquad \text{(B2)}$$

The detection probability of animals with school size s is then:

$$\Pr(I = 1 \mid s) = esw(s)/W \qquad \text{(B3)}$$

Here $esw(s)$ is effective search half-width for a sighting with school size s and W is the maximum perpendicular distance from the transect line. The probability distribution of detected schools is then:

$$\Pr(s \mid I = 1) = \pi^*(s) = \frac{esw(s)\pi(s)}{\sum_{s=1}^{\infty} esw(s)\pi(s)} \qquad \text{(B4)}$$

where W is cancelled out (Buckland *et al.*, 1993).

Taking into account negatively biased estimation for unconfirmed school sizes, it is further assumed that the observed unconfirmed school sizes (z) is less than true school size s and $E(z - 1 \mid I = 1, s) = b(s - 1)$, $0 < b < 1$. The parameter b is usually dependent on school size, environmental factors, and distance to sighting objects. Effects of covariates for the parameter b are incorporated through logistic link function, that is, $\mathrm{logit}(b) = a_0 + \Sigma a_i X_i$, where values of a are parameters and values of X are covariates. It is assumed that only school size s affects b, denoted $b(s)$, however it would be easy to incorporate environmental or other factors. A parametric probability distribution for unconfirmed school size z ($z = 1, 2, \ldots, s$) is then assumed to be:

$$\Pr(z \mid s) = \rho(z \mid s) = \frac{\Gamma(s)}{\Gamma(z)\Gamma(s - z + 1)} b(s)^{z-1}\{1 - b(s)\}^{s-z} \qquad \text{(B5)}$$

This is the binomial density for $z - 1$ given true school size s. The probability distribution of observed school size, given it is detected and unconfirmed is then:

$$\Pr(z \mid I = 1) = \rho^*(z) = \frac{\sum_{s=z}^{\infty} \rho(z \mid s) esw(s)\pi(s)}{\sum_{s=1}^{\infty} esw(s)\pi(s)} \qquad \text{(B6)}$$

where $\sum_{z=1}^{s}\sum_{s=z}^{\infty} \rho(z \mid s) esw(s)\pi(s) = \sum_{s=1}^{\infty} esw(s)\pi(s)$.

Equation (B6) implies that the mean of the unconfirmed school size minus 1 is equal to the mean of the confirmed school size minus 1 times the parameter b, i.e. $E_{\rho^*}(z - 1) = E_{\pi^*}\{b(s)(s - 1)\}$, where it is noted that the probability distributions are defined for $z - 1$ and $s - 1$. This is derived as follows:

$$E_{\rho^*}(z-1) = \sum_{z=1}^{\infty}(z-1)\rho^*(z) = \frac{\sum_{z=1}^{\infty}(z-1)\sum_{s=z}^{\infty}\rho(z \mid s) esw(s)\pi(s)}{\sum_{s=1}^{\infty} esw(s)\pi(s)}$$

$$= \frac{\sum_{s=1}^{\infty} esw(s)\pi(s)\sum_{z=1}^{s}(z-1)\rho(z \mid s)}{\sum_{s=1}^{\infty} esw(s)\pi(s)} = \frac{\sum_{s=1}^{\infty} esw(s)\pi(s)E(z-1 \mid I=1, s)}{\sum_{s=1}^{\infty} esw(s)\pi(s)}$$

$$= \frac{\sum_{s=1}^{\infty} b(s)(s-1) esw(s)\pi(s)}{\sum_{s=1}^{\infty} esw(s)\pi(s)} = E_{\pi^*}\{b(s)(s-1)\}$$

Therefore, $E_{\rho^*}(z)$ always has to be equal to or less than $E_{\pi^*}(s)$ because

$$\begin{aligned} E_{\rho^*}(z) - E_{\pi^*}(s) &= E_{\pi^*}\{b(s)(s-1)\} + 1 - E_{\pi^*}(s) \\ &= E_{\pi^*}[\{b(s) - 1\}(s-1)] \leq 0 \ (0 < \mathrm{b(s)} < 1,\ \mathrm{s} \geq 1). \end{aligned}$$

Finally a model of school confirmation is needed because confirmation status can change due to school size and environmental factors. The output of confirmation status is a sequence of 'Bernoulli trials' where each trial gives one of two possible outcomes, labelled 0 (unconfirmed) and 1 (confirmed). By letting the additional random variable c represent the outcome of each trial and the parameter d represent the probability that the animal is confirmed, the probability of confirmation status in each trial is $d^c(1–d)^{1-c}$. Effects of covariates for the parameter d are incorporated through logistic link function. However, it is assumed that only school size s and survey mode t affects d and denotes $d_t(s)$, where $t = 1$ denotes passing mode and $t = 2$ closing mode.

Genetic analyses (mtDNA and microsatellites) of Okhotsk and Bering/Chukchi/Beaufort Seas populations of bowhead whales

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ABSTRACT

Both North Pacific populations of bowhead whales (*Balaena mysticetus*) underwent heavy exploitation by commercial whalers in the 19th century, but their reduction in numbers was unequal and their contemporary population sizes differ by an order of magnitude. To investigate the genetic divergence of the different populations, tissue samples of bowhead whales representing the Okhotsk Sea (OS) population (25 samples) and the Bering/Chukchi/Beaufort Seas (BCBS) population (29 samples) were used to generate mtDNA control region sequences and genotypes for three microsatellite loci. There were 20 haplotypes represented in the contemporary BCBS samples and four in the OS samples, three of which were shared with the BCBS samples. The BCBS samples had a much greater haplotypic diversity (0.93) than the OS samples (0.61). Analyses of both types of data revealed significant genetic differences between the two populations, indicating that the populations represent discrete gene pools.

KEYWORDS: BOWHEAD WHALE; GENETICS; CONSERVATION; OKHOTSK SEA; BERING SEA; CHUKCHI SEA; BEAUFORT SEA

INTRODUCTION

Within decades of the discovery of North Pacific populations of bowhead whales (*Balaena mysticetus)* by commercial whalers in the 19th century, they had undergone a significant reduction in their numbers. The Bering/Chukchi/Beaufort Seas (BCBS) population was reduced to a quarter or a fifth of pre-exploitation levels (Woodby and Botkin, 1993), but has since substantially recovered (George *et al.*, 2002) and is still harvested in a subsistence hunt by Alaskan Eskimos. The Okhotsk Sea (OS) population was probably reduced by an even greater proportion and has shown little recovery since the cessation of commercial whaling, and is not hunted. One recent estimate for the BCBS population is 10,020 animals (George *et al.*, 2002) while the less-studied OS population is thought to number just a few hundred (Woodby and Botkin, 1993). Based on a genetic mark-recapture analysis, MacLean (2002) estimated the minimum population size for OS bowheads to be 247. Presently, the stocks are geographically isolated, separated by the Kamchatka peninsula, and there is no evidence that animals currently move between the regions.

The present allopatry of the two populations may not be static over large time scales, fluctuating instead with changing climatic factors. Moore and Reeves (1993) reviewed the distribution and movement of bowhead whales, suggesting that they are widely distributed along the boundary of the ice front in winter. The assumption that the distributions of ice and bowhead whales are closely tied led Dyke *et al.* (1996) to use the distribution of radiocarbon-dated bowhead whale subfossils to track changes in sea ice distributions over the last 10,500 years for the Canadian Arctic. Some of the distributional changes they inferred were abrupt and substantial. Although comparable paleontological data for the North Pacific are lacking, parallel changes in ice cover likely occurred for that region as well. Even in modern times, the extent of sea ice shows considerable interannual variability, extending in heavy ice years to the tip of the Kamchatka Peninsula (Niebauer and Schell, 1993). Indeed, Brueggeman (1982) included reports from 19th century commercial whalers of bowhead whales sighted along the eastern Kamchatka coast. While it is conceivable that some BCBS whales could follow the winter ice edge south in the western Bering Sea during heavy ice years and overlap with the OS population, there is no evidence that this has occurred recently. However, even if contact has not occurred in modern times, Overpeck *et al.*'s (1997) study of the 'Little Ice Age' of the last 400 years traces a pattern of cold periods in the Arctic up until the early 19th century. If 'heavy' ice years during this 'Little Ice Age' were more frequent or more extensive than modern records indicate, there may have been greater opportunity for contact in the not too distant past.

In light of the uncertainty regarding how recently contact between the two populations occurred, this paper investigates the degree to which the populations have diverged. With recent separation, genetic differentiation between them would be expected to be minimal. With contact in the more distant past, dependent on even larger-scale climatic change, stock discreteness should be more apparent and stable through time.

DNA sequence and microsatellite data are used to investigate genetic differentiation between the BCBS and OS populations of bowhead whales, and its implications for population management. Depending on the collection of comparable data from populations of bowhead whales in other areas (Eastern Canadian Arctic, Davis Strait, Spitsbergen), this may be an important first step in understanding the population structure of bowhead whales from all parts of their range.

MATERIALS AND METHODS

Okhotsk Sea bowhead whale samples were taken as biopsies from live whales in August 1995 (14 samples) and in August 1996 (11 samples). All were taken off the

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Ukurunru Cape of the Tugurskiy Peninsula, Russia (Brownell *et al.*, 1997). Tissue samples from the BCBS stock were all taken from animals killed in subsistence hunts in Alaska in 1992 (11 samples) and 1996 (18 samples). One of the 1992 subsistence hunt animals was taken in Nuiqsut, Alaska; the rest of the Alaskan samples came from Barrow. Seventeen of the Barrow samples were also used in a study by Rooney *et al.* (1998; 2001). In all of the above cases, skin samples were preserved in a saturated salt solution with 20% (v/v) DMSO (dimethyl sulphoxide), and kept there until processing. However, the BCBS samples were initially frozen and later transferred to the salt/DMSO solution.

Extraction of DNA from skin samples followed standard protocols as given in Sambrook *et al.* (1989). A 397 base pair (bp) region of the mitochondrial d-loop gene (5' end) was amplified and sequenced according to the methods given in O'Corry-Crowe *et al.* (1997). The primers used for amplification and sequencing were L15964 (5' −CCT CCC TAA GAC TCA AGG −3') and H16498 (5' −CCT GAA GTA AGA ACC AGA TG −3'), the latter from Rosel *et al.* (1994). One additional bowhead whale sequence was obtained from GenBank (accession number 72197) and was published in Árnason *et al.* (1993); the sample originated from Barrow, AK (Árnason and Best, 1991).

Microsatellite data were generated from the biopsy and subsistence harvest samples according to the methods given in Palsbøll *et al.* (1997); the GenBank sample was excluded from this part of the study. Microsatellite primers to EV1 and EV104 are from Valsecchi and Amos (1996) and GATA028 is from Palsbøll *et al.* (1997). One of the Russian samples failed to amplify for EV1. This locus was considered missing data for this individual in subsequent analyses.

Phylogenetic analyses of the sequence data from all samples using neighbour-joining methodology (from uncorrected *p*-distances) and maximum parsimony (MP) were conducted using PAUP 4.062a (Swofford, 1993). Additional analyses were performed using the programs GenePop 3.1b (Raymond and Rousset, 1995) and Arlequin 1.1 (Schneider *et al.*, 1997). The GenBank sequence was not included in the GenePop and Arlequin analyses, in order to keep the sequence and microsatellite sample sets directly comparable. Specific statistics are described in the table legends.

RESULTS AND DISCUSSION

For the d-loop data, the 55 bowhead whale sequences in the entire dataset contained 34 variable sites defining 22 haplotypes (Table 1). Seventeen sites were phylogenetically informative. Exclusive of the GenBank sequence, the 29 Barrow samples represented 20 haplotypes, and the 25 Okhotsk Sea biopsy samples included four haplotypes. Three haplotypes were shared between the two regions, leaving only one haplotype unique to the Okhotsk Sea samples. One must exercise caution in concluding that that one haplotype is unique to the OS population. Given the limited sampling, and the high diversity and large size of the BCBS population, it is plausible that that haplotype also occurs in the BCBS population, but has yet to be sampled. The low diversity in the OS samples is more telling in that there are probably many fewer unsampled haplotypes still extant in that population. In comparison to other small, endangered populations of baleen whales, the four haplotypes found in OS bowhead whales are much less than the 10 reported for western gray whales, *Eschrichtius robustus* (LeDuc *et al.*, 2002) and are more on a par with the five reported for North Atlantic right whales, *Eubalaena glacialis* (Malik *et al.*, 2000). There were no indels (insertions/deletions) among the contemporary Pacific Ocean samples, although the GenBank sequence, in comparison, had an extra base at bp 154.

Table 1

Variable sites; reference numbers from beginning of 5' end of the d-loop light strand.

Haplotype	1111111222222222222333333 1358890111244022555667789225899 56674581137413627458562851013601	Freq. BCBS	Freq. OS
A	AGCCCTCCCGCCGAGACGGTTCAATCGGCTCG	1	
B	AACCCCCCCGCCAAGACGGTTCAATTGGCTCG	1	
C	AACCTCCCCGCTAATACAGCTTAATTAGCTCG	1	3
D	AACCCTCCCGCCGAGACGGTTCAATCGGCTCG	5	13
E	AACCCCCCCGCCAAGACGGTTCAATCGGCTCG	1	
F	AACCCTCCCGCCGAGACGGTTCAATTGGCTCG	1	
G	AACCCTCCCGTCAAGATGGTTCAATCGGCTCG	1	
H	AACACTCCCGCCAAGATAGCTTAACCGGCCTG	2	
I	AACCCTCCCGCCAAGATATTTCAGTTGGCTCG	1	
J	AACCCTCCCGCTAAGACAGCTTAATTAGCCTG	3	
K	AACCCTCCCGCCGAGACGGTTCAATCGGTTCG	2	8
L	AACCCTCCCGCTAAGACAGCTTAATTAGCCCG		1
M	AACCCTCTTATCAGGACAGCTTAATCGGCCTG	1	
N	AACCCTCCCGCCAAGACGGTTCAATCGGCTCG	2	
O	AACCCTCCCGCCGAGACGGTTCAATTGGTTCG	1	
P	AACCCTCCCGCCAGGACGGCTTAACCGGCCCG	1	
Q	AACCCTCCCGCCAAGGTGGTTCAATTGGCTCG	1	
R	AACCCTCCCGCCGAGACGGTTCAGTCGGCTCG	1	
S	AACCCTCCCGCCGAGACGGTCCAATCGACTCG	1	
T	AACCCTCCCGCCAAGACATTTCAATTGGCTCG	1	
U	AATCCTTCCGCCGAGACGGTTCAATCGGCCCG	1	
GenBank	GACCCTCCCGCCGAGACGGTTCGATCGGCTCA		

The 80 MP trees had similar topologies to the unrooted neighbour-joining tree (Fig. 1), although the MP consensus tree showed less resolution. In any case, there was no geographic concordance with the topology of any of the trees. Diversity statistics for the sequences are given in Table 2 (exclusive of the GenBank sequence). The most notable difference is the lower haplotypic diversity shown by the OS samples (0.61) *versus* the BCBS samples (0.93), reflecting not only the fact that the OS sample set contained far fewer haplotypes than BCB, but also displayed a much greater skew in their frequency distribution (see Table 1 for haplotype frequencies). This pattern is consistent with a smaller historical population size in the Okhotsk Sea and the loss of haplotypes through genetic drift. However, a severe bottleneck of a historically large population could also result in low diversity. Given the uncertainty of estimating the pre-exploitation size of the OS population (Woodby and Botkin, 1993), it is not possible to determine which scenario (small historical population *versus* bottleneck) is more likely to have occurred with the present data. However, it is likely that additional haplotypic diversity was lost when 133 bowhead whales were killed from this already small population in 1968 (Doroshenko, 2000). The high haplotypic diversity value for the BCBS population is consistent with Rooney *et al.*'s (1999; 2001) conclusion that this population did not undergo a genetic bottleneck. Although the presence of only four haplotypes among the 25 OS samples resulted in the low haplotypic diversity calculated for that population, these four haplotypes were not particularly closely related to each other (Fig. 1). As a result, the phylogenetic analysis of the sequence data reveals little about relationships between the two populations.

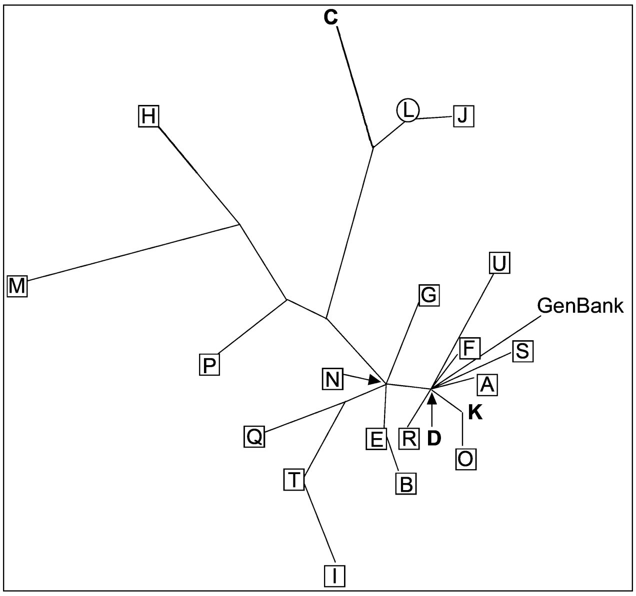

Fig. 1. Neighbour-joining tree determined using uncorrected *p*-distances among all haplotypes. Haplotypes in squares are those unique to the BCBS samples; those in circles are unique to the OS samples. Haplotypes in bold are shared between populations.

For the microsatellite data, locus EV104 exhibited a total of six alleles, EV1 had seven and GATA028 eight. Two of the alleles for EV104 were unique to the BCBS samples, as was one of the GATA028 alleles. EV1 contained a single allele that was unique to the OS samples. All other alleles for all loci were shared between the two populations. Frequencies of alleles and of homozygotes and heterozygotes are given in Table 3. The AMOVA and g-statistic analyses of the data showed small but significant differences between the populations for both microsatellite and sequence data (Tables 4 and 5). The microsatellite results are noteworthy because significant differences were found even though the use of only three loci would have made the power to detect those differences relatively low. These differences indicate that the two populations should be considered genetically and demographically separate for management purposes; gene flow between them is negligible at most. The results also seem to parallel those for gray whales (LeDuc *et al.*, 2002), another North Pacific species with a large eastern population showing high diversity and a small western population with considerably lower diversity.

The fact that the OS biopsy samples were taken from the same locality on successive days each year and in successive years, led to some concern about the possibility of replicate sampling of individuals introducing some bias into the data. However, none of the OS samples had identical genotypes for the three microsatellite loci examined, indicating that no animals were resampled.

Overall, the significance of the genetic differences is consistent with a lack of any appreciable recent gene flow between the two populations, but the small degree of those differences does not preclude the possibility that their most recent contact was in the not too distant past. Given the reduced population sizes, especially for the OS population, an increased rate of genetic drift in the last century could

Table 2

MtDNA genetic diversity by population. Values ± SD; $n = 29$ for the BCBS sample, and $n = 25$ for the OS one. For both populations, 398 nucleotide sites were sequenced. No insertions or deletions were observed. Nucleotide diversity is the mean number of pairwise nucleotide differences per observed nucleotide sites (Schneider *et al.*, 1997). Haplotype diversity: $h = 1 - \sum x_i^2$, where x_i is the frequency of the i_{th} haplotype (Nei, 1987).

Population	Number of transitions	Number of transversions	Nucleotide diversity	Haplotype diversity (*h*)
BCBS	26	3	0.015 ± 0.008	0.9275 ± 0.003
OS	11	1	0.008 ± 0.005	0.6112 ± 0.009

Table 3

Allelic frequencies and observed and expected numbers of homozygotes and heterozygotes (Raymond and Rousset, 1995) by population by microsatellite locus. $n = 29$ for the BCBS sample, and $n = 25$ for the OS sample. The null hypothesis of random union of gametes could not be rejected when tested against excess numbers of heterozygotes or excess numbers of homozygotes (Raymond and Rousset, 1995). "AA"= homozygotes; "Aa" = heterozygotes.

	Alleles							
EV1	1	2	3	4	5	6	7	
BCBS	0.224	0.138	0.086	0.224	0.310	0.000	0.017	
OS	0.146	0.104	0.167	0.167	0.292	0.083	0.042	
	"AA" BCBS		"Aa" BCBS		"AA" OS		"Aa" OS	
Expected	6.1		22.9		3.9		20.1	
Observed	4		25		6		18	
EV104	1	2	3	4	5	6		
BCBS	0.190	0.190	0.155	0.293	0.138	0.034		
OS	0.000	0.400	0.100	0.440	0.060	0.000		
	"AA" BCBS		"Aa" BCBS		"AA" OS		"Aa" OS	
Expected	5.5		23.5		8.9		16.1	
Observed	7		22		9		16	
GATA028	1	2	3	4	5	6	7	8
BCBS	0.241	0.155	0.069	0.121	0.034	0.103	0.241	0.034
OS	0.140	0.140	0.040	0.320	0.000	0.140	0.180	0.040
	"AA" BCBS		"Aa" BCBS		"AA" OS		"Aa" OS	
Expected	4.6		24.4		4.5		20.5	
Observed	2		27		6		19	

Table 4

Population differentiation based on mtDNA. Analysis of variance of pairwise mtDNA distances (i.e., number of nucleotide differences; Excoffier *et al.*, 1992) between and among individuals. The significance of measured fixation index, F_{st}, is obtained by permuting individuals among populations to determine the probability of obtaining, by chance, an F_{st} value greater or equal to the observed value; 1,000 permutations were used.

Source of variation	d.f.	Sum of squares	Variance components	Percent variation
Among populations	1	6.35	0.15	6.21
Within populations	52	118.94	2.29	93.79
Total	53	125.30	2.44	

Fixation index $F_{st} = 0.062$; significance $P = 0.026$

Table 5

Population differentiation based on three microsatellite loci. A. H_o = *allelic* distribution is identical across BCBS and OS populations (Fisher exact test; Raymond and Rousset, 1995), or B. H_o = *genotypic* distribution is identical across BCBS and OS populations (log-likelihood [G] based exact test; Raymond and Rousset, 1995).

A. Allelic differentiation
$\chi^2 = 21.5$
d.f. = 6
$P = 0.0018$

B. Genotypic differentiation
$\chi^2 = 20.6$
d.f. = 6
$P = 0.0021$

have enhanced a pre-existing level of differentiation. However, the present data are inadequate to evaluate this possibility.

In any analysis of this sort, conclusions drawn about population differentiation are limited by the sampling regime that was employed. When only a single locality is sampled for each population, any substructure or site fidelity within populations could introduce a sampling bias. This is likely not a factor for the BCBS samples, as the sampling locality is along a migration route, by which the vast majority of the population passes en-route to their feeding grounds. The OS samples, on the other hand, were collected from a single locality on the feeding grounds, and as such may not be as representative of the population. However, the structure and/or site fidelity in this population would have to be highly developed for any sampling bias to account for the observed genetic differentiation and differences in diversity. Increased sampling from more areas within the OS is obviously desirable to mitigate these concerns. It would also provide the basis for a better mark-recapture estimate of population size; the estimate of MacLean (2002) was based on only one between-year and one within-year resampling event. For the OS population, a genetic mark/recapture method is probably the most promising method for determining the current population size. This type of study is needed because of the difficulty in conducting photo-identification studies on this population. The OS bowhead whales, at least in our study area, appear to have a low frequency of distinctive markings compared to BCBS bowhead whales. In addition, a modelling study on populations of these sizes and incorporating their historical demographics could establish possible time-frames for recent contact and subsequent genetic drift.

ACKNOWLEDGEMENTS

We would like to thank the following for help in collecting and sharing samples: T. Albert, P.J. Clapham, D. Withrow, R. Suydam, T. Ohara, R.L. Pitman and B. Würsig. Special thanks to the Eskimo hunters in Alaska for their cooperation and assistance in procuring biopsy samples from harvested animals. Thanks to A. Rosenberg for generating the data at SWFSC. The CITES export permits were issued by the Russian State Committee of Environmental Protection for the Okhotsk Sea bowhead whale biopsy samples. Research on the Okhotsk Sea bowhead whales was conducted as part of the Marine Mammal Project under Area V: Protection of Nature and the Organization of Reserves within the US —Russia Agreement on Cooperation in the Field of Environmental Protection. Funding for this work was provided by the Bureau of Oceans and International Environmental and Scientific Affairs, US Department of State, through the International Whaling Commission, the Humane Society of the United States and the National Marine Fisheries Service.

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Date Received: March 2005
Date Accepted: March 2005

Genetic tagging of male North Atlantic minke whales through comparison of maternal and foetal DNA-profiles

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ABSTRACT

DNA-profiles from 288 mother-foetus pairs were used to obtain partial DNA-profiles for the fathers of the foetuses. The paternal profiles were subsequently matched against those of the males on the Norwegian DNA-register for minke whales using statistical analyses. Three likely instances of paternity were identified. An estimate of the number of reproductively active males in the population was calculated and found to be consistent with previous abundance estimates. However, the associated confidence interval was very broad since it was based on few 'recaptures'. Finally the scope and potential use of such genetic and population data is discussed.

KEYWORDS: ATLANTIC OCEAN; GENETICS; MARK-RECAPTURE; MOVEMENTS; REPRODUCTION; EUROPE; DNA FINGERPRINTING; COMMON MINKE WHALE

INTRODUCTION

Parentage studies based on DNA-profiles are now commonly conducted for many species of wildlife (Marshall *et al.*, 1998; Jones and Arden, 2004), however, so far there have been few for baleen whales (Clapham and Palsbøll, 1997; Nielsen *et al.*, 2001; Garrigue *et al.*, 2003). Determination of biological paternity *per se* is not usually the primary goal of such studies. Identification of father-offspring pairs can yield information about animal abundance (Nielsen *et al.*, 2001), gene flow between subpopulations (Amos *et al.*, 1993) and reproductive success in different behavioural groups of animals (Nielsen *et al.*, 2001).

A particularly advantageous situation for paternity studies arises when DNA-profiles from mother-offspring pairs, confirmed on non-genetic grounds, are available. By comparing their DNA-profiles, one of the father's two alleles can be inferred at each locus[1], yielding a partial paternal DNA-profile. This profile can subsequently be compared against a DNA-database of potential fathers. In the studies cited above, the database covers a large proportion of the male population. In the present study, on the other hand, only a small fraction of the males are present in the database, and hence a classical mark-recapture approach is used. The partial DNA profiles serve as tags for the fathers. Unless the number of genetic loci is very large, many tags will not be unique in the population, i.e. there may be males other than the true father that match an inferred partial DNA-profile. Thus, statistical analyses are required to calculate the 'specificity' of each father profile. The specificity is a measure of the usefulness of the tag in a mark-recapture setting. A related concept is that of the 'paternity probability' (Nielsen *et al.*, 2001). When a match with the database is obtained, one can calculate the probability that the true father has been found, as opposed to an unrelated male matching by chance.

The establishment of the Norwegian DNA-register for common minke whales (Olaisen, 1997) has provided an opportunity to perform paternity studies for northeastern Atlantic common minke whales (*Balaenoptera acutorostrata*). The register currently contains DNA-profiles (10 microsatellites loci and mtDNA) for 3,301 individuals caught by Norwegian whalers in the period 1997-2002. From the year 2000, foetal tissue samples have also been collected from pregnant females.

The migration pattern of common minke whales in the North Atlantic is not known but it has been speculated that they may enter the Northeast Atlantic feeding areas through the Denmark Strait and north of the British Isles. Recent sightings surveys (Skaug *et al.*, 2004) have revealed that common minke whales summer in fairly large numbers in the Norwegian, Greenland, North and Barents Seas. Although their numbers can vary through seasons and between years, no clear migration patterns are apparent from those data. According to Jonsgård (1951; 1955) common minke whales migrate into Norwegian and Arctic waters in the spring, are most frequent there in the summer, and leave these northern waters again more or less completely in the autumn. Immigration in the spring begins apparently in the southern and western areas and continues along the coast. There is segregation both with respect to length and sex (Jonsgård, 1951; Øien, 1988). Large females dominate in Skagerrak (Fig. 1, south-eastern part of the EN area) and in the main Barents Sea and off Spitsbergen, while large males dominate in the rest of the EN area (Fig. 1). During 1974-78, 333 minke whales were marked with Discovery tags in the Barents Sea. In addition, 18 individuals had been tagged prior to 1974 and 15 individuals have been tagged after 1978. Of the total 366 tags applied, 33 have been recovered in the commercial minke whale catches (Christensen and Rorvik, 1978; Beddington *et al.*, 1984). Locations for tagging and recaptures of the Discovery tags are shown in Fig. 1.

A key question is whether the 288 inferred partial DNA-profiles obtained in the present study are sufficiently specific to provide useful information about paternity. The number of fathers that can be identified also depends crucially on the proportion of the male population covered by the DNA-register. Simple calculations, based on the number of males present in the DNA-register and the best estimate of total population size (Skaug *et al.*, 2004), show that the expected number of recaptured fathers is rather low (approximately five). Thus, our ability to gain new

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[1] Not uniquely though, in the situation where a heterozygotous offspring shares both alleles with the mother.

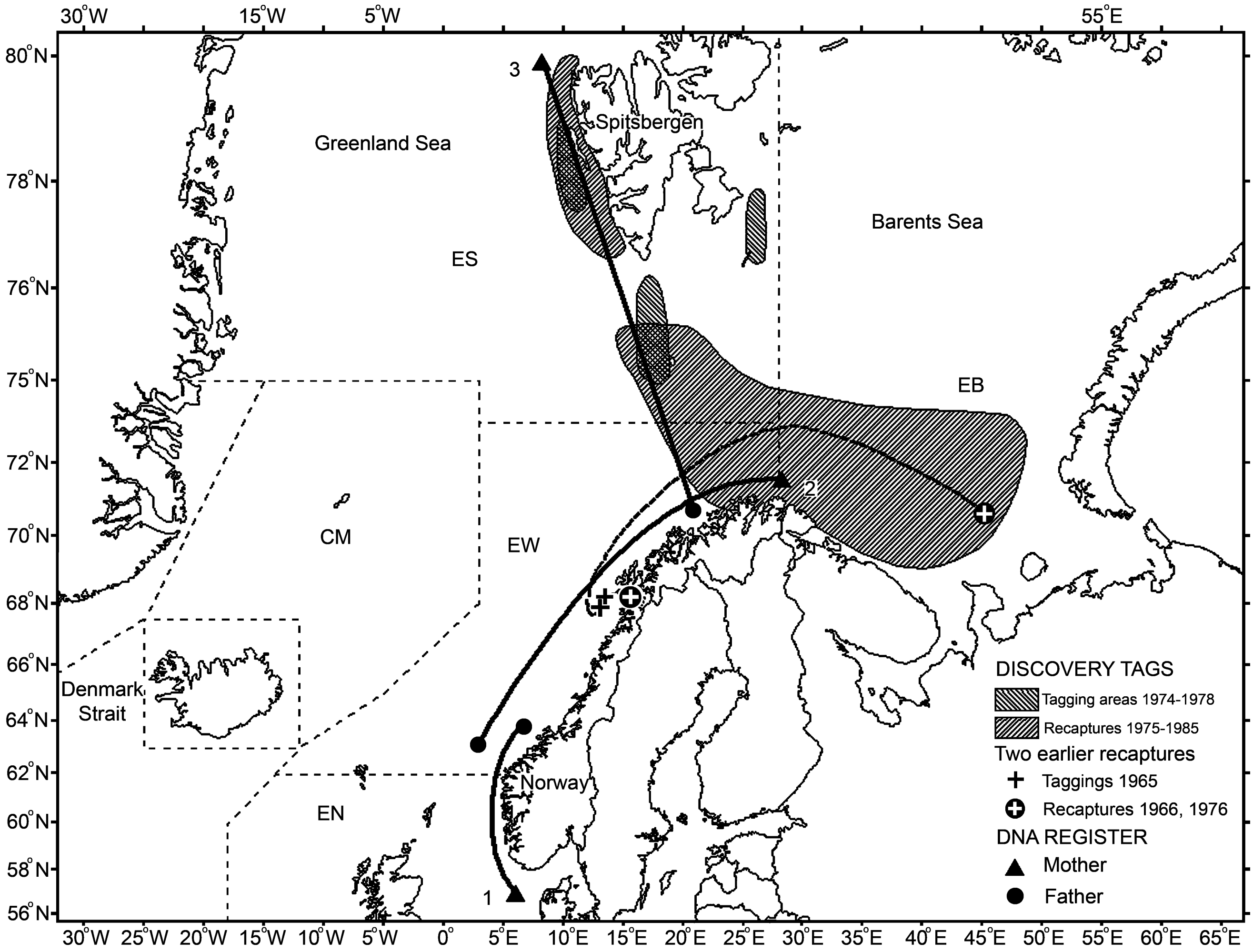

Fig. 1. Location of tagging and tag-recoveries, both for previously applied Discovery tags and for the genetic tags obtained in the present study. Dashed lines indicate borders between Small Areas. The numbers associated with mothers provide a link to Table 3.

biological information about common minke whales is rather limited. The goal was rather to report on the feasibility of the approach, and to point to potential applications if larger datasets should become available.

MATERIAL AND METHODS

Origin and nature of samples

The establishment of the Norwegian common minke whale DNA-register ensures that samples (muscle tissues) are taken from each animal caught under the Norwegian catch quota, and that a DNA-profile for each whale is established and stored in a database (Olaisen, 1997). The DNA-profile consists of 10 microsatellites, mtDNA and a sex-marker (Dupuy and Olaisen, 1998). In addition, for each animal, the register contains information about the time and geographical location of capture, as well as some biological parameters (length etc.). At the time of writing the register contained information (Table 1) on 3,301 individuals, out of the total of 3,392 individuals caught during the period 1997-2002. All individuals were caught in the season from April to September.

Starting from year 2000, foetal tissue samples have also been taken from pregnant females. In this study we have established the DNA-profiles of 288 foetuses, using the same protocol (Dupuy and Olaisen, 1998) and laboratory as has been used for the DNA-register. As mtDNA is maternally inherited, it does not carry information about the father and is only used for data checking, to guard against accidental sample switching during data collection.

Table 1

Norwegian catches of minke whales in the North Atlantic by Small Area for the period 1997-2002. The number of animals used in the present analysis is given in parenthesis.

	EN	EC	EB	ES	CM	Total
1997	57(53)	14(12)	283(280)	129(124)	20(19)	503(488)
1998	139(131)	15(14)	285(281)	129(126)	57(57)	625(609)
1999	122(116)	12(12)	287(277)	112(111)	58(55)	591(571)
2000	83(81)	16(8)	228(224)	103(101)	57(56)	487(470)
2001	128(124)	11(10)	262(257)	120(116)	31(31)	552(538)
2002	132(129)	13(13)	308(307)	146(141)	35(35)	634(625)
Total	661(634)	81(69)	1,653(1,626)	739(719)	258(253)	3,392(3,301)

Tag specificity and paternity probability

The specificity, p_{spec}, of a partial DNA-profile is a statement about how rare its constituent alleles are in the population. Thus, tag specificity can be calculated from maternal and foetal DNA-profiles alone, without consideration of any candidate fathers. Later, when given a database of candidate fathers, paternity probabilities can be assigned to each individual in the database according to formula (1) below, adopted from Nielsen *et al.* (2001).

The offspring and maternal DNA-profiles are denoted by O_i and M_i, respectively, for the *i*th foetus-female pair. Because the offspring inherits one allele from each parent, the part of O_i that is paternally inherited can be inferred by comparison of O_i with M_i (Table 2). At loci where the offspring is a heterozygote, it is not possible to determine which of the two alleles is inherited from the father (locus GT211 in Table 2). The partial DNA-profile (shaded part of the paternal-profile in Table 2) can be used to exclude potential fathers. Non-exclusion by this criterion cannot be taken as absolute evidence for paternity since consistency could occur by chance. The specificity, p_{spec}, of a genetic tag (a partial DNA-profile) is defined here as the probability that there are no males in the population, other than the true father, that are consistent with the tag. If f_l is the population frequency of the inferred allele at locus *l* then the probability that a given male (non-father) is consistent at *L* loci by chance is $p_0 = \Pi_{l=1}^{L}\left[1-\left(1-f_l\right)^2\right]$, and hence the specificity is given as: $p_{spec} = \left(1-p_0\right)^{N_m-1}$, where N_m is the number of reproductively active males in the population. A practical interpretation of p_{spec} is as a measure of 'tag quality', as a value of p_{spec} close to one means that the true father will be identified with near certainty if his profile is present in the database.

The DNA-profile of the *j*th male in the DNA-register is denoted by F_j. The paternity probability, $P_i(j)$, is defined as $P_i(j)$ = Pr(Male *j* is father of fetus *i*). Under the assumption that the *J* males contained in the DNA-register constitute a random sample from the N_m reproductively active males in the population, it follows (Nielsen *et al.*, 2001) that the paternity probability is given as:

$$P_i(j) = \frac{P(O_i \mid M_i, F_j)}{\sum_{k=1}^{J} P(O_i \mid M_i, F_k) + (N_m - J) P(O_i \mid M_i)} \qquad (1)$$

Here, $P(O_i \mid M_i, F_j)$ is the conditional probability of the offspring DNA-profile, given both maternal and paternal profiles. Similarly, $P(O_i \mid M_i)$ is the conditional probability of O_i given only the mother profile. Expressions for these probabilities can be derived from Mendel's law, together with the assumption that loci are independent, so that probabilities can be multiplied across loci. As pointed out by Nielsen *et al.* (2001), formula (1) can be interpreted as a Bayesian posterior probability. Formula (1) takes into account the fact that the DNA-register only covers a proportion J / N_m of the male population. The (posterior) probability that the DNA-register contains the true father of the *i*th foetus is $\sum_{j=1}^{J} P_i(j)$.

The year in which the *i*th mother-foetus pair was captured is denoted by y_i. Because the gestation period for common minke whales is suggested to be around 10 months (Horwood, 1990), only males in the DNA-register caught in year y_i or later were used to calculate $P_i(j)$. To emphasise this *J* is replaced by J_i, the number of males contained in the DNA-register caught in year y_i or later.

Abundance estimation

As with ordinary mark-recapture experiments, the data obtained in the present study can be used to estimate animal abundance, but for this case the uncertainty associated with the tag needed to be reflected. Expression (7) from Nielsen *et al.* (2001) was modified to obtain the log-likelihood function:

$$l(N_m) = \sum_{i=1}^{288} \log\left(\frac{N_m - J_i}{N_m} P(O_i \mid M_i) + \frac{1}{N_m} \sum_{j=1}^{J_i} P(O_i \mid M_i, F_j) \right)$$

An estimate of N_m was found by maximising $l(N_m)$, using a simple bisection algorithm.

RESULTS

Among the 288 genetic tags obtained in this study, five were consistent with two or more males in the DNA-register (matching at each of the 10 loci). All of these tags had very low specificities ($p_{spec} < 1 \times 10^{-8}$), showing that they were not useful as tags in a mark-recapture setting. There were 17 tags matching exactly one male in the DNA-register. A histogram of the specificities for all 288 tags is shown in Fig. 2. Sixty-eight tags had specificity higher than 0.9, and 127 tags were in the range 0.1-0.9. For calculation of p_{spec}, the value N_m = 36,000 was used. This number was derived from an abundance estimate of 107,200 minke whales (Skaug *et al.*, 2004), and the assumption that reproductively active males constitute 1/3 of these.

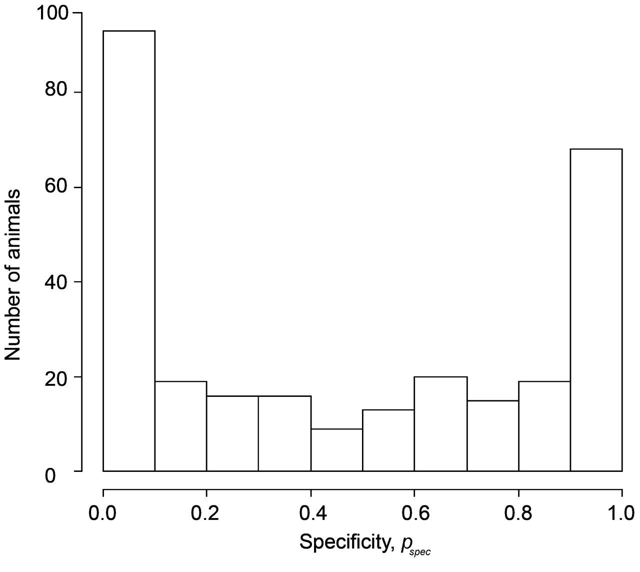

Fig. 2. Frequency distribution of tag-specificities for genetic tags obtained from the 288 minke whale mother-offspring pairs.

Table 2

DNA-profiles of a likely foetus-mother-father triplet. Alleles shared by both mother and offspring are shown in bold, while alleles shared by father and offspring are shaded grey. For locus GT211 it is not possible to infer which of the two alleles is inherited from the father. The column 'ID' gives the identification number used internally by the DNA-register.

	ID	GATA098	GT509	EV1	EV37	GT310	GT211	GT575	GT023	GATA028	GATA417
Foetus		95 **95**	**201** 205	**153** 157	201 **203**	**117** 121	104 106	154 **156**	**99** 99	**161** 206	**220** 236
Mother	104030	87 **95**	**201** 201	141 **153**	203 **203**	115 **117**	104 106	156 **156**	**99** 103	**161** 161	213 **220**
Father	201593	95 95	205 211	157 157	201 201	117 121	104 106	152 154	99 99	183 206	232 236

Four mother-father-offspring triplets had a paternity probability larger than 0.5 (Table 3). For each of these the positions and time points of capture were extracted from the database (Table 3). The male and female capture locations for the three triplets with a probability higher than 0.8 are shown in Fig. 1.

The log-likelihood as a function of N_m is shown in Fig. 3. The maximum likelihood estimate is $\hat{N}_m$ = 38,400, and the effective number of recaptures is m_e = 5. The lower bound in a 95% confidence interval is 13,000. The upper bound of the confidence interval is in practice infinity.

DISCUSSION

In Fig. 1, only mother-father-offspring triplets with paternity probabilities larger than 0.8 were plotted. The fourth triplet listed in Table 3 was excluded since its paternity probability was close to 0.5 and thus deemed not a 'certain' case. Nevertheless, paternity probabilities below 0.8 have various uses (Jones and Arden, 2004), one of them being abundance estimation.

In human genetics it has been estimated that the error rate in large-scale microsatellite screens of the type underlying the minke whale DNA-register is 0.25-2% per locus (Ewen *et al.*, 2000). Comparison of maternal and foetal DNA-profiles in the present study indicated that the error rate in the minke whale DNA-register is in the same range. Inconsistencies between maternal and foetal profiles discovered during this process were subsequently resolved by the genetics laboratory. However, errors in the unchecked half of the foetal profile, together with errors in the paternal profile when contained in the DNA-register, would cause the paternity probability to become zero, and hence lead to erroneous exclusion of the father. A simple sensitivity study was conducted to show that none of the excluded fathers in the database were likely to be excluded due to a typing error.

There is no evidence of monogamy in common minke whales, so it is very unlikely that the DNA-register would contain any full siblings of a given foetus. Half-siblings can be present, however, and we thus calculated the probability that a half sibling (same father as the foetus) is consistent with the inferred part of the father-profile by chance. This probability was found to be low (0.008), showing that half-siblings are unlikely to have caused problems in the study.

Based on the tagging programme carried out in the period 1974-1978, the Northeast Atlantic stock of common minke whales was estimated to be in the range 81,500 to 121,000 (Beddington *et al.*, 1984). More recent abundance estimates have been based on line transect methodology, and have given numbers in the same range (Skaug *et al.*, 2004). The estimate N_m = 38,400 for the reproductively active male population obtained in the present study is consistent with previous abundance estimates, but as it is based on few 'recaptures', the associated uncertainty is large.

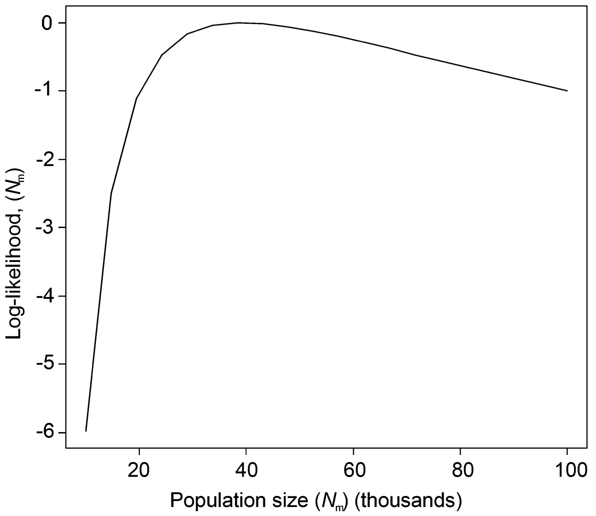

Fig. 3. Normalised log-likelihood as a function of male population size N_m (in thousands).

Mark-recapture methods rely on the assumption that all individuals have the same probability of being marked, as well as having the same probability of being recaptured on later occasions. If there are differences in reproductive success among males the first part of this assumption will be violated for the present method, because 'super-breeders' will have an increased chance of being tagged. There is no external information available on variation in reproductive success in common minke whales. Note that breeding opportunities prior to 2000 (the first year of collection of foetal samples) are not relevant in this context, and hence difference in age among males does not introduce heterogeneity in the marking probability. When recaptures are being recorded over a long period relative to the life span of the species, it may be necessary to apply mark-recapture estimators appropriate for open populations. As the recapture period in this study was only three years, this was not a concern.

A further assumption of mark-recapture methods is that of a single population, which translates into the assumption that northeastern Atlantic common minke whales are panmictic (i.e. constitute a single breeding unit). The fact that mtDNA markers for males and microsatellite markers (both males and females) have uniform haplotype frequencies across sub-areas indicate that there is only a single breeding population (IWC, 2004). The fact that there are significant differences in mtDNA haplotype frequencies between the central and eastern part of the North Atlantic for females, are likely to be caused by a learning process where the calves follow their mothers, and does not constitute evidence against the assumption of a single breeding stock.

Table 3

The four most likely foetus-mother-father triplets, as measured by the paternity probability (rightmost column). Information about time and position of capture, together with zoological length, is also given. The first column provides a link to Fig. 1 which displays capture positions. The column 'SMA' shows the corresponding IWC Small Area (Fig. 1).

	Female and offspring					Male				
Fig. 1	Date	Map reference	SMA	Length (cm)		Date	Map reference	SMA	Length (cm)	$P_i(j)$
				Moth.	Fet.					
1	10.05.01	56°59'N, 06°04'E	EN	775	14	11.08.02	63°50'N, 06°37'E	EW	864	1.00
2	30.05.01	71°35'N, 28°17'E	EB	785	44	08.06.02	63°10'N, 03°00'E	EW	770	0.99
3	28.05.00	79°55'N, 08°18'E	ES	810	48	18.07.01	70°46'N, 20°53'E	EW	820	0.87
	23.06.01	57°15'N, 04°34'E	EN	836	62	04.08.01	64°14'N, 05°44'E	EW	734	0.58

It is not known where breeding and calving take place. Studies of North Atlantic foetal growth data indicate a prolonged mating season with conceptions occurring December-May, with February as the peak month (Horwood, 1990). Hence, the whaling operations in one year end (in September) before next year's reproduction begins. Gestation has been calculated to last about 10 months and thus calves are born over the period October to March with a peak in December in the North Atlantic. None of the probable fathers listed in Table 3 were caught prior to the seasonal catch date of the female. This may be in accordance with the general belief inferred from catch statistics that mature females migrate into the summer feeding areas earlier than males (Øien, 1988).

Based on the observations from several studies of minke whale foetal growth rates, it has been found that the foetus has an average growth of approximately 1cm day^{-1} (Horwood, 1990). With this assumption all the foetuses in Table 3 must have been conceived in April, probably the latter half of the month. Although information on travel speeds of minke whales are sparse, results from satellite tracking in Norwegian waters indicate travelling distances of the order 50-80km day^{-1} (Heide-Jorgensen *et al.*, 2001). This means that the female caught in the Skagerrak part of the North Sea on 10 May 2001 with a foetus of length 14cm must have conceived within the North Sea area, and consequently, the father must also have been present in the North Sea area in this period. Combining this with the fact that the father was caught in the Norwegian Sea the year after, there are two locations in space and time for the father. This type of multiple recapture data provides a means of studying site fidelity in minke whales.

The links as given in Table 3 also give insight to reproductive parameters. Studies of Northeast Atlantic minke whales have given estimated lengths at sexual maturity of 7.15m for females and 6.75m in males. Both females and males listed in Table 3 show lengths well above these, namely 7.75m-8.36m and 7.34m-8.64m for females and males, respectively.

To verify the hypothesised relationships in Table 3, particularly the last two, one could type the involved individuals at a number of additional loci. This could also be done for putative fathers with probabilities lower than 0.5 (not shown in Table 3), and would be a way of partly getting around the fact that a large proportion of the tags have low specificities (Fig. 2). Such a two-stage approach is both time and cost efficient compared to an approach where all the males in the DNA-register are typed at additional loci.

In conclusion, the various genetic tagging methods that exist have a large potential to yield important new information about cetacean demography. This is especially true for common minke whales, which are difficult to study by other means. From a management point of view, it seems necessary to monitor the level of relatedness in catches for harvested whale populations. Even if laboratory costs should prevent DNA-profiles being established for the full catch, it is vital that tissue samples are taken from all individuals, and stored for future analysis.

ACKNOWLEDGEMENTS

We are grateful to Charlotta Lindblom at IMR for handling the tissue samples, and to the Norwegian Directory of Fisheries for providing funding for the study.

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Date Received: November 2004
Date Accepted: April 2005

J. CETACEAN RES. MANAGE. 7(2):119–135, 2005

Observations of cetaceans in the Maldives, 1990-2002

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ABSTRACT

Cetaceans observed in Maldivian waters were recorded during the period August 1990 to June 2002, from both vessels-of-opportunity and dedicated cetacean-watching cruises. A total of 1,829 cetacean sightings were recorded during 535 days at sea (equivalent to 261 standardised days). There were 83 multispecies sightings, plus a further 58 sightings without associated effort data and 129 strandings were recorded by the author and others, making a total of 2,108 cetacean records. In all, 20 different species were positively identified from sightings. Spinner dolphins were the most abundant species seen, accounting for 35% of sightings and 53% of numbers. This species showed a clear diurnal pattern of behaviour, with many schools entering the atolls in the early morning, and leaving in the late afternoon. Spinner dolphins regularly occurred with pantropical spotted dolphins and both species associated with yellowfin tuna. Bryde's whales also associated with yellowfin tuna and appeared to be most common in Maldivian waters during El Niño Southern Oscillation events. Blue whales were only recorded during November to April. Dwarf sperm whales were especially difficult to locate in rough weather but relatively common, making up one sixth of all sightings in flat-calm conditions. Melon-headed whales were particularly common in the south of the Maldives, but rare in the centre and north. Other species recorded were humpback whale, sperm whale, rough-toothed dolphin, Risso's dolphin, bottlenose dolphin, striped dolphin, Fraser's dolphin, pygmy killer whale, false killer whale, killer whale, short-finned pilot whale, Blainville's beaked whale, Longman's beaked whale and Cuvier's beaked whale.

KEYWORDS: INDIAN OCEAN; SANCTUARIES; INCIDENTAL SIGHTINGS; SCHOOL SIZE; MIGRATION; EL NIÑO; BRYDE'S WHALE; BLUE WHALE; DWARF SPERM WHALE; PANTROPICAL SPOTTED DOLPHIN; SPINNER DOLPHIN; MELON-HEADED WHALE

INTRODUCTION

The Republic of Maldives is a small island nation in the central Indian Ocean, to the southwest of India and Sri Lanka (Fig. 1). It lies at the heart of the International Whaling Commission's (IWC) Indian Ocean Sanctuary and has a particularly rich cetacean fauna. Until recently, however, it has received relatively little attention from cetologists.

Among those who made brief visits to the Maldives and left some record of their cetacean sightings were: the 19th century French merchant-shipowner and naturalist Jean-Jacques Dussumier (Arvy, 1972; Gilpatrick *et al.*, 1987); the Dutch sea captain Willem Mörzer Bruyns, who passed through or by the Maldives on several occasions in the 1950s and 1960s (Mörzer-Bruyns, 1971); Captain Jacques-Yves Cousteau, who visited the Maldives in 1967 (Cousteau and Diolé, 1971; 1972); Stephen Leatherwood and fisheries worker Charles Peters, who visited the Maldives separately in 1980-83 (Leatherwood *et al.*, 1984; with additional information on some sightings in: Leatherwood, 1986; Gilpatrick *et al.*, 1987; Wilson *et al.*, 1987; Leatherwood *et al.*, 1991); Japanese whaling researchers who passed through the Maldives on two scouting vessels in March 1982 (Kasuya and Wada, 1991); cetologists on the research yacht *Tulip* who visited the Maldives in late 1983 and early 1984 (Whitehead *et al.*, 1983; Alling *et al.*, 1984) during the course of their research elsewhere in the Indian Ocean Sanctuary (Alling, 1986; Whitehead, 1989; Gordon, 1991); and marine biologists Lisa Ballance and Robert Pitman who passed through Maldivian waters in April and June 1995 during the course of a cetacean survey of the western Indian Ocean (Ballance *et al.*, 1996; Ballance and Pitman, 1998).

Among reports by scientists based in the Maldives are those on: miscellaneous strandings and sightings (Anderson, 1990; 1996); the association of large yellowfin tuna (*Thunnus albacares*) with dolphins (Anderson and Shaan, 1998); all known cetacean strandings and specimens from the Maldives up to early 1999 (Anderson *et al.*, 1999); a 20-day cetacean survey in the north-eastern part of the Maldives during April 1998 (Ballance *et al.*, 2001); and a stranded Longman's beaked whale, *Indopacetus pacificus* (Dalebout *et al.*, 2003).

These studies between them reported a total of 18 species of cetacean from sightings in the Maldives, with a further two species reported from strandings. The 20 species (listed in the species accounts, below) include all of the expected pantropical varieties and all of the locally abundant species. However, most earlier studies were of limited duration and scale, and provided only limited information on local distribution, abundance, behaviour and ecology.

The aim of this paper is to summarise sightings of cetaceans in the Maldives made by the author over the 12-year period August 1990 to June 2002. Although not uniformly distributed, these sightings cover every month and every atoll and most have been recorded with associated effort data. While not comprehensive, they provide a broad overview of the cetacean species occurring in Maldivian waters including: a first impression of their distribution and relative abundance; some initial information on their local behaviour and ecology; and indications of promising avenues for more focussed future research.

METHODS

Survey area

The Maldives is composed entirely of coral atolls, which form a chain running north-south from about 7°N to about 0.5°S (Fig. 1). The atoll chain is single in the north and south but double in the central part of the archipelago. Maximum depths within the atolls are typically 50-60m but vary from about 10-100m. Outside the atolls the reef slopes drop steeply away to the ocean floor, at about 2-3,000m. An exception is found in the area between the double chain of atolls in the central Maldives, the 'inter-atoll sea', where bottom depths are of the order of 2-500m. While these general features of Maldivian bathymetry are well

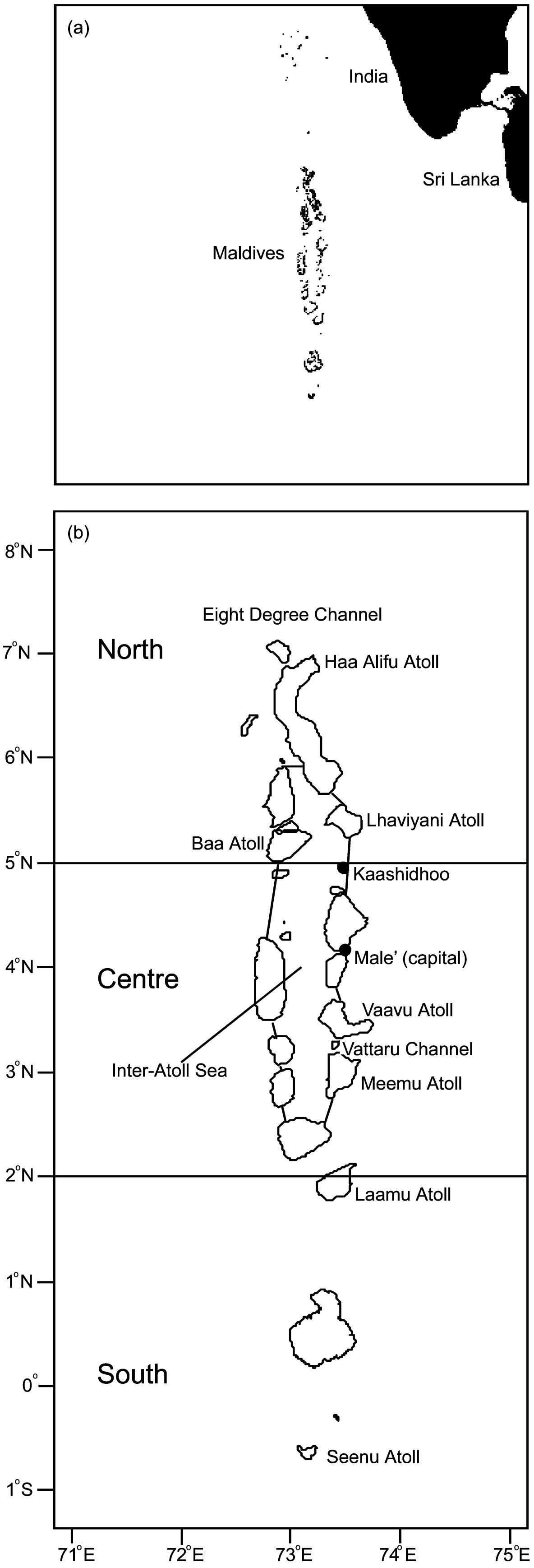

Fig. 1. The Maldives, showing location (a) and places and survey areas mentioned in the text (b).

established, there has been no detailed survey of the outer atoll slopes. As a result, discussion of this important cetacean habitat is restricted since bottom depths and gradients are not known accurately.

The Maldives is affected by the seasonal monsoons. The Northeast Monsoon lasts from about December to March, with winds and currents from the northeast or east. Winds can be quite strong in December and early January but are usually fairly calm in February and March. The Southwest Monsoon lasts from about May to October, with winds and currents mainly from the southwest and west. Winds can be particularly strong from late May to early August. April and November are inter-monsoon months, with variable but often light winds and currents. The south of the Maldives (south of about 2°30' or 2°00'N) is less affected by the monsoons than the north and centre of the country. Instead it is more under the influence of equatorial current systems.

Survey methodology

Between August 1990 and June 2002, 68 sea trips were undertaken, totalling 535 days at sea, during which cetacean sightings were systematically recorded. Observations were recorded from a wide variety of vessels (all mechanised), of lengths 10-45m (mostly 14-26m) with cruising speeds of 11-19km h^{-1} (6-11 knots). These included both vessels-of-opportunity (mainly local fisheries-research and diving boats) and dedicated cetacean-watching vessels. The latter included the cetacean survey trip reported by Ballance *et al.* (2001). The overall strategy was to make use of existing opportunities to accumulate sightings records from numerous sea trips covering a wide area and a long duration, rather than to conduct a systematic survey. In all cases, searching for cetaceans was with a combination of hand-held binoculars and naked eye. Different levels of observation effort were maintained during different sea trips, which can be grouped into four categories:

(1) Early trips (1990-95), mostly undertaken for fisheries research but also for diving, during which only one observer was present and little effort was made to search for cetaceans. Eye height was about 2-4m above sea level.
(2) Later fisheries and diving trips (1996-2002), during which 1-4 observers were present and some effort was made to search for cetaceans, although the main purpose of these trips was never cetacean observation. Eye height was 2-6m.
(3) Fifteen trips (1998-2002), the main purpose of which was whale and dolphin watching, during which a dedicated watch was maintained by 1-3 experienced observers, assisted by 1-6 inexperienced observers, for an average of about 7-8 hours per day. Eye height was 3-10m.
(4) One trip reported by Ballance *et al.* (2001), during which a dedicated watch was maintained by 5-8 experienced observers for an average of 7.8 hours per day 'on effort' with an additional average of about 2h d^{-1} at sea. Eye height was 4m. A slight difference in total number of sightings reported for this one trip in Ballance *et al.* (2001) and in this paper is the result of subjective differences in recording some adjacent cetacean groups as associated or not associated.

Major details of these four trip types are summarised in Table 1. Each atoll in the Maldives was visited at least five times during 1990-2002 and at least three sea trips were undertaken in each calendar month. In total, 1,829 sightings were recorded (Fig. 2). The uneven distribution of sightings largely reflects the distribution of sighting effort rather than any major pattern of cetacean abundance. For example, Fig. 2 shows a concentration of sightings in the east-central

Table 1

Summary of cetacean sightings and sighting effort.

Type of trip	No. sightings	No. trips	No. days	Sightings/ day	Raising factor	Std days
1. General (1990-1995)	195	27	197	1.0	0.141	27.8
2. General (1996-2002)	380	25	176	2.2	0.308	54.2
3. Whalewatch (1998-2002)	995	15	142	7.0	1.000	142.0
4. Cetacean survey (1998)	259	1	20	13.0	1.848	37.0
Sub-total	1,829	68	535	-	-	261.0
5. No-effort sightings	58					
6. Strandings	129					
Total	2,016					

Maldives in the area closest to Malé (the capital and my home base near which most effort was concentrated) and a relative dearth of sightings on the west of the atoll chain (reflecting limited effort there). Each sighting was coded for certainty of identification (definite, probable, possible, unidentified). Weather conditions were not recorded systematically. However, wind conditions were recorded for most sightings from 1996 and 92% of all such sightings were recorded in Beaufort force 3 or less (Table 3).

In addition to the 1,829 on-effort sightings, a further 58 sightings, without associated effort data, and 129 strandings were recorded by the author and others, making a total of 2,016 cetacean records. Stranding records are from Anderson *et al.* (1999) and subsequent unpublished reports held by the Marine Research Centre, Malé. Sightings from other observers were only included when the observer was known personally to the author, was known to be experienced and reliable, and was able to supply sufficient details, notes or photographs to confirm their record. Note that a single sighting could include more than one species: there were 83 instances of sightings involving more than one species, with nine involving more than two species (see further discussion below). As a result, the 1,829 on-effort sightings produced 1,921 on-effort species records and 2,108 total records (Table 4).

Analyses

Standardisation of sighting effort

Sightings were collected during four types of trip during which levels of observation effort were very different. With the information available there is no entirely satisfactory means to standardise effort. Nevertheless, the aim of this paper is to summarise findings from all sightings, not just a subset. Effort was therefore standardised by raising the numbers of days in each trip category by the ratio of sighting rates, using the trip category with the most sightings (category 3 above) as the standard (Table 1). It is estimated that the equivalent of 261 standardised days was spent at sea. A summary of standardised sighting effort by month and major area is provided in Table 2. Standardised effort was clearly not distributed uniformly across calendar months or major areas. This method of standardisation may introduce some biases but they are unlikely to be particularly large in relation to other sources of error and it is not possible to estimate actual sighting effort for trip categories 1 and 2 in a more rigorous manner. One tendency of this approach to standardisation will be to dampen indications of seasonal variations in abundance; in view of this and the very limited sighting effort in several months (Table 2) discussion of seasonal variation is kept to a minimum.

Table 2

Summary of sighting effort (standard days) by region and month.

Month	Inside atolls	Inter-atoll sea	Outside north	Outside centre	Outside south	Total
Jan	0.7	0.3	0.2	0.5	0.1	1.8
Feb	7.9	4.9	5.1	3.8	0.9	22.6
Mar	18.2	4.1	10.8	22.8	10.5	66.4
Apr	22.1	4.7	35.3	35.6	5.6	103.4
May	14.8	2.3		7.3		24.4
Jun	3.7	0.4	0.4	0.5		5.0
Jul	2.1	0.3		0.3	0.3	3.0
Aug	6.5	1.3	0.6	0.9	1.6	10.8
Sep	6.6	0.4		0.3	1.2	8.4
Oct	4.7	0.6	0.3	0.8	0.5	6.9
Nov	3.6	0.1	0.9	0.2		4.8
Dec	2.4	0.9		0.1		3.5
Total	93.3	20.1	53.6	73.2	20.7	261.0

Table 3

Cetacean sightings in relation to wind strength (for details of dwarf sperm whale see species account).

Beaufort	Total sightings	Dwarf sperm whale
0	187	32 (17.1%)
1	333	34 (10.2%)
2	462	6 (1.3%)
3	212	1 (0.5%)
4	76	0
5	25	0
6	4	0
Total	1,299	73 (5.6%)

Data limitations

Sightings from early trips (1990-95) were frequently unidentified and school-size estimates were erratic. Therefore these early data were not used in most analyses. For this study, all cetacean sightings recorded as ‘identification possible’ are treated as ‘unidentified’. In most analyses, only data from ‘identification definite’ sightings are used, unless stated otherwise. Estimates of relative abundance were calculated simply as estimates of numbers actually seen. They do not take account of differences in sightability and therefore undoubtedly underestimate the relative abundance of the more cryptic species.

Regional analysis and scope

To facilitate analysis of regional differences in cetacean distribution and abundance, five ‘major areas’ (illustrated in Fig. 1) are defined for the purposes of this study as follows:

(1) *Inside Atoll* – all waters inside all atolls, including reef channels into atolls;
(2) *Inter-atoll Sea* – the relatively shallow area of water in the middle of the double row of atolls in the central Maldives;
(3) *Outside North* – all waters outside the atolls north of 5°N, excluding the inter-atoll sea;
(4) *Outside Centre* – all waters outside the atolls between 2°N and 5°N, excluding the inter-atoll sea; and
(5) *Outside South* – all waters outside the atolls south of 2°N.

There are likely to be differences between the western and eastern portions of the offshore areas (Outside North, Centre and South), but the limited observation effort in the western portions (e.g. just 6.1 standard days in the west centre) precludes separate treatment. The Maldives claims a 200 n.mile Exclusive Economic Zone (EEZ) but has yet to formally declare all boundaries. As a result it is not clear if some published cetacean sightings lie within the Maldivian EEZ or not. This study was limited to sightings within about 50 n.miles (*ca* 90km) of the atolls. Most survey effort was actually carried out less than about 10 n.miles (*ca* 20km) from the atolls.

RESULTS AND DISCUSSION

Species accounts

A total of 20 species of cetacean were positively identified from sightings during 1990-2002 (Table 4). This included 19 of the 20 species previously recorded from the Maldives and one new record, the humpback whale (*Megaptera novaeangliae*).

Bryde's whale (*Balaenoptera edeni*)

Bryde's whales appear to be the most common baleen whale species in Maldivian waters (Tables 4, 6 and 7). The taxonomic status of this species in the north-central Indian Ocean remains uncertain but animals in Maldivian waters may be referable to *B. brydei* Olsen, 1913 (Rice, 1998; Ballance *et al.*, 2001; Wada *et al.*, 2003). One cow-calf pair was seen on 2 April 1999; the length of the calf was approximately one-third that of its mother.

For 17 dives by six individuals, mean dive time was 9.6min (SD=2.5min, range=6-12min). Blows varied considerably in strength, and exhalation sometimes took place underwater. Breaching was observed on two occasions. In four instances, Bryde's whales were observed lunge-feeding near the surface, sometimes on one side, sometimes vertically. Maldivian fishermen do not generally differentiate between different species of whale, calling them all *bodumas* (literally, big fish). However, they use the name *katterumas* (scissors fish) for whales that lunge through the surface with mouth agape; this name probably applies best to Bryde's whales.

Ballance *et al.* (2001) noted the presence of a concentration of Bryde's whales in the Vatteru Channel between Vaavu (=Felidhoo) and Meemu (=Mulaku) Atolls on 19-20 April 1998. Bryde's whales were actually present in this area from at least 26 March to 12 May 1998. A total of 77% of all on-effort sightings of Bryde's whales reported here (*n*=53 definite and probable identifications combined) were from this one concentration. As noted by Ballance *et al.* (2001) these whales appeared to be feeding: euphausiids were seen in the water near the whales on two days. On other occasions, Bryde's whales were seen feeding on anchovies (Engraulidae, once) and unidentified small red fish (three times).

Table 4

Summary of cetacean records by species (note that 'Other records' includes 129 strandings).

	On-effort sightings			Other records		
Species	ID definite	ID probable	% of all on effort sightings	ID definite	ID probable	Total
Spinner dolphin	624	44	34.8	21	2	691
Bottlenose dolphin	226	27	13.2	6	1	260
Risso's dolphin	211	8	11.4	5	0	224
Spotted dolphin	63	4	3.5	2	0	69
Striped dolphin	43	3	2.4	0	0	46
Fraser's dolphin	17	0	0.9	1	1	19
Rough-tooth dolphin	6	0	0.3	0	0	6
Short-finned pilot whale	79	2	4.2	6	1	88
Melon-headed whale	12	0	0.6	7	1	20
False killer whale	10	0	0.5	4	0	14
Killer whale	9	0	0.5	2	0	11
Pygmy killer whale	4	0	0.2	2	0	6
Melon-headed/pygmy killer	0	0	0.0	0	2	2
Cuvier's beaked whale	17	6	1.2	0	0	23
Blainville's beaked	3	7	0.5	0	0	10
Longman's beaked	1	3	0.2	1	0	5
Ginkgo-toothed beaked	0	0	0.0	1	0	1
UNID beaked whale	0	37	1.9	0	1	38
Bryde's whale	36	17	2.8	2	0	55
Blue whale	12	2	0.7	8	5	27
Humpback whale	1	0	0.1	1	0	2
UNID baleen whale	0	4	0.2	0	5	9
Dwarf sperm whale	74	6	4.2	0	0	80
Sperm whale	9	1	0.5	51	0	61
UNID dolphin	0	216	11.2	0	13	229
UNID cetacean	0	57	3.0	0	6	63
UNID whale	0	20	1.0	0	29	49
Total	1,457	464	100	120	67	2,108

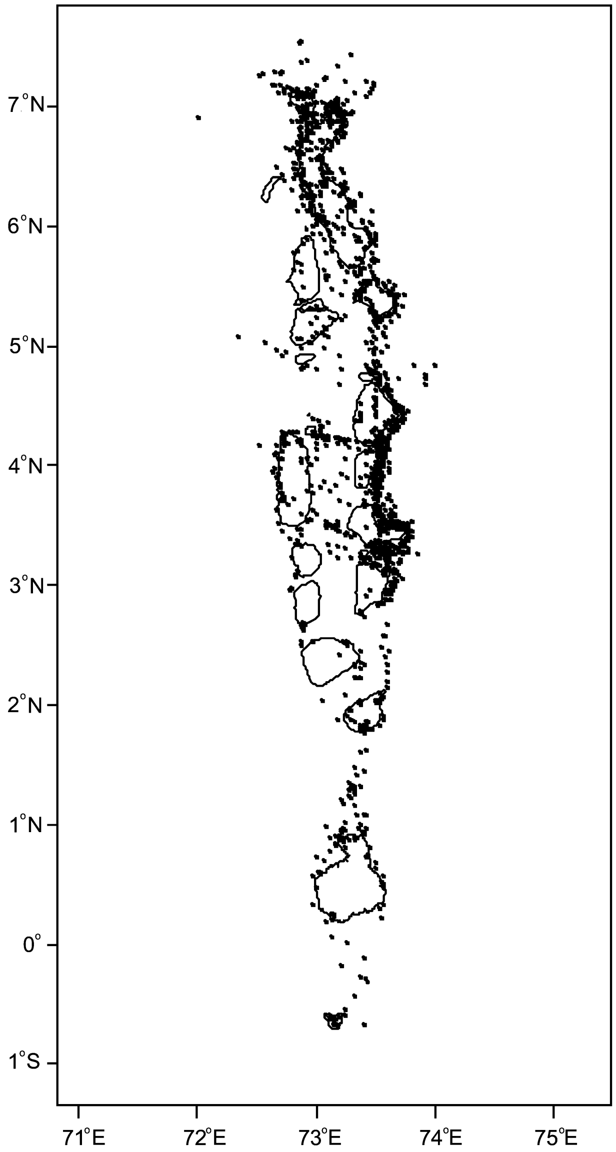

Fig. 2. Locations of cetacean sightings made during survey trips (*n*=1,829). The distribution of sightings largely reflects the distribution of sighting effort.

Anderson (1990) reported a baleen whale lunge-feeding off Lhaviyani Atoll in February 1988 which was tentatively identified as a Bryde's whale. Subsequent observations of this species confirm that sighting (from field notes) as a Bryde's whale. Anderson (1990) also reported sightings of many whales off Lhaviyani Atoll in 1972 (by N.T. Hasen Didi, formerly of Ministry of Fisheries, Maldives, pers. comm., 1990). Additional information (N.T. Hasen Didi, pers. comm., 1998) allows identification as probable Bryde's whales. As a result, and with further information from others, it appears that unusually large numbers of Bryde's whales (or probable Bryde's whales) were present in the following areas and years:

Lhaviyani Atoll	1972	N.T. Hasen Didi (pers. comm.)
Vattaru Channel	c. 1977-8	Meemu Atoll fishermen; Adam Hussein (pers. comm.)
Lhaviyani Atoll	1988	Lhaviyani Atoll fishermen; Anderson (1990)
Vattaru Channel	1998	Ballance *et al.* (2001); this study

The Maldives is influenced by interannual variations in oceanographic conditions, notably El Niño Southern Oscillation (ENSO) events, which affect the distribution and abundance of pelagic fishes (Anderson, 1993; Anderson *et al.*, 1998). Such ocean variability presumably also affects the distribution and abundance of at least some cetacean species in Maldivian waters. The years 1972, 1977, 1988 and 1998 were all ENSO years. It may be significant that anchovies appear to be more abundant than average during ENSO events and in the particular areas where Bryde's whale concentrations have been reported (Anderson and Saleem, 1994; 1995). In addition, yellowfin tuna (with which Bryde's whales often appear to associate, perhaps because they feed on the same prey) are most abundant in Maldivian waters during ENSO events (Anderson, 1993; Anderson *et al.*, 1998).

Table 5

Summary of cetacean school sizes by species.

Species	N	Mean	1.96 SE	Range	Mode
Spinner dolphin	466	58.2	6.6	6-750	20-30
Bottlenose dolphin	197	14.6	2.8	1-170	1-10
Risso's dolphin	184	33.3	5.1	2-300	2-15
Pantropical spotted dolphin	58	161	32.9	4-500	40-60
Striped dolphin	41	47.8	10.8	3-200	20-60
Fraser's dolphin	14	215	71	40-1,000	40-80
Rough-tooth dolphin	5	22.2	13.1	6-40	
Short-finned pilot whale	74	17.7	3.4	3-100	8-20
Melon-headed whale	12	412	218	30-1,200	100-120
False killer whale	12	36.0	15.3	1-100	40-50
Killer whale	9	6.3	1.2	5-11	5-7
Pygmy killer whale	4	16.5	9.1	9-30	
Melon-headed/pygmy killer	2	30		30	
Cuvier's beaked whale	17	2.3	0.4	1-4	2
Blainville's beaked	3	3.7		2-6	
Longman's beaked	4	6.5		2-20	2
UNID beaked	36	2.5		1-8	1-2
Bryde's whale	36	2.1	1.0	1-15	1
Blue whale	14	1.1	0.2	1-2	1
Humpback whale	2	2.0		2	2
UNID baleen whale	4	1.0		1	1
Dwarf sperm whale	74	1.7	0.2	1-6	1
Sperm whale	11	5.5	5.4	1-30	1
UNID dolphin	60	10.3	3.5	1-60	1-6
UNID cetacean	17	2.4	1.3	1-12	1-2
UNID whale	13	1.4	0.5	1-4	1

Blue whale (*Balaenoptera musculus*)

Blue whales in the northern Indian Ocean, including the Maldives, appear to be pygmy blues (*B. musculus brevicauda*) although their exact taxonomic status is uncertain and they may be referable to *B. m. indica* (*cf.* Yochem and Leatherwood, 1985; Mikhalev, 1996; Rice, 1998; Ballance *et al.*, 2001).

Blue whale dive times were distinctly bimodal: of 56 dives timed from eight whales (including those reported by Ballance *et al.*, 2001), 29 were short (range=5-9 min, mean=6.8min, SE=0.2min) while 25 were long (range=12-20min, mean=15.1min, SE=0.4min). Only two dives were of intermediate length (10 and 11min). The behaviour states associated with different dive times were not obvious, although the dive times of two whales did decrease when approached closely. Of 11 blue whales for which the information was recorded, 8 (73%) lifted their flukes high before diving, 1 (9%) barely lifted its flukes and 2 (18%) did not fluke at all.

Blue whale occurrence in Maldivian waters appears to be highly seasonal, with all sightings (not just those from this study) and strandings to date occurring between November and April. This is consistent with a hypothesis of a northern Indian Ocean stock (Yochem and Leatherwood, 1985;

Table 6

Estimated numbers of cetaceans seen by major areas within the Maldives. Note: Includes only sightings made during sea trips of categories 1-4 as defined in the Methods and summarised in Table 1.

Species	Outside north	Outside centre	Outside south	Inside atolls	Inter-atoll sea	Total
Spinner dolphin	5,304	5,996	2,181	20,924	3,518	37,923
Spotted dolphin	5,070	2,143	2,886	0	247	10,346
Risso's dolphin	2,190	2,452	15	32	299	4,988
Fraser's dolphin	1,110	1,520	610	0	300	3,540
Bottlenose dolphin	502	1,592	36	1,063	333	3,526
Melon-headed whale	100	650	2,588	0	0	3,338
UNID dolphin	772	552	306	684	383	2,697
Striped dolphin	879	1,138	0	0	55	2,072
Short-finned pilot whale	234	1,050	18	0	21	1,323
False killer whale	82	225	45	25	50	427
UNID cetacean	50	63	10	165	5	293
Dwarf sperm whale	61	69	0	0	2	132
Rough-toothed dolphin	101	18	0	0	0	119
UNID beaked whale	31	71	1	0	2	105
Bryde's whale	13	78	3	0	6	100
Sperm whale	60	10	0	0	0	70
Pygmy killer whale	45	21	0	0	0	66
Killer whale	21	31	5	0	0	57
Cuvier's beaked whale	22	24	6	0	0	52
Dense-beaked whale	5	22	0	0	0	27
UNID whale	10	4	11	0	1	26
Longman's beaked whale	2	22	2	0	0	26
Blue whale	12	2	2	1	0	17
UNID baleen whale	2	1	1	0	0	4
Humpback whale	0	0	0	2	0	2
Total	16,678	17,754	8,726	22,896	5,222	71,276

Table 7

Relative abundance of cetacean species by major areas within the Maldives (expressed as percentage of numbers of cetaceans seen in each area).

Species	Outside north	Outside centre	Outside south	Inside atolls	Inter-atoll sea	Total
Spinner dolphin	31.8	33.8	25.0	91.4	67.4	53.2
Spotted dolphin	30.4	12.1	33.1	-	4.7	14.5
Risso's dolphin	13.1	13.8	0.2	0.1	5.7	7.0
Fraser's dolphin	6.7	8.6	7.0	-	5.7	5.0
Bottlenose dolphin	3.0	9.0	0.4	4.6	6.4	4.9
Melon-headed whale	0.6	3.7	29.7	-	-	4.7
UNID dolphin	4.6	3.1	3.5	3.0	7.3	3.8
Striped dolphin	5.3	6.4	-	-	1.1	2.9
Short-finned pilot whale	1.4	5.9	0.2	-	0.4	1.9
False killer whale	0.5	1.3	0.5	0.1	1.0	0.6
UNID cetacean	0.3	0.4	0.1	0.7	0.1	0.4
Dwarf sperm whale	0.4	0.4	-	-	0.0	0.2
Rough-toothed dolphin	0.6	0.1	-	-	-	0.2
UNID beaked whale	0.2	0.4	0.0	-	0.0	0.1
Bryde's whale	0.1	0.4	0.0	-	0.1	0.1
Sperm whale	0.4	0.1	-	-	-	0.1
Pygmy killer whale	0.3	0.1	-	-	-	0.1
Killer whale	0.1	0.2	0.1	-	-	0.1
Cuvier's beaked whale	0.1	0.1	0.1	-	-	0.1
Dense-beaked whale	0.0	0.1	-	-	-	0.0
UNID whale	0.1	0.0	0.1	-	0.0	0.0
Longman's beaked whale	0.0	0.1	0.0	-	-	0.0
Blue whale	0.1	0.0	0.0	0.0	-	0.0
UNID baleen whale	0.0	0.0	0.0	-	-	0.0
Humpback whale	-	-	-	0.0	-	0.0
Total	100	100	100	100	100	100

Mikhalev, 1996), which migrates seasonally to feed on plankton associated with monsoonal upwelling off the coasts of Somalia and Arabia in May to October and disperses more widely (at least as far as the Maldives and Sri Lanka) during the leaner months of November to April (Anderson *et al.*, 1999).

Three blue whales seen in the Maldives in April were decidedly thin, i.e. with vertebrae clearly visible. Leatherwood *et al.* (1984) noted that blue whales seen off Trincomalee, east Sri Lanka, on 28 February 1983 were also thin. Whitehead (1989) presented a photo of another thin-looking blue whale off Trincomalee; although undated, the photo was probably taken in February or March 1984 (Jonathan Gordon, pers. comm., 17 July 2003). In contrast, Mikhalev (1996) described blue whales caught in the northwest Indian Ocean by Soviet whalers in the 1960s during October to December (mostly November) as being of 'good fatness'. This suggests that during October-December the whales are well fed, but by February-April they may be coming towards the end of a period with relatively little feeding. Around Sri Lanka, blue whales are regularly seen off the northeast coast near Trincomalee during December to April; they are rare later in the year, at least during October-November (Leatherwood *et al.*, 1984; Leatherwood and Reeves, 1989; Alling *et al.*, 1991). In 1983, blue whales had left the Trincomalee area by 24 April (Alling *et al.*, 1991). If at least some of the blue whales that spend the early part of each year off northeast Sri Lanka feed off Somalia and Arabia in May-October, then they might be expected to migrate via the Maldives in April. During this study, most sightings were made in April, while Ballance and Pitman (1998) recorded at least 27 blue whales in the Eight Degree Channel immediately north of the Maldives and in the area between the Maldives and Sri Lanka in April 1995.

Humpback whale (*Megaptera novaeangliae*)

Humpback whales in the Arabian Sea are believed to belong to a resident stock (Reeves *et al.*, 1991; Mikhalev, 1997; Papastavrou and Van Waerebeek, 1997; Minton *et al.*, 2002; Rosenbaum *et al.*, 2002). They appear to be rare in Maldivian waters, with only a single sighting by the author. This was of a cow-calf pair seen inside Seenu (= Addu) Atoll (0°37'S) in September 2001. The stock affinity of these whales is unknown, although they might have been from a southern population. Evidence for this includes: the timing of the sighting (during the austral winter); its location south of the equator; and the presence of a small calf approximately one third of the mother's length (at a time when Southern Hemisphere humpbacks are breeding).

The second sighting (Tables 4 and 6) was of another cow-calf pair, inside North Malé Atoll (4°14'N) in December probably of 1993 (Javier Martinez, Eurodivers Maldives, pers. comm., 1999). The timing of this sighting suggests that this pair might have been from the Arabian Sea stock.

These two sightings appear to be the first confirmed records of humpback whale from the Maldives although Brown (1957: fig. 4) recorded five sightings of humpback whales from merchant ship observers in the area immediately north of the Maldives and Slijper *et al.* (1964) also recorded several sightings of humpback whales in the general area of the Maldives. However, it is not clear how many, if any, of these records were made in what is now the Maldivian EEZ. Humpback whales were possibly not uncommon in the area of the Maldives prior to the mid-1960s. At that time (mostly in November 1966) Soviet whalers killed at least 242 humpback whales in the Arabian Sea (Mikhalev, 1997; 2000). Large numbers of blue, Bryde's and sperm whales were taken at the same time, many of them in the vicinity of the Maldives (Mikhalev, 1996; 2000). Some older Maldivians in the northern atolls recall frequent sightings of whale blows in the 1950s and early 1960s, but few sightings thereafter. Humpback whales remain particularly rare in Maldivian waters.

Sperm whale (*Physeter macrocephalus*)

There were few sightings of sperm whales in this study (0.5% of all sightings). Most sightings (82%, n=11) of sperm whales were of 1-3 individuals. These animals were thought to be males in all cases where details were noted (5 out of 9). Two other sightings (of 15 and 30 animals) were of groups of presumed females and juveniles.

Although there were so few sightings, relatively little time was spent offshore (beyond a few miles from the atolls) where this species might be expected to be most abundant. In fact, the sperm whale is the species most commonly reported stranded in the Maldives (Anderson *et al.*, 1999). During the 19th century, Yankee whalers took sperm whales in the northern Maldives (Clark, 1887: plate 183, map of whaling grounds; Wray and Martin, 1983). Sperm whales were encountered and studied in the waters between the Maldives and Sri Lanka by the *Tulip* project (Whitehead *et al.*, 1983; Whitehead, 1989) and were also the most frequently sighted cetacean in a more recent survey of the western Indian Ocean (Ballance and Pitman, 1998).

Dwarf sperm whale (*Kogia sima*)

Dwarf sperm whales are not uncommon in the Maldives (Table 4), with only four species being sighted more frequently. Dwarf sperm whales were most easily seen in calm weathers and seas; one sixth of all sightings made in flat, calm conditions (Beaufort 0) were of this species (Table 3). Of 73 sightings positively identified as dwarf sperm whale for which wind conditions were recorded, 90% were made in Beaufort 0-1. No sightings were made in winds stronger than Beaufort 3. The frequency distribution of sightings in relation to wind strength was significantly different from expectations based on sightings for all cetaceans (chi-squared=87.3, df=2, p<0.001). This is a reflection of this animal's undemonstrative behaviour (Caldwell and Caldwell, 1989; Chantrapornsyl *et al.*, 1991; Willis and Baird, 1998). During calm conditions, slicks or current lines were frequently seen. Dwarf sperm whales were regularly observed lying at the surface in these lines. The reason(s) for this apparent association are unknown.

All dwarf sperm whales were observed over the outer atoll slopes. No sightings were identified as pygmy sperm whale (*Kogia breviceps*). These two species have broadly overlapping ranges and both have been reported from the tropical Indian Ocean, although the details of their distributions are not well known. Nevertheless, these observations are consistent with suggestions that dwarf sperm whales are more common over slopes and in warm seas (Ross, 1979; Caldwell and Caldwell, 1989; Chantrapornsyl *et al.*, 1991; Rice, 1998; Willis and Baird, 1998; Wang *et al.*, 2002), although this species has also been recorded from the open western Indian Ocean (Ballance and Pitman, 1998).

Rough-toothed dolphin (*Steno bredanensis*)

Rough-toothed dolphins are relatively rare in the Maldives, with just six sightings recorded (Table 4). Four of these sightings were off Haa Alifu Atoll in the far north. In two instances rough-toothed dolphins appeared to be associated with bottlenose dolphins, a taxon with which they have previously been recorded interacting (Miyazaki and Perrin, 1994; Ritter, 2002). On one occasion, rough-toothed dolphins were seen diving near a fish aggregating device (FAD) and apparently feeding; on another occasion they were seen near some floating wood. The relatively frequent association of rough-toothed dolphins with floating objects has been noted by Pitman and Stinchcomb (2002). In one sighting, several rough-toothed dolphins were observed at the surface apparently playing with a pufferfish (*Arothron hispidus*) repeatedly pushing it with their snouts and flukes, and finally leaving it dead. Ritter (2002) recorded rough-toothed dolphins 'mistreating' a loggerhead turtle (*Caretta caretta*). The colour pattern observed was similar to that described by Miyazaki and Perrin (1994), but lips and bellies were often pink rather than white.

Moutou (1984) suggested that dolphins seen regularly between the islands of Malé and Vilingili in North Malé Atoll might have been rough-toothed dolphins. However, this seems most unlikely as rough-toothed dolphins were not recorded in this area during this survey; spinner dolphins occurred there regularly.

Risso's dolphin (*Grampus griseus*)

Risso's dolphins were the third most frequently recorded cetacean species, accounting for 11.4% of sightings and 7.0% of individuals seen (Tables 4 and 7). Risso's dolphins were nearly always seen outside the atolls, over the outer atoll slopes. Association with steep bottom topography appears typical for this species (Baumgartner, 1997; Kruse *et al.*, 1999). Several small groups were seen close to the outer atoll reefs, but only three groups were recorded inside an atoll.

Risso's dolphins were most frequently seen in small schools. Some 79% (*n*=184) of groups were of 30 or fewer animals. However, large groups did occur, with 9% of sightings of 60 or more animals. In these cases the group was usually spread in sub-groups over a large area, making determination of school boundaries somewhat subjective and estimation of school sizes particularly difficult.

Several types of behaviour were recorded for Risso's dolphins, but the most distinctive was holding the flukes high out of the water while maintaining a head-down position. This was noted in 15.6% of sightings for which some additional notes were made (*n*=154), and was not noted for any other dolphin species in the Maldives. The significance of this behaviour is not known. It was seen in schools of all sizes (range=4-200, mean=39.3, *n*=23, 1.96SE=22.6) and it occurred in schools demonstrating all other recorded types of behaviour.

Bottlenose dolphin (*Tursiops sp.*)

Most bottlenose dolphins seen in the Maldives appeared (on the basis of external morphology) to be *Tursiops truncatus*. However, the possibility that some *Tursiops* in Maldivian waters are Indo-Pacific bottlenose dolphins, *T. aduncus* (*cf.* Ross and Cockcroft, 1990; Rice, 1998; Hale *et al.*, 2000; Wang *et al.*, 2000), cannot be discounted. Bottlenose dolphins were the second most frequently sighted species (Table 4), but with a relatively low mean school size (Table 5) ranked only fifth in relative abundance (Table 7).

Bottlenose dolphin groups inside the atolls were smaller (mean=7.7, *n*=98, range=1-80, 1.96SE=1.8) than groups outside the atolls (mean=21.9, *n*=97, range=1-170, 1.96SE=4.9). This difference is statistically significant (*t*=5.3, df=193, *p*<0.001).

There were also differences in behaviour between bottlenose dolphins inside and outside the atolls. Inside the atolls they tended to avoid boats, did not readily bowride (only in 14% of sightings, *n*=101) and showed little aerial activity. In contrast, bottlenose dolphins outside the atolls bowrode more readily (in 37% of encounters, *n*=104) and were often active aerially. However, these differences might simply be a function of the larger school sizes outside the atolls. Although bottlenose dolphins inside the atolls did not associate with other species (apart from one group recorded with spinner dolphins), this may simply reflect the lack of other species inside the atolls. In comparison, 34% (*n*=105) of bottlenose dolphin groups outside the atolls were associated with another species.

In addition, there was some suggestion of colour differences between bottlenose dolphins in the two areas: those outside the atolls sometimes appearing darker with a more obvious diffuse pale patch behind the dorsal fin, while those inside the atolls appeared to show a more distinct white tip to the snout and at least one showed distinct ventral spotting. However, these differences were not always discernable. The underlying nature of the differences between bottlenose dolphins inside and outside atolls is not clear at this stage. In particular it is not known how these relate to the specific or sub-specific differences (e.g. *truncatus* versus *aduncus*) or ecomorphotypic differences (e.g. 'inshore' versus 'offshore') seen elsewhere.

Bottlenose dolphins were seen feeding, or apparently feeding, on 19 occasions, all except once inside the atolls. The single exception outside the atolls was adjacent to an anchored FAD. Inside the atolls, bottlenose dolphins were seen chasing bigeye scad (*Selar crumenopthalamus*, Carangidae), halfbeaks (Hemirhamphidae) and needlefish (Belonidae). Other possible prey items included swimming crabs (Portunidae), flying fish (Exocoetidae) and small jacks (Carangidae). A diving instructor (Carl Nichols, pers. comm.) filmed two large giant jacks (*Caranx ignobilis*, Carangidae) buzzing and then head-butting a single bottlenose dolphin in Baa Atoll. On seven occasions, bottlenose dolphins were seen feeding at night near anchored fish collection vessels. These ships regularly anchor at set locations within atolls to purchase fresh tuna from local fishermen. They have strong lights to facilitate transferring fish after sunset. These lights also attract numerous fish under the vessels. Local bottlenose dolphins appear to have learnt to hunt at these locations, as they can be seen regularly near particular collection vessels (e.g. in Haa Alifu and Laamu Atolls). On three occasions, bottlenose dolphins were noted feeding in atoll channels (where strong tidal currents promote fish concentrations).

Pantropical spotted dolphin (*Stenella attenuata*)

Pantropical spotted dolphins (referred to hereafter as spotted dolphins) were the second most abundant cetacean recorded (Tables 6, 7 and 8). They appeared to be particularly abundant in the north and south of the Maldives, in both areas making up over 30% of all cetaceans by number. In contrast, they contributed just 12% of cetaceans by number seen outside the atolls in the central Maldives. Spotted dolphins were not seen inside the atolls and they were uncommon in the inter-atoll sea between the central atolls. This distribution pattern is similar to that of large (>70cm fork length) yellowfin tuna, which are rare inside the atolls and in the inter-atoll sea and are commonest in the north and south of the country (Anderson and Shaan, 1998; Anderson *et al.*, 1998). Spotted dolphins were regularly associated with yellowfin tuna, seabirds and spinner dolphins (see below). The modal size of spotted dolphin schools was 40-60 individuals (Table 5), although a secondary mode was also apparent, with school sizes of 150-300 individuals. Schools associated with spinner dolphins had on average 50% more spotted dolphins (mean=182 individuals, *n*=35, 1.96SE=41) than those without (mean=122, *n*=26, 1.96SE=48).

Spinner dolphin (*Stenella longirostris*)

The spinner dolphin was the most common species recorded during this study. It accounted for 35% of all sightings and 53% of estimated numbers (Tables 4 and 7), and was ubiquitous in the areas studied.

Spinner dolphins regularly enter the atolls through reef channels (Maldivian = *kanduoli*) in the morning and leave in the afternoon (Fig. 3). Sunrise varies from about 05:50 to 06:20h and is at about 06:00h during March-April when most sightings were recorded. Sunset varies from about 17:50 to 18:25h and is at about 18:15h in March-April. The peak time for entering was between 06:40 and 07:20h, when 39% of all entering spinner schools (*n*=95) were recorded. Excluding one school recorded leaving at 08:45h, there was no overlap in times of entering and departing the atolls. The peak time for leaving the atolls was between 16:15 and 17:50h, when 60% of all leaving schools (*n*=117) were recorded. Note that early entries (before 06:30h) were probably under-recorded, for the obvious reason. Some late departures may also have been missed in the rapidly falling darkness after sunset; there were two records of spinner dolphin schools inside an atoll heading towards a channel after dark, at 18:20 and 19:00h. Elsewhere around tropical oceanic islands spinner dolphins are known to move inshore to rest in shallow, sheltered areas by day and to move offshore into deep water to feed on mesopelagic fishes at night (e.g. Norris *et al.*, 1994). The diurnal behaviour of Maldivian spinner dolphins thus appears typical for this species in this type of habitat.

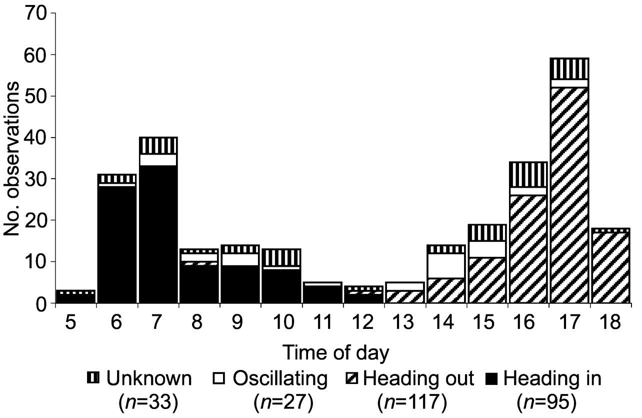

Fig. 3. Occurrence and direction of travel of spinner dolphin schools in atoll channels by time of day.

Reef channels break the atoll rim into a series of reefs, which vary considerably in length (from just a few metres to about 45km). Spinner dolphins use channels adjacent to long reefs more frequently than channels adjacent to short reefs. While this is partly because the longer reefs tend to face offshore (rather than into the inter-atoll sea), the main reason seems to be that spinner dolphins heading inshore in the morning towards a stretch of atoll rim with many short

Table 8

Relative abundance of cetaceans by major area within the Maldives (expressed as numbers of individuals seen per standard day).

Species	Outside north	Outside centre	Outside south	Inside atolls	Inter-atoll sea	Total
Spinner dolphin	99.0	81.9	105.4	224.3	175.0	145.3
Spotted dolphin	94.6	29.3	139.4	-	12.3	39.6
Risso's dolphin	40.9	33.5	0.7	0.3	14.9	19.1
Fraser's dolphin	20.7	20.8	29.5	-	14.9	13.6
Bottlenose dolphin	9.4	21.7	1.7	11.4	16.6	13.5
Melon-headed whale	1.9	8.9	125.0	-	-	12.8
UNID dolphin	14.4	7.5	14.8	7.3	19.1	10.3
Striped dolphin	16.4	15.5	-	-	2.7	7.9
Short-finned pilot whale	4.4	14.3	0.9	-	1.0	5.1
False killer whale	1.5	3.1	2.2	0.3	2.5	1.6
UNID cetacean	0.9	0.9	0.5	1.8	0.2	1.1
Dwarf sperm whale	1.1	0.9	-	-	0.1	0.5
Rough-toothed dolphin	1.9	0.2	-	-	-	0.5
UNID beaked whale	0.6	1.0	0.0	-	0.1	0.4
Bryde's whale	0.2	1.1	0.1	-	0.3	0.4
Sperm whale	1.1	0.1	-	-	-	0.3
Pygmy killer whale	0.8	0.3	-	-	-	0.3
Killer whale	0.4	0.4	0.2	-	-	0.2
Cuvier's beaked whale	0.4	0.3	0.3	-	-	0.2
Dense-beaked whale	0.1	0.3	-	-	-	0.1
UNID whale	0.2	0.1	0.5	-	0.0	0.1
Longman's beaked whale	0.0	0.3	0.1	-	-	0.1
Blue whale	0.2	0.0	0.1	0.0	-	0.1
UNID baleen whale	0.0	0.0	0.0	-	-	0.0
Humpback whale	-	-	-	0.0	-	0.0
Total	311.2	242.5	421.5	245.4	259.8	273.1

reef segments have many atoll channels to enter through, so any one channel receives relatively few entrants. In contrast, spinner dolphins approaching a long reef have to turn one way or the other and follow the reef along to the nearest entrance channel, which consequently receives dolphins from a wider area.

Spinner dolphin group size was highly variable (range=6-750). Mean school size was estimated at 58 ± 7 individuals, but there were major variations in mean size in different situations (Table 9). For example, there was a trend for mean school size to increase with distance offshore (inside atoll < channel < near offshore < further offshore). At a greater average distance offshore, in the wider western Indian Ocean, Ballance and Pitman (1998) estimated a still larger mean school size, of 170. These observations are consistent with a hypothesis of larger school size being an important anti-predation mechanism when offshore. However, it should be noted that spinner schools associated with spotted dolphins tended to be larger than those not associated with spotted dolphins (Table 9), since spotted dolphins are found offshore. The associations of spinner dolphins with spotted dolphins, tuna and seabirds are discussed below.

Most Maldivian spinner dolphins showed the tripartite colour pattern typical for the nominate sub-species (Perrin, 1990). Van Waerebeek *et al.* (1999) described a second ‘colour morph’ from Oman, which showed a dark stripe between the lateral medium grey field and the belly, which was pink rather than white or pale grey. A very similar colour pattern was noted on six occasions in the Maldives. However, the two main components of this ‘colour morph’ were also seen separately on a number of occasions. Several otherwise typically tripartite spinner dolphins were seen with pink bellies. Such a ‘flushed’ appearance has been noted for other dolphins in warm waters, and is related to thermoregulation (Perrin, 2002). On other occasions, animals with a dark lateral stripe were seen with pale, not pink, bellies; the significance of this striping is unknown.

Table 9

Spinner dolphin school size by major habitat and association.

Habitat (subset)	Mean	1.96 SE	Range	N
All	58.2	6.6	6-750	466
Inside atolls	41.0	9.6	6-400	95
Channels	53.7	8.4	6-350	193
Outside atolls (inter-atoll sea)	60.6	26.4	6-400	31
Outside atolls (offshore)	74.8	15.2	6-750	147
Outside atolls (≤1nm offshore)	56.8	13.0	6-250	76
Outside atolls (>1nm offshore)	94.0	27.6	6-750	71
With spotted dolphins	132.5	48.5	10-750	34
Without spotted (offshore)	57.4	11.7	6-400	113
Without spotted (>1nm offshore)	61.0	23.9	6-400	38
Without spotted (all others)	50.6	6.0	6-400	319

Striped dolphin (*Stenella coeruleoalba*)

Striped dolphins were moderately abundant, accounting for over 2% of sightings and individuals recorded, and ranking seventh in relative abundance (Tables 4 and 7). They only occurred outside the atolls and were not recorded in the south (Table 6). Striped dolphins were relatively less abundant around the Maldives than in the wider western tropical Indian Ocean, where they ranked second in abundance in a survey by Ballance and Pitman (1998). Even applying their sightability correction factor (Ballance and Pitman, 1998: table 2) would only raise striped dolphins to fifth ranking in the Maldives. This presumably reflects the striped dolphins’ preference for an open oceanic habitat.

Striped dolphins were often extremely active, with much aerial activity. However, they alternated such frenetic outbursts with periods of apparent calm, with little aerial activity, during which it was very difficult to locate or follow schools. Striped dolphins often had pink (flushed) bellies; this was specifically recorded on six occasions, compared with only one record of white bellies.

Fraser’s dolphin (*Lagenodelphis hosei*)

Fraser’s dolphins are one of the commonest cetaceans in the Maldives, ranking fourth in abundance (Tables 7 and 8), even though it accounted for less than 1% of sightings on effort (Table 4). This is a reflection of this species’ large mean school size (215 ± 71 individuals) (Table 5). Fraser’s dolphin schools had a very characteristic appearance, which permitted identification even at a distance. The schools appeared tight and purposeful, with all individuals swimming in the same direction, often porpoising, and in calm conditions leaving a distinct wake. Some 53% of Fraser’s dolphin schools were associated with other species, notably short-finned pilot whales and melon-headed whales (see below).

Melon-headed whale (*Peponocephala electra*)

Melon-headed whales had the largest estimated mean school size of any cetacean in the Maldives (412 ± 218 individuals) (Table 5). As a result, even though encounters were infrequent, just 0.6% of all sightings on effort (Table 4), this species ranked sixth in relative abundance (Tables 7 and 8). Melon-headed whales were much more common in the south of the Maldives than in the north and centre of the country (Fig. 4, Tables 7 and 8). This was the only species to show this pattern of regional distribution. Further afield, melon-headed whales appear to be rare in the Arabian Sea north of the Maldives (Leatherwood *et al.*, 1991; Ballance and Pitman, 1998; Van Waerebeek *et al.*, 1999).

Pygmy killer whale (*Feresa attenuata*)

Pygmy killer whales are one of the rarer cetaceans in the Maldives with just four on-effort sightings and two strandings records (Table 4). It is certainly uncommon, although these few sighting likely underestimate its true abundance, since it appeared to be relatively cryptic.

False killer whale (*Pseudorca crassidens*)

False killer whales accounted for just 0.5% of sightings and ranked ninth in relative abundance (Tables 4 and 7). There were several observations of false killer whales attacking or appearing to attack large prey, on one occasion a manta ray (*Manta birostris*) and on three occasions sailfish (*Istiophorus platypterus*). On another occasion, a pod of false killer whales was observed swimming out of an atoll channel as a school of spinner dolphins was entering. When the spinner dolphins were within about 400m of the false killer whales they abruptly changed course, increased speed and porpoised away from them. In contrast, two other schools of false killer whales were seen to swim though a group of Risso’s dolphins and to pass by a group of pilot whales, without causing any apparent disturbance. False killer whales are believed to be predators of spinner dolphins, billfish and other large fish (Norris *et al.*, 1994; Odell and McClune, 1999; Strickland in Kiefner, 2002).

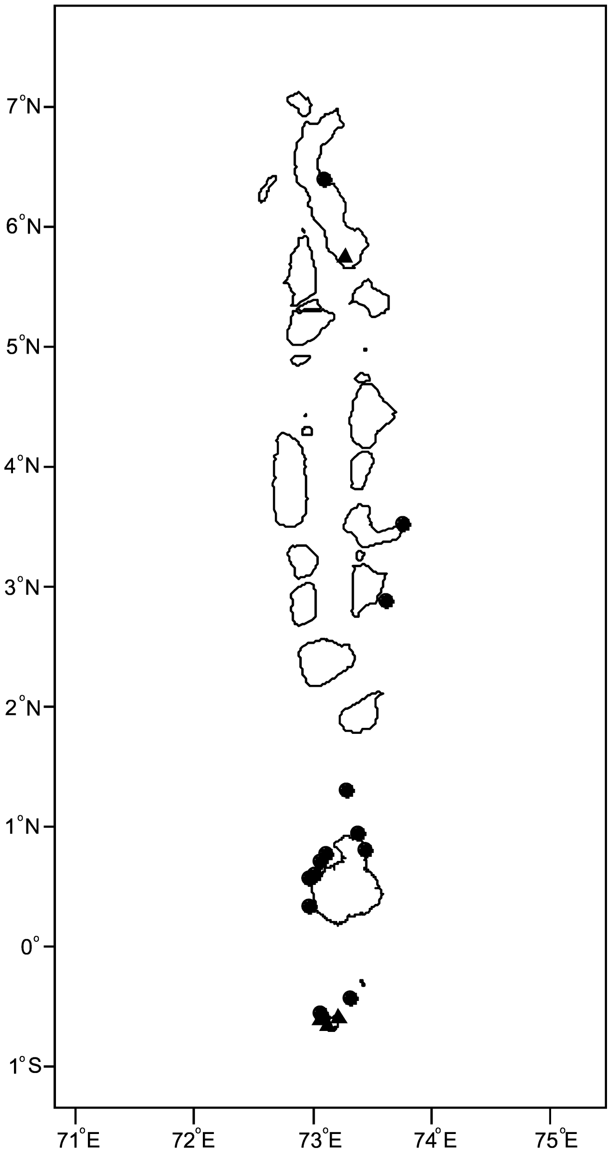

Fig. 4. Locations of sightings (circles, n=14) and strandings (triangles, n=6) of melon-headed whales. Note the concentration of observations in the south of the Maldives.

Killer whale (*Orcinus orca*)

Killer whales are not especially common in the Maldives (Tables 4, 6 and 7). School size ranged from 5-11 (Table 5). Eight of nine schools had 5-7 members; the ninth had 11 members. On one occasion the largest animal in a pod of about six was observed to have a large pink object in its mouth, probably the skinned carcass of a dolphin, shark or large tuna. On another occasion a pod of about six killer whales was observed apparently shadowing a school of spotted dolphins (which were associated with yellowfin tuna). There is also a report from a diving instructor of an underwater encounter with a pod of killer whales, which were seen toying with a manta ray, eventually leaving it dead (Tina Elgen, pers. comm.). Sivasubramaniam (1965) reviewed logbook records for damage to tuna longline catches by sharks and killer whales across the Indian Ocean, including the Maldives. He was not able to identify the 'killer whale' species implicated. Leatherwood *et al.* (1991) suggested that false killer whales were as likely as killer whales to have been involved.

Short-finned pilot whale (*Globicephala macrorhynchus*)

Pilot whales in the Maldives have been confirmed as short-finned pilot whales by: a pair of mandibles from a single stranding (Anderson *et al.*, 1999); close observation and photographs of live individuals (Ballance *et al.*, 2001; this study); and genetic analysis of biopsy samples collected by Ballance *et al.* (2001) (Susan Chivers, pers. comm.). They accounted for 4.2% of sightings and ranked eighth in relative abundance (Tables 4 and 6, Fig. 5). Pilot whales were usually observed over the outer atoll slope, most often just 1-2km offshore (see below). They were usually seen logging (apparently resting) or travelling. When travelling, most pilot whale groups (91% of groups for which direction of travel was recorded, n=46) tended to swim parallel to the atoll reef slope, presumably maintaining position over an appropriate feeding depth.

Pilot whales were rarely seen on the east side of the Maldives near Malé in the early part of the year. Indeed there were only two sightings off the east-central Maldives earlier than 29 March. Before that date the average sightings rate in the eastern central zone was 0.12 pilot whale sightings per day (n=16 days), whereas from that date the average sightings rate was 1.19 pilot whale sightings per day (n=48 days). This difference is statistically significant (chi-squared=14.7, df=1, p<0.01). The sudden arrival of pilot whales in that area at the end of March or in the first few days of April was noted each year from 1999 to 2002. It is not clear why pilot whales arrive in that area at that time; a possible explanation would be an increase in squid abundance, but there is no information on squid abundance in the Maldives. It is also not clear where the pilot whales come from, although they may come from the south. Among pilot whale groups encountered between 22 March and 21 April inclusive for which directions of movement were recorded (n=21), 76% were heading north, while only 24% were heading south. In contrast, for encounters from 30 April to 12 May inclusive, four pilot whale groups were heading south, while none were heading north.

One individual short-finned pilot whale, recognised by a distinctive cut on its dorsal fin, was seen three times over a 20-day period in 1998. On all three occasions it was recorded as being in a school of about ten individuals. It was first seen on 29 March off northeast Vaavu Atoll. On 13 April it was seen off northwest Lhaviyani Atoll (approximately 200km north). On 17 April it was seen near Kaashidhoo, an isolated island between Lhaviyani and North Malé Atolls (over 60km south of the second sighting). This pattern of individual movement is consistent with the pattern of school movement noted above, suggesting that pilot whales enter the area near Malé from the south in late March.

Beaked whales, Ziphiidae

Four species of beaked whale are known from the Maldives (Anderson *et al.*, 1999; Ballance *et al.*, 2001; Dalebout *et al.*, 2003): Cuvier's beaked whale (*Ziphius cavirositris*), Blainville's beaked whale (*Mesoplodon densirostris*), ginkgo-toothed beaked whale (*Mesoplodon ginkgodens*) and Longman's beaked whale (*Indopacetus pacificus*). The ginkgo-toothed beaked whale is so far known only on the basis of a tooth from a mature male in the National Museum, Malé (Anderson *et al.*, 1999).

All species together made up 3.9% of on-effort sightings. However, such were the difficulties of identifying beaked whales at sea with current knowledge, that only 28% of these sightings (n=75) were identified to species with

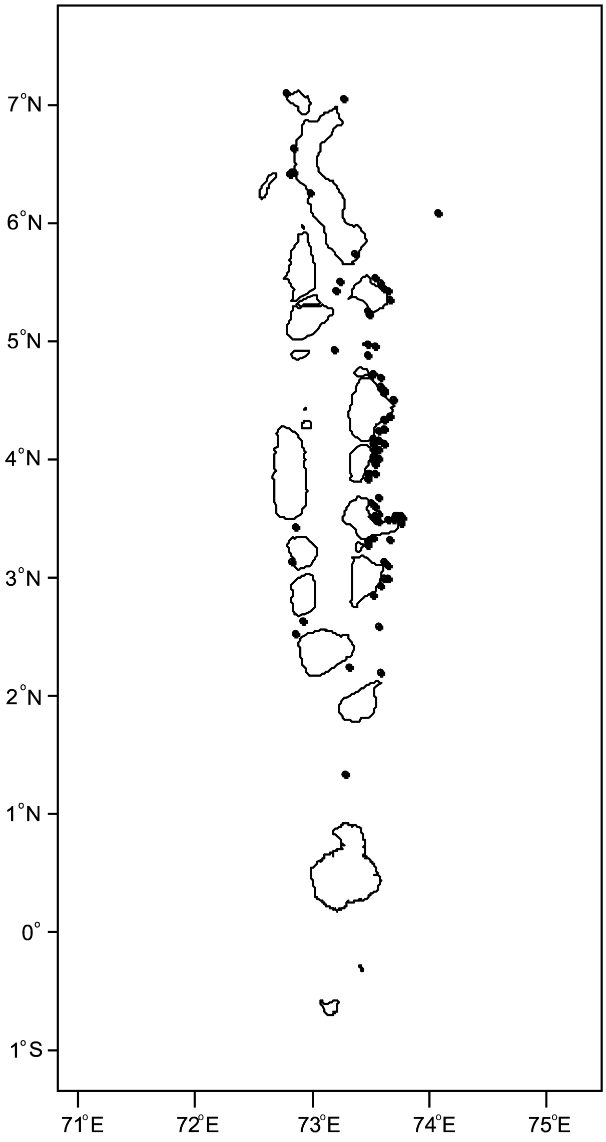

Fig. 5. Locations of sightings of short-finned pilot whales (*n*=84).

confidence. All beaked whales were seen in deep water outside the atolls, mostly over the outer atoll slopes. Only one was recorded from the rather flat-bottomed inter-atoll sea, and that was from the edge near the slope. The highest density of beaked whale sightings was off southeast Vaavu Atoll (Fig. 6), where the atoll reef juts out to form the most easterly point of the Maldives and where bottom topography is believed to be particularly steep.

Cuvier's beaked whale was the most frequently identified beaked whale (Table 4). Fourteen dives were timed for seven individuals. Mean duration of 13 dives was 26min (range=23-29min, SD=2.4min). One other dive, by a presumed mother and calf, was distinctly shorter at just 16min.

Blainville's beaked whale was difficult to identify positively at sea. The three definite sightings recorded here were all of (separate) groups containing a mature male with black barnacle tufts on their teeth (group size range=2-6 individuals). Nine dives by two individuals averaged 16min (range=13-22min, SD=3.8min).

Longman's beaked whale, long considered the least-known of all whales, was recorded from the Maldives by Dalebout *et al.* (2003) on the basis of a single stranding in 2000. There was one positive sighting of about 20 individuals, and three other sightings all of 2 individuals. Further details of these encounters will be published separately.

Other species

A total of 20 species of cetacean were positively identified at sea during the period 1990-2002. The only other species positively recorded from the Maldives so far is the ginkgo-toothed beaked whale, *Mesoplodon ginkgodens* (*cf.* Anderson *et al.*, 1999). There are as yet no confirmed live sightings of this species in the Maldives. The known cetacean fauna of the Maldives therefore currently stands at 21 species. A record of common dolphin (*Delphinus delphis*) from the Maldives by Deraniyagala (1956) is best regarded as unconfirmed (Anderson *et al.*, 1999; Jefferson and Van Waerbeek, 2002). A sighting tentatively identified as a fin whale (*Balaenoptera physalus*) by Anderson (1990) is now considered to have probably been a Bryde's whale. A photo of a minke whale (*Balaenoptera acutorostrata*) published by Kiefner (2002, p.30) was purportedly taken in the Maldives. According to the photographer (Helmut Debelius, pers. comm.) the photo was probably taken in the Maldives in the late 1970s, but the date and location cannot now be confirmed.

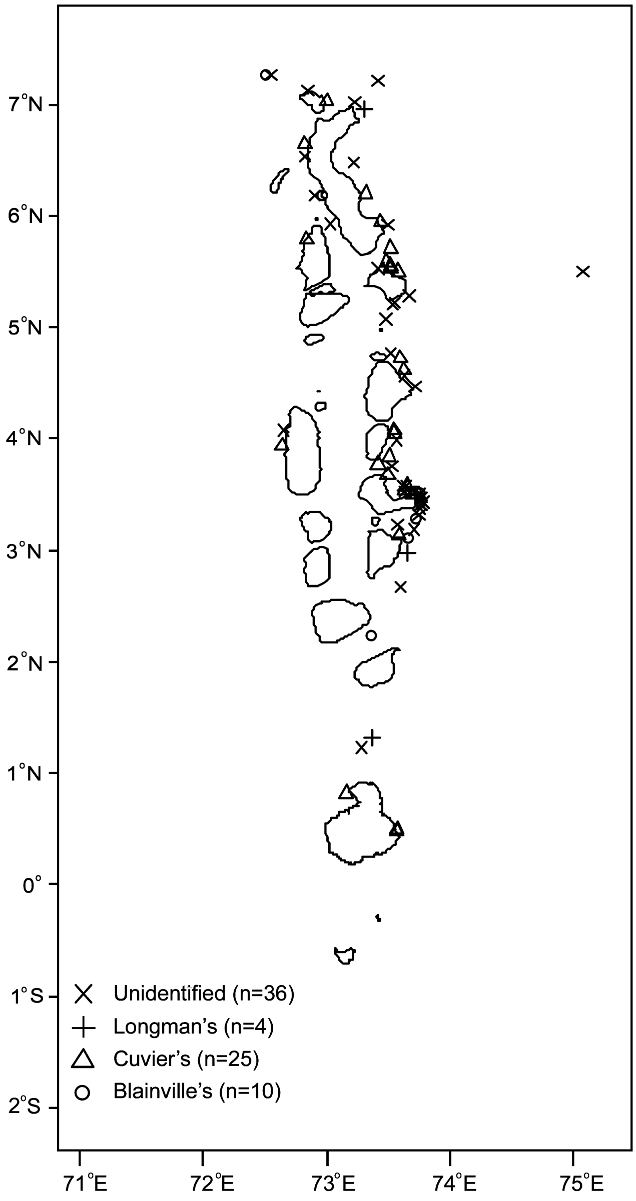

Fig. 6. Locations of sightings of beaked whales (*n*=75).

Inter-specific associations

A total of 83 sightings involved more than one species (Tables 10 and 11). Three or more species were associated in at least nine instances:

1 × spinner, spotted and striped dolphins;

1 × bottlenose dolphin, false killer whale and unidentified dolphin;

1 × bottlenose dolphin, pilot whale and Longman's beaked whale;

2 × bottlenose dolphin, pilot whale and Risso's dolphin;

3 × bottlenose dolphin, pilot whale and Fraser's dolphin;

1 × bottlenose dolphin, pilot whale, Fraser's dolphin and Risso's dolphin.

Spinner and spotted dolphins regularly associated only with each other, with 37 sightings of mixed schools. In 55% of sightings of spotted dolphins (*n*=67) they were associated with spinner dolphins. In contrast, in only 15% of sightings outside the atolls (*n*=244) were spinner dolphins associated with spotted dolphins. However, for spinner dolphins more than 1 n.mile (1.85km, the median distance of sightings) offshore, 46% (*n*=71) were associated with spotted dolphins. More than 2 n.miles (3.7km) offshore, 58% (*n*=55) of spinner dolphin sightings were associated with spotted dolphins.

Bottlenose dolphins associated with at least seven other cetacean species (six excluding a single observation with spinner dolphins), the largest number of associates for any cetacean in this survey. Bottlenose dolphins associated most frequently with pilot whales. Bottlenose dolphins were the only species associated with false killer whales, with which they were seen in four out of 10 on-effort false killer whale encounters.

Fraser's dolphins were associated with other cetacean species in 53% of sightings (Table 10). The species involved were melon-headed whales, short-finned pilot whales, Risso's dolphins and bottlenose dolphins (Table 11). While the association with melon-headed whales is well known, associations with other species appear to have been less frequently reported (Jefferson and Leatherwood, 1994; Perrin *et al.*, 1994; Perryman *et al.*, 1994; Dolar, 2002). In the south of the Maldives (where pilot whales appeared to be rare but melon-headed whales were common) 50% of Fraser's dolphin schools (*n*=4) were associated with melon-headed whales, whereas in the north and centre 42% (*n*=12) were associated with pilot whales. In addition to the five mixed groups recorded here, pilot whales were noted in the vicinity of Fraser's dolphin schools on another three occasions although they were not recorded as being associated at the time. Fraser's dolphins were often seen at some distance from associated pilot whales; the Fraser's dolphins usually moved faster than the pilot whales, but maintained contact by frequent changes of course, occasionally appearing to loiter while the pilot whales caught up. The significance of these observations is unclear but they might suggest that this association is more advantageous to the Fraser's dolphins than to the pilot whales. What that advantage might be and whether Fraser's dolphins reap a similar advantage from their association with melon-headed whales are matters for speculation at present.

Pilot whales and Risso's dolphins were the two most frequently sighted species associated with the outer atoll slopes (see below). Despite their relative abundance, and sharing a habitat of limited area, these two species were recorded as being associated with each other on only four occasions (Table 10). In one case, the two species were travelling in the same direction but not in close proximity. In the other three cases, the Risso's dolphins displayed what could be interpreted as aggressive behaviour towards the pilot whales, including tail slapping and breaching. Shane (1995) suggested that Risso's dolphins and short-finned pilot whales compete for squid. She noted four instances of apparent aggression by Risso's dolphins towards pilot whales, and suggested that the former displaced the latter off Santa Catalina Island, California, when squid resources were limited.

Table 10

Occurrence of cetaceans in mixed schools.

Species	No. mixed schools	Total sightings	% in mixed schools
Spinner dolphin*	38	244	15.6
Spotted dolphin	38	67	56.7
Striped dolphin	1	46	2.2
Bottlenose dolphin*	38	115	33.0
Risso's dolphin	9	219	4.1
Fraser's dolphin	9	17	52.9
Rough-toothed dolphin	1	6	16.7
Short-finned pilot whale	32	81	39.5
False killer whale	4	10	40.0
Melon-headed whale	2	12	16.7
Longman's beaked	1	3	33.3
Sperm whale	1	10	10.0
Unidentified dolphin	2		
Total	176		

*Note: for spinner and bottlenose dolphins, only sightings outside the atolls are included.

Associations with seabirds, tuna and other fishes

A summary of cetacean associations with seabirds and tuna is presented in Table 12. The spotted dolphin was the species most frequently seen with birds and tunas. Among 67 sightings of spotted dolphins, 64% were recorded as being associated with tunas. In all cases where it was possible to identify the tunas (54% of all sightings), they were identified as yellowfin tuna. Some 58% of spotted dolphin schools were associated with seabirds, of at least 15 different species, the most frequently recorded being Lesser Noddy (*Anous tenuirostris*) and Sooty Tern (*Sterna fuscata*). Overall, 76% of spotted dolphin schools were noted as associated with tuna and/or birds. Since it may not always be possible to detect the presence of tuna, and birds may not be present if the tuna are not feeding, it seems likely that 76% is an underestimate of the percentage of spotted dolphin schools associated with tuna. Spotted dolphins associated with yellowfin tuna were normally seen following the tuna, not vice versa. This behaviour is also reported by Maldivian pole and line tuna fishermen (Anderson and Shaan, 1998).

Spinner dolphins outside the atolls were associated with seabirds in 14% of sightings. At least 14 species of bird are involved, including Brown Noddy (*Anous stolidus*), Lesser Noddy, Sooty Tern, Bridled Tern (*Sterna anaethetus*) and Lesser Frigatebird (*Fregata ariel*). Spinner dolphins were recorded with tunas in 14% of sightings outside the atolls. In 26 cases the tunas were identified to species: 24 (9.8% of sightings) yellowfin tuna, 1 (0.4%) skipjack (*Katsuwonus pelamis*) and 1 (0.4%) kawakawa or little tuna (*Euthynnus affinis*). Spinner dolphins are known to associate regularly with yellowfin tuna, but not as frequently as spotted dolphins (Norris *et al.*, 1994). No bird or tuna associations with spinner dolphins were noted inside the atolls.

Table 11

Frequencies of inter-species associations.

	Spinner dolphin	Spotted dolphin	Bottlenose dolphin	Risso's dolphin	Fraser's dolphin	Pilot whale	False killer	Total
Spotted dolphin	37							37
Striped dolphin	1	1						2
Bottlenose dolphin	1	-						1
Risso's dolphin	-	1	5					6
Fraser's dolphin	-	-	5	2				7
Rough-toothed	-	-	1	-	-			1
Pilot whale	-	-	29	4	5			38
False killer	-	-	4	-	-	-		4
Melon-headed	-	-	-	-	2	-	-	2
Longman's	-	-	1	-	-	1	-	2
Sperm whale	-	-	-	-	-	1	-	1
UNID	-	-	1	1	-	-	1	3
Total	39	2	46	7	7	2	1	(208)

Note: totals in Tables 10 and 11 do not tally because some mixed schools contained more than two species.

Table 12

Occurrence of cetaceans with birds and tuna. Percent values are of total sightings for each species.

Species	Total sightings	With birds	With tunas	With birds or tunas
Pantropical spotted	67	39 (58.2%)	43 (64.2%)	51 (76.1%)
Spinner dolphin*	244	33 (13.5%)	34 (13.9%)	43 (17.6%)
Bryde's whale	53	5 (9.4%)	8 (15.1%)	8 (15.1%)
Striped dolphin	46	7 (15.2%)	3 (6.5%)	7 (15.2%)
Dwarf sperm whale	80	3 (3.8%)	1 (1.3%)	3 (3.8%)
Bottlenose dolphin*	115	1 (0.9%)	1 (0.9%)	2 (1.7%)
Rough-toothed dolphin	6	0	1 (16.7%)	1 (16.7%)
Killer whale	9	1 (11.1%)	0	1 (11.1%)
False killer whale	10	1 (10.0%)	0	1 (10.0%)
Melon-headed whale	12	1 (8.3%)	0	1 (8.3%)
Risso's dolphin	219	1 (0.5%)	0	1 (0.5%)
Unidentified		5	5	8
Total		97	96	127

*Note: for spinner and bottlenose dolphins, only sightings outside the atolls are included.

Experienced Maldivian tuna fishermen report that dolphins (presumably spinner dolphins) with associated tunas leave the tunas if they enter an atoll.

Bryde's whales were associated with tunas in at least 15% of sightings. In every case the fish were identified as yellowfin tuna, although in two instances skipjack tuna were also present. Each time Bryde's whales were seen feeding (*n*=6), yellowfin tuna were seen feeding in the same area and apparently on the same prey. Seabirds were present in 9% of Bryde's whale sightings; the birds included Lesser Noddies, Brown Noddies, Sooty Terns, Bridled Terns and Great Crested Terns (*Sterna bergii*).

Seabirds were seen with killer whales and false killer whales on one occasion each. In both cases the birds (Swinhoe's Storm-petrels, *Oceanodroma monorhis*, in the case of the false killer whales, Flesh-footed Shearwaters, *Puffinus carneipes*, with the killer whales) were scavenging scraps (Anderson and Baldock, 2001).

On three occasions baleen whales were seen in close proximity to other plankton feeders. Once whale sharks (*Rhincodon typus*) were seen feeding on krill in the same area as Bryde's whales. Manta rays (*Mobula* sp.) were observed on two occasions, in close proximity to a blue whale and five feeding Bryde's whales.

Remoras (Echeneidae) were recorded on four different species. Unidentified remoras were seen on spinner, striped and bottlenose dolphins. What appeared to be whale-suckers (*Remora australis*) were regularly seen and photographed on blue whales. One shark-sucker (*Echeneis naucrates*) was clearly seen and photographed on a bowriding spinner dolphin. This remora species has recently been confirmed to associate with cetaceans (Fertl and Landry, 1999).

Regional distribution

The cetacean fauna inside the atolls was very different from that outside (Tables 6, 7 and 8). Only two species, spinner dolphin and bottlenose dolphin, occurred regularly inside the atolls. In addition, both records of humpback whale were from inside the atolls. In contrast, every other species occurred most frequently, or exclusively, outside the atolls.

Outside the atolls, the south of the Maldives showed several distinct differences in its cetacean fauna compared to the north and centre. Most obviously, melon-headed whales were common in the south, but rare in the north and centre. Spotted dolphins also appeared to be especially common in the south of the Maldives. In contrast, several species appeared to be less common in the south than in the north and centre, including Risso's dolphin, bottlenose dolphin, short-finned pilot whale and striped dolphin. The southern Maldives is less affected by the seasonal monsoon currents than the north and centre of the country, but is instead much influenced by equatorial currents and their associated upwellings (Molinari *et al.*, 1990; Anderson *et al.*, 1998). Within the Maldives, several pelagic fish species show distinct differences in abundance between the south and north-central Maldives (Anderson, 1992; Anderson and Saleem, 1994; Anderson *et al.*, 1998). Within the wider Indian Ocean, some other marine organisms are confined mainly to equatorial waters within about 5° of the equator. These include at least one seabird, Matsudaira's Storm-petrel *Oceanodroma matsudairae* (Bailey *et al.*, 1968), and a planktonic copepod (Meenakshikunjamma, 1974). In the Eastern Tropical Pacific, melon-headed whales are known to associate with equatorial upwellings (Au and Perryman, 1985).

Differences between the north and centre of the Maldives (outside the atolls) are much less obvious than those with the south (Tables 7 and 8). Spotted dolphins are less abundant in the centre than in the north (and south); as noted above, this is probably related to the abundance of large yellowfin tuna in these regions (Anderson and Shaan, 1998; Anderson *et al.*, 1998).

The cetacean fauna of the inter-atoll sea between the double chain of central atolls appears to be intermediate between that inside the atolls and that of the oceanic waters outside the atolls. Many species show intermediate levels of relative abundance (Tables 7 and 8). The inter-atoll sea shows intermediate oceanographic characteristics: much of it is relatively flat-bottomed and sheltered (like the inside of the atolls) while parts of it adjoin the steep slope of the Maldives ridge and are fully exposed to oceanic conditions.

Association with outer atoll slopes

Several species appeared to be closely associated with the steep outer atoll reef slopes. These included dwarf sperm whale, Risso's dolphin, short-finned pilot whale, Cuvier's beaked whale and Blainville's beaked whale (see individual species accounts above). All of these species feed heavily on squid, and their association with outer atoll slopes likely reflects a concentration of squid in this habitat. Despite the apparent importance of this habitat for some cetaceans, the outer atoll slopes have not been considered in detail in this study, because lack of detailed bathymetric information from outside the atolls hinders analysis. For example, while it is clear that these species are seen most frequently over the general area of the slopes, it has not been possible to relate sightings to precise bottom depths or gradients. Nevertheless, the association of some species with the outer atoll slopes did influence the distribution of sighting effort. During most whalewatching cruises (sea trip category 3 as defined previously), one aim was to maximise cetacean sightings. This was best achieved by cruising over the atoll slopes.

CONCLUSIONS

The Maldives has a high diversity of cetaceans, with all the expected pantropical species being represented. Numbers of small delphinids were particularly high, and beaked whales also appeared to be relatively abundant. The Maldives undoubtedly offers considerable scope for both whalewatching tourism and cetacean research. Studies within the northwest Indian Ocean Sanctuary should illuminate the recovery, or otherwise, of stocks of large whale following exploitation in the 1960s. The northern Indian Ocean, including the Maldives, is oceanographically unique and cetacean studies here might therefore be expected to produce fresh insights into cetacean behaviour and ecology. Variations in cetacean distribution and abundance between the eastern and western sides of the atoll chain, and within regions between the northeast and southwest monsoons, were not dealt with here but warrant further study. In addition, there is scope for more detailed studies of any of the commoner species, of ecological interactions between slope-associated teuthivores, of baleen whale migrations and of the two forms of bottlenose dolphins.

ACKNOWLEDGEMENTS

Much of the early fieldwork reported in this study was carried out under the auspices of the Marine Research Centre; I am most grateful to the former Directors, the late Maizan Hassan Maniku and Ahmed Hafiz, for their support over many years. Most of the later fieldwork was carried out under the auspices of the Whale and Dolphin Company, Maldives. Thanks are due to the many people who provided details of sightings and to those who assisted with fieldwork, especially the staff of the Marine Research Centre (notably Zaha Waheed, Abdulla Shaan and Ibrahim Nadheeh), Michael Baldock and Stephen Akester. This analysis incorporates data collected during the survey reported by Ballance *et al.* (2001); I thank all those who facilitated and participated in that trip. For assistance with database development and data entry I am particularly grateful to my father Robert Anderson, and also to Glenys Latham, Stephen Lewis and Abdulla Shaan. Mohamed Shiham Adam produced the maps and also assisted with tracing literature. For assistance with various queries my thanks to Lisa Ballance, Susan Chivers, Helmut Debelius, James Mead, Bill Perrin and Bob Pitman. Drafts of this paper were reviewed by Mohamed Shiham Adam (Marine Research Centre, Maldives), Gianna Minton (Oman Whale and Dolphin Research Group), Robert L. Pitman (U.S. National Marine Fisheries Service), Graham J.B. Ross (Environment Australia) and two anonymous referees; I greatly appreciate their constructive comments. Finally, thanks to Susan for enthusiastic support and forbearance in equal measure.

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Date Received: May 2004
Date Accepted: June 2004

Fin whales (*Balaenoptera physalus*) summering in the Ligurian Sea: distribution, encounter rate, mean group size and relation to physiographic variables

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ABSTRACT

This paper investigates the distribution of Mediterranean fin whales (*Balaenoptera physalus*) between 1990-99 in the recently-established Pelagos Sanctuary for the Conservation of Mediterranean Marine Mammals. During the study period, 870 days were spent at sea, surveying a total of 73,046km, totalling 540 sightings of fin whales. Mean yearly whale encounter rates showed no significant differences in the first five years, but then steadily decreased between 1995-99. The highest encounter rates and largest mean aggregation size (mean=2.12; SD=1.32; SE=1.15) were in summer 1995 and the mean aggregation size throughout the study period was 1.75 (mode=1; SD=1.11; SE=0.05). Differences in mean aggregation size were significant between years, but not months. This is likely to be related to prey availability and to patchiness of plankton distribution. Generalised Linear Models were used to relate fin whale distribution to physiographic variables (mean, range and standard deviation of depth and slope, and distance from the nearest coast). Water depth was the most significant variable in describing fin whale distribution, with more than 90% of sightings occurring in waters deeper than 2,000m. This study demonstrates the deep water preference of fin whales in this area, emphasises the crucial role that this part of the western Ligurian Sea plays in the ecology of Mediterranean fin whales and provides recommendations for conservation and management measures in the area.

KEYWORDS: FIN WHALE; DISTRIBUTION; HABITAT; INDEX OF ABUNDANCE; CONSERVATION; EUROPE; MEDITERRANEAN SEA

INTRODUCTION

The fin whale (*Balaenoptera physalus*) is the only mysticete regularly occurring in the Mediterranean Sea (e.g. Duguy, 1990). Genetic analyses performed on Mediterranean specimens revealed the existence of a recently-diverged population, characterised by limited gene flow with North Atlantic conspecifics (Bérubé *et al.*, 1998). During the summer months, the species is known to concentrate in high numbers in the Corso-Ligurian Basin, described as one of the principal feeding grounds for fin whales in the Mediterranean Sea (Notarbartolo di Sciara *et al.*, 2003). Line-transect surveys, conducted in the western Ligurian Sea in August 1992 in order to assess the absolute abundance of cetaceans in the Basin during the summer months, yielded an estimate of 901 fin whales (SE=196.1, %CV 21.77, 95% CI 591-1,374), with a mean fin whale density ranging from 0.024 to 0.015 individuals km^{-2} (Forcada *et al.*, 1995; Gannier, 1997a; b). For a more detailed overview of the fin whale in the Mediterranean Sea see Notarbartolo di Sciara *et al.* (2003).

The oceanographic features of the Corso-Ligurian Basin result in an area of enhanced productivity (Jacques, 1990; Astraldi *et al.*, 1994) that hosts a richer cetacean fauna than bordering regions which are characterised by lower primary productivity (Notarbartolo di Sciara *et al.*, 1993). On 25 November 1999, in consideration of the local abundance of cetaceans, Italy, France and Monaco signed an Agreement for the establishment of an International Sanctuary for the Protection of Marine Mammals, which entered into force in 2002. The Sanctuary was listed among the Specially Protected Areas of Mediterranean Importance (SPAMIs) within the framework of the Barcelona Convention. The area encompassed by the Sanctuary lies between the French coast, northern Sardinia, and the coasts of Liguria and Tuscany in Italy (Fig. 1).

Mediterranean fin whales face a number of actual and potential anthropogenic threats, including collisions with vessels, chemical and acoustic pollution, entanglement in fishing gear (Notarbartolo di Sciara *et al.*, 2003) and disturbance by boats (Jahoda *et al.*, 2003). Collision events are common in Mediterranean waters (Anon., 1997; Pesante *et al.*, 2000) and may represent a major cause of non-natural mortality for fin whales. In fact, fin whales are the species most commonly struck by vessels worldwide (Laist *et al.*, 2001). Given the increasing number of ferries crossing the Pelagos Sanctuary, collisions are a growing source of concern for fin whales concentrating in this area during the summer months. Appropriate habitat use and distribution studies, to describe fin whales' habitat preferences and to investigate the existence of critical habitats for this species, are therefore urgently needed to aid implementation of management measures to regulate naval traffic, fishing and whalewatching within the Sanctuary.

This paper presents data collected in the waters of the Sanctuary during the summers of 1990-99. Dedicated cruises were organised to gather data on fin whale presence, distribution, encounter rate and aggregation size. The relationships with physiographic parameters such as water depth, slope and distance from the nearest coast were also investigated, as well as inter-annual patterns in mean aggregation size and encounter rate. The relevance of the results to the conservation of this species in the western Mediterranean Sea is presented at the end of the paper.

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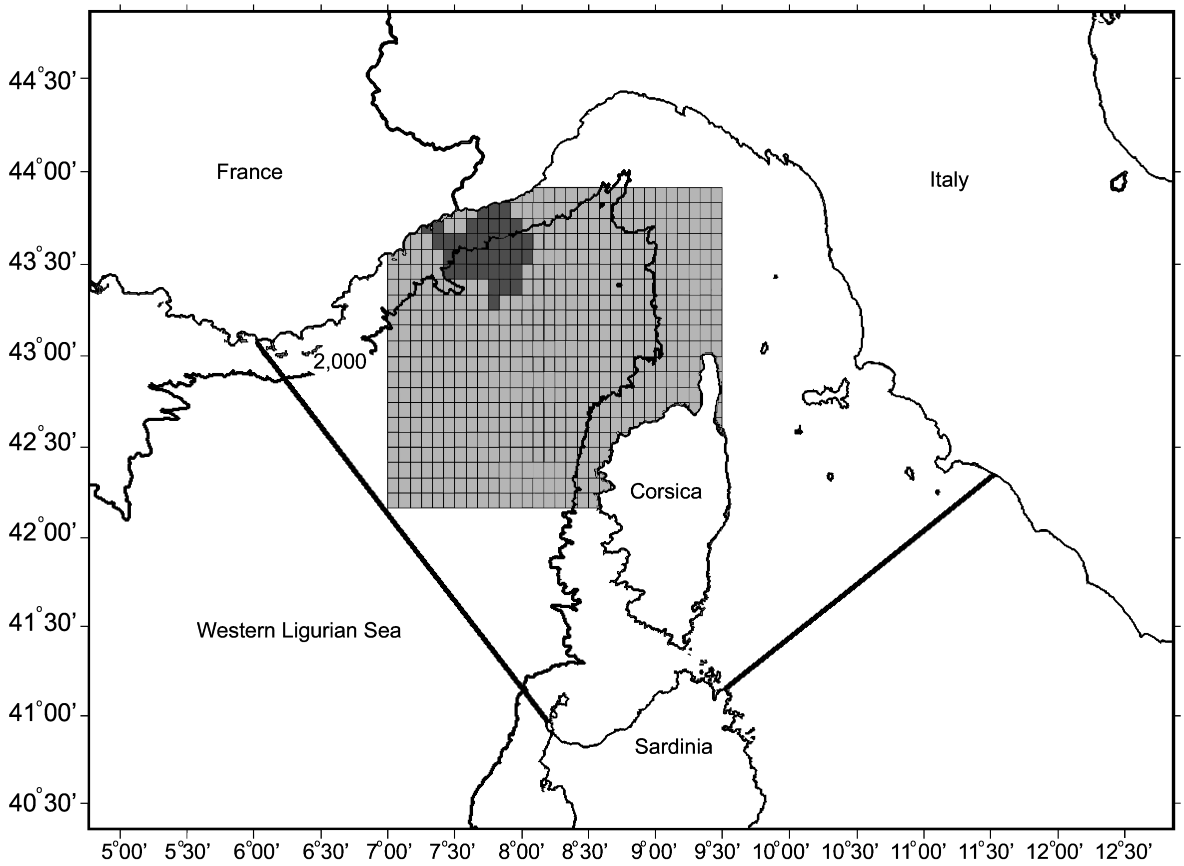

Fig. 1. The study area showing the 2,000m isobath, Sanctuary borders, 5' X 5' grid and in darker shading the sub-area.

MATERIALS AND METHODS

Study area

The study area included the continental shelf and offshore waters of the western Ligurian and Corsican Seas. Specifically, the study area was delimited by Saint Raphael (43°25'N, 6°50'E) on the French coast, Cape Mele (43°55'N, 8°10'E) on the Italian coast and Cape Corse (43°00'N, 9°25'E) and Girolata (42°20'N, 8°35'E) on the island of Corsica (Fig. 1). This area of approximately 24,000km^2 has a mean depth of 2,300m. The area is characterised by a narrow continental shelf, a marked cyclonic circulation present throughout the year, and strong upwelling currents (Jacques, 1994; Astraldi *et al.*, 1995).

Data collection methods and effort

This research was carried out between 1990 and 1999. Within each single year, effort varied in terms of length of field season and number of vessels used. The research platforms used in this study were auxiliary sailing vessels, equipped with inflatable craft, ranging in length from 15-20m, with a mean cruising speed ranging from 9-11km h^{-1}.

The tracks of the cruises were not designed to obtain an even coverage of the study area but rather to maximise encounters with whales (based on previous experience and available information), therefore increasing the number of sightings and the time spent with cetaceans.

During the searching effort, a minimum of one observer was positioned at each side of the vessel. Observations were made preferentially in flat seas and calm weather, defined as 'favourable conditions', and ceased when wind exceeded 3 on the Beaufort scale (wind speed = 5.4m s^{-1}). Searching effort start and end times were determined by departure and arrival times, start and end times of a sighting, sunrise and sunset, or major changes in weather conditions.

Whales were spotted by naked eye and were usually approached at short-distance to determine aggregation size, assess the presence or absence of sub-adults, and take pictures for photo-identification purposes (Agler *et al.*, 1990). In some cases the collection of biopsy samples for genetic (Bérubé *et al.*, 1998) and toxicological analyses (Marsili *et al.*, 1998; Fossi *et al.*, 2003), the assessment of possible disturbance caused by vessel approaches (Jahoda *et al.*, 2003) and tagging with time-depth-recorders (Panigada *et al.*, 1999; 2003) were also undertaken. Aggregation size was defined as the number of whales sighted within a radius of 1.5-2km of the research vessel. Whale sizes were compared visually to the sizes of nearby vessels of known length (i.e. the research or inflatable vessel), and all individuals <15m long were considered to be sub-adults; in accordance with data from the North Atlantic presented by Lockyer (1984) these whales were categorised as immature individuals and classified as suckling calves or weaning individuals following the criteria proposed by Orsi Relini (2000). Suckling and weaning whales were always accompanied by at least one adult (≥16m long). Sighting co-ordinates were recorded using a Global Positioning System (GPS) and plotted on a digital map in *ArcView 3.2*. The distance from the nearest coast and the water depth for each sighting location were determined from this. Environmental data, such as visibility, Beaufort wind force and sea state were recorded every 60 minutes, or more frequently if changes in conditions occurred.

Data analysis

To provide detailed information on the relative abundance of fin whales, the study area was divided into 5' squares with a surface area of approximately 62.5km^2 each (Fig. 1).

To calculate encounter rates, 38 squares that were surveyed every year from 1990 to 1999 were selected, and treated as a sub-sample of the study area (Fig. 1). This sub-area, covering a total of 2,375km², including coastal, slope and pelagic habitats and encompassing water depths up to 2,400m, was treated as representative of the entire study area.

Sighting effort was measured by computing the length of the track line surveyed under 'favourable conditions' in each 5' square. Encounter rates were then calculated by dividing the number of fin whale sightings in each square by the total distance covered under favourable conditions in the same square. These single values provided an index of fin whale sightings per unit effort. In order to avoid small sample biases, all the grids containing a sighting with less than 10km surveyed were eliminated from the dataset. Encounter rates for each year were obtained by averaging all the squares sampled in that year. The sampling variance of the encounter rate was then calculated using the following formula (Buckland *et al.*, 1993):

$$\frac{\sum_{i=1}^{k} \frac{l_i}{L}\left(\frac{n_i}{l_i} - \frac{n}{L}\right)^2}{k-1}$$

where l_i = length of transect in each square, n_i = number of sightings in each square, n = total number of sightings, L = total transect length, k = number of squares.

Encounter rates of individuals were calculated by multiplying yearly encounter rates by mean aggregation sizes.

In this study only whales sighted while searching under 'favourable conditions' and occurring within the sub-sample of the study area have been used for encounter rate calculations, while all sightings, including those off effort and those in unfavourable conditions, have been used for the analyses of aggregation size and for the measurements of depths and distances from the coast.

Clarke (1982) calculated an 'index of sighting conditions for surveys of whales and dolphins' and estimated that fin whales could be seen by the naked eye at a distance of one nautical mile, up to sea state 7 on the Beaufort scale with a heavy swell. In addition, Gunnlaugsson *et al.* (2002) while estimating fin whale abundance in the North Atlantic, found that Beaufort sea state did not affect estimation of the detection function. Therefore, when pooling all the sightings made under 'favourable conditions' it was assumed that detection rates were consistent for sea state conditions 0-3 on the Beaufort scale.

Group size is also known to affect detection rates (Buckland *et al.*, 2001). However, since fin whales in the Mediterranean tend to form aggregations of mainly 1-2 animals (D'Amico *et al.*, 2003; Notarbartolo di Sciara *et al.*, 2003; this dataset) and previous surveys in the same area demonstrated that encounter rates did not significantly differ between school size categories (Forcada *et al.*, 1996), the data were not stratified by group size.

Generalised Linear Models (GLMs)

GLMs were used to model the distribution of fin whales in relation to physiographic variables.

The response variable was the number of fin whale sightings in each square in each year. The survey effort, expressed in number of km searched in each square under favourable conditions, was treated as an offset. The explanatory variables were year treated as a factor, mean and range of depth, mean and range of slope and distance from the coast. These covariates were calculated for each square using *ArcView 3.2*. Depth and distance from the coast were measured in meters, while slope, calculated with the function 'derive slope' in *ArcView*, was measured in degrees.

Models were fitted assuming either a Poisson or Quasi Poisson distribution, both with the log link function; these distributions assume linearity on the scale of the link function rather than linearity between the covariates and the response on the raw scale. Linearity on the scale of the link function was checked using partial regression plots to ensure this assumption was reasonable. Before any models were fitted, variance inflation factors (VIFs) were calculated to ensure collinearity between covariates was not prohibitively high. A Poisson distribution was assumed when the dispersion parameter for the Quasi Poisson family was close to unity; in this case the Akaike Information Criterion (AIC) was used to select the best models performing backward and forward stepwise selection. A Quasi Poisson distribution was assumed when the dispersion parameter was ≠1; in this case the models were first fitted with all candidate variables and those with p-values greater than 0.05 were dropped from the model one by one. Models were fitted to data from the whole study area and from the selected sub-area. Year was treated both individually and as two five-year intervals (1990-94 and 1995-99). However, when fitting the models with data from the whole study area, neither single year nor year intervals were significant, therefore years were pooled in all further GLM analyses.

RESULTS

The duration of the field season, the number of days spent at sea each year and the number of km surveyed are shown in Table 1. In 1992 and 1993 two vessels operated, while in the remaining years only one boat was used for the data collection. A total of 540 fin whale sightings were made during the study period, comprising 942 individuals.

Table 1

Study period, number of days worked, total number of km surveyed, number of sightings and whales, referred to the whole study area.

Year	First date	Last date	No. of days worked	km surveyed	No. of sightings	No. of whales
1990	6 Jun.	4 Oct.	77	6,096	36	43
1991	2 Jun.	3 Oct.	99	10,960	70	110
1992	6 Jul.	25 Sept.	104	9,967	69	125
1993	16 Jun.	4 Oct.	137	10,709	78	153
1994	21 Jun.	29 Sept.	70	6,500	74	146
1995	3 Jun.	1 Oct.	85	6,849	73	155
1996	6 Jun.	12 Sept.	65	4,315	37	49
1997	12 Jun.	9 Oct.	82	6,604	36	52
1998	20 Jun.	24 Sept.	72	5,026	33	59
1999	20 Jun.	24 Sept.	79	6,290	34	50
Total			**870**	**73,046**	**540**	**942**

The sub-sample of the study area appeared to be homogeneously covered throughout the study period, as shown in Fig. 2.

Distribution

The research effort, in terms of km surveyed, during the 10-year research period covered 55.6% of the whole study area, but was mainly concentrated in the region closest to the Italian-French coasts and in the shipping lane between the mainland and Calvi, on the island of Corsica (Fig. 3a). The

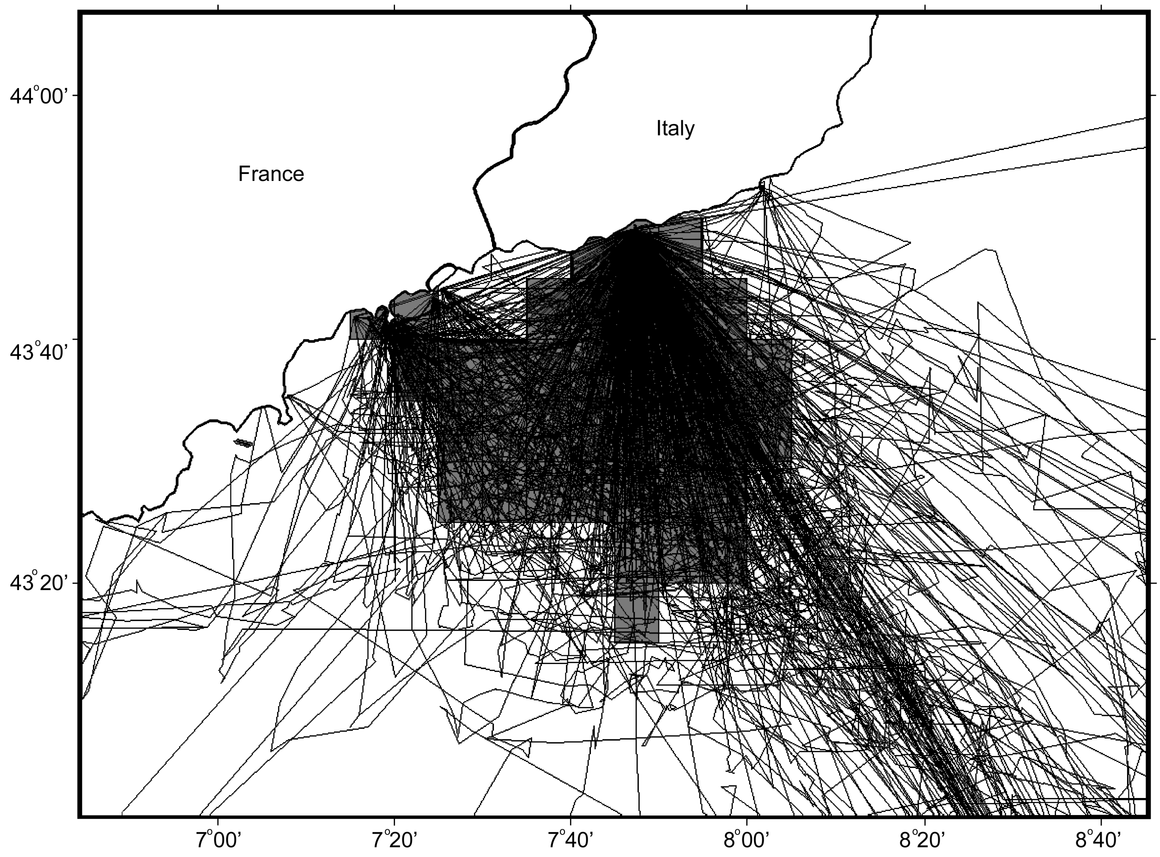

Fig. 2. The sub-sample of the study area showing the shipboard transects carried out in 1990-99.

540 fin whale sightings made from 1990-99 appeared to be concentrated in the central portion of the study area, in the zone between Nice, San Remo and the north-western coast of Corsica (Fig. 3b). The number of sightings in each 5' square is shown in Fig. 3c. The fin whale sightings generally reflected the distribution of effort, with a higher number of sightings close to the continental coast of Italy and France, in the centre of the study area and along the western coast of Corsica. The encounter rate values tended to be higher in the south-western portion of this area (Fig. 3d).

Whales were found predominantly in offshore waters, beyond the 2,000m isobath, with a relatively small number of sightings in shallower waters. More than 90% of sightings occurred in waters deeper than 2,000m and more than 23km from the nearest coast (Fig. 4). The mean water depth at sighting locations was 2,317m (SD=380, *n*=540, range 65-2,690), with a mean distance from the coast of 45.6km (SD=18.6, *n*=540, range 1.9-99.1). Distance from the nearest coast and sighting depth did not differ significantly throughout the study period.

Mean aggregation size, relative encounter rates of sightings and individuals in the sub-area surveyed each year are presented in Fig. 5. Encounter rates were stable for the years 1990-94, peaked in 1995 and steadily decreased in all successive years studied. The same trend could be seen for both aggregation and individual sightings.

An inverse variance-weighted linear regression was applied to the two time intervals. The first time interval (1990-94) did not show any particular trend (F-statistic = 0.064, $p= 0.8171$), while the second one, 1995-99, showed a significant decline (F-statistic = 185.5, $p= 0.0008561$).

GLM analysis

Two different data sets were used for the GLM analysis: one from the whole study area and one from the selected sub-area. The GLM analysis from the whole area revealed that mean depth was the most significant explanatory variable, with distance from the nearest coastline less significant, but still selected by the model (Quasi Poisson family, log link function) (Table 2). Bottom slope was never selected by the fitted models. Similar results were obtained when fitting the model for the sub-area (Poisson family, log link function) (Table 3); in that case, however, mean depth and depth range were highly significant, as well as year —treated as a factor.

The fit of each model was assessed using a pseudo-R^2 measure, calculated using the following formula (Hardin and Hilbe, 2001):

$$\text{Pseudo-R}^2 = 1 - \frac{\sum_{i=1}^{n}(y_i - \hat{y}_i)^2}{\sum_{i=1}^{n}(y_i - \bar{y}_i)^2}$$

Where y_i = the response variable, $\hat{y}_i$ = the fitted value and $\bar{y}_i$ = the mean of the observed response.

The model for the pooled data returned a pseudo-R^2 of 0.665, while the sub-area model gave a pseudo-R^2 of 0.413. Although the largest values for sightings per unit effort were under-predicted by the model, no systematic patterns were found in model residuals.

Aggregation size and composition

Fin whales were sighted mostly as singles or pairs (Fig. 6); these made up 81% of the sightings. Mean aggregation size in the overall study area over the study period was 1.74 individuals (mode=1, SD=1.11, *n*=540, range 1-7). Mean annual aggregation sizes ranged from 1.19 in 1990 to 2.12 in 1995, showing significant differences between years (ANOVA, F=4.14, $p<0.01$) (Fig. 7a).

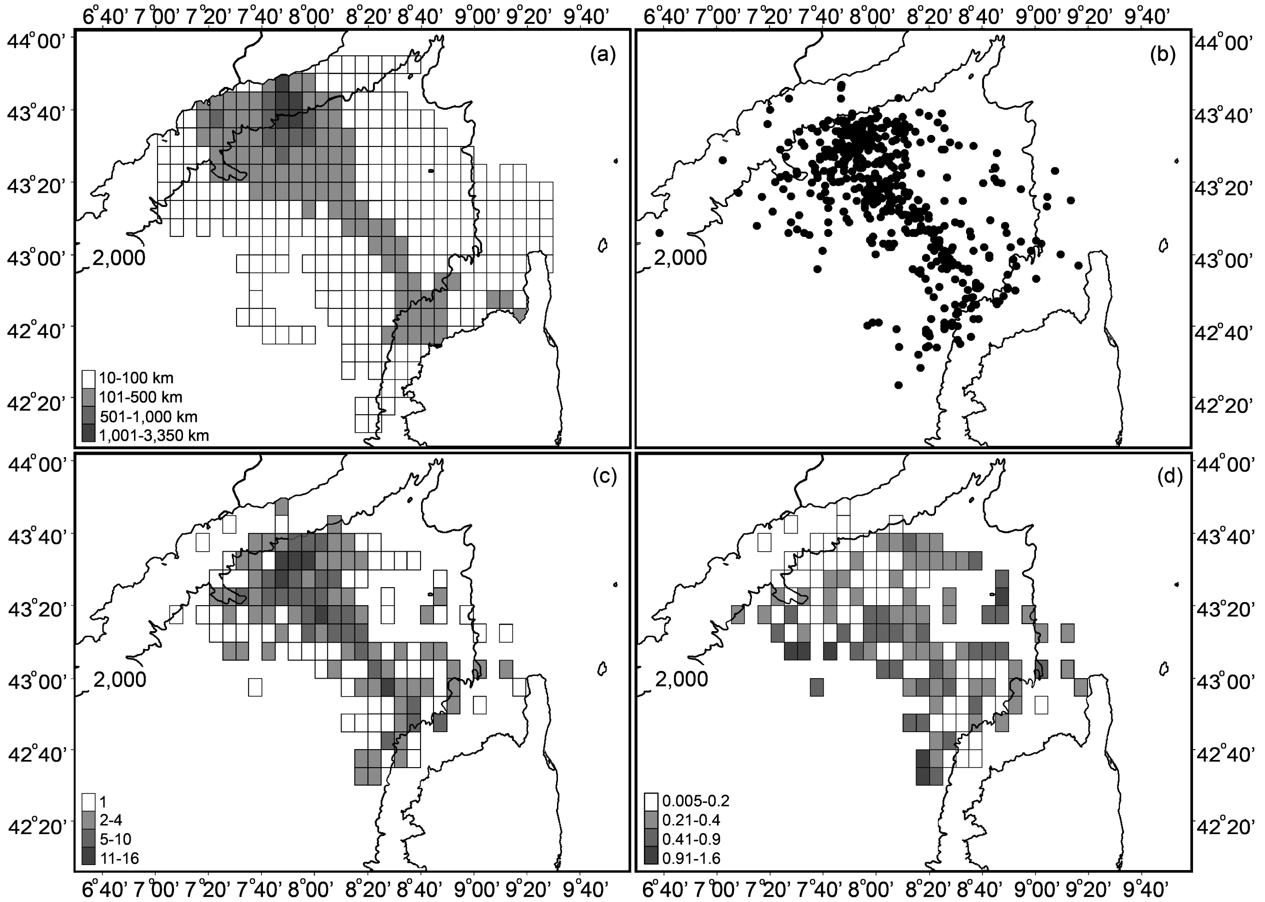

Fig. 3. (a) Research effort (km surveyed); (b) Fin whale sightings; (c) Number of sightings in each cell; (d) Encounter rate.

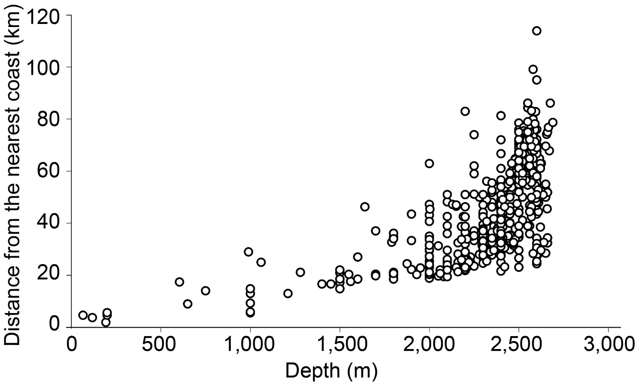

Fig. 4. Depth and distance from the nearest coast for all sightings.

Mean monthly aggregation size declined from 1.86 in June to 1.53 in September (Fig. 7b); however, this variation was not significant (ANOVA, F=1.02, *p*=0.349).

During the study period, 29 fin whales <15m long were recorded, representing 3.1% of the total. Following the age/size categories proposed by Orsi Relini (2000), these 'immature' whales were categorised as 13 suckling calves (6-11m long) and 16 weaning individuals (12-14m long).

DISCUSSION

This work summarises ten years (1990-99) of fin whale effort-weighed sightings in western Ligurian Sea waters. This area plays a key role for the ecology of cetaceans, particularly for whales, representing what is considered to be one of the most important feeding grounds in the Mediterranean Basin (Notarbartolo di Sciara *et al.*, 2003).

Considering that food is the driving force that influences cetacean distribution while in their feeding grounds (e.g. Sergeant, 1977), it can be assumed that Mediterranean fin whales summering in the Ligurian Sea strongly correlate their distribution and relative abundance with prey availability (Relini *et al.*, 1994; Orsi Relini *et al.*, 1992).

Fin whales in the Ligurian Sea were found predominantly in deep offshore waters, seldom occurring at depths less than 2,000m, which is in agreement with previous studies conducted both in the Mediterranean and the North Atlantic Ocean (Aguilar *et al.*, 1983; Sanpera *et al.*, 1984; Sigurjónsson *et al.*, 1989; Notarbartolo di Sciara *et al.*, 2003). However, in several locations within the species' known range, such as the Sicily Channel shelf near Lampedusa (Simone Canese, pers. comm.), or the continental shelf off the northeastern coast of the United States and Canada (Hain *et al.*, 1992) fin whales are mostly observed in shallow waters. These observations support the idea that habitat choice of fin whales when at their feeding grounds most likely depends upon the distribution of their prey (Woodley and Gaskin, 1996). In addition to prey distribution, depth preference is a widely used parameter to describe habitat choice by cetaceans (Davis *et al.*, 2001). Our results show that depth is the most important physiographic parameter that can be used to describe the distribution of fin whales in this study area. This underlines the offshore preferences of fin whales in the Ligurian Sea, which coincides with the presence of a large dome of cold water in the centre of the basin, characterised by high levels of nutrients and upwelling currents (Gostan and Nival, 1967; Pinca and Dallot, 1995). Such a pelagic distribution

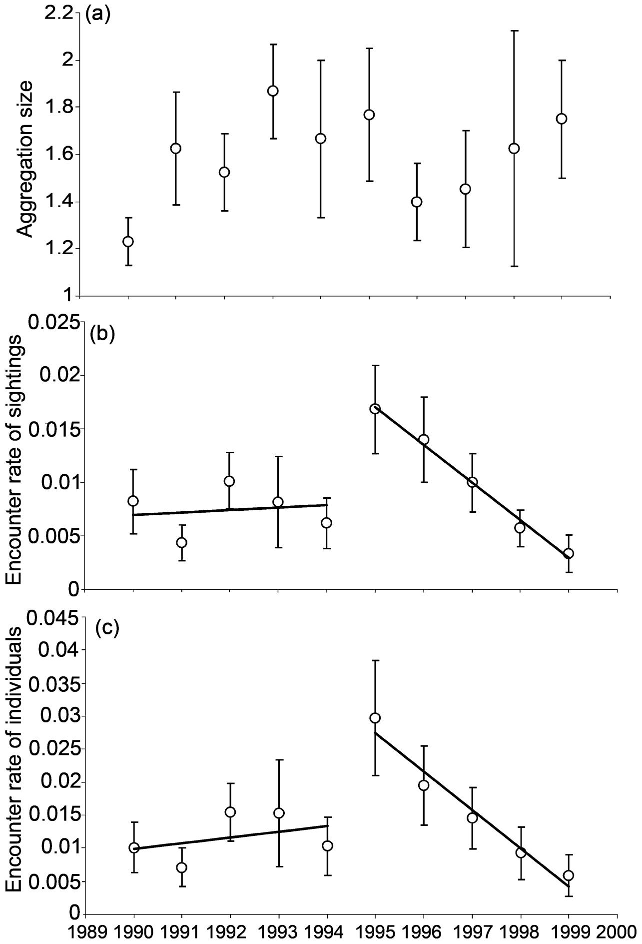

Fig. 5. Mean aggregation size and encounter rates for the sub-area, error bars represent ± one SE. (a) Mean aggregation size; (b) encounter rates of sightings; (c) encounter rates of individuals.

Table 2

Summary results of the GLM analyses, considering all data over the 10-year period and the whole study area (Quasi Poisson family, log link function).

	Estimate	SE	T	Pr (> | t |)
Intercept	-15.01	0.470	-32.1	< 0.001
Mean depth	-0.00154	0.000254	-6.05	< 0.001
Distance	0.0120	0.00503	2.39	0.0174

Table 3

Summary results of the GLM analyses, considering data over the 10-year period within the sub area (Poisson family, log link function). Year was considered as a factor.

	Estimate	SE	T	Pr (> | t |)
Intercept	-13.7500	0.9196	-14.9520	< 0.001
1991	-1.0220	0.3186	-3.2090	< 0.01
1992	-0.3285	0.2938	-1.1180	0.2635
1993	-0.5262	0.2681	-1.9630	< 0.05
1994	-1.6340	0.6048	-2.7020	< 0.01
1995	-0.2044	0.3396	-0.6020	0.547
1996	-0.2689	0.3721	-0.7230	0.469
1997	-0.4087	0.3597	-1.1360	0.256
1998	-1.1010	0.4044	-2.7210	< 0.01
1999	-1.5950	0.5374	-2.9680	< 0.01
Mean depth	-0.0015	0.0004	-3.9740	< 0.001
Depth range	-0.0013	0.0004	-3.3400	< 0.001

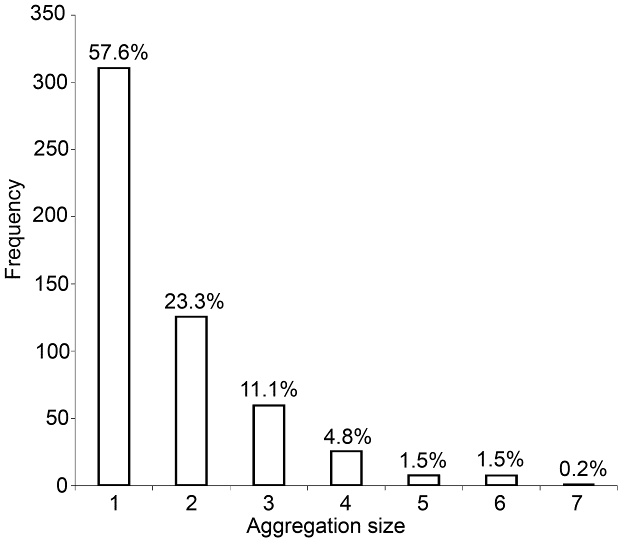

Fig. 6. Frequency distribution of aggregation sizes for all sightings.

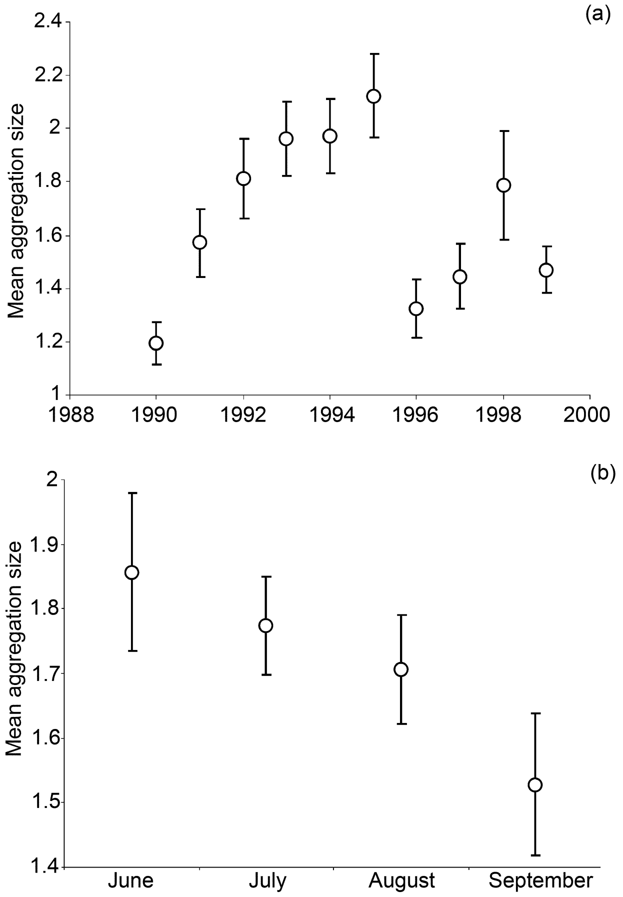

Fig. 7. (a) mean annual aggregation size for the whole study area; (b) mean monthly aggregation size for the whole study area. Error bars represent ± one SE.

most likely reflects the distribution of Northern krill (*Meganyctiphanes norvegica*), thus emphasising the strong link between habitat choice and prey distribution.

However, in the Mediterranean, there have been some years when fin whales were sighted close to the coast, over the continental shelf, as a possible consequence of coastal food aggregation (Notarbartolo di Sciara *et al.*, 2003). Airoldi *et al.* (1999) and Beaubrun *et al.* (1999) observed this unusual situation during summer 1997 in the Ligurian Sea and in the Gulf of Lions respectively, with whales observed less than 2km from shore, and often entering small bays and harbours. Our dataset did not show significant differences in mean depth and distance from the coast of sightings over the study period. An *ad hoc* GLM was fitted to test this hypothesis, considering the single year 1997 and testing it against all other years; GLM analysis again selected the model with mean depth, however year was not selected as an explanatory variable. The likely reason the coastal preference showed by fin whales during 1997 went undetected is that our effort was dedicated mainly to the offshore portion of the Ligurian Sea, with limited time spent in the coastal areas. Our results show that during summer 1997, fin whales were also present in offshore waters.

The steady decrease observed in the encounter rates from 1995-99 is cause for concern and stresses the need for further investigations. This decrease may be related to a geographical shift in the whales' distribution, perhaps induced by shifting oceanographic conditions, or to an altered prey distribution. However, the effects of a combination of human-induced threats, including naval traffic, anthropogenic noise and disturbance, habitat degradation and depletion of natural resources (Notarbartolo di Sciara and Gordon, 1997), cannot be disregarded. Nevertheless, although encounter rates varied considerably throughout the 10-year study period, they showed no overall trend. These results are in agreement with the GLM analysis for the sub-area, which selected year −treated as a factor −as a significant explanatory variable. This stresses the need for long term studies such as this which present natural fluctuations in encounter rate or distribution, that could be easily misunderstood if presented in a different time frame. Further investigations in the same area, including the repetition of surveys over wider areas and possibly encompassing the entire extent of the western Mediterranean summer feeding grounds, will help understanding of the reasons underlying such fluctuations across years, and provide better insight into fin whale relative abundance, and whether management measures are indeed required.

It has been hypothesised that cetacean group sizes largely depend on the distribution of their prey (Nemoto, 1964; Avocedo-Gutiérrez, 2002). Our data showed low mean aggregation size (1.74) compared with those (2.9) observed on the continental shelf off the northeastern coast of the United States and Canada (Hain *et al.*, 1992), but are consistent with data from the Gulf of Maine (Phil Clapham, pers. comm.). Forcada *et al.* (1996), also noted that mean aggregation sizes for Mediterranean fin whales were lower than that in other feeding grounds and proposed that aggregation sizes may be correlated with prey density. There may be a relationship between small mean aggregation size of fin whales and patchy distribution of *M. norvegica* −documented both in the Ligurian Sea (Labat and Cuzin-Roudy, 1996) and in other areas (Sameoto, 1983; Nicol, 1986) −as well as with the peculiar ecology in the Ligurian Sea of this euphausiid, which spends most of its time at considerable depth. The data presented here do not show a significant decrease in mean aggregation size from June-September, indicating that food may be evenly available throughout the season. These results match the seasonal abundance of *M. norvegica*, which is described as having two peaks of abundance, a major one in January/February and a less pronounced one during August-October (Sardou *et al.*, 1996). The recorded differences in yearly mean aggregation sizes indicate that prey availability or distribution might vary (e.g. with different patch size) across years. Inter-annual differences in prey biomass (Franqueville, 1971) may be related to different Beaufort states across winters; during calmer winter seasons low circulation may reduce the phytoplankton spring bloom and relative zooplankton high concentrations during the summer months.

The use of GLMs has provided valuable information regarding the distribution of fin whales in relation to physiographic variables. Future work will include the construction of cetacean habitat prediction models (Forney, 2000; Gregr and Trites, 2001), exploring the relationships between oceanographic conditions and cetacean distribution. In particular the relationship between biological parameters, including prey abundance and remotely sensed physical parameters (i.e. sea-surface temperature, ocean colour, wind speed), will contribute to the identification of particular areas that could be considered as critical habitats for this and other cetacean species in the Western Ligurian Sea.

Mediterranean fin whales are exposed to a number of threats, including direct human disturbance, anthropogenic noise, pollution and collisions with vessels. The latter represents a considerable source of concern in the study area (Laist *et al.*, 2001), due to the large and increasing number of ferries and commercial ships crossing the waters of the Ligurian Sea Sanctuary daily. Evidence of collisions has been reported both for stranded and free-ranging fin whales (data not shown), presenting high percentages of specimens struck by ships. The marked offshore distribution displayed by fin whales in the Ligurian Sea may serve to encourage, insofar as it is possible, the adoption of shipping lanes closer to coasts, thus reducing commercial traffic volume in offshore waters. Cetacean distributional differences throughout the study area should be further investigated to clearly determine whether zones of lower density exist, where ship crossings should occur to minimise their impact.

Throughout the study period 29 immature individuals (3% of the total) smaller than 15m were sighted. These whales were never seen alone, but always associated with at least one individual >16m, most likely representing a cow-calf association; nevertheless, given the difficulty in estimating length at sea, caution should be taken when dealing with these measurements. These data show that, even with a seasonal peak in births between September and January (Viale, 1985), Mediterranean fin whales may have adapted to the Mediterranean environment −which guarantees prey availability throughout the year and warm waters −by extending and overlapping both their calving and feeding seasons (Notarbartolo di Sciara *et al.*, 2003). Moreover, the observed immature individuals in the Pelagos Sanctuary during the summer months may also indicate that fin whales remain in the area year-round, suggesting that this area could represent also a significant breeding ground for them (Orsi Relini, 2000). This hypothesis is supported by the major peak in *M. norvegica* abundance described in the Ligurian Sea during January/February (Sardou *et al.*, 1996). Additionally, recent acoustic data, collected during autumn in the Corso-Ligurian Basin, confirmed the presence of vocally active fin whales during this period (Clark *et al.*, 2002), and analyses in progress of the same data set seem to demonstrate that fin whales are also present in the Western Ligurian Sea in winter and spring (Fabrizio Borsani, unpublished data).

ACKNOWLEDGEMENTS

Many people helped in the data collection throughout the years, and we are grateful to all of them. We would like to thank the captains of the boats we used for the data collection, in particular Giorgio Barbaccia and Ignazio Cavarretta. Our thanks go to the International Fund for Animal Welfare (IFAW), who provided the Logger Software, which was used for data logging during the cruises. Special gratitude goes to Portosole San Remo, for the continuous hospitality for our boats and especially to the memory of P.F. Gavagnin, who enthusiastically supported and followed our studies. Monique McKenzie provided valuable statistical inputs and support, which was greatly appreciated. We are also thankful to Ana Cañadas who was always available for help and support. We are thankful to Roberto Gramolini for his invaluable help with the GIS software and for the development of CR Tools. Giovanni Bearzi (Tethys Research Institute, Milan, Italy), Phil Clapham (Northeast Fisheries Science Center, Woods Hole, USA) and Sascha Hooker (Sea Mammal Research Unit, St. Andrews, UK) provided useful comments on earlier versions of the manuscript. Finally, we are particularly thankful to Phil Hammond (Sea Mammal Research Unit, St. Andrews, UK) who has provided valuable comments and continuous suggestions for the improvement of this manuscript. Funding for preliminary data analyses was provided by Saclant Undersea Research Centre, La Spezia, Italy. This research has been partly supported by a Marie Curie Fellowship of the European Community programme Quality of Life under contract number QLK5-CT-2002-51634. We would also like to thank Thorvaldur Gunnlaugsson and an anonymous reviewer for useful comments on the manuscript.

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Date Received: April 2004
Date Accepted: December 2004

J. CETACEAN RES. MANAGE. 7(2):147–152, 2005

Post-mortem stability of blubber retinoids in by-caught harbour porpoises (*Phocoena phocoena*): implications for the design of biomarker studies

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ABSTRACT

The effect of post-mortem time (0-48 hours) on retinoid concentrations in the blubber and liver of harbour porpoises under natural conditions is investigated to assess the stability of samples collected from animals after death. Organochlorine compounds and lipid content were also determined to assess their potential effects on retinoid status. Organochlorine concentrations remained low throughout the post-mortem period and were considered unlikely to influence retinoid body dynamics. Retinoid concentrations in liver were 5-6 times higher than those in blubber and both were highly correlated. In contrast with liver, blubber can be easily sampled from live individuals using non-destructive biopsy techniques and is therefore considered an alternative tissue to assess retinoid status in marine mammals. Neither significant differences nor trends were detected in the concentration of retinoids over the studied period, indicating that degradation agents (ultraviolet rays, oxygen exposure and heat) did not affect them. Blubber can thus be regarded as a reliable tissue for the assessment of the retinoid status of unpreserved specimens kept up to 48 hours in conditions similar to those of this study.

KEYWORDS: HARBOUR PORPOISE; ORGANOCHLORINES; INCIDENTAL CATCHES; BIOMARKERS; POLLUTANTS; BIOCHEMISTRY

INTRODUCTION

Retinoids comprise both natural molecules with vitamin A activity and synthetic analogues of retinol with or without biological activity (Blomhoff *et al.*, 1992). They are essential in a number of biological processes including vision, reproduction, growth, immune function, differentiation, embryonic development and general health maintenance (Blomhoff, 1994). Organochlorine compounds are known to alter metabolism and the accumulation of retinoids in the body (Brouwer *et al.*, 1989; Chu *et al.*, 1995; 1998; Rolland, 2000; Käkelä *et al.*, 2002; Nyman *et al.*, 2003), although the level at which this effect takes place may be species-specific (Håkansson *et al.*, 1991; Zile, 1992). In general, it is observed that exposure to polychlorinated biphenyls (PCBs), dioxin (TCDDs) and dichloro-diphenyl-trichloroethanes (DDTs) leads to depletion of retinoid reserves in mammalian tissues due to increased mobilisation of retinoids from storage sites, especially the liver and a subsequent increase in their degradation rate (Kelley *et al.*, 1998). Because of the sensitivity of retinoids to organochlorines, they have been proposed as biomarkers of the impact of this group of pollutants (Simms and Ross, 2000; Borrell *et al.*, 2002).

In mammals, retinoids are mainly stored in the liver (Blomhoff, 1994) and thus their body status is commonly assessed through determination of hepatic concentrations (Schweigert and Buchholz, 1995; Käkelä *et al.*, 2002). However, retinoids are lipophilic and they also accumulate in other fatty tissues. Marine mammals have a thick, extremely lipid-rich hypodermis, commonly known as blubber that acts as a thermoregulatory barrier and reserve depot. Blubber is the largest body fat compartment and represents a significant proportion of body mass: approximately 40% in pinnipeds (Schweigert *et al.*, 1987) and 15-45% in cetaceans (Aguilar *et al.*, 1999; Tornero *et al.*, 2004a). Therefore, it is an important body site for retinoid deposition in this group of animals (Schweigert *et al.*, 1987; Mos and Ross, 2002; Tornero *et al.*, 2004a; Tornero *et al.*, 2004b).

Retinoids are unstable compounds with extreme sensitivity to light, oxygen, trace metals, strong acids and excess heat (Blomhoff, 1994; Barua and Furr, 1998). Therefore, the appropriate conditions for the storage and treatment of samples can only be decided after conducting stability studies under controlled field and laboratory conditions. Earlier data suggest that samples must be kept frozen and shielded from light to prevent retinoid oxidation and/or isomerisation (Kishi *et al.*, 1981; Driskell *et al.*, 1985; Comstock *et al.*, 1993; Tanumihardjo *et al.*, 1996; Albalá-Hurtado *et al.*, 2000a; Gatti *et al.*, 2000; Dupertuis *et al.*, 2002). However, no information is available on the stability of retinoids during the time period from death to sample collection.

Bycaught cetaceans are a good source of samples for ecological studies because compared with those found stranded, they are relatively fresh and are representative of the overall population. Thus, they are expected to be neither affected by severe disease nor emaciated, which are common conditions in specimens washed ashore. Moreover, bycaught cetaceans provide biological data and allow the examination of tissues and organs, which are used to determine the main biological traits (age, sex, reproductive condition) and assess their toxicological status. However, in field conditions, a long interval of time between death and sample collection is often unavoidable. Tissue retinoid levels may vary owing to physiological alterations and breakdown. The quantitative determination of these changes

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is essential to calibrate the effect of post-mortem time on retinoid tissue concentrations and thus assess the validity of bycatches as a source of samples for evaluating retinoid status.

The harbour porpoise (*Phocoena phocoena*) is one of the most vulnerable cetaceans to incidental capture in fishing gear, particularly in the North Atlantic (e.g. Donovan, 1994), thus allowing samples to be readily obtained from a relatively large number of individuals. Taking advantage of this and also because this species inhabits waters ranging from pristine to highly polluted, the harbour porpoise was selected with the bottlenose dolphin (*Tursiops truncatus*) as target species for the International Whaling Commission's (IWC) POLLUTION 2000+ programme, an initiative that aims to elucidate pollutant cause-effect relationships in cetaceans (Reijnders *et al.*, 1999; Reijnders *et al.*, 2002). A first step in this project is the design and validation of sampling protocols. A previous paper (Borrell *et al.*, 2002), reviewed overall information on retinoids in cetaceans and the use of these compounds as biomarkers of organochlorine exposure in this group of animals. The objective of the present study, which is part of the IWC POLLUTION 2000+ project, is to calibrate the effect of post-mortem time on retinoid concentrations in the blubber and liver of harbour porpoises to assess the reliability of samples collected from dead animals. To our knowledge, this is the first time such a study has been undertaken for any cetacean.

Organochlorine compounds and lipid content were concurrently determined to evaluate their potential effect on the retinoid status of the sampled individuals. The correlation between blubber and liver retinoid concentrations was also investigated to determine whether the former is a reliable alternative for monitoring retinoids in this species.

MATERIAL AND METHODS

Sample collection

Six freshly by-caught harbour porpoises (5 males and 1 female) of known time of death were examined during the summer of 2001 in the weir fishery in Grand Manan, Bay of Fundy (Canada). They were measured and sexed, and a series of samples were collected from them with the objective of creating sequential replicates of each of the main tissues. Tissue collection, time intervals and preservation conditions followed the methods described in the 'Field Protocol for POLLUTION 2000+' (Reijnders *et al.*, 2002). Thus, an initial blubber sample was collected immediately following death. To mimic natural conditions, animals were then placed in a tank, at a depth of 2m underwater, and suspended beside the dock. Blubber was periodically re-sampled at 3, 9, 24 and 48 hours. Liver samples were not collected at all timepoints to maintain the integrity of the carcasses but, in all animals, a liver sample was collected at 48 hours. Water and carcass temperatures were monitored throughout the holding period. Carcass temperatures were measured using a needle temperature probe. After excision, samples were immediately wrapped in aluminium foil and stored at –20°C until analysis, a temperature at which retinoids in plasma and tissues are known to be stable for up to 10 years (Thomas *et al.*, 1998; Barua and Furr, 1998).

Retinoid analysis

Samples, analysed in triplicate, were treated at room temperature and under red light. The replicates, weighing about 100mg each, were saponified overnight in an ethanolic KOH solution (1g KOH, 2ml distilled H_20, 2ml ethanol, 20mg ascorbic acid) under nitrogen in a mechanical shaker. Retinoids were extracted by adding 8ml di-isopropyl ether and shaking for 30min. After separation from the aqueous phase, the organic extract was cleaned three times with 4ml of aqueous phosphate buffer (pH 7.4) [$KH_2PO_4 10^{-2}M/KOH6^{*}10^{-3}M$]. The extract was dried under nitrogen and reconstituted with 1ml methanol, 0.05% butylated hydroxy toluene (BHT) as an antioxidant and retinyl acetate as an internal standard. Reconstituted samples were filtered (0.20μm mesh) and a 20μl subsample was automatically injected (Waters 700 Satellite wisp) onto a high performance liquid Chromatography (HPLC) system (Waters 600 E System Controller Pump) equipped with a Restek column (Tracer Excel 120 ODS-A, 10cm length, 5μm bed, 0.46cm internal diameter) and a UV detector (Waters 486 Tuneable absorbance D) set at 326nm. Retinoids were eluted at a flow rate of 1ml min^{-1} using a mobile phase of methanol/water (80/20 V/V) for 1min followed by a linear gradient over 3min to 100% methanol. The column was then cleaned and equilibrated with 100% methanol for 14min at the same flow rate.

Organochlorine pollutant analysis

Lipids were extracted from blubber (samples weighing 0.2-1g) using n-hexane in Soxhlet apparatus, and lipid content was determined gravimetrically. Analysis of organochlorine compounds was carried out using capillary gas chromatography-electroncapture detector (GC-ECD) and following the procedures described by Borrell *et al.* (2001). The samples were analysed for the following compounds: HCB, α-HCH, β-HCH, γ-HCH, *pp'*-DDE, *op'*-DDE, *pp'*-DDD, *op'*-DDT, *pp'*-DDT and PCBs. Total hexachlorocyclohexane (tHCH) was the sum of all three isomers (α,β,γ). tDDT concentration was calculated as the sum of the five DDT compounds and total PCB concentration (tPCB) as the sum of 22 individual peaks (IUPAC number 28, 52, 95, 101, 151, 149, 118, 153, 105, 138, 187, 183, 128, 174, 156, 180, 170, 201, 195, 194, 206, and 209). Recoveries of organochlorine compounds ranged from 82-101% (n=12). The laboratory participated in interlaboratory calibration exercises for OCs in biota organised by Quasimeme (1998) and NIST/NOAA (2000 and 2003), obtaining fitting results.

Statistical analysis

The correlation between retinoid concentrations in liver (collected at 48h post-mortem) and blubber (mean of all blubber samples) was analysed by correlation/regression analysis. To compensate for the undesired variability between individuals, the analytical results of retinoids from each porpoise were standardised by calculating the proportion that the concentration at each timepoint (mean of the three replicates) represented in relation to the mean concentration of all timepoints (mean of the 15 replicates: three replicates × five timepoints). The proportions obtained by this method were used in the statistical comparisons. Data were tested for normality by a Kolmogorov-Smirnov test of goodness of fit. As the data distributed normally, differences in retinoid and pollutant levels were determined using analysis of variance (ANOVA) followed by the Tukey *t*-test to identify distinct sample pairs at $p<0.05$. The standardised retinoid values were also analysed for potential time trends using correlation/regression analysis. All calculations were carried out using the SPSS-x statistical package.

RESULTS AND DISCUSSION

Table 1 shows the biological characteristics of the sampled porpoises. The POLLUTION 2000+ field protocols (Reijnders *et al.*, 2002) require collection of tissues immediately after the porpoise's death and impose very strict sampling procedures. Proper protocol validation required adjustment to these conditions, and this made field sampling extremely laborious and demanding (see above in 'Sample Collection' section). As a consequence, the number of specimens studied was necessarily limited, though considered sufficient for the study.

Table 1

Sex, body length (cm), blubber lipid content (BLC) (%), and blubber pollutant concentrations of the harbour porpoises studied. Concentrations are determined at several times (hours) after death of the individuals and expressed as μg/g calculated on the basis of the lipids extracted.

ID code	Sex	Body length	BLC	Post-mortem time	tHCH	HCB	tPCB	tDDT
69	M	139	85.07	24	0.12	0.12	4.62	2.27
				48	0.13	0.14	5.45	3.18
84	M	119	80.15	0	0.15	0.11	5.33	2.69
				48	0.14	0.10	4.71	2.44
85	M	126	56.41	24	0.08	0.10	3.13	1.79
				48	0.09	0.09	3.92	1.88
184	M	109	80.62	0	0.10	0.10	3.85	1.67
				48	0.14	0.12	5.42	2.47
191	M	129	69.58	0	0.11	0.10	5.42	2.95
				48	0.10	0.11	4.98	2.65
199	F	150	77.81	0	0.09	0.04	4.76	2.00
				48	0.11	0.06	5.35	2.61

The sex ratio of the animals studied was skewed towards males. However, this was not considered to affect the calibration study because the harbour porpoise does not present significant sexual dimorphism either in body size or in any other anatomical trait that could affect retinoid decomposition. For example, the body surface area to volume ratio, which would affect thermal inertia of internal tissues after death and thus retinoid decomposition rates, is comparable in both sexes. Confirming this, the rate of decrease in the internal temperature of the only female sampled was not significantly different ($p>0.3$) to that of the males. Also, previous studies have showed that retinoid loads in harbour porpoises of comparable ages are also similar in both sexes (Borrell *et al.*, 2002).

The blubber lipid content ranged 56.41-85.07%, suggesting that sampled individuals were overall in good nutritive condition (Lockyer, 1995). The results of the blubber organochlorine analyses are also presented in Table 1. The concentrations of all compounds were higher than those found in harbour porpoises from Greenland (Borrell *et al.*, 1999; Bruhn *et al.*, 1999), of the same order of magnitude as those from Ireland (Smyth *et al.*, 2000), and lower than those from the Baltic Sea (Kannan *et al.*, 1993; Berggren *et al.*, 1999), the North Sea (Wells *et al.*, 1994), Denmark (Berggren *et al.*, 1999) and the United Kingdom (Law, 1994). As compared to studies carried out in the same population in 1989-1991, current organochlorine levels are significantly (approximately four times) lower (Tilbury *et al.*, 1997; Westgate *et al.*, 1997), in agreement with the trend of decreasing organochlorine pollution observed in most temperate regions of the Northern Hemisphere during the last decade (Aguilar *et al.*, 2002). The low concentrations found in this study seem unlikely to have influenced the retinoid dynamics of the porpoises studied. As expected, organochlorine concentrations in blubber did not vary during the 48 hour post-mortem period ($p>0.05$).

Table 2 shows the retinoid concentrations found in the blubber and liver of the specimens studied. Blubber concentrations varied widely between individuals, ranging from 42.6-224μg g^{-1}. These values were slightly higher than those reported in the same tissue in other cetaceans, such as harbour porpoises from West Greenland (Borrell *et al.*, 1999) and common dolphins (*Delphinus delphis*) (Tornero *et al.*, 2004a; b). Liver concentrations were, as expected, very high (131-1680μg g^{-1}) and similar to the highest values recorded in cetaceans, e.g. blue whales (*Balaenoptera musculus*), fin whales (*B. physalus*) and sperm whales (*Physeter macrocephalus*) (Schmidt-Nielsen *et al.*, 1934; Klem, 1935; Braekkan, 1948; Schweigert *et al.*, 1987).

Table 2

Blubber retinoid concentrations (0, 3, 9, 24 and 48 hour post-mortem replicates: mean ± SD) and liver retinoid concentrations (48 hour post-mortem replicates: mean ± SD) in the harbour porpoises studied. Concentrations are expressed as μg/g tissue.

Identification code	*n*	Blubber	*n*	Liver
69	15	140.04 ± 41.12	3	877.83 ± 88.82
84	15	74.23 ± 15.98	3	575.91 ± 118.95
85	12	103.10 ± 26.00	3	170.98 ± 25.27
184	15	42.60 ± 10.46	3	252.21 ± 10.57
191	15	224.03 ± 42.64	3	1,679.46 ± 643.92
199	14	88.26 ± 19.70	3	131.24 ± 52.59

As mentioned above, liver was only sampled at the 48 hour timepoint in order to preserve the integrity of the carcass. Given the absence of trends in blubber retinoid levels, it is assumed that liver was similarly unaffected by post-mortem times. Liver retinoid levels were approximately 5-6 times higher than those in the blubber. Similar studies on marine mammals have also described higher retinoid concentrations in liver than in blubber: more than 10 times higher in adult males and juveniles of grey seals (*Halichoerus grypus*) (Schweigert *et al.*, 1987), 7-8 times higher in ringed seals (*Phoca hispida*) (Käkëla *et al.*, 1997), eight times higher in precocious harbour seals (*Phoca vitulina*) (Mos and Ross, 2002) and approximately three times higher in common dolphins (Tornero *et al.*, 2004a; b).

Retinoid concentrations in blubber and liver were positively correlated (Fig. 1; $p<0.05$, $R^2=0.8$), suggesting that retinoid deposition in both tissues is subject to similar processes. This result concurs with that of Mos and Ross (2002), who reported a similar correlation in harbour seals. Therefore, both liver and blubber are equally reliable tissues for monitoring body retinoid status in these animals. However, access to the liver is not possible in free-ranging individuals, and the tissue decomposes rapidly post–mortem, so liver is in most cases an unsuitable tissue to monitor. As blubber can be easily sampled from both free-ranging and captured individuals using non-destructive biopsy techniques (Aguilar and Borrell, 1994), it is a reliable alternative to assess the retinoid status of marine mammals.

Fig. 2 shows the variation of the mean temperature of carcasses and seawater at various timepoints during the 48 hour post-mortem period. Holding water temperature ranged from 11.1-14.5°C (mean: 12.9°C). Carcass internal temperatures decreased drastically from the moment of

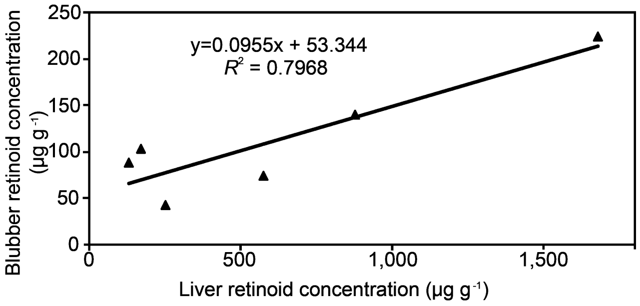

Fig. 1. Correlation between liver and blubber retinoid concentrations (µg g^{-1} tissue).

death (35.4-36.6°C) to the 48 hours timepoint (12.0-12.4°C). Fig. 3 shows the mean relative retinoid blubber concentrations at each sampling time in each studied individual. We did not find significant differences or trends in the concentration of retinoids over the studied period, neither in the ANOVA nor in the correlation/regression analyses (p>0.05). This indicates that the potential degradation agents did not affect blubber retinoid levels.

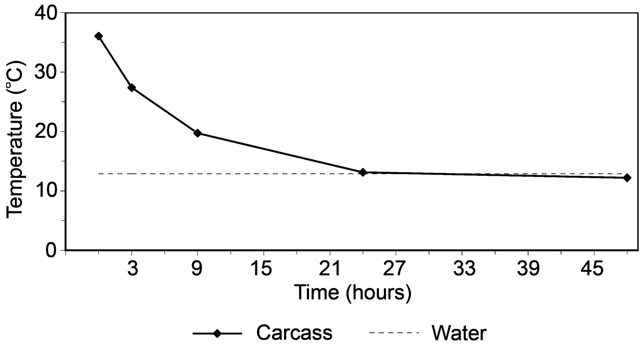

Fig. 2. Means of seawater and carcass temperatures at each sampling time: 0, 3, 9, 24 and 48h.

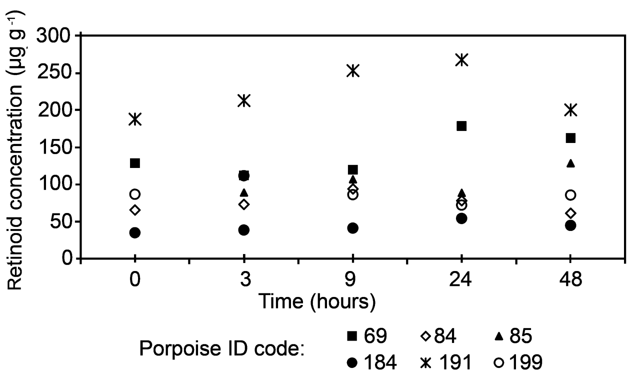

Fig. 3. Blubber retinoid concentrations at the different sampling times (0, 3, 9, 24 and 48h) in each harbour porpoise.

Three main agents have been reported to influence retinoid levels: ultraviolet (UV) rays, oxygen and heat. Although no information is available on the physicochemical stability of retinoids contained within the cellular structure of a tissue, direct exposure to the UV rays present in sunlight causes severe degradation of retinoids (Allwood and Plane, 1984; Chen *et al.*, 1996; Gatti *et al.*, 2000). Here, the skin cover apparently provided an effective barrier to UV penetration into the carcass. However, it should be noted that the corpse was kept 2m below the water surface and that the seawater in the Bay of Fundy is quite opaque owing to strong tidal mixing coupled with ample sediment sources. Thus, sunlight exposure at timepoints was strongly mitigated by the prevailing environmental conditions. From the moment of tissue collection to analysis at the laboratory, samples were protected from light by wrapping with aluminium foil and deep freezing, thus avoiding the effect of UV rays.

Exposure to oxygen also induces the loss of retinoids (Le Maguer and Jackson, 1983; McCarthy *et al.*, 1986). In previous studies, oxidative degradation had been prevented through special handling and preservation procedures, including storage under nitrogen or argon and addition of antioxidants like ascorbic acid or butylated hydroxy-toluene (BHT) (Wyss, 1990). Anoxia in the corpse occurs within hours of death and as a consequence, oxygen degradation did not appear to affect retinoid tissue concentrations before sampling. When the specimen was retrieved, the samples were quickly wrapped in aluminium foil to avoid dehydration and prevent direct exposure to the atmosphere; the analysis was performed under nitrogen and BHT was added. These precautions were sufficient to prevent retinoid oxidation.

Finally, the temperature of seawater also seemed to be sufficiently low to ensure the stability of retinoids during the study period. This is in agreement with previous studies reporting the stability of retinoids during storage in the dark at 2-8°C (Gatti *et al.*, 2000; Sforzini *et al.*, 2001), at room temperature (Nierenberg, 1985; Halbaut *et al.*, 1997; Albalá-Hurtado *et al.*, 2000b; Gatti *et al.*, 2000) and even at 20-40°C (Albalá-Hurtado *et al.*, 2000b; Sforzini *et al.*, 2001; Dupertuis *et al.*, 2002). In contrast, Sforzini *et al.* (2001) found high instability at room temperature, Chen *et al.* (1996) at 4, 25 and 35°C, and Halbaut *et al.* (1997) at 30°C. At higher temperatures, numerous authors have described considerable losses of retinoid content: the higher the temperature, the greater the loss (Albalá-Hurtado *et al.*, 2000a; Gatti *et al.*, 2000). Retinoid loss depends on the chemical nature of both the retinoids and the other species present in the sample (Albalá-Hurtado *et al.*, 2000a). The variable amount of molecular oxygen, the fat protective effect, and the possible synergetic effect between retinoids and other components, such as tocopherols, ascorbic acid and lipids, may account for the differences between authors' results (Billion-Rey *et al.*, 1992; Albalá-Hurtado *et al.*, 2000b; Dupertuis *et al.*, 2002). The protein-bound retinoids and the richness in natural antioxidants (Barua and Furr, 1998), as well as the high lipid content of cetacean blubber, 35-90% (Lockyer *et al.*, 1985; Aguilar and Borrell, 1990; Lockyer, 1991; 1993; 1995), may also have contributed to the stability of the retinoids.

We can conclude that, in the conditions of this study, retinoids remain stable at least during a 48 hour post-mortem period and, more generally, that retinoids are present in the blubber of harbour porpoises in such a state that they are not easily affected by degradation. As a consequence, blubber can be considered a reliable tissue for the assessment of the retinoid status of unpreserved specimens during periods and in conditions similar to those reported here. There are no grounds to extend this conclusion to longer periods, higher environmental temperatures or specimens of different body size. This is critical for the use of stranded individuals because corpses are often found over 48 hours post-mortem, directly exposed to sunlight and may have been subjected to temperature rises due to sun irradiation. As a consequence, the current protocol validation should not be unreservedly extended to stranded individuals. Given that this is the only attempt to calibrate sampling protocols so far undertaken for a cetacean species, further comparable studies are required to determine the actual range of conditions acceptable for retinoid monitoring in these animals.

ACKNOWLEDGEMENTS

This study was carried out as a part of the International Whaling Commission POLLUTION 2000+ programme. We are grateful to Teri Rowles, Arne Bjørge, Randy Wells, Todd O'Hara and Greg Donovan for comments and general support through the development of the project. V. Tornero was supported by a FPI fellowship from the Generalitat de Catalunya, and A. Borrell by a contract under the 'Ramón y Cajal' Program. Field and laboratory work was funded by the International Whaling Commission under the POLLUTION 2000+ project and the Fundació pel Desenvolupament Sostenible (FDS).

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Date Received: July 2004
Date Accepted: April 2005

Seasonal distribution and relative abundance of bottlenose dolphins, *Tursiops truncatus*, along the US mid-Atlantic Coast

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ABSTRACT

In the US mid-Atlantic, multi-disciplinary studies are underway to elucidate the complex stock structure of coastal bottlenose dolphins (*Tursiops truncatus*), as well as the degree of overlap between coastal and offshore ecotypes. In this study we use geo-referenced data, collected during aerial surveys in 2000-2002, to describe the distribution and relative abundance of bottlenose dolphins along the US mid-Atlantic coast. Two aerial survey designs were used: (1) onshore/offshore surveys out to 35 n.miles during winter from Georgia to Virginia; and (2) coastal surveys throughout the year along North Carolina (NC). The winter onshore/offshore surveys demonstrated that significantly more bottlenose dolphins occur in Raleigh Bay (between Cape Hatteras and Cape Lookout, NC), than in all other regions. Additionally, in winter most bottlenose dolphins occur in the coastal waters of NC; nearly half of all sightings occurred between the shoreline and 3km from shore. The year-round, coastal surveys demonstrated that this winter distribution pattern is the result of a distinct seasonal increase in the number of dolphins within the coastal waters of NC. Circular statistical analyses demonstrated a strong influence of season on dolphin abundance. Relatively few bottlenose dolphins were observed in late spring, summer, and early autumn, with increased numbers observed during winter. In all seasons but summer, dolphin numbers were highest in Raleigh Bay. Thus, the results of both surveys indicate the importance of the habitat surrounding Cape Hatteras to bottlenose dolphins. Dolphins may preferentially use these waters in response to changes in prey distribution and/or abiotic factors such as water temperature. These results reveal an overall seasonal movement pattern along the US Atlantic coast, which appears to be correlated, at least in part, to water temperature gradients and prey availability. Although the stock identity of dolphins sighted during these aerial surveys could not be ascertained, focused photo-identification efforts, together with enhanced genetic sampling, would provide insights into the movement patterns, and, thus, stock identity, of dolphins in this region.

KEYWORDS: BOTTLENOSE DOLPHIN; MANAGEMENT PROCEDURE; CONSERVATION; SURVEY–AERIAL; DISTRIBUTION; MOVEMENTS; ATLANTIC OCEAN; SITE FIDELITY; FOOD/PREY

INTRODUCTION

Coastal bottlenose dolphins (*Tursiops truncatus*) were the target of a directed drive fishery along the US mid-Atlantic coast from the late 1700s through the 1920s (Mead, 1975; Mitchell, 1975; Leatherwood and Reeves, 1982; Reeves and Read, 2003). These dolphins experienced a large-scale epizootic in 1987-88 (Geraci, 1989; Duignan *et al.*, 1996; McLellan *et al.*, 2002) and currently experience rates of fisheries bycatch that exceed their allowable removal levels (Waring *et al.*, 2002). Because of these impacts, coastal bottlenose dolphins in the mid-Atlantic are the focus of an ongoing, multi-disciplinary study to understand their stock structure and enhance their recovery (reviewed in Hohn, 1997). The present study provides insight into the temporal and spatial distribution and relative abundance of bottlenose dolphins along the US mid-Atlantic coast. These data were collected using two aerial survey designs: (1) an onshore/offshore survey out to 35 n.miles during winter from Georgia (GA) to Virginia (VA); and (2) a coastal survey throughout the year along North Carolina (NC).

The first goal of our study was to describe the winter distribution and relative abundance of bottlenose dolphins in US mid-Atlantic and southeastern US waters. In the northwest Atlantic there are two genetically separable and partially sympatric, but visually indistinguishable, populations of bottlenose dolphins. These are the coastal and offshore ecotypes (Hersh and Duffield, 1990; Mead and Potter, 1995; Hoelzel *et al.*, 1998; Torres *et al.*, 2003). Kenney (1990), using seasonal aerial survey data collected from Cape Hatteras, North Carolina (NC), north to the Gulf of Maine, determined that bottlenose dolphins were rarely observed north of Cape Hatteras in winter. Barco *et al.* (1999) demonstrated that dolphins were abundant in summer and absent in winter in the nearshore waters of Virginia Beach, VA. Kenney (1990) postulated that both the coastal and offshore ecotypes 'are seasonally migratory, with much lower abundance and a more southerly sighting distribution in the winter'. Using a 25-year database, McLellan *et al.* (2002) demonstrated that there were seasonal differences in the distribution of bottlenose dolphin strandings along the entire US Atlantic Coast. To date, though, there have been few survey efforts conducted south of Cape Hatteras, NC.

Torres *et al.* (2003), using both sightings and genetic samples collected during summer ship-board surveys, demonstrated that distance from shore and water depth could be used to stratify bottlenose dolphins into coastal and offshore ecotypes in the mid-Atlantic: all dolphins sampled within 7.5km of shore were of the coastal type and all those sampled beyond 34km and in waters deeper than 34m were of the offshore type. Torres *et al.* (2003) also described a 'gray zone' between 7.5 and 34km from shore and in waters less than 34m deep, where there was a dearth of samples of both ecotypes and an overlap between ecotypes. In the present study we use data gathered from recent winter aerial surveys (2000 and 2001) from VA to GA and spatial analytical techniques similar to those of Torres *et al.* (2003), to describe dolphin relative abundance and distribution in relation to distance from shore and depth.

The second goal of this study is to describe seasonal patterns of dolphin relative abundance and distribution in the coastal waters of NC. Dolphins inhabit both estuarine (Jones and Sayigh, 2002; Read *et al.*, 2003b) and coastal waters in NC (Waring *et al.*, 2002). Results of photo-identification studies (Urian *et al.*, 1999) and regional

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surveys (Friedlaender *et al.*, 2001) strongly suggest that seasonal differences in dolphin distribution exist within NC coastal waters. To date, however, no year-round, coast-wide survey data are available to evaluate such differences.

The above mentioned studies offer evidence of: (1) seasonal shifts in abundance and distribution of bottlenose dolphins along the US mid-Atlantic coast; and (2) spatial separation of coastal and offshore ecotypes. By analysing data from two aerial survey methods, our present study builds upon these results and offers a more comprehensive understanding of the spatial and temporal distribution of bottlenose dolphins along the US mid-Atlantic coast.

METHODS

Surveys were conducted in either single or twin-engine, over-wing planes. A Cessna 182 was used for coastal surveys and military versions of the Cessna 337 (O2) for onshore/offshore surveys. These aircraft designs provided high wing visibility, easy manoeuvrability, and retractable landing gear. The offshore flights were flown with additional safety equipment including an emergency position indicating radio beacon (EPIRB), an emergency locating transmitter (ELT), handheld VHF marine radios, a life raft and life vests.

Data collection

Both planes carried at least two global positioning system (GPS) units during each survey. One aviation GPS was used by the pilot to navigate tracklines, while sighting positions were collected and stored on a *Garmin* 12XL GPS with an external antenna. All sighting data were also recorded on data sheets in real time. Sighting locations were downloaded to a computer following surveys with associated sighting data, effort data and photography information. Standard event codes were used to differentiate between sighting events and effort events. The recorder collected data on cloud cover, visibility, Beaufort Sea State (BSS) and glare for each side of the plane on each trackline throughout the survey.

When an animal or group of animals was sighted, time and location on the trackline, species and the maximum, minimum and best estimate of the number of animals sighted were recorded. Observers used 7 × 50 *Fujinon* binoculars to confirm sightings. If large whales or large groups of dolphins were encountered, the track was broken and the plane circled over the sighting, collecting specific sighting locations and identification photographs. Group size was discussed among the observers and resolved to determine the best estimate. After identifying the species, the plane returned to the trackline at the position where it had left and continued the survey. Methodologies specific to each survey type are described below.

Onshore/offshore surveys

The crew for onshore/offshore surveys consisted of a pilot and a data recorder in the front seats and a left and right observer in the rear seats. The rear seat observers were responsible for reporting all animal sightings and shipping traffic. The individual in the co-pilot's seat acted as the data recorder.

The offshore survey area extended from 32°N at Savannah, GA to 37°N at the mouth of the Chesapeake Bay, VA. The tracklines started at the surf line and extended 35 n.miles (64.82km) offshore. In 2001, 76 tracklines were run in the survey area (Fig. 1). Tracklines were spaced parallel to each other at a distance of 4 n.miles apart and ran east to west. Tracklines at Cape Fear, Cape Lookout and Cape Hatteras were extended beyond 35 n.miles (64.82km) to provide additional offshore coverage. To increase coverage in 2002, while limiting tracklines to a length of 35 n.miles, the tracklines were flown at a 45% angle to latitude, in a northwest/southeast direction (Fig. 1). In 2002, the tracklines remained 4 n.miles apart, but 109 lines were flown from GA to VA.

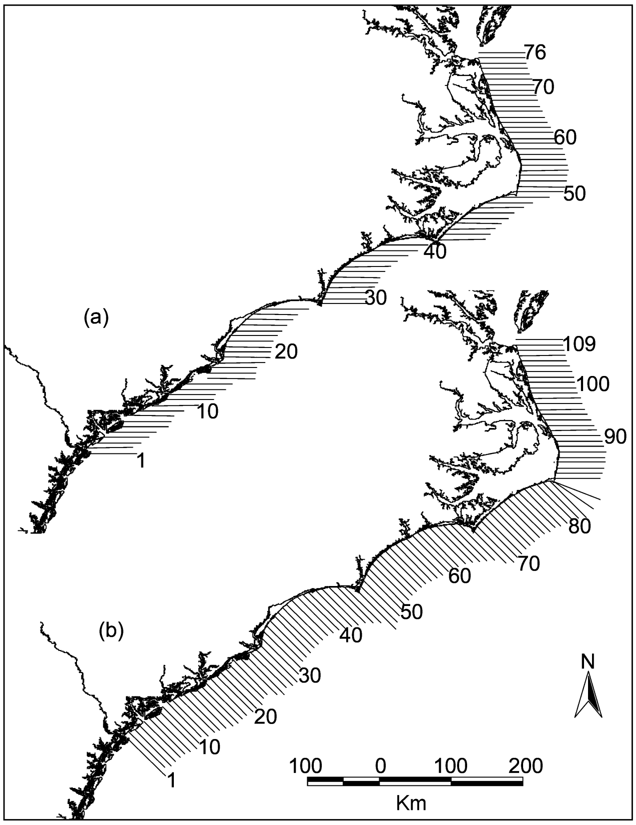

Fig. 1. Onshore/offshore survey tracklines in (a) 2001 and (b) 2002. Numbers denote individual trackline numbers.

The plane flew at 100kts, at a height of 300m. Observers were on-effort only in weather conditions of a BSS of 5 or less to standardise survey effort to optimal weather conditions. Given weather constraints across the geographically large survey area, tracklines were not systematically flown from north to south. Rather, survey effort was focused in areas with favourable weather conditions. Additional constraints were imposed by the necessity to adhere to closures imposed on military controlled airspaces in the nearshore waters of NC and VA and in coordination with the Air Defense Identification Zone (ADIZ). All tracklines were flown at least twice during the survey period, though some were flown as many as four times. However, only the first two surveys of each trackline in each year were used in this analysis, permitting similar effort to be analysed in both years. The offshore surveys were conducted from 6 February to 2 March 2001 and 22 January to 16 March 2002.

Coastal surveys

The coastal surveys were conducted along the NC coast from the South Carolina (SC) border, north to the VA border (See Table 1 for flight dates). The plane flew at 230m and at 100kts at a distance of approximately 500m offshore, parallel to the coastline. The crew for coastal surveys consisted of the pilot and a front seat recorder/observer and one left side rear observer. The plane flew northerly along the coast so that the rear observer monitored from the trackline to the shore while the front seat recorder/observer monitored from the trackline offshore. These surveys were occasionally broken to transit around regions of military activities that required restricted airspace. Due to unplanned military activity and occasional weather limitations, some surveys were terminated before they were completed. Only complete surveys, defined as one full survey of the entire NC coast in one day, were used in this analysis.

Table 1

Dates of coastal surveys, 2000 and 2001, with corresponding information on bottlenose dolphin sightings. The northernmost latitude indicates the latitude of the most northerly dolphin sighting; all surveys terminated at the NC/VA border (approximately latitude 36.6°N).

Date	Number of sightings	Total animals	Northernmost latitude (°N)
23 Feb. 00	46	296	35.9892
1 Mar. 00	92	633	35.6440
1 Apr. 00	63	441	36.0916
6 May 00	70	318	36.5114
9 May 00	12	72	36.5102
26 May 00	61	191	36.6200
1 Jun. 00	42	393	36.3156
17 Jun. 00	8	18	36.2677
22 Jun. 00	3	27	36.5305
30 Jun. 00	25	130	36.5055
3 Jul. 00	7	48	36.5474
15 Aug. 00	24	227	36.4791
19 Aug. 00	3	7	34.4677
20 Sep. 00	23	155	36.5498
4 Oct. 00	34	367	36.4502
13 Oct. 00	102	1,746	36.2160
20 Oct. 00	81	1,118	36.5490
13 Nov. 00	96	861	36.3727
27 Nov. 00	38	191	35.8521
29 Nov. 00	82	27	35.9357
17 Jan. 01	79	664	36.0695
2 Feb. 01	87	1,031	36.2344
23 Mar. 01	84	517	36.2742
20 Apr. 01	103	944	36.5054
14 May 01	52	420	36.5468
30 May 01	22	138	36.3632
12 Jun. 01	26	260	36.5349
19 Jun. 01	40	443	36.542001
26 Jun. 01	56	522	36.5057
16 Jul. 01	41	555	36.5543

Data analysis

Data from the onshore/offshore and coastal surveys were edited and sorted in Microsoft *Excel*. Graphs and figures were generated using Excel and the statistical package *SPSS* for Windows (SPSS Inc.; Version 11.5.0).

ArcGIS (ESRI; Version 8.2) was used to map tracklines and sighting locations from the onshore/offshore surveys. Despite the difference in survey methods used in 2001 and 2002, the same geographic area was covered in both years. Therefore, the mid-Atlantic coast was divided into six regions based on geographically prominent capes, bays or inlets: (1) Oregon Inlet, NC to the NC-VA border; (2) Cape Hatteras, NC to Oregon Inlet, NC; (3) Raleigh Bay; (4) Onslow Bay; (5) Long Bay; (6) south of Long Bay to the GA border (Fig. 2).

Values of depth and distance from shore for each sighting were sampled using *Arc/Info* (ESRI 1999; Version 8.0.1). The bathymetry coverage was created in *Arc/Info* (ESRI 1999; Version 8.0.1) from a combination of grids from the National Geophysical Data Center's Coastal Relief Model and the US Geological Survey's Gulf of Maine Bathymetry, points from the Geophysical Data System for Hydrographic Survey Data, and lines from the General Bathymetric Chart of the Oceans. The bathymetry grid was resampled to an integer grid with a cell size of 500m^2 and projected in *Albers*, assuming a spheroid Clarke 1866 projection. The eastern US coastline was created with data obtained from NOAA's Medium Resolution Digital Vector Shoreline. A 'distance from shore' grid was generated from this coastline coverage using the Euclidean distance to the closest point of land for each location.

Arc/Info was also used to determine the amount of survey effort relative to depth and distance from shore during the onshore/offshore surveys. Each trackline from 2001 and 2002 was buffered 2km on each side, the approximate visual sighting distance during the aerial surveys. These buffered tracks were then converted to grids and used to sample the total area of depth and distance from shore surveyed. These values were converted to square km of effort and used to make histograms of dolphins sighted per unit effort relative to depth and distance from shore.

Bottlenose dolphin group size tends to increase with increased water depth and openness of habitat (reviewed in Shane *et al.*, 1986). Therefore, group size was related to distance from shore using a Kruskal-Wallis non-parametric test.

For analysis of the coastal surveys, seasons were defined as winter (December-February), spring (March-May), summer (June-August), and autumn (September-November). Circular statistics were employed to analyse seasonal trends in relative abundance of bottlenose dolphins along the NC coast (*Oriana* software; Version 2.0; Kovach Computing Services). Unlike conventional linear statistical analysis, circular statistics assume there is no true zero, but rather 360 equal intervals called degrees. This statistical approach is appropriate for detecting seasonal trends in data collected across multiple years (e.g. Thayer *et al.*, 2003; Barlow, 1984). The date of each coastal survey was converted to a Julian day for all 32 complete surveys. Additionally, 31 was added to each Julian date to position the first day of winter at 0° and, thus, make each quadrant of the circular diagram representative of an individual season (see Fig. 3). This dating method made Julian day 1 = December 1 and Julian day 365 = November 30. The Julian date of each survey was then converted to a degree (based on a 360° circle) using the formula: $a = (360°)$ (Julian date) / 365 (366 for surveys in 2000 because it was a leap year) (Zar, 1984). An angular-linear correlation analysis was used to relate season and relative bottlenose dolphin abundance along the NC coast derived from the coastal surveys. The angular variable (date) was correlated with the linear variable (abundance). This correlation coefficient ranges from 0 to 1 and the significance of the correlation is calculated following the methods of Mardia and Jupp (2000).

RESULTS

Onshore/offshore aerial surveys (January-March 2001 and 2002)

Although their distribution was not uniform, a total of 494 sightings of bottlenose dolphins were made throughout the study area during the two winter seasons of onshore/offshore aerial surveys (Fig. 2). When corrected for effort (number of dolphins sighted per km of trackline flown within each region), there were significantly more

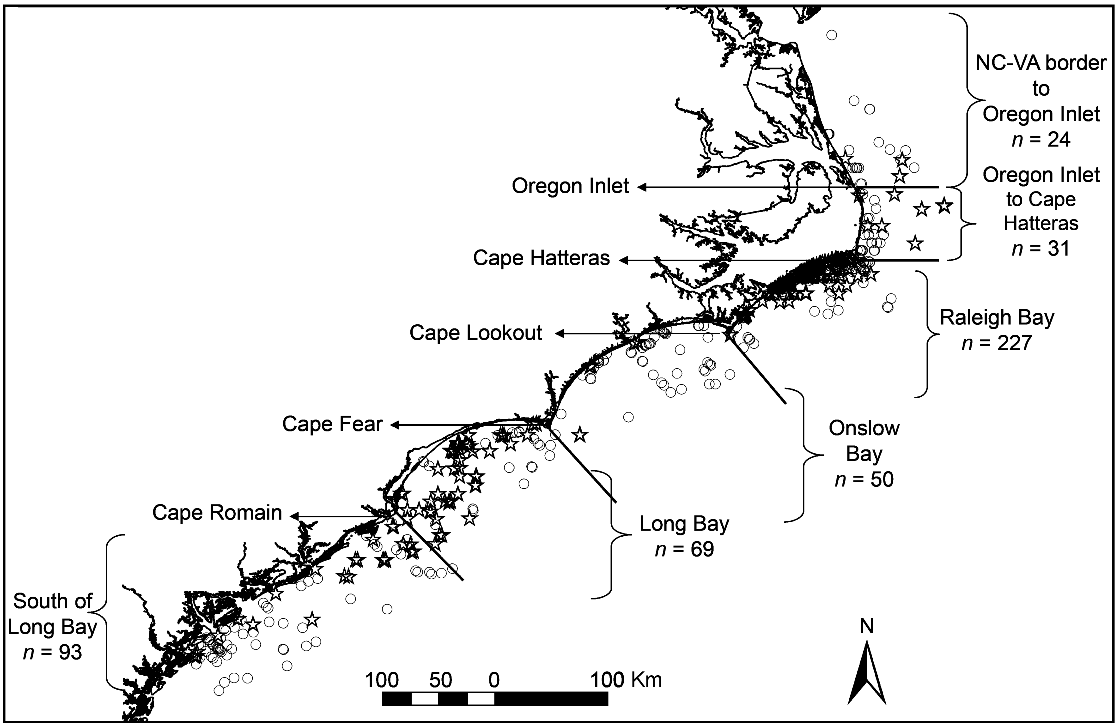

Fig. 2. The US mid-Atlantic coast was divided into six geographic regions based on prominent capes, bays and inlets, for analysis of bottlenose dolphin sightings from onshore/offshore aerial surveys in 2001 and 2002. The open stars indicate 2001 bottlenose dolphin sightings and the open circles indicate 2002 bottlenose dolphin sightings. *n* = total number of sightings within each region from the 2001 and 2002 surveys.

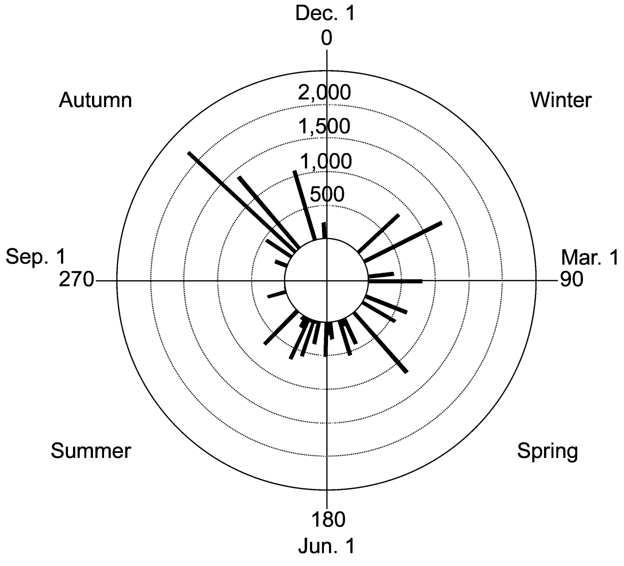

Fig. 3. A two-variable vector plot of all coastal surveys transformed into angles based on Julian date. Each bar corresponds to a single survey. The direction of the bar indicates the date (degree) of the survey, while the length of the bar denotes the total number of bottlenose dolphins counted on that survey. Each ring of the plot indicates the number of dolphins observed.

bottlenose dolphins counted in Raleigh Bay, between Cape Hatteras, NC and Cape Lookout, NC than all other regions (Exact Wilcoxon signed-rank test, V=21, *n*=6, *p*-value=0.0312) (Fig. 4). Nearly 30% of all bottlenose dolphin sightings occurred just south of Cape Hatteras, between 35.00°N and 35.20°N (Fig. 5b). Smaller peaks in sighting frequency occurred south of Cape Fear, south of Cape Romain, and north of Savannah, GA (Fig. 5b). The largest groups, containing more than 40 dolphins, were limited to the areas just south of Cape Hatteras, NC, in Raleigh Bay (14 sightings), and south of Cape Lookout, NC, in Onslow Bay (4 sightings). The four large group sightings in Onslow Bay were all offshore (>34.5km from shore). However, of the 14 sightings in Raleigh Bay, all but two large group sightings were within 2.5km of shore, including a single sighting of 150 individual dolphins 1km from shore. The remaining two large group sightings in Raleigh Bay were at 6 and 13km from shore.

Nearly half (45.7%) of all bottlenose dolphins sighted were within 3km of shore. Furthermore, 30.6% of dolphins were within 2km of shore and 9.3% were within 1km of shore (Fig. 6a). The greatest number of bottlenose dolphins sighted (871 individuals) was between 1 and 2km from shore. Bottlenose dolphins were observed frequently nearshore, but numbers of dolphins observed rapidly decreased beyond 3km of shore, with a slight increase between 34 and 46km. Beyond 46km from shore, very few bottlenose dolphins were sighted aside from a spike at 53km from shore.

There was no relationship between dolphin group size and distance from shore. A Kruskal-Wallis non-parametric test demonstrated that group sizes of sightings between 0-32, 33-46, and 33-64km from shore were similar. Moreover, of the 19 sightings beyond 50km from shore, no pattern of group size was evident.

The relative abundance of bottlenose dolphins in relation to water depth showed a similar trend as distance from shore. Sightings of bottlenose dolphins were most frequent in shallow waters and gradually declined with increasing depth (Fig. 6b). Beyond 10m depth, bottlenose dolphin observations were rare, except for two spikes in occurrence at 37m and between 401-500m. Twenty four percent of bottlenose dolphins were sighted in water less than 4m and nearly half (48.6%) were sighted in water less than 12m. All

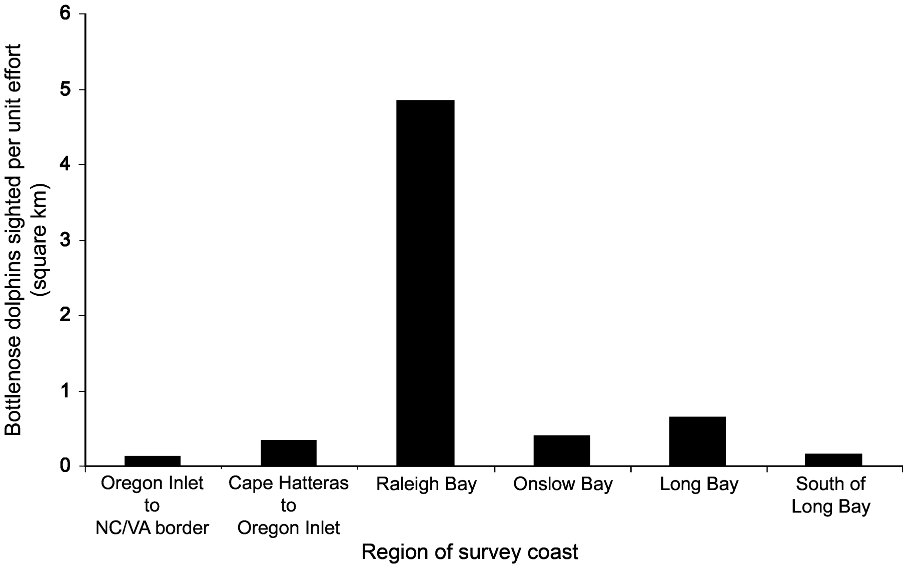

Fig. 4. Frequency of individual bottlenose dolphin observations during 2001 and 2002 onshore/offshore surveys, corrected for survey effort within each region.

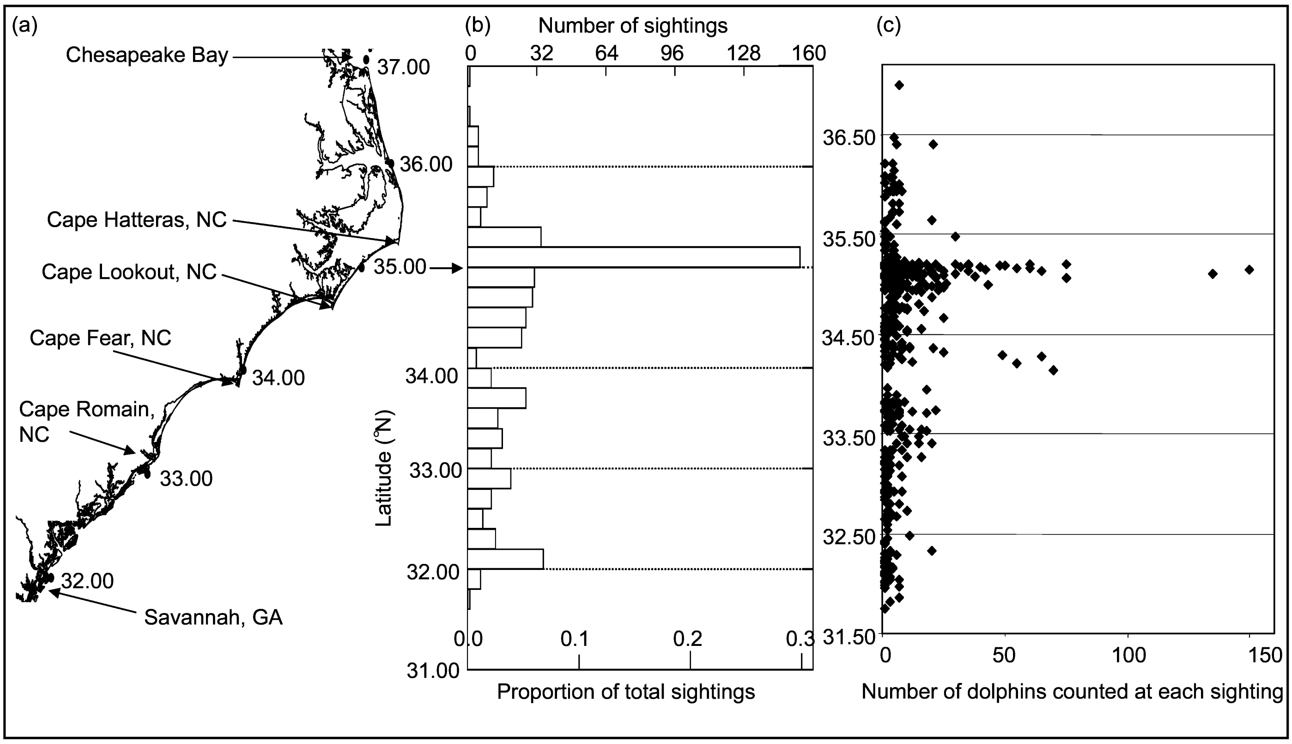

Fig. 5. Bottlenose dolphin sighting distribution from 2001 and 2002 onshore/offshore surveys relative to the coastline. (a) The onshore/offshore survey area for 2001 and 2002 (not to scale). (b) The proportional frequency of sightings by latitude. (c) The spatial frequency of sightings by group size relative to latitude.

17 sightings in water over 45m deep were between 34.81° N and 35.64° N, in offshore waters just north and south of Cape Hatteras, NC.

North Carolina coastal surveys (February 2000 – July 2001)

The onshore/offshore surveys demonstrate that, within the study area, in winter, most mid-Atlantic bottlenose dolphins occur in the coastal waters of NC (Figs 2, 4, 5 and 6). The NC coastal surveys permitted a quantitative description of seasonal patterns of bottlenose dolphin distribution within these nearshore waters.

A total of 5,431 bottlenose dolphins were observed on complete surveys during the two years of NC coastal aerial surveys. The relative abundance of bottlenose dolphins within NC coastal waters varied throughout the year. The circular statistical analysis demonstrated a correlation between dolphin abundance and season (Fig. 3). There was a significant correlation between the Julian date of each survey and total dolphins sighted (angular – linear correlation: r=0.436, p=0.006). Relatively few bottlenose dolphins were observed in late spring, summer, and early autumn (May-August). The greatest numbers of bottlenose dolphins were observed in late-autumn (October/

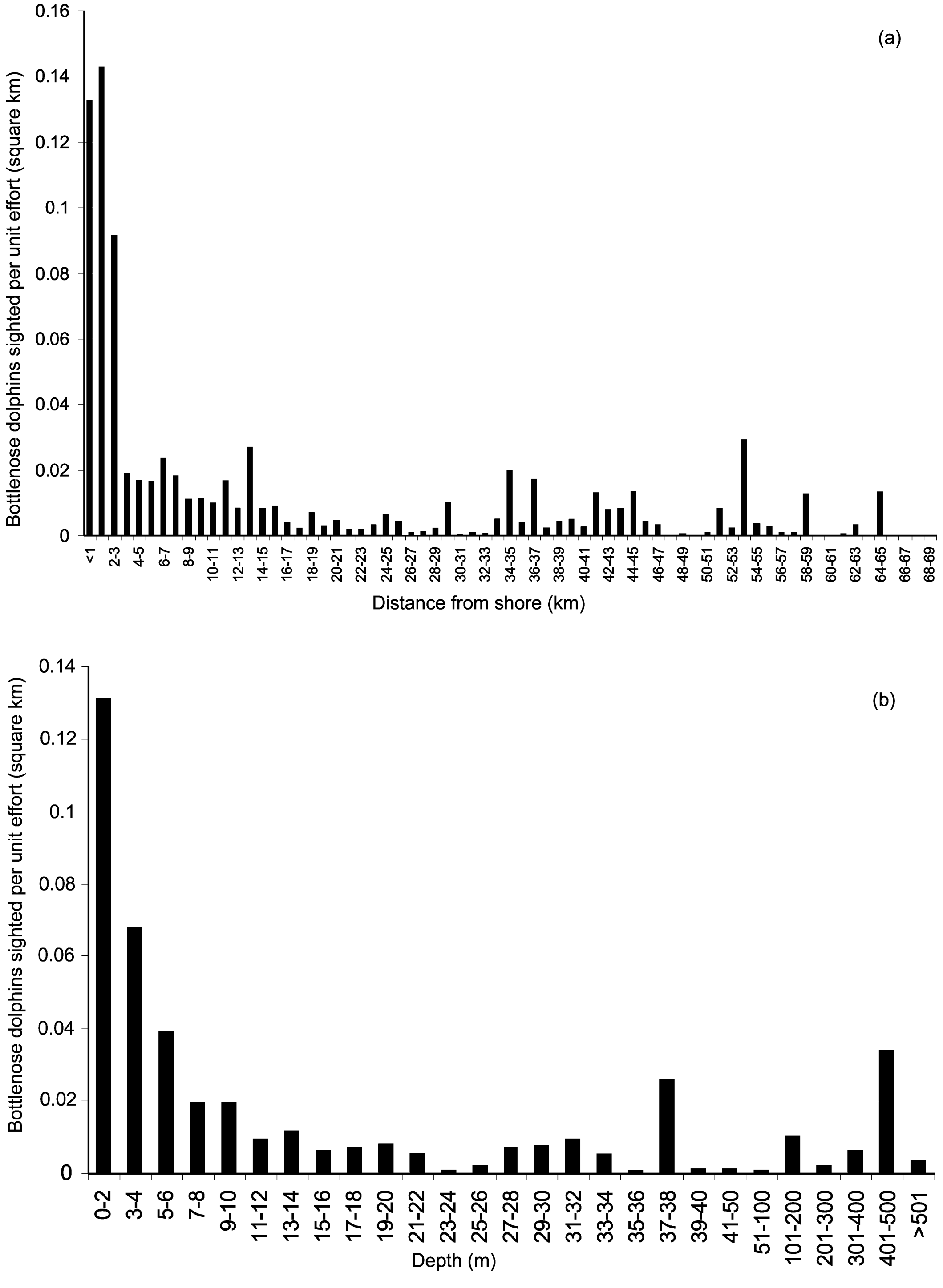

Fig. 6. Frequency of individual bottlenose dolphin observations per unit effort from 2001 and 2002 onshore/offshore surveys relative to distance from shore (a) and depth (b). The amount of survey effort conducted within each depth and distance from shore bin was calculated (see text for methods) in order to make relative sighting frequencies based on effort within each value range.

November). Intermediate numbers of bottlenose dolphins were sighted during the winter and early spring months of January-March.

This temporal fluctuation in relative abundance along the NC coast is also evident in Fig. 7, which spatially describes the seasonal distribution of bottlenose dolphin sightings. In winter, few bottlenose dolphins were sighted north of Cape Hatteras. During this period, bottlenose dolphin numbers were highest in the area just south of Cape Hatteras. In spring, more bottlenose dolphins were sighted north of Cape Hatteras than during winter. In summer, fewer dolphins were sighted than every other season and their distribution along the NC coast was more diffuse. During autumn, bottlenose dolphin sightings again clustered south of Cape Hatteras, with smaller peaks in abundance also observed at Cape Lookout and Cape Fear. In all seasons but summer, dolphin abundance was highest just south of Cape Hatteras.

Additionally, if season is ignored and sightings throughout the year are summed, individual bottlenose dolphin observations were most frequent at Cape Hatteras (Fig. 7, *n* values). A secondary peak in summed relative abundance occurred at Cape Lookout (742 dolphins sighted), and a third, slightly smaller peak at Cape Fear (398 dolphins sighted).

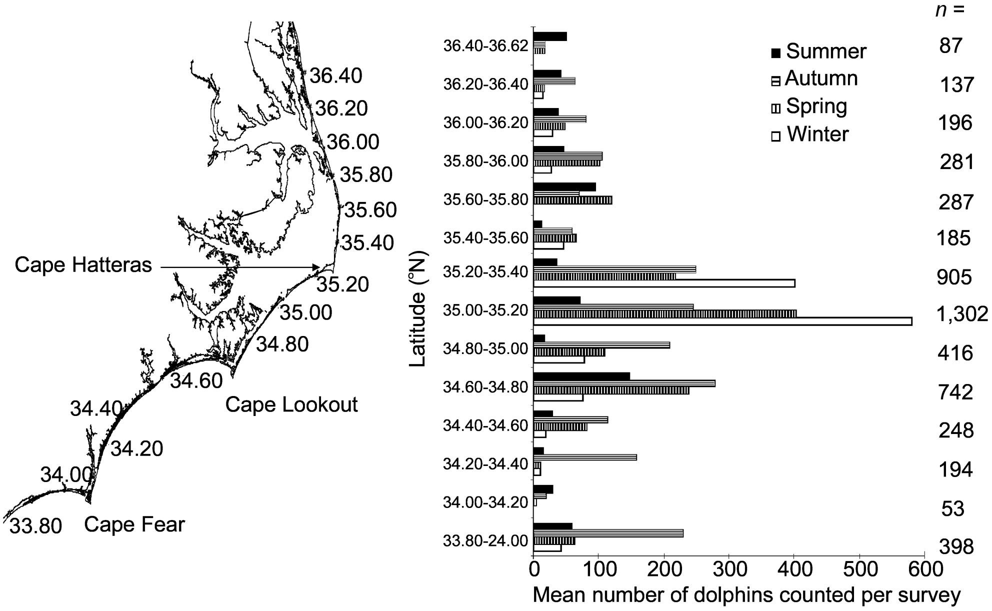

Fig. 7. Histogram of the seasonal distribution of bottlenose dolphins from 2000 and 2001 NC coastal surveys. Latitudinal bins were divided into equal 0.20° intervals. Note distinct peaks in abundance south of Cape Hatteras in all seasons but summer. *n* = number of dolphins observed within each latitudinal bin regardless of season. The NC coast is not drawn to scale.

The northernmost latitude of sightings in January, February and March of both years was further south than in all other months (Table 1). The mean latitude of bottlenose dolphin sightings November-March (late autumn through to early spring) was significantly less than the mean latitude between April-August (mid-spring through to summer) (one-tailed *t*-test: *p*=0.015).

DISCUSSION

This study used geo-referenced data from two complementary aerial surveys to describe the spatial and temporal distribution of bottlenose dolphins along the US mid-Atlantic coast. The onshore/offshore surveys demonstrate that in winter, dolphin abundance is greatest nearshore (<3km) in NC coastal waters, although dolphin abundance is relatively high out to 14km from shore. The coastal surveys demonstrated that dolphin relative abundance and distribution change seasonally in the nearshore waters of NC. Both surveys illustrate that bottlenose dolphin abundance is highest near Cape Hatteras, NC in all seasons except summer, suggesting that this area is an important habitat for bottlenose dolphins in the US mid-Atlantic.

Coupling our results with those of previous studies on bottlenose dolphin distribution north of Cape Hatteras, NC (Kenney, 1990; Barco *et al.*, 1999) reveals an overall seasonal movement pattern along the US Atlantic coast, which is likely correlated, at least in part, to water temperature gradients and prey availability. During the summer months, when water temperatures are relatively warm along the entire US east coast, Kenney (1990) found that bottlenose dolphins are distributed as far north as New Jersey (NJ). As water temperatures decline during the autumn, bottlenose dolphins appear to move south, reducing the frequency of sightings north of Cape Hatteras (Kenney, 1990) and increasing them south of Cape Hatteras (see Figs 3 and 7). When water temperatures decline further in winter, coastal bottlenose dolphins are extremely sparse north of Cape Hatteras, NC and abundant just south of Cape Hatteras. Finally, during the spring, as water temperatures rise, bottlenose dolphins are sighted more frequently north of Cape Hatteras. Thus, Cape Hatteras appears to be an important spatial boundary in the seasonal distribution of bottlenose dolphins along the US mid-Atlantic coast.

Although the stock identity of bottlenose dolphins sighted during these aerial surveys could not be ascertained, collaborative studies are being conducted to elucidate the movement patterns and stock identity of individual dolphins along the mid-Atlantic coast (Urian *et al.*, 1999). For example, in a photo-identification study conducted near Cape Hatteras during February/March 2003, Read *et al.* (2003a) matched individual dolphins from Cape Hatteras to dolphins photographed in the summer in NJ and VA. The results of this photo-identification study demonstrate that dolphins present in NJ during the summer move south to Cape Hatteras in winter. A combination of photo-identification techniques and temporal-spatial distribution analyses may provide further insight into the movement patterns of individual dolphins and, thus, their stocks along the US mid-Atlantic coast.

The onshore/offshore surveys demonstrated that, during winter, most dolphin sightings were within 3km of shore. Relative abundance remained high, though, out to 14km from shore. Because no genetic samples were obtained, we could not identify the dolphins as coastal or offshore ecotypes. However, we can speculate on the distribution patterns of the two ecotypes based on the results of Torres *et al.* (2003). Through spatial analysis of genetic samples of dolphins acquired during summer months, Torres *et al.* (2003) suggested spatial boundaries for each ecotype. All dolphins sampled within 7.5km of shore were of the coastal ecotype, while all those sampled beyond 34km of shore and in water deeper than 34m depth were of the offshore ecotype. Both ecotypes were found between 7.5km and this 34km/34m isoline, an area defined by Torres *et al.* (2003) as the ‘gray zone’. These results suggest that dolphins within 3km of shore, which represent nearly half of all dolphins sighted during the winter onshore/offshore surveys, are of the coastal ecotype. Likewise, those dolphins sighted beyond 34km from shore are probably offshore ecotype bottlenose dolphins. Unlike the study of Torres *et al.* (2003), however, which documented a dearth of dolphins sampled within the 'gray zone' in summer, our study demonstrated that dolphin sightings remained relatively high out to 14km in winter. Whether this offshore extension represents a seasonal increase of either ecotype's abundance, or an extension of either ecotype's range, is currently unknown. For these reasons, we recommend focused genetic sampling of dolphins in this area during the winter months in the US mid-Atlantic region to provide insight into the identity of dolphins inhabiting the 'gray zone'.

The winter distribution pattern described above coincides with a distinct seasonal increase in the relative abundance of dolphins within the coastal waters of NC, especially around Cape Hatteras (see Figs 3 and 7). It is likely that at least part of this increase is due to coastal dolphins moving into the area from the north (see Read *et al.*, 2003a). With more dolphins using the waters off Cape Hatteras, competition for prey resources and habitat is likely to increase, as well as conflicts with seasonally increased fishing activity in this area (Street, 1996; Thayer and Montgomery, 1996; Watterson, 1999).

The results presented here, from both aerial surveys methods, clearly depict the importance of the habitat surrounding Cape Hatteras to bottlenose dolphins. The onshore/offshore winter surveys demonstrated a distinct peak in abundance, accounting for nearly 30% of all dolphins sighted, in Raleigh Bay, just south of Cape Hatteras (Fig. 5b). The coastal surveys also demonstrated that dolphin abundance was highest in Raleigh Bay in all seasons but summer (Fig. 7). The high relative abundance of dolphins in the Cape Hatteras marine ecosystem suggests that dolphins may be moving into these waters in response to changes in prey distribution and/or abiotic factors such as water temperature (e.g. Gaskin, 1982; Barco *et al.*, 1999; Zolman, 2002). The seasonal coastal surveys and onshore/offshore surveys also show the importance of the Cape Lookout, Cape Fear and Cape Romain habitats for bottlenose dolphins during the autumn and winter months.

The precise oceanographic conditions and processes that make Cape Hatteras and the other less prominent capes a preferred habitat for bottlenose dolphins and their prey are difficult to identify. The waters off the capes of the US mid-Atlantic are dynamic, with vertical and horizontal currents constantly mixing and shifting to produce seasonally and spatially determined productive habitats for the prey species of the dolphins (Worthington, 1976; Auer, 1987; Frankignoul *et al.*, 2001; Grothues *et al.*, 2002). Although the causal relationship between ocean processes and the influx of prey species is difficult to determine, Friedlaender *et al.* (2001) demonstrated a correlation between bottlenose dolphin abundance and that of an important prey fish species, spot (*Leiostomus xanthurus*), in the coastal waters near Cape Fear, NC. Both dolphin and spot abundance peaked in autumn, suggesting that the seasonal increase in dolphin abundance in this area was in response to increased prey availability. Moreover, Barco *et al.* (1999) found that dolphin abundance in waters off Virginia Beach, VA was highly correlated with sea surface temperature. Future research should investigate these relationships between dolphin occurrence, cape prominence, sea surface temperature, current patterns, productivity, and prey availability.

Many factors contribute to the complexity of managing the mid-Atlantic bottlenose dolphin stocks and defining their spatial boundaries. These include the existence of both resident and transient stocks of coastal dolphins, overlapping ranges of coastal and offshore ecotypes, and complicated seasonal movement patterns (Hohn, 1997; Barco *et al.*, 1999; McLellan *et al.*, 2002; Read *et al.*, 2003a; b; Reeves and Read, 2003; Torres *et al.*, 2003). The temporally and spatially dynamic nature of the oceanographic processes in the US mid-Atlantic further challenges researchers and managers. However, by linking the driving processes of biological and physical oceanography together with the distributional ecology of dolphins (e.g. prey availability and thermal limits) a coherent picture of bottlenose dolphin biogeography will likely emerge. This study provides results from the first comprehensive seasonal survey of bottlenose dolphin distribution south of Cape Hatteras, NC and, when combined with the results from previous research (Kenney, 1990; Barco *et al.*, 1999; Read *et al.*, 2003a), depicts a clear seasonal north/south migration pattern of coastal bottlenose dolphins along the entire US mid-Atlantic coast. This research also demonstrates that the waters off Cape Hatteras, NC are an important habitat for the bottlenose dolphin, particularly during the winter season when bottlenose dolphins appear to congregate in this area.

ACKNOWLEDGEMENTS

Aerial survey efforts of this magnitude take significant logistic and personnel support to be successful. We wish to express our sincere thanks to the pilots, Steve Murray, Buzz Krauss, Don Carter and Bob Murphy. Numerous observers contributed hours of flying time including: Sue Zvalaren, Gretchen Lovewell, DJ Struntz, Kim Marks Lefler, Guen Jones, Sue Barco, Kirk Hardcastle, Erin Nill Kipps, Ari Friedlaender, Michelle Barbieri, Vicki Stegall, Shelley Etnier, Dan Robertson and Wendy Walton. The coastal surveys were supported by the National Marine Fisheries Service (NMFS), Northeast Region. The onshore/offshore surveys were supported by NMFS, Southeast Region. We thank Mike Tork (NMFS, NER) and Steve Swartz (NMFS, SER) for their support. These surveys were flown under Scientific Research Permit No. 1031 to UNC Wilmington. We would finally like to thank Andy Read of Duke University and two anonymous reviewers for their valuable comments on early drafts of this manuscript.

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Date Received: June 2004
Date Accepted: January 2005

A note on strandings and entanglements of humpback whales (*Megaptera novaeangliae*) in Ecuador

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ABSTRACT

Between June and September of each year, southeastern Pacific humpback whales, *Megaptera novaeangliae*, arrive on the Ecuadorian coast to reproduce. Between July 2001 and September 2002, seven new strandings of humpback whales were found at different places along the Ecuadorian coast. Three of them were related to incidental catches caused by fishing nets (gillnets) and one of them occurred outside of the humpback whales' reproductive season. Using non-proportional and proportional 95% confidence interval calculations, it is estimated that the average frequency of strandings of humpback whales is 1.55 individuals per year (95% CI: 0.27,2.83; range: 1-4) since 1994, principally in the central and southern parts of the Ecuadorian coast, and the proportion of strandings due to bycatch is estimated at 0.286 (95% CI: 0.105,0.533). A preliminary mortality rate of 0.035(95% CI: 0.019,0.055), including both unknown and anthropogenic causes is estimated for this stock. 50% of the strandings took place in August and most were registered in 2001 (*n*=4). Six humpback whales with fishing nets embedded in their pectoral fins and tails were also observed in the marine area of the Machalilla National Park and the island of La Plata July-September. 67% of these entanglements occurred in July, and in one case a mother, accompanied by her calf, was observed with cables and a net on her head. These incidental catches are possibly related to the strandings occurring at the same time along the Ecuadorian shoreline. The fishery device most frequently linked to bycatch is the surface gillnet. Technological changes in fishing gear are vital for the conservation of marine mammals. It is imperative that the Ecuadorian coast be divided into zones and certain areas be delimited for the conservation of humpback whales through agreements with local users of the marine areas.

KEYWORDS: HUMPBACK WHALE; STRANDINGS; INCIDENTAL CATCHES; GILLNETS; MONITORING; SOUTHERN HEMISPHERE; PACIFIC OCEAN; SOUTH AMERICA; MORTALITY RATE; FISHERIES

INTRODUCTION

From June to September of each year, a large number of humpback whales (*Megaptera novaeangliae*) arrive in Ecuadorian waters to breed (Haase and Félix, 1993; Scheidat *et al.*, 2000; Félix and Haase, 2001c). These whales are part of the southeast Pacific humpback whale population (Group 1 stock) that feeds in the Antarctic (Dawbin, 1966; Leatherwood *et al.*, 1983; IWC, 1999). Estimates of the number of animals using Ecuadorian waters range from 405 (95% CI: 221-531) (Scheidat *et al.*, 2000) to 2,683 (95% CI: 397-4,969) (Félix and Haase, 2001c) individuals. Félix *et al.* (1997) reported on the first recorded strandings of humpback whales along the Ecuadorian coast, with seven strandings occurring between August 1994 and October 1996, primarily along the southern coastline. At least one of the animals had been bycaught in industrial fishing nets (Félix *et al.*, 1997). In 1998, two humpback whale calves were captured in the nets of local fishermen near the island of La Plata (Scheidat *et al.*, 2000). Bycatches of cetaceans in fishing gear is one of the main threats to cetaceans (e.g. Perrin *et al.*, 1994; Reeves and Leatherwood, 1994; Carwardine, 1995; Reeves *et al.*, 2002). This note reports on new strandings of humpback whales along the Ecuadorian coast and provides the first observation of entanglements of this species observed at sea off Ecuador.

METHODS

From June to September 2001, four non-governmental organisations (Fundacion Natura, FEMM, Yaqu Pacha and the Pacific Whale Foundation), collaborated to collect field data and try to identify possible causes of reported stranding events. When possible, data on the length, age and sex of the stranded animals were collected. Stranding records are effectively opportunistic, although FEMM have been monitoring and investigating strandings of marine mammals along the Ecuadorian coast for ten years. Additionally, as part of an annual humpback whale population monitoring programme, two organisations (Yaqu Pacha and Pacific Whale Foundation) have recorded observations of entangled individuals around La Plata Island and Machalilla National Park (1°23'S, 80°58'W). These areas are considered important breeding grounds for the Group I humpback whales stock (Scheidat *et al.*, 2000; Félix and Haase, 2001c) (Figs 1 and 2). From 4 July to 2 October 2001, daily at-sea monitoring was carried out from commercial whalewatching boats based in Puerto Lopez (1°25', 79°55'W; Fig. 2) following a route to and from La Plata Island (Fig.1). The total effort comprised 240 hours (87 days and 149 trips). Observations were also made from land. Hand-held global positioning systems (GPSs) were used to record the locations of entangled whales.

RESULTS

Seven new strandings of humpback whales were recorded during July/August 2001 and January-September 2002 (Table 1; Fig. 1). The first stranding (no. 1) was found at the coastal area of Libertador Simón Bolívar. The animal (*ca* 14m) was in an advanced state of decomposition and the sex could not be determined. It appeared that both flippers and the caudal peduncle had been cut (Fig. 3) as well as about

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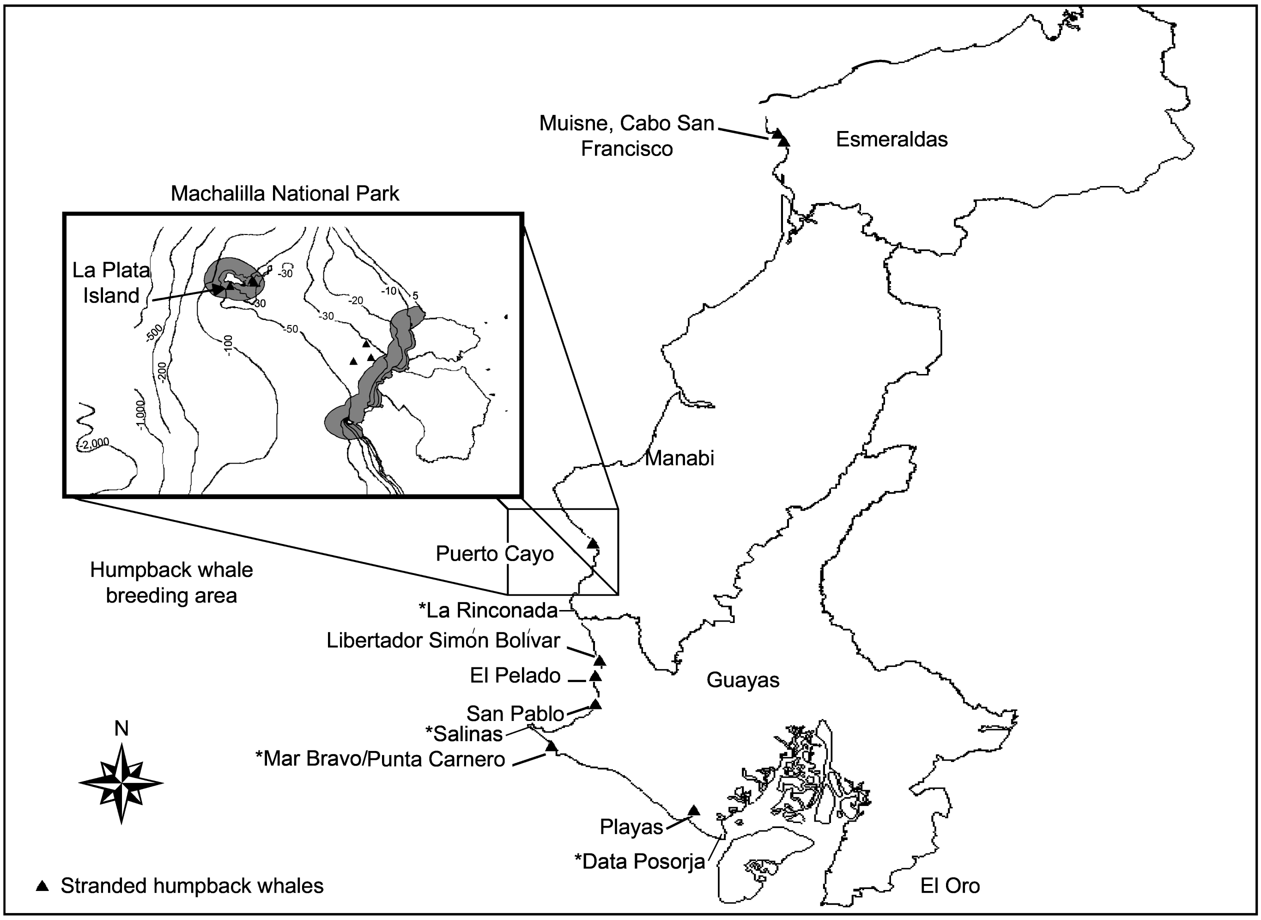

Fig. 1. Strandings of humpback whales on the Ecuadorian coast July 2001-September 2002 and locations of La Plata Island and Machalilla National Park. *=2004 strandings.

one-third of the upper jaw. The most probable cause of death appeared to be entanglement in either commercial or artisanal fishing gear; the animal was probably cut free while at sea (Ben Haase, pers. comm). Félix *et al.* (1997) had also reported a stranded humpback whale on Manglaralto (approximately 1km from Libertador Simón Bolívar), that had similar deep cable cuts on its tail and pectoral fins.

The second stranding (no. 2) was found at Punta Carnero. It was a smaller (9.5m), fresh animal. From its length, it was a sexually immature subadult (sexual maturity occurs at around 11-12m, Leatherwood *et al.*, 1988). It had an artisanal multifilament gillnet with floats embedded in its tail flukes, as well as deep cuts in the throat grooves and a ruptured humerus of the right pectoral fin (Fig. 4). It may have been one of a number of whales observed entangled in the Machalilla National Park (Table 2). The third stranding (No. 3) was of an adult at Muisne; the cause of the death could not be determined.

Stranding no. 4, found at Puerto Cayo, near the Machalilla National Park, was a small (almost 8m and probably a yearling) individual in such an advanced state of decomposition that its sex could not be determined. Wounds and injuries, in the throat and ventral areas. Stranding no. 5 was a small (6.8m) yearling or late season calf. It was found on 31 January 2002 at San Pablo, Santa Elena Peninsula, outside the typical breeding season. This suggests that adults and calves are found in Ecuadorian waters later than previously reported. It had bite wounds on its body (Ben Haase, pers. comm.; Haase and Félix, 2002) and no evidence of an encounter with fishing nets. The observed scars and wounds on these two individuals could have been caused by either scavengers post-mortem or predators pre-mortem. Killer whale (*Orcinus orca*) attacks in tropical South Pacific waters have been reported by Florez-Gonzalez *et al.* (1994). Transient killer whales around La Plata Island in the marine area of the Machalilla National Park (Carvajal and Gutierrez, 1995; Castro and González, 2002) and the Galapagos Islands (Merlen, 1999) have been documented.

The presence of killer whales in Ecuadorian waters is more common than previously thought. An attack of killer whales on humpback whales around La Plata Island was reported by Scheidat *et al.* (2000). Fourteen humpback whales were photo-identified (Félix and Haase, 2001a) with bite marks and mutilations presumably from killer whales (or more probably false killer whales, *Pseudorca crassidens*) in the same area. A stranded calf with signs of killer whale attack was recently found at Salinas (2°15’S, 80°40’W: Fernando Félix, pers. comm.). In 1992, 56 false killer whales beached at Chanduy (Félix, 1992) and more recently Castro (2004) reported large schools of pygmy killer whales (*Feresa attenuata*) around La Plata Island (1°34’S, 80°99’W).

The final two strandings occurred at the end of the season (September 2002, at the end of the breeding season. The first (no. 6), at the village of Playas, was an adult mature female (16.2m) that presented some evidence of fishery interaction (fishing nylon) whilst the other (no. 7), was a two week-old female calf (*ca* 5m) stranded on the beach at El Pelado (Table 1).

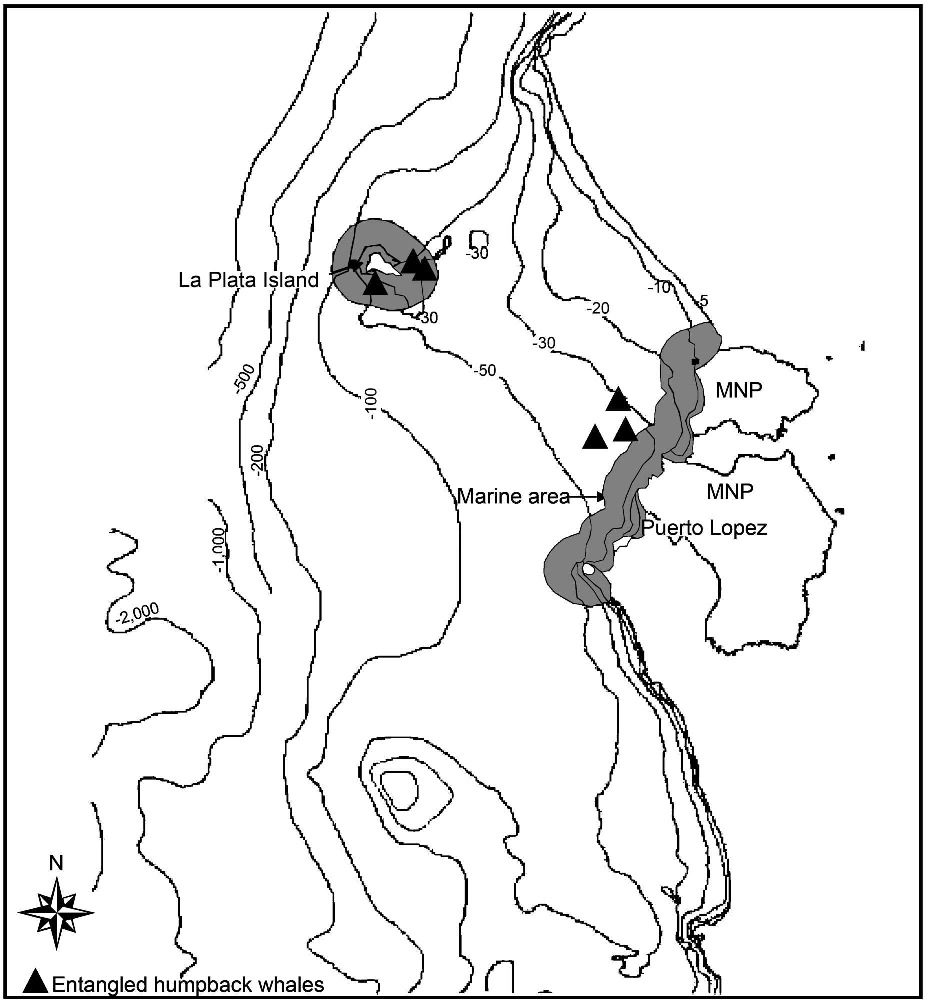

Fig. 2. Records of entangled humpback whales around La Plata Island and the Marine Area of Machalilla National Park July-September 2001.

Table 2 presents the sighting locations and details of the six reported humpback whale entanglements in the Machalilla National Park and La Plata Island during July-September 2001 (Fig. 2); four occurred in July (*n*=4). These included a mother and calf, with green cables and a net on the head. The entanglements were recorded in waters 30-50m deep within 5km offshore (Fig. 2), showing that entangled humpback whales were commonly seen close to the coast.

DISCUSSION

Bycatch in commercial and artisanal fisheries is known to be one of the most serious anthropogenic threats to cetaceans and indeed many other large marine organisms (Hall *et al.*, 2000). In Ecuador, artisanal fleets comprised some 7,000 vessels in the early 1990's, operating from around 70 communities (Campbell *et al.*, 1991). By the late 1990's this number had risen to an estimated 15,000 artisanal vessels

Table 1

Strandings of humpback whales on the Ecuadorian coast (July-August 2001 – January-September 2002). F = female.

No.	Location	Position	Date	Total length (m)	Sex	Remarks
1	Libertador Simón Bolívar	1°41'S, 80°50'W	24 Jul. 2001	~14	F*	Deep cuts in the caudal peduncle and both pectoral fins mutilated.
2	Punta Carnero-Mar Bravo	2°13'S, 80°59'W	01 Aug. 2001	9.5	F	Tail flukes embedded in a multifilament gillnet with floats.
3	Muisne, San Francisco	3°35'N, 79°59'W	Aug. 2001	-	-	Cause of death unknown.
4	Puerto Cayo, río Amargo	1°26'S, 80°50'W	20 Aug. 2001	7.7	-	Wounds and injuries present in the ventral side generated by bites.
5	San Pablo	1°41'S, 80°50'W	31 Jan. 2002	6.80	-	Wounds generated by bites.
6	Playas, General Villamil	2°37'S, 80°23'W	Sept. 2002	16.2	F	A cut in flukes and presence of fishing nylon on both caudal trunk and embedded within baleen in the upper jaw.
7	El Pelado	1°41'S, 80°50'W	Sept. 2002	5.43	F	Dismembered by people from the communities after stranding (cause of death unknown).

*Because of the whale's size it was classified as female.

Fig. 3. Adult humpback whale stranded in Libertador Bolivar, Guayas Province, Ecuador. Note the lack of the left pectoral fin (26 July 2001). [Photo: Raúl Carvajal]

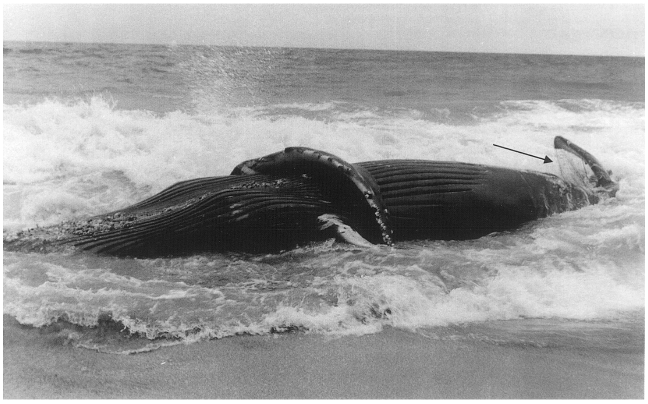

Fig. 4. Stranding of a juvenile humpback whale due to bycatch, Punta Carnero, Guayas Province, Ecuador. The arrow indicates the presence of a gillnet embedded around the tail flukes (1 August 2001). [Photo: Raúl Carvajal]

(Ormaza and Ochoa, 1999). The most common vessels are small (2-3 person) rafts with 20-50HP outboard motors, long wooden canoes for 3-4 fishermen and 10m wooden or fibreglass-open boats, with 75-100HP outboard motors (Massay, 1987). Fishing techniques include longlines (4-11.5km in length with about 100-1,500 hooks) and both surface (3km in length and 15m in depth) and deep (300-400m in length) gillnets (Cedeño, 1987; Martínez *et al.*, 1991). Humpback whales are protected by Ecuadorian law and also listed as vulnerable (Ministerial Decree No. 196 Official Register No. 458, June 1990).

The data from Félix *et al.* (1997) and this study (n=7) (Fig. 5), imply a minimum stranding frequency of 1.55 (=14/9) individuals year^{-1} (95% CI: 0.27, 2.83; range: 1-4), principally in the central and southern parts of the Ecuadorian coast. Four of the 14 individuals (*ca* 29%, 95% CI 11-53%) showed evidence of fishery interaction. The high occurrence during August and September is consistent with the study of Capella *et al.* (2001) for the coast of Colombia.

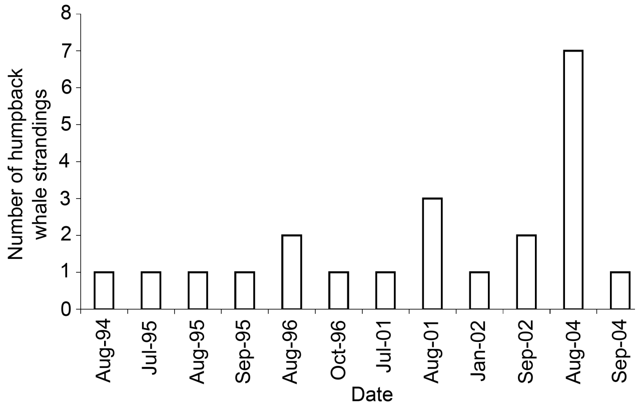

Fig. 5. Historical strandings data of humpback whales on the Ecuadorian Coast. Field data 1997-2001 and 2003 is not available because field data was not registered during that period. Data for 1994-1996 and 2004 were obtained from Félix *et al.* (1997) and Félix *et al.* (2004) respectively.

The potential effect of this mortality has yet to be determined and it is essential that better estimates of both anthropogenic mortality and abundance are obtained. However, depending on the assumptions made, the value could be in the region of 0.035, if the abundance estimate of 405 reported by Scheidat *et al.* (2000) is used. The estimates of bycaught animal mortality presented here may be underestimates; in 2001, the number of observed humpback whales entangled in fishing gear exceeded the number of stranded animals and the fate of these animals is unknown.

More recently, two and three adult humpback whales entangled in fishing gear were sighted at sea during whale watching and sightings surveys in the 2003 and 2005 breeding seasons (Fernando Félix, pers. comm.). No strandings were recorded in Ecuador for 2003. An unusually high number of strandings (three adults and five newborn calves) were recorded in 2004, but no cause of death was established (see Table 3; Félix *et al.*, 2004). Seven of these

Table 2

Cases of incidental catches and entanglement of humpback whales near the island of La Plata* in the Machalilla National Park (July-September 2001).

No.	Location	Date	Remarks
1	Coast of Machalilla, offshore	15 Jul. 2001	Adult humpback whale with fishing nets present in the pectoral fins.[a]
2	In front of Machalilla shoreline	20 Jul. 2001	Whale completely embedded in gillnets; tail flukes only free of the net; breathing with difficulty and abnormal swimming behaviour.[a]
3	Eastern sector of La Plata Island	26 Jul. 2001	Female with green ropes and net on its head and dorsal fin accompanied by a very small calf.[b,e]
4	La Plata Island, in front of Punta Escalera	30 Jul. 2001	Whale with pectoral fins encircled by net and fractured flukes (broken).[c]
5	In front of the Machalilla town coast	01 Aug. 2001	Whale with body surrounded by green and black net (probably a green and broken gillnet).[b, d]
6	Near the La Plata Island	10 Sept. 2001	Adult whale with green net in its mouth and 10 metres of rope and floats.[d]

*01°23'S, 80°58'W (between the island and continental Ecuador, waters of the Pacific Ocean); [a]Mrs. María Moreno de los Ríos (pers. comm.); [b]María José Barragán (pers. comm.); [c]Mr. Julio Pin (Machalilla National Park ranger) (pers. comm.); [d] Cristina Castro (pers. comm); [e] Daniela Rosero (pers. comm).

Table 3

Strandings of humpback whales on the Ecuadorian coast during 2004.*

No.	Location	Position	Date	Total length (m)	Sex
1	Playas	2°37'S, 80°23'W	5/08/04	>10	-
2	Playas	2°37'S, 80°23'W	5/08/04	4-5	-
3	La Rinconada	1°S, 80°W	13/08/04	14.3	M
4	Libertador Bolívar	1°41'S, 80°50'W	19/08/04	~5	-
5	Libertador Bolívar	1°41'S, 80°50'W	23/08/04	5	M
6	Data de Posorja	2°42'S, 80°14'W	24/08/04	14.5	F
7	Salinas	2°15'S, 80°40'W	31/08/04	~5	-
8	Mar Bravo	2°13'S, 80°59'W	14/09/04	~6	-

*Source: Data obtained and adapted from Felix *et al.* (2004).

strandings were found in August, although some were in an advanced state of decomposition. In 2003, six humpbacks washed ashore in September and October over less than 120km of the northern coast of Perú (Goya *et al.*, 2004). The cause of these mortalities during the southward humpback migration is thought to have been due to the presence of biotoxins.

As is the case elsewhere, entanglement may pose a greater threat to calves, yearlings and immatures than adults (Castro *et al.*, 1999). The prevalence of entanglements in waters 20-60m deep coincides with the distribution of most of the humpback whales (48-57%) reported by Félix and Haase (2001b; 2005). In addition to studies to better estimate the potential effect of bycatches on the population, it is important that efforts be made to develop effective mitigation strategies with the fishery sector in Ecuador and in the context of better fishery management for both artisanal and industrial fisheries. It is also important to explain potential problems to fishermen and recently, an environmental education program has been developed to address the artisanal fishermen in five fishing communities, near the Machalilla National Park. These communities were selected because of the high rate of incidental catches by surface gillnets known to occur in this area (Alava, 2001). Changes to fishing gear and operational procedures are being proposed as sustainable alternatives for the fishing industry, that will reduce bycatch per unit of effort (Hall *et al.*, 2000). Given the seasonal occurrence of humpback whales in the region, fishing restrictions during July and August, the prime breeding months is also likely to reduce bycatches (Hall *et al.*, 2000). Finally, serious consideration must be given to dividing the Ecuadorian coast be divided into conservation zones for humpback whales through agreements with local users of the marine areas.

ACKNOWLEDGMENTS

We would like to thank the Fundación Ecuatoriana para el Estudio de Mamíferos Marinos (FEMM) for sharing their knowledge of strandings registered on the Ecuadorian coast between 1994 and 1996, to Yaqu Pacha for supporting research in Ecuador since 1996, the Pacific Whale Foundation for its support, and the Fisheries Undersecretary for helping us with documentation and organising the training workshops for fishermen and divers of the Ecuadorian coast. The authors also thank Greg Kaufman (Pacific Whale Foundation), as well as the nature guides and tourism operators of the Machalilla National Park. We are indebted to all the FEMM volunteers for their valuable help during the stranding inspections. We would like to thank Ben Haase, Meike Scheidat, Merrill Kaufman and two anonymous reviewers for their suggestions and comments on this manuscript.

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Date received: February 2004
Date accepted: October 2004

J. CETACEAN RES. MANAGE. 7(2):169–175, 2005 169

Updated 1978-2001 abundance estimates and their correlations for the Bering-Chukchi-Beaufort Seas stock of bowhead whales

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ABSTRACT

The method of Cooke (1996) and Punt and Butterworth (1999) for computing abundance estimates for bowhead whales of the Bering-Chukchi-Beaufort Seas stock is reviewed. These abundance estimates are computed from estimates N_4 of the number of whales that passed within the 4km visual range of the observation 'perch' from which the whales are counted, the estimated proportions P_4 of the whales that passed within this range and the estimated standard errors (SE) of N_4 and P_4. Errors discovered while assembling the data used in developing previous estimates were corrected, and new estimated detection probabilities, N_4 and P_4 values and SEs were computed using the corrected data. The method of Cooke (1996) and Punt and Butterworth (1999) was then applied. The resulting 2001 abundance estimate was 10,545 (95% confidence interval 8,200 to 13,500), extremely close to the 2001 N_4/P_4 abundance estimate of 10,470 (95% confidence interval 8,100 to 13,500) (George *et al.*, 2004). The estimated rate of increase of this population from 1978 to 2001 was 3.4% per year (95% confidence interval 1.7% to 5%).

KEYWORDS: BOWHEAD WHALE; ABUNDANCE ESTIMATE; SURVEY-SHORE-BASED; ACOUSTICS; SURVEY-AERIAL; TRENDS

INTRODUCTION

Most estimates of abundance for the Bering-Chukchi-Beaufort Seas (BCB) stock of bowhead whales, *Balaena mysticetus*, have been based on data collected during ice-based visual 'census' studies conducted off Point Barrow, Alaska, during the spring migration of these whales from the Bering to the Beaufort Sea. From 1978 to 1988 counts were conducted annually, although in 1979 and 1984 they did not produce enough data to support an abundance estimate because of adverse environmental conditions. The primary documents describing the studies, including two successful studies conducted subsequently in 1993 and 2001, are listed in Table 1.

It was recognised fairly early in the period covered by these studies that visual detection of whales passing more than 4km offshore from the observers was extremely unlikely. Aerial transect surveys and acoustic monitoring were used to estimate the proportions of whales that passed within and beyond the 4km visual range (Table 1). Aerial surveys were conducted in 1979, 1981, 1984, 1985 and 1986 and acoustic monitoring in 1982, 1984, 1985, 1986, 1988, 1993 and 2001. Although both aerial transect survey and acoustic monitoring took place in 1984, the distributions obtained were not considered useful for assessing offshore distribution because heavy ice in the nearshore lead caused the visual census to fail and may also have affected the offshore distribution of the whales (Zeh *et al.*, 1993).

George *et al.* (2003; 2004) provide a brief summary of the history and methods of the studies. They also review the methods used to estimate abundance from the data. An estimate, N_4, of the number of whales that passed within the 4km visual range of the observation 'perch' from which the whales are counted is computed using methods developed

Table 1

Studies providing data for bowhead abundance estimation.

Year	Visual census	N_4?	P_4?	No. of perches[3]	Acoustic location data	Aerial transect survey
1978	Braham *et al.* (1979)	Yes	No	2	None	None
1979	Braham *et al.* (1980)	No[1]	Yes	2	None	Braham *et al.* (1980)
1980	Johnson *et al.* (1981)	Yes	No	2	None	None
1981	Marquette *et al.* (1982)	Yes	Yes	2	None	Marquette *et al.* (1982)
1982	Dronenburg *et al.* (1983)	Yes	Yes	2	Cummings *et al.* (1983), Cummings and Holliday (1985), Dronenburg *et al.* (1983)	None
1983	Dronenburg *et al.* (1984)	Yes	No	2	None	None
1984	Dronenburg *et al.* (1986)	No[2]	No[2]	1	Clark *et al.* (1986)	Nerini and Rugh (1986)
1985	Krogman *et al.* (1986)	Yes	Yes	2	Clark *et al.* (1986), Clark and Ellison (1988)	Nerini and Rugh (1986)
1986	George *et al.* (1987)	Yes	Yes	1	Clark and Ellison (1989)	Withrow and Goebel-Diaz (1989)
1987	George *et al.* (1988)	Yes	No	1	None	None
1988	George *et al.* (1990)	Yes	Yes	1	George *et al.* (1990)	None
1993	George *et al.* (1995)	Yes	Yes	1	Clark *et al.* (1996), Clark and Ellison (2000)	None
2001	George *et al.* (2003, 2004)	Yes	Yes	1	Clark *et al.* (2003)	None

[1] No counts were made 25 April-8 May because the lead in front of the perches was closed by ice or after 24 May because of weather. Thus too much of the season was missed to permit an abundance estimate.

[2] Heavy ice in the lead caused the visual census to fail. The acoustic and aerial survey data were consequently not considered usable for assessing offshore distribution in successful census years.

[3] Coded as 2 if two perches operated simultaneously to provide data for detection probability estimation, coded as 1 otherwise. The number of different perches used during the season is often a considerably larger number.

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by Zeh *et al.* (1986a; b; 1991). The estimated proportion of the whales that passed within the 4km visual range, P_4, is obtained from the aerial survey and acoustic data. The estimates N_4, P_4 and N_4/P_4 were first discussed by Raftery and Zeh (1991; 1993). The International Whaling Commission Scientific Committee (IWC SC) agreed to use the 2001 N_4/P_4 abundance estimate (George *et al.*, 2003) for its 2004 assessment of BCB bowhead whales (IWC, 2004, p.18).

Raftery *et al.* (1995) pointed out that P_4 for years lacking acoustic or aerial survey data could be computed from the years with such data, enabling the rate of increase of the BCB bowhead whales to be estimated from N_4/P_4 for all the years with successful visual censuses. Zeh *et al.* (1995) and Raftery and Zeh (1998) refined the method of Raftery *et al.* (1995) and applied it to the data used by Raftery *et al.* (1995), augmented by aerial survey data from 1981 and additional acoustic data from 1993. These methods were criticised by Cooke (1996) because covariances among the abundance estimates that resulted from using years with P_4 data to obtain the estimates for years without P_4 data were not computed, and the combination of process and observation error in P_4 values was handled in an *ad hoc* fashion. As in IWC (1994, p.75), Cooke (1996) used the term 'process error' to refer to the extent to which the variability of successive estimates exceeds their estimated variability after accounting for any trend over time; 'observation error' refers to the sampling error of the estimates. Process error arises when an estimated variance ignores some components of the true variance, e.g. year-to-year variability in the true proportion of whales that pass within visual range due to differences in ice conditions. Cooke (1996) presented a statistical model that overcame the problems he identified. Punt and Butterworth (1999) (Appendix A) applied the Cooke (1996) model to the N_4 and P_4 data in Zeh *et al.* (1995) and Raftery and Zeh (1998) to obtain the abundance estimates that have been used subsequently by the IWC SC, with coefficients of variation (CVs) and a correlation matrix.

George *et al.* (2003) investigated process error in the number of bowhead whales migrating past Point Barrow and in the proportion within visual range using the approach of Cooke (1996) and including the 2001 data. They found, as Cooke had, that there was no indication of process error in bowhead whale numbers, but considerable process error in the proportion within visual range.

The primary analysis of George *et al.* (2003) treated the N_4/P_4 value they obtained for 2001 as uncorrelated with the earlier abundance estimates in estimating rate of increase. They used the abundance estimates, CVs, and correlations given by Punt and Butterworth (1999) for the years before 2001. However, a careful reading of George *et al.* (2003) and discussions with George (pers. comm.) suggested that the 2001 data could and should be integrated with the earlier data using the Cooke (1996) method. Similarly, the primary references (Table 1) and subsequent discussions with some of the researchers (Cummings, pers. comm.; Ellison, pers. comm.; Rugh, pers. comm.) determined that aerial survey data from 1979, 1985 and 1986 and acoustic location data from 1982 that had not been used previously should be added.

It had been anticipated (IWC, 2004, p.18) that the 2001 N_4/P_4 abundance estimate would not be modified. However, in the process of assembling the data archive, errors were discovered in the visual census data from some of the early years of the census. This necessitated recomputing detection probability and abundance estimates from the archived data, resulting in small changes to all the N_4 values used previously and their standard errors (SE). Thus the estimates computed from the model of Cooke (1996) also changed.

Most of the corrections involved relatively minor adjustments to perch locations. A more significant set of corrections occurred for 1982, when a number of observers forgot to log out at the ends of their shifts. The correction of those errors resulted in reducing the number of hours in 1982 recorded as having more than two observers. Another significant error was discovered and corrected in the computer program *rawq.f* that extracted data for detection probability estimation. That error had led to incorrect determinations of whether whales were seen within or beyond 2km offshore from the perch. Whales seen and categorised as 'new' (seen for the first time) and 'conditional' (uncertain whether this is a new whale or a subsequent sighting of a whale seen previously) are used in computing N_4. Of the 20,262 new whales used in our analyses, only two were added as a result of correcting errors. Of the 3,633 conditional whales, only 18 were added.

The model and method of Cooke (1996) and Punt and Butterworth (1999) are reviewed here. Revised tables of detection probabilities, N_4 and P_4 values with SEs and N_4/P_4 values with CVs are provided. These are compared with the corresponding data used by Punt and Butterworth (1999). New abundance estimates, CVs and correlation matrix are provided and compared with those given in appendix A of Punt and Butterworth (1999) as well as with previously published estimates of bowhead abundance. The estimated 1978-2001 annual rate of increase for this bowhead population obtained by George *et al.* (2004) using our abundance estimates, CVs and correlation matrix is also reviewed.

METHODS

N_4 and P_4 data used to construct the abundance series

The available N_4 and P_4 data are summarised by year in Table 1. N_4 values (estimated numbers of whales that passed within visual range) were recomputed for the eleven years with adequate data using the corrected data. From 1978 to 1985, two perches were operated as described by George *et al.* (2003; 2004) so that detection probabilities could be estimated as a function of visibility, number of observers and distance of the whales offshore from the primary perch. A generalised linear model (McCullagh and Nelder, 1983) based on the removal method (Seber, 1982) was used (Zeh *et al.*, 1991). In each year with adequate visual effort to support an abundance estimate, counts made from the primary perch under particular conditions each day were corrected by dividing by the corresponding detection probability estimates. A linear combination of the corrected counts, adjusted for time without visual effort under acceptable conditions, provided the estimate for that day (Zeh *et al.*, 1986a; 1991). The daily estimates were summed to obtain the N_4 value for the year, after accounting for missed days using a time series interpolator, and SE(N_4) was estimated by a jackknife that omitted a day at a time (Zeh *et al.*, 1986b).

As described by George *et al.* (2003; 2004), P_4 values were computed as the proportion of acoustic locations directly offshore from the hydrophone array that fall within 4km offshore from the primary perch. Aerial transect survey data from 1979, 1981, 1985 and 1986 give km offshore from the ice edge for each bowhead seen on transect. These data also permit computation of P_4. At the resolution of the transect surveys, the location of the ice edge is equivalent to the location of the perch. Rugh (1990) reports that 90% of errors in aerial survey positions are <0.58km in magnitude, although some errors are as large as 1.89km. Only in 1983 (for 13% of the season) and 1986 (9%) were perches more than 0.58km back from the lead edge. Perches were always within 0.3km of the edge except for those years and 2001. They were never more than 1.5km from the edge.

Since there were both acoustic and aerial survey P_4 values for 1985 and 1986, weighted averages (by the inverse of the estimated variance) for those years were calculated. Variances for acoustic P_4 in 1985, 1986, 1988, 1993, and 2001 were obtained via a moving blocks bootstrap (Efron and Tibshirani, 1993) with 3-day blocks because samples of acoustic locations often covered more than a day. Variances for P_4 from the limited acoustic data in 1982 and the aerial transect data were obtained by an ordinary bootstrap that sampled days. In many cases, samples were a day or more apart, and even samples on adjacent days were generally hours apart. It therefore seemed reasonable to assume that samples from different days were independent.

Cooke's model

Cooke (1996) proposed the following statistical model for the analysis of the N_4 and P_4 data:

$$N_{4y} = N_y p_y e^{\nu_y} \qquad \nu_y \sim N(0;\sigma^2_{\nu,y})$$

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

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

where

N_{4y}	is the estimate N_4 for year y,
P_{4y}	is the estimate P_4 for year y,
N_y	is the number of whales in the population in year y,
p_y	is the proportion of the population within visual range in year y,
π	is the mean proportion of the population within visual range (the actual proportion varies from year to year as a consequence of process error),
$\sigma^2_{\nu,y}$	is the variance of the logarithm of N_{4y} (reflecting observation error),
$\sigma^2_{\varepsilon,y}$	is the variance of the logarithm of P_{4y} (reflecting observation error) and
σ^2_{η}	is the process error variance for the proportion of the population within visual range.

Note that Punt and Butterworth (1999) used P_y where N_y is used here[1]. Except for this change, the notation here matches that of Punt and Butterworth (1999). The parameters of this model to be estimated are N_y and p_y for each of the 11 years which have N_{4y} values, in addition to p_{1979}, π and σ^2_{η}. Note that p_{1979} is listed separately because 1979 is the only year judged to have usable P_{4y} data but without usable N_{4y} data.

The model assumes that the proportion p_y of the population within visual range varies from year to year around the mean value π. Thus, the natural logarithms of the estimates P_{4y} include two components of error, with only the first reflected in the estimated standard error of P_{4y}: (1) the measurement or observation error ε_y with variance $\sigma^2_{\varepsilon,y}$ and (2) the process error η_y with variance σ^2_{η}. For this reason, the estimate of the proportion p_y may differ from P_{4y} in years with P_{4y} data.

Estimation of model parameters

The estimates of the 25 parameters of this model are obtained by restricted maximum likelihood (REML), reviewed by Harville (1977). This involves finding the values for the parameters that minimise the following quantity:

$$0.5[(Y - X\beta)^T V^{-1}(Y - X\beta) + \ell\text{n}\left|V\right| + \ell\text{n}\left|X^T V^{-1} X\right|]$$

where Y is a column vector of length 31, X is the design matrix, β is a vector of length 24 containing the natural logarithms of all the parameters except σ^2_{η}, and V is a diagonal matrix with the first 11 elements on the diagonal the squared CVs of the N_{4y}, the next 8 the squared CVs of the P_{4y}, and the last 12 (corresponding to the years with either N_{4y}, P_{4y} or both) containing σ^2_{η}. Thus the diagonal elements of V are the variances of the elements of Y. The elements of Y are the natural logarithms of N_{4y} for y = 1978, 1980, 1981, 1982, 1983, 1985, 1986, 1987, 1988, 1993 and 2001; the natural logarithms of P_{4y} for y = 1981, 1982, 1985, 1986, 1988, 1993, 2001 and 1979; and 0s for the remaining 12 entries, i.e. a 0 for each year with either N_{4y} or P_{4y} data. According to the third model equation, $\eta_y = \ell\text{n}(p_y) - \ell\text{n}(\pi)$, and its expected value $E(\eta_y) = 0$. The only estimate we have for η_y is its expected value. This is the reason for the 0s in Y. Each of the first 11 rows of X consists of 0s except for a 1 to pick out the logarithm of N_y and another 1 to pick out the logarithm of p_y. Each of the next 8 rows has only a single 1 to pick out the logarithm of the correct p_y. Each of the next 12 rows represents η_y for one of the y, so each has a 1 to pick out the logarithm of p_y and –1 in the last column for the logarithm of π. The maximum likelihood estimate of π also provides an estimate of p_y for years in which P_{4y} data are not available.

RESULTS AND DISCUSSION

The revised estimates of detection probability $\hat{p}$ ± SE obtained from the 1978-1985 data are given in Table 2. Note that previous discussions and tabulations of detection probability data (Zeh *et al.*, 1986a; b; 1991; 1993) were in terms of the probability $\hat{q} = 1 - \hat{p}$ of failing to detect a whale. For comparison purposes, the detection probability estimates obtained by Zeh *et al.* (1991) are given in Table A.1 of Appendix A. The values in Table A.1 were used by Raftery and Zeh (1991; 1993; 1998) and Zeh *et al.* (1995) to compute N_4.

Table 2

Detection probability estimates $\hat{p}$ ± SE obtained as described by Zeh *et al.* (1991). These estimates are functions of distance of the whales offshore from the census perch, number of observers and visibility.

		Visibility		
Offshore distance	Number of observers	Excellent to very good	Good	Fair
≤ 2km	> 2	0.72 ± 0.06	0.65 ± 0.07	0.60 ± 0.08
	≤ 2	0.71 ± 0.03	0.63 ± 0.03	0.58 ± 0.05
> 2km	> 2	0.50 ± 0.11	0.40 ± 0.11	0.33 ± 0.12
	≤ 2	0.48 ± 0.08	0.38 ± 0.08	0.31 ± 0.09

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[1] N is commonly used to represent number of whales and P to represent a proportion or probability.

Values of $\hat{p}$ in Table 2 are quite similar to those in Table A.1 for the most part. However, Table 2 shows less effect of increasing the number of observers. Detection probabilities in 1982 were apparently high for reasons not captured by these factors, so when observers were correctly counted in that year, $\hat{p}$ was raised for ≤ 2 and lowered for > 2 observers. Table 2 also provides a somewhat clearer indication of the reduction in $\hat{p}$ when whales are more than 2km offshore from the perch. The incorrectly categorised offshore distance data used in estimating the values in Table A.1 blurred the effect.

Revised estimates N_4 and P_4 obtained from the archived data are given in Table 3. The CVs used in the first 19 elements on the diagonal of V are obtained by dividing Table 3 N_4 and P_4 standard errors (SE) by the corresponding estimates. Table 3 also lists the N_4/P_4 abundance estimates obtained by dividing N_4 by P_4 for years for which both N_4 and P_4 are available. Although the N_4/P_4 values in Table 3 are not used when computing abundance estimates using the method of Cooke (1996) and Punt and Butterworth (1999), they are of interest for comparison purposes. They are sometimes cited, e.g. for 2001 by George *et al.* (2004), because they are computed directly from the data obtained during a particular survey and the Table 2 detection probabilities.

Table A.2 gives the corresponding estimates used by Punt and Butterworth (1999). Comparing the values of N_4 in Table 3 with those in Table A.2, we can see the effects of the changes in the detection probability estimates. There were few hours with more than two observers in the early years of the census, so they show few changes related to the reduced effect of >2 observers except for 1982. From 1986 on, there were usually three observers. The effect of the additional observer in Tables A.1 and A.2 was to raise estimated detection probabilities and hence lower values of the estimate N_4. Because the estimated effect of the additional observer is less in Table 2 than in Table A.1, N_4 values from 1986 on tend to be greater in Table 3 than in Table A.2. Lower estimated detection probabilities when whales were farther offshore also contribute to increased N_4 values in Table 3 for years like 1983 when many whales were seen more than 2km offshore from the perch. This effect was exacerbated in 1983 because corrections to perch locations resulted in an increase in the number of whales >2km offshore compared to the 1983 data used in previous analyses.

The abundance estimates, $\hat{N}_y$, obtained using the method of Cooke (1996) and Punt and Butterworth (1999) are shown in Table 4, along with their CVs and correlation matrix. The mean proportion π within visual range was estimated to be 0.701, and the process error standard deviation σ_η was estimated to be 0.270.

Not surprisingly, the abundance estimates in Table 4 differ most from the N_4/P_4 values in Table 3 when P_4 has a large SE and/or differs quite markedly from the estimate of π (0.701). The abundance estimates for 1988, 1993 and 2001 have considerably lower CVs than the estimates for the earlier years and are not highly correlated with them. These estimates do not differ greatly from the corresponding N_4/P_4 values because acoustic monitoring was more

Table 3

Data used in the construction of the abundance estimates $\hat{N}_y$ for the Bering-Chukchi-Beaufort Seas stock of bowhead whales (Table 4). N_4/P_4 is shown for comparison with the estimates in Table 4.

	N_4/P_4		N_4		Acoustic P_4		Aerial survey P_4		Weighted average P_4	
Year	Estimate	CV	Estimate	SE	Estimate	SE	Estimate	SE	Estimate	SE
1978			3,338	295	NA		NA		NA	
1979			NA		NA		0.850	0.090	NA	
1980			2,722	491	NA		NA		NA	
1981	4,348	0.310	3,261	689	NA		0.750	0.166	NA	
1982	8,388	0.382	4,756	814	0.567	0.191	NA		NA	
1983			4,605	848	NA		NA		NA	
1985	6,547	0.271	3,136	583	0.500	0.131	0.457	0.132	0.479	0.093
1986	10,272	0.217	4,160	600	0.515	0.080	0.194	0.111	0.405	0.065
1987			3,712	544	NA		NA		NA	
1988	6,895	0.123	5,102	456	0.740	0.062	NA		NA	
1993	8,160	0.071	7,613	531	0.933	0.014	NA		NA	
2001	10,470	0.129	9,025	1,068	0.862	0.044	NA		NA	

NA = not available.

Table 4

Abundance estimates $\hat{N}_y$, CVs (actually standard errors of the logarithms) and the correlation matrix for the logarithms of the abundance estimates for the Bering-Chukchi-Beaufort Seas stock of bowhead whales based on the estimation procedure described above.

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

comprehensive during those years than during other years and provided relatively precise P_4 values. The addition of P_4 data for 1979 and 1982 in Table 3, compared to Table A.2, also contributes to lower between-year correlations in Table 4, compared to those in appendix A of Punt and Butterworth (1999) (their table A.1, our Table A.3).

The largest changes between the new abundance estimates in Table 4 and those in appendix A of Punt and Butterworth (1999) (their table A.1, our Table A.3) occur for the years for which additional P_4 data were used, particularly 1982 and 1986. In both of these cases, the added data suggested considerably fewer whales within viewing range than the data used previously. Withrow and Goebel-Diaz (1989) expressed concern that the transect distribution in 1986 did not reflect the distribution of whales they observed during photogrammetry flights. Those flights indicated a larger proportion within visual range. However, use of the Cooke (1996) model, as well as averaging P_4 from the transect surveys with P_4 from the acoustic locations, prevented that distribution from having undue influence.

Prior to the 2001 study, the most recent estimate of bowhead population size accepted by the IWC SC was 8,200 with 95% estimation interval from 7,200 to 9,400. This estimate was based on the Bayes empirical Bayes posterior distribution computed from 1993 data by Zeh *et al.* (1995) and Raftery and Zeh (1998). The 1993 estimate of 8,167 (Table 4) presented here is virtually identical to their estimate. The 95% confidence interval, computed as recommended by Buckland (1992), is 7,100 to 9,400. The 2001 estimate of 10,545 presented here has a 95% confidence interval of 8,200 to 13,500. This is almost the same as the corresponding interval based on N_4/P_4 given by George *et al.* (2004) as 8,100 to 13,500. George *et al.* (2004) estimated the annual rate of increase of this bowhead population from the data in our Table 4 by using generalised least squares to fit an exponential growth model. The estimated rate of increase from 1978 to 2001 was 3.4% per year, with a 95% confidence interval of 1.7% to 5%.

ACKNOWLEDGEMENTS

We thank the Alaska Eskimo Whaling Commission (AEWC) for their support of this research. We gratefully acknowledge funding provided by the North Slope Borough Department of Wildlife Management (NSB DWM) and the National Oceanic and Atmospheric Administration (NOAA, through the AEWC). We thank Sharon Hedley (University of St Andrews), Tore Schweder (University of Oslo) and Hans Skaug (Institute of Marine Research, Bergen, Norway) for helpful comments on drafts of this manuscript. We thank all who participated in the difficult and dangerous work of conducting the ice-based visual census, acoustic monitoring and aerial survey flights. We also thank all who helped to assemble the data included in our analyses and to make sure these data were correct. Two people who were instrumental in both the field work that produced the data and the work in assembling the data archives for the 2004 bowhead assessment deserve special mention for their contributions −without Craig George (NSB DWM) and Dave Rugh (NOAA), the data used in this paper could not have been gathered.

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Date received: August 2005
Date accepted: August 2005

Appendix A

THE DATA USED AND RESULTS FROM APPENDIX A OF PUNT AND BUTTERWORTH (1999)

For ease of comparison, Table A.1 gives the detection probabilities of Zeh *et al.* (1991) used by Zeh *et al.* (1995) and Raftery and Zeh (1998) to compute the N_4 values in Table A.2. The N_4 and P_4 values in Table A.2 were used in appendix A of Punt and Butterworth (1999) to construct their table A.1. Their table A.1, repeated here as Table A.3, gives the estimates, CVs and correlations they obtained.

Table A.1

Detection probability estimates $\hat{p}$ ± SE from Zeh *et al.* (1991).

		Visibility		
Offshore distance	Number of observers	Excellent to very good	Good	Fair
≤ 2km	> 2	0.74 ± 0.04	0.66 ± 0.04	0.63 ± 0.05
	≤ 2	0.70 ± 0.03	0.61 ± 0.04	0.57 ± 0.05
> 2km	> 2	0.55 ± 0.08	0.42 ± 0.09	0.38 ± 0.10
	≤ 2	0.49 ± 0.07	0.36 ± 0.08	0.32 ± 0.09

Table A.2

Estimates N_4, P_4 and N_4/P_4 with standard errors (Zeh *et al.*, 1995; Raftery and Zeh, 1998). The column of CVs in Table 8 of Punt and Butterworth (1999) has been added.

Year	N_4	SE(N_4)	P_4	SE(P_4)	N_4/P_4	SE(N_4/P_4)	CV(N_4/P_4)
1978	3,383	289	0.674*	0.189	5,019	1,476	0.294
1980	2,737	488	0.674*	0.189	4,061	1,365	0.336
1981	3,231	716	0.750	0.108	4,308	1,147	0.266
1982	4,612	798	0.674*	0.189	6,843	2,279	0.333
1983	4,399	839	0.674*	0.189	6,527	2,241	0.343
1985	3,134	583	0.519	0.131	6,039	1,915	0.317
1986	4,006	574	0.518	0.062	7,734	1,450	0.187
1987	3,615	534	0.674*	0.189	5,364	1,714	0.320
1988	4,862	436	0.739	0.053	6,579	757	0.115
1993	7,249	505	0.933	0.013	7,770	552	0.071

*Estimate obtained by Zeh *et al.* (1995) from the years with P_4 data. Not used in computing Table A.3.

Table A.3

Abundance estimates $\hat{N}_y$, *CV*s (actually standard errors of the logarithms) and the correlation matrix for the logarithms of the abundance estimates for the BCBS bowhead stock from Table A.1 of Punt and Butterworth (1999).

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