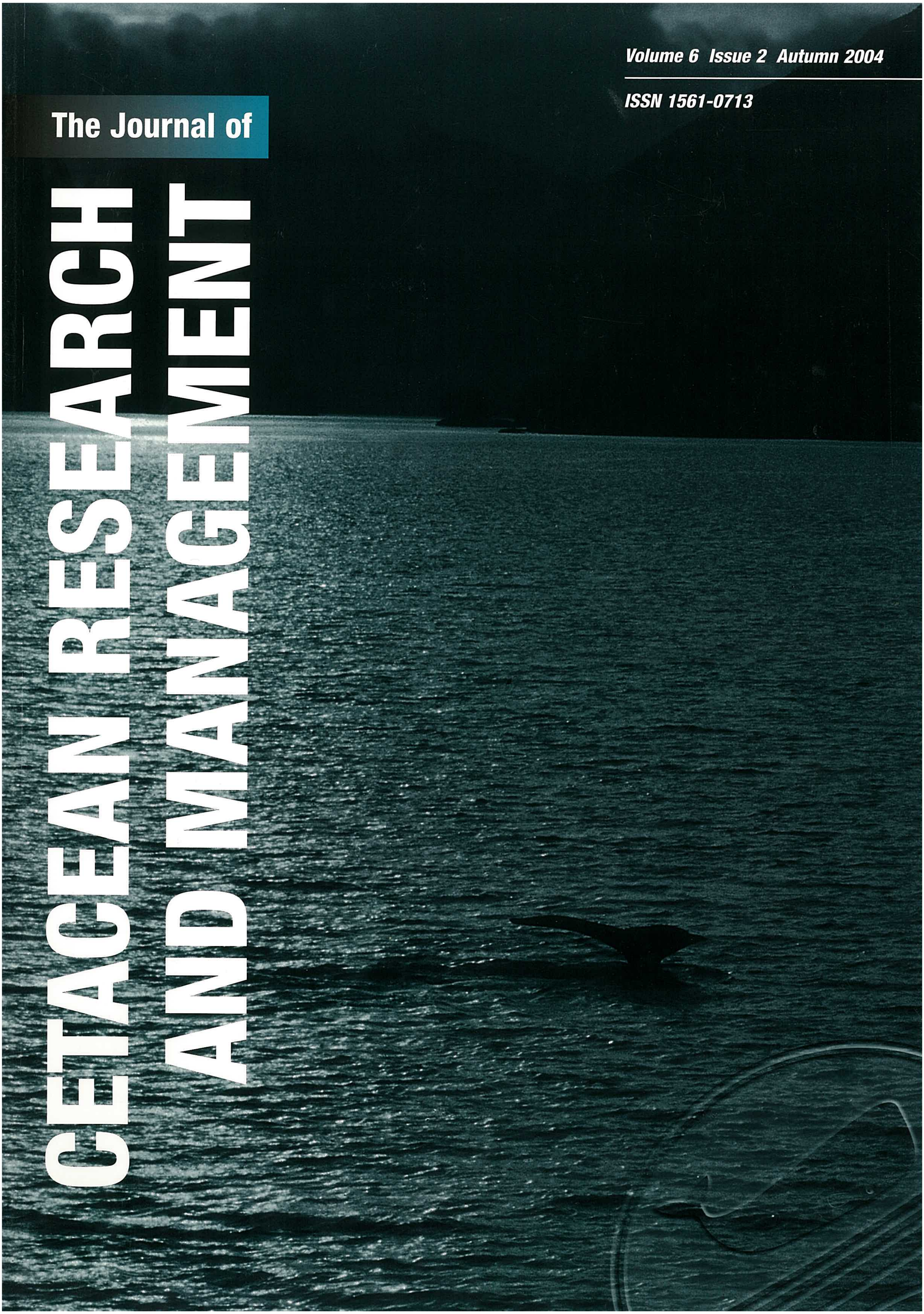
Volume 6 Issue 2 Autumn 2004

ISSN 1561-0713

The Journal of CETACEAN RESEARCH AND MANAGEMENT



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Editorial

This issue of the Journal follows the 2004 meeting of the International Whaling Commission held in Sorrento, Italy. 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 2005 as *J. Cetacean Res. Manage*. 7 (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). The RMS will also include a number of non-scientific matters, including inspection and enforcement. This has been the subject of a considerable amount of discussion within the Commission. The Commission received a proposal by the Chair for an RMS package of measures that he believed was a fair and balanced approach to move to the rapid completion of the RMS. Discussion of this will form a key part of the work of the Commission's RMS Working Group during the period leading up to the 2005 meeting in Ulsan, Korea.

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 it developed a document detailing the requirements and guidelines for the *Implementation* process. The Committee also updated 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. For a number of reasons, the Committee did not make as much progress as it had hoped on this issue in Sorrento. In order to ensure progress during the coming year it therefore agreed to hold an intersessional Workshop before the next annual meeting.

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*. This will begin at next year's annual meeting.

Bycatches of large whales

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

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, it will require further developments in sampling design with input from experts with detailed knowledge of market sampling issues. A proposal for a Workshop on that subject was developed and this Workshop will be held immediately prior to the next annual meeting in Ulsan, Korea. The objectives of the Workshop are:

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

It was also noted that the Workshop will be interested in the question of markets only insofar as determining whether or not such data can be used to provide reliable estimates of bycatch.

Work to further explore improved bycatch estimation methods for the two approaches noted above is continuing. Improved data reporting for large whale bycatches was also recommended and a *pro-forma* developed.

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, the Committee 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).

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 Sorrento. It believed that this *Gray Whale 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 and should sufficient data become available, an intersessional Workshop will be held before the next annual meeting to review progress.

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. Until the AWMP is completed the Committee continues to provide advice on an *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 catch limit 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. The primary focus of the in-depth assessment was: (a) the data required for the *Bowhead SLA*; and (b) examination of whether the present situation is within the tested parameter space for that *SLA*. The latter effort included 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 will examine in particular 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 year’s 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 this meeting showed that no change is needed to the current block quota for 2003-2007.

Minke and fin whales off West Greenland

In 2002, at the Commission, the same catch limits as previously in force were agreed by the Commission 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 and once again this year, the Committee received little new information on stocks of minke and fin whales off West Greenland. It stressed that this inability to provide any advice on safe catch limits is a matter of great concern, particularly in the case of fin whales where the best available abundance estimate dates from 1987/88 and is only 1,096 (95% CI 520-2,100); that for West Greenland common minke whales dates from 1993 and is 8,371 (95% CI 2,400–16,900). The Committee noted that an abundance survey would be undertaken this year.

The Committee stressed that obtaining adequate information for management must be seen as of very high priority by both the national authorities and the Commission. Without this information, the Committee will not be able to provide safe management advice in accord with the Commission’s management objectives, or develop a reliable *SLA* for many years, with potentially serious consequences for the status of the stocks involved. In particular, the Committee advised the Commission that in the absence of an agreed abundance estimate for fin whales arising out of the forthcoming survey, it will probably recommend immediately that the take of fin whales off West Greenland be reduced or eliminated.

Humpback whales off St Vincent and the Grenadines

In 2002, after considerable debate in the Commission, a catch limit of up to 20 whales for the period 2003-7 was agreed (the Scientific Committee must review this in 2005). This year, the Committee repeated that it believes it is most plausible that eastern Caribbean humpbacks are part of the West Indies breeding population (abundance in 1992/93 – 11,570, 95%CI 10,100–13,200). It recommended further collection of relevant data to confirm this. It also agreed that the catch limit set by the Commission would not harm the stock if it is part of the West Indies breeding population.

HISTORIC ABUNDANCE ESTIMATION, GENETIC METHODS

In the light of a paper by Roman and Palumbi (2003), the Committee agreed to consider the general methodological issue of estimating K and/or pre-exploitation population size in the context of the Committee’s assessment work, as well as to provide its view on the conclusions of the paper. The Committee was pleased that Palumbi was able to attend the meeting.

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. However, it noted that there are a number of limitations and uncertainties that must be considered when examining such data in a present-day management context as discussed above.

In view of this, the Committee agreed that the estimates of historic abundance provided in Roman and Palumbi (2003) 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 in particular 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 also identified further work necessary to assess if genetically-based estimates of ‘initial’ abundance can provide useful information for the management of cetaceans.

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, to ascertain 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 and discussed at the annual meeting later that year. 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).

It was recognised that such a complex project must proceed in an iterative fashion and the Workshop concentrated on specifying the various modular tasks needed for Phase I of the process (c.f. *Initial Exploration Trials* in the AWMP process), for which some results might be expected within a year, while also identifying the types of scenarios that would need to be covered in Phase II and beyond. The Workshop report was published in *J. Cetacean Res. Manage*. 6 (Suppl.). This year the Committee reviewed progress under Phase I of the TOSSM project (Testing Of Spatial Structure Models). It was pleased to see that great progress had been made on the most challenging module, i.e. the development and validation of a program to simulate realistic genetic datasets. 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 (1989). It can be considered as an in-depth evaluation of the status of all whale stocks in the light of management objectives and procedures; this would include the examination of current stock size, recent population trends, carrying capacity and productivity. Clearly, it is not possible to 'comprehensively assess' all whale stocks simultaneously, and the Committee has been working in an 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;
(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. This work will again be a priority item for discussion at next year's meeting. Particular attention will be given to the potential relationship between minke whale distribution and the extent and nature of sea ice.

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. 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, which it believes should commence in 2006. This year, the Committee reviewed a paper by Branch *et al.* (In Press). The Committee 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 (95% CI 1.4–11.6%); (2) had an estimated circumpolar population size of 1,700 (95% CI 860–2,900) in 1996; and (3) that this population is still severely depleted with the 1996 population estimate estimated to be at 0.7% (95% CI 0.3–1.3%) of the estimated pre-exploitation level.

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. An intersessional group was established last year to review progress and determine whether it is feasible to set a deadline for the assessment to be completed. Further work was identified this year and progress was reviewed. Further work remains to be completed.

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 special issue 2 of the Journal *Right whales: worldwide status*). The Committee is extremely concerned about this population, which, whilst probably the only potentially viable population of this species, is in serious danger (*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 from this stock 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 *J. Cetacean Res. Manage*. 6 (Suppl.). 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 the cumulative impact of multiple threats (from both natural and anthropogenic sources). Last year, the Committee adopted the Workshop report and endorsed its recommendations, including the research and monitoring plan.

In reviewing progress this year, the Committee noted with great concern that the evidence is compelling that this population is in serious danger of extinction. It reiterated that the population is small (only about 100 whales) and appears to have biological problems (only 23 reproductive females, three or more years calving interval, male biased sex ratio, and apparent low calf survival). Furthermore, there is only a single known coastal feeding habitat (approximately 60km long and 5km wide) used by females and calves which faces an obvious and immediate threat from industrial activities, including noise, vessel traffic and the potential for a catastrophic oil spill. Noting, its similarly strong concerns for North Atlantic right whales, the Committee recommended as a matter of absolute urgency that measures be taken to protect this population and its habitat off Sakhalin Island.

Plans for the Russia-USA research collaboration and national research plans from Russia and Korea were presented. As in previous years, the Committee strongly recommended that the ongoing Russia-USA and Russian and Korean national programmes on western gray whale research and monitoring continue and expand into the future. Results from these programmes will be the only way to monitor and assess the status of this critically endangered population.

The Committee also strongly recommended that all range states develop or expand national monitoring and research programmes on western gray whales. The Committee noted particularly that the precise location and status of the breeding grounds of this highly endangered whale (presumably in Chinese waters) are still unknown.

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) aims 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 this year's meeting.

Given the emergent threat of anthropogenic sound on cetaceans and other elements of marine ecosystems and also the potential for the Committee to assist in the development and interpretation of studies aimed at elucidating the potential impacts of anthropogenic noise on cetaceans, the Committee held a mini-symposium at this year's meeting, with presentations on the following topics: (a) the effects of anthropogenic noise on marine animals and the possible synergistic effects between ambient ocean noise levels and other environmental stressors; (b) physical acoustics and ambient noise in the ocean; (c) audition and the physiology of hearing in cetaceans and the effects of intense sounds on cetacean hearing; and (d) whale communication behaviour.

In conclusion, the Committee noted with great concern the impact on large whales in critical habitats of exposure to seismic sounds impulses, particularly with respect to severely threatened populations such as the western gray whale. It agreed that there is now compelling evidence implicating that military sonar has a direct impact on beaked whales in particular. It also agreed that evidence of increased sounds from other sources, including ships and seismic activities, were cause for serious concern. The potential for cumulative or synergistic effects of sounds, as found in other taxa, with non-acoustic anthropogenic stressors was noted. A number of detailed recommendations were made.

The Committee was pleased to hear that an intersessional Workshop on Habitat Degradation will take place in November 2004 at the University of Siena, Italy.

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 not yet happened.

This year, the primary topic considered was the franciscana. The franciscana is found along the Atlantic coasts of Brazil, Uruguay and Argentina, from approximately 18° to 42°S. The Committee reviewed available information on stock structure, abundance, life history, ecology, incidental catches and status. It made a number of research recommendations given the paucity of information for some areas. Bycatch in gillnet fisheries occurs throughout the range of the franciscana. The Committee expressed its concern that in some areas, annual removal rates due to bycatch were between about 1.6 and 3.3% exceeding the 1% removal level determined by the Committee as sufficient to warrant concern regarding the status of small cetaceans.

The Committee referred to its endorsement of the concept of a series of regional Workshops with the general objectives of developing a short- and long-term approach to the successful management and mitigation of the cetacean bycatch problems in a region, building upon work already undertaken by the Committee (see section on Regional Workshops).

The Committee also reviewed progress on previous recommendations it had made, particularly those concerning the critically endangered baiji and vaquita. The Committee received some information from China and welcomed the initiatives being taken, although it noted that the prospects for the baiji remain extremely poor.

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 reviewed the report of the third meeting of CIRVA. The Committee reiterated its endorsement of the fundamental conclusions drawn by CIRVA – that the current grave conservation status of this species is due to fisheries bycatch. The Committee noted at least six records of bycatch in the past seven months and, in general, was disheartened by the lack of any substantial progress in reducing bycatches since last year's meeting. Therefore, the Committee urged the Government of Mexico to implement the previous recommendations of CIRVA and to take immediate action to eliminate the bycatch of this species in the northern Gulf of California.

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

In the light of new evidence, the Committee repeated its concern over the catches and quotas for some stocks of white whales and narwhals, particularly in Greenland, east Hudson Bay and the Russian Arctic. 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 2004 meeting. The primary topic considered was a review of the results from the Workshop on the Science for Sustainable Whalewatching held in Cape Town, 6-9 March 2004. The Committee endorsed a number of recommendations from the Workshop concerning: (1) the value of experimental studies to measure the impacts of whalewatching; (2) new approaches and quantitative studies of relevance to the Scientific Committee; (3) further development of a framework for the management of whalewatching similar in concept to those codified in the FAO Code of Conduct for fisheries; (4) use of the precautionary approach in the absence of information of possible damaging effects of whalewatching; (5) use of case studies to promote broad conclusions about assessing impacts of whalewatching on different taxonomic groups at a variety of life history stages; (6) the development of whalewatching guidelines based on criteria that are simple, practical and objectively measurable under field conditions; (7) further development of the IWC's 1997 General Principles for the Development of Regulatory Frameworks for Whalewatching (see *www.iwcoffice.org*).

The Committee also reviewed whalewatching guidelines and regulations, and new information on dolphin feeding and 'swim-with' programmes.

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.

Most of the discussion at the 2004 meeting centred on reviewing the results of existing permits (Japan – Antarctic minke whales (JARPA); Japan – North Pacific common minke, sei, Bryde's and sperm whales (JARPN); Iceland – North Atlantic common minke, fin and sei whales) and reviewing proposals for their continuation. 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 agreed that it will undertake a full review of the JARPA programme when the complete set of results are available following the completion of the 16-year programme, i.e. some time after the 2005 annual meeting of the Committee.

WHALE SANCTUARIES

The Committee had been asked by the Commission to review the Southern Ocean Sanctuary (SOS) in 2004 and an intersessional working group had been appointed to develop a proposed framework to carry out the review. In summary, the Committee agreed that: (1) whales are not effectively protected from whaling in the SOS, because such Sanctuaries apply only to commercial whaling, and because (apart from stocks that migrate to the IOS) whales also migrate outside of the SOS boundaries; (2) the boundaries of the SOS were appropriately established for some, but not for all stocks; (3) it was not possible to completely evaluate the effectiveness of the SOS because the scientific objectives are not clear and are not associated with quantifiable performance measures. The Committee respectfully requested that the Commission considers clarifying the objective(s) of the SOS in order to allow the Committee to discriminate among designs that would, *inter alia*: protect whales; protect whale species diversity; and increase whaling yields outside the Sanctuary. The Committee also developed a series of recommendations that, once the overall objectives of the SOS have been refined, will allow these objectives to be evaluated, and will facilitate evaluation in future reviews. These recommendations were originally agreed by the participants of the Intersessional Meeting to Review the SOS, 28-29 June 2004, Sorrento (to be published in *J. Cetacean Res. Manage.* 7 (Suppl.)).

G.P. Donovan
Editor

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Migrations of individually identified humpback whales between the Antarctic Peninsula and South America

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ABSTRACT

Considerable uncertainty exists regarding the migratory destinations of humpback whales (*Megaptera novaeangliae*) from the Antarctic Peninsula region and the breeding grounds off the coasts of South America. Evidence is presented on the migratory patterns of Antarctic humpback whales based upon movements of individuals identified by natural markings as part of a large-scale international collaboration. Recapture rates were compared between animals from the low latitude breeding and calving areas along the northeastern (n=288) and northwestern (n=325) margins of South America with those identified in the high-latitude feeding areas in the region of the Antarctic Peninsula (n=535). The number of individuals re-sighted in the Antarctic Peninsula differed dramatically between eastern and western South America ($\chi^2=40.98$, $p=1.5 \times 10^{-10}$). No individuals from Brazil were re-sighted in either the Antarctic Peninsula or off western South America. In contrast, 43 individuals from western South America were identified off the Antarctic Peninsula. These findings suggest that the northwest coast of South America represents an important breeding ground destination for at least some of the humpback whales that feed near the Antarctic Peninsula, but provide no support for movement between the Antarctic Peninsula and the east coast of South America.

KEYWORDS: HUMPBACK WHALE; SOUTH AMERICA; ANTARCTIC; MIGRATION; PHOTO-ID

INTRODUCTION

In the Southern Hemisphere, humpback whales (*Megaptera novaeangliae*) feed in Antarctic waters during austral summer, and migrate to tropical areas for breeding and calving during the austral winter (for a species review see Clapham and Mead, 1999). Historically, six management areas for baleen whales in Antarctic waters were defined by the International Whaling Commission based principally on the density of commercial catches, but also on limited data on individual movements based on tag returns and limited data on pigment variations (reviewed by Donovan, 1991). More recently, seven geographically defined breeding and calving areas have been identified (Rice, 1998; IWC, 1998). The patterns of movement within some seasonal habitats and/or the migratory destinations of individuals have been examined by tagging with Discovery tags (e.g. Chittleborough, 1965) and by identification by natural markings (e.g. Kaufman *et al*., 1990; Stone *et al*., 1990; Garrigue *et al*., 2002). Discovery tagging was principally conducted in Areas IV and V (70°E to 170°W) and the breeding areas at corresponding longitudes leading to better documentation of migratory behaviour in these waters. In contrast, information on the long-distance movements of individuals from Antarctic Areas I and II (0° to 120°W) is more limited.

The waters of Area II were one of the principal areas of humpback whaling during the early years of the modern Southern Hemisphere industrial whale fishery (Tonnessen and Johnsen, 1982). Over 50,000 humpback whales were reported taken between 1909 and 1915, principally in the waters around South Georgia (Mackintosh, 1942). Antarctic humpback whaling in Area I was of considerably less importance, presumably reflecting a smaller pre-whaling population in the region (Mackintosh, 1965). On the breeding grounds, catches were made on both sides of South America by the 19th century non-mechanised whale fishery (Kellogg, 1929; Scammon, 1874; Townsend, 1935) and later by industrial whaling operations (Mackintosh, 1965; Tonnessen and Johnsen, 1982). A total of 1,542 humpbacks were taken off Paraíba, northeastern Brazil prior to 1963 and at least 10 were taken off Arraial do Cabo, Rio de Janeiro State, southeastern Brazil between 1960-1963 (Paiva and Grangeiro, 1965). A small-boat fishery in Abrolhos Bank, northeastern Brazil, killed an unknown number of humpbacks. The last whale harpooned was in

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1929 (Lodi, 1992). Along the western coast of South America, land stations in Peru and Chile processed 2,281 humpback whales between 1908 and 1975 (Clarke, 1980).

Much of the exploitation in these areas occurred before the advent of systematic collection of biological data on catches and before the development of the Discovery tag (Brown, 1978), limiting the amount of data available for analysis. Only one long-distance recovery of a Discovery tag has been reported for Area I (Dawbin, 1964) and none for Area II. The end of legal hunting of humpback whales in the Southern Hemisphere in 1963-1964 (Best, 1993) effectively ended the use of Discovery marks for the study of humpback movements. Illegal and unreported catches were numerous and widespread in the Southern Hemisphere both before and after the end of legal hunting (Tonnessen and Johnsen, 1982; Yablokov, 1994), but by their very nature these resulted in few data. Only two re-sightings have been reported between the Antarctic Peninsula and Colombia based upon natural markings (Garrigue *et al.*, 2002; Stone *et al.*, 1990). Considerable uncertainty exists, therefore, regarding the specific migratory destinations of humpbacks from the Antarctic Peninsula region and the breeding grounds off the coasts of South America.

This paper presents evidence of the migratory patterns of humpback whales between the high-latitude feeding areas in the region of the Antarctic Peninsula and the low-latitude breeding and calving areas along the eastern and western margins of South America. These results are based upon movements of individual whales identified by natural markings as part of a large-scale international collaboration.

METHODS

Individual humpback whales were identified from photographs of the natural markings and permanent scars on the ventral side of the flukes (Katona *et al.*, 1979). A collection of identification photographs from throughout the Southern Hemisphere is maintained at College of the Atlantic, Bar Harbor, Maine USA. This Antarctic Humpback Whale Catalogue (AHWC) is a collaborative effort involving numerous individual or institutional contributors. The majority of photographs were collected by research groups or by naturalists and tourists aboard cruise ships or whalewatching vessels. Because of the opportunistic nature of this collection there is considerable spatial and temporal variability in the distribution of sightings. Photographs included in these analyses were taken between 1984 and 2002. Photographic comparison was conducted as described in Katona and Beard (1990).

Analyses reported here utilised samples from three geographic regions (Fig. 1). The feeding area sample comprised photographs collected between 1981 and 2002 along the west coast of the Antarctic Peninsula, extending approximately from Elephant Island (61°01'S, 45°54'W) to Detaille Island (66°50'S, 66°50'W). All sightings were near the coast of the Peninsula or the adjacent islands. Most sightings are from Area I. A small number of sightings near the tip of the Peninsula were made east of 60°W and therefore in Area II, but no distinction is made in this analysis between animals sampled in the different management areas. Photographs from the eastern coast of South America were collected from Brazil from 1988 to 1999 principally in the waters around Abrolhos Marine National Park (17°20'-18°10'S, 38°35'-39°20'W) at Abrolhos Bank, and Cabo de Sao Tome (22°S, 40°W). Along the western margin of South America, most photographs were taken near Isla Plata off Machalilla National Park (01°16'S, 81°06'W) on the coast of Ecuador from 1988 to 2000 (Félix and Haase, 2001; Scheidat *et al.*, 2000), and off Colombia from 1986 to 2000 primarily in the region of Isla Gorgona in the Gorgona Island National Park (02°47'N, 78°18'W) (Flórez-González, 1991).

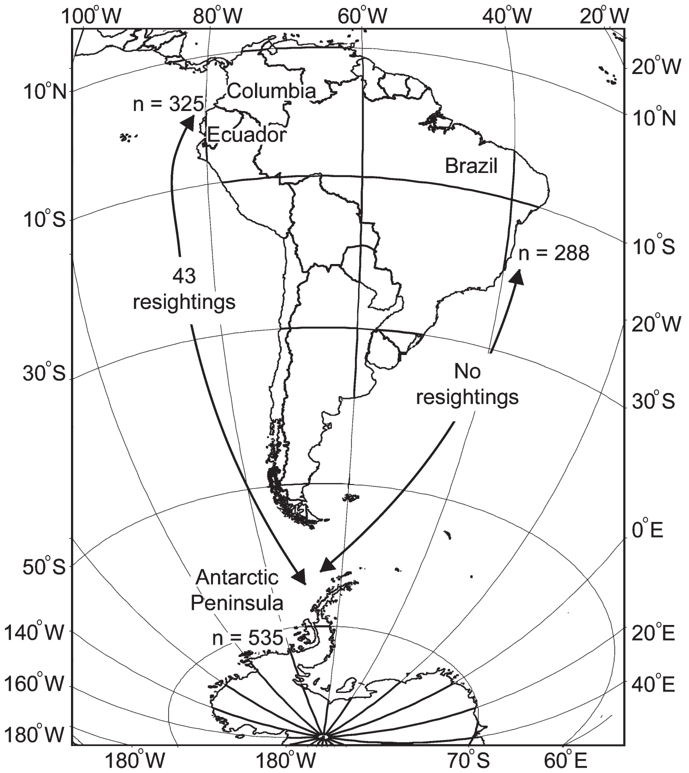

Fig. 1. Regions where photographs were collected, sample sizes and numbers of re-sightings. Arrows serve to connect potential migratory endpoints and are not intended to indicate routes of travel.

The rate of errors in identification by natural markings, and thus the re-sighting rate, is related to the quality of photographs used in comparison (Stevick *et al*., 2001). In these analyses only differences in photographic quality between eastern and western South America will produce bias in the results. The distribution of the poorest quality photographs does not differ significantly between the samples from these two areas (χ^2=2.18, p=0.14). The proportion of the poorest quality photographs is slightly higher in the sample from the west coast (west 0.24, east 0.18). Thus the probability of missing a re-sighting because of poor photographic quality is greater in the region with the higher re-sighting rate, and so any bias resulting from photo quality differences is conservative in this case. Therefore photographs of all qualities are included in order to maximise the available sample size.

RESULTS

A total of 1,105 individuals was identified. Table 1 presents the number of individuals identified in each sampling region and the number of re-sightings between regions. There were eight individuals in common to the Ecuador and Colombia samples, and re-sightings to the Antarctic Peninsula from these two regions occurred at a similar rate (χ^2=1.33, p=0.25). Movement of individuals between Ecuador and Colombia has been previously demonstrated (Flórez-González *et al*., 1998). Thus, although approximately 470km separate the sampling areas off Colombia and Ecuador, these two samples were combined into a single western South America sample.

Table 1

The numbers of individual humpback whales identified in each of the sampling areas and the number of individuals re-sighted between areas.

Region	Individuals	AP	B	E
Antarctic Peninsula (AP)	535			
Brazil (B)	288	0		
Western South America (WSA)	325	43	0	
Ecuador (E)	254	32	0	
Colombia (C)	79	14	0	8

Re-sightings to the Antarctic Peninsula differed dramatically between eastern and western South America. No individuals from Brazil were re-sighted in either the Antarctic or off western South America. In contrast, 43 individuals from western South America were identified off the Antarctic Peninsula (χ^2 = 40.98, p=1.54 × 10^{-10}).

DISCUSSION

Previous speculation on the migratory patterns of humpback whales from South American waters has been based primarily upon indirect evidence rather than on the movement of tagged individuals or shared genetic markers. For humpback whales generally, there is not a one-to-one correlation between feeding grounds and breeding grounds. Rather, individuals from different feeding areas may congregate at a common breeding area (Chittleborough, 1965; Katona and Beard, 1990; Calambokidis *et al*., 2001; Stevick *et al*., 2003) and individuals from different breeding areas may feed in the same area (Chittleborough, 1965; Calambokidis *et al*., 2001). This complicates interpretation of movement patterns when data are sparse, and different authors have reached contradictory conclusions.

There has been general agreement that humpback whales from the west coast of South America feed in Area I (Kellogg, 1929; Tomilin, 1957; Mackintosh, 1965; Slijper, 1979; Winn and Reichley, 1985; Evans, 1987). However some authors suggest a primary high-latitude destination in pelagic waters from 80°W to 120°W (Mackintosh, 1965; Winn and Reichley, 1985; Evans, 1987), while others propose a coastal distribution along the Antarctic Peninsula (Kellogg, 1929) or in the waters from the Peninsula west to about 80°W (Tomilin, 1957; Slijper, 1979). Few data have been available to bolster any of these suggestions. The single return for a Discovery tag to Area I was of an individual marked in Tonga recovered at 95°45’W in the Bellingshausen Sea (Dawbin, 1964). Surveys conducted between 1976/77 and 1987/88 have resulted in very low sighting rates for humpback whales from 80°W to 120°W, with substantially greater numbers observed near the Antarctic Peninsula (Kasamatsu *et al*., 1996). Two re-sightings between the Antarctic Peninsula and Colombia have been documented based upon natural markings (Stone *et al*., 1990; Garrigue *et al*., 2002). In addition to the movements of individuals demonstrated here, the distribution of mitochondrial genetic markers supports a strong affinity between animals sampled to the west of the Antarctic Peninsula and those from Colombian waters, and a lack of affinity between these individuals and those sampled elsewhere in the Southern Hemisphere (Olavarría *et al*., 2000; Caballero *et al*., 2001).

Two principal opinions have been advanced regarding the high-latitude destination of individuals from Brazil. Most authors suggest a destination in Area II, commonly in the waters near South Georgia (e.g. Slijper, 1979; Tomilin, 1957). Others, however, indicate (with varying levels of uncertainty) movement by some individuals from Brazil to the Antarctic Peninsula area (Mackintosh, 1965; Slijper, 1979; Evans, 1987). Modern sighting and stranding patterns off Brazil do not support a coastal migration to or from waters to the southwest, but are more consistent with an offshore migration, suggesting a feeding area to the south or southeast (Siciliano *et al*., 1999). The lack of re-sightings between Brazil and the Antarctic Peninsula is more consistent with the suggestion that humpback whales that breed in Brazil feed primarily in waters to the east of the Antarctic Peninsula. Because of the historical importance of humpback whaling near South Georgia, this region would appear to be a likely feeding area for whales breeding off Brazil (Mackintosh, 1965). However there is little evidence for any concentration of humpback whales in the region of South Georgia in recent years (Moore *et al*., 1999), and the sighting rate for humpback whales during systematic surveys conducted from 1976/77 to 1987/88 is low in the waters between 20°W and 40°W (Kasamatsu *et al*., 1996) where the highest historic concentration occurred (e.g. Slijper, 1979). Additionally, there has, to date, been little photographic coverage in Area II making it difficult to investigate movements of individuals in this region. Thus, the current feeding ground destination for Brazilian whales remains unknown (Siciliano *et al*., 1999) and there is not a clear candidate region within Area II.

Our findings suggest that the northwest coast of South America represents an important breeding ground destination for at least some of the humpback whales that feed near the Antarctic Peninsula. In contrast, they provide no support for movement from the Antarctic Peninsula to the east coast of South America.

ACKNOWLEDGMENTS

This project would not have been possible without the cooperation of many dedicated naturalists, tourists, tour operators and researchers from throughout the world. Over 120 individuals or groups provided photographs that contributed to these analyses. Photographic comparison was conducted with assistance from B. Holm, M. McOsker, P. Olson, J. Rock and O. Uz. Field assistance was provided by P. Acuña, M.I. Barraquer, M. Bassoi, R. Bernal, G. Bravo, D. Danilewicz, P. Falk, P.A. Flores, E. Pérez, L. González, L. Medrano, I. Moreno and M.C.O. Santos. A. Larrea edited the INACH catalogue. Versions of this work have benefited from critical reading by R. Reeves, J. Robbins, P. Hammond, S. Katona, C. Petersen and J. Anderson. The formation of the Antarctic Humpback Whale Catalogue, its growth and expanding collaborative nature owe much to the efforts of C. Carlson, S. Katona and G. Stone. Financial support for conducting the photographic analysis was provided by the Friends of Conservation, the International Whaling Commission, and numerous contributors to the Antarctic Humpback Whale Catalogue programme, with additional logistical and financial support from Allied Whale, College of the Atlantic. For support of field research and of the editing and comparison of photographic collections we would like to thank: the Brazilian Antarctic Programme (PROANTAR); Brazilian Council for Scientific Research and Development (CNPq); Cetacean Society International; Colciencias; Conservation Action Fund; Ecofondo; Fundación Yubarta; Instituto Antartico Chileno; Interministerial Commission for the Resources of the Sea (CIRM)/Brazilian Navy; International Fund for Animal Welfare; Pacific Whale Foundation; Parque Nacional Marinho dos Abrolhos/IBAMA; Parques Nacionales; Petróleo Brasileiro SA (PETROBRAS); Redley; Whale and Dolphin Conservation Society; World Wildlife Fund-Office Colombia; and Yaqu Pacha. Portions of Fig. 1 include intellectual property of ESRI and its licensor(s) and are used under license.

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Abundance of eastern North Pacific gray whales on the 1995/96 southbound migration

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ABSTRACT

Systematic counts of gray whales (*Eschrichtius robustus*) were conducted from 13 December 1995 to 23 February 1996 at Granite Canyon, California. This study was the second of three during the five-year period following the removal of gray whales from the US government list of endangered and threatened wildlife. The counts were made at the same research station used most years since 1975 by the National Marine Mammal Laboratory to observe the southbound migration of the eastern North Pacific stock. Counting methods were kept similar to those used in previous surveys and included double counting to assess observer performance. In addition, aerial surveys and high-powered binoculars provided documentation that a negligible fraction of migrating whales passed beyond the sighting range of the counting observers. A total of 2,151 pods (3,928 whales) was counted during 472.7hrs of standard watch effort with visibility recorded as fair to excellent. Data analysis procedures were substantially the same as in previous years with a modification to account for differential sightability by pod size. Population size is estimated to be 22,263 whales (CV=9.25%; 95% log-normal CI=18,700-26,500). This estimate is similar to the previous estimate of 23,109 (CV=5.42%; 95% CI=20,800-25,700) from the 1993/94 survey.

KEYWORDS: GRAY WHALE; ABUNDANCE ESTIMATE; PACIFIC OCEAN; SURVEY-SHORE-BASED

INTRODUCTION

The eastern North Pacific stock of gray whales has a predictable migration which has allowed researchers to conduct counts at regular intervals (Reilly, 1984). From mid-December to mid-February each year, gray whales migrate south past the Granite Canyon research station near Carmel, California. Convenient access to this site and the narrowness of the whale's migratory corridor there have permitted an efficient counting process that has been repeated through many seasons (see Reilly, 1984 and Laake *et al*., 1994). In recent years, the counting procedure has been tested in several ways: (1) aerial surveys (Shelden and Laake, 2002) and shore-based surveys using high-power binoculars (Rugh *et al*., 2002) have documented the distribution of sightings on the seaward side of the migratory corridor; (2) comparison of aerial observations with shore-based observations has determined the bias in pod size estimates by shore-based observers (Laake *et al*., 1994); (3) paired, independent counts of observers have allowed an estimate of whales missed within the viewing range during adequate visibility periods (Rugh *et al*., 1990; 1993); and (4) data from radio-tagged gray whales near Granite Canyon (Swartz *et al*., 1987) and thermal sensor images (Perryman and Laake, 1994) have been used to estimate the ratio of night to daytime passage rates.

Analytical techniques have followed the method described in Buckland *et al*. (1993). Aspects of this method were developed for earlier abundance estimates in Reilly *et al*. (1983) and Breiwick *et al*. (1988); the method was applied to the 1992/93 and 1993/94 census results in Laake *et al*. (1994). Buckland and Breiwick (2002) estimate trends in abundance for this population.

The objective of the 1995/96 study was to make a systematic count of gray whales passing the research station during the southbound migration. The basic counting effort was kept comparable to efforts used in previous seasons including paired, independent counts. In addition, an aerial survey (Shelden and Laake, 2002) and a 25× binocular study (Rugh *et al*., 2002) documented offshore distribution, while a thermal sensor study (Perryman *et al*., 1999) estimated whale passage rates during non-watch periods. The additional studies will be reported in separate documents with results included here as available. This study was the second of three to be undertaken (in 1993/94, 1995/96 and 1997/98) in the five years following the removal of gray whales from the United States List of Endangered and Threatened Wildlife on 16 June 1994 (Federal Rule 59 FR 31095).

METHODS

Field study

Systematic counts of gray whales were conducted from 13 December 1995 to 23 February 1996, covering the duration of the southbound migration past the Granite Canyon research station. The site, 13km south of Carmel, California, has been used by the National Marine Mammal Laboratory (NMML) for most years since 1975. Observation sheds, set on a 20.5m bluff, provide some protection from the elements and help to maximise concentration on the viewing area. Although the field of view covers more than 150°, observers generally search through only 40-50° north of the standard azimuth, a line perpendicular to the coastline (241° magnetic) at the survey site. A total of eight people took part in the shore-based counts. Seven were experienced in cetacean surveys, and six had previous experience with gray whale counts at Granite Canyon. As in previous seasons, three three-hour standard watch shifts covered the nine daylight hours from 07:30 to 16:30 hours. Observers were rotated to maintain equal effort in each of the three shifts.

Standard watch procedures were as in previous surveys (Rugh *et al*., 1990; 1993; Laake *et al*., 1994). When a gray whale pod was first sighted, the time, horizontal bearing and vertical angle were recorded. Magnetic compasses in *Fujinon* 7×50 binoculars provided horizontal bearings (±2°), and 14 reticle marks in the binoculars provided vertical angles relative to the horizon (detailed in Rugh *et al*., 1993). The pod was tracked by the observer as it proceeded south past the survey site. A chart was available to predict the time and vertical angle at which the pod would cross the standard azimuth. The time, horizontal bearing and vertical angle were recorded a second time as close to the standard azimuth as possible. An estimate of pod size was recorded along with any unusual behaviour, the presence of a calf and the number of times the pod was seen as it passed the site. In addition to whale sightings, observers recorded start and end times of systematic search effort and times of environmental change. The observation environment was characterised by visibility (subjectively categorised from 1 to 6, i.e. excellent to unacceptable), sea state (Beaufort scale) and wind direction.

In addition to the primary watch, a second, independent watch was conducted once or twice daily from 3-26 January 1996. The field of view, shed and station conditions of this paired watch were nearly identical to those of the primary watch station. This provided an independent sighting record, allowing for comparisons between observers and estimation of the fraction of whales missed by the primary observer. Methods were as described in Rugh *et al.* (1990; 1993). The 'south shed', the primary watch station, was used for the standard counts; the 'north shed' was used only when paired counts were being made.

To document the offshore distribution of whales independently from the paired counts on the standard watch, searches through shore-based 25-power binoculars and an aerial survey were conducted. Two high-power binoculars were mounted in separate observation sheds. In this study, few pods were seen beyond 3 n.miles. Further details and results are described in Rugh *et al.* (2002). Aerial surveys were conducted from 13-23 January 1996, as described in Shelden and Laake (2002). Tracklines were flown perpendicular to the coastline within 3 n.miles north and south of the counting station. Most tracklines were 10 n.miles long, but samplings were also conducted out to 20 n.miles. Only 1.28% of the whales encountered were beyond 3 n.miles, so the paired, independent counts of shore-based observers are considered adequate to represent the drop-off in sighting rates as a function of distance from shore. Thus, it was determined that no correction, other than for probability of detection by distance, was necessary for whales passing the site beyond 3 n.miles offshore.

In January 1993 and January 1994, pod size estimation experiments were conducted. An airplane circled pods of whales as 10 shore-based observers estimated pod sizes independently. This test resulted in a total of 240 estimates from 60 pods. The data were used in Laake *et al.* (1994) to estimate bias in recorded pod size and have also been used in this analysis.

Analysis

Population abundance calculations have been modified here from the analytical procedures developed in Buckland *et al.* (1993) and used by Laake *et al.* (1994) to account for: (1) differential sightability by pod size; and (2) covariance within the estimated number of whales sighted when corrections are applied to individual sightings of pods. Accordingly, the systematic counts of southbound whales are used to estimate the total number of whales passing the site during usable periods of watch effort. This was done by estimating the number of pods of each size passing during watch periods, multiplying by recorded pod size, then correcting for bias in estimating pod size and summing the result. The number thus obtained for total whales passing during watch periods was then multiplied by corrections for: (1) whales passing when no watch was in effect (including periods with poor visibility) (f_t); and (2) differences in diurnal/nocturnal travel rates (f_n). The total abundance estimate ($\hat{N}$) is calculated as:

$$\hat{N} = \hat{W} \cdot f_t \cdot f_n$$

where $\hat{W}$ is the estimated number of whales passing during watch periods. The coefficient of variation (CV) is estimated by:

$$CV(\hat{N}) \cong \sqrt{CV^2(\hat{W}) + CV^2(Q) + CV^2(f_t) + CV^2(f_n)}$$

where CV(Q) represents variability in the observed passage rate of whales about the fitted passage rate used to estimate (f_t).

Selection of usable effort periods

The analysis began by calculating the time and vertical angle at which each pod crossed the standard azimuth, assuming a travel speed of 3kts and travel parallel to the coastline (see Rugh *et al.*, 1993). The time from the beginning of the survey to the end was partitioned into effort periods and non-effort periods. The effort periods were further partitioned so that change in observer, visibility, wind direction or Beaufort sea state began a new effort period. Each sighting was assigned to the effort period into which its azimuth crossing time fell. The average sightings per hour by visibility code were compared, to determine the threshold visibility below which sighting rates drop off significantly. Effort periods with poorer quality visibility than this threshold were considered non-effort periods in the subsequent analysis.

Estimate of total whale pods passing during watch periods

Corrections for whale pods missed within the viewing area during systematic watch were estimated from the paired, independent observation records from the north and south sheds. Comparison of sightings from the two locations provided capture-recapture data. Rugh *et al.* (1993) established a scoring algorithm that defined matches between records based on time, offshore distance and pod size. Iterative logistic regression (Buckland *et al.*, 1993) was used to identify significant covariates to the probability of detecting a pod and to estimate the detection probability associated with each recorded pod. Possible covariates were shed (north or south), watch period, day, observer, distance offshore, pod size, sea state, wind direction and whales per hour. Once the matching record was established, all covariates were examined individually as binned categorical data. For numeric data, functional forms were chosen or bins were combined to represent the data with as few parameters as possible. All covariates were then entered into the model, and a backward step-wise model selection was followed until no step decreased the Akaike Information Criterion (AIC). The logistic regression model was used to estimate p_{ie}, the detection probability of the ith pod of size e recorded by the south shed observer. The total number of pods of size e passing during the effort periods of the survey, $\hat{M}_e$, and its variance were estimated as:

$$\hat{M}_e = \sum_{i=1}^{m_e} \frac{1}{p_{ie}}, \quad Var(\hat{M}_e) = \sum_{i=1}^{m_e} \left[\frac{1 - p_{ie}}{p^2{}_{ie}} \right] + D_\beta(\hat{M}_e)^T \hat{\Sigma}_\beta D_\beta(\hat{M}_e)$$

where m_e is the number of pods assigned size e sighted from the south shed, $D_\beta(\hat{M}_e)$ is the vector of partial derivatives of $\hat{M}_e$ with respect to the vector of parameters β estimated in the logistic regression evaluated at $\hat{\beta}$, the vector of parameter estimates, and $\hat{\Sigma}_\beta$ is the estimated variance-covariance matrix of $\hat{\beta}$ (c.f. Borchers, 1996). The estimated total number of pods passing the field site during watch periods, $\hat{M}$, is then:

$$\hat{M} = \sum_{e=1}^{E} \hat{M}_e,\ \mathrm{Var}(\hat{M}) = \sum_{e=1}^{E} Var(\hat{M}_e) + 2\sum_{j=1}^{E-1}\sum_{k=j+1}^{E} D_\beta(\hat{M}_j)^T \hat{\Sigma}_\beta D_\beta(\hat{M}_k)$$

where E is the largest observed pod size.

Bias in recorded pod sizes

Bias in the mean recorded pod size results from differential sightability of pods by size and from underestimation of pod size by observers. The differential sightability was accounted for by using the estimated number of pods passing during a watch, $\hat{M}_e$, in place of the number of pods recorded, m_e, (c.f. Buckland *et al.*, 1993; Laake *et al.*, 1994). An additive correction for pod size estimation bias was estimated for each pod size, e, from data collected during earlier surveys. Variances and covariances for these corrections and the standard deviation of the sub-sample were estimated by a bootstrap method in which seven observers and 60 pods were drawn at random, with replacement, from a pod size estimation experiment dataset to generate 10,000 samples of equivalent size. The variances and covariances were estimated from the correction factors calculated from these datasets. The total number of whales passing the observation site during watch periods represented by pods recorded as size e, $\hat{W}_e$, was estimated as:

$$\hat{W}_e = \hat{M}_e(e + b_e) \quad , \quad Var(\hat{W}_e) = Var(\hat{M}_e)(e + b_e)^2 + \hat{M}_e^2 \hat{\sigma}_{be}^2 + \hat{M}_e s_e^2$$

where b_e is the estimated additive bias correction for pods estimated as size e from Laake *et al.* (1994), $\hat{\sigma}_{be}^2$ is the bootstrap estimate of the variance of b_e, and s_e is the bootstrap estimate of the standard deviation of the bias estimation samples for pods estimated as size e. Note that the variance consists of three summands. The left and center summands represent the estimation errors in $\hat{M}_e$ and b_e, and the right summand is the variation due to classification errors in assigning pod size. The total number of whales passing the site during usable watch periods was estimated as:

$$\hat{W} = \sum_{e=1}^{E} \hat{W}_e \quad , \quad CV(\hat{W}) = \frac{1}{\hat{W}} \sqrt{\sum_{e=1}^{E} Var(\hat{W}_e) + 2\sum_{j=1}^{E-1}\sum_{k=j+1}^{E} \begin{bmatrix} (j + b_j) D_\beta(\hat{M}_j)^T \hat{\Sigma}_\beta\ D_\beta(\hat{M}_k)(k + b_k) \\ +\hat{M}_j\ \hat{M}_k \hat{\sigma}_{bjk} \end{bmatrix}}$$

where $\hat{\sigma}_{bjk}$ is the bootstrap estimated covariance of b_j and b_k.

Correction for whales passing during non-watch periods (f_t)

The rate of whales passing the site through time was modelled by a normal distribution with Hermite polynomials added to adjust for skewness, kurtosis and higher moments (Buckland *et al.*, 1993). The model defines a bell-shaped rate function, $q(t)$, of expected whales per day integrated to correct for periods when no watches were conducted. The correction factor, f_t, was defined as the ratio of the total area under the function, Q, to the sum over all watch effort periods of the area under the function during each effort period, (for the kth effort period). Components of $CV(N)$ that resulted from this analysis were the $CV(f_t)$, from the variance of the parameters of $q(t)$, and $CV(Q)$, which represents the variance about the Q_k of the corrected number of whales in the kth effort period.

Correction for difference in diurnal/nocturnal travel rates (f_n)

The night passage rate, f_n, used by Buckland *et al.* (1993) was also used here. It was based on data from radio-tagged gray whales near Granite Canyon (Swartz *et al.*, 1987).

RESULTS

There was a total of 524.5 hours of survey effort during the 73 days on which standard watches were conducted from 13 December 1995 to 23 February 1996. The average encounter rate of pods per hour in fair to excellent viewing conditions (visibility ≤4) was 4.550 (SE=0.409) and dropped off significantly to 2.991 pods per hour (SE=0.437, *p*=0.005) at visibility below fair (>4) (Table 1). Visibility 4 was thus selected as the threshold value for usable effort periods. There was a total of 472.7 hours of watch in usable effort in the standard watch and 51.8 hours when visibility was too poor (>4) to be included in the analysis. During the standard watch, a total of 2,300 southbound pods (4,197 whales) were recorded, of which 2,151 pods (3,928 whales) were seen with visibility ≤4 (Table 1). Average recorded pod size was 1.83 (CV=1.46%) during usable effort periods.

Table 1

Rates of sightings of gray whale pods by visibility code.

Visibility	Visibility code	Pods/hr	SE	Hours of effort	Number of pods
Excellent	1	10.800	0.480	2.5	27
Very good	2	5.483	0.729	76.8	421
Good	3	4.157	0.303	240.1	998
Fair	4	4.596	0.358	153.4	705
Poor	5	2.991	0.437	49.8	149
Unacceptable	6	0.000	0.000	2.0	0
All effort				524.5	2,300
Usable effort	1 - 4	4.550	0.409	472.7	2,151

The passing rate of the migration was symmetrical around the peak of the migration on 16 January 1996 (day 47.8 with 1 December 1995 = day 1) with a standard deviation of 12.1 days (Fig. 1). No Hermite polynomial corrections to the normal distribution were necessary. The correction factor for whales passing when no watches were in effect, f_t, was estimated to be 3.30 (CV=0.10%). The mean sighting rate during visibility ≤4 for the period 15-19 January 1996 of 9.1 pods/hr, was lower than the 11 pods/hr seen during 15-19 January 1994 and 10.7 pods/hr seen during 15-19 January 1995.

The mean offshore distance of gray whale pods seen with visibility ≤4 was 1.05 n.miles (1.94 km; SD=0.397 n.miles; Fig. 2). When corrected for differential sightability by pod size and distance, the mean offshore distance was 1.25 n.miles (2.31km; SD=0.807 n.miles, SE=0.17 n.miles). This was comparable to the mean sighting distance of 1.21 n.miles (SE=0.06) found during aerial surveys conducted in January 1996 (Shelden and Laake, 2002).

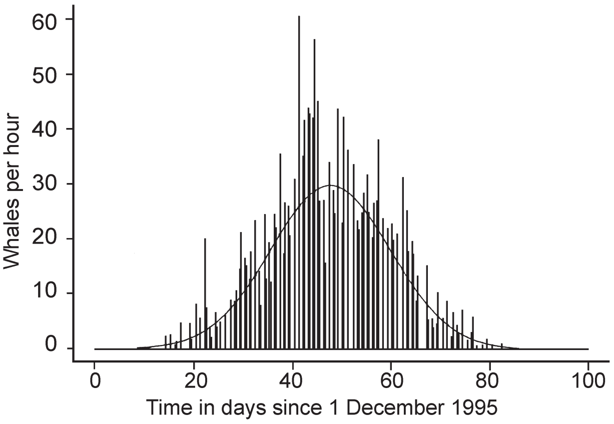

Fig. 1. Sighting rates of gray whales in the standard watch effort periods 13 December 1995 to 23 February 1996 during the southbound migration past Granite Canyon, California. Only effort periods with visibility ≤4 were included. Curve is fitted passage rate, *q*(*t*).

A total of 640 pods passed during periods of double counts with visibility ≤4. Of these, 456 were seen by both observers and 184 by only one observer. Examination of the individual categorical parameter fits of the possible covariates indicated that a third order polynomial would be sufficient to model the effect of distance offshore. The pod size effect appeared linear up to size five where it levelled off. Consequently, pod size was truncated at five and entered as a linear effect. All other numeric data were entered as linear effects. A stepwise logistic regression model selection resulted in significant effects of distance offshore (a second order polynomial), pod size, sea state and observer (Table 2). Pair-wise interactions were considered between each of these factors, the interaction between distance offshore and pod size was found to be significant. The resulting model was applied to the south shed data to estimate the correction for pods missed during watch. The logistic regression showed differential sightability by pod size and it was thus necessary to correct each pod size class separately.

Bias estimates (Table 3) from Laake *et al.* (1994) were used to correct the pod sizes (Table 4) so that mean corrected pod size was estimated as 2.56 (CV=8.80%). The estimated number of whales passing during watch periods was 6,611 (CV=8.62%). The total number of whales passing Granite Canyon during the 1995-96 southbound migration was estimated to be 22,263 (CV=9.25%; 95% CI=18,700-26,500; Table 5).

Table 2

Covariates and fitted parameters used to model the pod detection probability. Covariates are distance (D), pod size (PS), sea state (SS) and observer (OBS).

	Value	SE	t-value	Df	Sum of squares	Residual sum of squares
Constant	-1.407	1.094	-1.287			1,245.4
D(n.mile)	4.504	1.354	3.326	1	11.1	1,256.5
D^2	-1.681	0.423	-3.971	1	15.8	1,261.2
PS	1.421	0.714	1.990	1	4.0	1,249.4
DxPS	-1.681	0.875	-1.921	1	3.7	1,249.1
D^2xPS	0.517	0.259	1.999	1	4.0	1,249.4
SS	0.178	0.086	2.063	1	4.3	1,249.7
OBS				7	25.2	1,270.6

Table 3

Estimated biases by pod size from Laake *et al.* (1994) where b_e is the additive pod size correction, s_e is the bootstrap derived standard deviation around b_e and $\hat{\sigma}^2_{be}$ is the bootstrap derived standard error of b_e.

Pod size	b_e	s_e	$\hat{\sigma}^2_{be}$
1	0.941	1.273	0.071
2	0.646	1.262	0.064
3	0.607	1.229	0.155
4+	0.250	1.916	0.432

DISCUSSION

The population estimate calculated for the 1995/96 season (22,263) was very close to the Laake *et al.* (1994) estimate for 1993/94 (23,109; CV=5.42%, 95% CI=20,800-25,700) and that for 1987/88 (21,296; CV=6.05%, 95% CI=18,900-24,000) (Buckland *et al.*, 1993), but all of these were significantly higher than the Laake *et al.* (1994) estimate for 1992/93 (17,674; CV=5.87%, 95% CI=15,800-19,800). Variations in estimates may in part be due to undocumented vagaries in sampling or to differences in the proportion of the gray whale population that migrates as far south as

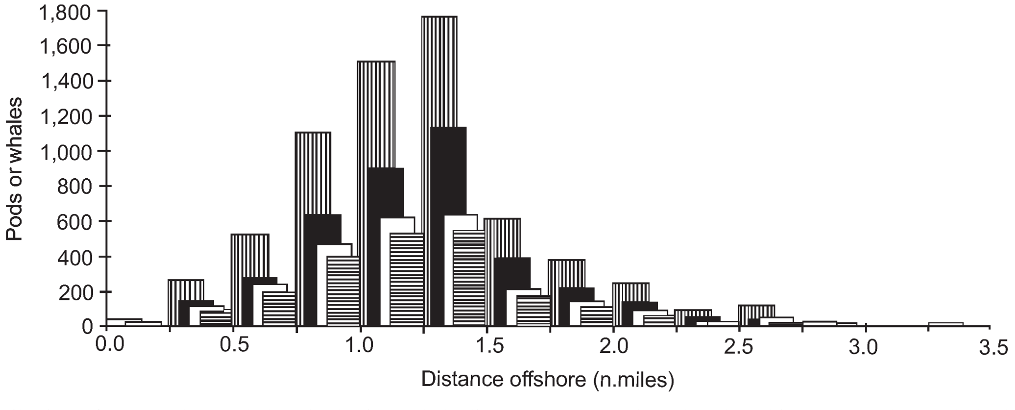

Fig. 2. Offshore distribution of: (1) total recorded pods (horizontal shading); (2) corrected total pods (white); (3) total recorded whales (black); (4) corrected total whales (vertical shading) from sightings of gray whales made between 13 December 1995 and 23 February 1996 during the southbound migration past Granite Canyon, California. Only effort periods with visibility ≤4 were included.

Table 4

Estimation of total whales passing during watch periods.

Pod size	Number of recorded pods	Average correction for missed pods	Corrected pod size	Estimated total whales	CV of total whales (%)
1	1,180	1.234	1.941	2,826	14.9
2	538	1.161	2.646	1,653	10.8
3	235	1.157	3.607	980	12.6
4	105	1.138	4.250	507	17.9
5	50	1.127	5.250	295	15.6
6	19	1.187	6.250	140	16.8
7	14	1.085	7.250	110	14.3
8	6	1.110	8.250	55	18.2
9	3	1.068	9.250	30	20.4
10	1	1.071	10.250	11	31.9
All	2,151	1.198		6,611	8.62

Carmel each year. Gray whale migrations have become increasingly delayed, particularly since the 1970s (Buckland and Breiwick, 2002). The 1995/96 migration continued this trend with its median date being later than for nearly all other surveyed years. In the autumn of 1995, sea ice in the northern Chukchi Sea was unusually late in forming (J.C. George, pers. comm.). The mild ice conditions may have meant that whales were distributed farther in the Arctic than usual and thus took longer to migrate south. This may explain the lower peak and perhaps the broader shape (reflected in the standard deviation) of the migration distribution observed in 1995/96 (Fig. 1) relative to previous years. This trend in increasingly later dates for the onset of southbound migrations may be a function of increased population size. Possibly, with the increased density of gray whales in the summer feeding areas, food resources have become more limited such that whales are dispersed more prior to their migration south while building up fat reserves (Rugh *et al*., 2001). An alternative would be that the number of pregnant females has not increased as much as the rest of the population in the past decade, owing to a slowing growth rate in the population. Pregnant females lead the southbound migration (Rice and Wolman, 1971), and thus the difference between numbers of pregnant females and numbers of all other whales would result in an apparent delay in the first phase of the migration.

The analysis followed a slightly different course to that of Buckland *et al.* (1993) and Laake *et al.* (1994) because detection probability of pods varied significantly with recorded pod size. If this effect were to be ignored and the method of Buckland *et al.* (1993) and Laake *et al.* (1994) followed, the abundance estimate would be 22,571 whales (CV=5.24%; 95% CI=20,400-25,000). Although that results in a slightly decreased abundance (*ca* 1.5%), the CV is nearly double, primarily owing to the use of bootstrap variances for pod size corrections and to including the covariance components of the variance of total whales passing during watch periods, thereby suggesting that CV(*N*) has been underestimated for earlier years.

ACKNOWLEDGEMENTS

The NMML sponsored the study with funds for field support through NOAA's F/PR Marine Mammal Research Plan. Shore-based observers included L. Baraff, D. DeMaster, L. Gerber, S. Hill (NOAA Corps), R. Hobbs, J. Lerczak, D. Rugh, K. Shelden and J. Waite from the NMML, T. Martin (NOAA Corps) and A. Von Saunder (NOAA Corps) from the Southwest Fisheries Science Center (SWFSC), and M. Scillia from the Moss Landing Marine Laboratory. W. Perryman (SWFSC) provided ideas and field support, including the loan of two high-powered binoculars from SWFSC. K. Shelden (NMML) led the aerial surveys with J. Gilpatrick (SWFSC) and a rotation of Hill, Martin and Von Saunder as observers. Use of the Granite Canyon research station, operated by the State of California's Department of Fish and Game as their Marine Pollution Studies Laboratory, was supported by M. Puckett (Director) and J. Lytle. J. Laake provided much useful advice during the analysis. Manuscript reviews by Laake, Lerczak, P. Boveng (NMML) and two anonymous reviewers provided many helpful comments.

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Table 5

Estimated abundance and intermediate parameters, Eastern North Pacific stock of gray whales, 1995/96.

Parameter	Estimate	SE	CV (%)
Total pods recorded by south observer during watch periods (m)	2,151		
Estimated total pods ($\hat{M}$)	2,578	46.8	1.82
Mean recorded pod size	1.83	0.027	1.46
Corrected mean pod size	2.56	0.226	8.80
Estimated number of whales passing Granite Canyon during watch periods ($\hat{W}$)	6,611	570	8.62
Correction for pods passing outside watch periods (f_t)	3.30	0.003	0.09
Estimated total whales without night travel correction (Q)	21,827	1,882	8.62
Correction for night travel (f_n)	1.02	0.023	2.25
Estimated number of whales passing Granite Canyon ($\hat{N}$)	22,263	2,060	9.25

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An examination of assessment models for the eastern North Pacific gray whale based on inertial dynamics

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ABSTRACT

Bayesian assessments of the eastern North Pacific stock of gray whales are conducted using the standard BALEEN II model and the inertia model developed by Witting (2000; 2001; 2003). The analyses confirm the increase in gray whale population size since 1968, but indicate that catches up to 256 animals per annum will lead to population decline if the inertia model is correct. However, analyses based on the standard BALEEN II model with a starting year of 1930 or 1968 fit the calf count data better than the inertia model, and indicate a population at its (current) equilibrium level and that the current catches are sustainable. The results of both the BALEEN II model and the inertia model are sensitive to the choice of the functional form used to represent density-dependence and those of the inertia model to the starting year for the analyses.

KEYWORDS: GRAY WHALE; POPULATION ASSESSMENT; TRENDS; MODELLING; WHALING-ABORIGINAL

INTRODUCTION

The eastern North Pacific (ENP) stock of gray whales (*Eschrichtius robustus*) was reduced substantially due to the impact of large and unsustainable harvesting during the late 19th Century (Fig. 1). No direct estimates of historical population size nor of the population size following the large historical commercial removals are available, although Townsend (1886) believed the stock to be only 160 individuals. Following the cessation of commercial harvesting, and under low aboriginal harvests, the population began to recover and surveys during the 1990s placed the population between 20,000 and 30,000 animals. The two most recent estimates of abundance (in 2001 and 2002) are, however, lower (18,200 and 16,900) prompting hypotheses that the population may have reached (or even exceeded) its (current) equilibrium level in the absence of harvest.

Given the lack of information on abundance prior to the commencement of the surveys at Granite Canyon in 1967, the only way to determine historical population sizes is through the use of population dynamics models. The models commonly used to assess whale populations assume that some population component (usually the birth rate/infant survival rate) is subject to density-dependent regulation. However, the inability of simple density-dependent population dynamics models to reconcile the catch history and abundance estimates for the ENP gray whales is well-known (Reilly, 1981; 1984; Cooke, 1986; Lankester and Beddington, 1986; Butterworth *et al.*, 2002). The inconsistency between these data sources arises because the stock must be relatively productive given the trend in population size inferred from the surveys off California. However, this implies that the stock should have recovered to its pre-exploitation level given the relatively low catches over the past 80-100 years. Reasons advocated to explain this inconsistency include large changes over time in carrying capacity and that the historical catches have been substantially under-estimated (Butterworth *et al.*, 2002).

Recent (Bayesian) assessments of this stock (Punt and Butterworth, 2002; Wade, 2002) have adopted a different approach to dealing with this inconsistency; they have not attempted to model the entire exploitation history but have instead started the population projections in a more recent year. The philosophy underlying these Bayesian assessments is to place a prior distribution on the abundance in a particular year (in general 1930) and to assume that the population had a stable age-structure at the start of that year. The population is then projected forwards to 2002 and the likelihood for the projection is calculated. The assumption that the population had a stable age-structure in 1930 is not unreasonable given the low catches for many of the years prior to 1930 (Fig. 1). The results are, in any case, insensitive to the first year considered in the analysis within a fairly wide range (Punt and Butterworth, 2002). The *Evaluation Trials* developed for the ENP gray whales (IWC, 2002; 2003) are based on a similar approach to assessing this stock.

Witting (2000) introduced the concept of inertial dynamics to discussions of large whales. An 'inertia model' involves the intrinsic values for some of the model parameters (e.g. the birth rate) differing among individuals and being determined from the state of the population (i.e. its size relative to some reference level) when they were born. The values for these parameters do not change over time. This concept leads to time-varying carrying capacity and the possibility of cyclic dynamics. Witting (2001; 2003) extended the concept of an inertial model by incorporating inertial dynamics into the BALEEN II model (de la Mare, 1989; Punt, 1999) and conducting Bayesian assessments of the ENP gray whales. These assessments were simultaneously able to both start the population projections prior to 1930 and provide adequate fits to the abundance data. They suggested, however, a much lower current replacement yield than indicated by previous assessments, essentially because they predicted a reduction in carrying capacity in the future. The analyses of Witting (2001) suggest a marked decline in abundance in the future, even in

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the absence of exploitation, although those of Witting (2003), which were based on a different data set, were less pessimistic.

Even ignoring inertial dynamics, the assumptions on which the analyses conducted by Witting (2001; 2003) are based differ somewhat from those underlying the most recent assessments of the ENP gray whales (Punt and Butterworth, 2002; Wade, 2002). This paper therefore develops an approach to including inertial dynamics into the model (BALEEN II) on which most recent assessments of the ENP gray whales are based (i.e. the conventional BALEEN II model is a special case of this extended model).

The analyses by Witting (2001; 2003) imply marked changes over time in birth rate. Therefore, consideration is given to validating the results of the alternative models using the data on calf counts (e.g. Poole, 1984; Perryman *et al.*, 2002). No attempt is made in this paper to fit the population dynamics model to the calf count data.

METHODS

Extensions of the BALEEN II model

The BALEEN II model and the extensions thereof needed to start the population projections for a year other than that in which the population was last equal to its pre-exploitation size with the corresponding age-structure are described in detail by Punt (1999). The key extension needed to include inertial dynamics in the BALEEN II model is (after Witting, 2001; 2003) to allow the age-specific birth rate/infant survival rate to be 'intrinsic' and related to the conditions when an animal was born (i.e. each cohort has a different 'intrinsic' birth rate/infant survival rate). The equation that defines the number of 0-year-olds (of both sexes) at the start of year t, B_t, is given by:

$$B_t = \sum_{a=a_m+1}^{x} \tilde{\gamma}_{t,a}\, \beta_a (R^{\mathrm{f}}_{t,a} + U^{\mathrm{f}}_{t,a}) \qquad (1)$$

where:

$R^s_{t,a}$	is the number of recruited animals of sex s (f= female/m=male) and age a at the start of year t;
$U^s_{t,a}$	is the number of unrecruited animals of sex s and age a at the start of year t;
a_m+1	is the lowest age that a female can reach first parturition;
β_a	is the fraction of females of age a which have reached the age at first parturition;
$\tilde{\gamma}_{t,a}$	is the birth rate for females of age a during year t:

$$\tilde{\gamma}_{t,a} = \begin{cases} 0 & \text{if } f_t\,\gamma_{t,a} < 0 \\ f_t\,\gamma_{t,a} & \text{if } 0 \le f_t\,\gamma_{t,a} \le f_{\max} \\ f_{\max} & \text{if } f_t\,\gamma_{t,a} > f_{\max} \end{cases} \qquad (2)$$

$\gamma_{t,a}$	is the 'intrinsic' birth rate for females of age a during year t;
$f_{\max}$	is the maximum possible birth rate;
f_t	is the impact during year t of density-dependence on the birth rate/infant survival rate for those age-classes for which all females have reached the age at first parturition, multiplied by the birth rate at pre-exploitation equilibrium, either:

$$f_t = \begin{cases} f_0\, e^{\kappa(1-D_t/D_{-\infty})} & \text{exponential} \\ \max(0, f_0[1 + A\{1-(D_t/D_{-\infty})^z\}]) & \\ & \text{Pella-Tomlinson} \end{cases} \qquad (3)$$

A	is the resilience parameter for the Pella-Tomlinson model;
z	is the density-dependence parameter for the Pella-Tomlinson model;
κ	is the resilience parameter for the exponential model;
f_0	is the birth rate at pre-exploitation equilibrium;
x	is the maximum age-class (treated as a plus-group and taken to be age 15);
D_t	is the size, at the start of year t, of the component of the population to which density dependence is functionally related – density-dependence is assumed to be functionally related to the number of females that have reached the age at first parturition, P^M_t, for the calculations of this paper for consistency with the assumptions underlying previous assessments of the ENP gray whales), and
$D_{-\infty}$	is the value of D_t at pre-exploitation equilibrium.

The dynamics of the 'intrinsic' birth rate are given by:

$$\gamma_{t+1,a} = \begin{cases} g_{t+1} \dfrac{1}{P^M_{t+1}} \displaystyle\sum_{a=a_m+1}^{x} \gamma_{t+1,a}\, \beta_a (R^f_{t+1,a} + U^f_{t+1,a}) & \text{if } a = 1 \\ \gamma_{t,a-1} & \text{if } 2 \le a \le x-1 \\ \dfrac{1}{R^{\mathrm{f}}_{t+1,x}} \begin{pmatrix} \gamma_{t,x}\, R^{\mathrm{f}}_{t,x}(1-F^{\mathrm{f}}_{\mathrm{r},t,x})S^{\mathrm{f}}_x \\ +\gamma_{t,x-1}\, R^{\mathrm{f}}_{t,x-1}(1-F^{\mathrm{f}}_{\mathrm{r},t,x-1})S^{\mathrm{f}}_{x-1} \end{pmatrix} & \text{if } a = x \end{cases} \qquad (4)$$

where:

$F^s_{\mathrm{r},t,x}$	is the exploitation rate on 'recruited' animals of sex s and age a during year t (see Punt (1999) for details);
S^s_a	is the (density-independent) survival rate for animals of sex s and age a;
P^M_t	is the number of females that have reached the age at first parturition:

$$P^M_t = \sum_{a=a_m+1}^{x} \beta_a (R^{\mathrm{f}}_{t,a} + U^{\mathrm{f}}_{t,a}) \qquad (5)$$

g_t	is the impact of density-dependence on the 'intrinsic' birth rate (governed by one of the following functional forms and constrained to be less than 5):

$$g_t = \begin{cases} e^{\phi\kappa(1-D_t/D_{-\infty})} & \text{exponential} \\ \max(0, 1 + A\phi\{1-(D_t/D_{-\infty})^z\}) & \text{Pella-Tomlinson} \end{cases} \qquad (6)$$

ϕ	determines the magnitude of 'inertial' dynamics.

The values for the $\gamma_{t,a}$ for the first year of the population projection, y_1, are set equal to 1. The function g determines the extent of inertial dynamics. The model outlined above collapses to the standard density-dependent population dynamics model (i.e. BALEEN II) if ϕ is set equal to 0, i.e. $\gamma_{t,a}$ = 1 for all t and a.

Data and likelihood function

Fig. 1 plots the historical commercial and aboriginal catches. The sex-ratio of the commercial and recent aboriginal catch is known to be biased towards females. However, as no information is available about the sex-ratio of the historical (pre-1944) aboriginal catches, a 50:50 sex-ratio is assumed for these catches for consistency with previous analyses (e.g. IWC, 2002; 2003).

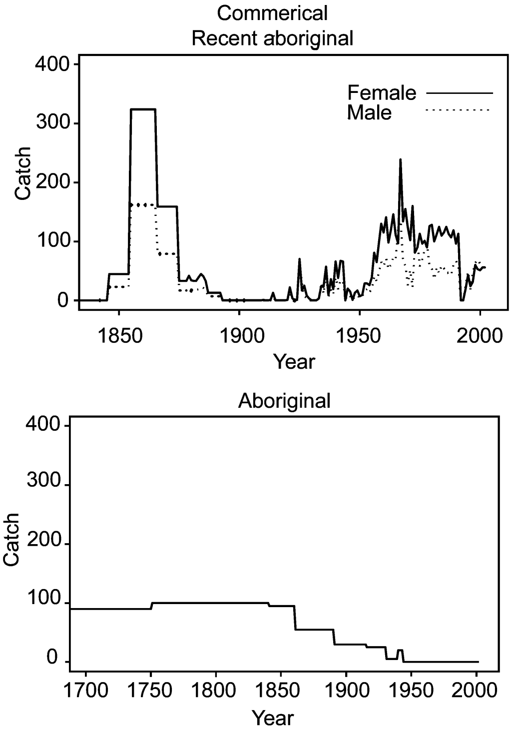

Fig. 1. The commercial and recent aboriginal (post-1943) catches (upper panel) and the historical (pre-1944) aboriginal catches (lower panel). The sex-ratio of the historical aboriginal catches is assumed to be 50:50.

The data used to estimate the values for the 'free' parameters of the model are the estimates of 1+ abundance from the surveys conducted at Granite Canyon, California. The sampling coefficients of variation for these estimates are known to underestimate the actual extent of observation error variability, so, following Wade (2002), these coefficients of variation are inflated by an 'additional variance' term. For consistency with the approach used to condition the AWMP *Evaluation Trials* (IWC, 2003) for the ENP gray whales, the 1+ abundance estimates are assumed to be independently and identically log-normally distributed. This assumption leads to the following likelihood function (ignoring constants independent of the model parameters):

$$L = \prod_t \frac{1}{\sqrt{\sigma_t^2 + E(CV_{\mathrm{add},t}^2)}} \exp\left(-\frac{(\ell n P_t^{\mathrm{obs}} - \ell n \hat{P}_t^{1+})^2}{2(\sigma_t^2 + E(CV_{\mathrm{add},t}^2))} \right) \quad (7)$$

where:

P_t^{obs} is the shore-count-based estimate of the (1+) abundance at the start of year t (the data point for year t is the survey that straddled years t-1 and t);

$\hat{P}_t^{1+}$ is the model-estimate of the (1+) abundance at the start of year t;

σ_t is the standard deviation of the logarithm of P_t^{obs} (approximated by its coefficient of variation);

$E(CV_{\mathrm{add},t}^2)$ is the square of the model-predicted CV of the additional variation for year t:

$$E(CV_{\mathrm{add},t}^2) = CV_{\mathrm{add}}^2 \frac{0.1 + 0.013\tilde{K}_{1+}/\hat{P}_t^{1+}}{0.1 + 0.013\tilde{K}_{1+}/\hat{P}_{1968}^{1+}}$$

CV_{add}^2 is the additional variation associated with the estimate of 1+ abundance for 1968; and

$\tilde{K}_{1+}$ the current equilibrium level for the 1+ component of the population[1].

The square of the total CV for the abundance estimate for year t is therefore modelled as the sum of two components: the square of the CV of the estimation error associated with the sampling variation (σ_t^2), and the square of the CV associated with the additional variance ($CV_{\mathrm{add},t}^2$). The size of the latter component is assumed to be density-dependent with the extent of density-dependence modelled as for the AWMP *Evaluation Trials* (IWC, 2003). The value for CV_{add} for 1968 is treated as an estimable parameter of the model. Data are also available on the extent of variation due to school size estimation error. However, these data are only available since the 1995/96 survey and consequently are ignored for the purposes of the analyses of this paper. IWC (2003) includes these data when conditioning the AWMP *Evaluation Trial*s for the ENP gray whales. This is because the performance of alternative *Strike Limit Algorithms*[2] for the ENP gray whales may be sensitive to the source of the additional variation in the abundance estimates.

Note that this approach to constructing the likelihood function implies that, although information on calf counts is available (e.g. Poole, 1984; Perryman *et al.*, 2002), these data are not used when fitting the model. Rather the calf count data are used to independently validate some of the predictions of the model.

Parameterisation and parameter estimation

The 'free' parameters of the model depend on whether the birth rate/infant survival rate is 'intrinsic' or not and the functional form assumed to model density-dependence. For the conventional density-regulated model (BALEEN II), these parameters are: $\tilde{K}_{1+}$, S_0 – the calf survival rate, S_{1+} – the survival rate for animals aged one year and above, a_m – the age-at-maturity, P_{1968}^{1+} – the 1+ population size in 1968, CV_{add} – the additional variance parameter, and the parameters of density-dependence function (A – the resilience parameter and z – the degree of compensation for the Pella-Tomlinson model, and κ for the exponential model; see Equation 3). The parameters of the 'intrinsic' model are the same as those of the density-regulated model, except that the value of ϕ (see Equation 6) is an estimated parameter rather than being assumed to be equal to 0.

The age at recruitment is not estimated. Instead, all of the analyses of this paper assume knife-edged recruitment at age 5 (IWC, 1993; Butterworth *et al.*, 2002). A Bayesian approach is used to estimate the 'free' parameters of the model based on the prior distributions in Table 1 and the Sampling/Importance Resampling (SIR) algorithm (Rubin, 1988).

The SIR algorithm for drawing a set of equally likely vectors of model parameters from the posterior distribution is as follows (the population projections are assumed to start in year y_1):

(a) Draw values for the parameters S_{1+}, $f_{\max}$, a_{m}, $MSYR_{\mathrm{mat}}$, $MSYL_{\mathrm{mat}}$, $\tilde{K}_{1+}$, P_{1968}^{1+}, CV_{add}, κ, and ϕ from the priors in Table 1.

(b) If density-dependence is assumed to be governed by the Pella-Tomlinson model, the system of equations that

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[1] Unlike the norm for baleen whale assessments, when y_1, the first year considered in the analysis, is greater than 1846, $\tilde{K}$ is not necessarily equal to the pre-exploitation size of the resource, because (for example) this analysis does not preclude a change over time in the environmental carrying capacity. Rather, when $y_1 > 1846$, $\tilde{K}$ should be considered to be the *current* (and assumed future) environmental carrying capacity.

[2] Algorithms that produce limits on the number of strikes for a stock of whales subject to aboriginal harvest.

relate *MSYL*, *MSYR*, S_0, S_{1+}, $f_{\max}$, a_m, *A* and *z* assuming that there is no inertial dynamics (Punt, 1999; Equations 18-21) are solved to find values for S_0, *A* and *z*.

(c) If density-dependence is assumed to be governed by the exponential model, the value of S_0 is chosen so that the relationship $f_0 = f_{\max} / e^{\kappa(1+\phi)}$ is satisfied.

(d) If y_1 >1846 (e.g. 1930), find the population size in year y_1 and the population rate of increase in this year, so that, if the population is projected from year y_1 to 1968, the total (1+) population size in 1968 equals the generated value for P^{1+}_{1968}.

(e) If y_1 = 1600 or 1846, find the value of $\tilde{K}_{1+}$ so that, if the population is projected from year y_1 to 1968, the total (1+) population size in 1968 equals the generated value for P^{1+}_{1968} (see Butterworth and Punt (1995) and Punt and Butterworth (1999) for full details of how $\tilde{K}_{1+}$ is calculated given a value for P^{1+}_{1968}).

(f) Compute the likelihood for the projection (see Equation 7).

(g) Steps (a)-(f) are repeated a very large number (typically 1,000,000) of times.

(h) 5,000 parameter vectors are selected randomly from those generated using steps (a)-(f), assigning a probability of selecting a particular vector proportional to its likelihood.

The above formulation implies that the year for which a prior on abundance is specified (1968) is not necessarily the same as the first year of the population projections (y_1). Analyses are conducted for four alternative starting years (i.e. y_1=1600, 1846, 1930 and 1968). Those analyses with starting years of 1600 and 1846 begin the population projection at pre-exploitation equilibrium while those analyses with starting years of 1930 and 1968 begin the population projections at a stable age-structure. *MSYR* and *MSYL* do not have their conventional definitions when there are inertial dynamics (i.e. $\phi \neq 0$). These parameters are included to provide a link with the previous assessments and because they provide a 'natural' way to place priors on the parameters *A* and *z* when density-dependence is governed by the Pella-Tomlinson model.

The prior distributions assumed for the bulk of the parameters (Table 1) are taken to be those on which the 1997 assessment of the ENP gray whales (IWC, 1998) was based. The prior distributions for the parameters that determine the extent of inertial dynamics (κ and ϕ) are taken to be uniform with bounds chosen to encompass the values supported by the data.

Differences from Witting (2003)

Although the population dynamics model underlying the analyses of this paper (Equations 1-6) is identical to that on which the analyses of Witting (2003) are based, there are several notable differences between the approach used for parameter estimation in this paper and that used by Witting (2003).

(1) The analyses of this paper are based on the 'backwards' approach to conducting Bayesian analyses (see step (e) above), i.e. a uniform prior is placed on the population size in a recent year (1968) instead of a uniform prior being placed on the equilibrium level, $\tilde{K}_{1+}$. The main reason for parameterising the model in this way (Butterworth and Punt, 1997) is that it avoids the priors for the parameters that determine productivity (*MSYR* for the BALEEN II model and ϕ and κ for the inertia model) being updated purely by the process of projecting the model forward (because combinations of low productivity and low *K* lead to extinction before 2002 and are consequently assigned zero likelihood). The process of sampling parameter vectors from the prior is also more efficient if the 'backwards' approach is adopted. This approach to conducting Bayesian assessments forms the basis for the trials used to evaluate *Strike Limit Algorithms* for the ENP gray whales and the Bering-Chukchi-Beaufort Seas stock of bowhead whales (IWC, 2002; 2003).

(2) A prior is placed on the maximum possible birth rate rather than on the survival rate for calves. In contrast, Witting (2003) places independent uniform priors on S_{1+} and S_0 and a U[0.3, 0.6] (or U[0.2,0.6] for a start year of 1600) prior on the maximum possible birth rate. The approach of this paper (through steps (b) and (c) above) implies that the maximum possible birth rate can be achieved at very low population size; this is not case with the approach taken by Witting (2003). This paper also imposes the constraint that S_0 be less than S_{1+}, a constraint not imposed by Witting (2003) who assumed independent priors for these two parameters.

(3) Witting (2003) restricts the number of population size cycles between the first year of the assessment and 2005 to one when the analysis starts in 1846 and to two when it starts in 1600 – no such restriction (which is equivalent to adding a new prior) is imposed here; rather the data are used to determine the relative likelihood of alternative parameter values (and hence number of cycles).

Table 1

The prior distributions.

Parameter	Prior distribution
Non-calf survival rate, S_{1+}	U[0.95, 0.999]
Age-at-maturity, a_m	U[5, 9][a]
$\tilde{K}_{1+}$[b]	U[0, 70,000]
1968 abundance, P^{1+}_{1968}	$\ell n P^{1+}_{1968} = N(\ell n 12,921; 0.0746^2 + CV^2_{\mathrm{add}})$
$\mathrm{MSYL_{mat}}$ (%)	U[40, 80]
$\mathrm{MSYR_{mat}}$ (%)	U[0, 10]
Extent of density-dependence, κ	U[0, 4]
Extent of inertial dynamics, ϕ	U[0, 4]
Maximum birth rate, $f_{\max}$	U[0.3, 0.6]
Additional variation (population estimates), CV_{add}	U[0, 0.35]

[a]Discrete uniform distribution; [b]The prior for $\tilde{K}_{1+}$ is ignored if the population projections start at pre-exploitation equilibrium (i.e. $y_1 \leq 1846$).

(4) The priors for some of the remaining parameters are slightly different and there are some slight differences in how the model is parameterised (e.g. Witting (2003) defines the function g as $\exp(\phi\kappa(D_t - D_{-\infty}))$ rather than as $\exp(\phi\kappa(1 - D_t/D_{-\infty}))$).

Apart from (3) the differences between the approach of this paper and that of Witting (2003) relate to how the model is implemented within a Bayesian estimation framework. Maximum likelihood results do not depend on how the model is parameterised nor on the priors for the model parameters so the two approaches should be fully comparable had the analyses been based on maximum likelihood rather than Bayesian techniques.

RESULTS AND DISCUSSION

Management related quantities

The results are summarised by the posterior medians, means and 90% credibility intervals for the following management-related quantities:

(a) $MSYR_{\text{mat}}$ – the Maximum Sustainable Yield rate (in terms of harvesting of the mature component of the population and expressed as a percentage);
(b) $\tilde{K}_{1+}$ – the equilibrium level for the 1+ component of the population;
(c) $P^{1+}_{2002} / \tilde{K}_{1+}$ – the number of 1+ animals at the start of 2002, expressed as a percentage of that corresponding to the equilibrium level;
(d) $P^{1+}_{2002} / MSYL_{1+}$ the number of 1+ animals at the start of 2002, expressed as a percentage of that at which *MSY* is achieved;
(e) *Slope* – the average annual increase of the total (1+) population from 1968 to 1988 as estimated from a linear regression fit to the logarithms of the model estimates of (1+) population size over this period – this statistic is used to assess the extent to which model is able to mimic the abundance data – a log-regression through the actual abundance estimates for 1968-88 leads to a value for *Slope* of 0.032;
(f) RY_{2002} – the replacement yield during 2002;
(g) $\lambda_{\max}$ – the maximum rate of increase (given a stable age-structure); and
(h) κ and ϕ - the parameters of the inertia model.

The values for the quantities related to *MSY* are meaningless for the analyses that allow for inertial dynamics. Therefore, 100-year population projections under (constant) future annual catches of 0, 128, and 256 (split equally among males and females) were conducted and the results summarised by the 5th, mean, median and 95th percentiles of $P^{1+}_{2102} / \tilde{K}_{1+}$.

Sensitivity to alternative population dynamics models

Table 2 provides the values for the management-related quantities for assessments of the ENP gray whales using the standard BALEEN II model (the 'basic' model) and the inertia model, when the inertial dynamics are based on the exponential formulation (see Equations 3 and 4). Two variants of each model based on varying the first year of the historical projection period (y_1) are considered. The choices y_1=1930 and 1968 for the standard BALEEN II model were made for consistency with the most recent assessments conducted by the Scientific Committee of the International Whaling Commission (IWC, 1998; Punt and Butterworth, 2002; Wade, 2002) The choice y_1=1846 for the inertia model was made because Witting (2001) initiated his historical projections in this year while the choice y_1=1600 reflects the first year for which estimates of aboriginal removals have been postulated (Fig. 1). Witting (2003) also presented results for analyses that begun both in 1846 and in 1600. The posterior medians and 90% credibility intervals for the time-trajectories of total (1+) population size and calf numbers for period 1950-2025[3] from the four baseline analyses are shown in Fig. 2. This figure also displays the estimates of absolute abundance and the calf counts[4].

All four baseline analyses are able to mimic the change in population size over the period 1968-98 adequately (Fig. 2), although the posterior distribution for the rate of change in population size from 1968-88 obtained from the inertia model with y_1=1846 is shifted to noticeably lower values compared with the posterior distributions obtained from the other three baseline analyses (Table 2; column *Slope*). None of the four analyses is able to mimic the calf counts particularly successfully, although the two analyses based on the BALEEN II model perform better at this than the two analyses based on the inertia model (Fig. 2). Specifically, the BALEEN II models mimic the calf counts better than the inertia model (in terms of the posterior medians) for all years except 1996-98 and achieve a lower mean square error than the inertia model.

It is not straightforward to compare the results of the analyses based on the standard BALEEN II model with those based on the inertia model because many of the standard BALEEN II model outputs refer to Maximum Sustainable Yield, *MSY*, in some way (e.g. *MSYR*) whereas the inertia model does not include *MSY*[5]. However, it is possible to compare the posterior distributions for the biological parameters, the current population size, the 2002 replacement yield, and the future time-trajectories of population size. The analyses based on the standard BALEEN II model indicate that the population is currently at its (estimated) equilibrium population size and consequently the current replacement yield is negative. In contrast, the analyses based on the inertia model suggest a higher current population size that is substantially in excess of its pre-exploitation (1600 or 1846) population size, and a positive current replacement yield. The posterior distributions for $\lambda_{\max}$ are, however, remarkably similar among the four baseline analyses.

Fig. 3 explores the consequences of annual catches from 2003 of 0 and 256 for each of the four baseline analyses in terms of the time-trajectories of 1+ population size from year y_1 to 2200. Except for the inertia model: y_1=1600 analysis, all of the analyses suggest that under a regime of zero catches in the future, the 1+ population will stabilise close to its current population size (Fig. 3; Table 2). In contrast, the inertia model: y_1=1600 analysis predicts a continuing decline in 1+ population size even with zero future catches. Projections to 2102 indicate that annual catches of up to a level of 256 will not have a substantial impact on the population size if the standard BALEEN II model is correct (Table 2). This is perhaps not surprising given that *MSY* is estimated to be larger than 600 for the two analyses based on this model. The projections based on the inertia model do predict future declines in population size

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[3] The projections beyond 2002 are based on a catch of zero.

[4] The calf counts are displayed in Fig. 2 even though the analyses on which the population trajectories are based ignore these data when fitting the population dynamics model.

[5] The outputs that depend on *MSY* are consequently omitted from Table 2.

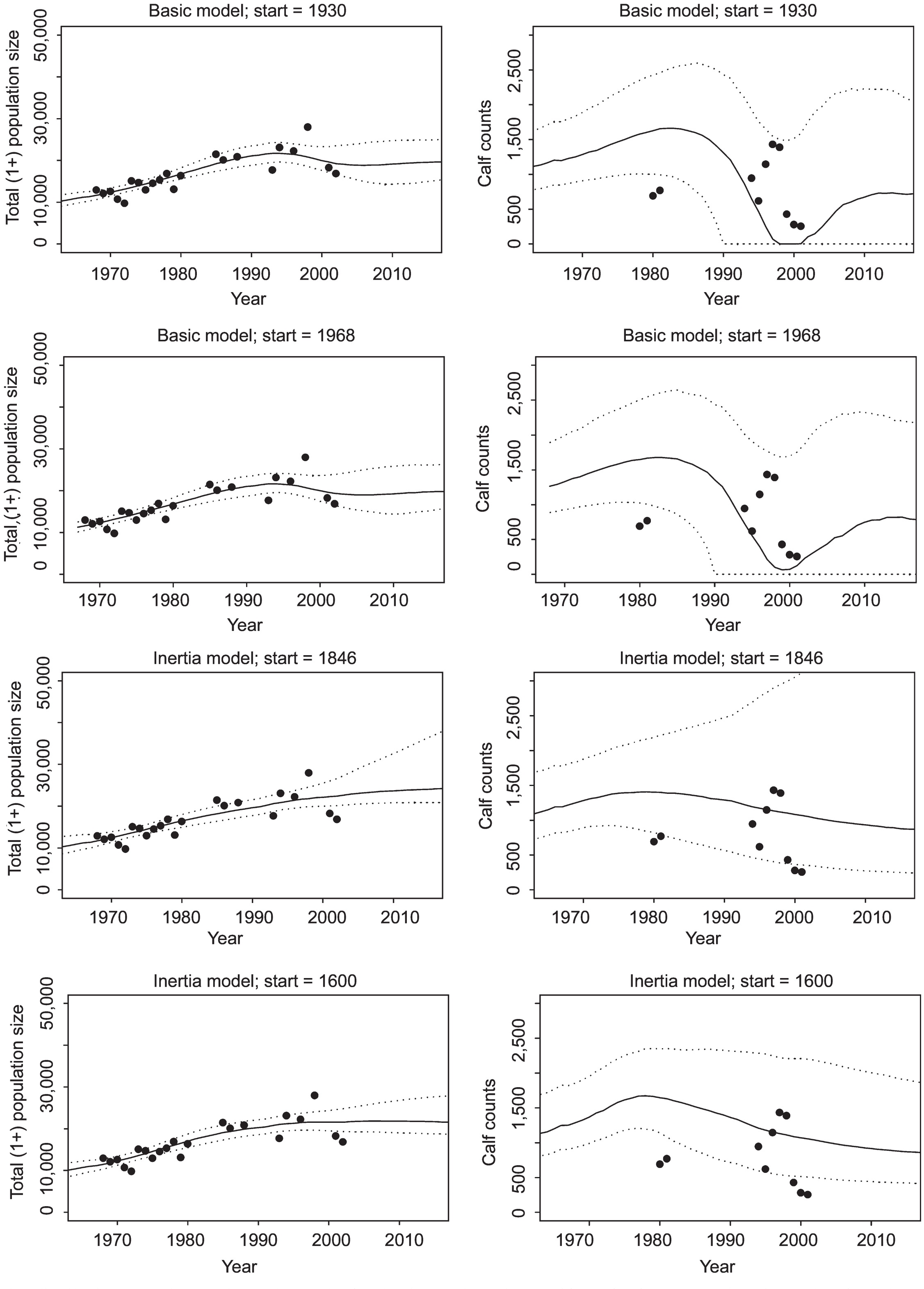

Fig. 2. Posterior distributions (medians and 90% intervals) for the time-trajectories (1965-2015) of 1+ population size and calf numbers for the four baseline analyses. The dots indicate the data points available for use in the analyses. The projections beyond 2002 assume zero catches.

for annual catches of 256 but the population still exceeds its pre-exploitation size substantially in 2102 (Table 2). Projections beyond 2102 are more pessimistic for the inertia model:y_1=1846 analysis which predicts population collapse in over 5% of cases.

The posterior median for $\tilde{K}_{1+}$ is largest for the analyses based on the standard BALEEN II model, lower for the inertia model:y_1=1846 analysis and lowest for the inertia model:y_1=1600 analysis. The latter result is perhaps unexpected given that the total historical catch is highest for the y_1=1600 analysis. The reason for the differences in $\tilde{K}_{1+}$ between the two analyses based on the inertia model relate to differences in the estimates of ϕ and κ (Table 2) which lead to there being two cycles for the y_1=1600 analysis but to only one cycle for the y_1=1846 analysis (Fig. 3). The posterior for the replacement yield for 2002 from the y_1=1846 analysis assigns more probability to high values than that for the y_1=1600 analysis.

Table 2

Estimates of twelve management-related quantities for the eastern north Pacific stock of gray whales. The point estimates given are posterior medians, followed by posterior means in round parenthesis. Posterior 90% credibility intervals are given in square parenthesis.

	$MSYR_{mat}$ (%)	$\tilde{K}_{1+}$	$P_{2002}^{1+} / \tilde{K}_{1+}$ (%)	$P_{2002}^{1+} / MSYL_{1+}$ (%)	Slope	RY_{2002}	$\lambda_{\max}$	κ	ϕ	$P_{2102}^{1+} / \tilde{K}_{1+}$		
										Catch=0	Catch=128	Catch=256
Basic model; y_1=1930												
Baseline	7.0 (7.0)	18,454 (19,355)	106 (106)	124 (125)	2.92 (2.91)	-193 (-191)	1.057(1.059)			101 (103)	101 (103)	103 (104)
	[4.8; 9.2]	[15,553; 24,900]	[89; 123]	[96; 158]	[1.94; 3.82]	[-685; 399]	[1.041; 1.085]			[85; 121]	[85; 121]	[91; 124]
Exponential form		40,094 (42,375)	59 (59)	82 (86)	1.93 (1.94)	447 (449)	1.058 (1.061)	1.524 (1.516)		100 (99)	92 (91)	83 (82)
		[26,640; 65,103]	[37; 82]	[44; 143]	[1.28; 2.59]	[299; 612]	[1.041; 1.090]	[0.148; 2.843]		[95; 100]	[85; 94]	[74; 88]
No surveys since 2000	5.2 (5.3)	38,190 (39,973)	76 (79)	108 (107)	2.58 (2.60)	713 (639)	1.049(1.053)			100 (101)	100 (100)	99 (99)
	[3.5; 7.5]	[19,333; 66,363]	[44; 117]	[58; 155]	[1.97; 3.34]	[-73; 1,067]	[1.038; 1.083]			[91; 108]	[93; 110]	[90; 111]
Post-model-pre-data	5.3 (5.3)	39,781 (40,353)	84 (78)	111 (103)	2.33 (2.31)	411 (577)	1.051(1.051)			100 (97)	100 (92)	99 (86)
	[1.4; 9.3]	[15,956; 66,730]	[22; 121]	[34; 155]	[-.82; 5.26]	[-358; 1,913]	[1.017; 1.085]			[69; 110]	[17; 112]	[0; 116]
Basic model; y_1=1968	6.8 (6.8)	18,927 (20,002)	104 (103)	119 (120)	2.97 (2.99)	-195 (-189)	1.054(1.057)			101 (101)	101 (102)	102 (104)
	[4.4; 9.1]	[16,078; 26,735]	[85; 121]	[92; 154]	[1.97; 3.97]	[-685; 419]	[1.039; 1.082]			[84; 118]	[84; 121]	[89; 124]
Inertia model; y_1=1846		14,835 (15,273)	151 (150)		2.56 (2.52)	255 (310)	1.061(1.059)	0.116 (0.369)	1.492 (1.611)	159 (162)	145 (147)	134 (135)
		[13,187; 18,936]	[125; 168]		[1.43; 3.53]	[135; 682]	[1.032; 1.085]	[0.074; 2.065]	[0.307; 3.216]	[143; 190]	[131; 171]	[118; 155]
Inertia model; y_1=1600												
Baseline		10,079 (10,621)	214 (209)		2.94 (2.95)	131 (151)	1.057(1.058)	0.239(0.326)	1.096 (1.180)	172 (169)	154 (151)	140 (136)
		[8,573; 14,443]	[152; 240]		[2.00; 3.85]	[-25; 404]	[1.040; 1.081]	[0.071; 0.911]	[0.611; 1.988]	[121; 197]	[93; 180]	[78; 169]
Pella-Tomlinson form		12,254 (12,311)	155 (156)		2.76 (2.75)	-290 (-309)	1.049(1.050)			108 (112)	109 (112)	115 (115)
		[9,379; 15,100]	[116; 208]		[1.65; 3.75]	[-738; 77]	[1.034; 1.069]			[85; 152]	[82; 148]	[72; 157]
50:50 sex-ratio		10,502 (10,914)	207 (205)		3.00 (2.98)	155 (176)	1.052(1.051)	0.311 (0.414)	0.965 (1.026)	171 (165)	151 (145)	134 (127)
		[8,873; 14,186]	[167; 235]		[2.10; 3.75]	[20; 415]	[1.036; 1.066]	[0.081; 1.005]	[0.534; 1.719]	[118; 196]	[91; 179]	[67; 169]
No surveys since 2000		12,976 (14,925)	202 (192)		2.62 (2.66)	498 (549)	1.047(1.048)	0.662 (1.078)	0.826 (0.891)	176 (183)	156 (159)	134 (137)
		[9,688; 26,308]	[113; 239]		[1.96; 3.50]	[97; 1,088]	[1.038; 1.062]	[0.115; 3.360]	[0.264; 1.789]	[112; 284]	[95; 243]	[80; 204]
U[0.2, 0.6] prior on $f_{\max}$		10,223 (11,125)	213 (204)		2.91 (2.86)	149 (182)	1.055(1.056)	0.244 (0.355)	1.103 (1.181)	174 (172)	157 (153)	140 (137)
		[8,802; 17,298]	[131; 236]		[1.74; 3.78]	[-2; 494]	[1.036; 1.079]	[0.069; 1.013]	[0.575; 2.055]	[126; 202]	[98; 182]	[82; 170]
Post-model-pre-data		16,580 (18,203)	155 (160)		1.83 (1.75)	342 (492)	1.046(1.048)	1.230 (1.490)	0.541 (0.699)	172 (175)	148 (149)	126 (126)
		[9,469; 30,305]	[35; 295]		[1.20; 4.66]	[25; 1,458]	[1.014; 1.092]	[0.075; 3.574]	[0.149; 1.812]	[92; 278]	[45; 246]	[0; 231]

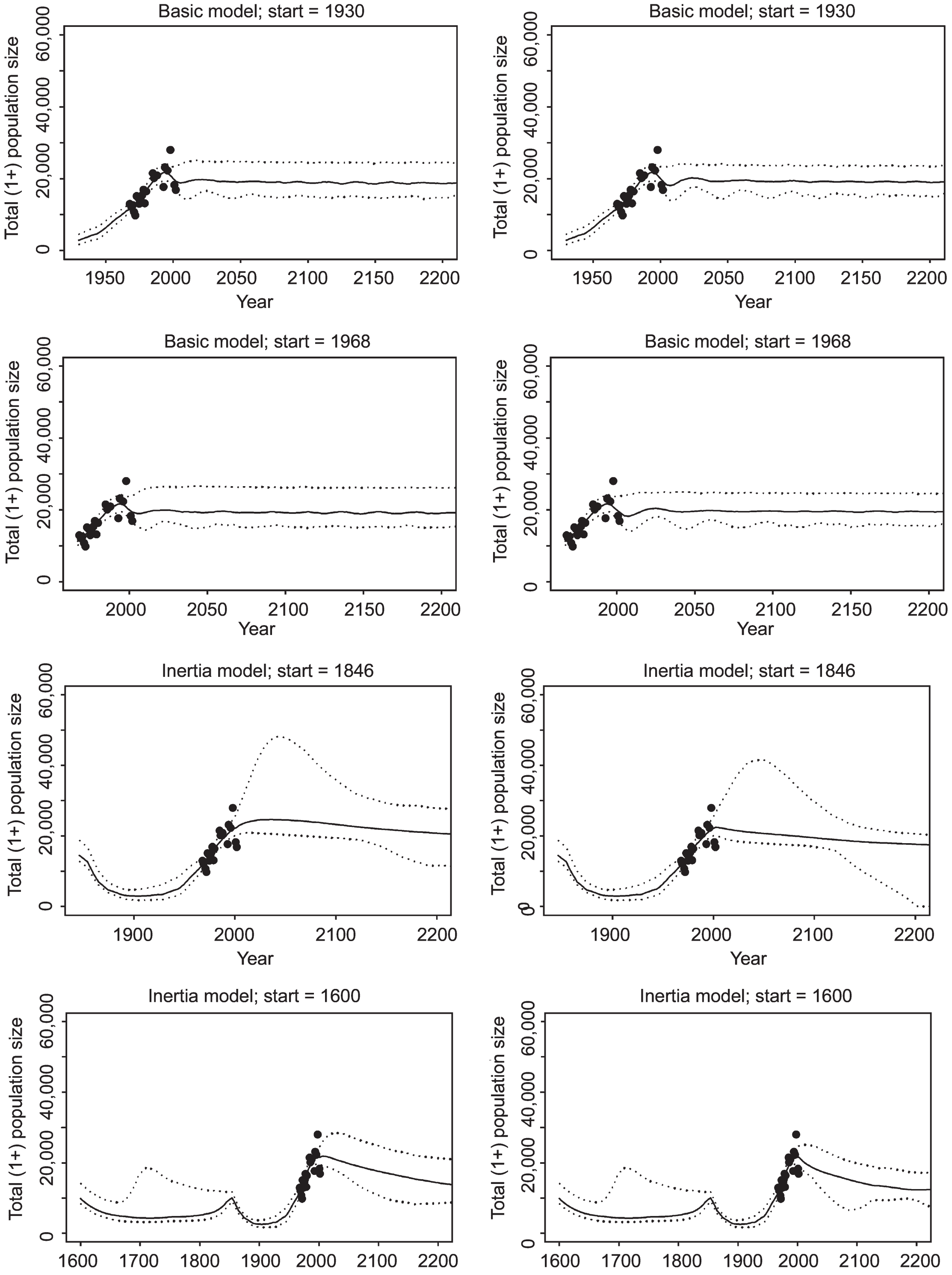

Fig. 3. Posterior distributions (medians and 90% intervals) for the time-trajectories (year y_1-2200) of 1+ population size for the four baseline analyses. The projections beyond 2002 assume zero catches (left panels) and 256 animals annually (right panels).

Table 2 provides results for some variants of the BALEEN II model when y_1 is set to 1930 and of the inertia model when y_1 is set to 1600. Changing the functional form used to model inertial dynamics from the exponential model to the Pella-Tomlinson model (Equations 3 and 5) lowers the current depletion (though it still exceeds 100%), suggests a negative rather than a positive current replacement yield, and indicates a much smaller impact of future catches of 256 on 1+ population size compared to that of future catches of zero (Table 2). The time-trajectory of the future population size is more oscillatory for the Pella-Tomlinson model than for the exponential model (Fig. 4 top right panel), one consequence of which is that, even for a zero catch, there is a substantial drop in 1+ population size by 2102. The oscillatory behaviour of the Pella-Tomlinson model occurs because this functional form leads to zero calves when the number of mature animals exceeds $(1 + A\phi) / A\phi$ of that in 1600 (Equation 6). This effect is present in both the density-regulated and the inertia models but is more pronounced for the inertia model because the impact of inertial dynamics can be to drive the population substantially in excess of the 1600 level. The fit of the model to the abundance data is, however, poorer for this model variant (the median for *Slope* in Table 2 is only 2.76% for the Pella-Tomlinson model compared to 2.94% for the baseline model and 3.22% for a log-regression through the data points for 1968-88).

The results for the standard BALEEN II model are also sensitive to the form assumed for the density-dependence function. For example, changing the density-dependence function for the basic model from the Pella-Tomlinson model to the exponential model (Table 2, row 'exponential form'; the value of the quantity *slope* for the exponential model is substantially less for this model than based on the data) leads to markedly poorer fits to the data. The poorer fit to the data may be a consequence of the reduction in the number of parameters governing density-dependence (two for the Pella-Tomlinson model compared to only one for the exponential model).

The posterior medians for the management-related quantities are not notably sensitive to assuming that the sex ratio of the historical harvest since 1944 is 50:50 rather than the actual sex ratio, which is biased towards females (Fig. 1). However, the probability of resource extirpation exceeds 5% for projections based on a future catch of 256 (Fig. 4, bottom left panel). This result is consistent with the maximum likelihood results obtained by Witting (2003) who predicted drastic reductions in population size after 2000 had the sex-ratio of the historical catches been 50:50. The results are insensitive to reducing the lower limit of the prior for $f_{\max}$ from 0.3 to 0.2.

The posterior distribution for the 1+ population size trajectory based on the post-model-pre-data distribution[6] (lower right panel of Fig. 4) is, as expected, much less precise than the corresponding posterior from the baseline analysis (upper left panel of Fig. 4).

Ignoring the two most recent total population size estimates has a marked impact on the results of assessments based on the standard BALEEN II model (Fig. 5; Table 2). Instead of the population being at (or above) its (current) equilibrium level, it is estimated to be only 80% of this level (posterior median). As a consequence of this, the replacement yield for the 'no surveys since 2000' analysis is markedly higher than those for the analyses that include these two data points (Table 2). Ignoring these two data points also increases the posterior median for $\tilde{K}_{1+}$ markedly. Previous analyses (e.g. Punt and Butterworth, 2002) have concluded that assessments which start the population projections after 1900 and that are based on data until 1998 provide essentially no information about the upper bound for $\tilde{K}_{1+}$. The two most recent data points provide such information and hence have a marked impact on the posterior distributions. These two estimates are therefore the first evidence from population counts that the population has reached its current 'carrying capacity'. In contrast, the calf count data suggest that evidence in this regard has been available for several years (Fig. 2).

Ignoring the 2001 and 2002 data points for the inertia model:y_1=1600 analysis (Fig. 6) again leads to higher values for the posterior median for $\tilde{K}_{1+}$ (but not to the extent evident for the standard BALEEN II model). However, the posterior distributions for current depletion and the consequences of future catches of 0, 128 and 256 whales per annum are affected much less.

General discussion

The analyses of this paper confirm the conclusion of Witting (2001; 2003) that a model which incorporates inertial dynamics can reconcile the catches and population count data for the ENP gray whale population. Furthermore, the results confirm that assessments based on this model structure reveal the current population size to be larger than the pre-exploitation size, and that catches of less than 256 would cause some population decline, rather than just reducing the rate of (further) population increase, as suggested by past assessments based on the standard BALEEN II model. However, the future declines do not lead to the collapses suggested by Witting (2001), at least within the 300-year time-frame considered in the analyses of this paper. This is probably because, in common with the analyses of Witting (2003), the analyses of this paper are based on the actual catches by sex rather than on assuming a 50:50 sex ratio for the historical catches.

Although the inertia model is as effective as the standard BALEEN II model at replicating the absolute abundance data when the population projections for the standard model begin in 1930 or 1968, it is less able to mimic the changes over time in the calf counts (Fig. 2).

The results from the standard BALEEN II model and inertia model are both very sensitive to exactly how density-dependence (exponential or Pella-Tomlinson) is formulated, while the results from the inertia model are somewhat sensitive to the choice of the first year considered in the analysis (contrast the results for y_1=1846 and y_1=1600 in Table 2). 1600 was clearly not the first year in which aboriginal takes of gray whales occurred, raising the question of how to choose an appropriate first year for the application of an analysis based on the inertia model. In contrast, the results for the standard BALEEN II model are insensitive to a choice for y_1 between 1900 and 1968 (Punt and Butterworth, 2002).

The results for the baseline case of this paper for y_1=1846 are quite similar to those for the corresponding case in Table 3 of Witting (2003). However, the results for y_1=1600 are notably different (the posterior median for $\tilde{K}_{1+}$ is lower and that for the current depletion higher in this paper than in Witting (2003)). As noted above, there are some differences in exactly how the Bayesian estimation is implemented in the analyses and it appears that these differences have some notable impacts on the results for the choice y_1=1600.

The inertia model formally incorporates changes over time in carrying capacity into the population dynamics through Equation 6. This differs in concept from previous attempts to reconcile the catch and abundance data for the ENP gray whales by postulating changes in carrying capacity in which the extent of change was estimated as a free parameter of the model (e.g. Butterworth *et al.*, 2002). An untested (and possibly untestable even in the medium term) assumption of the inertia model is, however, that cycles have occurred prior to 1846 (e.g. Fig. 3, bottom right panel) and will occur in the future. This is because the only data to compare alternative formulations for how carrying capacity may have changed are the abundance data which exhibit an increasing trend over the period 1967-88. The inertia model predicts that carrying capacity is declining at present whereas predictions based on formulations of the standard BALEEN II model (e.g. Butterworth *et al.*, 2002; Punt and Butterworth, 2002; Wade, 2002) have been predicated on the assumption that carrying capacity will remain at its current level. Apart from the calf count information, there are no other data not already included in

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[6] The post-model-pre-data distribution is the joint distribution for the parameters that arises when the parameter combinations that are unfeasible (e.g. correspond to extinction prior to 1968) are excluded.

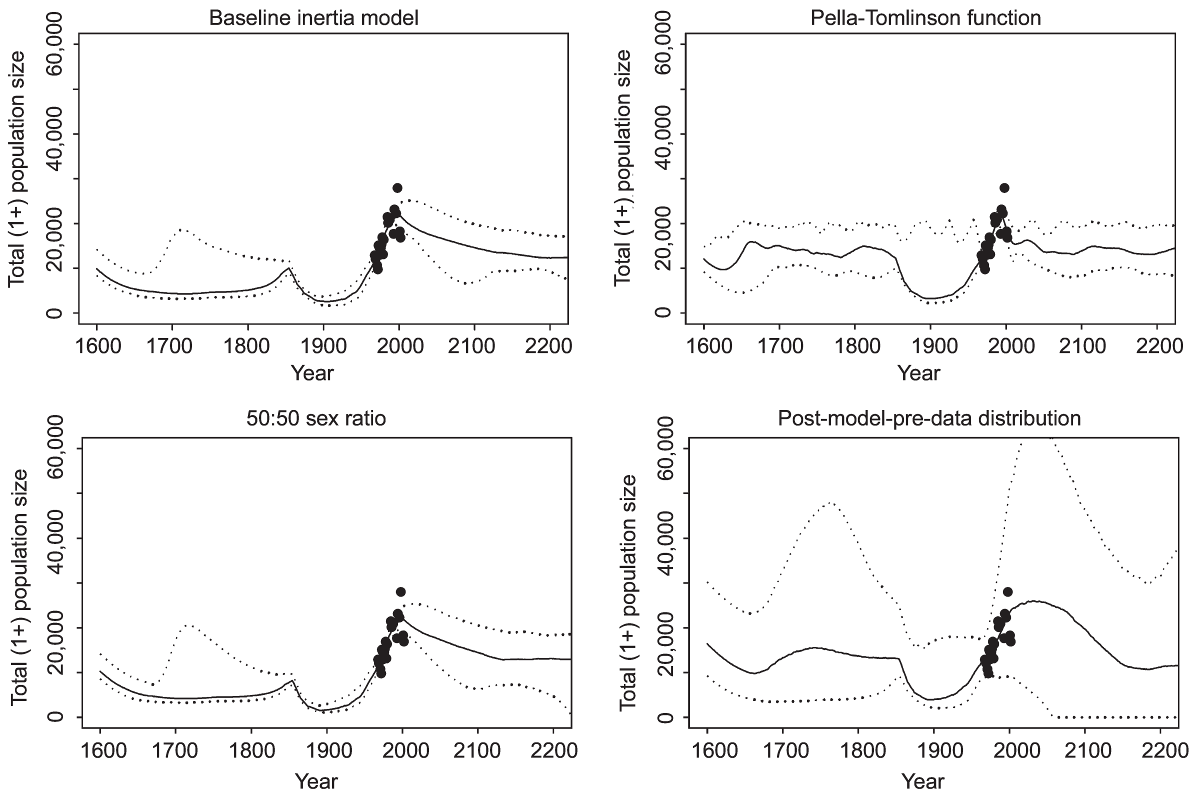

Fig. 4. Posterior distributions (medians and 90% intervals) for the time-trajectories (1600-2200) of 1+ population size for variants of the inertia model: y_1=1600 analysis. The projections beyond 2002 assume an annual catch of 256 animals.

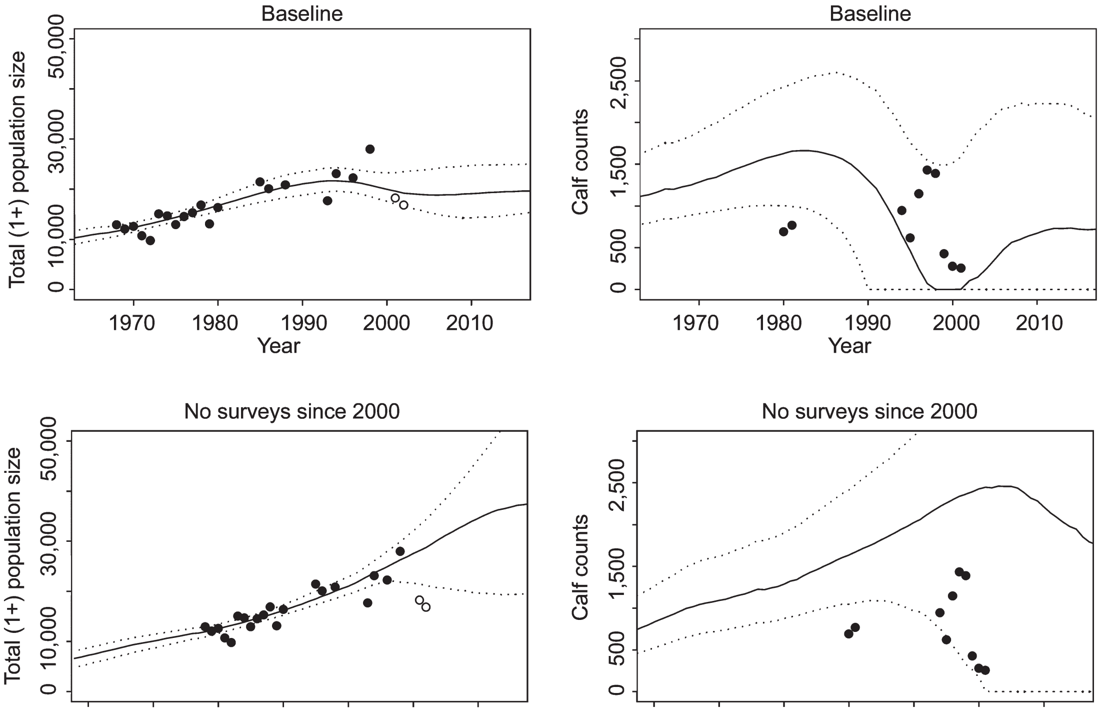

Fig. 5. Posterior distributions (medians and 90% intervals) for the time-trajectories (1965-2015) of 1+ population size and calf numbers for the baseline basic model: y_1=1930 analysis and a variant thereof that ignores the data from the surveys since 2000. The dots indicate the data points available for use in the analyses. Note that the 2001 and 2002 abundance estimates (the open circles in the left panels) were not included in the 'no surveys since 2000' analysis.

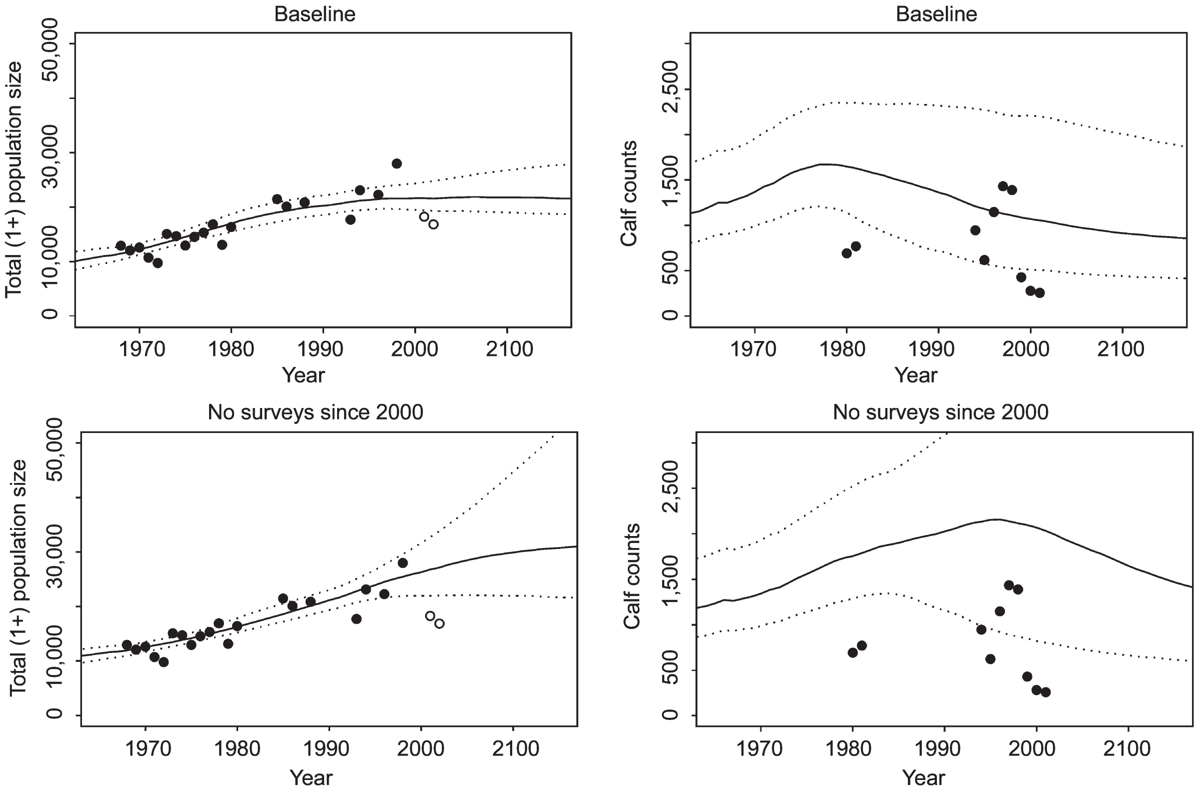

Fig. 6. Posterior distributions (medians and 90% intervals) for the time-trajectories (1915-2015) of 1+ population size and calf numbers for the inertia model: y_1=1600 analysis and a variant thereof that ignores the data from the surveys since 2000. The dots indicate the data points available for use in the analyses. Note that the 2001 and 2002 abundance estimates (the open circles in the left panels) were not included in the 'no surveys since 2000' analysis.

the analyses to distinguish between these two approaches to making future predictions.

ACKNOWLEDGEMENTS

Support for this work was provided to AEP and GF by NOAA/NMFS. Lars Witting is thanked for discussions regarding the inertia model and its implementation. Discussions with Paul Wade and Jeff Breiwick (NMML) are also gratefully acknowledged. Jeff Breiwick provided the most-recent time-series of estimates of absolute abundance and the time-series of calf counts. The paper was substantially improved by comments by Lars Witting and an anonymous reviewer.

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A note on gray whale distribution and abundance in the Magdalena Bay Complex, México during the 1997 winter season

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ABSTRACT

The goal of this study was to determine the distribution and abundance of gray whales, distinguishing between cow-calf pairs and single whales, in the different areas forming the Magdalena Bay Complex at Baja California Sur, Mexico. The lagoon complex comprises three well-defined zones: Santo Domingo Channel or Puerto Adolfo López Mateos region in the north; the central part properly known as Magdalena Bay; and the southern portion, Almejas Bay. The study period spanned eight weeks during the 1997 winter season. Fifteen surveys were conducted: 5 at Santo Domingo Channel, 7 at Magdalena Bay and 3 at Almejas Bay. Maximum combined counts by area and date were as follows: Santo Domingo Channel: 100 whales (83 cow-calf pairs and 17 single whales) on 27 February; Magdalena Bay: 81 whales (9 cow-calf pairs and 72 singles) on 14 February; and Almejas Bay: 109 whales (15 cow-calf pairs and 94 single whales) on 28 February. Santo Domingo Channel was the main calving zone within the lagoon complex and had the highest number of cow-calf pairs; for every count in this zone the number of cow-calf pairs was always higher than that of single whales. In contrast, Magdalena and Almejas Bays were mainly used for courtship and mating, or aggregation areas for young and immature whales. It is recommended that these studies continue and attempt to cover the entire season, and complete even coverage of all areas within the Complex. This will allow more effective management and regulation of human activities affecting gray whales within the Magdalena Bay lagoon complex.

KEYWORDS: GRAY WHALE; BREEDING GROUNDS; MONITORING; PACIFIC OCEAN

INTRODUCTION

Gray whales (*Eschrichtius robustus*) are today found only in the North Pacific (Mead and Mitchell, 1984). Two populations exist: the heavily depleted western stock (Weller *et al*., 2002); and the abundant eastern stock that is subject to aboriginal subsistence whaling (IWC, 2004). The eastern gray whales regularly take refuge from the open sea by entering lagoons during their annual migration (Dedina, 2000). Their breeding grounds are located in Mexico, along the Baja California peninsula (Fig. 1). The main concentrations are the lagoons of Ojo de Liebre (53%), San Ignacio (11%), Guerrero Negro (9%), La Soledad estuary (17%), with the remaining 10% concentrated in the bays of San Juanico, Magdalena and Almejas (Rice *et al*., 1981).

Magdalena and Almejas Bays were the site of the first gray whaling operations in the mid-19th Century. This was primarily due to the nature of the whaling operations (taking calves first), easy access and suitable water depths. It was only later, when the number of whales at these sites decreased, that the whalers began to use San Ignacio and Ojo de Liebre (Scammon's) lagoons (Henderson, 1984). After a break in harvesting about 1886, gray whaling resumed in 1914 with the highest intensity focused again on Magdalena Bay (Reeves, 1984).

Although the Magdalena Bay Complex has been considered a priority area for conservation by the Mexican Government and others, it is not included in the 2,700,000 hectare area that the state of Baja California Sur recognises under several conservation agreements (Breceda *et al*., 1991).

Previous studies conducted on these breeding grounds for gray whales are scarce and most are focused on only part of the Complex (e.g. Norris *et al*., 1983; Fleischer and Contreras U., 1986; Gardner and Chávez-Rosales, 2000).

In most of these studies, no distinction was made between the areas of the Complex that appear to be used by the whales in different ways. The primary aim of the present study was to provide information on the use, distribution and abundance of the gray whales in the lagoon complex during the winter of 1997, as a contribution towards the development of effective management plans for the region in the context of human activities.

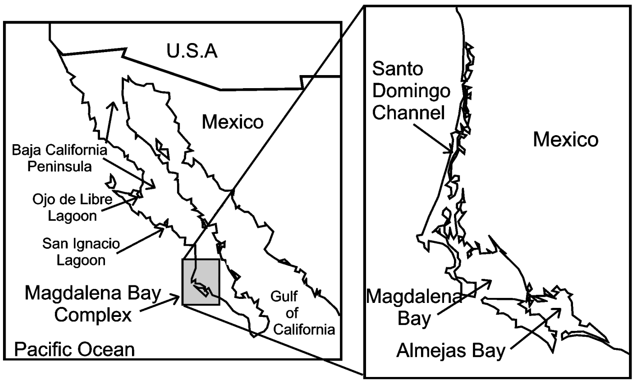

Fig. 1. The Baja California peninsula, showing the gray whale breeding sites: Ojo de Liebre and San Ignacio lagoons; and the Magdalena Bay Complex.

METHODS

Study area

The Magdalena Bay Complex is located on the western coast of the Baja California peninsula between 24°20'N-25°20'N and 111°30'W-112°10'W (Fig. 1). It includes three

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separate, well-defined areas from north to south: Santo Domingo Channel; Magdalena Bay; and Almejas Bay (Fleischer and Contreras U., 1986; Loreto *et al.*, 1996).

The Santo Domingo Channel, also known as La Soledad estuary, is approximately 32km^2 (Fig. 2). The town of Puerto Adolfo López Mateos is located in this area and fishing is the main economic activity. Whalewatching is conducted from the town between January and March. The area is connected to Magdalena Bay through a shallow and narrow channel formed by Magdalena Island (Rice *et al.*, 1981).

Magdalena Bay is 31km long and 22km wide and connects with the Pacific through a 6km wide mouth (Fig. 3). The town of Puerto San Carlos includes an energy plant and commercial docks, as well as several whalewatching companies. The bay is connected to Almejas Bay by La Gaviota Channel.

Almejas Bay is 22km long and 15km wide (Fig. 4). It is connected with the Pacific Ocean through Rehusa Channel, a 2km wide mouth. The entrances to Magdalena and Almejas Bays are formed by Margarita Island (Rice *et al.*, 1981). Puerto Cancun is an (almost) permanent fishing town – the human population here varies depending on the season's activities. Whalewatching is not permitted in the area.

The total area of the Complex is 1,370km^2, of which 1,030km^2 is at least 4m in depth. The oceanic influence is great due to the connections with the Pacific (Rice *et al.*, 1981).

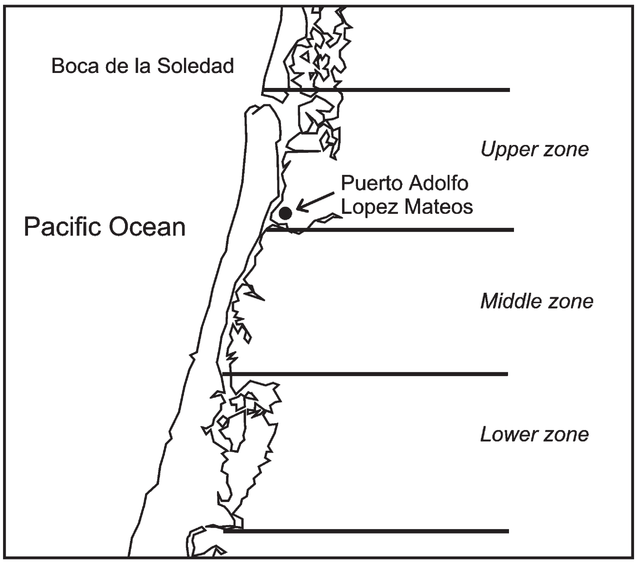

Fig. 2. Santo Domingo Channel and zones considered in this study.

Whale counts

Censuses were conducted following the methodology used by Jones and Swartz (1984) to study the distribution and abundance of gray whales. The same methods have been used on the other breeding grounds (Urbán-R *et al.*, 1997; 1998; 2001), thus the results are comparable among all the wintering sites.

The counts were conducted from 6-7m outboard engine vessels, sailing at a mean speed of 11km h^{-1}. The crew comprised the driver, two observers (one on each side of the vessel) and a recorder. In order to avoid double counting, whales were only recorded when at 90° from the transect line. With the aid of hand-held binoculars (10x), cow-calf pairs and single whales were recorded separately. If there was doubt as to the presence of a calf, the sighting was recorded as a single whale. The start and end times of each survey and the exact location of each sighting was recorded. The different regions within the Complex were divided into zones to allow examination of any differences in distribution and abundance. Sightings effort terminated when the sea state was Beaufort 3 or higher.

Following Fleischer and Contreras (1986), the Santo Domingo Channel was divided into three zones (upper, middle and lower). A single transect was followed along the middle of the channel from Boca de la Soledad in the north to Devil's Bend in the south (Fig. 2). Since both coasts are visible all the time it was assumed that every whale along the transect was counted.

Given the large extent of Magdalena Bay, four zones (west, southeast, central and mouth) were designated after examining the distribution of the whales at the beginning of the season (Fig. 3). As shown in the figure, three transects were surveyed whilst at the mouth of the bay, circular scans were carried out when the vessel was stationary. The transects were located in zones which were of an adequate depth for whales. Although no other areas were systematically surveyed, they were checked to confirm the absence of whales.

Similarly, Almejas Bay was divided into three zones: west, southeast and mouth (Fig. 4). As shown in the figure, two transects were covered with circular scans occurring at two sites in the mouth region.

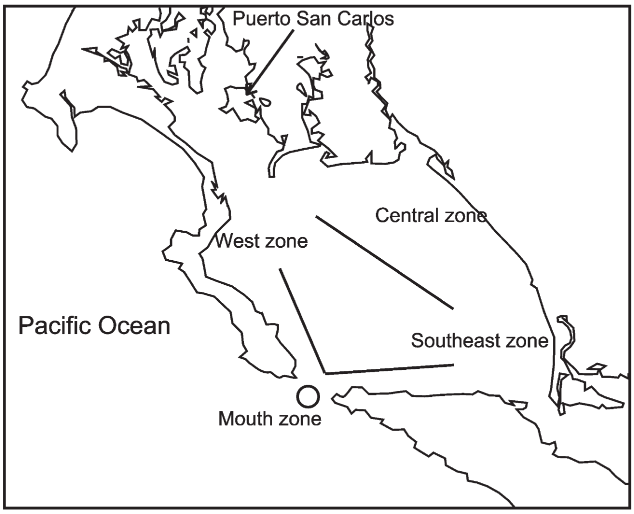

Fig. 3. Magdalena Bay and location of the transects.

RESULTS

The study period lasted for 8 weeks (13 February to 3 April 1997) during which fifteen censuses were completed (Table 1). Since the fieldwork started late in the season, it was not possible to determine the dates of the whales' arrival at the Complex, nor the exact length of stay.

The maximum combined counts (the highest sum of cow-calf pairs and single whales) were recorded as follows: 100 whales (83 cow-calf pairs and 17 singles) on 27 February at Santo Domingo Channel; 81 whales (9 cow-calf pairs and 72 singles) on 14 February at Magdalena Bay; and 109 whales (15 cow-calf pairs and 94 singles) on 28 February at Almejas Bay (Table 2).

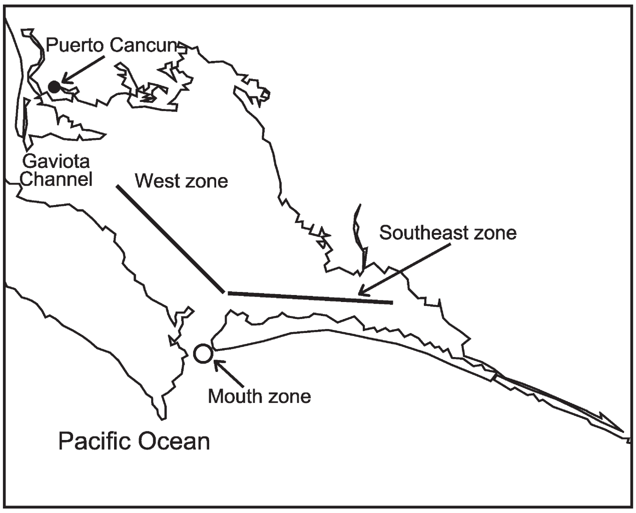

Fig. 4. Almejas Bay showing the position of the transects covered.

In order to determine if cow-calf pairs showed a preference for a particular region, percentages of these groups and single whales were compared in the maximum combined counts. As shown in Fig. 5, Santo Domingo Channel was mostly used by calving whales (83%) while Magdalena and Almejas Bays were dominated by single whales (89% and 86% respectively).

The highest maximum combined count for the three regions of the lagoon complex was observed at Almejas Bay.

Table 1

Number of gray whales by region, zone and type of whale at the Magdalena Bay Complex during censuses in the 1997 winter season. The counts for each area and zone are divided into single whales and cow-calf pairs (C-c).

Santo Domingo Channel

	Upper		Middle		Lower		Total	
Date	Single	C-c	Single	C-c	Single	C-c	Single	C-c
13 Feb.	9	31	3	22	0	0	12	53
20 Feb.	3	10	10	13	3	26	16	49
27 Feb.	8	46	8	27	1	10	17	83
04 Mar.	10	41	11	27	2	7	23	75
20 Mar.	0	20	0	5	0	1	0	26

Magdalena Bay

	West		Mouth		S-East		Central		Total	
Date	Single	C-c	Single	C-c	Single	C-c	Single	C-c	Single	C-c
14 Feb.	12	0	9	3	11	0	40	6	72	9
27 Feb.	6	0	4	0	0	0	16	0	26	0
06 Mar.	8	0	8	2	3	0	3	2	22	4
13 Mar.	4	0	0	0	0	0	4	0	8	0
20 Mar.	0	2	0	2	0	1	1	1	1	6
25 Mar.	1	1	0	0	2	0	0	2	3	3
03 Apr.	1	0	0	0	0	0	0	0	1	0

Almejas Bay

	S-East		Mouth		West		Total	
Date	Single	C-c	Single	C-c	Single	C-c	Single	C-c
28 Feb.	58	4	24	2	12	9	94	15
07 Mar.	20	12	34	7	2	0	56	19
19 Mar.	0	0	1	11	0	2	1	13

Table 2

Summary of surveys conducted at Magdalena Bay complex. Counts of single whales (sgl.) cow-calf pairs (C-c) and sum of both are included.

Region	Number of surveys	Sum of whales for all surveys					Maximum combined count	
		sgl.	C-c	Total	sgl.	C-c	Total	Date
S. Dom.	5	68	286	354	17	83	100	27 Feb.
B. Mag.	7	133	22	155	72	9	81	14 Feb.
B. Alm.	3	151	47	198	94	15	109	28 Feb.

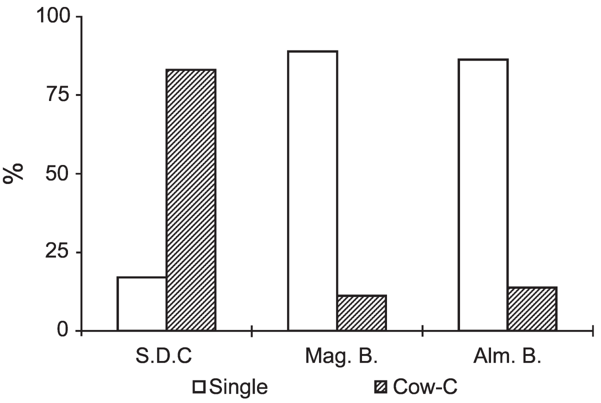

Fig. 5. Percentage of gray whales (single whales and Cow-calf pairs) during the maximum combined count at the different regions of the Magdalena Bay Complex: Santo Domingo Channel (S.D.C.) Feb 27; Magdalena Bay (Mag.B.) Feb 14; and Almejas Bay (Alm.B.) Feb 28.

Santo Domingo Channel

Abundance

Five censuses were carried out at Santo Domingo Channel between 13 February and 20 March. During the first census, 65 sightings (12 singles and 53 cow-calf pairs) were made. This accounted for 18.3% of the maximum combined count for the season. Total sightings of cow-calf pairs showed a general increase during February before declining during March; sightings of single animals increased up until early March before declining to zero by 20 March (Fig. 6; Table 1). Throughout the period, there were many more sightings of cow-calf pairs than singles and the former were seen throughout the study period whereas the latter were not present on the final survey.

Distribution

Maximum combined counts were as follows: 54 in the upper zone, 35 in the middle zone and 35 in the lower zone (Table 1).

Most of the whales were recorded in the upper zone, with cow-calf pairs more abundant than single whales. This area was determined to be the most important for calving in the lagoon complex in the winter of 1997 (Fig. 6; Tables 1 and 2).

UPPER ZONE

During the maximum combined count in this zone, 8 single whales and 46 cow-calf pairs were observed. This accounted for 54% of the whales in the area. Since this zone had the highest occupation (Table 1) it is clearly a calving zone within the region of Santo Domingo Channel.

MIDDLE ZONE

Eight single whales and 27 cow-calf pairs were recorded during the maximum combined count, accounting for 35% of the total. As for the entire Santo Domingo Channel, more cow-calf pairs than single whales were observed in this zone. This zone accounted for most of the single whales in the region and has the second highest occurrence of cow-calf pairs (Table 1).

LOWER ZONE

Only 11% of the total whales observed during the maximum combined count were observed here: 1 single whale and 10 cow-calf pairs. During the study period more cow-calf pairs than single whales occupied this zone. The lowest counts for both cow-calf pairs and single whales in Santo Domingo Channel were recorded in the lower zone (Table 1).

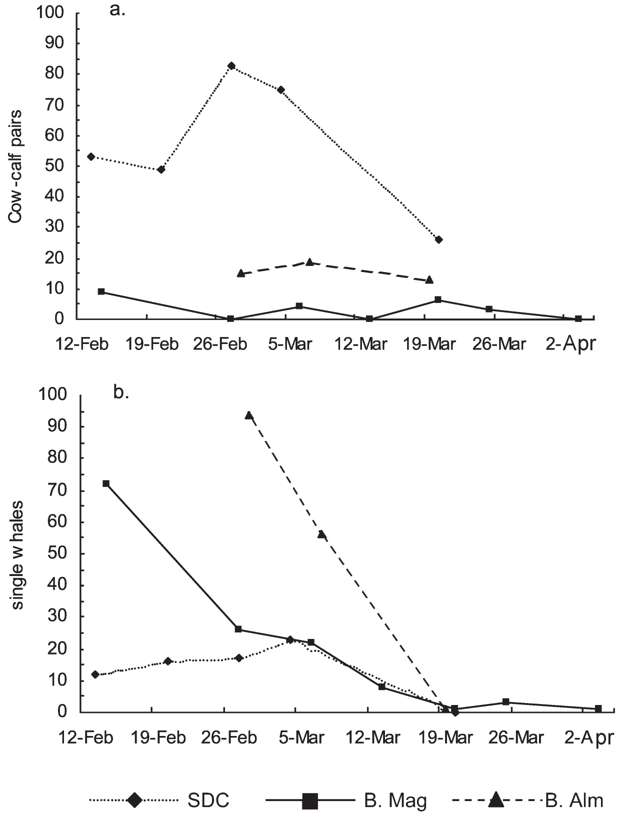

Fig. 6. Gray whale counts at the different parts of the Magdalena Bay lagoon Complex. (a) Cow calf pairs; and (b) single whales.

Magdalena Bay

Abundance

At the beginning of the study period, the number of both cow-calf pairs and single whales was higher than later in the season. The first count of 81 whales (72 singles and 9 cow-calf pairs) was the maximum combined count, recorded on 14 February. After this date the number of whales decreased.

The numbers of both single whales and cow-calf pairs decreased from February to the beginning of March. The number of single whales was higher than that of cow-calf pairs over the entire study period (Fig. 6).

Distribution

The maximum combined count was recorded as follows: 12 in the west zone, 12 at the mouth, 11 in the southeast zone and 46 in the central zone (Table 1).

WEST ZONE

Twelve single whales and no cow-calf pairs were recorded during the maximum combined count, accounting for 14.8% of the total. During the study period, the counts of single whales were always higher than of cow-calf pairs (Table 1).

MOUTH

The maximum combined count for this zone accounted for 14.8% of the whales: 9 singles and 3 cow-calf pairs. The single whales were more abundant than the cow-calf pairs. Almost one third (31.8%) of the cow-calf pairs in Magdalena Bay were recorded in this zone.

SOUTHEAST ZONE

Only 13.6% of the whales (11 singles and 0 cow-calf pairs) during the maximum combined count were observed in this zone. This zone was the least used by the whales in the region but single whales were found throughout the study period, decreasing in number towards the end of the season.

CENTRAL ZONE

Forty single whales and 6 cow-calf pairs made up the maximum combined count for this region, accounting for 56.8% of the whales. This was the main aggregation zone within Magdalena Bay. Single whales were particularly abundant at the beginning of the season. Although the number of single whales was higher than cow-calf pairs, this was the most important zone for calving at Magdalena Bay.

Almejas Bay

Abundance

Three surveys were conducted in this area from 28 February to 19 March 1997. The number of whales recorded on the first count was the highest: 109 whales (94 singles and 15 cow-calf pairs). For the following counts the number of single whales gradually decreased while the number of cow-calf pairs slightly increased (Fig. 6; Table 1).

Distribution

The maximum combined count distribution was as follows: 62 in the southeast zone, 26 at the mouth and 21 in the west zone.

Percentages of whales during the maximum combined count showed that most of the whales congregated in the southeast zone, where single whales were more abundant. In contrast, cow-calf pairs were more abundant in the west zone but the total number of whales in this region was the lowest during the combined count (Table 1).

SOUTHEAST ZONE

During the maximum combined count this zone accounted for 56.8% of the whales (58 singles and 4 cow-calf pairs). This was the highest number of whales observed in this part of the Complex (Fig. 5). This zone was the main congregation site for single whales and the second for cow-calf pairs (Table 1).

MOUTH

Twenty-four single whales and 2 cow-calf pairs were observed during the maximum combined count, accounting for 23.8% of the whales (Fig. 5). This zone was the second most important for single whales and the third for cow-calf pairs. Single whales were more abundant than cow-calf pairs (Table 1).

Towards the end of the season whales were observed gathering around two sandbanks in the Rehusa Channel called ‘los filetes’. These shallow sites are close to the mouth of the bay and are separated from each other by approximately 1.5km. The changing direction of the currents in the zone and the accumulation of sediments allow the whales to ‘rest’ on the bottom, surfing almost effortless.

WEST ZONE

This zone accounted for 19.26% (12 singles and 9 cow-calf pairs) of the maximum combined count (Fig. 5). Both singles and cow-calf paris were less numerous in this zone than in the rest of the bay (Table 1). The number of single whales was always higher than cow-calf pairs.

DISCUSSION

Although the three aggregation regions of the lagoon complex were surveyed several times, the counts were initiated late in the season. Thus it was not possible to determine the dates of arrival. Previous studies in the area indicate that gray whales are present at the lagoon complex from at least the beginning of January (Villa-Ramírez *et al.*, 1981; Fleischer and Contreras U., 1986). The late start also affected the attempt to estimate more accurately the peak dates of abundance.

The whales were evenly distributed in the three areas of the lagoon complex by the date of the maximum combined count. Out of the total 290 whales, Santo Domingo Channel accounted for 100 (34%), Magdalena Bay 81, (27%) and Almejas Bay 109 (37%). It is important to recognise the size differences for the various parts of the Complex: Santo Domingo Channel is the smallest and Magdalena Bay the largest. Thus, as pointed out by Dedina (2000) gray whales are found more densely congregated in the narrower Santo Domingo Channel.

The Magdalena Bay Complex is often referred to as a single wintering area for gray whales (Rice and Wolman, 1971; Jones and Swartz, 2002). This study shows that the three parts of the Complex should be considered as separate wintering locations for this species that are utilised by the whales in different ways. In contrast with Santo Domingo Channel, where more cow-calf pairs are observed, Magdalena and Almejas Bays are sites where more single whales were counted. Whale occurrence did not change to other areas during the 1997 winter, although this was noted for subsequent years by Gardner and Chavez (2000).

Santo Domingo Channel was clearly the most important calving area of the Complex having the greater number of cow-calf pairs throughout the season. This situation was unique for the entire lagoon complex. The same situation had been observed in 1981, 1982 and 1986 (Villa-Ramírez *et al.*, 1981; Fleischer and Contreras U., 1986). At San Ignacio and Ojo de Liebre lagoon, the other breeding grounds, the number of cow-calf pairs is greater usually only towards the end of the season when single whales are departing to the north (Urbán-R *et al.*, 1997; 2003). It appears that the upper and lower zones are the most important for the aggregation of whales whilst the middle zone is only the area where whales were seen in transit between zones.

No previous studies have been conducted in Magdalena and Almejas Bays. Since both areas are mostly used by single whales, these regions appear to be aggregation sites for courting and mating whales or for young and immature animals.

Thus it seems that the portion of Santo Domingo Channel utilised by gray whales during the winter, although very limited geographically, represents an important breeding location for the population.

The Santo Domingo Channel is the only region of the Complex where a similar study has been conducted. Fleischer and Contreras (1986) reported on whale censuses in the region between 11 January and 10 March 1983. The maximum combined count reported was observed on 10 February with 159 whales (33 singles and 123 cow-calf pairs). Although these counts were higher than those presented here, the rate of cow-calf pairs and single whales is similar.

Prior to this study, Almejas Bay had not received sufficient attention and the results in this paper show that is an important winter aggregation area. However, the presence of whales here might be more irregular due to its geographic situation at the southern limit of the normal gray whale wintering range. Any change in the population or in its distribution will certainly become evident in this particular area. It is pertinent to add that Almejas Bay is not open for whalewatching activities and there are no plans by the Mexican government to permit the activity in the foreseeable future (Diario Oficial, 2000).

Dedicated and continued surveys starting in late December or early January (including photo-identification effort to better examine movements and residency) would provide better data to determine arrival dates, occupation peak and total length of stay at the different parts of the Complex.

ACKNOWLEDGEMENTS

Octavio Maravilla and Gabriela Velázquez were especially helpful acting as observers and also participating in other parts of the work. William McCready, former Director of the School for Field Studies (SFS) assisted us during the development of the fieldwork at Magdalena Bay. We also acknowledge the whalewatching operators of Unión de Lancheros Turísticos de Puerto Adolfo López Mateos for their help with boat time. The study was conducted under permit No. D00750.-1458. We are grateful to the anonymous reviewers whose comments helped to improve this manuscript. The authors very much appreciate the kind efforts of G. Donovan and all the editorial staff of this Journal for patiently reviewing and correcting this paper. We also appreciate the efforts of the Instituo Nacional de Ecologia and the Federal Delegation of SEMARNAP.

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Behaviour and physiological effects of transmitter attachments on a captive harbour porpoise (*Phocoena phocoena*)

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ABSTRACT

A captive harbour porpoise (*Phocoena phocoena*) was monitored for 80 consecutive days, 10 days before attachment of a satellite dive recorder and a VHF-radio tag, 30 days during attachment and 40 days after removal of the transmitters. Dive data recorded by the satellite transmitter was collected during the attachment. Daily food intake was measured and each week the porpoise was taken out of the water for a physical examination. Behavioural observations logged on the handheld computer showed an immediate effect of the tagging in time spent resting at the surface (logging), which was four to six times higher on the day of attachment. Digital video recordings showed a significant increase in the mean duration of rolls at the surface immediately after attachment. The mean duration of dives was shorter before attachment than both after the tagging and after removal of the transmitters. Furthermore the frequency of surfacings farthest away from where the porpoise was taken out of the pool for tagging, was highest the first five days following the tagging. Dive data from the satellite tag showed a semidiurnal diving pattern, with increased mean dive depth in the first 24 hours after attachment. The heart rate was fairly constant during the tagging, but the mean heart rate increased significantly from 161 beats per minute (bpm) to 180 bpm after the first hole in the dorsal fin was made. The body weight of the porpoise increased up to the time of tagging (16 May 2000), after which it decreased until six days prior to release (28 July 2000); this was probably due to the seasonal trend in blubber thickness of harbour porpoises rather than an effect from the tagging. After one month of attachment, a reaction occurred around the frontal pinhole and the transmitters were removed. This reaction was probably due to drag from two tags and seaweed attached to the tags during the last part of the attachment period. After the tags were removed epithelia closed the pinholes after two days.

KEYWORDS: HARBOUR PORPOISE; BEHAVIOUR; PHYSIOLOGY; CAPTIVITY; SATELLITE TAGGING; TELEMETRY

INTRODUCTION

During the past decade, telemetry studies have helped elucidate the behaviour and population structure of cetaceans. Due to the relatively large size of the transmitters, tagging of smaller species, such as the harbour porpoise (*Phocoena phocoena*) has been limited until the recent availability of smaller tags.

Many kinds of tags have been used in studies on cetaceans, including VHF transmitters, satellite tags and dataloggers. Satellite tags in particular are popular since data are transmitted to an earth-based station via a satellite, making retrieval of the tag unnecessary. Several small cetacean species have been followed for long periods using VHF or satellite tags, e.g. white whales (*Delphinapterus leucas*): 30-126 days (Richard *et al*., 2001), 14-104 days (Suydam *et al*., 2001); harbour porpoises: 2-212 days (Read and Westgate, 1997); 50 days (Westgate *et al*., 1998), 6-349 days (Teilmann *et al*., 2003); Dall's porpoise (*Phocoenoides dalli*) 2-378 days (Hanson, 2001); and narwhals (*Monodon monoceros*): 6-145 days (Dietz *et al*., 2001). Dataloggers have also been deployed on small cetaceans, including the harbour porpoise. A datalogger stores high resolution dive data within the instrument usually for a few hours or days (Westgate *et al*., 1995; Otani *et al*., 1998; Schneider *et al*., 1998; Teilmann, 2000; Baird *et al*., 2001; Laidre *et al*., 2002).

Transmitters are attached to smaller odontocetes in several ways. In some cases they are secured to the front or the side of the dorsal fin or the dorsal ridge, usually with two to four nylon, delrin, stainless steel or titanium pins (4-9mm diameter) through the dorsal fin (e.g. Read and Westgate, 1997; Richard *et al*., 2001). Other approaches include the attachment of the transmitters to the dorsal fin or the body using suction cups (Schneider *et al*., 1998); in the case of male narwhals the tags can be secured around the tusk of the animals (Dietz *et al*., 2001). The pins ensure that the tag stays attached for a longer period of time, but boring two to three holes through the dorsal fin may be a stressful procedure for the animal. Furthermore the pinhole wounds are at a potential risk of infection due to their exposure to the water and foreign material. Using suction cups for attachment allows the tag to stay on for only some hours, but there is no risk of infection. However, suction cups can cause localised skin damage (Read *et al*., 1997); after eight hours of attachment blisters developed under the suction cups and they appeared to cause the porpoise much discomfort for several days.

So far there have been no systematic studies on how invasive attachments affect behaviour and physiology of the animals. However, one study did attempt to re-sight tagged animals to evaluate tag attachment and animal condition (Hanson, 2001). The reason for this limited number of studies is due to logistical difficulties associated with following and observing wild cetaceans for longer periods of time, both before and after attachment of transmitters. In general, only small changes in behaviour have been observed (Martin and Smith, 1992; Read and Westgate, 1997; Otani *et al*., 1998). These observations were however undertaken without baseline information, and could only reveal a difference in behaviour immediately after tagging and later; this cannot be interpreted to show that tagging does not change behaviour on a longer-term scale. Tag attachment by pinning through the dorsal fin was found to cause slight behavioural short-term reactions on the Amazon River dolphin (*Inia geoffrensis*; Martin and da Silva, 1998). These reactions were limited to the first few minutes following the tagging.

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This study documents the first systematic record on possible changes in behaviour of a cetacean equipped with a satellite and a VHF radio transmitter. Behavioural observations were focused on changes immediately after tagging and over a longer period. The physiological effects of the transmitters on the animal were also studied.

METHODS

Study site

The experiment was carried out at the Cetacean Rehabilitation and Research Center, Neeltje Jans, The Netherlands, in an outdoor enclosure placed in a harbour in a firth without any boat traffic. Two harbour porpoises were kept in an outdoor floating pen 34×20m wide, with the deepest part varying from 4-7m depending on the tide. Large floating pontoons surrounded the pen, the sides and the bottom were made of net (twine thickness: 3mm) with a stretched mesh size of 9cm, which allowed seawater to continuously flow through the pen. Within the floating pen were two smaller holding pens (3.6 × 2.9m; 1.2m deep) situated at the north end (Fig. 1).

Study animal

Only one of the two harbour porpoises was used in this study. The study animal was a stranded mature female (code PpSH057). It was kept in an indoor pool for rehabilitation at the Netherlands Cetacean Research and Rehabilitation Centre at the Harderwijk Marine Mammal Park, Harderwijk, The Netherlands, approximately 4.5 months prior to the start of the study. After this period the animal was transferred to Neeltje Jans on 12 April 2000, where the experiment was carried out over a period of 80 days. At the time of tagging, the porpoise was 141.5cm long and weighed 39.4kg. Each week the porpoise was taken out of the water for approximately 15 minutes for a physical examination. Blood samples were taken from the fluke and the weight, length and girth of the animal was measured. Furthermore, food intake was measured on a daily basis from 8 May 2000 until the end of the study; the porpoise had unlimited access to fish at each feeding. After rehabilitation, the animal was released into the North Sea on 3 August 2000 (with no tags attached).

Transmitters and attachment

A VHF radio tag (Sirtrack Ltd, New Zealand) and a satellite dive recorder (SDR-T16 with 2 × M1 cells, Wildlife Computers, Seattle, USA) were attached, on each side of the dorsal fin (Fig. 2). The external measurements of the VHF tag were 5.0(l) × 3.7(h) × 0.7(w)cm. The VHF tag was glued (Loctite 414) to a conveyer rubber belt padded with 3mm neoprene in which three holes for the pins were made. The maximum external measurements of the satellite transmitter were 10.0(l) × 6.5(h) × 2.1(w)cm with a triangular pointed tip towards the front (Fig. 2). The satellite transmitter had three holes in the epoxy casting, one in front and two on top of the tag. The back of the transmitter was lined with 3mm neoprene. The total weight of the dorsal pack was 180g in air and 20g in water. A detailed description of how dive data are collected and transmitted by the SDR-

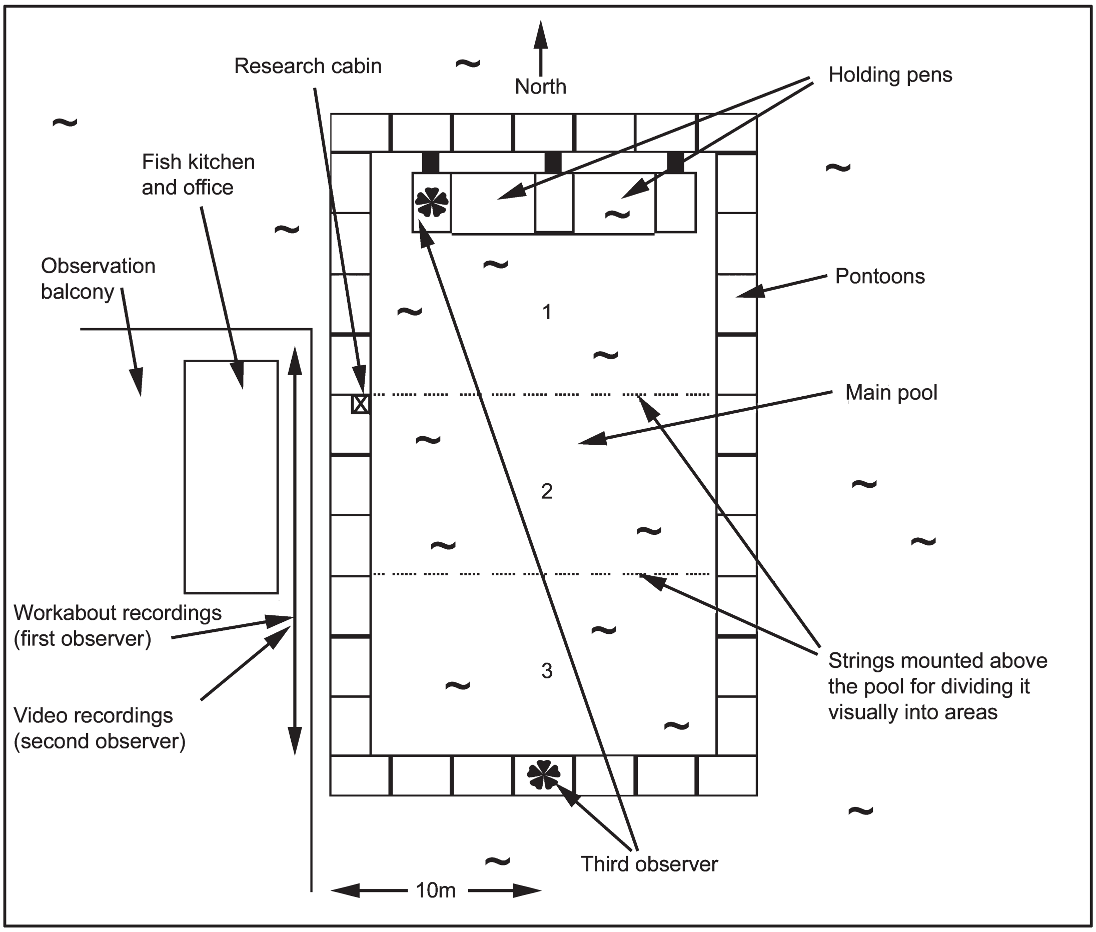

Fig. 1. Schematic view of the pen. The main pool is divided into three areas. The Workabout and video recordings were made from the observation balcony and were recorded by the first and second observer respectively. The third observer followed the animal from one of two different positions (*).

T16 tag can be found in Teilmann (2000). In addition to the transmitted dive data, the tag also stored the depth of the animal every 10 seconds on its internal memory. However the transmitter had to be recovered for downloading of these data to a computer. The pressure transducer had a resolution of 1m with an accuracy of ±1% of the depth reading. The 10 seconds depth readings were recorded continuously for 87 hours after tagging until the memory was full. Two hours of these data were discarded; one hour in the beginning that represented a period before and during tagging, and approximately one hour at the end comprising corrupted data. A total of 85 hours of data, representing 30,600 depth recordings, was available for analysis. The dive data were grouped into one-hour periods, and the mean depth of each hour was used for analysis.

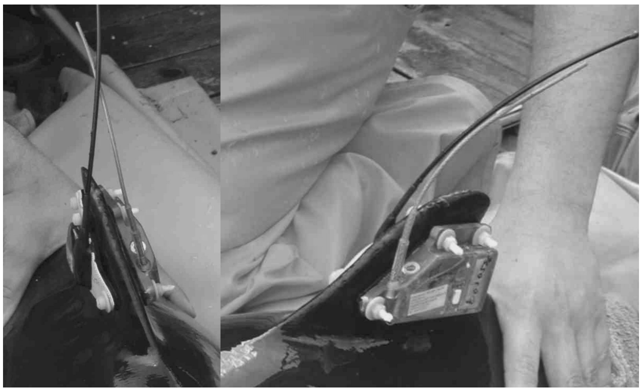

Fig. 2. Pictures of the SDR-T16 satellite tag (transparent) and the VHF tag (black) glued to a piece of conveyer belt and the three pins attaching the tags to the dorsal fin.

Prior to the attachment, the animal was tranquillised with Valium and local anaesthesia was applied to the dorsal fin (Lidocain ointment 5%, and Scandicain 3% injections). Three holes were then bored in the dorsal fin with a 5mm cork borer-type utensil. The transmitters were attached with three pins (polyoxymethylen (POM), 5mm in diameter) sheathed with smooth nylon tubes and coated with antibacterial ointment (Fucidin 2%). The pins were fastened with nylon nuts, but not too tightly so that water could still flow between the neoprene and the skin. During attachment of the transmitters, the harbour porpoise was fitted with a heart rate instrument to monitor the cardiac response to tagging. The heart rate monitor consisted of a Polar transmitter fitted on an elastic belt, and a Polar Vantage NV wrist monitor (Polar Electro). The elastic belt was strapped around the chest of the porpoise just anterior to the pectoral fins. On the inside of the belt two electrodes, connected to the transmitter, measured the electrical potential from the heart and transmitted the data to the wrist monitor via an electromagnetic field (Edwards, 1997). The heart rate was measured in beats per minute (bpm) giving an average value every 5 seconds. By observing the wrist monitor it was possible to closely follow the heart rate while the tagging progressed. After the porpoise was released, the heart rate data were transferred to a computer using a wireless interface (Advantage Interface, Polar Electro).

Observations

One observer measured behavioural changes immediately after the tagging and after removal of the transmitters using a handheld computer (Psion Workabout). A second observer followed the porpoise closely with a Sony digital video camera also immediately following transmitter attachment and after removal, while a third observer monitored the animal regularly for 80 consecutive days focusing on possible behavioural changes before, during and after transmitter attachment.

The first observer collected a total of 15 hours of data on the Workabout, one day before attachment (3.1hrs), two days immediately after attachment (3.9hrs and 5.4hrs, respectively) and the seventh day after the transmitters were removed 16 June 2000 (2.6hrs). The Workabout was programmed to log duration of dives, frequency and duration of surfacings in each of the three areas of the enclosure as well as the number of loggings. A ‘logging’ was recorded each time the porpoise remained at the surface between two breaths.

One day before tagging, the two days following tagging and on the seventh day after removal of the transmitters, digital video recordings provided data on the exact duration of each roll during the observation period. A roll was defined as a surfacing followed by a single breath, and then a dive (Amundin, 1974). The duration of rolls was measured to give an indication of whether the transmitters had an impact on the swimming pattern of the harbour porpoise. The duration of each roll was calculated by tallying the number of picture frames in the video recordings, starting with the first appearance at the surface and ending when the porpoise disappeared again. One frame represented 0.04 seconds and only fully recorded and clearly visible rolls were analysed. The mean duration of 45-50 rolls was calculated from the afternoon as well as for the morning immediately after tagging.

The third observer followed the porpoise visually while taking notes from either of the two locations marked in Fig. 1. Harbour porpoise behaviour was observed in two periods of 10 minutes (around 10:00 and 14:00 hours) each day, over 80 days, resulting in a total of 26.7 hours of observation. The observation period was divided into four sub-periods, based on when the transmitters were attached. Day 1-10 was the baseline period, before the attachment of the transmitters, day 11-15 was the first five days after attachment, day 16-40 when transmitters were attached, and day 41-80 after removal of the tags. Two types of behaviours were recorded: duration of each dive and distribution of surfacings in the pool. Durations of 4,273 dives were recorded and grouped in 5 second intervals. The pool was divided into three areas to facilitate analysis of the distribution of surfacings (Fig. 1). The area in which the porpoise surfaced following each dive was recorded and the distribution of surfacings among the three areas were compared. Area 1 contains the holding pool where the porpoise was taken out of the water for attachment of the transmitters and for medical examinations.

Data analysis

Animal behaviour software (Observer version 3.0, Noldus, the Netherlands) was used to analyse the data collected on the Workabout. SAS 8.02 (SAS Institute Inc., Cary, NC, USA) was used for statistical analysis. All data proved to be distributed normally and the statistics used were descriptive statistics, one-way ANOVA, Tukey test and chi-square test. The results were considered significant at the 5% level.

RESULTS

The transmitters were attached to the dorsal fin of the animal during a routine weekly physical examination at 08:30-09:00 on 16 May 2000. During the tagging, the porpoise generally reacted as if it had been a normal physical examination, although when the holes were made in the dorsal fin, the porpoise reacted a few times by arching its back. The heart rate measurements showed a relatively constant pulse of 161 bpm (STD=13.1) until the first hole was made. Thereafter the heart rate increased significantly to 180 bpm (STD=10.3, *t*-test, $p<0.0001$, Fig. 3) until the animal was released into the water and the heart rate measurer was removed.

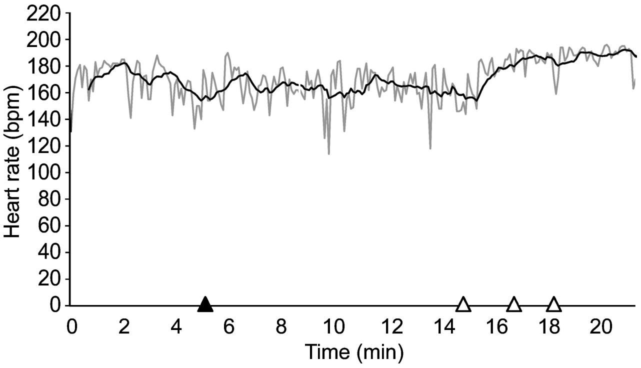

Fig. 3. Heart rate of the porpoise (bpm) during tagging. The black triangle on the x-axis represents when the blood samples were taken and the white triangles represent when the holes were bored in the dorsal fin. The black line is a running average.

Behavioural effects caused by the transmitters

Loggings (Fig. 4)

A total of 15.0 hours of observation on the handheld computer yielded data on 132 loggings. The number of loggings per hour was five to six times higher on the day of tagging, than the day before tagging, the day after tagging and on one day a week after removal of the tags.

Duration of rolls (Fig. 5)

The mean duration of rolls varied significantly (one-way ANOVA: $p<0.0001$, $F=120.65$). There was a significant difference in the duration of rolls during all days of observation, except for the 16 May seven hours after attachment and the seventh day after removal of transmitters (Tukey test, critical value 3.89).

Dive duration (Fig. 6)

Dive duration varied between 1-163s with an overall mean of 22.2s. The mean dive duration whilst the tag was attached (23.8s) was significantly higher than both the mean dive duration before (19.0s) and after removal of transmitters (21.7s; one-way ANOVA: $p<0.01$, $F=6.6$).

Surfacing areas

In the first period after the attachment (day 11-15), the porpoise surfaced more in area 3, the area furthest away from the medical pool (89%) compared to the other three periods (45-56%). Consequently surfacings in area 1 and 2 for the period from day 11-15 were less frequent (area 1=2% and area 2=9.5%) than in the other periods (area 1=15-24% and area 2=28-31%) (Fig. 7). There was a significant difference in the distribution of areas where the porpoise surfaced when comparing the four time periods (chi-square, $p<0.001$).

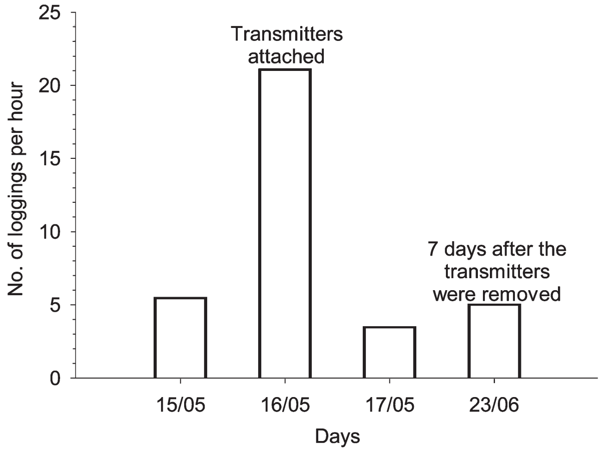

Fig. 4. Frequency of loggings per hour on four days of observation. There were 15 hours of observation in total: 3.1hrs on the day before attachment of the transmitters; 3.9 and 5.4hrs on the two days following attachment; and 2.6hrs on the seventh day after the removal of the transmitters.

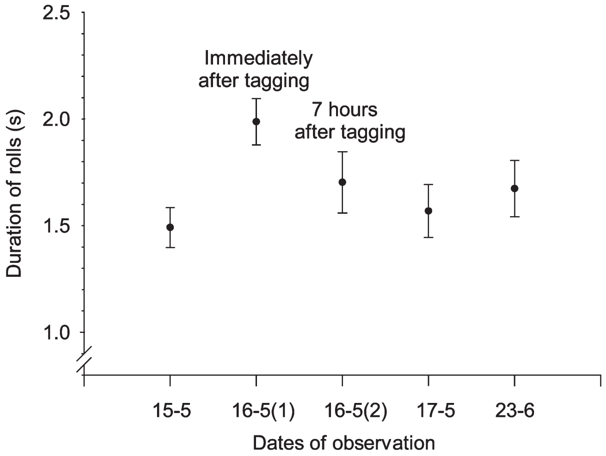

Fig. 5. The mean duration of rolls on four days of observation. All rolls were measured from recordings made between 13:20 and 17:00, except 16-5 (1), where recordings were made between 09:00 and 10:00. The mean duration of rolls each day are represented by dots, while the bars represent one standard deviation.

Depth of dives

A clear semidiurnal dive cycle was evident during the first 85 hours after tagging. Shallower mean depth of dives were recorded around noon and again around midnight (dive depth 0-1m), and deeper mean depth of dives were recorded in a short period around 06:00 and 18:00 (dive depth 1.5-2.2m) (Fig. 8). In the first 24 hours after attachment, the semidiurnal pattern was similar, but with 1-2m deep mean depth during all hours compared to the rest of the experimental period. The tide varied about 3m with high tide around 01:30-3:30 in the morning and 13-15:30 in the afternoon during 16-19 May 2000. There was no obvious connection between dive cycle and tide cycle.

Body weight and food intake of the porpoise

A decrease in body weight from 35 to 33kg was seen for the first two weeks after the porpoise was stranded (4 December 1999). After that, the porpoise steadily gained weight, except for a period between mid-January and late February 2000 when its body mass remained fairly constant (Fig. 9). At the time of transfer to the outdoor enclosure in Neeltje Jans (12 April 2000), the porpoise weighed 38.8kg and in the period up to the tagging (16 May 2000) the body weight

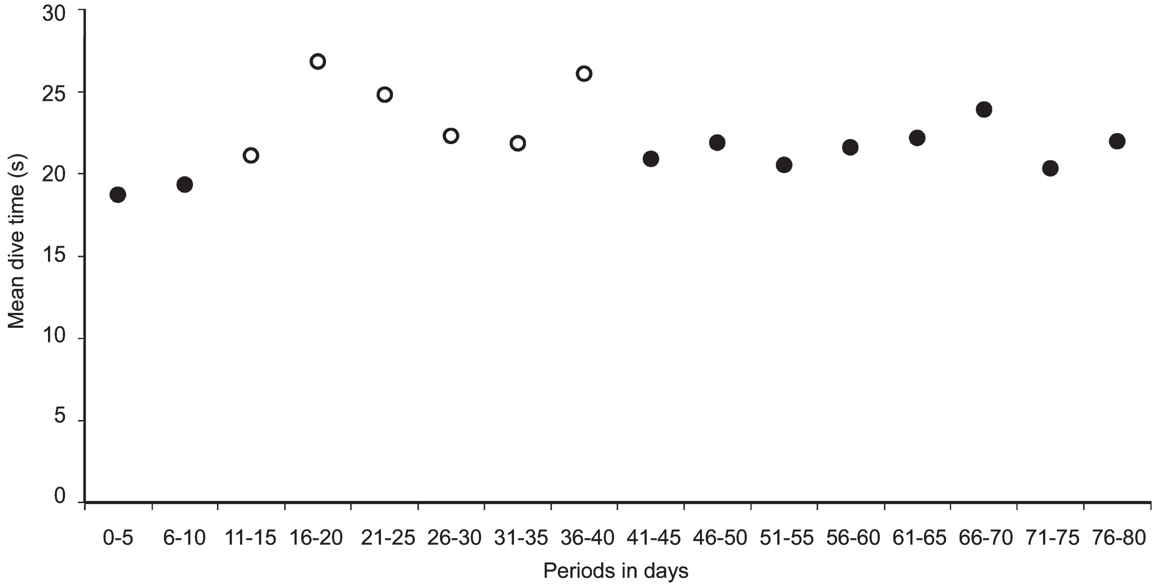

Fig. 6. The mean dive time of 16 five-day periods in seconds. The black dots represent time periods where the porpoise was not tagged and the white dots represent time periods where the porpoise was tagged.

increased to 39.4kg. During transmitter attachment period, the body mass decreased to 37.2kg and after the transmitters were removed the porpoise continued to lose weight until the last week of July, just prior to the release of the porpoise, where the animal gained 1kg. The relative weight loss between mid-May and late July was 7.6% of the total body weight.

The daily food intake decreased from 1.7 to 1.4kg in the week up to the tagging. From the time of transmitter attachment until three weeks after the removal of the transmitters, the daily food intake increased steadily from 1.4kg to 1.9kg. Following that period the food intake increased much more rapidly than previously seen, thus from 6 July 2000 until the end of the study period the daily food intake increased from 1.9kg to 3.5kg (Fig. 9).

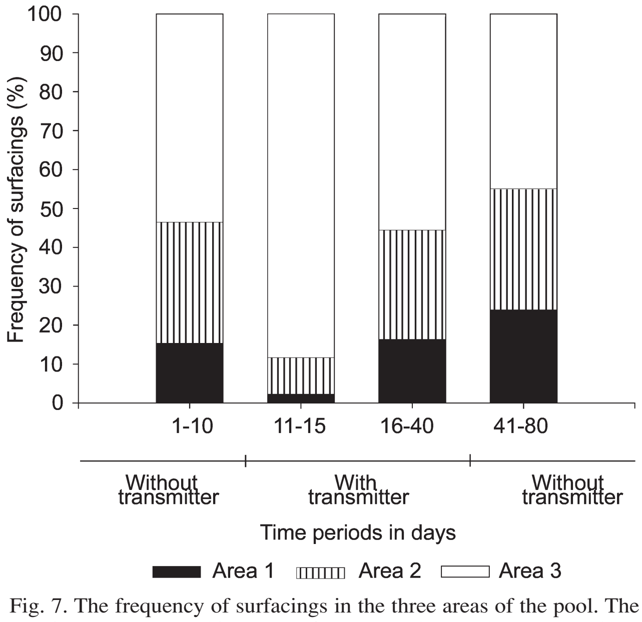

Fig. 7. The frequency of surfacings in the three areas of the pool. The animal was released in area 1 after the tagging on day 11 (see Fig. 1 for areas).

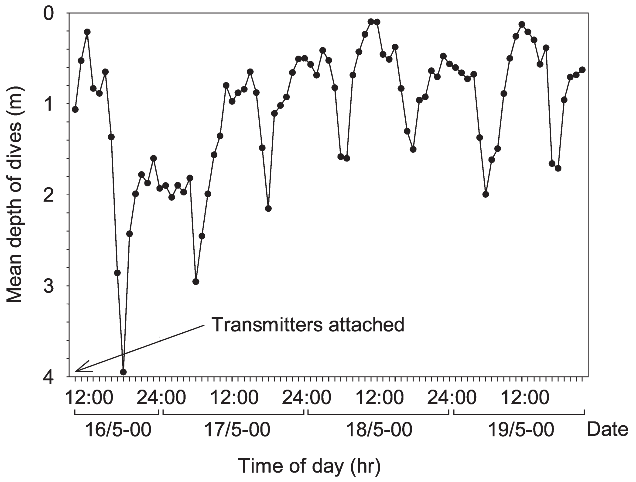

Fig. 8. The mean depth of dives during 85 hours. The depth of the porpoise was measured every 10 seconds and 360 measurements were averaged over 1 hour. The mean depth of each hour is displayed against time of day starting immediately after the attachment of the transmitters. Note the apparent semidiurnal rhythm of diving.

Removal of the tags

Due to a lighter skin colour around the pinholes and a sudden reaction when the front hole was touched, the transmitters were removed on 16 June after one month of attachment. When the pins were removed a reddish exudate was present inside the holes but no swelling was observed. This tissue reaction that apparently emerged after about one month could be due to the additional drag associated with the seaweed that tended to get stuck on the antennas and pins during the last part of the experiment. The animal was often seen with long 'tails' of seaweed up to 0.5m in length trailing after it when it swam.

On the second day after transmitter removal, the holes were closed but the porpoise still reacted when the front hole was touched. After seven days all holes were healed, but touching the front hole still caused the animal to react. After 28 days the porpoise did not react to any pressure on the holes.

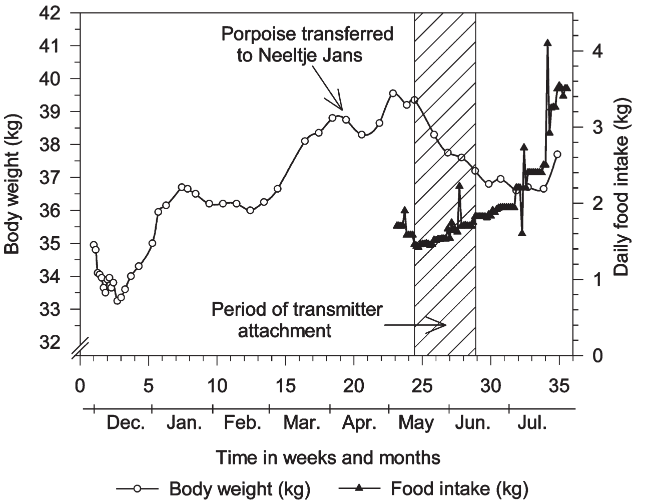

Fig. 9. The variation in body mass (primary y-axis) from 4 December 1999 to 28 July 2000 and the daily food intake (secondary y-axis) from 8 May 2000 to 2 August 2000. The time is given in both weeks after the porpoise stranded and months of the year.

When the transmitters were removed, an imprint of 1mm in depth was observed on the upper and lower part on both sides of the dorsal fin. The colour of the skin at the imprint was lighter than the normal skin. The imprint on the lower part of the dorsal fin was gone after five days, while the one on the upper part did not disappear until 35 days after the transmitters were removed. Several times during these 35 days the skin sloughed at the imprints. The imprints did not seem to cause the porpoise any discomfort.

DISCUSSION

Heart rate measurements

There was no clear effect on the heart rate of the animal when blood samples were taken. However, the mean heart rate increased significantly following the boring of the first hole. Geertsen (2002) presents heart rate data during handling and tagging of 20 harbour porpoises. During nine of these taggings, the time of the boring and blood sampling were recorded. Three of the porpoises experienced a clear and significant increase in heart rate after the first hole was bored. Therefore we suggest that the state of the animal during tagging should be monitored closely, particularly during the boring of the holes through the dorsal fin. Furthermore, measuring the heart rate of the animal during tagging is important for monitoring its wellbeing.

Short-term effects on behaviour

The dramatic increase in logging behaviour we observed has also been documented for a captive adult female harbour porpoise regularly carrying a datalogger attached with suction cups for approximately one hour at a time (Teilmann, 2000). In this experiment, logging increased significantly when the datalogger was attached compared to before and after the attachment. In another study, Otani *et al.* (1998) observed two female harbour porpoises in a small circular tank before and after attachment of a datalogger. Although logging behaviour was not recorded, no changes in either breathing frequency, body weight, swimming or feeding behaviour, were reported after the attachment of the dataloggers. The observed increase in logging in the present study during the first day after tagging was probably a result of the animal acclimatising to the touch of a foreign object on its dorsal fin and the sensation of associated drag during diving. Furthermore, the Valium that was used as a tranquilliser could have had an effect on the animal's behaviour in the first hours after tagging.

Immediately after the attachment, the harbour porpoise made significant longer lasting rolls than on the day before attachment. The mean duration of rolls decreased with time following the period after attachment, but in none of these periods was the mean duration of rolls as low as the day before attachment. Teilmann (2000) recorded the behaviour of a harbour porpoise in captivity before and after a datalogger was attached to the dorsal fin with suction cups. The porpoise was resting (immobile) for 11% of the observation time before and 37% during the attachment of the datalogger (Teilmann, 2000). Furthermore the frequency of breathings that terminated by the porpoise submerging/sinking backwards after resting at the surface increased significantly after the attachment of the datalogger (Teilmann, 2000). The 'sinking backwards' behaviour was not observed in the present study, but in another study also conducted at Neeltje Jans, such behaviour was observed in two different male porpoises tagged with satellite transmitters (Ron Kastelein, unpubl. data). Irvine *et al.* (1982) also observed this behaviour in two out of 10 bottlenose dolphins tagged in the wild with radio tags attached with one pin through the dorsal fin. The slower rolls at the surface and the slow sinking backwards could be an adaptation to reduce the possible discomfort when the tag hits the water surface during a normal roll. The differences in mean duration of dives, before, during and after tagging, show that the porpoise increased its dive duration during tagging. Although the mean dive duration only increased by about 5s, this may also be an adaptation to reduce the number of surfacings and thereby the numbers of impacts with the water surface.

During the first 24 hours after tagging, the mean dive depth was 1-2m deeper than during the following 61-hour period, where the semidiurnal diving pattern was rather constant. Since the dive depth could only be recorded by the satellite tag, it is not known whether the deeper dive depth after tagging was a reaction to the tagging or if the shallower dives recorded after 24 hours was a reaction to the presence of the tag.

In the first period after deployment of the transmitters (day 11-15), the animal surfaced almost exclusively in area 3, compared to the other three periods. This behaviour suggests that the porpoise connected the stressful tagging experience with the holding pen in area 1. Therefore it tended to stay as far away as possible from that end of the pool in the first days following the tagging. A similar behaviour was observed in a satellite tagging study of wild porpoises in Denmark where tagged animals tended to move rapidly away from the tagging location immediately after release but often returning to the same general area after some days (Teilmann, 2000).

The increase in logging behaviour as well as the clear avoidance behaviour towards area 1, suggest a reaction to the tagging experience. However, the results presented in this paper indicate that the change in behaviour may only last a few hours or days. Considering that harbour porpoises exhibit a high degree of individual behavioural variability (Westgate *et al.*, 1995; Read and Westgate, 1997; Teilmann, 2000), and that the experiment in this paper is based on only one animal, the results must be interpreted with caution.

Long-term effects on behaviour

Only a few experiments have succeeded in resighting tagged animals after several days (Martin and Smith, 1992; Read and Westgate, 1997; Hanson, 2001). Read and Westgate (1997) reported resightings seven days after release of a male harbour porpoise deployed with a satellite tag mounted on the front of the dorsal fin, and a VHF transmitter attached to the trailing edge of the dorsal fin. The animal appeared to swim normally, and was in a large group of feeding porpoises. Martin and Smith (1992) were able to observe a tagged white whale on several occasions in the days following the release of the animal. The animal was often seen together with other white whales, and its behaviour appeared normal. Furthermore, a satellite tagged harbour porpoise was resighted in Danish waters in the company of another porpoise for a few hours two months after tagging. There was no apparent difference in behaviour between the two porpoises (Jonas Teilmann, pers. comm.). Hanson (2001) observed a tagged free-ranging harbour porpoise periodically over a 203 day period. Although the porpoise was commonly observed near other porpoises, the animal appeared to log at the surface with greater frequency than its conspecifics (NMML, unpublished data).

Physiological effects

Attaching a satellite tag and/or a VHF transmitter onto small cetaceans using pins through the dorsal fin gives rise to concern about potential adverse impacts associated with the tag and the attachment. The drag from transmitters is a potential problem and has been discussed in relation to both tissue and energetics for several marine animals (Bengtson *et al.*, 1993; Watson and Granger, 1998; Hanson, 2001). In small cetaceans, where the tag is attached with pins through the dorsal fin, the drag is transferred from the transmitter to the pins, and ultimately to the adjacent tissue (Hanson, 2001). This may cause tissue degradation around the holes and result in migration of the pins through the fin, resulting in the tag detaching from the animal. Irvine *et al.* (1982) report of several cases of pins migrating through the dorsal fin of bottlenose dolphins deployed with VHF-transmitters. Hanson (2001) found from wind tunnel experiments that positioning a tag on each side of the dorsal fin of a harbour porpoise increased the drag considerably compared to attachment of a single tag onto the side of the dorsal fin. Careful attention to streamlining the design of the tag can probably reduce the drag significantly (Hanson, 2001). Furthermore, the fast closure of the holes suggests that it was only a local reaction and that the ability to regenerate tissue is very fast in the dorsal fin.

During tag attachment and after the transmitters were removed, the porpoise continued to lose weight despite the increase in food consumption. Lockyer *et al.* (2003) reports on clear seasonal fluctuation in both body weight and food intake of a mature male and a mature female captive harbour porpoise kept in a semi-natural outdoor enclosure over a period of five years in Kerteminde, Denmark. The body weight of both porpoises peaked during the winter months, after which it decreased during spring and reached the lowest values in the summer. The daily food consumption declined after January until the end of June where it increased rapidly until late summer or early autumn. The mean weight loss (percent of the total body weight) in the period 1997-2001 was larger for the female than for the male (19.9% and 15.7% respectively, Lockyer *et al.*, 2003). The relative weight loss was less pronounced for the porpoise in the present study, but the porpoises in the two studies showed similar patterns in daily food intake. Therefore it is possible that the variations in body weight and daily food intake for the porpoise in this study were due to seasonal fluctuations rather than an effect of the extra drag caused by the transmitters and the seaweed. However, contrary to the hypothesis that the drop in body weight was part of a seasonal body weight cycle, is the fact that the drop was less pronounced after the transmitters were removed. In addition, the female had been housed indoors over the previous winter, and thus did not create an extra thick blubber layer like the porpoises in Kerteminde that live in cold water in the winter.

CONCLUSIONS

Although the results presented in this paper are gathered from one captive harbour porpoise, which did not have to capture its own food, it appears that the attachment of satellite tags had minor long-term effects on the animal's behaviour. Changes in behaviour were evident in the first hours or days after the tagging, but thereafter the animal appeared to behave normally apart from a slight increase in the mean dive duration.

The shape of the tag, antenna and saddle should be carefully designed according to hydrodynamic principles to reduce drag as much as possible (Hanson, 2001). Furthermore we recommend rounding all edges, pins etc., to avoid catching seaweed. New smaller and more hydrodynamic tags have been designed with internal pins (e.g. SPOT2 and SPOT3, Wildlife Computers, Seattle, USA), or recessed nuts (Hanson, 2001) to reduce drag and seaweed attachment. As it is difficult to get quantitative data on the effects of tagging on cetacean species in the wild, we recommend that more long-term captive studies be conducted. These studies should focus on: (1) the effect of various tag designs on the tissue of the dorsal fin; (2) the effect of various pin materials, as well as their size and number used for attachment on the dorsal fin tissue; (3) the effect of various tag designs on the behaviour and energetics of the animal; and (4) developing a reliable release mechanism for long-term deployments that releases the tag when e.g. battery is drained. Such studies will help developing tags and methods of attachment that have the least impact on the animals and thereby increasing the value of the results obtained from animals tagged in the wild and not compromising their well-being.

ACKNOWLEDGEMENTS

We would like to thank the staff at Neeltje Jaans for excellent training and caretaking of the porpoise. Genevieve Desportes and Christina Lockyer provided useful information on various aspects of the physiology of harbour porpoises. We would also like to thank Rune Dietz and Jakob Tougaard for constructive criticism on an earlier draft as well as Bent Jørgensen and Frank Riget for comments on the statistics and Brad Hanson and another external reviewer. This study was financed by the Danish Forest and Nature Agency as a part of the tagging study of wild harbour porpoises in Denmark and by the Danish National Research Foundation.

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A note on improving the mechanism of pinger attachment for the Danish North Sea gillnet fishery

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ABSTRACT

This paper describes development of a better mechanism for the attachment of pingers to fishing gear, aimed particularly at the Danish bottom-set gillnet fishery. In a cooperative effort involving gillnet fishermen, the fishermen's organisations and researchers, modifications to the physical shape of a pinger and its attachment to the gear were developed, taking into consideration the acoustic functioning of the pinger, battery life, robustness to operational rigours, weight, volume, buoyancy, environmental effects, cost and handling. The suggested attachment (THOR-1) has a number of important advantages in this fishery compared to the more common head rope attachment. THOR-1 was tested for ease of handling on board a gillnet vessel and found to perform very well, with minimal interference with normal fishing operations. The main disadvantage of THOR-1 is the need for an effective range of around 200m.

KEYWORDS: GILLNETS; INCIDENTAL CATCHES; EUROPE; FISHERIES; SMALL CETACEANS; HARBOUR PORPOISE

INTRODUCTION

Bycatch of small cetaceans is a major problem in a number of gillnet fisheries around the world (see e.g. review in Perrin *et al*., 1994). For the North Sea it was estimated that more than 8,000 harbour porpoises (*Phocoena phocoena*) were bycaught annually in the mid-1990s (Vinther, 1999; Northridge and Hammond, 1999); the need to mitigate this bycatch has been identified by both ASCOBANS and the IWC (IWC, 1996; ASCOBANS, 1997). An experiment conducted in the Gulf of Maine sink gillnet fishery demonstrated that bycatch of harbour porpoises could be reduced significantly by using acoustic alarms (pingers) attached to the nets (Kraus and Brault, 1997; Kraus *et al*., 1997) and it was recommended that pinger experiments should be conducted in other fisheries to further test this mitigation measure (IWC, 1996).

In 1997, a trial was conducted by the Danish Institute for Fisheries Research (DIFRES) in cooperation with a number of Danish fishermen to investigate whether pingers could reduce bycatch of harbour porpoises in the commercial bottom-set gillnet fishery for cod in the North Sea (Larsen, 1999). The results showed that the pingers almost eliminated the incidental catch, but it was also clear from the experience that the mechanism used for attaching the pingers to the fishing gear would present problems during normal fishing operations in the Danish bottom-set gillnet fisheries. This was not unexpected as the pinger attachment mechanism had been designed based on the special requirements of the trial, including the requirement for each vessel to switch between active and control pingers on a daily basis. For this reason, pingers used during the trial were attached to the head rope of the nets with a snap hook on a short strap and a 50mm wide Velcro-strap glued to the mid-part of the pinger and strapped around the head rope. The pingers were attached to the tail-ends, i.e. the bridles used to tie the nets together into strings. The report of the study (Larsen, 1999) recommended that if pingers were to be used in commercial fisheries, pinger housing and attachment to the fishing gear should be designed so that they would interfere as little as possible with the fishing operations.

To ensure a wide acceptance among fishermen it is important that pingers are not seen as an impediment to the efficient conduct of fishing operations. If pingers interfere with the practical operations of the fishing gear, fishermen will be inclined to use them as little as possible. Another important consideration for the fishermen is the cost of using the pingers, which is affected by such factors as battery life and the ability of the pinger to stand up to operational rigours. The IWC Scientific Committee, having agreed that pingers can be an effective mitigation means for harbour porpoise bycatch, recommended that field trials be carried out to address such practical operational issues as mentioned above (IWC, 2000). This point was also made by Northridge *et al.* (1999) in the report of their sea trial of pingers in the Celtic Shelf gillnet fishery.

Most commercially available pingers have been developed with head rope attachment in mind. However, this attachment places considerable constraint on the size and shape of the pinger, which in turn limits the amount of energy that can be included with the pinger. This requires batteries to be changed more often, or limits the pinger's lifetime if batteries cannot be changed. In some fisheries, like the Danish cod gillnet fishery, head rope attachment also puts considerable physical stress on the pinger, e.g. when the pinger hits the railing or steel post (see below) during shooting of the nets and when it goes through the net hauler during retrieval of the nets.

To help resolve these problems, DIFRES initiated a study in 1999 to develop a better mechanism for attachment of pingers to fishing gear, aimed particularly at the Danish bottom-set gillnet fishery. The project was conducted in cooperation with the Danish Fishermen's Association (DFA) and with active fishermen. The results of the study are presented here in the hope that they will be useful for other fisheries as well.

METHODS

A working group was established including active bottom-set gillnetting fishermen, members of the DFA Gillnet Fishermen's Committee, a representative of the DFA and researchers from DIFRES. The working group was given the task of developing modifications to the physical shape of the pinger and its attachment to the gear, taking into consideration the acoustic functioning of the pinger, battery life, robustness to operational rigours, weight, volume, buoyancy, environmental effects, cost and handling.

Practical handling trials with models of the suggested designs were subsequently conducted on board a commercial gillnetting vessel. These handling trials were intended to identify immediate problems related to shooting, hauling and storing nets with pinger models attached. Longer term trials with actual prototype pingers are considered the next step in the development process, but are outside the scope of the present project.

GEAR TYPES AND FISHING PRACTICE

Gillnets in the Danish North Sea cod fishery are normally 1,000 meshes long, typically 21.5-26.5 meshes high and stretched mesh size is 150-170mm. The head rope is 8 or 10mm and 60-70m long giving hanging ratios of around 0.5. In the fishery on wrecks a string is 2-4 nets long and typically 2-4 strings are placed on each wreck, with an anchor at each end of each string. In the fishery on flat bottom/stony grounds, nets are typically tied together into strings of 5 (sometimes 10) nets in length. These strings are equipped with strong snap hooks at the ends to facilitate fast and easy coupling of these small strings into strings 20-60 nets long, depending on whether they are set in parallel rows or, less common, as a single meandering string. When set in parallel rows, the distance between neighbouring rows can be as little as 10m. The strings are kept in place by anchors attached at the end of the strings, and at regular intervals (normally for every 10 nets) along the strings. Buoys mark the end of each string as well as the anchors in between. Fishing depths are typically 20-80m. In the most recent years there has been a tendency towards setting the nets in long meandering lines or circles and using fewer anchors.

Nets are stored on board in large sacks or in small wooden compartments called pounds. The nets are most often shot over the side of the vessel around a steel post on the railing, and at speeds up to 6 knots. The nets are hauled using hydraulic net haulers, of which a variety of different designs are in use. After the catch has been removed, the nets are often run through a machine, which stretches and cleans the nets from seaweed and other items, before placing them back into the pound or sack. Nets can be moved between pounds using small portable net haulers, in some cases through metal tubes from one end of the vessel to the other.

Because of the very short strings used in the Danish wreck fishery, pinger handling is much less of a problem than in the flat bottom fishery. In the wreck fishery, pingers can be attached at each end of a string and still ensonify the whole string as a string is rarely more than 200m long.

In other Danish bottom-set gillnet fisheries (e.g. for hake, plaice and turbot) the mesh size, hanging ratios, height of nets, buoyancy of head ropes and fishing depths vary, but the nets are handled in ways similar to the handling in the cod fishery.

RESULTS

The pinger development working group considered low interference with net handling, low cost and long lifetime to be the most important criteria for the acceptance of pingers among fishermen. The last two factors are to some degree linked and inversely related, so an acceptable compromise has to be found between them.

The working group evaluated a number of different pinger designs, including two commercially available products, the Dukane Netmark1000 and the Aquatec AQUAmark100, in the light of these criteria. All are designed to be attached to the head rope. The working group did not find head rope attachment an optimal solution; the reasons for this include:

(1) concern over crew safety when nets with pingers attached to the head rope are moved around the vessel using net haulers and when nets are shot over the side at high speed;
(2) concern over pingers button-holing the mesh while the nets are kept in pounds or sacks;
(3) concern over pingers not being able to withstand the repeated hits on the steel post during net shooting;
(4) the need to keep pingers as small as possible, thereby reducing the amount of energy that can be included (and thus lifetime) and reducing the possibilities for protecting the pinger against damage due to physical impacts;
(5) head rope attachment normally requires permanent or semi-permanent attachment, which results in excessive pinger use and waste of pinger energy in fisheries where nets are set close to each other.

There are technical solutions to some of these problems, but these solutions can lead to other problems.

The working group considered alternative ways of attaching the pingers, and suggested one in particular for practical handling tests on board a commercial fishing vessel. This solution, named THOR-1 (see Figs 1 and 2) after the port Thorsminde, where the working group met, takes advantage of the anchors that, in the Danish gillnet fisheries in the North Sea, are placed for every 10 nets along a string, and of the vessel having to slow down to set these anchors. A pinger can be attached to the anchor spring line (the line between the tail-end and the anchor) at the same time as the anchor is set, without delaying the shooting of the nets. The pinger needs to be positively buoyant and attached with a line of 1.5-2m to keep the pinger off the seabed. A snap hook on the pinger line will facilitate fast attachment to the anchor spring line. If the pinger is not positively buoyant on its own, a float can be attached to the pinger line.

Handling trials

The handling trials were carried out on board a commercial gillnet vessel in the North Sea in October 1999. The vessel was typical for a Danish North Sea gillnet vessel: 19.85GRT, a crew of four, and equipped with a hydraulic net hauler. Weather conditions during the trials were fine with almost clear skies, winds around 8ms^{-1} and waves of 1.5-2m. Two strings of five gillnets each were used, with dimensions as described above for cod fishing.

Dummy pingers machined in solid polyethylene cylinders with rounded edges were used (see Fig. 2). The dimensions of the dummy pingers were: length=180mm; diameter=80mm; rounding=10mm. A 15mm diameter hole was drilled through one end and a 2m length of 10mm polypropylene line was fed through this hole and the ends tied together to form a double string. A heavy snap hook of the same type used by the fishermen to connect strings of nets was tied to the other end of the double string for attachment to the gear. The dummy pingers were positively

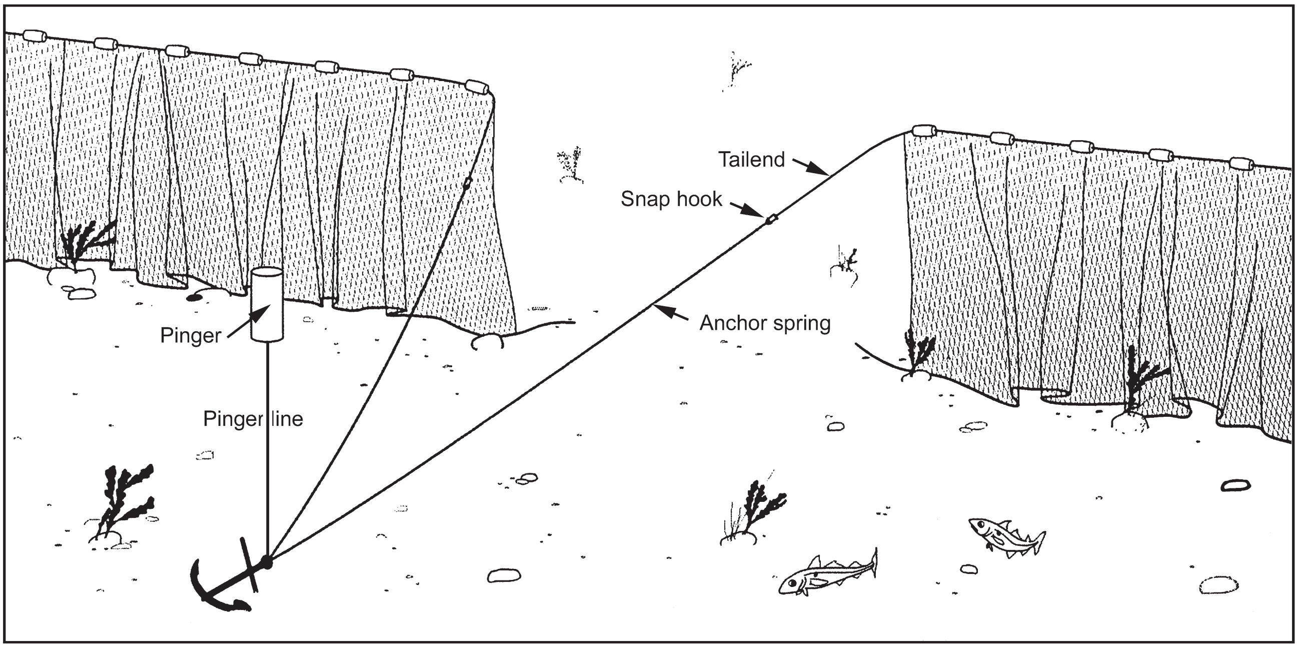

Fig. 1. The attachment of THOR-1 to the anchor spring line on a bottom-set gillnet.

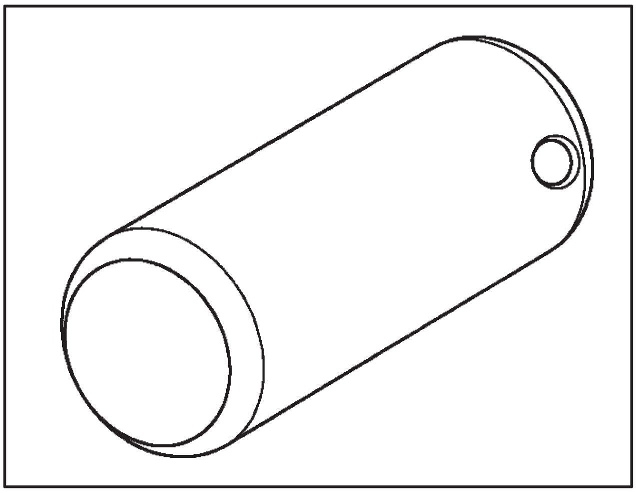

Fig. 2. Diagram of the dummy pingers used during the handling trials (not to scale).

buoyant. The dimensions of the dummy pinger were chosen to make it considerably larger than pingers designed for head rope attachment, and large enough to carry three D-cell batteries, to determine if this size would present a problem in handling.

The nets were shot and hauled twice, with dummy pingers attached at both ends as well as to the snap hook between the two five-net strings. The dummy pingers were attached by the crewmember also attaching the nets to the anchor lines. There were no problems in attaching the dummy pingers to the anchor spring lines without interfering with the normal handling of the nets. Similarly, a dummy pinger was attached to the snap hook between the two five-net strings without interference or delay. At the first haul of the nets, the dummy pingers were removed before the nets entered the net hauler. This requires the attention of one of the crewmembers, who are normally all busy removing the catch from the nets during hauling. At the second haul, the dummy pingers were removed at the table where the catch is also removed, thus demanding less attention from the crew, but requiring the dummy pinger to pass through the net hauler. The fishermen noted that when the pingers are removed at the table, it would facilitate removal if the ends of the pingers were more rounded, this would make them easier to take through the mesh in cases where they have ended up underneath the net.

The pinger development working group discussed the results of the handling trials and concluded that this way of attaching pingers to the nets did not interfere with the normal handling of the nets. The working group also discussed various ways of making the pingers easily available for fast attachment during shooting of the nets. However, the working group agreed that, given the variability in net handling practices among vessels, this problem would be best solved by individual solutions for each vessel.

DISCUSSION

In June 2000, use of pingers became mandatory in the months August-October in the Danish North Sea wreck net fishery. This fishery was selected primarily because of the particularly high harbour porpoise bycatch rate observed but also because problems regarding pinger attachment were expected to be minor in this fishery as a result of the way nets are handled. However, the wreck net fishery has now almost completely disappeared because of the severely reduced quotas for the North Sea cod stock, and the fishing effort has moved into other types of gillnetting or into hook fishing. If pinger use becomes mandatory in some or all of these other types of gillnetting, as suggested by a recent proposal from the EU-Commission, the importance of developing solutions to the problems related to attaching pingers to fishing gear becomes apparent.

The mechanism and procedure for attaching pingers to bottom-set gillnets suggested by the Danish working group is one way of solving the attachment problems. It has a number of important technical advantages over head rope attachment, some of which are particular to the Danish gillnet fisheries, while others are of a more general nature.

The main advantages of the suggested attachment compared to head rope attachment are:

(1) it avoids the safety problems related to shooting nets with pingers over the side of the vessel at high speed;
(2) the pingers are easily removed and do not have to go through the net cleaning machinery, which reduces handling problems;
(3) because the pingers are not permanently attached to the nets, physical stress on the pingers is minimised;
(4) size and shape constraints on the pinger are reduced, thus it can carry more energy and can also be better protected against physical damage;
(5) because the pingers are not permanently attached to the nets, they can easily be used in different fisheries over the year;
(6) fishermen can optimise pinger use and avoid wasting pinger energy because just the required number of pingers necessary to ensonify all nets can be attached;
(7) it will be easier to design a housing for changing the batteries in this kind of pinger;
(8) replacement of failed pingers is considerably easier.

In other field trials of pingers, head rope attachment has been the precedent. Gearin *et al.* (2000) tied the pingers to the head rope using nylon tie wraps, but made no comments on their experience with this attachment. Kraus *et al.* (1997) put the pingers in bait bags tied to the head rope, but also did not comment on whether any problems were experienced with this attachment. Northridge *et al.* (1999) also used bait bags, but noted that this attachment would not necessarily be a long term solution. Use of bait bags avoids the problem of 'button-holing' and probably also to some extent protects the pinger against hard impacts. Otherwise, this method has the same problems as tying the pinger directly to the head rope, but how severe these problems are will vary with vessels, net types and hauling techniques.

The major disadvantage of THOR-1 is that it requires a pinger that is able to ensonify more than half the distance between two adjacent anchors, i.e. more than 300m. Although this is not a technical problem, it means that the porpoise free zone around the nets will be larger than may be necessary to avoid incidental catch. A solution to this problem would be to attach pingers for every five nets, where many Danish fishermen already have a snap hook, which the pinger could be attached to. This would reduce the required efficient pinger range to maybe around 200m, depending on how large an overlap is necessary between adjacent pingers. This will clearly lead to larger habitat exclusion for the porpoises than using pingers with a smaller effective range. However, the results presented by Larsen and Rye Hansen (2000) suggest that even with an effective pinger range of 400m, only a very small fraction of the North Sea would be unavailable to the porpoises at any given time if all gillnets in Danish fisheries that have incidental catch of porpoises were equipped with pingers.

A further advantage of the suggested solution is that it has been developed with the active participation of the fishermen who will be affected, if pingers are made mandatory in Danish bottom-set gillnet fisheries other than the wreck fishing. Active involvement of the affected fishermen has two main advantages. One is that the solution will be based on the collective body of experience among the fishermen regarding the practical possibilities. The other is that active involvement in the decision process will help both to legitimise the regulations as well as increase compliance with the regulations.

The handling trials suggest that this way of attaching pingers would be a workable solution for fisheries like the Danish bottom-set gillnet fisheries, but only after intensive use will it be possible to conclude that there are no other significant disadvantages than the ones identified here.

ACKNOWLEDGEMENTS

I thank the fishermen who participated in this project for their valuable contributions and Carsten Krog (DFA), Morten Vinther (DIFRES), Simon Northridge (SMRU) and an anonymous reviewer for their very valuable comments on the draft manuscript.

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Incidental mortality of dolphins in the eastern Pacific Ocean purse-seine fishery: correlates and their spatial association

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ABSTRACT

A zero-inflated Poisson model was used to identify typical fishing practices that contributed to incidental mortality of dolphins in the eastern Pacific purse-seine fishery between 1993 and 2001. The presence of hazardous net conditions (net canopies and net collapses), the duration of the backdown procedure (the primary method of releasing dolphins from the net), the size and species composition of the encircled dolphin herd and the amount of tuna encircled, were all found to consistently contribute to increased dolphin mortality per set. In particular, the presence of net canopies and large biomass in the net contributed to both the development of problematic situations in which mortality could occur and to the mean mortality per set, once a problematic situation had developed. On the other hand, lengthy backdown procedures and the presence of net collapses contributed to the development of problematic situations, but had less effect on the mean mortality per set once a problematic situation had developed. Because some of these variables are partially correlated, the overall conclusion of this analysis is that one of the primary causes of dolphin mortality continues to be the encirclement of large herds. Dolphin mortality can increase with the number of dolphins encircled because: (1) the more animals encircled, the greater the likelihood of entanglement and mortality while confined in the net; and (2) the duration of the backdown procedure increases with the number of animals encircled. The duration of the backdown procedure may, in turn, contribute to increased dolphin mortality by: (1) keeping dolphins in close contact with the net for longer periods of time, thereby increasing the chances for entanglement; and (2) leading to the formation of net canopies. Dolphin mortality increases in the presence of net canopies because animals can be trapped below the sea surface in the areas of canopies. Spatial distributions of encircled herd size, duration of the backdown procedure, presence of net canopies and presence of dolphin mortality show similar patterns. Encircled herd size tended to be greatest south of the equator and north of the equator along the offshore margin of the fishery. In these areas, the duration of the backdown procedure tended to be longer and there was often an increased probability of net canopies and dolphin mortality, but also larger catches of tuna. These consistent spatial patterns suggest that reallocation of fishing effort to other areas may be an effective means of reducing the current level of dolphin mortality. Predictive models could be developed to assess tradeoffs between dolphin mortality and tuna catches at varying levels of fishing effort in areas where large herds are targeted by fishermen and different strategies for reallocation of fishing effort to other areas or to purse-seine sets on unassociated tunas.

KEYWORDS: DOLPHIN; INCIDENTAL CATCHES; FISHERIES; PACIFIC OCEAN; BYCATCH; MODELLING

INTRODUCTION

In the eastern Pacific Ocean (EPO), purse-seine fishermen use the association of tunas with dolphins as one means of locating and catching tunas (National Research Council, 1992). Yellowfin tuna (*Thunnus albacares*) is found in association with several species of dolphins in the EPO, primarily the spotted dolphin (*Stenella attenuata*), the spinner dolphin (*S. longirostris*) and to a lesser extent the common dolphin (*Delphinus delphis*) (Allen, 1985; Hall *et al.*, 1999). Fishermen search for signs of dolphins at the sea surface such as splashes, associated birds or the mammals themselves. To catch the tuna, the fishermen chase and attempt to encircle the herd of dolphins with the purse-seine net. If the fishermen are successful, encircling some percentage of the dolphin herd will also result in capture of tuna. Once the bottom of the net has been pursed to prevent the tuna from escaping, fishermen attempt to release the dolphins before loading the fish. This is made possible because vertical stratification of the tuna and dolphins typically occurs within the net, with the dolphins being closest to the surface. Incidental mortality of dolphins can occur if they become entangled prior to release.

Efforts to reduce dolphin mortality have resulted in a decrease in incidental mortalities from an estimated hundreds of thousand of animals annually in the 1960s (Lo and Smith, 1986; Wade, 1995) to less than 5,000 animals per year since 1993 (IATTC, 2002). Mortality reduction has been approached from several angles. Modifications to fishing gear and adoption of release techniques since the late 1950s (National Research Council, 1992) have made significant gains toward eliminating dolphin mortalities. Perhaps the most important release technique developed, the 'backdown' procedure, allows fishermen to pull the net, once pursed, out from under the dolphins, which being air breathers, remain close to the surface. The backdown procedure forms the net into a channel and dolphins are able to swim out over the net at the end of the channel. Smaller mesh netting in the backdown channel (Medina Panel or dolphin safety panel) helps reduce entanglement. Rescue efforts by vessel crew, from rafts and as swimmers within the net, or from small boats outside the net, have also contributed to the reduction in mortality. During such rescue efforts, crewmembers attempt to free any entangled animals and guide them out of the net.

Analyses of data collected by fisheries observers onboard tuna vessels have also been undertaken as part of efforts to reduce the incidental mortality of dolphins. Previous studies have been conducted to explore the efficacy of gear modifications and rescue efforts in reducing mortality (e.g. Fox and Lenarz, 1975 and references therein; Everett *et al.*, 1976; Powers *et al.*, 1979; IATTC, 1984). Previous studies have also shown that mortality of dolphins per set varied with fishing parameters such as the catch of tunas, the species of dolphin and the size of the encircled herd, the area of the set, the time of the set (sets completed during the day versus sets completed in darkness), the duration of the backdown procedure and the presence of strong currents, gear malfunctions, net canopies (billows of netting formed along the sides of the net) and net collapses (collapses of the

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purse) (e.g. Fox and Lenarz, 1975 and references therein; Everett *et al.*, 1976; Powers *et al.*, 1979; IATTC, 1984; 1987; 1989). Insights gained from these analyses are still used in seminars to advise new captains of risky fishing conditions (IATTC, 2002). However, fishery parameters that affect dolphin mortality may not act independently or may be correlated (see below) and to our knowledge, recent analyses of relationships between dolphin mortality and fishery parameters have considered only one parameter at a time. Thus, there may be new information to be learned from application of multivariate approaches.

Over the last decade, the large reductions in mortality have been spurred by international agreements, yet corresponding analyses of fishery observer data that would provide insight on any changes in the relationships between mortality and fishery parameters have not kept pace. National legislation to establish fleet-specific incidental dolphin mortality limits has served to promote reductions in mortality since the early 1970s (Joseph, 1994; Hall, 1998; Gosliner, 1999). In 1993, an international agreement (Bayliff, 2001) established annual individual-vessel dolphin mortality quotas for the first time in this fishery. Following the implementation of these annual vessel limits, mortality per set has decreased to about one seventh the 1992 level (IATTC, 2002). With such a substantial reduction in mortality per set, it is of interest, especially from a management perspective, to determine which aspects of typical fishing conditions continue to lead to dolphin mortality. Generalised linear model (GLM) techniques are used to identify typical fishing practices and environmental conditions that contributed to dolphin mortalities over the 1993-2001 period. Spatial relationships between the most influential variables identified by the GLM analyses and dolphin mortality are summarised and areas for further study to reduce mortality are proposed.

DATA

Data collected by observers onboard tuna vessels of the international purse-seine fleet between 1993 and 2001 were used in this analysis. Sampling coverage by Inter-American Tropical Tuna Commission (IATTC) observers over this nine-year period was greater than 65% annually. Data collected by the national observer programme of Venezuela for 2000-2001 were also used. Only purse-seine sets targeting tunas associated with dolphins ('dolphin' sets) were considered. Dolphin sets for which data were not available on all the variables of interest (Table 1) were excluded prior to analysis.

In addition, some dolphin sets were excluded prior to analysis for a variety of reasons: (1) sets during which the visibility was less than two nautical miles – low visibility may interfere with the observer's ability to view the encirclement process; (2) sets during which fishing operations violated procedures prohibited under the Agreement on the International Dolphin Conservation Program (available at *www.iattc.org*), such as sets completed after sunset – the Agreement bans setting after sunset (Bayliff, 2001) and thus sets that occur during these conditions are likely the result of gear malfunctions that have severely hampered the normal fishing activities; (3) sets on species other than spotted dolphins, spinner dolphins and common dolphins, the three species typically found in association with tunas (Allen, 1985; Hall *et al.*, 1999); (4) sets where the observer's estimate of the number of dolphins encircled was zero – either the observer was not able to obtain a good estimate of the number of animals encircled or dolphin mortality was not an issue because no animals were in the pursed net (mortalities that are hypothesised to occur outside the period of observation of the dolphins by the observer (Archer *et al.*, 2001) were not considered); (5) repeat sets on the same herd – multiple sets can be made on the same herd of dolphins, if, for example, the fish escape capture during the first set; (6) sets for which speedboats were not used during the backdown procedure and, for the 1998-2001 period, sets for which no rescue swimmers were used during the backdown procedure – there were too few sets without speedboats and rescue swimmers during the backdown procedure in the database to create their own category and pooling with other categories seemed unwise.

Finally, one set in 2001 was excluded because of exceptionally high mortality. Preliminary analysis suggested that this set, which had a mortality almost 17 times the next largest mortality per set value in 2001, was very influential on model fit. This set was excluded because the goal of this analysis is to identify typical rather than unusual fishing operations that led to mortality.

After trimming the dataset, 3,173 to 4,557 dolphins sets were available annually for final analysis. On average, 54% of the mortality and 59% of the dolphin sets were retained annually.

The goal of this analysis was to identify typical fishing practices that continue to lead to dolphin mortality. Environmental conditions, operational problems, fishing operations, use of rescue equipment and biomass characteristics were considered in this analysis. These variables are discussed briefly below; a detailed description of each variable is presented in Table 1. Environmental variables that may hamper fishing operations include the presence of strong currents, the sea state and the weather (e.g. fog or rain). Season was also included as a factor to address environmental effects that were possibly missed. Habituation of animals to the fishery may affect their behaviour during fishing operations. Because the historical presence of the fishery has been greatest closest to the coast, the fishing grounds in the EPO were divided into three areas, based on the cumulative fishing effort from 1959 to 1992 (Fig. 1). Operational problems potentially contributing to mortality were modelled by including variables indicating the presence of gear malfunctions, net collapses, net canopies and the extent to which the dolphin safety panel covered the backdown channel. A net collapse refers to the condition when the sides of the net come into contact, reducing the size of the unobstructed volume within the pursed net. A net canopy refers to a billowing in the netting that forms along the sides of the net. The analysis also included an indicator of the level of the captain's skill at fishing for tuna associated with dolphins. Captains with more experience at setting on tuna associated with dolphins may handle gear malfunctions or adverse environmental conditions more effectively. The average number of dolphin sets made by captains in the previous three years was used as an indicator of the level of captain skill. The effects of temporal aspects of fishing operations on dolphin mortality were explored by including in the analysis the start time of the set and the durations of the various components of the setting process: the approach, the chase, the capture, the pre-backdown net retrieval and the backdown procedure. Variables indicating the use of equipment to rescue dolphins during the backdown procedure, such as speedboats and rafts and the deployment of swimmers and divers, were included to model the effects of rescue efforts on mortality. Finally, variables describing characteristics of the biomass in the net were also included: number and species of

Table 1

Variables considered in the analysis of mortality per set. The abbreviations used in Tables 2-4 are shown in parentheses. For continuous variables, the minimum, median and maximum, are shown (data pooled across years). For categorical variables, the number of levels is shown in parentheses.

Variable	Type	Units (or levels)
Environmental variability (E)		
Weather (WTH)	Categorical (3)	Fog, rain, haze.
Season (SSN)	Categorical (3)	January through April; May through August; September through December.
Strong currents (CUR)	Categorical (2)	Presence/absence.
Sea state (BEA)	Continuous	Beaufort scale (0;2;8).
Fishing area (FSH)	Categorical (3)	Historical fishing activity (number of dolphin sets, 1959-1992, all vessels sizes) (Fig. 1): (1) ≤ 3,000 sets; (2) 3,001-6,092 sets; (3) >6,092 sets. Estimates of numbers of dolphin sets are based on the sum of observer tallies of sets for sampled trips of the IATTC, and national observer programmes of the USA and Venezuela, and tallies from fishermen's logbooks for unsampled trips. This sum was adjusted upwards using tuna catch information to account for trips for which neither observed data nor logbook data were available.
Operational problems (O)		
Gear malfunctions (MLF)	Categorical (3)	No malfunctions, minor malfunctions and major malfunctions. Major malfunctions include: webbing wrapped on purse cable; failure of the vessel's main hydraulics; failure of the net skiff; winch failure; ripped purse-seine net; broken purse cable; fouled/broken bunch line or corkline; netting caught on vessel's stern. Minor malfunctions include: speed boat failure; failure of vessel's bow thrusters, main engine failure, power block failure; broken chain; broken skiff tow, broken vang cable; webbing in the rings; other. Major malfunctions directly affect the ability of captain and crew to manipulate the net and release marine mammals.
Net collapse (CLP)	Categorical (2)	Presence/absence. Net collapses occur when opposite sides of the purse-seine come together. Presence does not include intentional net collapse.
Net canopies (CNP)	Categorical (2)	Presence/absence. Net canopies are billows of webbing that form along the sides of the net.
Dolphin safety panel (SPC)	Categorical (2)	Presence/absence of adequate coverage of the backdown channel.
Captain skill (CPT)	Categorical (2)	Previous fishing activity (average number of dolphin sets per year for the previous three years, computed using a moving average): <30 dolphin sets per year; ≥30 dolphin sets per year. On average, about 30 dolphin sets were made per trip for those trips of fishermen fishing on tunas associated with dolphins.
Fishing operations (F)		
Start time of the set (TME)	Continuous	Local time of the release of the net skiff, 24-hour clock (05:45; 12:08; 18:46).
Duration (decimal hours) of:		
Approach (APR)	Continuous	Time between initial sighting and release of the first speed boat (0.02; 0.57; 7.58).
Chase (CHS)	Continuous	Time between the release of the first speed boat and release of the net skiff (0.02; 0.43; 5.73).
Capture time (ENC)	Continuous	Time between the release of the net skiff and the point at which the bottom of the net is pursed and the rings are above the water ('rings up') (0.02; 0.67; 4.47).
Net retrieval (RET)	Continuous	Pre-backdown net retrieval. Time between 'rings up' and the start of the backdown procedure (0; 0.57; 10.07).
Backdown (BCK)	Continuous	The backdown procedure (0; 0.2; 2.73).
Rescue equipment use during backdown (R)		
Speedboats (SPB)	Categorical (2)	Rescue, rescue with mask.
Rafts (RFT)	Categorical (3)	None, rescue with raft, rescue with raft and mask (either snorkeling or SCUBA).
Swimmers, divers (SWM)	Categorical (3)	None (only used for 1993-1997 because of sample size), swimmer with or without mask, SCUBA diver.
Biomass characteristics (B)		
Number of dolphins (DPH)	Continuous	Number of animals in the purse-seine net once the net has been pursed. Computed as the sum of the observer's individual estimates of the number of animals that were killed, injured, or unknown status, escaped over the net, released before backdown, released through the backdown procedure, released by hand during backdown, released after backdown, and released from the sack. When any of these estimates were unavailable, the observer's estimate of the number of animals in the net at the time it is pursed was used, if available. The former is preferable to the latter because it is typically based on the sum of smaller counts that the observer can edit as he feels necessary over the course of the set. On the other hand, the observer's estimate of the number of animals in the net at the time it was pursed is used for management purposes and must not be changed after the beginning of the backdown procedure. (1; 369; 5,000).
Dolphin species (SPP)	Categorical (3)	Species of dolphin encircled: spotted dolphins, spotted and spinner dolphins or spinner dolphins alone, common dolphins.
Tons of tuna (TUN)	Continuous	Metric tons of tuna in the purse-seine net once the net has been pursed. (0; 13.61; 300).
Herd cohesion (HCC)	Categorical (3)	Number of groups in the herd at the time of chase: all animals in one group; animals in several groups; animals in many groups.

dolphins encircled, the degree of cohesiveness of the herd at the time of chase (a possible indicator of behaviour prior to encirclement) and the amount of tunas encircled.

The total mortality of dolphins reported by the observer for each set was used for dolphin mortality per set. Although it is not known exactly when during the set that the mortality occurred, it is generally believed that most of the reported mortality occurs before the end of the backdown procedure. A rough annual estimate of the number of mortalities that occurred after the backdown procedure was computed as the sum of the number of animals reported to be alive in the net after the end of backdown less the sum of the number of animals reported to be released alive after the end of backdown (IATTC data). For six of the nine years, this difference was less than or equal to 5% of the total mortality.

Both the amount of tuna captured and the number of dolphins encircled were log transformed (natural logarithm) prior to analysis. This transformation linearised the relationship between tuna capture and the number of dolphins encircled. A value of 1.0 was added to the tuna capture prior to computing the transformation; tuna may escape during encirclement leaving only dolphins in the pursed net. On average, annually only 3% of the sets involved no catch of tunas.

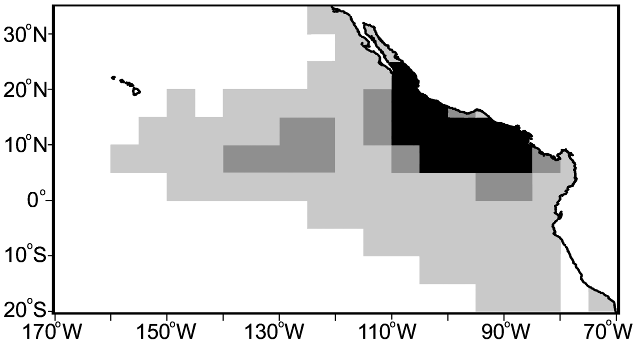

Fig. 1. Areas representing the different levels of historical fishing effort, based on the number of dolphin sets during 1959-1992. Light grey: =3,000 sets; dark grey: 3,001 to 6,092 sets; black: >6,092 sets.

METHODS OF ANALYSIS

Few dolphin sets presently result in mortalities (Fig. 2). A preliminary analysis of these data was done using log-linear models (e.g. McCullagh and Nelder, 1989). However, the data were found to be over-dispersed with respect to the Poisson model. In particular, results of a score test for extra zeros (van den Broek, 1995) suggested that the data contained more zeros than would be expected under the Poisson model. To address this issue, a final analysis of these data was undertaken using a zero-inflated Poisson model (ZIP; Lambert, 1992; Hall, 2000) which accommodated the excess zeros (Fig. 3). Alternative models explored for these data included the delta-gamma model (e.g. Stefánsson, 1996) and the negative binomial model (e.g. McCullagh and Nelder, 1989). The delta-gamma model was ultimately not used to avoid inconsistent parameter estimates resulting from improper specification of the conditional distribution of positive mortalities (Grogger and Carson, 1991; proper specification requires the use of a truncated distribution). As measured by Akaike's Information Criterion (Akaike, 1974; Burnham and Anderson, 1998), both the negative binomial model and the ZIP model were superior to a simple Poisson model, with the negative binomial model out-performing the ZIP model. However, there was some evidence of lack of fit of both negative binomial and ZIP models to the positive counts; the ZIP model was selected over the negative binomial because we believe a zero-inflated model to be more consistent with the process that generated the data. The fitted negative binomial models accommodated the excess zeros by way of large variances for mortality per set, $\mu + \hat{\alpha}\mu^2$, 2.6 $\hat{\alpha} \leq 4.6$, μ the mean mortality per set. On the other hand, we believe that the large proportion of zeros in the data arise from efforts on the part of fishermen to avoid dolphin mortality throughout the set, not from large between-set variability in mortality rates of an otherwise unmodified Poisson process. The observed information matrices from ZIP models fitted with all variables were nonsingular for each year, suggesting that the ZIP model should be estimable for these data (Lambert, 1992).

The ZIP model (Lambert, 1992; Hall, 2000) for dolphin mortality Y in the i^{th} set is given by:

$$Y_i \sim \begin{cases} 0 & \text{probability } p_i \quad \text{('zero-mortality' state)} \\ \text{Poisson } (\lambda_i) & \text{with probability } (1\text{-}p_i) \quad \text{('Poisson' state)} \end{cases}$$

The vectors of parameters p and λ are related to matrices of covariates G and B through canonical GLM relationships (McCullagh and Nelder, 1989): a logistic regression model for the probability of being in the zero-mortality state, $\text{logit}(p)=\text{G}\gamma$ and a log-linear model for the mean mortality per set in the Poisson state, $\log(\lambda) = \text{B}\beta$. No parameters are assumed shared between these two parts of the ZIP model. The covariates are taken to be known without error because of a lack of data with which to do otherwise. Since it is unknown which zero-mortality sets belong to the zero-mortality state and which belong to the Poisson state, this model is fitted iteratively using an EM algorithm (Hall, 2000), where the missing data are indicator variables Z_i: $Z_i = 1$ if the i^{th} set belongs to the zero-mortality state and $Z_i = 0$ if it belongs to the Poisson state. The expectation step of the EM algorithm is the estimation of Z by its conditional mean, given the current estimates of (γ, β). The maximisation step of the EM algorithm involves two parts, one which equates to using logistic regression to update γ and one which equates to using a weighted log-linear Poisson regression to update β. To avoid model misspecification due to changes in the fishery over the nine-year period, the data for each of the nine years were analysed separately.

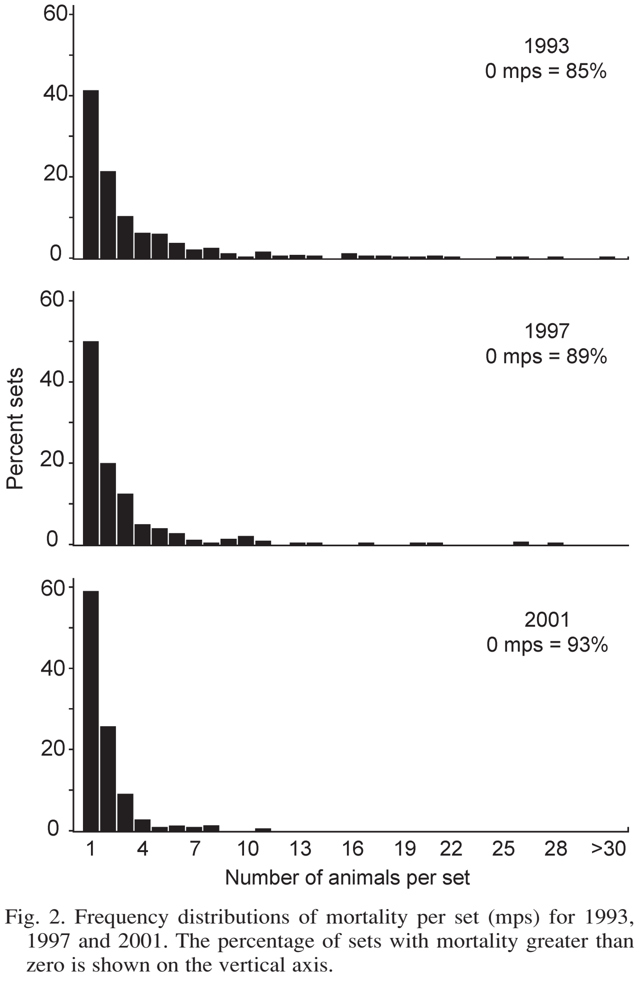

Fig. 2. Frequency distributions of mortality per set (mps) for 1993, 1997 and 2001. The percentage of sets with mortality greater than zero is shown on the vertical axis.

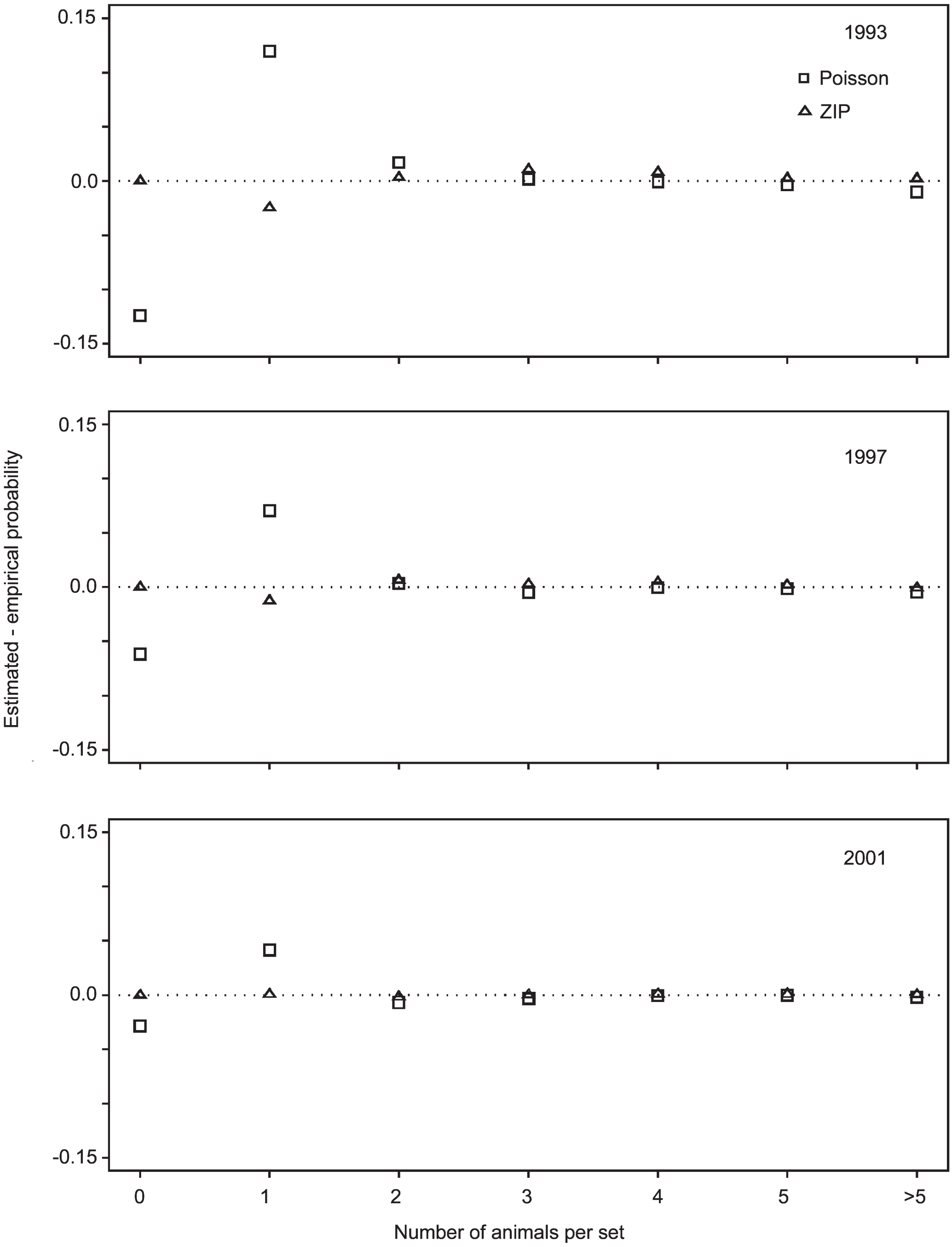

Fig. 3. Difference between estimated and empirical probabilities of mortality for 1993, 1997 and 2001. Empirical probabilities were computed as the sum of the number of sets with a specific mortality value, divided by the total number of sets. Estimated probabilities were based on Poisson and ZIP models fitted to the data using all variables (Table 1).

Given the data, it was of interest to determine if any variables in Table 1 could be identified as consistently contributing to dolphin mortality. Thus, the ZIP model was used as a variable screening/selection technique, not to develop the optimal predictive model for mortality per set. It is likely that only a subset of those variables listed in Table 1 strongly influence dolphin mortality and some may have no effect at all. Some of the variables shown in Table 1 are correlated (Table 2). The influence of certain variables on dolphin mortality may depend on other variables present in the model. In addition, because of the opportunistic nature of the data collection, confounding is also an issue. For example, the offshore area of the fishery with low levels of fishing effort (Fig. 1) tends to be the area fished predominantly in the summer months (Hall *et al.*, 1999), likely producing the apparent relationship between fishing area (E-FSH) and season (E-SSN) (Table 2). Stepwise model selection over all variables (main effects and two-variable interactions) was thus used to select an influential subset of the variables shown in Table 1. The 'null' model, a model that includes only an overall constant, was taken as the starting model. At each step, the model retained was that which best fit the data, where fit was measured by the model deviance plus twice the number of parameters (Akaike's Information Criterion as defined by Hastie, 1987; AIC_H). The deviance (McCullagh and Nelder, 1989) is a log-likelihood measure of the discrepancy between the data and the model. AIC_H was used as opposed to the classic AIC (Akaike, 1974) because this measure of fit was automatically supplied by the statistical software used to

Table 2

An illustration of relationships between predictor variables (Table 1), based on data for 1994. Shown are: (A) sample correlations between pairs of continuous variables; (B) p-values from a chi-square test of independence (Rice, 1988), applied pairwise to categorical variables; and (C) p-values from a chi-square test of independence applied pairwise to categorical and continuous variables, where continuous variables were discretized into values of zero (≤median) and one (>median). In (B) and (C), categorical variables with more than two levels were reduced to presence-absence by taking the first level as 'absence' and the other levels together as 'presence'. A value of 0.00 in (B) and (C) indicates a p-value <0.01.

(A)

	E-BEA	F-TME	F-APR	F-CHS	F-ENC	F-RET	F-BCK	B-DPH
F-TME	0.07							
F-APR	0.01	0.16						
F-CHS	-0.02	0.09	0.06					
F-ENC	-0.03	-0.04	0.04	0.10				
F-RET	0.05	-0.04	-0.01	-0.01	0.12			
F-BCK	-0.01	0.02	0.01	-0.04	-0.01	0.01		
B-DPH	0.07	0.07	0.13	0.11	-0.01	-0.03	0.28	
B-TUN	0.02	0.05	0.18	0.04	0.07	-0.01	0.11	0.45

(B)

	E-WTH	E-SSN	E-CUR	E-FSH	O-MLF	O-CLP	O-CNP	O-SPC	O-CPT	R-SPB	R-RFT	R-SWM	B-SPP
E-SSN	0.02												
E-CUR	0.00	0.52											
E-FSH	0.94	0.00	0.00										
O-MLF	0.05	0.00	0.00	0.23									
O-CLP	0.01	0.35	0.00	0.61	0.00								
O-CNP	0.88	0.02	0.00	0.00	0.00	0.05							
O-SPC	0.00	0.24	0.00	0.18	0.00	0.60	0.44						
O-CPT	0.05	0.00	0.42	0.00	0.20	0.07	0.94	0.00					
R-SPB	0.06	0.10	0.00	0.00	0.00	0.31	0.13	0.00	0.00				
R-RFT	0.08	0.00	0.00	0.59	0.08	0.00	0.02	0.00	0.23	0.00			
R-SWM	0.07	0.00	0.92	0.00	0.26	0.08	0.08	0.01	0.00	0.00	0.28		
B-SPP	0.08	0.00	0.01	0.00	0.26	0.99	0.00	0.00	0.16	0.39	0.00	0.00	
B-HCC	0.30	0.26	0.20	0.00	0.95	0.46	0.17	0.99	0.23	0.02	0.08	0.03	0.40

(C)

	E-BEA	F-TME	F-APR	F-CHS	F-ENC	F-RET	F-BCK	B-DPH	B-TUN
E-WTH	0.00	0.54	0.39	0.08	0.96	0.56	0.11	0.32	0.10
E-SSN	0.00	0.90	0.00	0.07	0.00	0.90	0.01	0.01	0.00
E-CUR	0.00	0.86	0.49	0.46	0.00	0.00	0.00	0.99	0.94
E-FSH	0.00	0.00	0.10	0.14	0.00	0.00	0.00	0.00	0.00
O-MLF	0.00	0.44	0.55	0.24	0.00	0.00	0.33	0.92	0.24
O-CLP	0.09	0.46	0.01	0.35	0.67	0.24	0.00	0.07	0.07
O-CNP	0.12	0.68	0.78	0.59	0.19	0.53	0.00	0.00	0.00
O-SPC	0.76	0.95	0.00	0.00	0.00	0.09	0.00	0.00	0.00
O-CPT	0.00	0.56	0.00	0.84	0.04	0.75	0.10	0.00	0.00
R-SPB	0.20	0.37	0.60	0.37	0.00	0.36	0.40	0.16	0.89
R-RFT	0.00	0.75	0.75	0.00	0.47	0.00	0.00	0.22	0.37
R-SWM	0.00	0.41	0.00	0.00	0.02	0.00	0.00	0.00	0.00
B-SPP	0.01	0.62	0.00	0.49	0.07	0.32	0.00	0.00	0.00
B-HCC	0.52	0.12	0.07	0.00	0.86	0.00	0.22	0.97	0.12

perform the stepwise analysis. Both forward and backward stepping were allowed. Preliminary analyses showed that the most substantial reductions in AIC_H occurred within the first few steps and that reductions in AIC_H thereafter were relatively small (see also Results below). Given the goal of this analysis, the number of steps was limited to 20 to ease the computational burden of both stepwise selection and the EM algorithm. The change in deviance between the null model and the model reached after 20 steps is presented as a rough indicator of model utility.

A stability analysis was performed to determine sensitivity of the fitted ZIP models to unusual observations and relationships amongst predictor variables. The stability analysis borrows conceptually from a technique referred to as bootstrap aggregation (Breiman, 2001 and references therein), but without the final model averaging. The stability analysis was performed by fitting a ZIP model to each of 50 bootstrap samples of the data (drawn with replacement), for each year. Given the results of the stepwise procedure applied to the original data (see below), the stepwise selection for the bootstrap data was limited to seven steps. In each year, the percentage of times each variable was selected within the first seven steps of the 50 fitted models was tabulated. Similarity among the dominant variables selected in the resampling procedure and those of the original fitted model is an indication of model stability.

RESULTS

Changes in the AIC_H statistic versus iteration of the stepwise fitting procedures showed large initial decreases in the first two to three steps, followed by a long series of steps during which other variables and two-variable interactions were added with relatively small improvements (Fig. 4, Table 3). The average reduction in deviance after 20 steps was 32% for the logistic models and 51% for the log-linear models

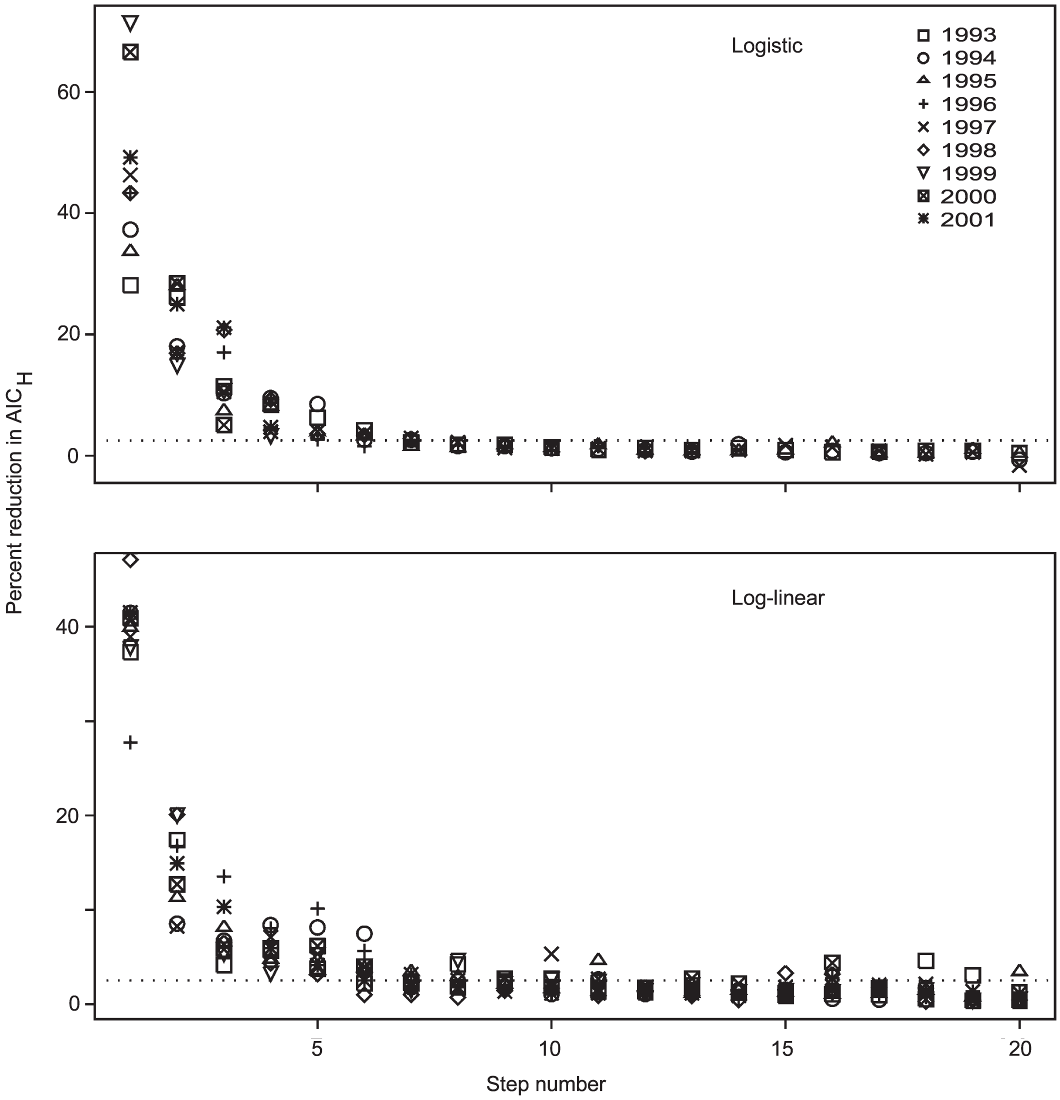

Fig. 4. Percent reduction in AIC_H between sequential steps in the stepwise fitting procedure for the logistic model of the probability of being in the zero-mortality state (upper panel) and the log-linear model of the mean mortality in the Poisson state (lower panel). The percent reduction in AIC_H was computed as the difference in AIC_H between sequential steps, divided by the total reduction in AIC_H achieved over the 20 steps. Different plot symbols represent the different years. Dashed horizontal lines indicate 2.5%.

(Table 3). Once entered, variables were rarely removed. Variables selected across the nine years for the logistic models were largely the same as those selected for the log-linear models. The most notable exception to this, fishing area (E-FSH), appeared in log-linear models in five of the nine years, but in none of the nine years for the logistic model. For both models, when interaction terms were present, they were not consistently the same terms from year to year and most interaction terms appeared in only one to two years, even though some of the variables themselves appeared in more than half the years (e.g. presence of net canopies, F-CNP). Beyond about seven to 10 steps, the relative reduction in the AIC_H levelled off and was typically less 2.5% (Fig. 4) and, thus, in what follows the focus is on the variables that entered within the first seven steps.

Based on fitting the logistic model, it was found that the probability of being in the zero-mortality state decreased in the presence of hazardous net conditions, increasing time animals remained in close contact with the net and characteristics of the biomass in the net, but increased with captain experience (Table 3; Fig. 5). The probability of being in the zero-mortality state was found to decrease consistently with the occurrence of net canopies (O-CNP) in nine of nine years, net collapses (O-CLP) in six of nine years, the duration of the backdown procedure (F-BCK) in eight of nine years, the amount of tuna in the net (B-TUN) in five of nine years and the species of dolphin encircled (B-SPP) in six of the nine years. On the other hand, the probability of being in the zero-mortality state was found to increase consistently with the level of captain experience at fishing on tunas associated with dolphins (O-CPT) in four out of nine years. The probability of being in the zero-mortality state also increased with the use of rescue swimmers and SCUBA divers during the backdown procedure (R-SWM) in three out of the five years where adequate data were available on swimmer/diver use (1993-1997; Table 1), primarily due to the effect of SCUBA divers. Differences between the use of swimmers versus SCUBA divers was not found to strongly influence dolphin mortality in later years (Table 3).

Based on fitting the log-linear model, mean mortality in the Poisson state was found to increase in the presence of hazardous net conditions, gear malfunctions and the characteristics of biomass in the net, but decrease with

Table 3

Variables selected, and their order of selection, in the stepwise procedure for the logistic model of the probability of being in the zero-mortality state (A), and the log-linear model of the mean mortality in the Poisson state (B). Abbreviations are defined in Table 1. Two abbreviations, separated by a colon, indicate an interaction term. Sample size (number of dolphin sets) is shown in parentheses at the top of each column (sample sizes are the same for both models). At the bottom of each column in parentheses is the reduction in deviance (null deviance less residual deviance), associated degrees of freedom, and the percent reduction in deviance (relative to the null deviance). Dashed horizontal lines indicate that no further iterations were taken in the stepwise selection procedure. Abbreviations shown in italics indicate variables (or interactions) that were removed.

	1993 (3,173)	1994 (3,724)	1995 (3,647)	1996 (3,336)	1997 (3,777)	1998 (4,557)	1999 (3,465)	2000 (3,806)	2001 (3,878)
(A)									
(1)	O-CNP	F-BCK	O-CNP	F-BCK	F-BCK	F-BCK	F-BCK	F-BCK	F-BCK
(2)	B-SPP	B-SPP	B-DPH	O-CLP	O-CNP	O-CNP	O-CNP	O-CNP	O-CNP
(3)	F-BCK	O-CNP	O-CLP	R-SWM	B-DPH	B-DPH	B-TUN	B-TUN	B-SPP
(4)	B-TUN	O-CLP	B-SPP	O-MLF	O-CLP	O-CLP	B-SPP	----	F-BCK:O-CNP
(5)	O-CLP	B-TUN	F-BCK	B-TUN	B-SPP	O-CPT	----	----	----
(6)	O-CPT	F-BCK:O-CLP	R-RFT	O-CNP	O-CPT	B-TUN	----	----	----
(7)	R-SWM	R-SWM	O-CPT	F-BCK:O-CNP	R-RFT	B-TUN:F-BCK	----	----	----
(8)	O-MLF	O-CNP:R-SWM	F-RET	F-CHS	B-TUN	----	----	----	----
(9)	O-CLP:O-CPT	B-TUN:R-SWM	O-CLP:R-RFT	R-SPB	E-SSN	----	----	----	----
(10)	O-SPC	F-BCK:R-SWM	E:CUR	F-RET	R-SPB	----	----	----	----
(11)	F-BCK:O-CLP	B-TUN:O-CLP	B-DPH:E-CUR	B-TUN:F-RET	B-SPP:O-CLP	----	----	----	----
(12)	B-SPP:O-SPC	B-SPP:F-BCK	F-APR	B-TUN:F-BCK	B-DPH:F-BCK	----	----	----	----
(13)	E-CUR	R-SPB	O-CLP:O-CNP	F-RET:O-CNP	O-CNP:B-SPP	----	----	----	----
(14)	E-CUR:O-SPC	R-SPB:R-SWM	E-CUR:O-CNP	----	O-SPC	----	----	----	----
(15)	B-TUN:F-BCK	E-BEA	E-WTH	----	O-SPC:R-SPB	----	----	----	----
(16)	F-BCK:O-CNP	B-TUN:E-BEA	F-RET:R-RFT	----	O-SPC:R-RFT	----	----	----	----
(17)	E-CUR:R-SWM	B-TUN:R-SPB	E-WTH:O-CLP	----	B-DPH:O-CNP	----	----	----	----
(18)	F-CHS	B-SPP:O-CLP	F-TME	----	F-BCK:O-CNP	----	----	----	----
(19)	B-SPP:F-CHS	B-SPP:O-CNP	E-CUR:F-TME	----	B-TUN:F-BCK	----	----	----	----
(20)	R-RFT	*B-SPP:O-CNP*	F-BCK:O-CLP	----	*B-SPP:O-CLP*	----	----	----	----
	(787, 25; 33%)	(799, 28; 32%)	(819, 24; 36%)	(741, 15; 43%)	(822, 25; 38%)	(718, 7; 40%)	(320, 5; 28%)	(344, 3; 26%)	(138, 5; 13%)
(B)									
(1)	O-CNP	O-CNP	O-CNP	O-CNP	O-CNP	O-CNP	O-CNP	O-CNP	F-BCK
(2)	B-DPH	F-BCK	F-BCK	B-SPP	E-BEA	B-SPP	B-DPH	B-DPH	O-CNP
(3)	O-MLF	F-ENC	B-TUN	O-MLF	O-CPT	B-SPP:O-CNP	E-FSH	O-MLF	B-TUN
(4)	R-RFT	B-DPH	O-CPT	O-CPT	B-DPH	B-TUN	B-SPP	E-WTH	B-SPP
(5)	B-DPH:O-MLF	B-DPH:O-CNP	B-SPP	B-DPH	O-MLF	E-FSH	B-SPP:O-CNP	E-WTH:O-CNP	E-SSN
(6)	E-BEA	B-HCC	B-SPP:F-BCK	B-DPH:O-MLF	E-SSN	F-APR	B-DPH:E-FSH	E-CUR	E-CUR
(7)	O-SPC	F-RET	E-CUR	R-SWM	E-BEA:E-SSN	F-APR:O-CNP	F-RET	O-CPT	O-SPC
(8)	E-BEA:O-SPC	F-BCK:F-RET	E-CUR:O-CNP	B-HCC	B-TUN	F-BCK	E-FSH:F-RET	B-SPP	B-DPH
(9)	B-DPH:E-BEA	B-DPH:B-HCC	B-SPP:B-TUN	O-CNP:O-MLF	B-SPP	B-SPP:B-TUN	F-ENC	R-RFT	B-DPH:O-CNP
(10)	E-BEA:O-MLF	R-SWM	E-WTH	B-HCC:O-CPT	B-SPP:E-SSN	B-TUN:F-BCK	E-CUR	B-SPP:O-CNP	O-CPT
(11)	O-CNP:O-SPC	B-DPH:R-SWM	E-CUR:E-WTH	B-SPP:O-MLF	B-TUN:O-CNP	R-SPB	E-CUR:O-CNP	O-CNP:R-RFT	B-SPP:E-CUR
(12)	E-BEA:R-RFT	B-SPP	F-BEA	B-TUN	O-CPT:O-MLF	F-APR:R-SPB	O-CLP	B-HCC	E-SSN:O-SPC
(13)	O-MLF:O-SPC	B-SPP:O-CNP	F-RET	E-BEA	E-SSN:O-CPT	O-CNP:R-SPB	E-WTH	B-HCC:E-CUR	B-DPH:B-SPP
(14)	B-DPH:O-CNP	B-DPH:B-SPP	E-FSH	B-DPH:B-HCC	B-DPH:O-CPT	E-SSN	E-CUR:E-WTH	B-HCC:E-WTH	B-DPH:O-CPT
(15)	O-SPC:R-RFT	B-SPP:B-HCC	B-SPP:F-RET	B-DPH:O-CPT	B-DPH:B-TUN	B-TUN:E-SSN	E-SSN	R-SPB	F-ENC
(16)	F-TME	F-BCK:O-CNP	B-SPP:E-CUR	B-SPP:R-SWM	E-FSH	B-SPP:E-SSN	B-SPP:E-SSN	E-CUR:O-SPB	E-CUR:F-ENC
(17)	E-FSH	R-RFT	B-TUN:F-BCK	O-CPT:R-SWM	B-DPH:B-SPP	B-TUN:F-APR	E-FSH:E-SSN	B-SPP:R-SPB	F-BCK:F-ENC
(18)	E-FSH:O-MLF	B-HCC:R-RFT	E-FSH:O-CPT	B-SPP:B-DPH	B-TUN:O-MLF	F-BCK:O-CNP	F-RET:O-CLP	E-CUR:R-RFT	O-CLP
(19)	E-FSH:O-SPC	O-CNP:R-RFT	B-HCC	B-DPH:O-CNP	E-BEA:O-CPT	E-SSN:F-BCK	F-BCK	E-CUR:O-CNP	B-SPP:F-ENC
(20)	E-SSN	F-RET:R-RFT	B-HCC:O-CPT	B-HCC:O-MLF	B-DPH:E-SSN	E-CUR	F-BCK:O-CNP	O-CLP	F-BCK:O-CNP
	(1,114, 37; 46%)	(1,288, 36; 49%)	(1,752, 29; 57%)	(2,320, 46; 70%)	(852, 33; 48%)	(752, 30; 44%)	(871, 33; 52%)	(840, 31; 54%)	(490, 27; 42%)

captain experience (Table 3; Fig. 5). The mean mortality in the Poisson state increased consistently with the presence of net canopies (O-CNP) in nine of nine years, the number of dolphins encircled (B-DPH) in four to six of the nine years, depending on interactions, and the species of dolphins encircled (B-SPP) in five of the nine years. The mean mortality in the Poisson state was found to vary with the presence of gear malfunctions (O-MLF) in four of nine years, but the direction of the effect was not consistent. In two of the four years, malfunctions sometimes led to increased mortality through interactions with encircled herd size (B-DPH:O-MLF). The mean mortality in the Poisson state set decreased consistently with the level of captain experience at setting on tunas associated with dolphins (O-CPT) in four of the nine years.

Neither the probability of being in the zero-mortality state nor the mean mortality in the Poisson state were found consistently to vary strongly with the duration of phases of the set other than that of the backdown procedure (F-BCK), or with environmental conditions (Table 3). The time of the set (F-TME) and the duration of the approach (F-APR), chase (F-CHS), encirclement (F-ENC) and pre-backdown net retrieval (F-RET) were only identified as strongly influencing dolphin mortality in one-two of the nine years. Similarly, the weather (E-WTH), season (E-SSN), sea state (E-BEA) and the area of the set (E-FSH), were only identified as strongly influencing dolphin mortality in one-two of the nine years and the presence of strong currents (E-CUR) in one-three of the nine years.

Although not included expressly in the list of variables, the duration of the set (from the initial sighting to the end of the backdown procedure) was not found to have a strong influence on dolphin mortality per set. No more than three duration variables entered into any one model within the first 20 steps (Table 3). In addition, fitted models that included all variables, without interaction terms, never yielded coefficients for the durations of the various phases of the setting process that were consistently of the same

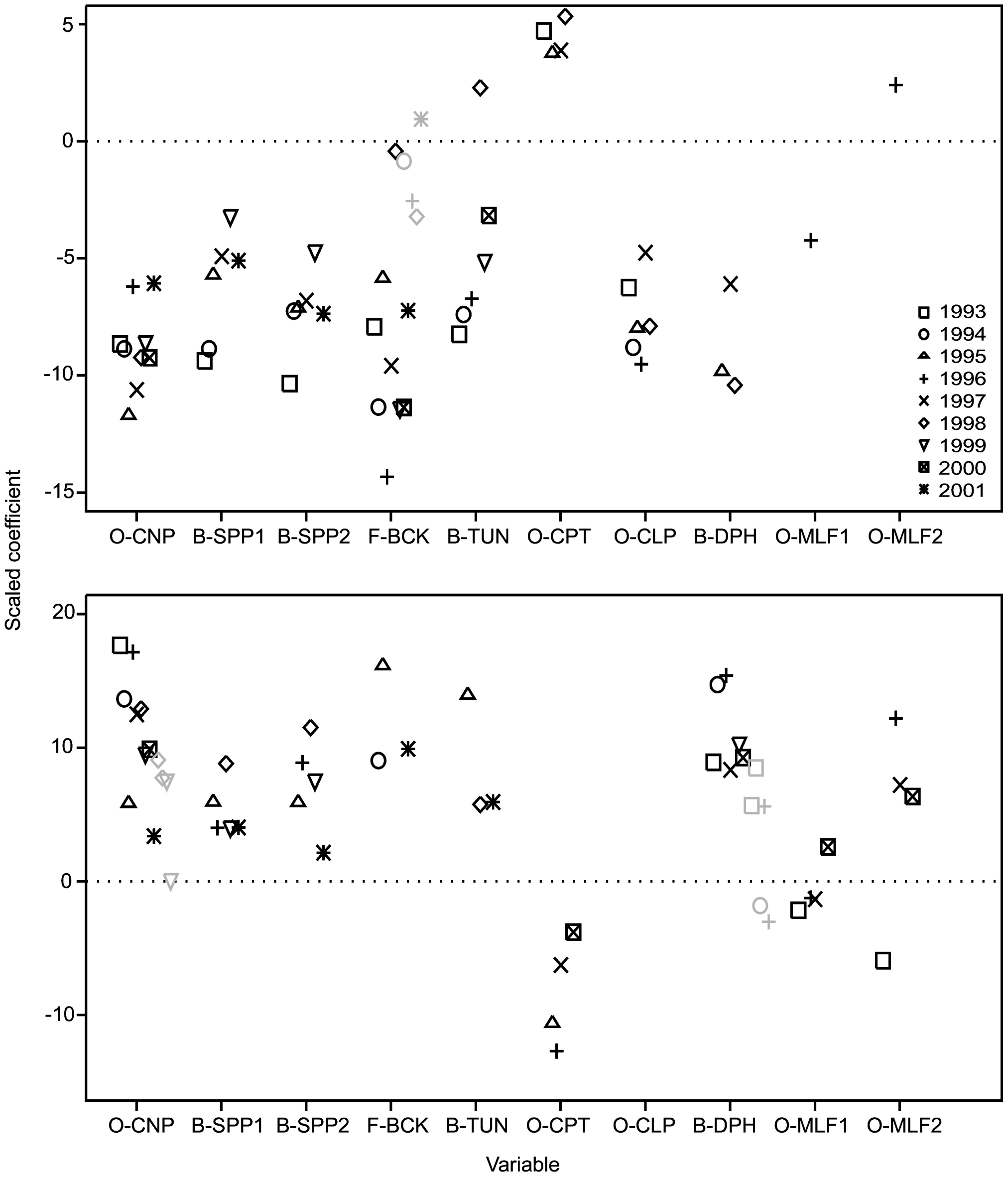

Fig. 5. Estimated coefficients for individual variables, divided by their standard errors, from logistic models of the probability of being in the zero-mortality state (top panel) and log-linear models of the mean mortality in the Poisson state (bottom panel). Models were based on the terms selected within the first seven steps of the stepwise fitting procedure (Table 3). Coefficients adjusted for interaction terms are shown in grey. Interaction terms between continuous and categorical variables are shown as a modified coefficient for the continuous variable.

sign, suggesting that the duration of the entire setting process is likely of secondary importance as compared to the duration of the backdown procedure (F-BCK) (Table 3). A principal components analysis (Seber, 1984) did not yield any reasonable simplification of the description of the setting process, with at most 26% of the variability in durations explained by the first principal component.

Results of the stability analysis (Table 4) support the importance of those variables selected repeatedly within the first several steps of the original models. Most of the variables frequently selected in the logistic models within the first several steps were selected in the stability analysis with high frequency. In particular, net canopies (O-CNP) and the duration of the backdown procedure (F-BCK) were selected in at least 88% of the models fitted to the bootstrap samples in each year. The species of dolphins encircled (B-SPP), the tons of tuna captured (B-TUN) and net collapses (O-CLP) were also frequently selected in six of nine years. Present to a lesser extent in multiple years were the size of the encircled herd (B-DPH), the level of captain experience (O-CPT) and the use of rescue swimmers and divers (R-SWM). The presence of other terms in the models fitted to the bootstrap data sets in 1999-2001 as compared to the original fitted models (Table 3) suggests decreased model stability in those years. Variables selected repeatedly within the first seven steps of the log-linear original models (Table 3) also tended to be selected consistently in the stability analysis. Net canopies (O-CNP) was selected in at least 96% of the models fitted to the bootstrap samples in each year. The species of dolphin (B-SPP) and size of the encircled herd (B-DPH) were selected with high probability in four to five of the nine years. In addition, the effect of correlation between the encircled herd size (B-DPH) and the tuna captured (B-TUN) can be seen, particularly in the results of for the log-linear models (Table 4B). Either the encircled herd size was a dominant term or encircled herd size and tuna captured were selected with relatively similar frequency.

DISCUSSION

This analysis has attempted to identify the variables consistently contributing to increased dolphin mortality between 1993-2001. Results of fitting a ZIP model to

Table 4

Results of the stability analysis. Shown is the percentage of models fitted to bootstrap samples that contained each variable (or interaction) for: (A) the logistic model of the probability of being in the zero-mortality state, and (B) the log-linear of the mean mortality in the Poisson state. Only those variables found in over 20% of the models in at least two years are shown.

	1993	1994	1995	1996	1997	1998	1999	2000	2001
(A)									
O-CNP	100	100	100	90	100	96	100	100	94
O-CLP	96	100	88	100	86	84	54	4	44
F-BCK	100	100	88	100	100	88	96	98	96
B-SPP	100	100	98	66	62	46	86	70	36
B-TUN	88	86	51	68	40	76	48	44	26
B-DPH	0	0	55	12	34	46	26	2	34
O-CPT	62	2	51	4	52	44	0	20	14
R-SWM	40	32	8	88	20	12	0	0	0
E-CUR	8	0	6	0	0	0	42	36	24
R-RFT	8	2	20	2	22	0	0	0	16
F-RET	0	6	24	18	2	2	14	28	0
O-MLF	6	16	2	40	4	0	8	22	2
O-SPC	10	0	0	0	18	2	28	4	26
F-BCK:O-CNP	4	0	6	18	48	14	8	6	72
F-BCK:O-CLP	26	56	8	0	0	10	10	2	4
B-SPP:O-CNP	6	2	10	8	12	22	10	48	16
B-SPP:F-BCK	2	40	2	6	14	2	20	4	12
(B)									
O-CNP	100	100	100	96	98	100	100	100	98
B-DPH	90	94	45	76	60	64	80	96	44
B-SPP	32	14	78	43	76	96	64	36	88
F-BCK	34	84	92	31	22	36	38	28	88
B-TUN	20	4	61	32	60	40	24	4	58
O-CPT	4	0	59	86	86	6	2	66	18
O-MLF	54	18	12	78	66	2	2	82	0
E-FSH	30	4	8	6	32	52	56	18	0
E-CUR	2	0	29	8	8	10	38	60	34
F-RET	4	32	25	2	2	14	32	2	8
E-SSN	10	6	20	16	8	8	12	8	60
F-ENC	8	60	14	0	2	6	18	4	30
B-HCC	10	90	24	0	6	30	6	6	10
R-SWM	28	24	0	42	10	0	0	0	0
R-RFT	20	8	2	22	0	0	0	8	6
B-SPP:F-BCK	0	0	22	4	0	4	0	0	24
B-SPP:O-CNP	4	0	0	0	8	64	38	24	4

dolphin mortality per set data suggest that only a few variables were of primary importance (Tables 3-4, Fig. 4). The presence of net canopies (O-CNP) was found to contribute to increased dolphin mortality in all nine years (Table 3, Fig. 5). In addition, the duration of the backdown procedure (F-BCK), the number (B-DPH) and species (B-SPP) of dolphin encircled, the amount of tuna captured (B-TUN) and the presence of net collapses (O-CLP) were also found to contribute to increased dolphin mortality in at least five of the nine years (Table 3, Fig. 5). On the other hand, dolphin mortality was found to decrease with increased captain experience at fishing on tunas associated with dolphins (O-CPT) in four of the nine years (Table 3, Fig. 5).

Comparison of these results with those of earlier studies suggests that some of the variables that can be identified as strongly affecting dolphin mortality have remained the same for the last three decades. Consistent with these results, previous analyses of dolphin mortality per set data (Fox and Lenarz, 1975; Everett *et al.*, 1976; Powers *et al.*, 1979; IATTC, 1984; 1987; 1989) indicated that mortality per set increased with the size of the dolphin herd encircled, the amount of tuna captured, the duration of the backdown procedure, the presence of net canopies, net collapses and gear malfunctions and varied with the dolphin species involved. The results here differ from those of previous studies in that use of a ZIP model has enabled separation of influential variables into those that may contribute to the development of problematic situations (i.e. low probability of being in the zero-mortality state) and those that may influence the amount of mortality that occurs, once a problematic situation has developed (i.e. the mean mortality per set in the Poisson state). For example, lengthy backdown procedures (F-BCK) and the presence of net collapses (O-CLP) were found to contribute consistently to the development of problematic situations (Tables 3-4), but have less influence on the mean mortality per set in problematic situations. On the other hand, the presence of net canopies (O-CNP) and large biomass in the net (B-TUN, B-DPH) contributed consistently to both the development of problematic situations and to the mean mortality per set in problematic situations. In addition, to our knowledge, previous analyses did not incorporate a measure of captain skill, which was indicated in this analysis as reducing mortality per set.

Correlations among these variables (Tables 2, 4) make interpretation of the results, in terms of ‘cause and effect’, difficult. For example, the number of dolphins encircled (B-DPH) was found to be correlated with the number of tons of tuna captured (B-TUN) and with the duration of the backdown procedure (F-BCK), which was, in turn, related to the presence of net canopies (O-CNP). Nonetheless, all four variables contributed strongly to improving model fit (Tables 3-4, Fig. 4). Clearly, variables may contribute to increased dolphin mortality for several reasons and the process is likely complex. Nonetheless, it is useful to determine if any synthesis of these results can lead to a clearer picture of at least one of the ways in which dolphin mortality occurs. Because net canopies (O-CNP) were identified in both stages of the analysis in all nine years (Table 3) and because net canopies was selected frequently in the stability analysis (Table 4), the presence of net canopies and their relationship to other predictor variables (Table 1) were considered first. The species of dolphins encircled in the net will not be considered further. Consistent with the results (Tables 3-4, Fig. 5), spinner dolphins and especially common dolphins, have been found to have higher mortality rates (Fox and Lenarz, 1975; IATTC, 1989), which may be the result of differences in behaviour within the pursed net (IATTC, 1986; Pryor and Shallenberger, 1991; Schramm, 1997). Historical efforts to reduce such behaviourally-based causes of mortality have included US bans on setting on herds of pure spinner dolphins (*US Federal Register Vol. 51 (2) January 3, 1986*); spinner dolphins are typically encountered by the fishery in mixed herds with spotted dolphins (Scott and Cattanach, 1998; Hall *et al.*, 1999), the species more frequently involved in the fishery (Hall *et al.*, 1999). Although mortality rates of common dolphins can be high, sets on common dolphins occur much less frequently (Hall *et al.*, 1999) and, as a result, common dolphin mortality only accounted for an average of about 11% of the total dolphin mortality annually since 1993 (IATTC, 2002).

Although the data do not reveal the exact timing of the formation of net canopies, available information suggests that long backdown procedures are strongly associated with the formation of net canopies. Results of building a logistic model for the probability of a net canopy, in a stepwise manner using all other predictor variables in Table 1, indicated a strong relationship between the duration of the backdown procedure and the presence of net canopies. The duration of the backdown procedure was selected first in all nine years, resulting in a 6-12% reduction in deviance (71-156, 1 degree of freedom). A likely mechanism for this

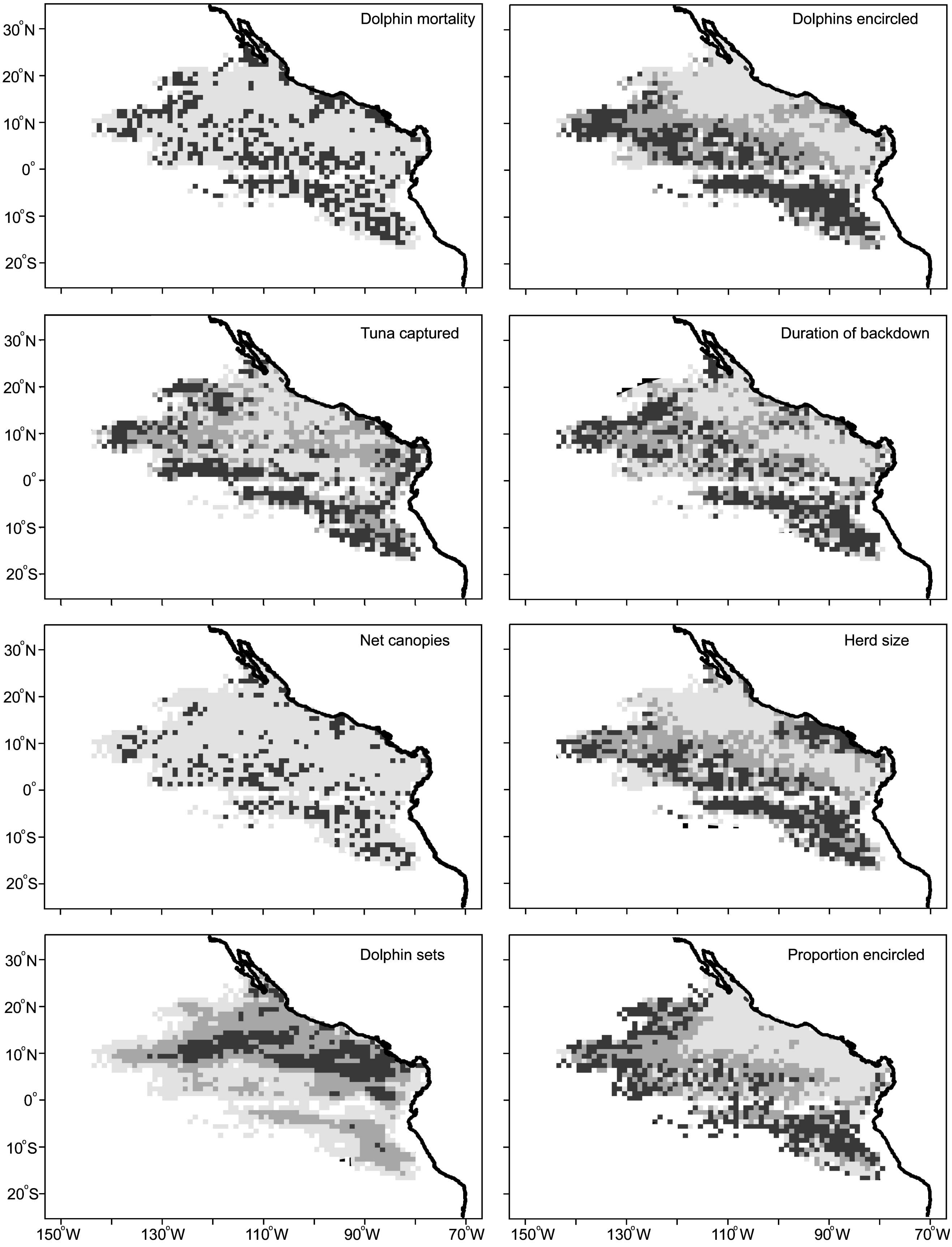

Fig. 6. Spatial distributions of the proportion of sets with dolphin mortality ($\leq$0.15; >0.15), standardised number of dolphins encircled per set, standardised capture of tunas per set, standardised duration of backdown, proportion of sets with net canopies ($\leq$0.10; >0.10), standardised herd size, number of dolphin sets ($\leq$10 sets; 11-50 sets; >50 sets) and the standardised ratio of the number of dolphins encircled to the herd size (proportion encircled), 1993-2001. For standardised quantities, light grey indicates 1° square areas with values $\leq$ the 0.40th quantile of standardised values, dark grey indicates 1° square areas with values between the 0.40-0.70th quantiles of standardised values, black indicates 1° square areas with values > the 0.70th quantile of standardised values. Standardisation was done in the following manner. First, the average of the particular quantity (e.g. number of dolphins encircled) was computed by 1° square area for each year. Annually, 1° square averages were then standardised by subtracting the median of 1° square values and dividing by the inter-quartile range of 1° square values. These annual standardised values were combined across years for each 1° square by computing a weighted average, weights equal to the number of dolphin sets in each year in the particular 1° square.

association is the physical dynamics of extended backdown procedures. Long backdown procedures tend to cause the floor of the purse-seine to rise toward the surface. This deformation of the net can produce net canopies along the sides of the backdown channel.

The duration of the backdown procedure was, in turn, found to be strongly associated with the size of the encircled herd. This relationship was demonstrated clearly in the stepwise procedures for fitting the ZIP models. The significance of the number of dolphins encircled was often reduced once the duration of the backdown procedure was added to the model (and vice versa). In a stepwise GLM procedure modelling the natural logarithm of the duration of the backdown procedure (assuming a gamma distribution for the stochastic component), the number of dolphins encircled was selected first in all nine years, resulting in a 13-24% reduction in deviance (89-143, 1 degree of freedom). The duration of the backdown procedure was, however, not found to be strongly related to the amount of tuna captured (see also Table 2). In fact, correlation between the duration of the backdown procedure (F-BCK) and the number of dolphins encircled (B-DPH) (Table 2) is likely the reason that the amount of tuna captured (B-TUN) was most influential on the probability of being in the zero-mortality state, while the number of dolphins encircled was most influential in determining the mean mortality in the Poisson state (Tables 3-4). Because tuna capture is correlated with encircled herd size (Table 2), we believe the importance of tuna capture in the ZIP models to largely reflect complications associated with manipulating large dolphin biomass within the pursed net.

Thus, we believe that the results of this analysis support a continuing relationship between dolphin mortality and the encirclement of large herds. The results would be consistent with the following scenario. Encirclement of large herds leads to dolphin mortalities because of the sheer magnitude of the number of animals confined within the pursed net and because it extends the duration of the backdown procedure, which, in turn, leads to prolonged close confinement of the dolphins within the backdown channel and may, in turn, lead to the formation of net canopies. It is also believed that dolphin mortalities result from setting in areas of strong currents and from poor gear maintenance, which leads to failure of equipment essential to the release of dolphins from the pursed net. Consistent relationships between strong currents and dolphin mortality and between gear malfunctions and dolphin mortality, were not identified in this analysis of these data. This may be because these factors are of secondary importance in the present fishery, because the definitions of strong currents and gear malfunctions are not adequate to reveal relationships to dolphin mortality with these data, given the current low levels of reported mortality and/or because their effects on mortality are instead captured by variables such as the presence of net canopies and net collapses (Table 2).

Spatial distributions of the occurrence of mortality, the presence of net canopies, the duration of the backdown procedure and the size of the encircled herd show very similar patterns (Fig. 6). In general, the largest encircled herds occurred south of the equator and along the offshore margin of the fishery north of the equator. This area tended to be where the duration of the backdown procedure was longest and where net canopies were more common. This was also an area that yielded some of the largest captures of tunas (Fig. 6). Although large encircled herds show a spatial correspondence with areas of high probability of dolphin mortality, the areas of the largest encircled herds were not always the areas where the largest herds were targeted by fishermen (Fig. 6). For example, large herds were targeted consistently by fishermen nearshore between the Gulf of Tehuantepec, Mexico and Cabo Velas, Costa Rica, as well as north of the equator along the offshore margin of the fishery and south of the equator. However, the proportion of the herd that was encircled was typically greatest south of the equator and north of the equator along the offshore margin of the fishery (Fig. 6).

Low values of the proportion of the herd that was encircled between the Gulf of Tehuantepec and Cabo Velas (Fig. 6) have been related to spatial differences in evasive behaviour of dolphins (IATTC, 1986; Heckel *et al.*, 2000; Lennert-Cody and Scott, In press). Spatial patterns in evasive behaviour have been hypothesised to arise from spatial differences in the amount of exposure to the fishery (Heckel *et al.*, 2000; Lennert-Cody and Scott, In press) and from the timing of first exposure to the fishery since purse-seining on tunas associated with dolphins began in the late 1950s (Lennert-Cody and Scott, In press). This suggests that dolphin behaviour may be involved in determining the occurrence of mortality, not only as a result of the species involved, but also indirectly as a result of learned evasive behaviours.

Given the dependence of dolphin mortality on the encirclement of large herds, the results suggest that the current level of dolphin mortality could be further reduced by increasing efforts to avoid encircling large herds of dolphins and by reallocating fishing effort to areas where encircled herd size is typically small. Currently, fishermen encircle fewer dolphins by attempting to split the herd prior to the beginning of encirclement. This technique is productive if the tuna remain with only part of the dolphin herd. On the other hand, establishing a maximum targetable herd size is not likely to be a realistic management option because herd size is difficult to estimate accurately. An observer's best estimate of herd size is based on having the opportunity to observe the herd for an extended period of time over the entire setting process.

Reallocating fishing effort to areas where encircled herd size is typically small warrants further consideration because spatial patterns in encircled herd size do not appear to be sensitive to short-term environmental fluctuations such as those caused by El Niño events. A major El Niño event occurred in the EPO in 1997-98, resulting in distinct spatial variability in biological measures such as surface chlorophyll (Wilson and Adamec, 2001), but no overall change in the spatial relationship between encircled herd size and dolphin mortality. While the southern area of the fishery and the offshore margin of the fishery north of the equator are areas of larger catches of tunas, large catches of tunas can be seen to occur in other areas of the fishery, including inshore areas where lesser numbers of dolphins were encircled (Fig. 6). Predictive models could be developed to estimate spatial distributions of dolphin mortality, encircled herd size and tuna captures. Results of these models could be used to assess the tradeoffs between dolphin mortality and tuna catch at varying levels of fishing effort in areas where large herds are typically targeted by fishermen and to develop strategies for reallocation of fishing effort to dolphin sets in other areas or to sets on unassociated schools of tunas, which are sometimes made in similar areas as dolphin sets (Hall *et al.*, 1999; Watters, 1999).

Because of the goal of this analysis, we believe that addressing the extra zeros through a zero-inflated model accounts for the largest relative departure of the data from a classical Poisson model (Fig. 3). However, lack of fit of the ZIP model to the positive mortalities suggests that the ZIP model, as well as other zero-inflated (or zero-truncated) models (e.g. Mullahy, 1986; Ridout *et al.*, 2001) and overdispersed Poisson alternatives (e.g. the negative binomial) are not good candidates for predictive models with this type of data. Although these models have been shown to be useful for prediction in other situations where data with excessive zeros arise (Mullahy, 1986; Lo *et al.*, 1992; Stefánsson, 1996; Hall, 2000), lack of fit in our case likely arises because of efforts on the part of fishermen to actively reduce mortality, which may evolve over the course of the set. Had prediction of mortality been our goal, algorithmic models (e.g. Breiman, 2001 and references therein) might yield superior performance; results of algorithmic models are generally more difficult to interpret and thus were not used in this analysis.

ACKNOWLEDGEMENTS

The authors thank Robin Allen, William Bayliff and Michael Scott (IATTC, 8604 La Jolla Shores Drive, La Jolla, California USA 92037-1508) and two reviewers, for comments and suggestions that greatly improved this manuscript. The authors thank Ernesto Altamirano, David Bratten, Enrique Urena and Nickolas Vogel for comments regarding interpretation of the results of the analysis and Nickolas Vogel for database assistance. The first author thanks N. Chyan-huei Lo for helpful discussions regarding many aspects of this manuscript. Observer data were kindly provided by the national observer programmes of the USA and Venezuela.

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Interactions between common bottlenose dolphins (*Tursiops truncatus*) and the artisanal fishery in Asinara Island National Park (Sardinia): assessment of catch damage and economic loss

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ABSTRACT

In 1999, the Italian Central Institute for Applied Marine Research (ICRAM), in response to reports made by local fisheries, began a study into the interactions between common bottlenose dolphins (*Tursiops truncatus*) and the artisanal fishery in the Asinara Island National Park (Sardinia). Using onboard observers, fishing boat surveys were carried out to determine the frequency of interactions, variations in the catch of target species and damage to two different types of trammel net caused by dolphins. Interactions occurred primarily with trammel nets targetting striped red mullet (*Mullus surmuletus*; the less valuable peacock wrasse, *Simphodus tinca*, was also caught). Interactions also occurred with trammel nets set for lobster (*Palinurus elephas*), cuttlefish (*Sepia spp.*) and scorpionfish (*Scorpaena spp.*), but these were considered negligible. The target species, catch and damage inflicted on the catch was recorded, both in the presence and absence of dolphins, in an effort to ascertain associated damage and economic cost. Loss of catch was found to be significant only in the case of nets deployed during the red striped mullet fishing season. Although the level of interaction was high relative to the narrow red striped mullet fishery season, the overall economic impact on the fishing community was found to be modest. The presence and regulations of the national park area may provide an opportunity for investigating mitigation activities compatible with both cetacean conservation and the maintenance of the traditional fisheries.

KEYWORDS: FISHERIES; COMMON BOTTLENOSE DOLPHIN; COMPETITION; EUROPE

INTRODUCTION

Interactions between fisheries and marine mammals have been frequently reported and involve almost all existing fishing gears (e.g. Northridge and Hofman, 1999). Such interactions generally have negative consequences for both fishery economics and the conservation status of marine mammals (Perrin *et al*., 1994; Hall and Donovan, 2002). Two types of interaction can be distinguished: biological and operational. Biological interaction is the competition for the same biological resource, at the population level (Northridge and Hofman, 1999). Operational interaction is associated with individual animals causing direct damage by stealing fish from the gear or becoming entangled in gear (Harwood, 1992). This latter interaction can result in damage to the fishing gear, spoilt prey in the net, fish taken from the net and reduced catch rate. Bottlenose dolphin distribution is often related to the distribution of prey (e.g. Barros and Odell, 1990; Barros *et al*., 2000); interactions with fisheries will thus be more likely where the distribution of their preferred prey overlaps with the distribution of the target species of a fishery.

There are examples of competitive interactions with coastal fisheries from several European countries, e.g. Greece (Labropolou, pers. comm.; Casale *et al*., 1999), Croatia (Drasko Holcer, pers. comm.), Spain (Alonso *et al*., 2000; Lopez *et al*., 2000; Gazo *et al*., 2001), Tunisia (Naceur Lofti, 2000) and others. Within Italy descriptive studies have been conducted in Western Sicily (Quero *et al*., 2000) and Sardinia (Cannas *et al*., 1994). The common bottlenose dolphin (*Tursiops truncatus*) is the most frequently involved species, probably due to its coastal distribution and opportunistic feeding habits (Barros and Odell, 1990). Despite increased research effort, the nature and seasonality of the interactions and the damage to fisheries, through gear and loss of catch, have never been quantified. To evaluate the need for mitigation measures and/or economic compensation related to damage caused by the interactions, it is necessary to fill these knowledge gaps.

This study, conducted between 1999 and 2001, details the interaction between small-scale fisheries and common bottlenose dolphins in the Asinara Island National Park, northwest Sardinia. It evaluates the damage to the catch in order to estimate the magnitude of the impact on the local economy. This area was selected for the study for two main reasons: (1) reports and requests for help from the local fisheries; and (2) the relatively pristine nature of the area around Asinara Island due to the establishment of a penitentiary which had isolated it from the public since 1885 (Gessa, 1998). After the closure of the penitentiary in 1997, the area was designated as a national park. In the area, 39 dolphins have been photo-identified in a six year period; variability in re-sighting frequencies suggests that some individuals have a high site fidelity whilst others frequent the study area more sporadically (Lauriano *et al*., 2003). The frequency of newly identified individuals has decreased in recent years, suggesting that the majority of the population frequenting this area has been identified (Lauriano *et al*., 2003). Preliminary investigations, conducted through interviews with fishermen, had indicated that interactions occured predominantly with trammel nets; interactions with long-lines and creel traps were considered insignificant. Hence this study has focused on the trammel net fishery.

MATERIALS AND METHODS

Study area

The study area is approximately 480km^2 wide, comprising the Asinara National Park and its adjacent waters (Fig. 1). The western shore of the island is characterised by high rock cliffs and the sea floor drops quickly to a depth of 45m and

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is highly influenced by strong wave dynamics due to prevailing north and north-westerly winds (Delitala *et al.*, 1998). In contrast, the eastern coast has a wide continental slope extending across the Asinara Gulf. This eastern shoreline, sheltered from the prevailing winds and hence not subject to the strong 'wave movements' of the open sea, is dominated by a lush sea grass meadow (*Posidonia oceanica*).

Fishing operations

The fishing fleet of Stintino, the main fishing port within the study area, comprises 21 boats. The average gross tonnage is 3.41 (range 1.19-9.26), average overall length (LOA) is 7.36m (range 4.8–12.65) with an average engine power of 47.49hp (range 13.5–230). The fishery activities are conducted in accordance with park regulations; bottom-set fishing gear, such as trammel nets, are the main fishing gear whilst other gear, such as long—lines and traps, are sporadically used. The fishery is closed for 45 days every winter; apart from this restriction, fishing activity is carried out throughout the year. Two main types of trammel net are deployed separately, according to the period of the year, as described below.

B-type[1] *nets*, with mesh size between 32 and 72mm, are used between January and April mainly to catch seabream (*Diploidae*), cuttlefish *(Sepiidae*) and scorpionfish (*Scorpaenidae*), and between May and August for lobster (*P. elephas*). This type of net is left soaking continuously and is inspected by fishermen every 24 hours. The average length was 823m and height 1.6m (Table 1).

S-type[2] *nets*, with mesh size of 27mm, are used between September and December only and target striped red mullet (*M. surmuletus*). The net is set before dawn and haul starts at sunrise. The average length was 919m and height 1.6m (Table 1).

Table 1
Characteristics of fishing operations.

Net type	N	Mean depth (m)	Depth range (m)	Mean length (m)	Length range (m)	Mean duration of the fishing operation (mins)		
						Set-up	Soak	Haul
B	67	63±21	20-102	823±102	550-1,000	-	>1,200	56±18
S	88	31±12	10-65	919±362	500-2,000	22±8	172±74	42±15

Data collection

To collect data on fishing activities, observers were placed aboard up to three fishing boats each day. The following data were collected: mesh size; net length; time of net setting and hauling; catch composition; total weight of individual species; morphological damage to the fish; geographic location and depths at each net end; presence/absence of dolphins; the beginning and end of any interactions; and the number of dolphins sighted.

Interactions were defined as occasions when dolphins were observed within 400m of the nets. 'Set up duration' was defined as the time between the start and the end of the

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[1] Large mesh size.

[2] Small mesh size.

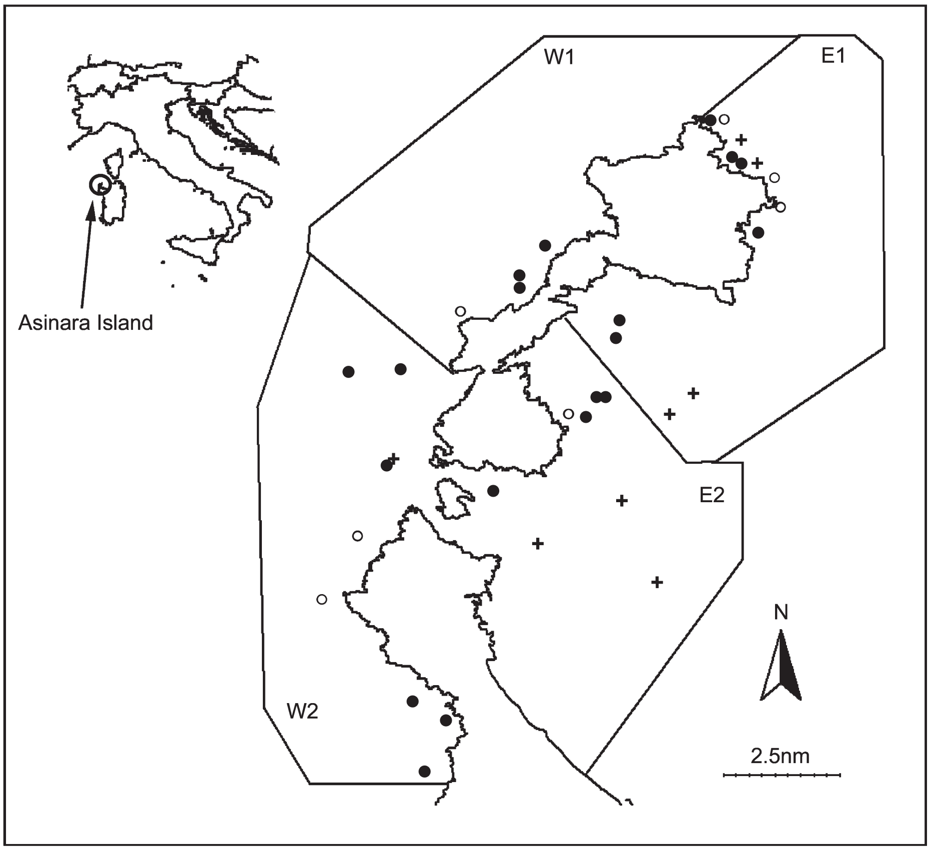

Fig. 1. The study area between 1999 and 2001 (solid circle = interactions S-type nets; open circle = interactions B-type nets; + sightings during the monitoring B-type net fishing season). E=East; W=West. S and B type nets are not overlapping; they are deployed in different seasons.

set up operation; ‘Haul duration’ as the time between start and end of the hauling operation; and ‘Soak duration’ as the time between set-up end and the start of the hauling time. Accordingly, the total fishing time was the sum of these three operations.

Each net monitored was considered to represent a fishing experiment; in a single day several fishing experiments could occur.

Catch-per-unit-effort (CPUE) was defined as the total catch (kg) divided by the length of the net (km). Analyses were performed for each type of net separately.

For those fish species recorded in more than 50% of the total observations, multiple regression analyses were carried out in order to evaluate factors affecting catches, in terms of both the CPUE and morphological damage. Independent variables – year, season, area, depth, presence/absence of dolphins, group composition – were tested for their unconditional interrelation. Explanatory variables were chosen using the Akaike Information Criterion, AIC (e.g. Akaike, 1974).

The economic damage caused by the loss of catch due to interactions, was calculated only for S-type nets by considering: (1) the average catch loss of the main target species per km of net; (2) the local commercial value of the target species per kg; (3) the mean net length used daily by each vessel; (4) the average number of fishing days during each fishing season; and (5) the overall frequency of interactions.

The annual frequency of interactions was estimated from the number of interactions observed during the overall number of fishery experiments. Data on the duration of the fishing season and the commercial value of each target species were provided by the local fishery consortium.

In order to assess damage to the catch, each specimen caught was analysed and the morphological damage classified into following five categories (Lauriano and Di Muccio, 2002): (a) ‘Head’, when only the head remained, the body removed at the level of the gills; (b) ‘Tail’, only the tail remained; (c) ‘Bite’, the specimen showed one or more parts removed; (d) ‘Fragment’, only parts of the specimen remain; (e) ‘Vestigial’, empty bodies with only the skin and bones left (see Fig. 2).

To collect data on dolphin behaviour and movements during interactions, a 5.8m rigid inflatable boat (RIB) was towed by the fishing boat and used by an independent team of researchers in order to avoid interference with fishing activities and dolphin behaviour. Successive boat locations recorded from the RIB, using a GPS receiver, were assumed to describe the locations of the dolphins being observed.

Due to the different soak times for B- and S-type nets, the monitoring of fishing operations was conducted in two different ways.

S-type net. The observation (by on-board observers) of S-type nets was continuous during the entire fishing operation, starting from the set up to the end of hauling. In order to achieve maximum coverage of the fishing area (such as a bottom rocky area) the nets were set in a winding pattern resulting in a smaller length than it would be if deployed straight. Since one end was anchored, with other was attached to the fishing boat, observers were able to listen for dolphins in the area around the net or to see them after sunrise. No fishing operations were performed in poor sea conditions (sea ≤ 2 on the Douglas sea and swell scale[3]).

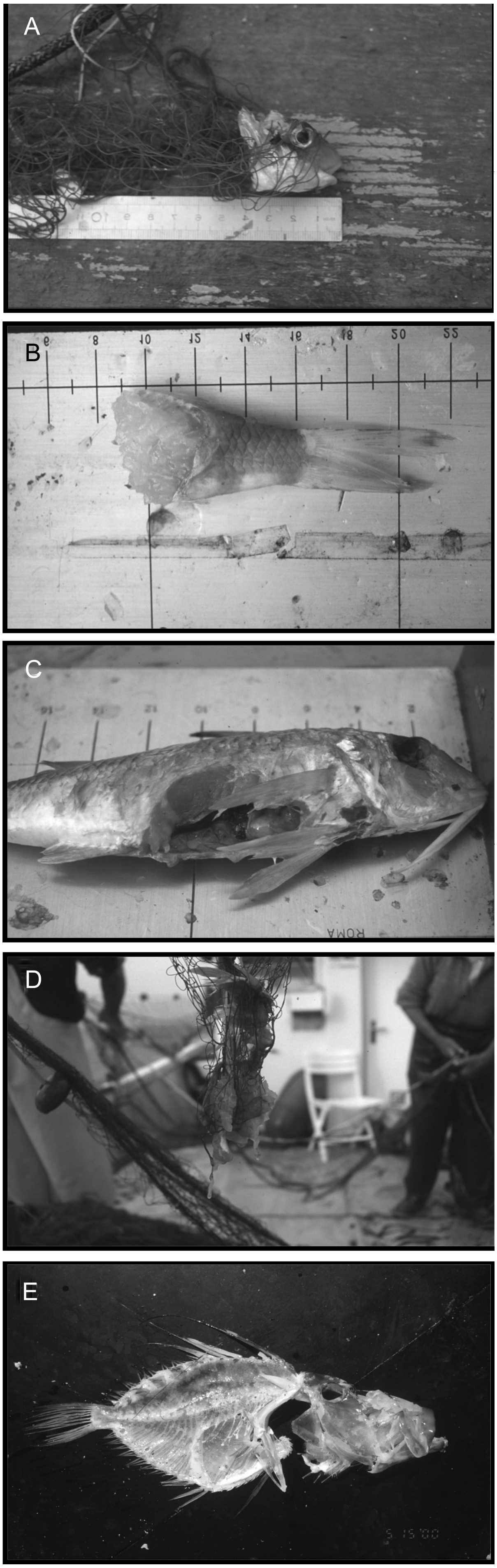

Fig. 2. Photographs of categories of morphological fish damages. (A) Head. (B) Tail. (C) Bite. (D) Fragment. (E) Vestigial.

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[3] e.g. see http://www.dcmnr.ie/display.asp?pg=1093

B-type net. By contrast, B-type nets were monitored only during the set up/hauling period. However, during the day, since the interactions could occur at any time during the 24-hour fishing period, the fishing area was also monitored with the RIB ('Monitoring surveys'). During these monitoring surveys, the number of nets in the study area and the presence/absence of dolphins were recorded. Data were only considered for analysis when the sea state was $\leq$ 3 Beaufort scale[4].

Data were georeferenced using a Geographic Information System (GIS). The study area was subdivided into four sectors (Fig. 1) of equal dimensions (E1, E2, W1,W2) and the relative densities of dolphins and buoys for each sector were calculated in order to establish the possible overlap between dolphins and fishing areas. The relative density was expressed as the total numbers of encounters weighted by effort (n/km), in each sector.

RESULTS

S-type net

Composition of the catch

A total of 88 fishing experiments were conducted between October 1999 and October 2001 on 24 different days. Of these, 41 took place off the eastern and 47 off the western coasts of the island.

Catches were characterised by the overwhelming predominance of striped red mullet over forkbeard (*P. phycis*), pandora (*Pagellus spp.*), seabream (*Diplodus spp.*) and scorpionfish. Species caught more than three times are indicated in Table 2.

Bottlenose dolphin frequency during fishing operation (Hauling/setting and soak)

Bottlenose dolphins were recorded interacting with the fishing operations on 29 occasions out of 88 experiments (0.33). The annual frequencies of interactions, during year 1999, 2000 and 2001, were 0.27 (n=11), 0.25 (n=51) and 0.50 (n=26) respectively. The first sightings occurred between 05:55 and 09:57 hrs. The dolphins arrived 12 times during soaking time and 17 times during hauling. When interactions occurred, dolphins spent a mean of 20 minutes (SD=27, n=29) around the nets. The mean group size was 6.8 (SD=3.04, range 1-12) and calves were present on eight occasions.

Factors affecting catch levels

Table 3 shows the significant results of multiple regression analysis of explanatory variables explored; the total catch of fish was negatively correlated with the duration of the soak time and dolphins interactions, but was positively correlated with depth.

Multiple linear regression analyses were performed on the catch rate of nine main species (Table 4): striped red mullet (97% of the total catch on discrete occasions), common seabream (85%), black scorpionfish (*S. porcus*) (76%), large-scaled scorpionfish (65%), annular seabream (*D. annularis*) (65%), comber (*S. cabrilla*) (64%), common pandora (*P. erythrinus*) (59%), common cuttlefish (*S. officinalis*) (58%), and peacock wrasse (*S. tinca*) (51%). Only for striped red mullet and peacock wrasse were the total catches significantly affected by dolphins.

Effect of dolphins on catches

LEVEL OF CATCHES

When dolphin interactions occurred, the total CPUE (kg/km) was reduced from 17.68 (SD=12.12) to 10.27 (SD=11.66) for all years combined (t-value=2.73, df=86, p=0.008). The red striped mullet CPUE decreased from 7.63 (SD=6.35) to 4.15 (SD=6.73) in the presence of dolphins for all years combined (t-value=2.37, df=86, p=0.02). The average red striped mullet CPUE with and without bottlenose dolphins varied by year and was 1.98 and 11.51 in 1999, 5.36 and 7.69 in 2000 and 3.45 and 5.06 in 2001 respectively. For peacock wrasse, with or without interactions, the CPUE was 0.20 and 0.52 in 1999, 0.30 and 0.19 in 2000 and 0.41 and 0.21 in 2001 respectively.

DAMAGE

Damage of various kinds were detected on fourteen species (Figs 3 a, b). Of those variables examined, only the presence of dolphins showed a positive correlation (see Table 5). The 'Head' damage category was observed only for striped red mullet (15 cases) and comber (1 case only): 'Bites' were the most common form of damage irrespective of the presence of dolphins (Figs 3a and b). It is notable that 'Head' and 'Fragment' damage were both positively correlated with the presence of dolphins (p=0.007; and p=0.001, respectively) and negatively correlated with the year (Head-Year2000: p=0.003; 'Year2001': p=0.002; and Fragment-'Year2000': p=0.00003; 'Year2001': p=0.00000003). 'Head' damage was also positively correlated with the presence of groups composed by adults ($p=1.3^{-11}$) while 'Fragment' was positively correlated with the presence of sub-adults in the group (p=0.002).

Estimate of Economic Damage (ED)

The economic reduction of the net fishing yield was mainly related to the red striped mullet catch. This species has a much higher commercial value than the peacock wrasse (on average €9.90/kg compared to €1.03/kg) and economic loss was only calculated for the most valuable species. The estimated economic loss per boat per season varied quite widely with the annual mean for the three year period being over €1,100 (see Table 6).

B-type net

Composition of the catch

Sixty-seven fishing operations were carried out in 17 days; of these, eleven took place off the eastern shore and 56 off the western shore of the island. Catches mainly comprised lobster, large-scaled scorpionfish (*S. scrofa*), common octopus (*Octopus vulgaris*) and skate (*Raja spp.*). The species caught are listed in Table 2.

Bottlenose dolphin frequency during fishing operations (hauling/setting nets)

Dolphins were recorded during fishing operations (hauling/setting nets) on 7 out of 67 (0.10) fishing experiments. The frequencies for 2000 and 2001 were 0.17 (out of 35) and 0.3 (out of 32) respectively. The first sightings occurred between 05:22 and 09:30hrs. During the hauling/setting operation dolphins spent an average of eight minutes (SD=5) around the nets. The mean group size was 1.6 (SD=0.55, range 1-2) and groups comprised only adults.

Factors affecting catch levels

Correlations among explanatory variables on total catch are show in Table 7.

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[4] e.g. see http://www.dcmnr.ie/display.asp?pg=1094

Table 2

Fish catch checklist in each net type (species caught less than 3 times are not reported).

				Net B		Net S	
N	Class	Family	Species	No. obs.	CPUE	No. obs.	CPUE
1	Osteichthyes	Carangidae	*Seriola dumerilii* (Risso, 1810)	3	0.450	3	0.011
2		Centracanthidae	*Spicara maena* (Linnaeus, 1758)	1	0.003	32	0.155
3		Congridae	*Conger conger* (Linnaeus, 1758)	1	0.010	5	0.036
4		Gadidae	*Phycis phycis* (Linnaeus, 1766)	25	0.816	40	0.906
5			*Trisopterus minutus capelanus* (Linnaeus, 1758)	3	0.006	8	0.115
6		Labridae	*Labrus bimaculatus* (Linnaeus, 1758)	2	0.018	4	0.006
7			*Labrus merula* (Linnaeus, 1758)	1	0.030	18	0.099
8			*Labrus viridis* (Linnaeus, 1758)	0	0.000	12	0.129
9			*Symphodus mediterraneus* (Linnaeus, 1758)	0	0.000	5	0.012
10			*Symphodus roissali* (Risso, 1810)	0	0.000	25	0.136
11			*Symphodus tinca* (Linnaeus,1758)	0	0.000	45	0.252
12		Lophiidae	*Lophius piscatorius* (Linnaeus, 1758)	18	0.732	0	0.000
13		Mullidae	*Mullus surmuletus* (Linnaeus, 1758)	3	0.013	85	5.301
14		Sciaenidae	*Sciena umbra* (Linnaeus, 1758)	3	0.043	36	0.164
15		Scomberesocidae	*Scomberesox saurus* (Walbaum, 1792)	3	0.015	2	0.007
16		Scorpaenidae	*Scorpaena porcus* (Linnaeus, 1758)	13	0.165	67	0.560
17			*Scorpaena scrofa (*Linnaeus, 1758)	45	1.613	57	0.651
18		Serranidae	*Serranus cabrilla* (Linnaeus, 1785)	6	0.017	56	0.446
19		Soleidae	*Solea impar* (Bennett,1831)	6	0.077	0	0.000
20			*Solea vulgaris* (Quensel, 1806)	4	0.024	0	0.000
21		Sparidae	*Boops boops* (Linnaeus, 1758)	2	0.003	13	0.025
22			*Dentex dentex* (Linnaeus, 1758)	5	0.322	22	0.134
23			*Diplodus annularis* (Linnaeus, 1758)	0	0.000	59	0.200
24			*Diplodus puntazzo* (Cetti, 1789)	2	0.009	16	0.044
25			*Diplodus sargus* (Linnaeus, 1758)	3	0.042	8	0.034
26			*Diplodus vulgaris* (E.Geoffrey Saint-Hilaire, 1817)	6	0.039	75	0.479
27			*Pagellus acarne* (Risso, 1826)	9	0.034	7	0.077
28			*Pagellus erythrinus* (Linnaeus, 1758)	16	0.219	52	0.415
29			*Sarpa salpa* (Linnaeus, 1758)	0	0.000	10	0.027
30			*Spondyliosoma cantharus* (Linnaeus, 1758)	12	0.164	35	0.120
31		Sphyraenidae	*Sphyraena sphyraena* (Linnaeus, 1758)	0	0.000	4	0.033
32		Trachinidae	*Trachinus araneus* (Cuvier, 1829)	13	0.168	2	0.010
33			*Trachinus draco* (Linnaeus, 1758)	12	0.102	8	0.030
34			*Trachinus radiatus* (Cuvier, 1829)	6	0.053	2	0.004
35		Triglidae	*Trigloporus lastoviza* (Brûnnich, 1768)	3	0.013	16	0.032
36		Uranoscopidae	*Uranoscopus scaber* (Linnaeus, 1758)	22	0.359	15	0.055
37		Zeidae	*Zeus faber* (Linnaeus, 1758)	14	0.148	15	0.046
38	Chondrichthyes	Rajidae	*Raja asterias* (Delaroche, 1809)	22	2.468	0	0.000
39			*Raja brachyura* (Lafont, 1873)	6	2.087	1	0.007
40			*Raja clavata* (Linnaeus, 1758)	3	0.109	2	0.012
41			*Raja miraletus (*Linnaeus, 1758)	16	0.439	0	0.000
42			*Raja* sp.	4	1.497	0	0.000
43			*Dasyatis pastinaca* (Linnaeus, 1758)	1	0.024	4	0.020
44		Scyliorhinidae	*Scyliorhinus canicula* (Linnaeus, 1758)	20	0.179	8	0.516
45	Cephalopoda	Loliginidae	*Loligo vulgaris* (Lamark, 1798)	0	0.000	7	0.024
46		Octopodidae	*Octopus vulgaris* (Cuvier, 1797)	16	1.330	19	0.258
47		Sepiidae	*Sepia elegans* (Blainville, 1827)	0	0.000	4	0.032
48			*Sepia officinalis* (Linneus, 1758)	5	0.138	51	0.438
49			*Sepia orbignyana* (Ferussac, 1826)	0	0.000	28	0.094
50	Crustacea	Palinuridae	*Palinurus elephas* (Fabricius, 1787)	59	3.197	9	0.044
51		Majidae	*Maja squinado* (Herbest, 1788*)*	3	0.091	1	0.001

No significant differences ($p>0.05$) were found in the total catch for when dolphins were or were not present during the hauling/setting operation (CPUE=17.11; $n=7$; SD=13.96 and CPUE=17,81; $n=60$; SD=15.16, respectively).

Damage

A total of 248 fish (33 species) showed damage. The most frequent category (77%) was 'Vestigial' damage ($n=190$), followed by (18%) 'Bites' ($n=44$). The remainder accounted for only the 6% of the total.

The number of damaged specimens was positively correlated only with the year (hauling/setting operations only) ($p=0.020$). 'Bite' ($p=0.032$) and 'Vestigial' ($p=1.7^{-11}$), were positively correlated with depth.

Monitoring of the study area from the rigid inflatable boat (January-August)

During 50 days of field work days, 1,758km were covered and a total of 903 buoys were recorded; on only 10 occasions were bottlenose dolphins encountered. On three of these they were following working bottom trawlers, and these encounters are not included in Fig. 1. The mean group size was 4.0 (range 1-9, SD=2.79, $n=10$), with an average of 1.7 sub-adults per group. Buoy and relative sighting density, weighted by effort (km covered within each quadrant), are

Table 3

S-type net: multiple regressions analysis on total catch.

	Estimate	SE	t-value	p[1]
(Intercept)	10.06378	3.43266	2.932	0.00434 **
Durat. exp.	-1.62088	0.80258	-2.020	0.04662 *
Depth	0.25663	0.08861	2.896	0.00481**
Dolphins	-5.10512	2.06585	-2.471	0.01549 *
Residual SE	277.7	DF	79	
F-statistic	5.908	DF	3 & 79	0.001044 **

[1] Level of significance. ***=0.001 ; **=0.01 ; *=0.05.

Table 4

S-type net: multiple regressions analysis on species' catch.

	Estimate	SE	t-value	p[1]
P. erithrynus				
(Intercept)	-0.4896	0.5053	-0.969	0.3355
Year 2000	-0.6904	0.3252	-2.123	0.0368*
Year 2001	-0.3671	0.3037	-1.209	0.2303
Area E2	0.5332	0.2699	1.975	0.0516
Area W1	0.3003	0.3008	0.998	0.3210
Area W2	-0.1412	0.2876	-0.491	0.6248
Depth	0.0414	0.0099	4.181	7.3^{-5}***
Residual SE	24.61	DF	79	
F-statistic	8.22	DF	6 & 79	5.91^{-6} ***
S. porcus				
(Intercept)	5.2289	1.4399	3.631	0.0005 ***
Year 2000	-1.5758	0.9483	-1.662	0.1003
Year 2001	0.0964	0.9340	0.103	0.9181
Depth	-0.1042	0.0274	-3.809	0.0003 ***
Dolphins	-1.2722	0.5921	-2.149	0.0516
Residual SE	76.67	DF	79	
F-statistic	4.981	DF	4 & 79	0.0012 **
S. cabrilla				
(Intercept)	-1.5630	0.5635	-2.774	0.0068 **
Year 2000	-0.3402	0.3711	-0.917	0.3619
Year 2001	0.1812	0.3655	0.496	0.6213
Depth	0.0809	0.0107	7.553	5.01^{-11} ***
Dolphins	-0.3273	0.2297	-1.425	0.1581
Residual SE	30.01	DF	79	
F-statistic	24.64	DF	4 & 79	1.829^{-13} **
S. tinca				
(Intercept)	1.0308	0.2364	4.360	3.79^{-5} ***
Area E2	-0.1078	0.1851	-0.583	0.5615
Area W1	0.3512	0.2001	1.755	0.0830
Area W2	0.6378	0.1811	3.523	0.0007 ***
Durat.exp	-0.0706	0.0483	-1.462	0.1476
Depth	-0.0218	0.0062	-3.515	0.0007 ***
Dolphins	1.0308	0.2364	4.360	3.79^{-5} ***
Residual SE	16.12	DF	79	
F-statistic	5.834	DF	6 & 79	5.834^{-5} **
D. annularis				
(Intercept)	0.4496	0.1521	2.956	0.0041 **
Area E2	0.0761	0.1252	0.608	0.5450
Area W1	0.0584	0.1418	0.412	0.6815
Area W2	0.2976	0.1317	2.259	0.0265 *
Depth	-0.0108	0.0045	-2.470	0.0156 *
Residual SE	11.86	DF	79	
F-statistic	3.789	DF	4 & 79	0.00706 **
M. surmuletus				
(Intercept)	2.7816	1.6935	1.643	0.1042
Depth	0.1306	0.0492	2.653	0.0095 **
Dolphins	-3.0560	1.2727	-2.401	0.0187 *
Residual SE	156.3	DF	79	
F-statistic	5.776	DF	2 & 79	0.0045 **
S. officinalis				
(Intercept)	0.5044	0.2293	2.200	0.03062 *
Area E2	0.9873	0.2378	4.152	7.94^{-5} ***
Area W1	0.1525	0.2411	0.632	0.5289
Area W2	0.6593	0.2405	2.741	0.0075 **
Durat.exp	-0.1891	0.0635	-2.979	0.0038 **
Residual SE	21.7	DF	79	
F-statistic	7.757	DF	4 & 79	2.32^{-5} ***

[1] Level of significance. ***=0.001 ; **=0.01 ; *=0.05.

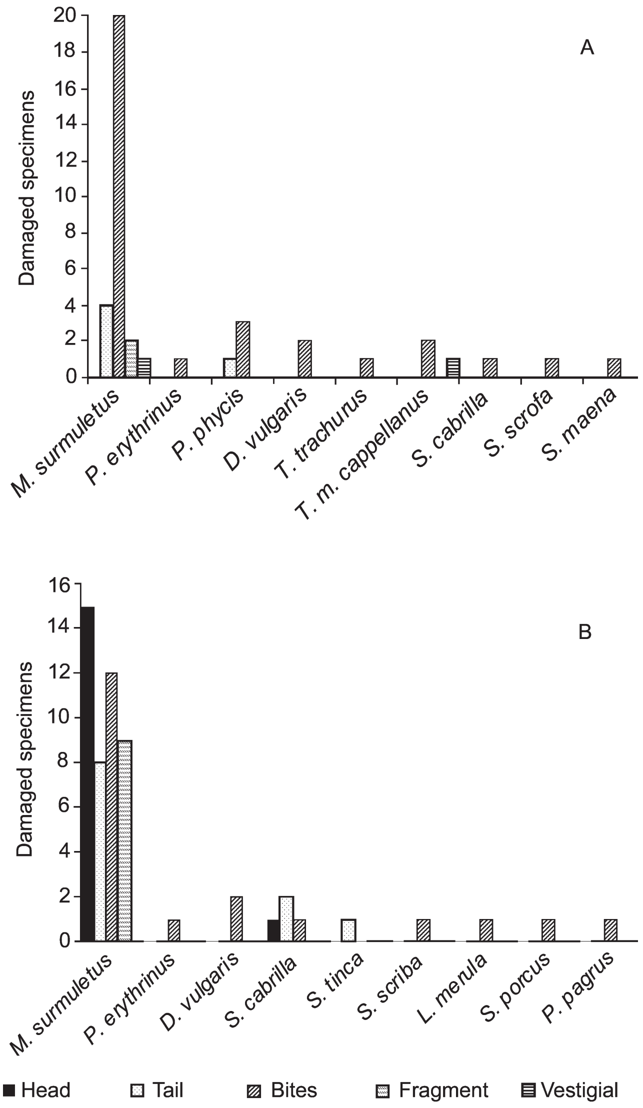

Fig. 3. Fish damage categories and damaged specimens without (A) and with (B) interaction.

Table 5

S-type net: multiple regressions analysis on morphological damages.

	Estimate	SE	t-value	p[1]
(Intercept)	0.3873	0.1396	2.773	0.00684 **
Dolphins	0.3156	0.1049	3.008	0.00347 **
Year 2000	-0.1377	0.1508	-0.913	0.36386
Year 2001	0.1669	0.1584	1.054	0.29495
Residual SE	13.78	DF	83	
F-statistic	5.563	DF	3 & 83	0.0001819 ***

[1] Level of significance. ***=0.001 ; **=0.01 ; *=0.05.

Table 6

Economic damage (ED) in euro (€) of red striped mullet catch (1999-2001). L=mean catch loss (kg) per species per km of net; l=mean length of net used by each boat daily; F=frequency of interaction; D=mean fishing season (days) for red striped mullet.

Year	L (kg/km)	l (km)	F	D (days)	Kg price (€)	ED per boat (€)
1999	9.53	2.63	0.27	30	9.81	1,992.26
2000	2.33	2.64	0.25	38	9.81	573.42
2001	1.61	3.13	0.50	37	10.07	939.03
Total mean economic damage (€)						**1,168.24**

Table 7

B-type net: multiple regressions analysis on catch.

	Estimate	SE	t-value	p[1]
(Intercept)	5.397e+03	1.920e+04	0.281	0.779636
Season SU	9.370e+00	1.053e+01	0.890	0.376994
Season W	-1.896e+01	9.286e+00	-2.042	0.045642 *
Area W1	2.428e+00	5.241e+00	0.463	0.644796
Area W2	-3.219e+00	5.727e+00	-0.562	0.576238
Depth	-3.016e-01	8.034e-02	-3.753	0.000401 ***
Dolphins	-4.392e+00	5.223e+00	-0.841	0.403812
Residual SE	348	DF	59	
F-statistic	2.83	DF	7 & 59	0. 013 *

[1] Level of significance. ***=0.001 ; **=0.01 ; *=0.05.

shown in Table 8. The highest relative density of common bottlenose dolphin encounters was found in fishing area E1 followed by W2. Buoy relative density was higher along the western shore of Asinara (W1 followed by W2).

Table 8

Daylight monitoring of fishing areas (B-type net season).

Area	E2	E1	W1	W2
Buoys	193	197	217	296
Effort (km)	867	371	164	356
Sightings	1	3	1	2
Buoys density	0.222	0.531	1.323	0.831
Dolphin density	0.001	0.008	0.006	0.007

DISCUSSION AND CONCLUSION

This study represented the first attempt in the Mediterranean basin to quantify depredation by bottlenose dolphins to artisanal fisheries. Despite widespread complaints in the region, an increase of attention to the problem and persistent requests for subsidy, little if any detailed information was available on this topic. A wide range of fishing gears is deployed in different regions and seasons and it is possible that different species of cetaceans may be involved in others kinds of competitive interactions.

This study highlights the existence of what was called 'operational competitive interaction' (Northridge and Hofman, 1999; Reeves *et al.*, 2001) between bottlenose dolphins and fishermen. Nevertheless, striking differences were revealed in the type and importance of interaction in the two types of trammel net. Because of differences in the operational activity and consequently in methodology, detailed analysis of the interaction was possible for trammel S-type nets only, whereas the level of the interaction for trammel B-type nets could only be inferred. Nevertheless, all evidence suggests a low degree of depredation with trammel B-type net in comparison to trammel S-type net.

S-type net

S-type nets showed a high frequency of interactions (up to half of the experiments in 2001) and the relatively prolonged mean duration of the interactions (20 mins) was consistent with active exploitation of the catch by the dolphins.

The diversity of fish species in the catch decreased in the presence of dolphins and the total CPUE showed a significant reduction. Of the nine fish species analysed, however, only catches of striped red mullet and peacock wrasse were adversely affected by dolphins.

On a closer investigation of the damage to the fish, the 'Head' category was recorded only for nets for which the presence of dolphins had been noted; it was particularly associated with all-adult groups. Such remains can be associated with the bottlenose feeding strategy and the mode of entanglement of the fish species. In fact, fish are entangled in the medium panel of the trammel net (Anon., 1998; Ferretti *et al.*, 2002) such that only the rear portion is left exposed and open to a predator. It is also believed that, when a large amount of prey is available, marine mammals have the ability to select the most nutritious portion of the prey (Harwood, 1992). Thus a trammel net may represent a 'supermarket' for the dolphins characterised by a high concentration of preferred prey, allowing for a selection of both the species and the 'best bite'. This is consistent with the fact that only striped red mullet heads were recorded when an interaction occurred. In addition, the frequency of 'fragments' was correlated with the number of sub-adults which may reflect the lack of skill of sub-adults to most effectively exploit the catch. Despite the clear impact of dolphin presence on the total catch of striped red mullet, the number of 'Heads' recorded was relatively low (*n*=15). This suggests the possibility of a more complex feeding strategy, not only restricted to the use of the nets as a 'supermarket', but also as a barrier to stop fleeing prey, as described for Mauritanian bottlenose dolphins (Brusnell, 1973) and killer whales (Similä and Ugarte, 1993).

The morphological damage category 'Bite', with its characteristic shape and size, seems more attributable to the action of other predators such as cuttlefish (*Sepia spp.*), common octopus (*O. vulgaris*), european conger (*Conger conger*) and Mediterranean moray (*Murena helena*) (Lauriano and Di Muccio, 2002). Interestingly, the frequency 'Bites' decreased when dolphins were present, which may reflect an impact of the presence of a top predator on other predators.

B-type nets

Bearing in mind the difference in monitoring methodology linked to the particular fishery activities, the rate of dolphin interaction during the hauling and setting operations was negligible. The total catch seemed not to be affected by the presence of dolphins but rather by environmental and temporal factors, e.g. depth and season, as possible consequence of fish ecology and different conservation status of fish stocks around Asinara Island (Tunesi *et al.*, 2001).

None of the morphological damage categories detected on the specimens caught in B-type nets was correlated with the presence of dolphins. In these nets the most frequent category, 'Vestigial', was rather related to 'Depth' and 'Season' and was probably caused by scavenging organisms (mostly Isopoda). The category 'Head' detected in the S-type nets and considered as a proxy of dolphin depredation was never recorded for B-type nets. We would have expected that such damage would have been recorded if interactions had occurred during unmonitored phases of the fishing process. Finally from the data collected during the monitoring survey and despite the high density of B-type nets in certain areas and their daily availability to dolphins, no evidence of direct competitive interactions with dolphins was observed.

General

Our results suggest that in this area, bottlenose dolphins are adapting their feeding strategies to the red mullet fishery – this may reflect their energetic requirements in different seasons and years (e.g. the calving period) and availability. In the Gulf of Asinara, there is also an intense and profitable trawling activity all year around, except for September.

Trawlers usually harvest red mullet (*Mullus barbatus*), European hake (*Merluccius merluccius*) (Ardizzone and Corsi, 1997) and other sandy and mud bottom circumlittoral species that have been reported in the Mediterranean bottlenose dolphin diet (Miokovic *et al*., 1997; Relini, O.L. *et al*., 1994). It has been suggested that bottlenose dolphins in this area take advantage of the presence of trawlers (Lauriano, 1997), as described in other regions (Fertl and Leatherwood, 1997). When trawling ends due to the closure of the fishery, the bottlenose dolphins seem to switch their attention to the trammel net fishery for striped red mullet, which at that time of the year becomes gregarious and coastal (Pipitone *et al*., 1995; Relini, G. *et al*., 1999). In this context, we propose that the bottlenose dolphins augment their energy intake by taking advantage of these particular two fisheries. A positive balance between the cost and benefits of feeding activities related to the exploitation of certain fisheries compared to 'no-aided' free ranging hunting strategies (Fortuna *et al*., 1998), the possible ease of hunting and/or a risk minimisation due to the gear characteristics, also reflected by the presence of calves in the group (Ashford *et al*., 1996), and the higher concentration of preferred prey around the fishing gear, might explain the bottlenose dolphins preferences for small mesh size nets and trawlers, compared to large mesh size nets or long-lines.

Mitigation

Recognising the existence of competitive interactions between bottlenose dolphins and fishermen is considerably easier than devising a strategy to minimise such interactions. Considerable flexibility of approach in addressing this issue will be required. The nature and level of interactions will be dependent on several factors and the bottlenose dolphin is well known to be extremely adaptable. A single, one-time solution is unlikely to be found; a combination of mitigation methods seems to be the best approach.

Dolphins approached S-type nets mainly during the hauling period. This suggests that dolphins might be reacting to a cue which attracts them to full nets. Characteristic noises (the 'dinner bell' theory), whilst setting and hauling the net, such as the low engine revolutions or the noise of the winch may represent such cues. This hypothesis is consistent with a lack of interactions with the long-line fishery, where the fishing gear is hauled manually. Bottlenose dolphins have been reported to be able to distinguish operational noises of shrimp fishing boats produced by winch and engine and adjust their behaviour accordingly (Gunther, 1954 as cited in Shane *et al*., 1986; Norris and Prescott, 1961; Gruber, 1981 as cited in Shane *et al*., 1986). A cue effect of winch noise has also been demonstrated for killer whales (Matkin, 1986; Yano and Dahlheim, 1995). Another potential cue could be the collective noise of several fishing boats leaving the harbour at the same time at night. With respect to that possibility, local fishermen also pointed out the general absence of interactions after a period of fishing inactivity due to bad weather, they suggested some correlation between previous fishing activity and the presence of dolphins.

One approach to consider, therefore, is to develop fishing strategies that reduce possible cues. This could be achieved, for example, by introducing: (i) modifications to the fishing gear; (ii) time/area closures; and (iii) greater fishing area and gear turnover, and/or (iv) through a process of 'stealth fishing', as suggested by Tregenza (2001). It has also been suggested that a parsimonious use of pingers could also help to ease this problem. However, the cost of untested new technologies, such as the deployment of 'pingers' in this case should be considered (Reeves *et al*., 2001) along with a risk assessment to investigate possible negative effects on dolphins and the habitat. It should be noted that these fisheries operate in marine protected areas; the use of the deterrent devices may thus be inconsistent with the main aim of the marine reserve which is the preservation of the habitats and biodiversity.

It is also important to note that the overall economic damage caused by dolphins to the fishery, at least as calculated in this initial study, is small, affecting only on strictly seasonal activity. Despite this, the interaction represents a strong psychological factor in the perception of the fishermen because almost every year it affects up to a third of their income during the two months of the striped red mullet fishery. Our data also highlight annual differences in economic damage according to the total catch, frequencies of interaction and mean length of net.

We recognise that in order to develop a complete estimate of the economic damage, gear damage and the consequent reduced catching capacity should be considered. In this context it should be noted that tears in the net are not sewn up daily, but only when serious damage occurs and meticulous repairs are only made in autumn during the biological fishing closure.

Provided an agreed mechanism to estimate economic costs could be agreed, the National Park Authority could support a compensation scheme for predator damage. In addition or alternatively, it could assist with mitigation research. This approach has been tested at the national level in Sweden for terrestrial mammals (Swedish Environmental Protection Agency – *http://www.internat.naturvardsverket.se/*). In fact some economic refunds are already established by a regional law[5], provide reimbursement for damage caused by dolphins. Reimbursement is intended for net damage only, and requires the fisherman to hand in the net to the coastguard who must verify the extent of the damage. This practice interrupts fishing activities, and is inconvenient for fishermen who wish to apply.

Whatever other approach is adopted, public awareness programmes, should also be established. For example, in this study several factors were found to be correlated with the decrease in fish catches (for example season, depth, area, and other predators). Nevertheless, fishermen perceived that only dolphins were detrimental to their activities. In the past this attitude has lead to extreme 'solutions'. For example until the 1950s in Italy and former Yugoslavia, rewards were paid for killed dolphins, considered as vermin to be eradicated (Holcer, 1994).

ACKNOWLEDGEMENTS

We thank Giovanna Barbieri, Giovanni Bearzi, Corrado Buonuomo, Andrea Cardinali, Stefano Di Muccio, Marta Manca-Zeichen, Giovanna Pesante, Eva Salvati, Umberto Scacco, Ornella Sanna, Enrico Tarulli, and Carola Vallini for helping in the fieldwork. We are grateful to the Management Board of the Parco Nazionale dell'Asinara for providing the scientific permits and to the Cooperativa di Pescatori di Stintino for their collaboration in the field work. Many thanks also to Dr. Claudio Agostinelli for his help with statistics and to Peter Mackelworth for its invaluable editing

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effort. Special thanks are due to A.J. Read (Duke University Marine Laboratory, Beaufort, North Carolina, USA), S. Northridge (Sea Mammals Research Unit, University of St. Andrews, St. Andrews Fife UK) and the Editor for their useful comments on this manuscript.

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Stratification of lipids, fatty acids and organochlorine contaminants in blubber of white whales and killer whales

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ABSTRACT

The biopsy — via dart, trocar or surgery — is becoming the preferred protocol for sampling skin and blubber of many cetacean species, because a small sample from a healthy animal may provide better information than a larger sample collected via necropsy from an ill or emaciated animal. Furthermore, the biopsy is often the only means of obtaining samples (e.g. for threatened or endangered species). Because biopsy darts collect only a small sample of tissue — and blubber can be heterogeneous in structure and composition — it is essential to compare the results obtained from biopsies to those found by analysing full-thickness blubber samples obtained via necropsy. This manuscript compares blubber stratification in two odontocete species, white whales (*Delphinapterus leucas*) and killer whales (*Orcinus orca*). Five parameters (i.e. lipid percent and classes, contaminant concentrations and profiles, fatty acid profiles) were measured by blubber depth. Results of these comparisons strongly suggest that biopsy results must be interpreted with caution and in conjunction with results from species-specific blubber depth profiling. For example, lipid classes measured in biopsy samples of white whales and killer whales were similar to those for equivalent-depth samples obtained by necropsy. In addition, lipid-adjusted contaminant concentrations measured in dart or trocar samples adequately represented those obtained by necropsy of both species. Conversely, the lipid content in biopsy samples was lower than that found in same-depth necropsied samples due to loss of lipid during sampling. Also, because of the high level of fatty acid stratification observed, fatty acid profiles from the outer blubber layer collected via biopsy from both species are less likely than the metabolically active inner layer to be useful in determining the prey species consumed by these odontocetes. This study demonstrates, for white and killer whales, that properly interpreted results from blubber biopsies can provide valuable information about the body condition, health and life history of individual animals.

KEYWORDS: POLLUTANTS; ORGANOCHLORINES; STRANDINGS; BIOPSY SAMPLING; KILLER WHALE; WHITE WHALE; PACIFIC OCEAN

INTRODUCTION

Lipid (fat) comprises a large proportion of the body mass of many cetaceans, with most of the lipid consolidated as a blubber layer. Analysis of blubber can provide a great deal of information about the body condition and health of marine mammals. For example, blubber thickness and lipid content can be indicative of the nutritive condition of cetaceans (Aguilar and Borrell, 1990) and profiles of fatty acids in blubber can be used to infer the diet of marine mammals (Adams *et al*., 1997; Iverson *et al*., 1997; 2002; Walton *et al*., 2000). In addition, measuring concentrations of lipophilic organochlorine contaminants (OCs) in the blubber of top predators (e.g. odontocetes) provides information on potential adverse health effects resulting from contaminant exposure, because high OC concentrations have been associated with immunosuppression, reproductive impairment, alteration in bone development and growth and increased susceptibility to disease (Reijnders, 1986; Olsson *et al*., 1994; De Guise *et al*., 1996; 1997; De Swart *et al*., 1996; Kamrin and Ringer, 1996; Ross *et al*., 1996; Zakharov *et al*., 1997; Beckmen *et al*., 1999; 2003). However, when measuring OC concentrations, changes in lipid class profiles (i.e. proportions of triglycerides, free fatty acids, phospholipids, wax esters and cholesterol) should be considered because these factors may influence the concentrations of contaminants in a blubber layer (Koopman *et al*., 1996).

Collecting biopsy samples (i.e. blubber and epidermis) from wild cetaceans — through surgical or punch biopsies on captured-released individuals and through remote biopsy darting — is becoming routine as part of an effort to develop non-destructive techniques for studying genetics, contaminant exposure and feeding ecology (stable isotope ratios and fatty acid profiles) of populations (Barrett-Lennard *et al*., 1996; Fossi, F.C. *et al*., 1997; Fossi, M.C. *et al*., 1997; 1999; 2000). In addition, biopsy samples from presumably healthy animals are preferred over samples collected from necropsies of stranded cetaceans, because strandings often involve animals in compromised health that are not representative of the overall population (Brown, 1985; Aguilar *et al*., 1999). However, only a few studies have tested whether blubber biopsies provide a sample that is representative of the entire blubber layer in cetaceans (Aguilar and Borrell, 1991; Gauthier *et al*., 1997) and these studies have looked primarily at the distribution of OCs within the blubber of mysticetes.

Differences in OC concentrations by blubber depth appear to be species-specific, i.e. some species show pronounced stratification and others have blubber that is more homogenous. Aguilar and Borrell (1991) found higher lipid-normalised PCB and DDT concentrations in the outer blubber layer compared to the inner layer in fin whales (*Balaenoptera physalus*) and in male sei whales (*B. borealis*) (by factors of 1.1 to 1.5), but female sei whales showed little variation in OC concentrations between these layers. The authors concluded that blubber samples collected from cetaceans for pollutant analyses should include all layers in order to be representative of an individual animal's pollutant load. In another study, Gauthier *et al.* (1997) found no statistically significant differences in lipid-normalised OCs among the outer,

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middle or inner blubber layers in minke (*B. acurostratra*) and blue whales (*B. musculus*).

Recently, as interest in using blubber fatty acids to provide information about diet has increased, researchers have questioned whether biopsy samples can provide adequate samples for fatty acid signature analysis. Koopman (1996; 2001; 2002) found that significant vertical stratification of fatty acids was evident between the inner and outer blubber layers in odontocetes, suggesting that the inner blubber layer is more active metabolically than the outer layer in terms of lipid deposition and mobilisation. Similarly, Olsen and Grahl-Nielsen (2003) observed significant vertical stratification of fatty acids in minke whale blubber and concluded that studies to trace dietary influence of fatty acids should be made using the inner blubber layer. Furthermore, Hooker *et al.* (2001) reported that fatty-acid stratification was present throughout the depth of the blubber in northern bottlenose whales (*Hyperoodon ampullatus*), but was much less pronounced than that found in the blubber of smaller cetaceans (Koopman, 2001; Koopman *et al.*, 2002).

Because the dart biopsy is becoming a standard protocol for obtaining tissue samples from many cetacean species, it is essential to compare the results obtained from analysing biopsy samples to those for blubber collected by necropsy. This paper compares blubber stratification in two odontocete species – white whales (*Delphinapterus leucas*) and killer whales (*Orcinus orca*) – by measuring five parameters (i.e. percent lipid, lipid classes, OC concentrations, OC patterns and fatty acid profiles) by blubber depth in samples obtained both by biopsy and necropsy. In addition, two biopsy-sampling techniques – darts and trocars – have been compared.

METHODS

Cetaceans sampled

Blubber samples from five white whales from the genetically distinct Cook Inlet and Bristol Bay populations (O'Corry-Crowe *et al.*, 1997), as well as from three stranded killer whales, were studied (Table 1). Two of the killer whales were marine mammal-eating transient ecotypes and one was a piscivorous resident ecotype (Black *et al.*, 1997; Ford *et al.*, 2000). Although non-stranded animals are preferred for blubber stratification studies, neither of the killer whales stranded in 2002 (L60 and CA189) was believed to have died from a chronic illness resulting in emaciation, so the results should not be biased from this cause. The cause of death of the Alaskan transient killer whale that stranded in 2003 (ATx; a currently unidentified member of the AT1 pod; see Table 1) is not known, but lipid content of the blubber from this animal was in the same range as previously found for wild Alaskan transients (Ylitalo *et al.*, 2001), so emaciation was unlikely.

Subsampling of blubber by depth and position on animal

Thickness of blubber from the necropsied white whales CI-73, CI-76 and BB-75 was sufficient to allow subdividing the samples by depth. However, because of differences in blubber thickness, blubber from CI-73 and CI-76 was divided into fourths and blubber from BB-75 (a juvenile) was divided into thirds.

Initial attempts to obtain full-thickness blubber samples from white whales using trocars were unsuccessful due to the fluidity of the blubber. Lipid seeped from the trocar tip, so these samples have not been included in this paper. However, samples CI-01-05 and CI-01-06 (6mm core) were frozen rapidly in the trocar and were removed while still frozen. The resulting samples were of sufficient length and mass to allow division into halves – near-epidermis and near-muscle subsamples.

Blubber was collected from the dorsal region of killer whales CA189 and ATx and also from the mid-lateral region of CA189. Subsequently, blubber was subdivided by depth into three layers from 0-2cm (from the epidermis), 2-4cm and >4cm. Blubber from L60 was collected from the dorsal and lateral body regions and from the anterior, central and posterior (to the dorsal fin) regions of the saddle patch. Blubber from each region was subdivided into three layers by depth from 0-2cm (from the epidermis), 2-4cm and >4cm (the lateral sample was not thick enough to include a third layer; see Table 4). At the same time, biopsy samples were taken using a dart (5 × 20mm) that was thrust fully into the anterior, central and posterior regions of the saddle patch. The samples were estimated to be ~2cm in depth. To simplify references, the near-epidermis blubber layer was termed the 'outer' layer, the layer nearest to the muscle the 'inner' layer and the other layer(s) were 'middle' layer(s).

TLC/FID lipid percent and lipid class determinations

Blubber samples were analysed for total lipids by thin layer chromatography coupled with flame ionisation detection (TLC/FID) using an Iatroscan Mark 5 (Shantha, 1992). The lipid sample extracts (i.e. a portion of the extract prepared for fatty acid analyses; see below) were spotted on Chromarods (Type SIII) and developed in a solvent system containing 60:10:0.02 hexane:diethyl ether:formic acid (v/v/v). The various classes of lipids (i.e. wax esters, triglycerides, free fatty acids, cholesterol and phospholipids) were separated based on polarity, with the nonpolar compounds (e.g. wax esters) eluting first, followed by the more polar lipids (e.g. phospholipids). The Iatroscan was operated with a hydrogen flow rate of 160mL min^{-1} and airflow of 2000m min^{-1}. A four-point linear external calibration was used for quantitation. Duplicate TLC/FID analyses were performed for each sample extract and the mean value reported. Total lipid concentrations were calculated by adding the concentrations of the five lipid classes for each sample and reported as total percent lipid relative to the original sample.

Fatty acid concentrations and profiles

The analytical method used to measure fatty acid concentrations in these tissues, which was recently developed in the Northwest Fisheries Science Center laboratory, integrates several methodologies reported in the literature. Briefly, the method involves: (1) extracting approximately 1g of tissue (mixed with sodium and magnesium sulphates to remove water) by Accelerated Solvent Extraction (ASE) using 50ml methylene chloride at 100°C and 2000psi (Sloan *et al.*, 2004); (2) partitioning the extract into three fractions [approximately 46% for OC analysis, 46% for gravimetric lipid and 8% for fatty acid and lipid class (Iatroscan) analysis]; (3) derivatising the fatty acid fraction to fatty acid methyl esters (FAMEs) using 3% sulphuric acid in methanol; (4) extracting the FAMEs into iso-octane; (5) drying the extract over a bed of sodium sulphate; and finally (6) separating and analysing the FAME extracts on a DB-23 capillary column using quadruple gas chromatography/mass spectrometry (GC/MS) operated in the selected ion monitoring (SIM) mode. In most cases, the molecular ion was chosen for quantitation and a confirmation ion was also monitored. Eighty-three different fatty acids were determined (as methyl esters; Table 2). A

Table 1

Life history and other parameters of the white whales and killer whales sampled.

	Sample type	Date sampled/ stranded	Location	Age class	Sex	Length (cm)	Ecotype	Comments
White whales								
CI-73	Subsistence/ necropsy	7/2001	Cook Inlet	Adult	F	345		Lactating
CI-76	Subsistence/ necropsy	7/2002	Cook Inlet	Adult	M	457		
BB-75	Subsistence/ necropsy	5/2002	Bristol Bay	Juvenile	M	287		
CI-01-05	Trocar/live	8/2001	Cook Inlet	Adult	F	362		Captured for satellite tagging and released.
CI-01-06	Trocar/live	8/2001	Cook Inlet	Adult	F	401		Captured for satellite tagging and released.
Killer whales								
CA189	Stranded/ necropsy	1/2002	Inland waters of Washington state	Adult	F	671	Transient	According to necropsy results, CA189 was ‘fresh-dead’ with a ‘good’ body condition and no emaciation. CA189 may have given birth to a stillborn calf or aborted a late-term foetus. Most often observed in California waters (Black et al., 1997).
L60	Stranded/ necropsy (biopsy*)	4/2002	Outer coast of Washington state	Adult	F	606	Resident	Southern Resident from a pod that inhabits the inland waters of Puget Sound in the summer months (Black *et al.*, 1997; Ford *et al.*, 2000). She had given birth to at least two calves, the first died (1990-1998), but the second calf is still alive (1995-) (Ford *et al.*, 2000).
ATx	Stranded/ necropsy	4/2003	Prince William Sound, AK	Adult	M	700	Transient	Likely a member of the AT1 pod that frequents the waters of Prince William Sound and the Kenai Fjords. Genetic analyses are currently underway to assist in identifying this individual.

* Biopsy samples were simulated by thrusting a biopsy dart into the saddle patch area of the killer whale (see Methods).

standard nomenclature system was used for naming these fatty acids, where ‘n’ followed by a number refers to the position of the first double bond relative to the alkyl end of the molecule.

OC contaminant concentrations and profiles

Blubber samples (1 to 3g) of both cetacean species were extracted, following addition of internal standards, using the ASE procedure (Sloan *et al.*, 2004). The methylene chloride extract was then filtered through a column of silica gel and alumina and concentrated for further cleanup by high-performance liquid chromatography (HPLC) using a size-exclusion column that separated lipids and other biogenic material from the OC fraction (Krahn *et al.*, 1988; Sloan *et al.*, 2004). Finally, the fraction containing OCs was analysed by GC/MS to measure analyte concentrations. ΣPCB is the sum of the following 46 congeners (only 40 peaks because some congeners elute together) −17, 18, 28, 31, 33, 44, 49, 52, 66, 70, 74, 82, 87, 95, 99, 101/90, 105, 110, 118, 128, 138/163/164, 149, 151, 153/132, 156, 158, 170, 171, 177, 180, 183, 187/159/182, 191, 194, 195, 199, 205, 206, 208, 209; and ΣDDTs is the sum of *o,p*’-DDD, *p,p*’-DDD, *o,p*’-DDE, *p,p*’-DDE, *o,p*’-DDT and *p,p*’-DDT.

Statistical analyses

Prior to all statistical calculations, both OC and fatty acid concentration data were tested for normality by computing the skew and kurtosis of the individual analyte distributions; all were found to be substantially non-normal. In an attempt to improve the homogeneity of the data, the concentration data were both arcsine and square root transformed but neither of these transforms resulted in a consistent improvement in data normality nor resulted in an appreciable difference in any of the final PCA results. Therefore, the untransformed data were retained in the final analyses. All statistical comparisons among univariate variables were computed using a two sample, one-tailed, t-test of significance assuming unequal variances.

Principal Component Analysis (PCA) of OCs in blubber was conducted using JMP Statistical Discovery Software® (Macintosh version 5.01) to determine the similarity of contaminant and fatty acid patterns. Analyte concentrations were normalised by dividing concentrations of each OC analyte by total OCs (sum of the PCBs and pesticides measured). PCA was then computed on both the correlation and covariance matrices of these normalised data. When PCA is used, the number of samples should exceed the number of variables, preferably by a factor of two (McGarigal *et al.*, 2000). Because of the need to further reduce the number of variables (64 variables and 15 samples for white whales; 58 variables and 23 samples for killer whales), only those OC analytes exhibiting the largest positive and largest negative eigen vector projections along the first three principal component axes were used for the final PCA analysis. For white whales, these analytes were PCB congeners 28, 52, 70, 118, 151, dieldrin, *p,p*’-DDD, *o,p*’-DDT; and for killer whales, analytes were congeners 52, 74, 99, 149, 156, 183, beta-HCH, alpha-chlordane, t-nonachlor, mirex, *o,p*’-DDE, *p,p*’-DDE. Also, all analytes that had values below the limits of quantitation were excluded from the dataset because values below this limit distort the pattern and strongly affect the PCA analysis.

Fatty acid concentrations were normalised by dividing concentrations of each analyte by the sum of all FAME analytes measured. All analytes that had values below detection limits were excluded and PCA was computed on both the correlation and covariance matrices. For white whales, the eight fatty acids that had the largest contribution to the first three principal components were used in the final PCA analysis − C16:1n7, iso-C18:0, C18:1n9, C18:1n13,

Table 2

Fatty acids analysed (as methyl esters) in the blubber of marine mammals. The fatty acid number (as shown in figure 3), abbreviation, systematic name and trivial (common) name are provided.

#	Abbreviation	Systematic name	Trivial name	#	Abbreviation	Systematic name	Trivial Name
1	C10:0	n-Decanoic acid§	Capric	43	C18:1n5	13-Octadecenoic acid	
2	C11:0	n-Undecanoic acid§	Hendecanoic	44	C18:1n7	11-Octadecenoic acid§	Vaccenic
3	C11:1	10-Undecenoic acid§	Hendecenoic	45	C18:1n9	9-Octadecenoic acid§	Oleic
4	C12:0	n-Dodecanoic acid§	Lauric	46	C18:2n4	11,14-Octadecadienoic acid	
5	C12:1	11-Dodecenoic acid§		47	C18:2n6	9,12-Octadecadienoic acid§	Linoleic
6	Me4812C13:0	4,8,12-Trimethyltridecanoic acid		48	C18:2n7	8,11-Octadecadienoic acid	
7	C14:0	n-Tetradecanoic acid§	Myristic	49	C18:3n1	11,14,17-Octadecatrienoic acid	
8	isoC14:0	12-Methyltridecanoic acid§		50	C18:3n3	9,12,15-Octadecatrienoic acid§	alpha-Linolenic
9	Me11C14:0	11-Methyltetradecanoic acid		51	C18:3n4	8,11,14-Octadecatrienoic acid	
10	C14:1n5	9-Tetradecenoic acid§	Myristoleic	52	C18:3n6	6,9,12-Octadecatrienoic acid§	gamma-Linolenic
11	C14:1n7	7-Tetradecenoic acid		53	C18:4n1	8,11,14,17-Octadecatetraenoic acid	
12	C14:1n9	5-Tetradecenoic acid		54	C18:4n3	6,9,12,15-Octadecatetraenoic acid§	
13	C15:0	n-Pentadecanoic acid§		55	C19:0	n-Nonadecanoic acid§	
14	isoC15:0	13-Methyltetradecanoic acid§		56	C20:0	n-Eicosanoic§	Arachidic
15	anteisoC15:0	12-Methyltetradecanoic acid		57	C20:1n11	9-Eicosenoic acid	Gadoleic
16	tMeC15:0	2,6,10,14-Tetramethylpentadecanoic acid		58	C20:1n15	5-Eicosenoic acid§	
17	C15:1n5	10-Pentadecenoic acid§		59	C20:1n5	15-Eicosenoic acid	
18	C16:0	n-Hexadecanoic acid§	Palmitic	60	C20:1n7	13-Eicosenoic acid	
19	isoC16:0	14-Methylpentadecanoic acid§		61	C20:1n9	11-Eicosenoic acid§	Gondoic
20	anteisoC16:0	13-Methylpentadecanoic acid		62	C20:2n11	6,9-Eicosadienoic acid	
21	Me7C16:1	7-Methylhexadecenoic acid		63	C20:2n6	11,14-Eicosadienoic acid§	
22	Me78C16:1na	7,8-Dimethylhexadecenoic acid		64	C20:2n9	8,11-Eicosadienoic acid	
23	C16:1n11	5-Hexadecenoic acid		65	C20:3n3	11,14,17-Eicosatrienoic acid§	
24	C16:1n5	11-Hexadecenoic acid		66	C20:3n6	8,11,14-Eicosatrienoic acid§	homo-gamma-Linolenic
25	C16:1n7	9-Hexadecenoic acid§	Palmitoleic	67	C20:4n3	8,11,14,17-Eicosatetraenoic acid	
26	C16:1n9	7-Hexadecenoic acid		68	C20:4n6	5,8,11,14-Eicosatetraenoic acid§	Arachidonic
27	C16:2n4	9,12-Hexadecadienoic acid		69	C20:5n3	5,8,11,14,17-Eicosapentaenoic acid§	EPA
28	C16:2n6	7,10-Hexadecadienoic acid		70	C21:5n3	6,9,12,15,18-Heneicosapentaenoic acid	
29	C16:3n4	6,9,12-Hexadecatrienoic acid		71	C22:0	n-Docosanoic acid§	
30	C16:3n6	4,7,10-Hexadecatrienoic acid		72	C22:1n11	11-Docosenoic acid	
31	C16:4n1	6,9,12,15-Hexadecatetraenoic acid		73	C22:1n5	17-Docosenoic acid	
32	C16:4n3	4,7,10,13-Hexadecatetraenoic acid		74	C22:1n7	15-Docosenoic acid	
33	C17:0	n-Heptadecanoic acid§	Margaric	75	C22:1n9	13-Docosenoic acid§	Erucic
34	anteisoC17:0	14-Methylhexadecanoic acid		76	C22:2n6	13,16-Docosadienoic acid§	
35	isoC17:0	15-Methylhexadecanoic acid§		77	C22:3n3	13,16,19-Docosatrienoic acid§	
36	C17:1n7	10-Heptadecenoic acid§		78	C22:4n3	10,13,16,19-Docosatetraenoic acid	
37	C17:1ne	Heptadecenoic acid		79	C22:4n6	7,10,13,16-Docosatetraenoic acid§	
38	C18:0	n-Octadecanoic acid§	Stearic	80	C22:5n3	7,10,13,16,19-Docosapentaenoic acid§	DPA
39	isoC18:0	16-Methylheptadecanoic acid§		81	C22:6n3	4,7,10,13,16,19-Docosahexaenoic acid§	DHA
40	anteisoC18:0	15-Methylheptadecanoic acid		82	C24:0	n-Tetracosanoic acid§	
41	C18:1n11	7-Octadecenoic acid		83	C24:1n9	15-Tetracosenoic acid§	Nervonic
42	C18:1n13	5-Octadecenoic acid					

§ These fatty acids were identified using known standards. The other fatty acids (unmarked) were tentatively identified based on GC retention time and mass spectral data.

C18:2n7, C18:3n3, C19:0, C20:1n7. For killer whales, the final PCA analysis was performed using the nine fatty acids exhibiting the largest statistically significant differences in concentrations when comparing all transient blubber samples (at all depths and locations) with all resident blubber samples. Those were 2,6,10,14-Me-C15:0, iso-C15:0, C16:3n4, iso-C18:0, C18:3n3, C18:1n13, C20:1n11, C22:1n11, C24:1n9.

Quality assurance

Quality assurance procedures for determining OC and fatty acid concentrations and percent lipid included use of Standard Reference Materials (SRMs), certified calibration standards, method blanks, solvent blanks and replicate samples. SRMs used (from the National Institute of Standards and Technology) were SRM 1945 for OC contaminants and percent lipids and SRM 1946 for fatty acids. Acceptance criteria for analyses of NIST SRM 1945 and SRM 1946 were those that NIST uses for its Intercomparison Exercises. In addition, our laboratory has successfully participated in NIST and other quality assurance intercomparison exercises each year.

To determine whether differences by depth in the lipid content and OC concentrations were larger than the variability inherent in the analyses, relative standard deviations for replicate analyses (n=8) of these analytes were determined for the SRM analysed with each set of samples. RSDs were relatively low (RSDs = 3.7% for lipid content, 8.3% for ΣPCBs and 8.4% ΣDDTs) and generally less than the differences reported between different depths or techniques. Replicates of samples analysed in the same set showed lower OC variability (RSDs = 0.4-2.8% for ΣPCBs and 0.2-2.3% ΣDDTs) than reported for the SRMs that were analysed over a period of months with each set.

RESULTS

Percent lipid in blubber

Percent lipid did not vary greatly by blubber depth in the samples from the necropsied white whales (RSDs = 1.6-14%; Table 3), although the middle layer(s) tended to have higher percent lipid compared to the outer (near-epidermis) or inner (near-muscle) layers. For each individual, the outer layer had percent lipid that was very close to the mean of the three or four layers analysed (Table 3). In contrast, blubber samples collected by trocar showed a large variation in percent lipid between the halves (Table 3). Furthermore, both the inner and outer layers sampled by trocar had much lower percent lipid values than those in the corresponding layers of blubber samples collected via necropsy.

There was greater variability in total lipid by blubber depth in the necropsied resident killer whale L60 (Table 4) than in the necropsied white whales. For the body positions (i.e. anterior, central, posterior, dorsal) having blubber thick enough to be split into three layers, RSDs for mean percent lipid ranged from 12-53%. The middle layer generally had the highest percent lipid and the inner layer had the same or lower percent lipid than was found in the outer layer. For each body position sampled, the outer layer had percent lipid that was similar to the mean of the two or three layers analysed (Table 4). Samples of L60 collected by dart biopsy showed substantially lower percent lipid (8.3-10%) compared to the samples from the same body positions and depth (0-2cm) collected by necropsy (28-40%).

Percent lipid varied less by depth in the transient killer whales (RSDs = 14-22%; Table 4) than in the resident whale, but more than in the white whales. For CA189, the middle layer from each of the two positions sampled had the highest percent lipid. However, the inner layer had lower percent lipid than the outer layer in the dorsal sample and the reverse was true for the mid-lateral sample. For ATx, the highest percent lipid was found in the middle layer (dorsal position), whereas lipid content was lower and approximately equal in the inner and outer layers. As found for the resident killer whale, the outer layers from the transient whales generally had percent lipid that was similar to the mean of the three layers analysed.

Lipid classes

Triglycerides were the predominant lipid class found in blubber samples from all the white whales, irrespective of depth in the blubber layer (Fig. 1). Necropsy samples CI-73 and CI-76 and trocar sample CI-01-05 also showed a small proportion (~5%) of free fatty acids.

The lipid classes in killer whale blubber varied substantially by depth at all body positions (Fig. 2). Both the resident and transient animals had a high proportion (>50%) of wax esters in the outer layer (0-2cm) and that proportion decreased rapidly with depth. As the wax ester proportion decreased, the triglyceride proportion increased to >80% in the layer nearest the muscle. The lipid in blubber sampled by dart biopsy from the resident killer whale contained about 40% wax esters and most resembled the equivalent layer (outer) in the sample taken by necropsy from the same animal. Two of the samples showed a small proportion (<5%) of free fatty acids (L60 0-2cm necropsy and L60 biopsy).

Table 3

Concentrations of ∑PCBs and ∑DDTs determined by GC/MS in white whale blubber sampled at various depths.

		ng/g, wet weight		ng/g, lipid	
Blubber depth*	%Lipid**	∑PCBs	∑DDTs	∑PCBs	∑DDTs
BB-75; necropsy; juvenile male					
Outer third	66	1,100	1,000	1,700	1,500
Middle third	85	1,500	1,300	1,800	1,500
Inner third	69	2,400	2,000	3,500	2,900
BB-75 necropsy (mean)	73	1,700	1,400	2,300	2,000
SD	10	670	510	1,000	810
RSD (%)	14	39	36	43	41
CI-73; necropsy; adult female					
Outer quarter	71	860	920	1,200	1,300
2nd quarter	73	820	790	1,100	1,100
3rd quarter	73	650	610	890	840
Inner quarter	71	590	560	830	790
CI-73 necropsy (mean)	72	730	720	1,000	1,000
SD	1.2	130	170	170	240
RSD (%)	1.6	18	24	17	24
CI-76; necropsy; adult male					
Outer quarter	68	2,200	3,000	3,200	4,400
2nd quarter	85	2,600	3,200	3,100	3,800
3rd quarter	73	1,300	1,400	1,800	1,900
Inner quarter	74	1,200	1,400	1,600	1,900
CI-76 necropsy (mean)	75	1,800	2,300	2,400	3,000
SD	7.2	690	990	840	1,300
RSD (%)	9.6	38	43	35	43
CI-01-05; trocar biopsy; adult female					
Outer half	10	66	70	660	700
Inner half	37	120	120	320	320
CI-01-05 trocar biopsy (mean)	24	93	95	490	510
SD	19	38	35	240	270
RSD (%)	79	41	37	49	53
CI-01-06; trocar biopsy; adult female					
Outer half	5.8	110	150	1,900	2,600
Inner half	13	230	280	1,800	2,200
CI-01-06 trocar biopsy (mean)	9.4	170	220	1,800	2,400
SD	5.1	85	92	70	280
RSD (%)	54	50	42	3.9	12

*A full-thickness portion of blubber from the necropsy samples was subdivided into quarters or thirds; the 'outer' portion was the layer nearest the epidermis and the 'inner' was nearest the muscle; CI-73's blubber layer was 5 cm thick, BB-75's was 2.2 cm and CI-76's was 6 cm. The trocar biopsy samples were divided in half; the outer half was the layer nearest the epidermis and the inner was nearest the muscle; CI-01-05's sample measured 6.8 cm and CI-01-06's was 3.3 cm (see Methods). **TLC/FID lipid analyses (see Methods).

Fatty acid profiles

Fig. 3 shows the fatty acids in the blubber of the white whale CI-73 (divided into four layers), those from the 'central' position on the saddle patch of the resident killer whale L60 (divided into three layers) and those from the transient killer whale ATx (divided into three layers). The identities of the 83 fatty acids are given in Table 2. The lines at 25%, 50% and 75% (white whale sample) and at 33.33% and 66.66% (killer whale samples) indicate the proportion of each fatty acid that would be expected if these acids were homogeneously distributed among the layers. Some fatty acids appeared to be fairly evenly distributed (e.g. 29, 45, 46 and 66 in the white whale; 6, 21 and 35 in the resident killer whale; and 1, 24, 34, 35 and 37 in the transient killer whale). Other fatty acids appeared to be more heterogeneously distributed among layers (e.g. 1 and 4 in the white whale; 80 and 81 in both killer whales). Furthermore, the lower molecular weight fatty acids (those having lower identification numbers) were found in higher proportions in

Table 4

Concentrations of ∑PCBs and ∑DDTs determined by GC/MS in blubber sampled at various depths and positions in one resident and two transient killer whales.

			ng/g, wet weight		ng/g, lipid	
Blubber position	Blubber depth*	%Lipid**	∑PCBs	∑DDTs	∑PCBs	∑DDTs
Female resident (L60) - necropsy						
Anterior	0 - 2 cm	40	5,800	6,400	15,000	16,000
	2 - 4 cm	40	8,800	8,600	22,000	22,000
	> 4 cm	12	3,700	4,800	31,000	40,000
	Anterior mean	31	6,100	6,600	23,000	26,000
	SD	16	2,600	1,900	8,000	12,000
	RSD (%)	53	43	29	35	46
Central	0 - 2 cm	28	5,300	6,100	19,000	22,000
	2 - 4 cm	35	7,300	8,200	21,000	23,000
	> 4 cm	11	6,200	6,900	56,000	63,000
	Central mean	25	6,300	7,100	32,000	36,000
	SD	12	1,000	1,100	21,000	23,000
	RSD (%)	50	16	15	66	64
Posterior	0 - 2 cm	37	5,900	6,400	16,000	17,000
	2 - 4 cm	46	8,600	8,400	19,000	18,000
	> 4 cm	38	8,800	9,300	23,000	24,000
	Posterior mean	40	7,800	8,000	19,000	20,000
	SD	5	1,600	1,500	3,500	3,800
	RSD (%)	12	21	19	18	19
Dorsal	0 - 2 cm	42	6,800	7,700	16,000	18,000
	2 - 4 cm	51	9,400	10,000	18,000	20,000
	> 4 cm	17	3,700	4,100	22,000	24,000
	Dorsal mean	37	6,600	7,300	19,000	21,000
	SD	18	2,900	3,000	3,000	3,000
	RSD (%)	48	44	41	16	14
Lateral	0 - 2 cm	31	6,000	7,500	19,000	24,000
	2 - 4 cm	38	6,700	7,500	18,000	20,000
	Lateral mean	35	6,400	7,500	19,000	22,000
	SD	5	500	0	700	3,200
	RSD (%)	14	8	-	3.7	15
	L60 - necropsy (mean n=14)	33	6,600	7,300	22,000	25,000
	SD	12	1,800	1,600	11,000	12,000
	RSD (%)	37	27	23	47	49
Female resident (L60) - dart biopsy***						
Anterior	0 - ~2 cm	10	2,600	2,700	26,000	27,000
Central	0 - ~2 cm	9.0	2,600	2,700	29,000	30,000
Posterior	0 - ~2 cm	8.3	2,300	3,000	28,000	36,000
	L60 - dart biopsy (mean n=3)	9	2,500	2,800	28,000	31,000
	SD	0.9	170	170	1,500	4,600
	RSD (%)	9.9	6.8	6.1	5.4	15
Female transient (CA189) - necropsy						
Dorsal	0 - 2 cm	48	480,000	1,800,000	1,000,000	3,800,000
	2 - 4 cm	64	690,000	2,600,000	1,100,000	4,100,000
	> 4 cm	42	540,000	2,600,000	1,300,000	6,200,000
	Dorsal mean	51	570,000	2,300,000	1,100,000	4,700,000
	SD	11	110,000	460,000	150,000	1,300,000
	RSD (%)	22	19	20	14	28
Mid-lateral	0 - 2 cm	42	670,000	2,600,000	1,600,000	6,200,000
	2 - 4 cm	64	770,000	3,000,000	1,200,000	4,700,000
	> 4 cm	58	760,000	3,100,000	1,300,000	5,300,000
	Mid-lateral mean	55	730,000	2,900,000	1,400,000	5,400,000
	SD	11	55,000	260,000	210,000	750,000
	RSD (%)	21	8	9	15	14
	CA189 (mean n=6)	50	650,000	2,600,000	1,300,000	5,100,000
	SD	13	120,000	460,000	210,000	1,000,000
	RSD (%)	26	18	18	16	20
Male transient (ATx) - necropsy						
Dorsal	0 - 2 cm	26	110,000	170,000	420,000	540,000
	2 - 4 cm	34	140,000	200,000	410,000	590,000
	> 4 cm	28	140,000	190,000	640,000	790,000
	ATx (mean n=3)	29	130,000	190,000	490,000	640,000
	SD	4	17,000	15,000	130,000	130,000
	RSD (%)	14	13	8	27	20

*Measured from bottom of epidermis. **TLC/FID lipid analyses (see Methods). ***Dart was thrust into the skin/blubber by hand. ∑DDTs (wet weight) were measured as described by Ylitalo *et al.* (2001).

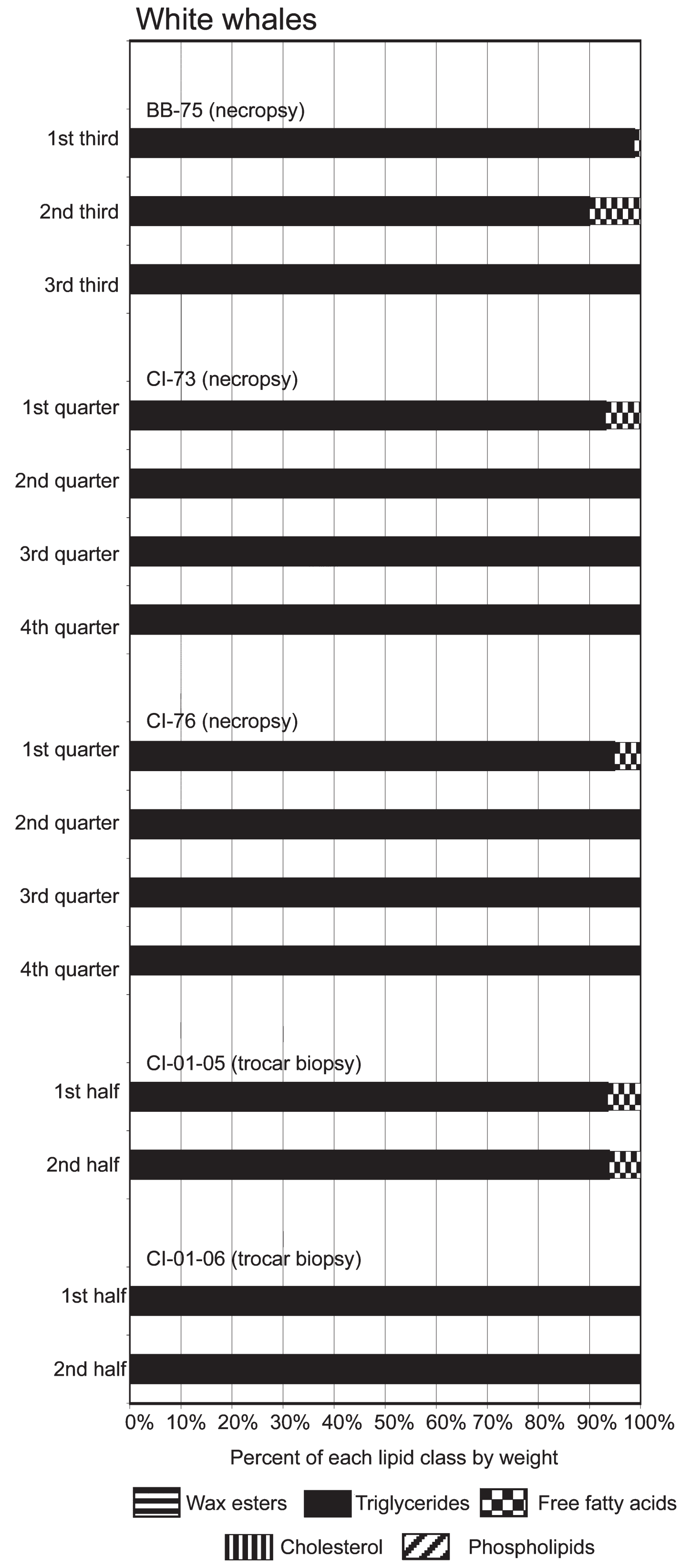

Fig. 1. Lipid classes (i.e. wax esters, triglycerides, free fatty acids, cholesterol and phospholipids) determined in each layer of white whale blubber by depth (i.e. each half, third or quarter). The layer labeled '1st' is the one nearest the epidermis.

the outer (epidermis) layer than in the inner layer – particularly in the white whales and also to a lesser extent in the killer whales.

PCA was used to further assess the homogeneity of the fatty acids profiles in the white whale blubber samples. In this plot (Fig. 4A), the eigen vectors exhibiting the highest factor loadings on the first three principal component axes were: C16:1n7 and C18:2n7 (PC1); C18:3n3 and C18:1n9 (PC2); and iso-C18:0 (PC3). The fatty acid profiles for each white whale generally did not group closely by depth in the blubber layers (evenly dashed ovals – Fig. 4A), again indicating a high degree of depth stratification for these

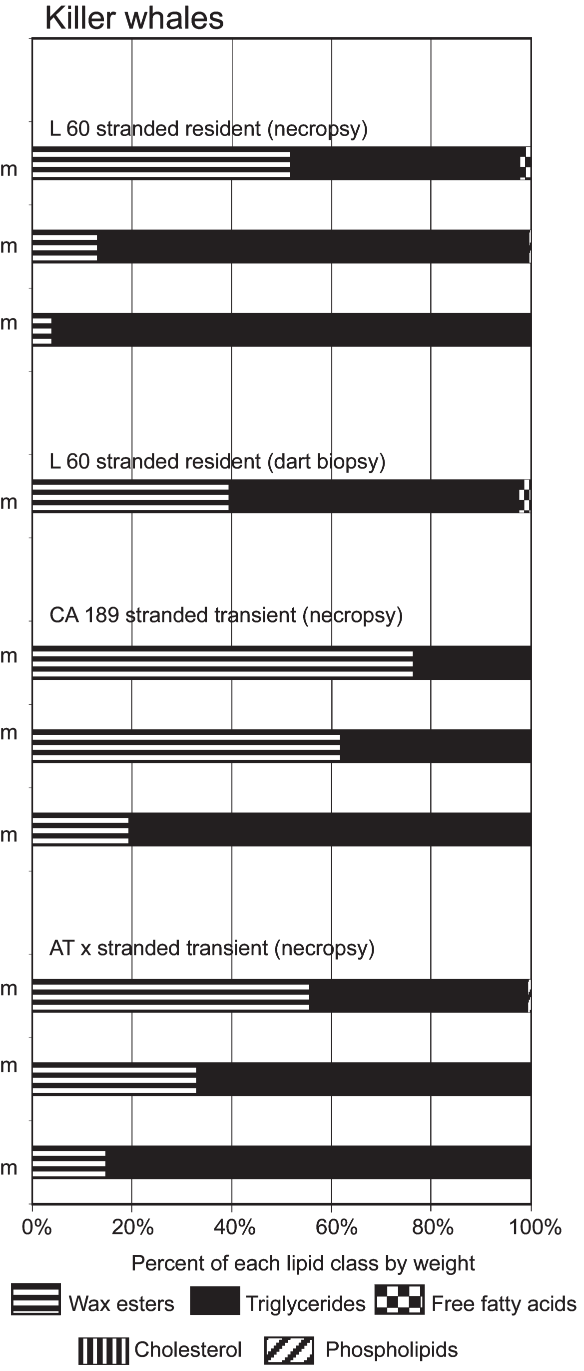

Fig. 2. Lipid classes (i.e. wax esters, triglycerides, free fatty acids, cholesterol and phospholipids) determined in each layer of killer whale blubber by depth from the epidermis (i.e. 0-2cm, 2-4cm, >4cm). The data for each depth represent the mean from all body positions sampled.

animals. However, the four animals from Cook Inlet could be distinguished from the single animal from Bristol Bay by their fatty acid profiles, regardless of which blubber depth was used for comparison (unevenly dashed ovals – Fig. 4A). This distinction was predominantly due to a larger relative abundance of branched-chain fatty acids in BB-75 (in particular, iso-C18:0). A pair-wise univariate analysis of the relative concentration of iso-C18:0 in each of the five animals in Fig. 4A indicated that this compound was significantly higher (by approximately a factor of 2) in the animal from Bristol Bay than in any of the four Cook Inlet animals, regardless of the sampling depth or lateral location of the blubber sample ($p<0.02$). Because replicate measurements of iso-C18:0 in the standard reference material ($n=5$), indicated that the analytical uncertainty in this particular fatty acid was low (RSD = 10.0%), the observed 2-fold difference cannot be attributed to measurement error.

When PCA was used to depict patterns for the killer whale fatty acids, all body positions sampled on each killer whale were clustered when grouped by depth (solid ovals – Fig. 4B). For example, the fatty acid profiles of the five body positions sampled for the resident killer whale (L60) were highly similar and clustered when grouped by depth (solid ovals). Similarly, the fatty acid profiles for the dorsal and mid-lateral positions of the transient CA189 were grouped by depth. However, in all the whales, it is the outer layer that is the most different from all the other layers sampled (Fig. 4B). In this plot, the eigen vectors exhibiting the highest factor loadings along the first three principal component axes were: C20:1n11 and C22:1n11 (PC1); C22:1n11 and iso-C15:0 (PC2); C18:3n3 and C18:1n13 (PC3). Regardless of the blubber depth or body position at which the blubber sample was acquired, the two killer whale ecotypes could be readily distinguished from one another by means of their fatty acid profiles (unevenly dashed ovals in Fig. 4B). Separation of the two ecotypes appeared to be greatest along PC1 indicating that the concentrations of C20:1n11 and C22:1n11 were substantially different between the transient and resident killer whale(s). A univariate analysis of the concentrations for these two fatty acids in each of the three animals indicated both fatty acids were significantly greater in the resident animal than either of the two transients ($p<0.01$). Again, the analytical uncertainty in each of these fatty acids measured from replicate analyses of the SRM material (RSDs = 1.3% and 5.5%, respectively) was negligible and contributed little to the observed separation of the two ecotypes.

Contaminant concentrations

Concentrations of selected contaminants (ΣPCBs and ΣDDTs) for all depths and positions sampled are given in Table 3 (white whales) and in Table 4 (resident killer whale L60 and transient killer whales CA189 and ATx). In white whales, the highest wet weight contaminant concentrations were found in CI-76 (an adult male), next was BB-75 (a juvenile male) and then CI-73 (a lactating female). The lowest concentrations were found in the two adult female white whales sampled by trocar. Although reproductive status of these females is unknown, they were not accompanied by calves. Concentrations of ΣPCBs and ΣDDTs (wet weight) in the outer layer of white whales differed from concentrations in the inner layer, but generally by no more than a factor of two, with higher concentrations sometimes in the outer layer and other times in the inner layer (Table 3). 'Normalisation' of wet weight concentrations to lipid (i.e. concentrations reported in ng/g lipid in Table 3) did not equalise the distribution of the contaminants among layers. Instead, the outer layer had consistently higher concentrations (ng/g lipid) of ΣPCBs and ΣDDTs than those found in the inner layer for Cook Inlet white whales and the reverse was true for the Bristol Bay whale.

Blubber samples (necropsy) from the resident killer whale L60 had mean concentrations of ΣPCBs and ΣDDTs (Table 4) that were about 3-fold higher (wet weight) or 9-fold higher (lipid weight) than those found in the most heavily contaminated white whale (CI-76). In general, the highest concentrations of OCs (wet weight) in L60 occurred in the middle blubber layer. Lipid normalisation of ΣPCBs

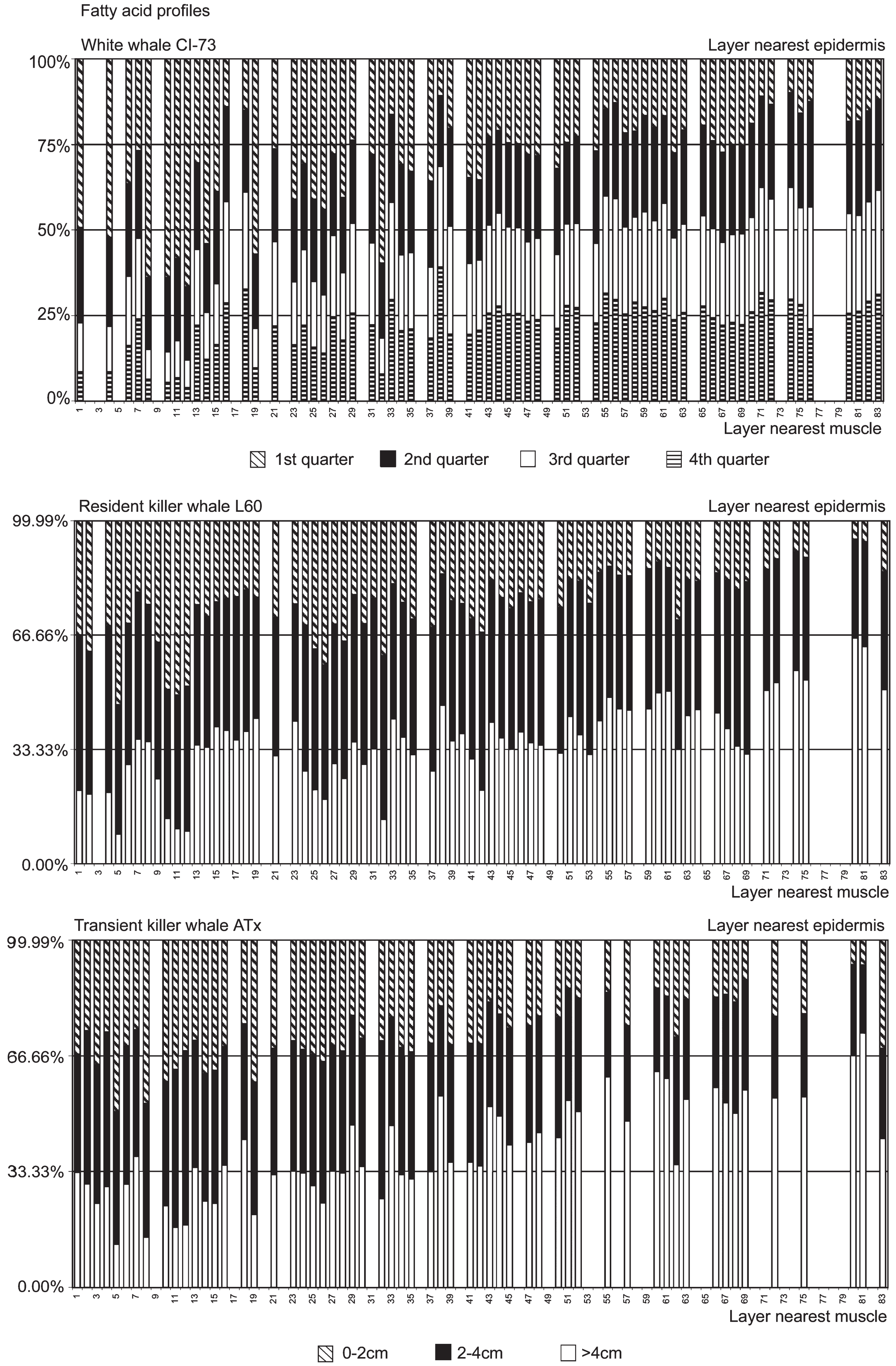

Fig. 3. Proportions of 83 fatty acids (see Table 2 for identification) found in the blubber layers of a white whale from Cook Inlet (CI-73), the resident killer whale L60 and the transient killer whale ATx. Blubber from CI-73 was divided into quarters and that from L60 and ATx was divided into three layers (0-2cm, 2-4cm and >4cm). Data are not shown when fatty acids concentrations were below the limit of quantitation for one or more layers.

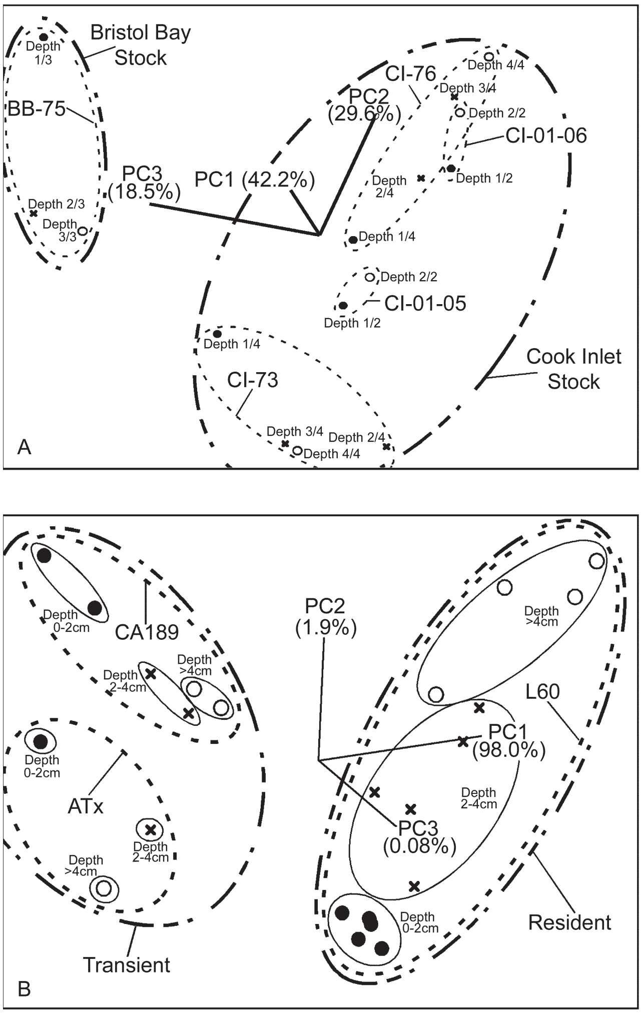

Fig. 4. Plot of the first three principal components derived from the fatty acid composition of (A) white whale blubber and (B) killer whale blubber. The quartered white whale blubber samples are grouped by animal (evenly dashed ovals) and by stock (unevenly dashed ovals). Killer whale blubber samples from each body position (individual symbols) were divided into thirds and grouped by depth from epidermis (solid ovals), by animal (dashed ovals) and by ecotype (unevenly dashed ovals). The percent of the total variation among samples explained by each principal component is given on the label for each axis. Depth 1 is the layer closest to the epidermis and depth 4 is closest to the muscle.

and ΣDDTs contributed to increased (or equal) contaminant homogeneity (decreased RSDs) for the posterior, dorsal and lateral samples, whereas the anterior and central positions showed decreased homogeneity (increased RSDs). Except for the lateral position, the lipid-adjusted OC concentrations were highest in the inner layer. The samples taken by dart biopsy had wet weight concentrations of ΣPCBs and ΣDDTs that were about half the concentrations in the necropsied samples from the same depth and body position. When the concentrations of ΣPCBs and ΣDDTs were lipid-adjusted, the biopsy samples had OC concentrations that were 1.5-2 times those in the necropsied samples.

The transient killer whales, CA189 and ATx, had mean concentrations of ΣPCBs and ΣDDTs (wet weight) in blubber that were much higher than those of the necropsied resident killer whale (by a factor of about 100 for ΣPCBs and about 400 for DDTs for CA189 and by about 20 for both ΣPCBs and ΣDDTs for ATx; Table 4). For samples from the two body positions of CA189, variability by depth in mean wet weight concentrations of ΣPCBs and ΣDDTs was low (RSDs = 8-20%). When the concentrations were expressed as lipid weight, the variability among layers increased (RSDs = 14-28%). The layer with highest lipid-normalised concentrations of ΣPCBs and ΣDDTs differed between the two sampling positions – the inner layer had higher lipid normalised concentrations than the outer layer for the dorsal sampling position, but the reverse was true for the mid-lateral position. For ATx, variability in wet weight concentrations of ΣPCBs and ΣDDTs among the layers was also low (RSDs = 8-13%), but increased when the concentrations were expressed using lipid weight (RSDs = 20-27%). As found for the dorsal samples in CA189 and L60, ATx's inner layer sample had higher lipid normalised concentrations of ΣPCBs and ΣDDTs than were found in the outer layer.

Contaminant profiles

PCA was used to depict patterns in the OC data for both the white whales and killer whales (Figs 5A and B). For white whales, the OC profiles of samples from different blubber depths of each individual animal were somewhat clustered (evenly dashed ovals in Fig. 5A) and were well separated from each other. The OCs having the highest factor loadings along the first three principal component axes were: PCB 28 and PCB 70 (PC1); PCB 118 and *p,p*'-DDD (PC2); PCB 52 and *o,p*'-DDT (PC3). The two white whale stocks, Cook Inlet and Bristol Bay, were also distinct based on their OC profiles (unevenly dashed ovals), separated primarily along the second principal component axis (PC2). A univariate analysis of the concentration data for the two eigen vectors contributing most to PC2 (i.e. PCB 118 and *p,p*'-DDD) indicated that both were significantly different when comparing the Bristol Bay whale with each of the four whales from the Cook Inlet stock ($p<0.07$). Again, the analytical measurement errors for these particular OCs (RSD = 8.1% for PCB 118 and 9.3% for *p,p*'-DDD) were very small relative to their respective inter-stock concentration differences.

The OC profiles of the five body positions sampled for the resident killer whale L60 were observed to be quite similar when grouped by depth (solid ovals in Fig. 5B), indicating much greater variability in OC patterns by depth than by body position. Depth stratifications of OCs (primarily along PC3) were much lower in the two transient killer whales, with CA189 demonstrating the least stratification. However, OC profiles from all blubber depths of the transient killer whales were well-separated from each other and from those of the resident L60 (evenly dashed ovals in Fig. 5B), principally along PC1. The OCs having the highest factor loadings along the first three principal component axes were: *p,p*'-DDE and PCB 74 (PC1); PCBs 52 and 99 and t-nonaclor (PC2); PCB149 and beta-HCH (PC3). Thus, *p,p*'-DDE and PCB 74 were the OCs primarily responsible for separating these three whales from one another (and perhaps also separating them by ecotype). A univariate analysis of the concentration data for these two OCs indicated both were significantly different in the resident compared to either of the transients ($p<0.01$).

DISCUSSION

Percent lipid in blubber

Percent lipid was fairly uniform by depth in blubber samples for necropsied white whales (Table 3). Furthermore, the lipid percent in the outer layer provided a good measure of the mean for the entire blubber layer for each white whale.

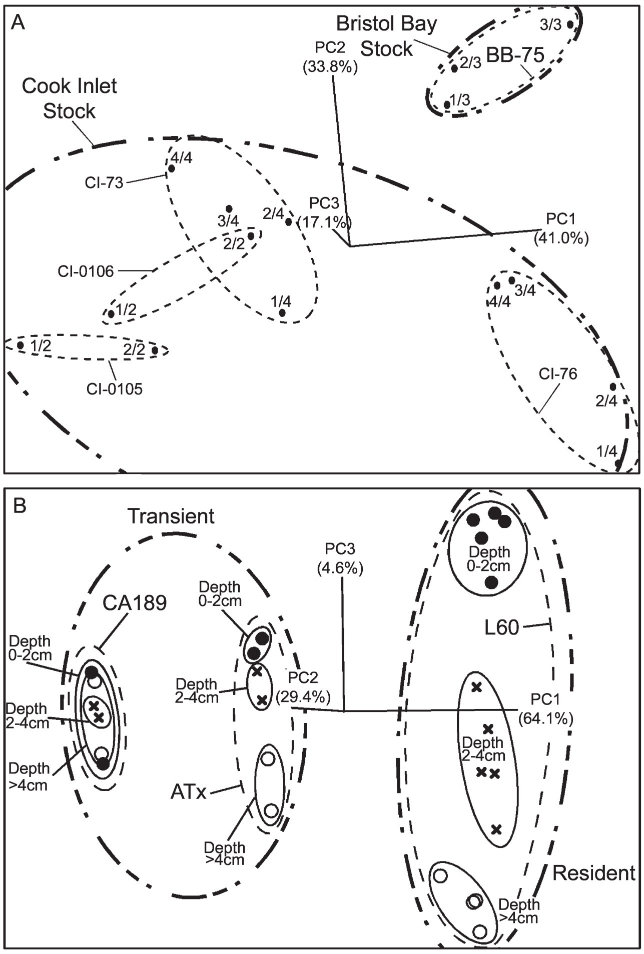

Fig. 5. Plot of the first three principal components derived from the OC composition of (A) white whale blubber and (B) killer whale blubber. The quartered white whale blubber samples are grouped by animal (dashed ovals) and by stock (unevenly dashed ovals). Killer whale blubber samples from each body position (individual symbols) were divided into thirds and grouped by depth from epidermis (solid ovals) and by animal (dashed ovals). The percent of the total variation among samples explained by each principal component is given on the label for each axis. Depth 1 is the layer closest to the epidermis and depth 4 is closest to the muscle.

These results are similar to those found by Gauthier *et al.* (1997) for minke and blue whales and by Aguilar and Borrell (1991) for fin whales, where no significant difference in lipid content was found among blubber layers. In contrast, Aguilar and Borrell (1991) found a significant difference in lipid content between the inner and outer layers of sei whales (the outer layer had higher percent lipid).

The trocar blubber samples collected from live Cook Inlet white whales had comparatively low lipid content, as well as an uneven distribution of lipid between halves, compared to necropsy samples from Cook Inlet whales (Table 3). Blubber thickness and lipid content for the four live-whale samples should, in fact, be similar because they were all sampled during the same season (summer), were of the same approximate age and were feeding within the same geographic location. Although the samples were frozen in the trocar soon after collection, lipid was likely lost when the trocar was removed from the animal due to the consistency of the blubber. Thus, the large differences in measured lipid content between trocar and necropsy blubber samples likely represent a true sampling bias. In contrast, Gauthier *et al.* (1997) reported that their 'deep' (19-26mm) biopsy samples were within the ranges measured in the blubber of necropsied blue and minke whales.

For resident and transient killer whales, the outer blubber layer provided a good estimate of mean percent lipid for the full blubber layer, similar to the results found for white whales. As in the trocar samples from white whales, dart biopsy samples taken from the resident whale had lower percent lipid than found for necropsied samples at equivalent depth (outer layer) and body positions (Table 4). These results are consistent with previous results for dart biopsies of wild cetaceans that showed lower percent lipid than would be expected from blubber sampled via necropsy. For example, Krahn *et al.* (2001) reported that mean lipid levels in gray whale blubber sampled by biopsy (10±1.0%; *n*=38) were substantially lower than those found for subsistence animals sampled by necropsy (43±2.7%; *n*= 17).

A number of theories have been advanced to explain the lower percent lipid in dart biopsy samples: (1) lipid seeping from the blubber structural matrix as the biopsy dart is ejected from the animal; (2) lipid washing away when the dart falls into the water before being retrieved; and (3) the dart hitting at an oblique angle so that more epidermis and connective tissue than blubber are collected. Because the laboratory-simulated biopsy dart technique used to acquire the killer whale samples in the current study entered the blubber as vertically as possible and did not fall into water, the low percent lipid in these biopsy samples most likely resulted from lipid that seeped from the blubber matrix as the dart was removed.

Lipid class profiles

For the white whales, triglycerides comprised the greatest proportion of the lipid regardless of depth (Fig. 1). These results agree with previous studies showing that blubber of healthy cetaceans contained primarily neutral lipids, e.g. triglycerides and nonesterified free fatty acids (Kawai *et al.*, 1988; Tilbury *et al.*, 1997; Krahn *et al.*, 2001). Furthermore, the trocar samples showed the same profile of lipid classes as found for the necropsy samples.

Unlike the blubber of white whales, blubber layers of killer whales contained 15-75% wax esters, with greater proportions found in the outer layer (Fig. 2). These results were unexpected because a previous study by Litchfield *et al.* (1975) that examined the lipid composition of fatty tissues of 20 different species of odontocetes (*O. orca* were not sampled) found that the blubber of Delphinidae contained mostly triglycerides, with the exception of false killer whales which contained 96% triglycerides and 4% wax esters. Similarly, other studies (Koopman *et al.*, 1996; Koopman, 2001) reported that blubber of odontocetes was composed primarily of triglycerides and contained little or no wax esters. In fact, the only odontocetes that have been reported to contain appreciable proportions of wax esters (>40%) in their blubber were whales from the Ziphiidae (beaked whale) and Physeteridae (sperm whale) families (Litchfield *et al.*, 1975; Hooker *et al.*, 2001).

The lipid class profile of the resident killer whale from the dart biopsy (outer layer) had only slightly smaller proportions of wax esters than were found in the outer layers from necropsy samples (Fig. 2). Therefore, the biopsy dart sample could provide lipid class information that adequately portrays the profile of the same-depth sample obtained via necropsy. However, unless a deeper biopsy sample were obtained, a biopsy could not provide information about the manner in which lipid class profiles of killer whales change by blubber depth.

Fatty acid profiles

Fatty acid profiles of a predator have been statistically linked to fatty acid profiles of potential prey species to provide an estimate of relative proportions of specific prey species consumed (Adams *et al*., 1997; Iverson *et al*., 1997; 2002; Walton *et al*., 2000). Because the inner blubber layer is more metabolically active than the outer layer, it is thought to better indicate prey fatty acid profiles (Hooker *et al*., 2001). Thus, it is important to ascertain whether biopsy sampling of the outer layer can be representative of the fatty acid profiles of the metabolically active inner blubber layer.

In both white whales and killer whales, fatty acids were disproportionately distributed among the blubber layers (Fig. 3), similar to the results reported by other researchers (Hooker *et al*., 2001; Olsen and Grahl-Nielsen, 2003). When PCA was used to determine how the various blubber layers were grouped based on the fatty acids present, profiles from the white whales showed that the inner and outer layers were not highly correlated (Fig. 4A). Similarly, fatty acid profiles of the inner blubber layer were very different from the outer layer for the resident and transient killer whales (Fig. 4B). Thus, a biopsy sample comprising only the outer blubber layer of either species would not accurately represent the metabolically active inner layer and thus would likely fail to correlate well with the fatty acid signatures of their primary prey species.

Olsen and Grahl-Nielsen (2003) have indicated that blubber fatty acid profiles may also be suitable for population (stock) identification in minke whales. Furthermore, a recent study by Moller *et al*. (2003) demonstrated that the blubber fatty acid composition of North Atlantic minke whales supported the existence of a three-region population model, regardless of the depth at which the blubber sample was acquired (deep vs superficial). In the current study, fatty acid profiles were able to distinguish the single Bristol Bay white whale from the Cook Inlet animals at all blubber depths (Fig. 4A). Similarly, the two ecotypes (resident and transient) of killer whales were readily classified from their profiles (Fig. 4B), so ecotype identification based on fatty acid profiles seems possible. Due to the small number of white and killer whales represented in this study, it is impossible to determine with any certainty whether it is differences in diet, genetics or both that are primarily responsible for the separations observed between the white whale stocks, as well as the killer whale ecotypes. However, from these very limited data, it has been observed that the fatty acid profiles of outer blubber layers (thought to contain a higher proportion of endogenous biosynthesised fatty acids, perhaps under genetic control) were nearly as effective as the inner blubber layers (believed to best reflect exogenous diet composition) in resolving white whale stocks, as well as killer whale ecotypes. This preliminary observation suggests that odontocete blubber fatty acid profiles may be subject to both dietary and genetic control. Many additional samples from white whales of different populations and killer whales with identified ecotypes are needed to confirm this hypothesis.

Contaminant concentrations

The adult female white whales had lower concentrations of ΣPCBs and ΣDDTs than were found in the adult male (Table 3), in agreement with previous studies showing maternal transfer of contaminant burdens to offspring during gestation and lactation (Muir *et al*., 1992; Aguilar and Borrell, 1994; Norstrom and Muir, 1994; Ridgway and Reddy, 1995; Krahn *et al*., 1997; 1999; Aguilar *et al*., 1999). Furthermore, OC levels in necropsied Cook Inlet whales (Table 3) were in the same range as those reported previously for animals of the same sex in the Cook Inlet population (Krahn *et al*., 1999).

The ΣPCBs and ΣDDTs found in the female transient killer whale CA189 (Table 4) were higher than any reported previously for either males or females from that ecotype (Ross *et al*., 2000; Ylitalo *et al*., 2001). Transient ATx also had higher levels of ΣPCBs and ΣDDTs than were found in the resident L60, but lower than those found in transient CA189 (Table 4). The high contaminant concentrations found in the transient killer whales compared to those found in the resident animal can be explained by the diets of the two ecotypes, i.e. transient killer whales feed largely on marine mammals and resident animals are primarily piscivores (Baird, 1994). Thus, the transients feed on prey that contain higher contaminant levels as a result of OC bioaccumulation (Muir *et al*., 1988; Kucklick *et al*., 1994; Fisk *et al*., 2001). These results agree with previous studies in Alaska (Ylitalo *et al*., 2001) and in Canadian waters (Ross *et al*., 2000).

ΣPCBs and ΣDDTs in blubber were inconsistently distributed in the white whales – sometimes the outer layer had the highest concentrations, similar to results reported by Aguilar and Borrell (1991), and other times (e.g. the Bristol Bay juvenile male) the inner layer had the highest concentrations (Table 3). Similarly, both ecotypes of killer whales showed an inconsistent OC distribution by depth, with more variation when contaminant concentrations were expressed on a lipid weight basis. These variations in contaminant concentrations within the blubber layer of both species point out the need to have a full-thickness blubber sample, as suggested by Aguilar and Borrell (1991), to accurately represent contaminant concentrations in blubber.

White whales sampled via trocar contained much lower wet weight concentrations of ΣPCBs and ΣDDTs than reported for the necropsied female (Table 3) or previously for subsistence white whales (Krahn *et al*., 1999). However, because these trocar samples also had very low percent lipid, contaminant concentrations expressed as lipid weight increased up to 20-fold, resulting in lipid normalised concentrations of OCs that were in the same ranges as those reported previously (Krahn *et al*., 1999). Thus, OCs in samples collected by trocar should be lipid adjusted to compensate for lipid loss during sampling.

Similar to the white whale trocar samples, samples collected by dart from killer whale L60 contained ΣPCBs and ΣDDTs (wet weight) that were substantially lower than those in necropsied samples from the equivalent depth and position. When these OCs were lipid adjusted, the resulting biopsy concentrations had a high bias relative to their equivalent necropsy samples, thus over-compensating for the lipid loss during sampling. Regardless, lipid-adjusted ΣPCBs and ΣDDTs in biopsies are a sufficiently good measure of these contaminants to allow comparison to OC levels in other marine mammals or to threshold levels for contaminant-related health effects (Nilsson and Huntingdon, 2002).

Additional work on dart and trocar design, as well as on sampling techniques, is warranted to improve their suitability for obtaining more representative OC contaminant data, particularly for wet weight concentrations. For example, researchers report using darts that are larger in diameter (6.4mm O.D.) (Barrett-Lennard, 2000) or longer (30mm) (Matkin, pers. comm.) than the one used in this study.

Contaminant profiles

PCA analysis of OC contaminants in white whale blubber collected by necropsy have been used to distinguish among stocks, both in Alaska (Krahn *et al*., 1999) and Canada (Muir *et al*., 1996). In this study, OC profiles in white whale blubber (necropsy or trocar) indicated that the intra-animal variation with depth was small relative to the inter-animal differences, such that each individual animal can be readily distinguished from the others (Fig. 5A). Furthermore, OC patterns for the single whale from Bristol Bay differed from those of the Cook Inlet whales (Fig. 5A). However, additional samples from each area will be needed to determine whether these stocks can be distinguished by contaminant patterns alone. Among the Cook Inlet whales, the OC patterns from three females were grouped, whereas the sample from the only male was an outlier. This was not surprising, because white whales have previously demonstrated resolution of OC profiles by sex (Krahn *et al*., 1999).

As found for white whales, the intra-animal variation in OC profiles with depth or body position for the killer whales was small relative to the inter-animal differences (Fig. 5B). Thus, the OC patterns for the resident L60 were different from those of the transients, as would be expected due to their different trophic positions and diets (Baird, 1994). However, because only three animals were sampled, it is difficult to predict whether the resident and transient ecotypes could routinely be distinguished using PCA contaminant profiles.

CONCLUSIONS

This study showed that the degree of stratification varied both by species and parameter measured, so biopsy techniques that sample only an outer blubber layer must be interpreted with caution and in conjunction with results from species-specific blubber depth profiling. However, when carefully interpreted, results from chemical analyses of biopsy blubber samples can provide valuable information for many applications. For example, lipid classes determined in biopsy samples of white and killer whales were similar to those obtained for equivalent-depth samples obtained by necropsy. In addition, lipid-adjusted contaminant concentrations measured in dart or trocar samples were representative of those obtained by necropsy of white and killer whales. Therefore, following lipid normalisation of OCs, biopsy techniques can be used to determine whether these species are highly contaminated and thus at risk for contaminant-related health effects. In contrast, fatty acid profiles from outer blubber layers of these cetacean species were largely different from those in the metabolically active inner layer and are therefore unlikely to be useful in attempting to make correlations with the fatty acid profiles of potential prey.

In spite of the limitations of biopsy sampling, a small biopsy sample from a healthy cetacean may provide better information than a larger sample collected via necropsy from an ill or emaciated animal. In the future, improved design of biopsy darts or trocars could prevent lipid loss during sampling and also increase the size of each sample, allowing increased comparability of biopsy results to those obtained from necropsy. Finally, additional biomarkers and analytical methods should be developed specifically for biopsy samples, so each small sample can provide a large array of data about the animal's life history, body condition and health.

ACKNOWLEDGEMENTS

White whale samples were provided by subsistence hunters from Bristol Bay and Cook Inlet, Alaska. The 2001 Cook Inlet white whale tagging crew collected the trocar necropsy samples. Brent Norberg, Robyn Angliss and other members of the Northwest Regional Stranding Network, Marine Mammal Health and Stranding Response Program, sampled killer whales CA189 and L60. Marilyn Dahlheim, Stephanie Norman and Brad Hanson (National Marine Mammal Laboratory, Alaska Fisheries Science Center), Debbie Duffield (Northwest Regional Stranding Network, Portland State University Vertebrate Biology Museum), Pete Schroeder (Marine Mammal Research Associates), Dave Huff (Vancouver Aquarium), Stephen Raverty (Ministry of Agriculture, Food and Fisheries), Brad Smith (Alaska Regional Office, NOAA Fisheries) and Kathy Burek (Alaska Veterinary Pathology Services), as well as personnel from the Olympic Coast National Marine Sanctuary, the Whale Museum and the Washington Department of Fish and Wildlife, were also involved in the necropsy of the killer whales. We value the technical assistance of Don Brown, Daryle Boyd, Richard Boyer, Ron Pearce, Jennie Bolton and Karen Tilbury in sample and data analysis. We thank two reviewers, Donald Brown and David Baldwin, for their helpful comments. We are grateful for the support of Teri Rowles and for funding, in part, from the Marine Mammal Health and Stranding Response Program of NOAA Fisheries.

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J. CETACEAN RES. MANAGE. 6(2):191–198, 2004

The estimation of the detection function and *g*(0) for short-beaked common dolphins (*Delphinus delphis*), using double-platform data collected during the NASS-95 Faroese survey

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ABSTRACT

This paper examines the data for common dolphins collected during a general double-platform line transect cetacean survey carried out in waters around the Faroe Islands in 1995 (from southeastern Iceland to western Ireland) in order to determine the extent to which a correction factor can be estimated to account for animals missed on the trackline and for responsive movement towards the vessel. A major assumption of conventional distance-based methods is that all objects at zero distance from the line are detected (i.e. $g(0)=1$). If this assumption is violated the estimated density and hence abundance will be negatively biased. It also assumes that animals do not respond to the survey vessel before they are detected by the observers. If the animals are attracted to the vessel, for example, this will result in a positively biassed estimate. The $g(0)$ estimate was obtained using the method of Borchers *et al.* (1998). Visual inspection of the data suggested that the dolphins were attracted to the vessel and this was accounted for following the Buckland and Turnock (1992) approach. Coefficients of variation (CVs) and confidence intervals (CIs) were estimated using a non-parametric bootstrap procedure. During the survey, almost 1,700 n.miles were sailed on primary research effort. There were 153 common dolphin sightings including 52 duplicates. The chosen model for the detection function incorporated perpendicular distance, group size and Beaufort sea state. The resulting estimate of $g(0)$ was 0.7961 (CV=0.14). Density estimates obtained under an assumption of no responsive movement are almost six times higher than when it is taken into account, highlighting the importance of collecting appropriate data to allow analysis of this potential problem in cetacean surveys.

KEYWORDS: ABUNDANCE ESTIMATE; *g*(0); SURVEY-VESSEL; COMMON DOLPHIN; ATLANTIC OCEAN; EUROPE

INTRODUCTION

The short-beaked common dolphin (*Delphinus delphis*, common dolphin hereafter) is widespread in the northeastern Atlantic. Although typically found in oceanic and shelf-edge waters, it can also be seen in neritic waters (e.g. Forcada *et al.*, 1990; Carlisle *et al.*, 2001; Harwood and Wilson, 2001; Hammond *et al.*, 2002; Lopez, 2003; Silva and Sequeira, 2003). In recent years, concern has been expressed over its conservation status in these waters, largely due to large bycatches of the species in certain fisheries (e.g. Goujon *et al.*, 1993; 1994; Tregenza and Collet, 1998; Morizur *et al.*, 1999; Lopez *et al.*, 2003; Silva and Sequeira, 2003). However, quantitative knowledge of the abundance and stock structure of the species in this area is sparse and this, combined with a lack of reliable estimates of bycatch levels and population dynamics, make a good evaluation of conservation status problematic (e.g. see Hall and Donovan, 2002).

Of primary importance in understanding the status of a population is knowledge of its abundance. The most commonly used method for estimating abundance of cetaceans is distance-based line-transect sampling, in which the visual observer(s) travels along a pre-determined trackline recording ‘sightings’ (individuals or clusters of individuals) and estimating the perpendicular distances to the trackline. These data (together with covariates that may be affecting the detection of the targets), can be used to estimate the effective strip width of the survey and ultimately density and abundance estimates (Buckland *et al.*, 2001).

For reliable estimates to be obtained, a number of assumptions must either be met or violations corrected for. One major assumption is that all animals on the trackline are detected, commonly expressed as $g(0)=1$[1]. In practice, this is unlikely to be fully met for cetaceans, as for example, it is probable that some animals will be missed because they are submerged. If this assumption is indeed violated, and no correction is made, the estimated density and abundance will be negatively biased to some degree (Buckland *et al.*, 2001; Hammond, 2001).

A number of methods to attempt to estimate $g(0)$ have been developed over the last two decades. These generally involve double-platform surveys where two visually and acoustically independent teams of observers (usually located one above the other on the same vessel) survey the same area (e.g. Barlow, 1988; Butterworth and Borchers, 1988; Buckland *et al.*, 1993). Analyses combine distance sampling and mark-recapture methodology (Borchers *et al.*, 1998; 2002). The process can be seen as an experiment in which each sighting corresponds to a trial with four possible outcomes: detection by platform 1, detection by platform 2, detection by both platforms (a duplicate sighting) or detection by neither of the platforms. A set of covariates, one of which would typically be perpendicular distance of the sighting to the transect, is associated with each trial. The probability that a group is detected by a platform is modelled as a logistic function of the detection covariates. Each trial represents a capture event, and duplicate sightings represent ‘recaptures’. The proportion of duplicate sightings is then used to estimate $g(0)$ (Borchers *et al.*, 1998; 2002; Buckland *et al.*, 2001).

In recent years, more robust methods have been developed which incorporate corrections for responsive movement and for groups missed on the transect line

[1] $g(y)$ is the probability that an object at distance y from the line is detected.

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(Buckland and Turnock, 1992; Borchers *et al.*, 1998). In these, one of the independent observation platforms searches further ahead of the vessel than the other (e.g. using high-powered binoculars), ideally detecting the animals before they respond to the approaching vessel. The observers then track the sightings until they are detected by the other (primary) platform or have passed abeam.

A further assumption of line-transect methods is that animals do not respond to the survey vessel before they are detected by the observer; again, if violated and not corrected for, this will result in either an overestimate (if animals are attracted to the vessel) or an underestimate (if animals move away from the vessel). Different approaches have been used to account for responsive movement (e.g. Palka and Hammond, 2001; Mullin and Fulling, 2003). Common dolphins are known to be attracted to vessels, although the extent of this behaviour is unknown.

This paper examines the data from the first double-platform survey with sufficient duplicate sightings of common dolphins to allow an estimation of *g*(0). The data (Desportes *et al.*, 1995; 1996) were obtained by the Faroese vessel that took part in the third multinational NASS (North Atlantic Sighting Surveys) survey held in summer 1995 and co-ordinated by the North Atlantic Marine Mammal Commission (NAMMCO, 1997). Earlier NASS surveys took place in 1987 (Gunnlaugsson and Sigurjónsson, 1990) and 1989 (Sigurjónsson *et al.*, 1991). The present analysis estimates *g*(0) for common dolphins for the first time incorporating a correction for both animals missed on the trackline and responsive movement. Resultant abundance estimates and a discussion of the distribution of common dolphins as revealed by the full series of NASS surveys is given in Cañadas *et al.* (In press).

METHODS

Survey design and data collection

The primary target species of the Faroese vessel in 1995 was the long-finned pilot whale (*Globicephala melas*) and this was reflected in the survey design (in terms of survey area and methodology). However, data were collected on all species encountered.

The survey area for the Faroese vessel comprised the area between southeastern Iceland and western Ireland (see Fig. 1). The area was divided into two blocks, an Eastern block (between 5^{0}W-18^{0}W and 52^{0}N-62^{0}N) and a Western block, added to cover an area extended to the west, (between 18^{0}W-28^{0}W and 52^{0}N-57^{0}30'N). The Eastern block (Block E hereafter) had an area of 232,858 n.miles^{2} (798,708km^{2}), and the Western block (Block W hereafter) an area of 108,325 n.miles^{2} (371,557km^{2}). The total area was surveyed between 8 July and 6 August 1995.

Given the limited amount of vessel time available and the unpredictability of the weather, two cruise tracks were planned: primary and secondary (solid and dashed lines respectively, Fig. 1). The primary cruise track (1,841 n.miles) was designed to fulfil the necessary statistical requirements for line transect surveys and be expected to result in a reliable estimate. Effort was allocated to each block depending on their areas and the encounter rates observed in 1989 (Sigurjónsson *et al.*, 1991). The secondary cruise tracks were planned to enhance coverage if time and weather permitted, once the primary track was covered.

The research vessel was a 36m modified long-liner, *Miðvingur*, equipped with two observation platforms. The cruising speed was about 9.5 knots.

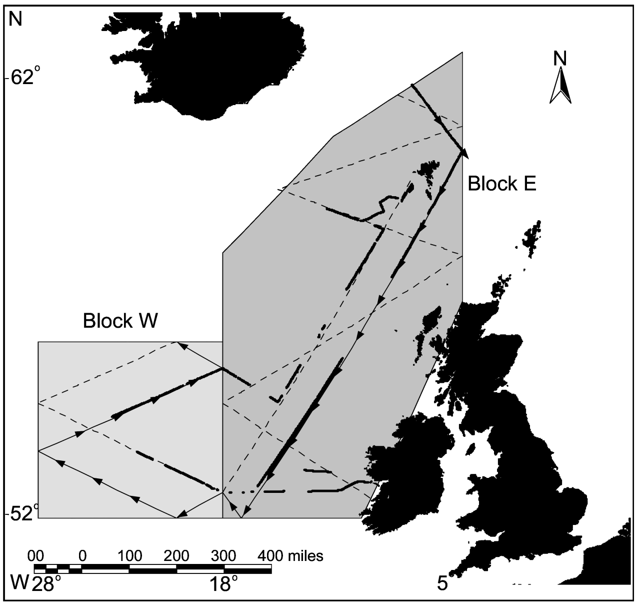

Fig. 1. Survey area showing blocks W and E, planned cruise tracks (solid thin line with arrows = primary cruise track; dashed line = secondary cruise track) and tracks realised on effort (thick solid line).

The double-platform method used in this survey (hereafter BT mode), was based on that developed for the 1994 SCANS[2] survey (Hammond *et al.*, 1995; 2002) following Buckland and Turnock (1992); only one-way independence between the platforms is required.

The primary platform (PP) was situated on the forward mast with an eye height of 11.5m. It was visually and acoustically independent from the tracking platform. The PP housed two observers searching with naked eyes (binoculars were only used for species identification), concentrating on the surface within the 1,000m of the vessel and 90° either side of the trackline. Distances to sightings were estimated by eye and angles were measured with mounted angleboards.

The tracking platform (TP) was situated above the navigation bridge, with an eye height of 9.35m. Two observers and one duplicate identifier (DI) were present. The TP observers used 7 × 50 reticule binoculars to search an area ahead of the primary searching area of the PP observers (>1,000m). One TP observer concentrated on a band 60° on either side of the trackline whilst the other searched a wider band 90° either side of the trackline. It was hoped that this search area was sufficiently wide and far ahead of the vessel to ensure that animals were detected prior to any responsive movement to the ship. Once sighted by the TP, animals were tracked until either being detected by the primary platform or passing abeam of the vessel.

The DI received information from both the TP observers and the PP observers (by telephone) as soon as a sighting was made; it was the DI's responsibility to determine if duplicate sightings were made and to record effort data and sighting conditions onto a computer in real time. GPS positions were recorded automatically every 30s. Data on effort and sighting conditions were recorded every 15 minutes or whenever changes occurred (including observers on watch, sea state (Beaufort), swell height and angle, glare width and strength, horizontal and vertical angle of the sun, wind direction and weather type). The following data were

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[2] Small Cetacean Abundance in the North Sea.

recorded for each sighting or re-sighting: time, platform, estimated distance, angle, observer, cue, behaviour, aspect, species, group size, calves, duplicate class (definite, likely, probable) and comments.

A total of 10 experienced observers rotated in two hours shifts (two hours on duty and two hours off). The observers remained assigned to the same platform during most of the cruise. Research was not conducted if visibility was less than 1,000m, if it was raining or if sea state exceeded Beaufort 4.

Data analysis

Organisation of the data

Several legs (transects) were defined within each block: two for block W and 10 for block E, and effort was calculated for each leg. In addition, each leg was divided into segments of approximately 20 n.miles each (except for 1 leg in block E which contained one single segment) for bootstrapping purposes (non-parametric bootstrap). Sections of transect were considered different segments when there was more than one hour off effort between them (e.g. due to bad weather conditions or night) even if they had a length of less than 20 n.miles. A total of 106 segments were thus defined, of which 22 were in block W.

Estimation methods

The estimation of the detection function and $g(0)$ followed the methods of Borchers *et al.* (1998), implemented in S-Plus. The estimation functions and associated documentation are available on request (email: *dlb@mcs.st-and.ac.uk*). The essentials of the method (described in detail in Borchers *et al.*, 1998) are as follows:

(1) Only the PP detection function is estimated.
(2) TP sightings provide binary trials for estimation of the PP detection function, in which detection by the PP constitutes a 'success'. Binary regression on these data, using generalized linear model (GLM) methods and a 'logit' link function provides estimates of the PP detection function (details below).
(3) Abundance of animals within the searched strip (N_w) is estimated using only PP sightings in a Horvitz-Thompson-like estimator in which the detection probability of the *i*th sighting is estimated by evaluating the logistic detection function estimated in (2) above, using the explanatory variables associated with the *i*th sighting (details below).
(4) Density is estimated by dividing the estimate of N_w by the area of the searched strips.

The form of the detection function, with r explanatory variables in addition to perpendicular distance (x), is:

$$g(x,\underline{z}) = \frac{\exp[\beta_0 + \beta_x x + \sum_{k=1}^{r} \beta_k \underline{z}_k]}{1 + \exp[\beta_0 + \beta_x x + \sum_{k=1}^{r} \beta_k \underline{z}_k]} \qquad (1)$$

where: g(x,z) is the detection probability as a function of the available explanatory variables (x = perpendicular distance and $z_1,...,\underline{z}_k = k$ other explanatory variables), β_0 is an intercept parameter, β_x is a parameter relating to the effect of distance and the β_ks are parameters relating to the effects of other explanatory variables. All these parameters are estimated.

The explanatory variables considered were perpendicular distance and any of the variables (animal or environment related) recorded during the sightings: group size, cue, behaviour, aspect, sea state, glare width and intensity, swell height and angle, sun angle horizontal and vertical and wind direction. Model selection was done manually using the Akaike Information Criterion (AIC). Following Borchers *et al.* (1998), $g(0)$ is estimated as:

$$\hat{g}(0) = \hat{E}_z[g(0,\underline{z})] = \sum_{j=1}^{n} \frac{\hat{g}(0,\underline{z}_j)}{\hat{g}(\underline{z}_j)\hat{N}_w} \qquad (2)$$

where:

$$\hat{g}(\underline{z}_j) = \int_0^w \hat{g}(x,\underline{z}_j)\frac{1}{w}\,dx \qquad (3)$$

Coefficients of variation (CVs) for $g(0)$ were estimated using a non-parametric bootstrap procedure (1000 iterations), in which segments were the sampling units. Resampling was performed separately within each block. Confidence intervals (CIs) were estimated using a simple percentile method.

Visual inspection of the data suggested substantial movement of the animals towards the ship between the detection from the tracking and the primary platform (probably due to attractive responsive movement): see Figs 2, 3 and 4. These plots should not be over-interpreted; more duplicate detections of animals moving in toward the trackline after being seen by the TP would be expected, even if there is random, non-responsive movement, because animals that move in are more likely to be seen by PP. However, estimation of the expected fraction of duplicate detections that show movement towards the trackline is not simple and the apparent movement in the plots is enough to suggest that it would be wise to use a method which accommodates responsive movement. If the TP detects animals before they respond, the BT method is able to do this. The version of this method which is described in detail in Borchers *et al.* (1998) was implemented in the set of Splus functions mentioned above.

Abundance within the searched strip of half-width w about the trackline was estimated by :

$$\hat{N}_w = \sum_{j=1}^{n} \frac{s_j}{\hat{g}(\underline{z}_j)} \qquad (4)$$

where s_j is the group size of the j^{th} detected school and the sum is over all PP detections. The density of dolphins in the survey area, D, is estimated as follows:

$$\hat{D} = \frac{\hat{N}_w}{2Lw} \qquad (5)$$

where L is the total length of all lines and w is the chosen truncation distance.

RESULTS

Data collection

Bad weather conditions meant that only 43% of the available research time could be spent on effort. This prevented even completion of the primary cruise track and a number of modifications to the tracklines had to be made during the survey itself.

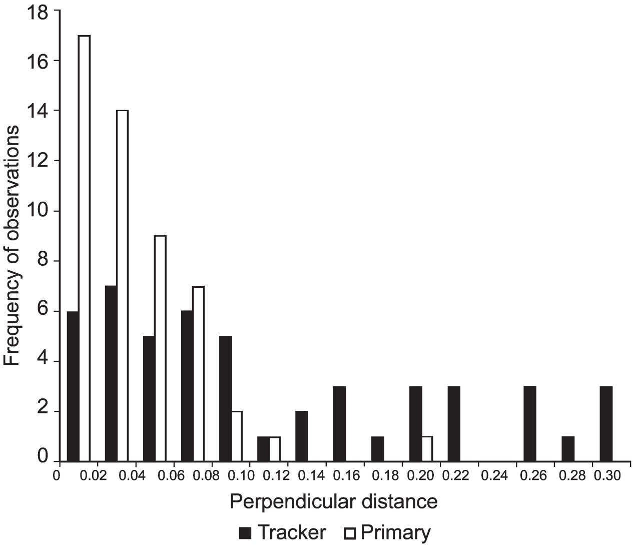

Fig. 2. Frequency of observations at different perpendicular distances (in nautical miles) for duplicate sightings, both from the tracker and primary platforms.

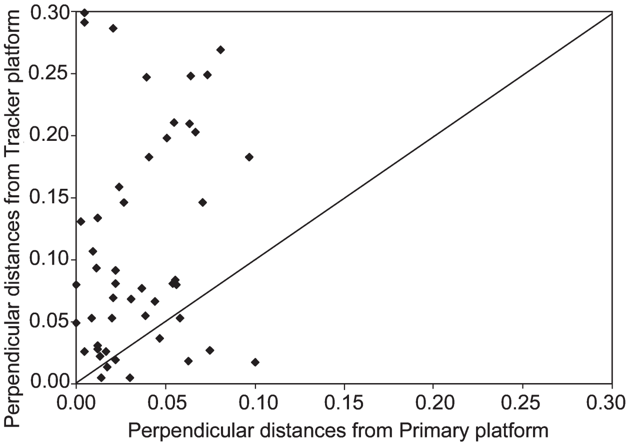

Fig. 3. Scatterplot of perpendicular distances measured both from tracker and primary platforms. Each dot represents a duplicate sighting.

Shelter from forecast extended bad weather was sought in the city of Galway on the west coast of Ireland. The tracks to and from Galway, conducted in searching effort, were added to the original cruise track. In contrast, some additional time was available at the end of the survey and thus some searching effort was conducted on the western edge of the Faeroe Bank following part of the secondary trackline. The final tracks performed under effort are shown in Fig. 1 (solid thick line). However, these changes to the original design give rise to some concern over the representativeness of the survey, especially in block E (see below).

In total, 1,672.8 n.miles were sailed on effort, of which 1,321.8 n.miles were in block E and 351 n.miles in block W. About 64% of the effort was in Beaufort 3 or 4 and only 4% was in Beaufort 0 or 1. Of the 471 cetacean sightings recorded, 153 (including 52 duplicates) were of common dolphins (i.e. *n*=101). Sightings by block and platform are given in Table 1 and the position of the sightings is given in Fig. 5.

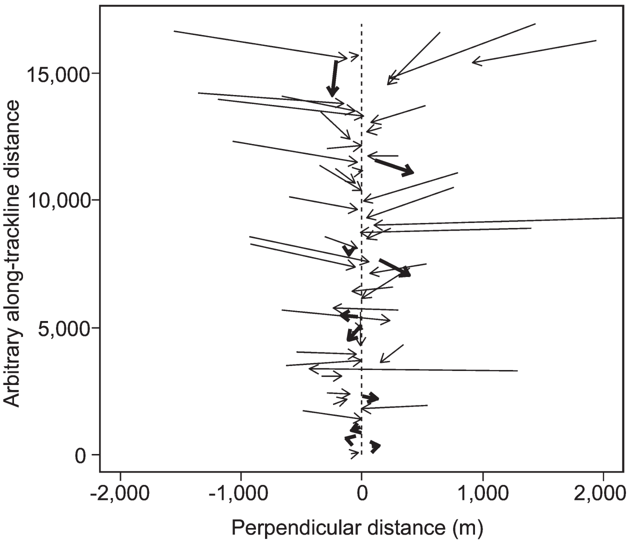

Fig. 4. Perpendicular distance movement of duplicates. Arrows represent the movement of duplicates from the time they were detected by the tracker until the time they were detected by the primary observers. All positions are relative to the survey vessel. Each detection has been shifted by 300m along the trackline relative to the previous detection in order to separate the arrows. The single arrow extending beyond the right edge of the box originated at 4,000m. All arrows corresponding to movement away from the trackline appear in bold.

Table 1

Numbers of schools of common dolphins detected on effort from primary (PP) and tracker (TP) platforms, together with the number of duplicates (D), for each block and in total.

Species	PP	TP	D
Block W	49	46	29
Block E	27	31	23
Total	76	77	52

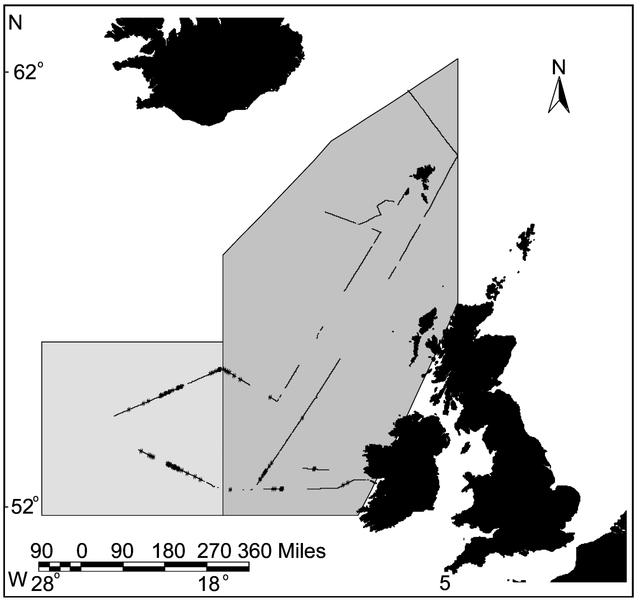

Fig. 5. Sightings of common dolphins on effort.

Data analysis

Estimation of g(0)

For the estimation of $g(0)$, data from both blocks were pooled to increase sample size, since no differences in detectability were expected between them (same vessel, observers and similar environmental conditions). A truncation distance of 0.3 n.miles was chosen given (1) the distribution of the data, with most sightings very close to the trackline and (2) that for estimating $g(0)$, sightings of primary interest are those relatively close to the trackline. With this truncation distance, only 2.5 % of the data was discarded.

Fig. 6 shows the frequency distributions of the perpendicular distances of primary detections (detections from the PP), trials (detections from the TP) and duplicates, together with the proportion of duplicates within the truncation distance. Within this distance, no trend in the proportion of duplicates is apparent (i.e. the proportion of duplicates was not influenced by distance from the trackline; bottom right plot of Fig. 6). The fact that the PP perpendicular distance distribution of detections falls off and the duplicate proportion does not, may reflect either: (a) unmodelled heterogeneity which increases as distance increases (in which case the duplicate detection function is a biased estimate of the detection function – it should fall off more); (b) that the PP perpendicular distance distribution is a biased estimate of the shape of the PP detection function, because animals have moved towards the trackline by the time they are detected, making the distribution too peaked near distance zero; or (c) some combination; in this application (b) appears the most likely (see below).

Several combinations of the potential explanatory variables listed in ‘Methods’ were considered for modelling the detection function. The two models with the lowest AICs (differing by only 0.008) were a model using perpendicular distance and group size (AIC = 62.925; and see Fig. 7) and a model with the same two variables plus sea state (AIC = 62.917; and see Fig. 8). Although the first is more parsimonious, the second seems more appropriate given that external information shows that sea state is very likely to be affecting detectability, even if in this case sample size is inadequate to detect this. In addition, this model gives a more plausible detection function shape. The coefficients of the final model and their standard error and *t* value are shown in Table 2.

Table 2

Coefficients of the variables included in the chosen model of the detection function, with their standard error (SE), *t* values and approximate *p*-values.

	Coefficients	CE	*t* value	*p*-value
Intercept	1.895	1.348	1.41	0.16
Perpendicular distance	-1.063	4.592	-0.231	0.82
Group size	0.121	0.077	1.56	0.12
Beaufort	-0.453	0.345	-1.31	0.19

Group size was selected by AIC as an important explanatory variable for the detection function. In addition the detection function parameter associated with group size has a positive sign (Table 2). This implies that the effect of increasing group size in the model is to increase detection probability, and that detection probability at any given distance (and at distance zero in particular) is greater for large groups than small groups. The fitted model implies that larger groups have greater $g(0)$ values than smaller groups, as one might expect.

The resulting overall estimate of $g(0)$ was 0.796 for the whole area. Non-parametric bootstrapping with 1,000 resamples gave a CV of 0.13 (CI: lower 95%=0.577, upper 95%=0.961). Results by block are given in Table 3.

Estimation of density

When applying the Horwitz-Thompson estimator to the fitted values obtained from the logistic regression (i.e. incorporating responsive movement), an estimated density of 2.52 animals n.mile^{-2} (0.74 animals km^{-2}) for block W was obtained. The mean value obtained by bootstrapping with 1000 resamples was similar − 2.58 with a CV of 0.13. Results for the whole area and for each block are shown in Table 3. Although results can be obtained for both blocks, the actual tracks carried out in block E (see Fig. 1) most of which lie in the middle of the stratum and roughly parallel to depth contours, combined with the small sample size in that area give rise to concern as to its reliability. In effect, given the coverage, the density estimate obtained, even for block W, applies to the east of this block. This is considered further in Cañadas *et al.* (In press).

To compare the density estimates incorporating and ignoring the effects of responsive movement, an estimate was also obtained using the DISTANCE program (Thomas *et al.*, 2002) under the assumption that animals were uniformly distributed with respect to distance from the transect at the time they were detectable by the primary platform. Although the same covariates used in the BT method (group size and sea state) were considered when modelling the detection function, the best model fit to the data was a hazard-rate key function with hermite polynomial series expansion and no covariates other than perpendicular distance. The $g(0)$ estimate for the whole area given above was incorporated as a multiplier. Results are shown in Table 3. The detection function for the primary platform (with a right truncation distance of 0.07 n.miles, discarding 8% of the data) is shown in Fig. 9. The density estimate obtained, 14.74 animals n.miles^{-2}, was 5.9 times higher than that obtained using the BT method[3].

DISCUSSION

There have been relatively few double platform shipboard surveys in Europe. Perhaps the best example is the summer 1994 SCANS survey conducted in the North Sea (Hammond *et al.*, 2002). Estimates of $g(0)$ were obtained for the three most abundant species in the area: the harbour porpoise (*Phocoena phocoena*), minke whales (*Balaenoptera acutorostrata*) and whitebeaked dolphins (*Lagenorhyncus albirostris*), as well as for a fourth group: *Lagenorhyncus* sp. The small duplicate sample size for common dolphins (which were found almost exclusively in the Celtic Sea) precluded estimation of $g(0)$ for that species; the estimate of abundance presented assumed that $g(0)=1$.

The $g(0)$ estimate obtained here for common dolphins (0.80, CV=0.13) is relatively high compared to those obtained for other small cetacean species in the North Sea during SCANS (Hammond *et al.*, 1995): 0.31 (CV=0.15) for the harbour porpoise, 0.57 (CV=1.41) for white-beaked dolphins, 0.54 (CV=0.27) for the group *Lagenorhyncus* sp.

Common dolphins are usually sociable and conspicuous animals, with frequent surface and aerial behaviour. In addition, the mean school size in this study was 8.3,

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[3] This difference is larger than that reported in Buckland *et al.* (2004). This is due to an error in their analysis which was discovered after publication.

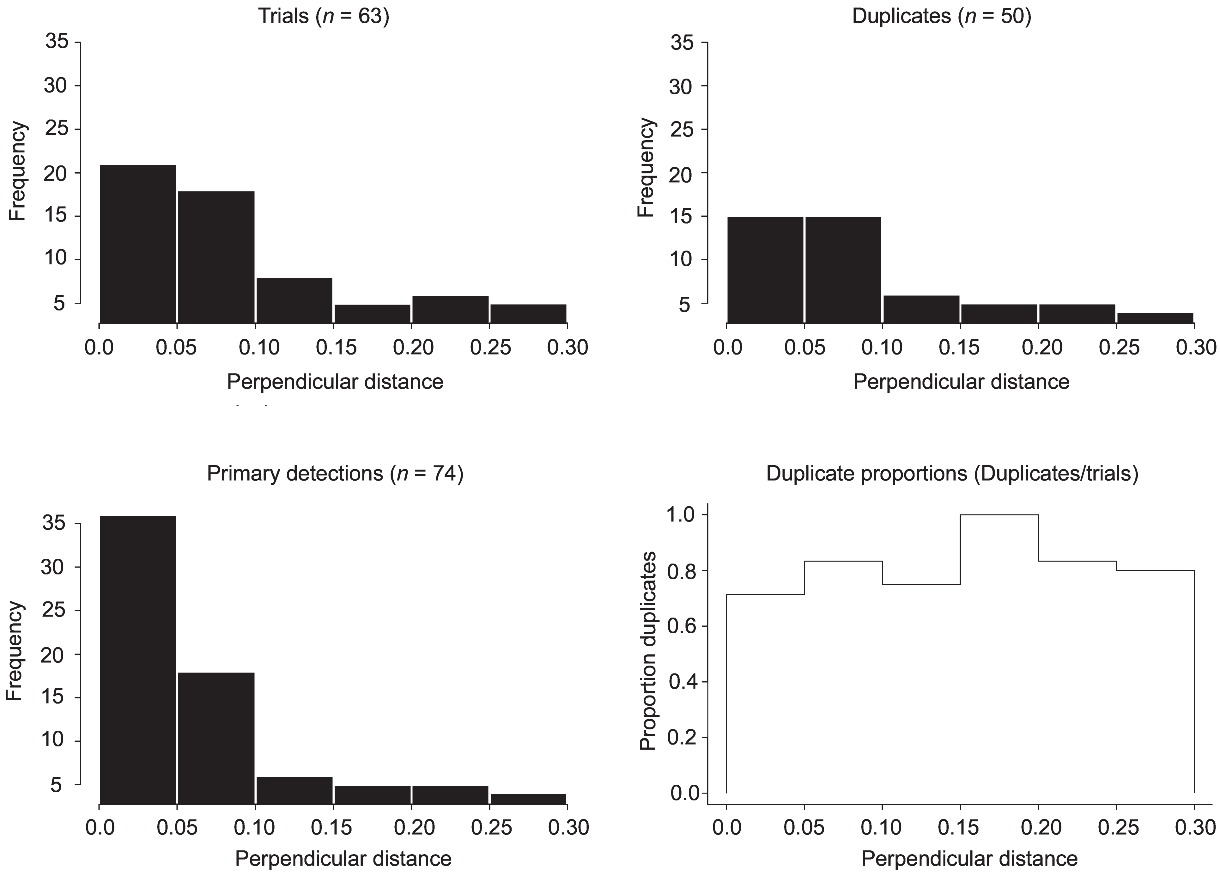

Fig. 6. Frequency distributions of the perpendicular distances of primary detections (detections from the primary platform), trials (detections from the tracker platform) and duplicates, and proportion of duplicates within truncation distance from the trackline.

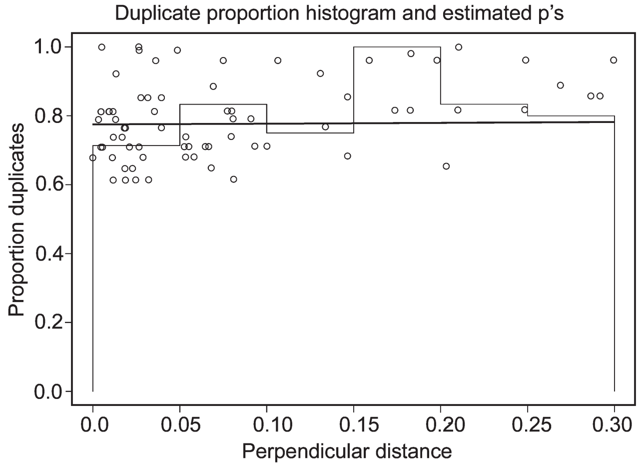

Fig. 7. Histogram of proportion of duplicates against perpendicular distance. The detection function obtained from including perpendicular distance and group size in the model is shown as a solid line. The dots represent the predicted detection probability for individual detections.

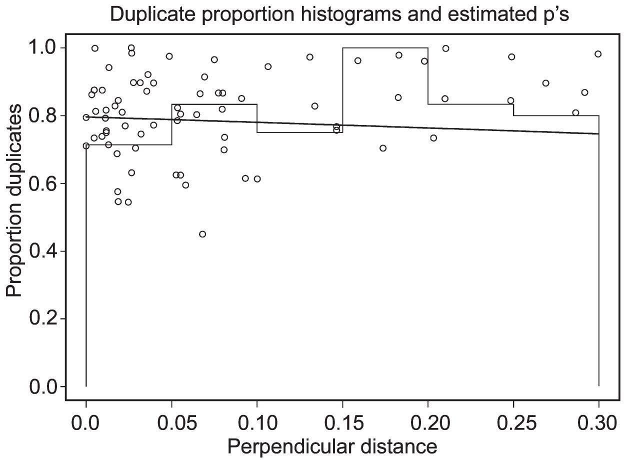

Fig. 8. Histogram of proportion of duplicates against perpendicular distance. The detection function obtained from including perpendicular distance, group size and Beaufort sea state in the model is shown as a solid line. The dots represent the predicted detection probability for individual detections.

considerably larger than for the species considered in the SCANS survey: 1.5 for harbour porpoise, 3.8 for white-beaked dolphins, and 4.3 for *Lagenorhyncus* sp. Taking this into account, it does not seem very surprising that the *g*(0) value for common dolphins in this paper is higher, even though the adverse weather conditions on this survey would tend to reduce *g*(0).

Estimates of *g*(0), of course, take into account other factors than the behaviour and school size of the target species. In particular they take into account characteristics of a specific survey such as the type and speed of the vessel, height of the platforms, individual observers, predominant environmental conditions (e.g. sea state and visibility) etc. This makes it problematic to consider using *g*(0) values across surveys. Despite this, the present results suggest that relatively little negative bias may occur if an assumption of *g*(0)=1 is made for common dolphins for surveys where *g*(0) cannot be estimated (such as SCANS).

By contrast, the present study has revealed that potential responsive movement of common dolphins to the vessel must be taken into account when estimating their abundance from vessel surveys. In this regard it should be noted that

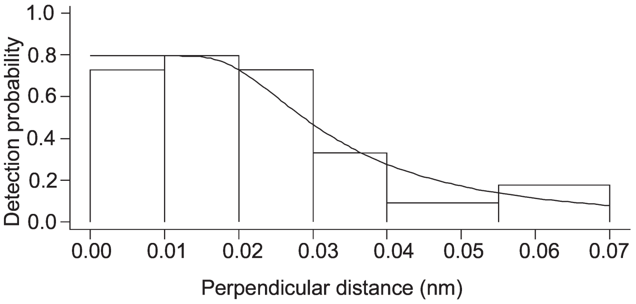

Fig. 9. Perpendicular distance distribution of detections by the primary platform. The line is the detection function fitted with DISTANCE software to data truncated at 0.07 n.miles. The histogram and fitted line have been scaled to give the line an intercept equal to the estimated $g(0)$. The estimated effective strip width was 0.038 n.miles.

Table 3

Estimates of $g(0)$, encounter rate (n/L), group size (E[s]), density of schools (Dschool) and animals (Dindiv) and abundance of schools (Nschool) and animals (Nindiv) for the whole area and stratified for blocks. Mean (Mean$_{bs}$) and coefficients of variation (CV$_{bs}$) after 1000 resampling bootstrap are given, together with the 95% confidence intervals (CI). Area and densities are given in n.miles^2, length and encounter rates are given in n.miles. Truncation distance was 0.3 n.miles. Estimates from DISTANCE for block W are also shown, calculated from PP data and with a truncation distance of 0.07 n.miles.

	n	Dschool	Dindiv	g(0)
Total area				
Estimate	74	0.124	1.028	0.796
Mean$_{bs}$	74	0.133	1.052	0.788
CV$_{bs}$	0.21	0.32	0.24	0.13
Lower 95%$_{bs}$	47	0.072	0.618	0.577
Upper 95%$_{bs}$	105	0.226	1.583	0.961
Block E				
Estimate	25	0.040	0.333	0.807
Mean$_{bs}$	25	0.042	0.34	0.799
CV$_{bs}$	0.36	0.51	0.43	0.14
Lower 95%$_{bs}$	10	0.017	0.109	0.556
Upper 95%$_{bs}$	44	0.078	0.661	0.985
Block W				
Estimate	49	0.304	2.522	0.791
Mean$_{bs}$	49	0.329	2.578	0.785
CV$_{bs}$	0.25	0.37	0.26	0.13
Lower 95%$_{bs}$	27	0.159	1.416	0.542
Upper 95%$_{bs}$	73	0.592	4.017	0.957
Distance (W)				
Estimate	45	2.145	14.737	0.796
CV		0.35	0.38	
Lower 95%		1.069	7.052	
Upper 95%		4.303	30.798	

there is no guarantee that even the 7x binoculars allow detection before responsive movement occurs, especially for small groups in rough sea states. It is thus not inconceivable that the effect of responsive movement is greater than calculated here. It is clear that if surveys aim to estimate the abundance of common dolphins, data should be collected in such a way that attempts to allow most sightings to be detected before responsive movement occurs and that allows responsive movement to be accommodated in analysis, should it occur.

It is beyond the scope of this paper to provide a detailed comparison of density estimates for common dolphins obtained from this study with estimates from other parts of the North Atlantic or to develop an abundance estimate; this is covered in Cañadas *et al.* (In press).

ACKNOWLEDGEMENTS

The primary funding for the survey was provided by the Government of the Faroe Islands and by the North Atlantic Marine Mammal Commission (NAMMCO). In addition, Føroya Sparikassi, Føroya Banki and Føroya Shell sponsored aspects of the study; Atlantic Airways provided the travel of the cruise leader. The EU project SCANS provided the sightings and effort data entry software used during the cruise. Various pieces of equipment were kindly lent by the Faroese Museum of Natural History, the Faroese Telephone Company, Danbiu APS (Copenhagen, Denmark), le Centre de Recherche sur les Mammifères Marins (La Rochelle, France), l'Institute Français de Recherche et d'Exploitation des Mers (IFREMER, Brest, France) and the Sea Mammal Research Unit (Cambridge, UK). Thanks are due to T. Johannesen, captain of the Miđvingur, and his crew for their co-operation in conducting the research, as well to all the observers onboard. Very special thanks are due to the Faroese Natural History Museum, and especially D. Bloch, for taking care of the survey logistics and financing, and for allowing the use of the data in the present study. Special thanks are due also to S. Buckland and S. Cumberworth for their advice and help in the design of the survey, S. Chalis for modifying the SCANS software, and L. Thomas and P.S. Hammond for their valuable comments and advice during data analysis. The comments of two anonymous reviewers helped considerably in improving the manuscript.

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