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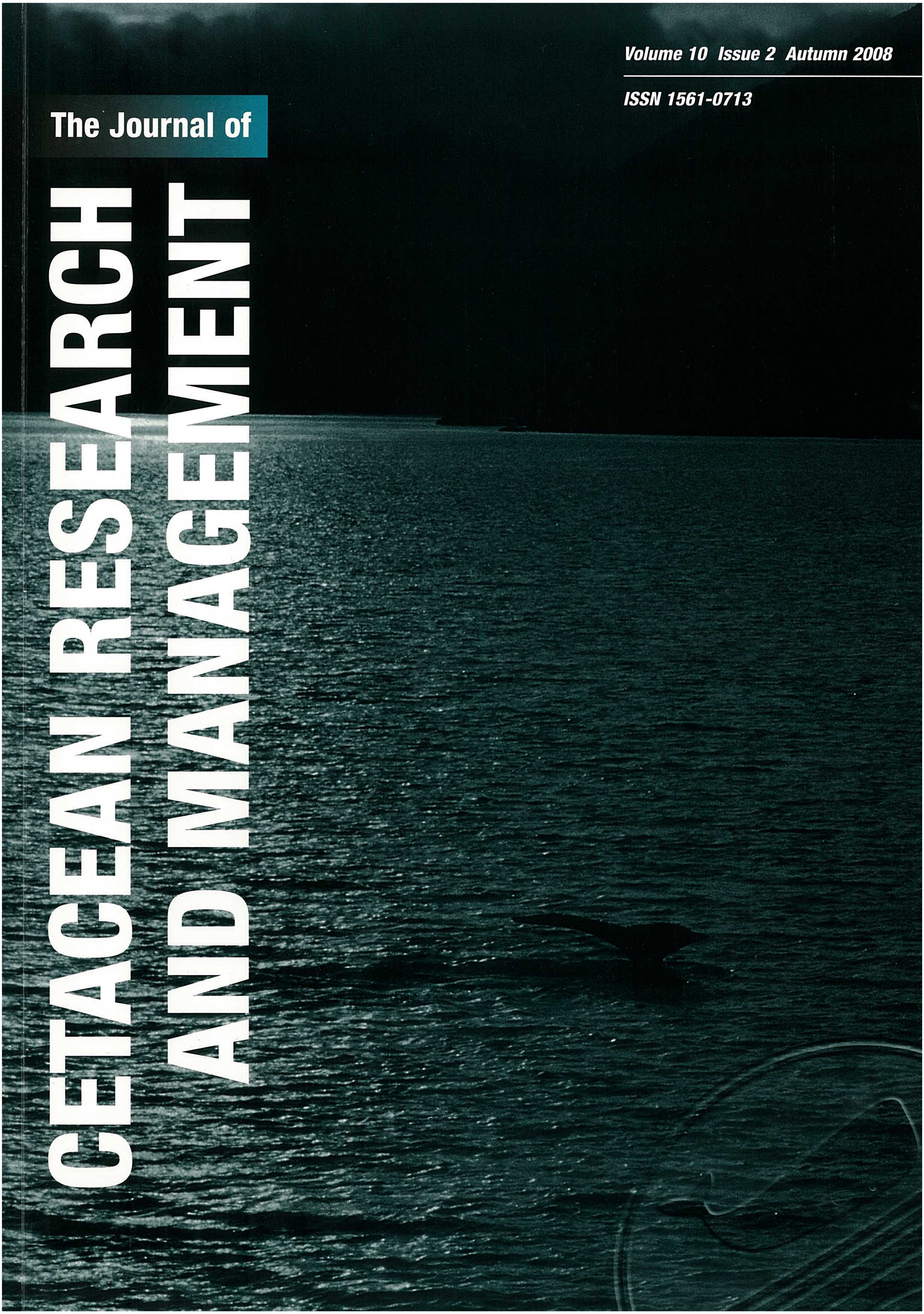

Contents

Editorial

This summary of the work of the Scientific Committee at the recent annual meeting follows the 2008 meeting of the International Whaling Commission held in Santiago, Chile. 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 2009 as *J. Cetacean Res. Manage.* 11 (Suppl.).

REVISED MANAGEMENT PROCEDURE

After the adoption of the moratorium on commercial whaling in 1982, the Committee spent over eight years developing the Revised Management Procedure (RMP) for baleen whales. In brief, the RMP is a generic management procedure designed to estimate safe catch limits for commercial whaling of baleen whales. This was adopted some time ago by the Commission, at the 1992 meeting. However, the Commission has stated that it will not set catch limits for commercial whaling for any stocks until it has agreed and adopted a complete Revised Management Scheme (RMS) which will include a number of non-scientific matters, including inspection and enforcement. The RMS has been the subject of a considerable amount of discussion within the Commission and this is ongoing in the context of a broader debate about the future of the Commission[1].

Process for revision of the *CLA*

The *CLA* (*Catch Limit Algorithm)* is used to determine safe removal limits under the RMP and was agreed in 1992. As a result of a request by Norway (IWC, 2006), the Committee reviewed the process for considering revisions to the *CLA* agreed in 1992 and clarified some issues. The result of the review was to:

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

This year, the Committee agreed to hold an intersessional Workshop on (2) with a view to making a decision on this at the 2009 Annual Meeting.

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. In 2005, the Committee developed requirements and guidelines for the *Implementation* process (IWC, 2005). Some final details had required further analytical work and this was completed in 2007 (IWC, 2008c).

North Pacific Bryde's whales

In 2007, the Committee had successfully completed the *Implementation* for western North Pacific Bryde's whales. This was the first *Implementation* undertaken using the new requirements and guidelines and it had provided for the option of the 'variant with research' (IWC, 2008b). The Committee received documentation on how such an option may be implemented at this year's meeting but further work is required. Abundance estimates were agreed this year, with a total estimate of around 20,500 whales (approx 95% CI 10,700-39,200).

North Atlantic fin whales

At the 2005 Annual Meeting, the Committee initiated the *pre-Implementation Assessment* of North Atlantic fin whales (IWC, 2006, p.7). To progress this work, a co-operative intersessional Workshop was held in March 2006 with the NAMMCO scientific committee on general scientific issues of common interest, particularly with respect to stock structure, abundance and catch history (IWC, 2007b). The results of that workshop were discussed and endorsed at the 2006 Annual Meeting and it was agreed that the *pre-Implementation Assessment* was complete (IWC, 2007c, pp.11-12). For practical reasons, it was agreed that the *Implementation* would begin after the 2007 Annual Meeting. The *Implementation* process takes a two year period, encompassing three annual meetings and two intersessional workshops. The first Intersessional Workshop took place successfully in spring 2008 (IWC, 2009) and the results were reviewed in Santiago. In addition to reviewing and approving the results of the 'conditioning' specified intersessionally, the Committee completed its work with respect to the following:

(1) final specification and weighting (with respect to plausibility) of the *Implementation Simulation Trials*;
(2) discussion of what data/research may reduce the number of hypotheses and possible time-frames for this research/data collection;

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[1] E.g. see *http://www.iwcoffice.org/commission/future.htm*

(3) updates/improvements to standard data sets (i.e. abundance, catches, bycatches) for use by the *CLA* in final trials and when evaluating the plausibility of hypotheses and hence assigning weights to trials (new data are not used when conditioning the trials);
(4) specification of operational features (geographical and temporal) and management variants;
(5) development of a timetable for the remaining work (including circulation of trial results and format); and
(6) initial discussion of the inputs for actual application of the *CLA* (catches, bycatches, estimates of abundance and projected future anthropogenic removals).

North Atlantic common minke whales

The Committee began an *Implementation Review* of North Atlantic common minke whales in Santiago – the last review occurred in 2003 (IWC, 2004a, pp.12-13). Progress was made and the review should be completed next year.

Bycatches of large whales and other sources of anthropogenic mortality such as ship strikes

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. This year the Scientific Committee addressed mortality due to bycatch in fishery operations, ship strikes, marine debris (e.g. risk from entanglement and ingestion) and noise.

The Scientific Committee reviewed progress towards estimating bycatch using: (1) fisheries data and observer programmes; and (2) genetic data from market sampling. The Scientific Committee has been collaborating with FAO on collation of relevant fisheries and bycatch data with the aim of identifying fisheries where further monitoring would be valuable. With respect to market sampling, while recognising the differing views of various member governments over this issue, the Committee reaffirmed its view that availability of data from DNA registers will improve estimates of total take from market surveys and its ability to review papers containing the results of market sampling. The Committee requested that these be made available through the Committee's Data Availability Agreement.

With respect to ship strikes, the results from studies of collisions between whales and vessels off the Canary Islands and New Zealand and papers on modelling collision risk were reviewed. Substantial progress with the global IWC database of ship strikes has been made. The database design was agreed by the Scientific Committee last year and has also been approved by ACCOBAMS for its work. Subsequently, a small group of scientists have been populating the database. To date, 763 records, mainly from published sources, have been entered. Consideration is now being given to the best way to continue the data collection process, including ongoing maintenance and quality control of the database and the development of a web-based data entry system via IWC's website. Mortality due to ship strikes is a concern not only with respect to setting commercial and aboriginal subsistence catch limits, but also in evaluating threats to the survival of endangered populations.

With respect to noise, the Scientific Committee agreed that there is a need for internationally co-ordinated research to address gaps in knowledge on sonar-related cetacean strandings including improving the ability to conduct necropsies as quickly as possible, standardising data collection on the animal's environment at the time of the death/stranding, and co-ordinating with military or other government agencies so that all factors related to the stranding are examined. The impacts of noise are also addressed under Environmental Concerns (see below).

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 (IWC, 1994). In other areas, however, little progress has been made and, as a result, a growing number of cetacean species (both large and small) face critical conservation problems as a result of fisheries bycatch. Rather than holding another large generic workshop, it was agreed that given the case- and area-specific nature of the problem, a series of broad-based regional workshops would be more effective, focusing on regions where bycatch problems have been given priority by the Scientific Committee and are not already being addressed.

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

DEVELOPMENT OF AN ABORIGINAL WHALING MANAGEMENT PROCEDURE

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

At the 2002 meeting, the Committee completed its work with respect to the Bering-Chukchi-Beaufort Seas stock of bowhead whales. It agreed a *Strike Limit Algorithm (SLA)* for bowhead whales and the scientific aspects of a Scheme;

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

The situation for the Greenlandic fisheries for fin and minke whales is more difficult but considerable progress has been made in the last two years and high priority is being accorded to this work. In the meantime, the Scientific Committee developed a safe method to provide interim advice on catch limits for these whales for a limited period (10 years).

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.

The catch limits presently in force are:

- Bering-Chukchi-Beaufort Seas stock of bowhead whales (taken by native peoples of the USA and the Russian Federation): A total of up to 280 bowhead whales can be landed in the period 2008-2012, with no more than 67 whales struck in any year (and up to 15 unused strikes may be carried over each year).
- Eastern North Pacific gray whales (taken by native peoples of the USA and the Russian Federation): A total catch of 620 whales is allowed for the years 2008-2012 with a maximum of 140 in any one year.
- Caribbean humpback whales (taken by St. Vincent and The Grenadines): For the seasons 2008-2012 the number of humpback whales to be taken by the Bequians of St. Vincent and the Grenadines shall not exceed 20.
- West Greenland fin whales: The number struck shall not exceed 19 in each year.
- West Greenland common minke whales: The number struck shall not exceed 200 in each year (and up to 15 unused strikes may be carried over each year).
- West Greenland bowhead whales: The number struck shall not exceed 2 per year (and up to 2 unused strikes may be carried over each year). The quota for each year shall only become operative when the Commission has received advice from the Scientific Committee that the strikes are unlikely to endanger the stock.
- East Greenland common minke whales: The number struck shall not exceed 12 in each year (and up to 3 unused strikes may be carried over each year).

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. New information on abundance, distribution, catches and ecology was presented. The population is believed to be close to carrying capacity. The Committee confirmed that the present catch limit was acceptable this year using the *Gray Whale SLA*. An *Implementation Review* will take place in 2009.

Bering-Chukchi-Beaufort Seas stock of bowhead whales

In addition to the work on the *Bowhead SLA*, the Committee has also been examining the status of the Bering-Chukchi-Beaufort Seas stock of bowhead whales. The most recent abundance estimate (for 2001) is 10,500 (95%CI 8,200-13,500) giving a rate of increase between 1978 and 2002 of 3.2% (95%CI 1.4%, 5.1%). After a thorough *Implementation Review* in 2007 the Committee agreed that the *Bowhead SLA* remains the most appropriate tool for providing management advice for this harvest (IWC, 2008a, p.18). In Santiago it was confirmed that the present catch limits will not harm the stock.

Minke and fin whales off West Greenland

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

In 2006, the Committee was pleased to receive and accept a new abundance estimate for the common minke whale (3,500, 95%CI 1,500-7,700) off West Greenland.

However, despite the considerable progress made in developing an assessment method based on the observed sex ratio in the catch, the Committee was not in a position to provide unequivocal advice on catch limits and recommended that the Commission exercise caution when setting catch limits, noting that the replacement yield was between around 170 and 230 whales if the lower bound of the abundance estimate is used. The Committee has also developed a workplan to finalise the development of an appropriate assessment method by 2009.

For the fin whale, the Committee accepted a new abundance estimate of 4,656 (CV 0.46; 95% CI 1,890-11,470). Using the method agreed for providing interim advice, it agreed that the current catch limit will not harm the stock.

Bowhead whales off West Greenland

The bowhead whales off West Greenland are probably part of a single eastern Arctic stock off Canada and West Greenland. It agreed that an abundance estimate of 6,344 (95%CI=3,119-12,906) for the single eastern Arctic bowhead stock is suitable for use in development of management advice for aboriginal harvest of bowheads off West Greenland. Using the agreed method for providing interim management advice, the Committee agreed that the current catch limit will not harm the stock. The question of stock structure will be reviewed again next year.

Humpback whales off St. Vincent and the Grenadines

The Committee has received positive confirmation that eastern Caribbean humpback whales are part of the West Indies breeding population (abundance in 1992/93 – 11,570, 95%CI 10,100-13,200) and agreed that the present catch limit set by the Commission will not harm the stock.

Humpback whales off West Greenland

Last year, the Committee had noted that the humpback whales found off West Greenland belong to a separate feeding aggregation whose members mix on the breeding grounds in the West Indies, with individuals from other similar feeding aggregations (IWC, 2008a, p.21). It therefore had agreed that the West Greenland feeding aggregation was the appropriate management unit to consider when formulating management advice.

HISTORIC ABUNDANCE ESTIMATION, GENETIC METHODS

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

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

STOCK IDENTITY

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

A specialist Workshop to examine the use of simulation testing to assess the performance of methods to identify population structure was held in January 2003 (IWC, 2004b) – known as TOSSM[2]. 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). Subsequently, progress has been made in the development and validation of a program to simulate realistic genetic datasets (IWC, 2007a) and the Committee has begun to receive papers that are beginning to test boundary setting algorithms in a management context. Work is continuing to develop this approach and it has now reached the point where it can be used to test more complex and realistic scenarios.

COMPREHENSIVE ASSESSMENT OF WHALE STOCKS

The 'Comprehensive Assessment' of whale stocks

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

Antarctic minke whales

The Committee has carried out annual surveys in the Antarctic (south of 60°S) since the late 1970s. The last agreed estimates for each of the six management Areas for minke whales were for the period 1982/83 to 1989/90[3]. At the 2000 meeting, the Committee agreed that whilst these represented the best estimates for the years surveyed, they were no longer appropriate as estimates of current abundance. An initial analysis of available recent data had suggested that current estimates might be appreciably lower than the previous estimates.

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

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

Completion of revised circumpolar abundance estimates for Antarctic minke whales continues to be a high priority as there is no agreed current estimate. Data from the IWC-IDCR/SOWER cruises are being used for this purpose. The cruises from 1978/79 to 2003/04 can be divided into three circumpolar series (the CPI, II and III). Standard analyses of minke whale abundance estimates from these surveys have shown an appreciable decline for CPIII. For some years now

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[2] *http://swfsc.noaa.gov/TOSSM.aspx*

[3] *http://www.iwcoffice.org/conservation/environment.htm#sower*

the Committee has been trying to obtain abundance estimates from more sophisticated analyses as part of its examination as to whether the decreases represent a real decline in abundance or whether there are other explanations for the differences (e.g. changes in the number of whales in the pack ice which is outside the survey area). The Committee had hoped to present revised estimates this year using three new model approaches, but although considerable progress was made, this had not been possible. To ensure estimates that can be agreed upon are available next year, a detailed work plan and an intersessional Workshop have been scheduled.

Southern Hemisphere blue whales

The Committee is beginning the process of reviewing the status of Southern Hemisphere blue whales. An important part of this work is to try to develop methods to identify pygmy blue whales from 'true' blue whales at sea and progress is being made on this. Work on genetic and acoustic differentiation techniques is continuing and there is considerable progress with morphological methods. Good progress was made by the Committee in collating information on Southern Hemisphere blue whales as part of the Comprehensive Assessment process. Information received on pygmy blue whales confirmed that their presence in Antarctic waters is rare. Evidence was also received suggesting that the Chilean blue whales probably represent a discrete population or even subspecies.

Over 300 individual blue whales have been identified thus far from over 20,000 photographs taken during the IWC-IDCR/SOWER cruises. The Committee recommended that photographs taken during the Japanese scientific research programmes in the Southern Ocean should be added to those taken on IWC-IDCR/SOWER cruises and that analysis of the Japanese photos should be presented next year. The Japanese samples will increase the overall sample size and this greatly enhances the scientific value of both sets of photographs. A proposal to establish a central web-based catalogue of blue whale identification photographs, primarily for the Southern Hemisphere was endorsed. The system will be designed to facilitate the matching of blue whale photographs among a wide number of researchers and should result in a considerably increased capacity to understand some of the basic questions relating to Southern Hemisphere blue whale populations with respect to movements, basic biology and stock structure.

The Committee endorsed the results of a paper (Branch, 2008) that suggests a pre-exploitation abundance of Antarctic blue whales of some 256,000 animals (95% credibility interval of 235,000-307,000) and that the minimum population size reached was as low as only 395 whales (95% credibility interval of 235-804), i.e. only 0.15% of the pre-exploitation level. The positive news is that the population has recently been increasing at an estimated annual rate of 6.4% (95% credibility interval of 2.4-8.4%). (The estimated maximum rate of increase for blue whales is about 8.5%.) The most recent survey abundance estimate (for 1997/98) was about 2,300 blue whales (95% CI 1,150-4,500) – however, that is still less than one percent of the pre-exploitation abundance levels.

The Committee agreed that the circumpolar assessment for Antarctic blue whales is now complete.

Southern Hemisphere humpback whales

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

In Santiago, high priority was given to completion of the Comprehensive Assessment of Southern Hemisphere humpback whale Breeding Stocks B and C off the western and eastern African coasts respectively. Information presented to the Committee suggests that the stock structure for both stocks is complex; work to clarify this will continue intersessionally. Abundance estimates presented for Breeding Stock B off Gabon range from around 6,600 (95% CI 4,900-8,800) to 8,200 (95% CI 6,500-10,400). Estimates for Stock C3 (C stock comprises four sub-stocks, C1-C4) suggest numbers in the range 4,500-7,700. Work to complete the assessment will continue intersessionally.

The Committee reviewed information on other stocks of humpback whales including the stocks wintering off western South America and feeding from Isla Chiloe to the Antarctic Peninsula, humpbacks off eastern Australia, New Zealand and the South Pacific Islands and humpbacks off Oman. A study confirmed that the high growth rate of the east Australian humpback population has continued and yielded a long-term annual rate of increase of 10.9% (95% CI 10.5-11.4%). This population was estimated to number around 9,683 whales in 2007 (95% CI 8,556-10,959). Humpback whales off Oman in the Arabian Sea seem to be one discrete population and the Committee stressed the importance of increasing research on the status of, and threats to this geographically isolated population

North Pacific common minke whales

In light of the results of the RMP *Implementation* completed in 2003 (IWC, 2004a), the Scientific Committee began work on the in-depth assessment of western North Pacific common minke whales, with a special emphasis on the J-stock (found primarily in the Sea of Japan); that work continues. One of the difficulties facing this assessment is the apparent complexity of the population structure of common minke whales in the waters around Japan; there are at least four stock structure hypotheses and possibly more. The Committee hopes to clarify stock structure next year. Abundance estimates from sighting surveys in Russian Federation and Korean waters were reviewed but further analytical and field work is required before a final new abundance estimate for the area can be agreed. The Committee expressed concern about the continued high levels of reported bycatch of common minke whales from the J-stock and other coastal populations as well as recent suspicion of illegal catches from the J-stock.

Southern Hemisphere right whales

The Committee received a considerable amount of new information on southern right whales. Much of the information comes from long-term monitoring programmes; the Committee frequently notes the importance of such programmes to its work. Right whales off southern Australia have been increasing at around 8% annually (approx. 95% CI 4.5-11.8%). The value of satellite telemetry studies was illustrated by the information on feeding strategies and movements of animals tagged off South Africa. The Committee was pleased to receive information from South America and encouraged further work, noting the value of partnerships amongst local and national governments, researchers and other stakeholders. It was also pleased to receive the results of a Workshop held on the right whales found off Chile and Peru. That Workshop had concluded that the right whales in this region were critically endangered and that further work is needed to better understand their status and to enable measures to mitigate anthropogenic disturbance to be developed. The Committee recommended further international co-operation amongst researchers and increased photo-identification and biopsy sampling effort. It also encouraged research into the value of protected areas and the conduct of stock-specific assessments. This latter recommendation will be considered further next year.

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 and is extremely concerned about this population, which, whilst probably the only potentially viable population of this species, is in serious danger (*ca* 300 animals). By any management criteria applied by the IWC in terms of either commercial whaling or aboriginal subsistence whaling, there should be no direct anthropogenic removals from this stock.

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

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

Western North Pacific gray whales

The Committee and the Commission have expressed great concern over the critically endangered western gray whale on a number of occasions. It is one of the most endangered populations of large whales in the world with a population size of around 130 individuals and only about 23 breeding females. The primary feeding grounds lie along the north-eastern coast of Sakhalin Island, where existing and planned oil and gas developments pose potentially serious threats to the population, through habitat damage, ship strikes, noise pollution and oil spills. Entanglements in fishing gear throughout the range also pose a serious threat to the population.

The Committee welcomed a progress report on the valuable work undertaken since 1995 by a collaborative Russia-US programme, particularly with respect to photo-identification and genetic data. Information from that programme was incorporated into an updated assessment of the stock. It is encouraging that the population has been slowly increasing, at least up until 2005. However, its low absolute abundance and the news that five females had died in fishing gear during the past three years reaffirmed its critical status; projections incorporating this absolute number of additional mortalities indicate about a 25% probability of population decline and a substantial risk (about 10%) of extinction by 2050. The introduction by Japan of a new regulation in its 'Fisheries Resource Protection Law' aimed at reducing risk of incidental mortalities of gray whales in fisheries was welcomed.

The Committee made a number of recommendations with respect to the reduction of anthropogenic mortalities and disturbance. Development of efficient mitigation is greatly hampered by lack of information on migration routes and breeding destinations of the gray whales. The Committee noted the value of telemetry work in this regard, but also the need to exercise great care before undertaking such work on an endangered population. It will discuss this further next year. The Committee also reaffirmed its support for the IUCN Western Gray Whale Advisory Panel (WGWAP)[4] with respect to the Sakhalin area. It especially welcomed the work being undertaken by the WGWAP to: (1) prepare for a forthcoming seismic survey in 2009; and (2) compare the photo-identification data from the Russia-US programme and an industry-sponsored Russian programme. It strongly encouraged continued collaboration between these two complementary programmes. With respect to threats caused by fishing gear, the Committee recommended that range states make every effort to determine whether stranded or entangled whales match animals found in the photo-identification catalogues and/or genetic archive and to report such events (including photographs) as soon as possible. Identification of the causes of anthropogenic mortality is important in developing mitigation efforts.

The Committee reaffirmed the urgent need to reduce anthropogenic mortality to zero in this population. The work of the WGWAP towards the conservation of this population was endorsed and the participation of the Sakhalin Energy Investment Company in the Panel process was commended. It stressed the need for information on all activities and planned seismic surveys and urged all oil exploration companies to participate fully in the process of providing timely information.

Northeast Atlantic bowhead whales

About 20 bowhead whales were sighted at almost 81°N between Svalbard and Greenland in April 2006. There has been an apparent increase in observations of bowhead whales in these waters in recent years but it is not known if these few animals are stragglers from other populations or if they are survivors from the historic Spitsbergen population. If they are survivors of the Spitsbergen population, they are probably from one of the most endangered populations of the large whales in the world. The Committee recommended additional work to clarify their status as soon as practicable.

North Pacific bowhead whales

In the Okhotsk Sea, whaling on bowheads started in 1846 and was pursued intensively for two decades and then continued sporadically until 1913. Illegal catches resumed in 1967, but the numbers taken remain unknown. In light of

[4] *http://cms.iucn.org/wgwap/the_panel/index.cfm*

the small population size and recent catch history, the Committee expressed great concern and recommended that further work to investigate status be conducted as soon as possible.

EFFECTS OF ENVIRONMENTAL CHANGE ON CETACEANS

There is an increasing awareness that whales should not be considered in isolation but as part of the marine environment; detrimental changes to their habitat may pose a serious threat to whale stocks. The Committee has examined this issue in the context of the RMP and agreed that the RMP adequately addresses such concerns. However, it has also emphasised that the species most vulnerable to environmental threats might well be those reduced to levels at which the RMP, even if applied, would result in zero catches. Over a period of several years, the Committee has developed two multi-national, multi-disciplinary research proposals. One of these, POLLUTION 2000+, has two aims: to determine whether predictive and quantitative relationships exist between biomarkers (of exposure to and/or effect of PCBs) and PCB levels in certain tissues; and to validate/calibrate sampling and analytical techniques. The report of the first phase of the programme has been published (Reijnders *et al*., 2007). The other, SOWER 2000, is examining the influence of temporal and spatial variability in the physical and biological Antarctic environment on the distribution, abundance and migration of whales.

This year the Committee focussed on a number of environmental matters, including cetacean diseases, ecosystem modelling, climate change effects, pollution, anthropogenic noise and SOCER (State of the Cetacean Environment Report).

With respect to diseases, the Cetacean Emerging and Resurging Disease (CERD) group established last year prepared information on cetacean pathogens, biotoxins and disease reports. It also reviewed progress on disease identification and standardisation, case definition, diagnostic laboratories and data sharing. Given the paucity of available or targeted diagnostic laboratories and diagnostic tests specific for marine mammals, a list of laboratories and experts for specific or general diagnostic capabilities by country, continent and/or region will be compiled and maintained.

The Committee received a report from a two-day pre-meeting Workshop on skin diseases in cetaceans held in Santiago on 30-31 May. The Workshop reviewed the state of knowledge on the examination of, distribution of, and causes of skin diseases in cetaceans with a focus on cetaceans of South America. The potential for impacts of skin diseases in small populations in areas where there are high levels of environmental degradation was recognised and it was agreed that special action should be given to prevalence and impact of skin diseases in dolphins from southern and south-eastern Brazil. With respect to global action, recommendations were made for research, standardisation and on data sharing.

Due to time constraints, the POLLUTION+ Phase II modelling workshop planned for spring 2008 was not held. However, a new Steering Group has been assembled which is finalising plans for an intersessional workshop that will develop Terms of Reference for Phase II of the programme. Inter alia the workshop will establish a framework for modelling pollution effects, identify key cetacean populations to be studied, develop a protocol for validating the use of biopsy sampling techniques with respect to pollutant studies and then begin to apply this protocol to large whale species.

The Committee received new information on anthropogenic noise in relation to the potential impacts of seismic surveys on cetaceans, mid-frequency sonar and a cetacean stranding event. It noted a call by a recent International Workshop on Shipping Noise and Marine Mammals for global action to reduce the contributions of shipping to ambient noise with targets being set for the next 10 and 30 years.

Ecosystem modelling

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

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

This year's focus was planning for a joint CCAMLR/IWC Workshop, to be held in August 2008, to review input data required for ecosystem models to provide advice on krill predators in the Antarctic marine ecosystem. Expert Working Groups for each of the key taxa were preparing for the Workshop. The Committee agreed that the approach taken by these groups, and the progress being made towards the Workshop, was appropriate.

The use of the ECOPATH with ECOSIM software to explore the potential impact of cetaceans on fishery yields was also discussed. The Committee agreed that simulation testing of multiple models is a valuable approach, reaffirming its conclusion of 2002 that at this stage, no single approach could be recommended to provide reliable information of value to consideration of cetacean dynamics in an ecosystem context. While this does not necessarily rule out the possibility that inferences could be drawn if a number of different approaches yield qualitatively similar results, the Committee agreed that it may be some time before this situation changes.

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 Committee can study and provide advice on them. As part of this programme, the Committee has reviewed the biology and status of a number of species and carried out major reviews of significant directed and incidental catches of small cetaceans.

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

This year the Scientific Committee undertook a regional review of conservation issues regarding the (at least) 39 species of small cetaceans in the southeast Pacific (Columbia, Ecuador, Peru and Chile). The Committee noted that little is known about the distribution and abundance of many of the coastal species that are probably most impacted by anthropogenic activities, including Burmeister's porpoise, Peale's dolphin, bottlenose dolphin and the Chilean dolphin. A number of recommendations were made to improve the knowledge of the abundance, distribution, pattern of residency, population structure, life history and ecology of these and other small cetacean species. The Committee expressed concern with respect to both habitat degradation and the exclusion of small cetaceans from their habitat by aquaculture developments and recommendations were also made with respect to direct and incidental takes. A number of small coastal populations, including bottlenose dolphin, Peale's dolphin and spotted dolphins may be threatened by unregulated and undocumented takes for bait. It recommended that the impacts of such removals be assessed and the status of the affected populations be documented. The Committee also recommended that range states establish programmes for monitoring and reporting of bycatch of small cetaceans as part of their regular fisheries monitoring and that existing bycatch monitoring programmes be continued, particularly in relation to mitigation efforts. Recommendations for further research and regional collaboration (e.g. with IOC/UNESCO11) were made.

The Committee also reviewed progress on previous recommendations including those with respect to the vaquita, harbour porpoise (exposed to high bycatch throughout its range), franciscana (at risk from harbour development and bycatch), illegal takes of botos, the hand-harpoon hunts for Dall's porpoise in Japan (concern regarding sustainability) and Hector's dolphins (bycatch in gill net fisheries).

With respect to the vaquita, the Committee noted that the entire population is most likely to be no more than 150 animals and that there has been an extraordinary rapid decline of approximately 75% in a decade. It further noted that if the current mortality due to bycatch in fishing gear continues, it is likely that the species will be extinct in five years and probably less. The Committee therefore re-iterated its extreme concern about the conservation status of the vaquita which is the most endangered cetacean species in the world. It expressed its great frustration that despite more than a decade of warnings, this species has continued on a rapid path towards extinction due to a lack of effective conservation measures in Mexico (although it welcomed news that Mexico is taking measures to remove fishing gear that entangle these animals). It strongly recommended that, if extinction is to be avoided, all gillnets should be removed from the upper Gulf of California immediately. In the extremely unfortunate circumstance that this does not occur immediately, the Committee indicated that it must certainly occur within a three-year period starting in 2008. To meet this schedule, the Committee encouraged the international community including IWC member countries and non-governmental organisations (NGOs), to assist the government of Mexico in this task. In the Commission, Mexico confirmed that by Presidential Decree, over 50 million USD is being made available to remove gillnets throughout the range of the vaquita.

The Committee reaffirmed its concern over the conservation status of the boto and that directed killing of this species continues without restriction or catch limits. It recommended that immediate steps be taken by Brazil, Colombia, Peru and Venezuela to stop this hunt and that range states report to next year's meeting regarding progress made. In the Commission, Brazil reported that it has established a national working group of cetacean biologists, fisheries experts and environmental managers to devise better regulations for the fisheries that are the major cause of mortalities of the boto. The Committee re-iterated its concerns for stocks of Dall's porpoise and repeated earlier recommendations that catches should be reduced to sustainable levels, that the bycatch levels be quantified and that a full assessment of each of the affected populations be conducted as soon as possible.

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

SCIENTIFIC ASPECTS OF WHALEWATCHING

Over recent years there has been emerging evidence that disturbance from some whalewatching activities may have population-level effects in cetaceans. The Committee is therefore planning a large-scale whalewatching experiment to assist in describing such effects, to improve understanding of the mechanisms involved and to develop mitigation measures. Work will continue intersessionally and a final research proposal is expected to be available at next year's meeting. An overview of whalewatching in South America raised concerns that aerial whalewatching in Chile and Brazil using helicopters has the potential to disturb whales. The Committee reviewed aspects of short-term and long-term methods to assess biological impacts of whalewatching on cetaceans and gave advice on further developments.

With respect to guidelines and regulations for whalewatching, the Committee expressed some concern at the apparent trend of government agencies to use voluntary codes of conduct rather than legal regulations. The Committee recommended that in general, codes of conduct should be supported by appropriate legal regulations and modified if necessary as new biological information emerges. The world-wide compendium of whalewatching guidelines and regulations around the world was updated and is available on the IWC web site (*http://www.iwcoffice.org/conservation/whalewatching.htm#regulations*).

REVIEW AND COMMENT ON SCIENTIFIC PERMITS ISSUED FOR SCIENTIFIC RESEARCH

Improving the procedure for reviewing scientific permit proposals

An improved procedure to review special permit proposals as well as the periodic and final review of results from special permit programmes was agreed by consensus by the

Scientific Committee and endorsed by the Commission. In this approach, reviews will be undertaken at intersessional workshops of independent experts. A limited number of scientists associated with a proposal will be allowed to attend such workshops in an advisory role, primarily to present their proposal or results and to answer questions of clarification. To ensure that the composition of any expert group is considered balanced and fair, the experts will be chosen by the Chair and Vice Chair of the Scientific Committee and IWC's Head of Science in consultation with a Standing Steering Group representing a range of experience and expertise within the Scientific Committee.

Review of results from existing permits

The Scientific Committee reviewed results from Japan's current research programmes in the Antarctic (i.e. JARPA II) and North Pacific (JARPN II) and Iceland's programme in the North Atlantic.

JARPA II is a large-scale Antarctic programme that commenced with the first year of a two-year feasibility study during the austral summer of 2005/06. The objectives are defined by Japan as: (1) monitoring of the Antarctic ecosystem; (2) modelling competition among whale species and developing future management objectives; (3) elucidation of temporal and spatial changes in stock structure; and (4) improving the management procedure for Antarctic minke whale stocks. JARPA II will focus on Antarctic minke, humpback and fin whales and possibly other species in the Antarctic ecosystem that are major predators of Antarctic krill.

With respect to JARPA II, 2007/08 was the first year of the full-scale research programme. While permits were issued for minke, fin and, for the first time, humpback whales, Japan subsequently agreed to delay the taking of humpback whales at least until after the 2008 Annual Meeting. In the event, 551 Antarctic minke whales were taken and no fin whales.

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

In the JARPN II programme in 2007, a total of 207 (plus one lost) common minke, 100 sei, 50 Bryde's and 3 sperm whales were taken. A review of the first six years of JARPN II will take place intersessionally prior to next year's Annual Meeting following the new approach mentioned above.

Iceland's programme was primarily for feeding ecology studies and involved the proposed take of 100 common minke whales, 100 fin whales and 50 sei whales in each of two years. In the event, Iceland issued permits to take 38 common minke whales in 2003, 25 minke whales in 2004, 39 minke whales in 2005, 50 minke whales in 2006 and 39 minke whales in 2007. The total number of common minke whales taken has been 200, the last being taken in 2007. Currently the samples and data are being analysed and when this has been completed, the programme will be subject to an IWC review following the agreed new procedure.

Again, as in the past, different views on the value of these research programmes were expressed in the Scientific Committee and in the Commission. The deep division within the organisation regarding scientific permit whaling is one of the main reasons why a better approach to the review of proposals and results has been developed.

WHALE SANCTUARIES

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

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

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

REFERENCES

Branch, T.A. 2008. Current status of Antarctic blue whales based on Bayesian modeling Paper SC/60/SH7 presented to the IWC Scientific Committee, June 2008, Santiago, Chile (unpublished). 10pp. [Paper available from the Office of this Journal].

International Whaling Commission. 1994. Report of the Workshop on Mortality of Cetaceans in Passive Fishing Nets and Traps, 22-25 October 1990. *Rep. int. Whal. Commn (special issue)* 15:1-71.

International Whaling Commission. 2004a. Report of the Scientific Committee. *J. Cetacean Res. Manage. (Suppl.)* 6:1-60.

International Whaling Commission. 2004b. Report of the Workshop to Design Simulation-based Performance Tests for Evaluating Methods Used to Infer Population Structure from Genetic Data, 21-24 January 2003, La Jolla, USA. *J. Cetacean Res. Manage. (Suppl.)* 6:469-85.

International Whaling Commission. 2005. Report of the Scientific Committee. Annex D. Report of the Sub-Committee on the Revised Management Procedure. Appendix 2. Requirements and Guidelines for *Implementation. J. Cetacean Res. Manage. (Suppl.)* 7:84-92.

International Whaling Commission. 2006. Report of the Scientific Committee. *J. Cetacean Res. Manage. (Suppl.)* 8:1-65.

International Whaling Commission. 2007a. Report of the 2nd TOSSM (Testing of Spatial Structure Models) Workshop. *J. Cetacean Res. Manage. (Suppl.)* 9:489-98.

International Whaling Commission. 2007b. Report of the Joint NAMMCO/IWC Scientific Workshop on the Catch History, Stock Structure and Abundance of North Atlantic Fin Whales, 23-26 March 2006, Reykjavík, Iceland. *J. Cetacean Res. Manage.* 9:451-68.

International Whaling Commission. 2007c. Report of the Scientific Committee. *J. Cetacean Res. Manage. (Suppl.)* 9:1-73.

International Whaling Commission. 2008a. Report of the Scientific Committee. *J. Cetacean Res. Manage. (Suppl.)* 10:1-74.

International Whaling Commission. 2008b. Report of the Scientific Committee. Annex D. Report of the sub-committee on the revised management procedure. Appendix 5. Pro-forma for research programmes associated with the 'variant with research' option. *J. Cetacean Res. Manage. (Suppl.)* 10:115.

International Whaling Commission. 2008c. Report of the Scientific Committee. Annex D. Report of the sub-committee on the revised management procedure. Appendix 7. New text for requirements and guidelines for conducting surveys and analysing data within the Revised Management Scheme (RMS). *J. Cetacean Res. Manage. (Suppl.)* 10:117.

International Whaling Commission. 2009. Report of the First Intersessional RMP Workshop on North Atlantic Fin Whales, 31 March to 4 April 2008, Greenland Representation, Copenhagen. *Journal of Cetacean Research and Management (Suppl.)* 11:in press.

Reijnders, P., Wells, R., Aguilar, A., Donovan, G., Bjørge, A., O'Hara, T., Rowles, T. and Siebert, U. 2007. Report of the Scientific Committee. Annex K. Report of the Standing Working Group on Environmental Concerns. Appendix 2. Report from POLLUTION 2000+: Phase I. *J. Cetacean Res. Manage. (Suppl.)* 9: 261-74.

Roman, J. and Palumbi, S.R. 2003. Whales before whaling in the north Atlantic. *Science* 301: 508-10.

Mitochondrial genetic variation in bowhead whales in the western Arctic

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ABSTRACT

Bowhead whales in the Western Arctic are managed as a single stock by the International Whaling Commission (IWC). In response to recent concerns about the potential existence of multiple stocks in the region, we examined genetic variation in the mitochondrial control region among various spatial, temporal and age-related strata. Sequences from 382 samples were used in the comparisons. No significant differences were detected in spatial comparisons or in temporal comparisons along Alaska's North Slope. However the $\chi\chi^2$ analysis showed evidence of genetic heterogeneity between some of the age cohorts, specifically between animals born prior to 1918 (*n*=8) and those born after 1979 (*n*=34) (*p*=0.030), between those born 1918-1949 (*n*=13) and those born after 1979 (*p*=0.050), and between the two aforementioned older cohorts and those born after 1979 (*p*=0.009). There was also a significant F_{st} difference between autumn (*n*=13) and spring (*n*=11) whales from St. Lawrence Island (*p*=0.049). The age data were insufficient to determine if this seasonal difference was due in part to the difference between age cohorts.

KEYWORDS: BOWHEAD WHALE; GENETICS; WHALING; ARCTIC; NORTHERN HEMISPHERE

INTRODUCTION

Bowhead whales (*Balaena mysticetus*) in the western Arctic were heavily exploited in the 19th century, their numbers reaching a nadir of approximately 1,500 whales early in the 20th century (Brandon and Wade, 2006). This population, which inhabits the Bering, Chukchi and Beaufort Seas (BCB), has since increased to about 10,000 whales (George *et al*., 2004; Zeh and Punt, 2005), and is estimated to be growing at about 3% per annum (George *et al*., 2004). Fig. 1, based on information presented in Moore and Reeves (1993), depicts the basic movements and seasonal ranges of bowhead whales in the western Arctic. Although the map reflects the basic pattern of known movements exhibited by the majority of the population, traditional knowledge, historical catch records (Bockstoce *et al*., 2005) and recent scientific observations indicate that there is considerable variation around this model. Although the commercial harvest has long ended, subsistence hunting by aboriginal communities continues in Alaska and along the Chukotka Peninsula in Russia, with an annual take of 30-40 whales per year over the past two decades (Braham, 1995; Suydam *et al*., 2006). Since 1977, the IWC has managed this population as a single stock (IWC, 2001; Rugh *et al*., 2003). However, in recent years, there have been questions raised regarding the possible presence of multiple stocks within the BCB population (Anon., 2005), which if true may necessitate a revision of management practices (e.g. IWC, 2006)[1].

Some multi-stock hypotheses involve spatial separation within the range of the population, while others invoke a temporal difference in the timing of migration. Another alternative is that there is only a single stock, but that genetic differences among age cohorts have arisen from the unusual demographic history of the population together with the unusual life history of bowhead whales, which live much longer than any other cetacean. A considerable amount of research, including the use of genetic markers, has been directed at examining these hypotheses (e.g. Jorde *et al*., 2007). Taylor *et al*. (2007) reviewed the different lines of evidence that bear upon the stock issue, including life history parameters, distribution and movements, catch records and genetic variability, concluding that the preponderance of evidence indicates the presence of a single stock. For genetic studies, it is reasonable to expect that most possible genetic subdivisions will be more easily detectable by the use of mitochondrial markers than nuclear genes; the haploid nature and maternal inheritance of the mitochondrial genome result in a smaller effective population size that is more strongly influenced by the effects of genetic drift (Avise, 1995). The magnitude of differentiation will be larger for mtDNA; however, mtDNA used alone will be unable to differentiate strata if the strata themselves contain samples from multiple stocks. Here, the results from an examination of genetic diversity are presented, both spatial and temporal, in BCB bowhead whales using mitochondrial control region sequences.

MATERIALS AND METHODS

Samples came primarily from whales taken in subsistence hunts, with additional samples taken from biopsies and stranded whales. The supplemental data contain a complete

[1] Subsequent to the completion of this paper, the IWC Scientific Committee found that the bowhead *SLA* (*Strike limit algorithm*) used to provide management advice was robust to a wide range of stock structure hypotheses (IWC, 2008a).

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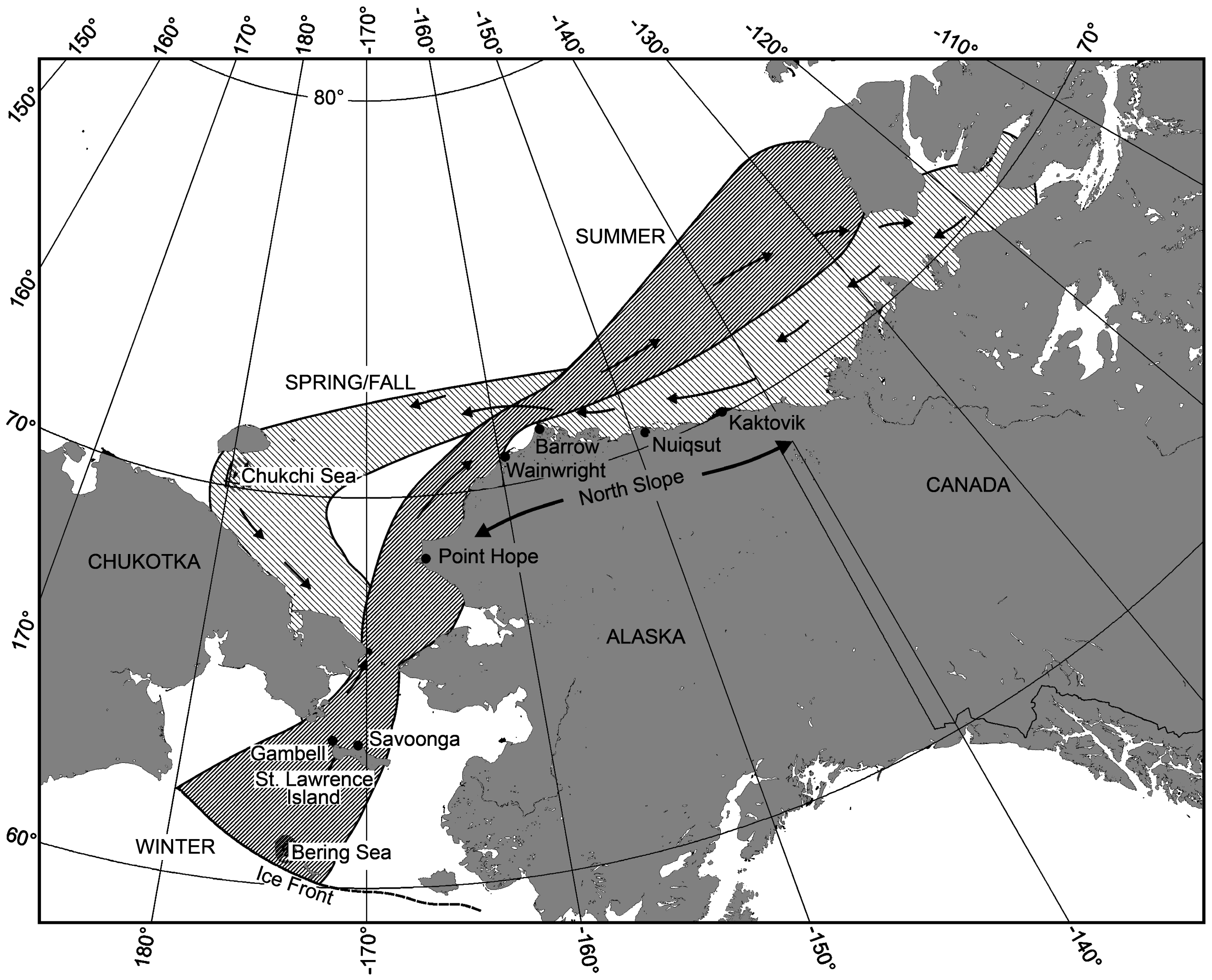

Fig. 1. Basic pattern of seasonal movements of bowhead whales in the western Arctic, based on information from Moore and Reeves (1993). The dark shading indicates spring migration (March to June), and the lighter shading is summer-autumn (July to November). The wintering area is Bering Sea south of the Bering Strait and north of 60°N; but mainly in the NW Bering Sea including Anadyr Gulf and within the seasonal sea ice.

list of samples, with their collection information, stratification and haplotype information. DNA extraction, amplification, and sequencing of skin samples were conducted using standard protocols (LeDuc *et al.*, 2005) and also see additional material[2]). DNA was extracted from samples of bone and baleen as in Morin *et al.* (2006).

The data set was stratified according to various temporal, spatial and age-related criteria. The spatial and temporal strata consisted of samples pooled over multiple years. The spatial strata applied were Barrow (the village on Alaska's North Slope with the largest hunt), the entire North Slope of Alaska (NS), St. Lawrence Island (SLI), Gambell and Savoonga (two villages on SLI), Alaska (comprised of NS plus SLI), and Chukotka, Russia. In addition, the Barrow and NS strata were divided into Fall (F; Aug-Oct) and Spring (S; Apr-Jun). Seasonal stratification for SLI was F (Nov-Jan) and S (Apr-May). For the age comparison, samples were divided into birth-year strata, based on the year of catch and the estimated ages of the samples based on baleen growth increments and aspartic acid racemisation (George *et al.*, 1999; Lubetkin *et al.*, In prep; Rosa *et al.*, 2004). One stratum was comprised of animals born prior to the low point in the population's history (prior to 1918). The rest of the age-related strata were based on approximately 30-year increments after and including 1918 (i.e. 1918-49, 1950-79, and after 1979). In addition, a subsequent stratification was used wherein the two oldest cohorts were combined in order to increase the sample size of the oldest group. The sorting of individual samples into all the strata is given in the supplemental data. The calculation of Φ_{st} was performed using uncorrected pairwise differences in *Arlequin* 1.1. (Schneider *et al.*, 1997). F_{st} and χ^2 (Roff and Bentzen, 1989) were calculated using a program written by KKM. For all analyses 10,000 permutations were used to calculate the *p*-value.

Due to the large number of samples obtained from skulls and baleen, there was some concern regarding some individual whales being duplicated in the dataset, either as multiple samples of hard tissue or as hard tissue and skin samples. Since the sample size from SLI is so limited, the potential effect of duplication of samples on the results is large. To address this, comparisons involving strata from SLI were reanalysed after incorporating putative matches into the dataset. To date, there have been two efforts to associate samples of bone and baleen with particular harvested whales. In the first, whale-ID numbers were assigned to the Gambell whale skulls used for the present study from the record of harvested whales going back to 1961, which included whale-ID number, body length, sex, date taken, and whaling captain. A whaling captain had been assigned to these skulls by one of the Gambell locals. Whale body length was then calculated using regression equations with skull length and skull width predicting body length.

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[2] *http://www.iwcoffice.org/_documents/publications/additions/mtDNA_sequences.xls*

These regression equations were derived using combined data for all whales with cranial measurements (e.g. male and female, data quality 1-3, 1974-2004); so they are NOT sex specific: (skull length (cm)2.3945+181.29)/100 = body length (m); (skull width (cm)5.7528+48.866)/100 = body length (m).

Using information from the whaling captain, the derived body length and any information in the comments mentioning if it was an old or recent skull, the skulls were matched to a whale-ID number from the harvest record. Those for which correct matches were fairly certain were considered as putative matches for the reanalysis. Less certain matches were not incorporated. These were usually due to uncertainty regarding the year of harvest for a particular skull, or the whaling record including multiple whales of a given size caught during the estimated time of harvest. In the second analysis, presented in Morin *et al.* (2007), nineteen single nucleotide polymorphisms (SNPs) were used to genotype samples and look for genetic matches. Although both methods produce equivocal results, they do provide some basis for detecting putative duplicates. All analyses involving SLI were therefore conducted twice; first with all samples treated as separate and independent and second incorporating SNP-based and 'fairly certain' matches from the aforementioned studies. These included matches within sample types (e.g. baleen – baleen) and between sample types (e.g. baleen – bone or bone – skin). The effect of incorporating theses matches was to reduce the sample size for most comparisons. However, since some of the matches were of skulls to previously unsampled whales, this meant that some of the skull samples now had collection dates associated with them. This allowed the seasonal comparison of SLI to have a greater sample size. Detailed sample information and stratifications used can be found on the IWC website[3]. The putative matches have been added to the table[3] in a separate column and the putative collection info (for whales not already represented by other samples) has been included in parentheses.

RESULTS AND DISCUSSION

There were 68 different haplotypes recorded, defined by 44 variable sites. For details about the frequencies and specific sequences, see Appendix 1 and additional data[3]. Complete sequences are available on Gen Bank, accession numbers FJ744425-FS744492. Results of the pairwise comparisons are summarised in Table 1. None of the spatial comparisons yielded significant differences. Significant differences were seen in χ^2 analyses between the animals born before 1918 and those after 1979, between those born 1918-1949 and those after 1979, as well as between the two oldest cohorts combined and the youngest. There was near significance (p=0.088) when the youngest cohort was compared to those born 1950-1979. It may be that the historical population dynamics of the BCB bowhead whales – extreme reduction followed by rapid recovery – have led to changes in haplotype frequencies across generations, at least between those generations on either side of the population's nadir (Martien *et al*., 2007; Ripley *et al*., 2006). Shifting haplotype frequencies over time have also been found for a recovering population of humpback whales (Rosenbaum *et al*., 2002). For the bowhead whales, additional samples from aged whales are desirable to further assess the variability between cohorts.

There have been several multi-stock hypotheses proposed for this population in recent years (IWC, 2008b). In some of those hypotheses, the stocks are spatially segregated, with one stock migrating past and being hunted along the North Slope, and the other predominating around either St. Lawrence Island or the Chukotka Peninsula. The results presented here do not support these multi-stock hypotheses, as all the comparisons were non-significant at the 0.05 level. In comparison, LeDuc *et al*. (2005) found that BCB and Okhotsk Sea bowhead whales were different in their mitochondrial sequences in an F_{st} analysis (p=0.026), and that the Okhotsk Sea population had a much lower level of haplotypic diversity (0.61 vs. 0.93). However, there is a caveat attached to the comparisons involving Chukotka. Available samples do not allow adequate testing for a resident stock of bowhead whales off the Chukotka Peninsula because samples for Chukotka were only available in the autumn, which is a period when some whales that migrate to the Canadian arctic are known to move to Chukotka for autumn feeding (Krutzikowsky and Mate, 2000; Mate *et al*., 2000; Moore and Reeves, 1993). To test for the potential of a resident Chukotka group, samples need to be collected there in spring or early summer when all the whales that migrate along the North Slope are thought to be in Alaskan and Canadian waters.

Other multi-stock hypotheses that have been suggested postulate the existence of temporally segregated stocks. Under these hypotheses, the animals migrating past Barrow in the spring constitute a single, pure stock, while those passing Barrow in the autumn represent a mixed-stock assemblage. This hypothesis would predict some level of genetic differentiation between Barrow animals hunted in the spring and autumn. No such differentiation was found.

There was a significant difference found between autumn and spring whales from SLI when putative matches were incorporated into the dataset. Although intriguing, this may not necessarily be indicative of the presence of multiple stocks. Given that one season (fall) occurs just before the mating season, the whales caught in this season may include a higher proportion of older whales than those caught in spring, and the difference may therefore be age-related. At present there are not enough data to test this hypothesis because only one SLI sample came from an animal that had been aged.

For all the comparisons, the results should not be considered conclusive. Many of the strata had small samples sizes, and non-significant p-values may reflect low power (Type II error) – the addition of more samples may lead to different results. On the other hand, Type I errors are also possible. In seasonal comparisons (F v S) for Barrow and the North Slope, there were significant and near significant differences that were found in earlier studies (Taylor *et al*., 2004) that have disappeared with the addition of more samples (present results). Although an explicit calculation of statistical power would provide readers with a stronger ability to interpret the data, specific alternate hypotheses regarding the magnitude of expected differentiation between strata are needed for such calculations. It had been hoped that such specific alternate hypotheses could have been obtained from analyses of nuclear DNA data together with reviews of other data relevant to population structure (reviewed in Taylor *et al*., 2007). However no specific alternate hypotheses with specific hypothesised abundances and levels of dispersal arose from those other data sources.

In addition to the statistical considerations discussed above, interpretation of genetic data for bowhead whales is further complicated by various factors: a population known

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[3] *http://www.iwcoffice.org/_documents/publications/additions/mtdnaSTRATAnew.xls*

Table 1

Results of the analyses of mitochondrial sequence data. Note: Data set includes two stranded whales that were used in large-scale spatial analyses (e.g., NS v SLI) but were omitted from temporal analyses or those strata specific to a village.

Strata (sample size)	F_{st}	*p*	χ^2 (per df)	*p*	Φ_{st}	*p*
Spatial						
Barrow (258) v SLI (63) I	-0.0006	0.469	0.995	0.493	0.006	0.122
Barrow (258) v SLI (52) II	-0.003	0.820	0.865	0.772	0.0003	0.357
Barrow (258) v Savoonga (21) I	-0.002	0.495	0.856	0.688	-0.002	0.464
Barrow (258) v Savoonga (20) II	-0.004	0.587	0.857	0.687	-0.003	0.494
Barrow (258) v Gambell (42) I	0.002	0.218	1.133	0.243	0.012	0.069
Barrow (258) v Gambell (32) II	-0.004	0.731	0.935	0.597	0.001	0.342
Barrow (258) v Chukotka (22)	-0.009	0.919	0.707	0.877	-0.009	0.764
AK (360) v Chukotka (22) I	-0.008	0.856	0.752	0.792	-0.006	0.605
AK (349) v Chukotka (22) II	-0.008	0.879	0.750	0.799	-0.007	0.631
NS (297) v SLI (63) I	0.0004	0.359	1.026	0.429	0.005	0.147
NS (297) v SLI (52) II	-0.003	0.728	0.895	0.709	-0.0001	0.390
NS (297) v Savoonga (21) I	0.00003	0.394	0.883	0.643	-0.0009	0.409
NS (297) v Savoonga (20) II	-0.002	0.506	0.880	0.637	-0.002	0.436
NS (297) v Gambell (42) I	0.003	0.211	1.150	0.226	0.011	0.082
NS (297) v Gambell (32) II	-0.004	0.714	0.955	0.563	-0.0001	0.382
NS (297) v Chukotka (22)	-0.009	0.913	0.711	0.860	-0.008	0.695
Temporal						
Barrow F (133) v S (125)	0.0003	0.357	0.984	0.546	0.002	0.210
NS F (154) v S (141)	-0.001	0.640	1.026	0.421	0.0003	0.346
SLI F (13) v S (11) I	0.054	0.070	1.180	0.176	-0.013	0.481
SLI F (14) v S (17) II	0.056	0.024	1.193	0.154	0.011	0.268
Age cohort						
Birth-year <1918 (8) v 1918-1949 (13)	-0.010	0.513	1.102	0.320	-0.035	0.714
Birth-year <1918 (8) v 1950-1979 (25)	-0.013	0.680	1.001	0.686	-0.027	0.698
Birth-year <1918 (8) v >1979 (33)	0.003	0.357	1.519	0.030	0.005	0.361
Birth-year 1918-1949 (13) v 1950-1979 (25)	-0.010	0.652	0.745	0.981	0.006	0.315
Birth-year 1918-1949 (13) v >1979 (33)	0.010	0.230	1.390	0.050	0.007	0.294
Birth-year 1950-1979 (25) v >1979 (33)	0.008	0.182	1.194	0.088	-0.009	0.566
Birth-year <1950 (21) v 1950-1979 (25)	-0.007	0.652	0.910	0.829	0.004	0.322
Birth-year <1950 (21) v >1979 (33)	0.009	0.204	1.386	0.009	0.010	0.236

to be out of demographic equilibrium because of recent population dynamics, sampling that is known to be non-random with respect to the age structure of the population and limited sample sizes outside of the migratory corridor that includes Barrow. The unusual longevity of bowhead whales means that the sample set contains both whales born during the commercial whaling era over 100 years ago, who represent a relatively pristine population, and whales born in recent decades, representing a population in the process of increasing from around 1,500 whales to the current 10,000. The genetic sample set has the potential to exaggerate the patterns of disequilibrium by disproportionately selecting the oldest and youngest individuals. Bowhead whales are known to migrate according to age and reproductive condition (Moore and Reeves, 1993). Some of the smaller villages prefer the largest whales, while Barrow whalers prefer smaller whales. The present mtDNA results are consistent with a single stock with genetic heterogeneity related to age cohorts, and patterns of genetic heterogeneity found in other markers (e.g. Jorde *et al*., 2007) could also result from similar age-related processes as those that were suggested here. However, samples sizes for many strata are small, and some hypotheses of stock structure do not lend themselves to testing with the present dataset. Ideally, samples would be obtained from breeding grounds and season to directly test for the presence of multiple stocks.

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REFERENCES

Anon. 2005. *Final report of the workshop on bowhead whale stock structure studies in the Bering-Chukchi-Beaufort Seas: 2005-2006, 23-24 February 2005, Seattle, WA*. NOAA/AFSC/NMML and NSB/ Dept. of Wildlife Management. 19pp.

Avise, J.C. 1995. Mitochondrial DNA polymorphism and a connection between genetics and demography of relevance to conservation. *Conserv. Biol*. 9(3): 686-90.

Bockstoce, J.R., Botkin, D.B., Philip, A., Collins, B.W. and George, J.C. 2005. The geographic distribution of bowhead whales in the Bering, Chukchi, and Beaufort Seas: evidence from whaleship records 1849-1914. *Mar. Fish. Rev*. 67(3): 1-43.

Braham, H.W. 1995. Sex and size composition of bowhead whales landed by Alaskan Eskimo whalers. pp.281-313. *In*: McCartney, A.P. (eds). *Hunting the Largest Animals: Native Whaling in the Western Arctic and Subarctic. Occasional Pub. No. 36*. The Canadian Circumpolar Institute, Edmonton, Alberta. 355pp.

Brandon, J. and Wade, P.R. 2006. Assessment of the Bering-Chukchi-Beaufort Sea stock of bowhead whales using Bayesian model averaging. *J. Cetacean Res. Manage*. 8(3): 225-40.

George, J.C., Bada, J., Zeh, J., Scott, L., Brown, S.E., O'Hara, T. and Suydam, R. 1999. Age and growth estimates of bowhead whales (*Balaena mysticetus*) via aspartic racemization. *Can. J. Zool.* 77: 571-80.

George, J.C., Zeh, J., Suydam, R. and Clark, C. 2004. Abundance and population trend (1978-2001) of western Arctic bowhead whales surveyed near Barrow, Alaska. *Mar. Mammal Sci.* 20(4): 755-73.

International Whaling Commission. 2001. Report of the Second Workshop on the Development of an Aboriginal Subsistence Whaling Management Procedure (AWMP), Seattle, Washington, November 1999. *J. Cetacean Res. Manage. (Suppl.)* 3:417-47.

International Whaling Commission. 2006. Report of the Scientific Committee. *J. Cetacean Res. Manage. (Suppl.)* 8:1-65.

International Whaling Commission. 2008a. Report of the Scientific Committee. Annex E. Report of the standing working group on the development of an aboriginal subsistence management procedure. *J. Cetacean Res. Manage. (Suppl.)* 10:121-49.

International Whaling Commission. 2008b. Report of the second Intersessional Workshop to prepare for the 2007 bowhead whale *Implementation Review*, Seattle, 12-17 January 2007. *J. Cetacean Res. Manage. (Suppl.)* 10:513-25.

Jorde, P.E., Schweder, T., Bickham, J.W., Givens, G.H., Suydam, R. and Stenseth, N.C. 2007. Detecting genetic structure in migrating bowhead whales off the coast of Barrow, Alaska. *Mol. Ecol.* 16(10): 1993-2004.

Krutzikowsky, G.K. and Mate, B.R. 2000. Dive and surfacing characteristics of bowhead whales (*Balaena mysticetus*) in the Beaufort and Chukchi seas. *Can. J. Zool.* 78: 1182-98.

LeDuc, R.G., Dizon, A.E., Burdin, A.M., Blokhin, J.C., George, J.C. and Brownell, R.L., Jr. 2005. Genetic analyses (mtDNA and microsatellites) of Okhotsk and Bering/Chukchi/Beaufort Seas populations of bowhead whales. *J. Cetacean Res. Manage.* 7(2): 107-12.

Lubetkin, S.C., Zeh, J., Rosa, C. and George, J.C. In prep. Age estimation for young bowhead whales (*Balaena mysticetus*) using baleen growth increments and their rates of change. 28pp.

Martien, K.K., Archer, E., Ripley, B.J. and Taylor, B.L. 2007. The genetic consequence of non-equilibrial dynamics in bowhead whales. 12pp. Paper SC/59/BRG16 presented to the IWC Scientific Committee, May 2007, Anchorage, USA (unpublished). 12pp. [Paper available from the Office of this Journal].

Mate, B.R., Krutzikowsky, G.K. and Winsor, M.H. 2000. Satellite-monitored movements of radio-tagged bowhead whales in the Beaufort and Chukchi seas during the late-summer feeding season and fall migration. *Can. J. Zool.* 78: 1168-81.

Moore, S.E. and Reeves, R.R. 1993. Distribution and movement. pp.313-86. *In*: Burns, J.J., Montague, J.J. and Cowles, C.J. (eds). *The Bowhead Whale.* Special Publication No. 2. Society for Marine Mammalogy, Lawrence, KS. 787pp.

Morin, P.A., Hancock, B.L. and George, J.C. 2007. Development and application of single nucleotide polymorphisms (SNPs) for bowhead whale population structure analysis. Paper SC/59/BRG8 presented to the IWC Scientific Committee, May 2007, Anchorage, USA (unpublished). 7pp. [Paper available from the Office of this Journal].

Morin, P.A., LeDuc, R.G., Robertson, K.M., Hedrick, N.M. and Perrin, W.F. 2006. Genetic analysis of killer whale (*Orcinus orca*) historical bone and tooth samples to identify western US ecotypes. *Mar. Mammal Sci.* 22(4): 897-909.

Ripley, B.J., Martien, K. and Taylor, B.L. 2006. A simulation approach to understanding non-equilibrial dynamics in a recovering long-lived species: the bowhead whale. Paper SC/58/BRG13 presented to the IWC Scientific Committee, May 2006, St. Kitts and Nevis, West Indies (unpublished). 12pp. [Paper available from the Office of this Journal].

Roff, D.A. and Bentzen, P. 1989. The statistical analysis of mtDNA polymorphisms: chi-square and the problem of small samples. *Mol. Biol. Evol.* 6(5): 539-45.

Rosa, C., George, J.C., Zeh, J., Botta, O., Zauscher, M., Bada, J. and O'Hara, T.M. 2004. Update on age estimation of bowhead whales (*Balaena mysticetus*) using aspartic acid racemization. Paper SC/56/BRG6 presented to the IWC Scientific Committee, July 2004, Sorrento, Italy (unpublished). 15pp. [Paper available from the Office of this Journal].

Rosenbaum, H.C., Weinrich, M.T., Stoleson, S.A., Gibbs, J.P., Baker, C.S. and DeSalle, R. 2002. The effect of differential reproductive success on population genetic structure: Correlations of life history with matrilines in humpback whales of the Gulf of Maine. *J. Hered.* 93(6): 389-99.

Rugh, D., DeMaster, D., Rooney, A., Breiwick, J., Shelden, K. and Moore, S. 2003. A review of bowhead whale *Balaena mysticetus* stock identity. *J. Cetacean Res. Manage.* 5(3): 267-79.

Schneider, S., Kueffer, J.M., Roessli, D. and Excoffier, L. 1997. *Manual Arlequin: A Software for Population Genetic Data Analysis, Version 1.1.* University of Geneva, Switzerland. 82pp.

Suydam, R.S., George, J.C., Hanns, C. and Sheffield, G. 2006. Subsistence harvest of bowhead whales (*Balaena mysticetus*) by Alaskan Eskimos during 2005. Paper SC/58/BRG21 presented to the IWC Scientific Committee, May 2006, St. Kitts and Nevis, West Indies (unpublished). 5pp. [Paper available from the Office of this Journal].

Taylor, B.L., LeDuc, R.G. and George, J.C. 2004. Interpreting genetic heterogeneity in the B-C-B stock of bowhead whales: a response to SC/56/BRG32. Paper SC/56/BRG44 presented to the IWC Scientific Committee, July 2004, Sorrento, Italy (unpublished). 10pp. [Paper available at the Office of this Journal].

Taylor, B.L., LeDuc, R.G., George, J.C., Suydam, R.S., Moore, J.E. and Rugh, D. 2007. Synthesis of lines of evidence for population structure for bowhead whales in the Bering-Chukchi-Beaufort region. Paper SC/59/BRG35 presented to the IWC Scientific Committee, May 2007, Anchorage, USA (unpublished). 12pp. [Paper available from the Office of this Journal].

Zeh, J.E. and Punt, A.E. 2005. Updated 1978-2001 abundance estimates and their correlations for the Bering-Chuckchi-Beaufort Seas stock of bowhead whales. *J. Cetacean Res. Manage.* 7(2): 169-75.

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A calf index for monitoring reproductive success in the Bering-Chukchi-Beaufort Seas bowhead whale (*Balaena mysticetus*) population

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ABSTRACT

The percentage of calves in a whale population can provide information on whether a population is increasing, stable or decreasing and is an input to population models. In this paper a method for estimating the percentage of calves in the Bering-Chukchi-Beaufort Seas (B-C-B) bowhead whale population in any given year by obtaining information on the percentage of calves passing Point Barrow, Alaska, during the last three weeks of the spring migration is presented. The method incorporates information on the timing of the migration with the percentage of calves detected during calf index surveys conducted during weekly periods from 14 May to early June. Historic data provide the different proportions of the migration during the weekly periods during low, medium and high calf years. The index is adjusted to allow for calves passing before 14 May and calves that are born after their mothers pass Point Barrow. The calf index was calculated for eight years using data from aerial photographic surveys near Point Barrow from 1985 to 2004 and the mean percentage of calves in the sampled years was 6.1%. Power analyses indicate that nine years of calf index data are required following a decline to detect a 60% reduction in the calf index. Additional calf index surveys prior to a decline would increase the power to detect a decline. This method can provide a robust estimate of the percentage of calves in the population each year with a modest aerial survey or photographic effort at Point Barrow. The data would be valuable in evaluating whether calving rates are within the range tested for the purpose of reviewing the B-C-B bowhead whale *Strike Limit Algorithm*.

KEYWORDS: ARCTIC; BEAUFORT SEA; CHUKCHI SEA; BOWHEAD WHALE; CALVES; PHOTOGRAMMETRY; POPULATION PARAMETERS; REPRODUCTION; SURVEY-AERIAL; NORTHERN HEMISPHERE; BIRTH RATE

INTRODUCTION

The Bering-Chukchi-Beaufort (B-C-B) population of bowhead whales (*Balaena mysticetus*) has increased at a rate of 3.4% per annum (95% CI=1.7-5.0%) from 1978 to 2001 (George *et al*., 2004b; Zeh and Punt, 2005) despite a subsistence harvest conducted under a quota administered by the International Whaling Commission (IWC). Under the current management agreement a new population estimate is obtained at least every 10 years to confirm population trends, but because the confidence intervals around these estimates are broad, changes in population trends cannot be confirmed by a single estimate. Therefore, a cost effective technique is needed to gauge the health of the population across shorter time intervals. This could be done by monitoring calving success through a complete calving cycle, which is thought to be 3-4 years (George *et al*., 2004a; Koski *et al*., 1993). Such data would also be valuable to evaluate whether calving rates were within the range tested for the purposes of reviewing the bowhead whale *Strike Limit Algorithm* (*SLA*) and would provide data for evaluating the effect of environmental variability on calving rates. The latter has been identified by IWC (2009) as an important input to future stochastic operating models for evaluating effects of harvests on stocks such as the B-C-B bowhead whale.

Changes in sea ice cover have been found to impact marine mammals in different ways. Species that avoid ice, such as gray whales (*Eschrichtius robustus*), have lower calf production and are in poorer condition during years when ice lingers late into the summer feeding season (Perryman *et al*., 2002; Perryman and Lynn, 2002). Species that rely on ice as a feeding or resting habitat, such as walruses (*Odobenus romarus*) and polar bears (*Ursus maritimus*), have reduced reproductive success when ice cover is reduced (Cooper *et al*., 2006; Stirling *et al*., 1999; Stirling and Parkinson, 2006). Concerns that reductions in ice cover in the Arctic might affect bowhead whale reproductive success because of their strong affiliation with sea ice and that increased oil and gas exploration activity might impact the population further motivate development of a more frequent and economical measure of reproductive success for this population.

Aerial photogrammetry studies of bowhead whales have been conducted near Point Barrow, Alaska, during their spring migration from the Bering Sea toward summer feeding areas in the Beaufort Sea and Amundsen Gulf. Data from these studies have been used to document the length-frequency distribution of the population and hence the percentage of calves in the population (Koski *et al*., 2006). The migration past Point Barrow is size structured (Angliss *et al*., 1995; Koski *et al*., 2006; Withrow and Angliss, 1992; 1994). Few calves are seen before mid-May, so annual recruitment can be estimated by monitoring the numbers of calves migrating past Point Barrow from mid-May to early June, the latter part of the spring bowhead whale migration. Note that the gray whale spring migration off California is also monitored for calves only during the latter half (Perryman *et al*., 2004).

In this paper a method of monitoring the reproductive success of B-C-B bowhead whales is described. Mothers and calves passing Point Barrow during the mid-May to

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early June period were counted or photographed and these data integrated with historic data on the proportion of the migration passing during weekly periods, with the weekly proportions varying among low, medium and high calf years. This permits an estimate of the percentage of calves in any given year without sampling the entire migration if calves born later in the season than surveys are conducted or after their mothers pass Point Barrow are accounted for (Koski *et al.*, 2004; 2006). If the data that are collected include information on whale lengths obtained from photogrammetry, the size structure of the sampled whales permits evaluation of whether the season is a typical or unusual season with respect to the timing of the migration.

METHODS

Aerial photogrammetry surveys

Aerial photogrammetry surveys were flown near Point Barrow, Alaska, in each of 1985-87, 1989-92, 1994 and 2003-04 by the National Marine Mammal Lab (NMML), Alaska Fisheries Science Center, NOAA Fisheries Service and/or LGL Limited. All of these years except 1987 and 1994 covered the latter part of the spring migration well. The methods employed build on the approach used by Koski *et al.* (2006) to estimate the length-frequency distribution of B-C-B bowhead whales by combining information on the proportion of the population passing during weekly periods with the length structure of the population during those same periods. This approach minimised biases caused by low sampling rates during some weekly periods. The calf index is an extension of this approach and does not require sampling during the first four weekly periods because no or few calves pass Point Barrow before 14 May (fig. 3 of Koski *et al.*, 2006).

The weekly proportions of the migration passing Point Barrow late in the season vary among low, medium and high calf years with a higher proportion of the migration passing later in the season during years when higher numbers of calves are present. Although the mean weekly proportions used by Koski *et al.* (2006) were appropriate when averaging several years of data, year-specific proportions are necessary to compute an unbiased calf index for a specific year. Visual, acoustic and aerial survey data from the ice-based surveys of bowhead whales in 1985, 1986, 1988, 1993 and 2001 (George *et al.*, 2004b; Zeh and Punt, 2005) were analysed to estimate the proportion of the migration that passed Point Barrow during the periods 14-20 May, 21-27 May and >27 May. These were the years when ice-based effort supplemented by aerial surveys spanned the entire migration. Based on earlier studies, 1986 and 2001 were categorised as high calf years (Angliss *et al.*, 1995; George *et al.*, 2004b) and 1985 and 1988 as low calf years (Angliss *et al.*, 1995; George *et al.*, 1995). Based on number of calves seen as a percentage of number of whales seen by the ice-based survey (George *et al.*, 1995; 2004b) it is likely that 1993 was a medium calf year. The low survey proportions after 13 May in 1993 compared to those in the high calf years 1986 and 2001 (Table 1) also suggest that 1993 was not a high calf year.

Calculation of calf index

The calf index is calculated by multiplying the proportion of the migration estimated to pass Point Barrow during a weekly period by the percentage of calves detected during that same period and then summing the resulting products for the last three weekly periods of the season (i.e. 14-20 May, 21-27 May and >27 May). The percentage of the calves during each period can be obtained either from aerial surveys or from photogrammetry studies. If aerial surveys are used, each whale sighted should be circled to confirm whether or not it has a calf. Calves can be very difficult to detect during aerial surveys because they are small and frequently travel below their mothers (Davis *et al.*, 1983).

Koski *et al.* (2004; 2006) noted that the spring photography data are positively biased towards larger numbers of mother-calf pairs than other whales for two reasons. First, calves which are recently born in the spring, have much shorter dive times than non-calves and so the calves (and hence their mothers) are approximately 1.69× (SE=0.14) more likely to be detected than non-calves (Koski *et al.*, 2004). Thus, when calculating the percentage of calves during each weekly period from survey data, the weekly counts of mothers and calves should be divided by 1.69. Second, researchers conducting photographic studies made extra effort to photograph mothers and calves (including mothers accompanied by yearlings), resulting in 1.46× (SE=0.17) more photographs of mothers and calves than of other whales (Koski *et al.*, 2006). Thus, when photographs provide the data for calculating the calf index, as in this paper, the number of images of mothers and calves seen together in each week needs to be divided by $1.69 \times 1.46 = 2.47$. The 1.46 factor also needs to be applied to mother-yearling pairs in spring to avoid giving them too much weight when estimating the percentage of calves because extra effort was also made to photograph mother-yearling pairs. However, the dive times of yearling bowheads whales are much longer than spring-born calves and so the 1.69 correction factor is not applied to mother-yearling pairs.

To accomplish these corrections, each image of a whale was given a weight. The single image of an unaccompanied calf identified by a post-survey length measurement was given a weight of 1/1.69. All other images of calves were given weights of 1/2.47, as were the images of their mothers. Images of a mother-yearling pair were given a weight of 1/1.46. All other images had weights of 1. Thus, summing the weights of the images of calves and of other whales during a given week of a given year and computing the percentage of calves as

$$100 \times (\text{sum of calf weights}) / (\text{sum of calf weights} + \text{sum of other whale weights})$$

is equivalent to counting the images requiring each correction factor, dividing by the correction factor and computing the percentage of calves from the corrected counts.

Compared to previous estimates based on aerial and ice-based surveys and photogrammetry studies, a relatively accurate and fully-corrected estimate of the percentage of calves in the population can be obtained by applying corrections for calves that pass before 14 May or are born after their mothers pass Point Barrow to the raw calf index described above. No calves were seen before 14 May during photogrammetry studies in years with low calf production (1985 and 1992, raw calf index <2%). Thus no correction for calves that passed before 14 May was made for low-calf years. During years with medium (2-5%) or high (>5%) calf production (1986, 1989-91 and 2003-4), an augmented calf index including a weekly period covering calves seen before 14 May was computed. The mean (augmented calf index)/(raw calf index) over these years is 1.046 (SD=0.054). Koski *et al.* (1993) compared the length-frequency distribution of mothers photographed at Point Barrow in spring with that of mothers in the summering

Table 1

The proportion of the migration estimated to pass Point Barrow, Alaska, during each weekly period as estimated from ice-based survey data from 1986, 1988, 1993 and 2001. Calf production was high in 1986 and 2001, relatively low in 1988 and 1993.

Years	<23 Apr.	23-29 Apr.	30 Apr.-6 May	7-13 May	14-20 May	21-27 May	>27 May
1986	0.0065	0.1110	0.1536	0.3144	0.2386	0.1025	0.0734
1988	0.0850	0.1554	0.2186	0.4030	0.0829	0.0104	0.0448
1993	0.0302	0.1701	0.2378	0.3417	0.1135	0.0719	0.0350
2001	0.0757	0.1275	0.2593	0.2192	0.1501	0.0821	0.0861
Mean proportions:							
All years	0.0494	0.1410	0.2173	0.3196	0.1463	0.0667	0.0598
High calf years	0.0411	0.1193	0.2065	0.2668	0.1944	0.0923	0.0798
Low calf years	0.0576	0.1628	0.2282	0.3724	0.0982	0.0412	0.0399

areas. They found that smaller mothers tended to have their calves later in the season, and most appeared to have calved after they had passed Point Barrow. Based on those data, they estimated that ~11% of bowhead whale calves were born after their mothers passed Point Barrow. Thus the fully-corrected estimate of percentage of calves is (raw calf index)/0.89 in low-calf years and 1.046 × (raw calf index) /0.89 in medium- and high-calf years.

Standard errors

Standard errors were obtained by bootstrapping with 100 bootstrap replications. The standard deviation (SD) of the 100 bootstrapped values provides the SE for the estimated correction factor or raw calf index value.

The dataset from which the 1.46 factor was computed included the number of photographs for each of 75 mother-calf pairs and 1,656 other whales. For each of 100 replications, a bootstrap sample of the mother-calf pairs and a bootstrap sample of the other whales was drawn and the bootstrapped value computed as

(mean photos per mother-calf pair) / (mean photos per other whale).

The SE for the 1.69 factor was computed similarly from a dataset with paired data on dive time and time at the surface following the dive for 248 dives made by 13 calves and 302 dives made by 77 other bowhead whales during spring migration near Point Barrow. In this case, bootstrapping was done on whales rather than dives since diving and surface times for the same whale are likely to be correlated; all the paired data for each whale in each calf and other bootstrap sample were included in the computations.

The variability of the 1.46 and 1.69 factors was incorporated in the SE of the raw calf index for a given year by computing bootstrapped values $B_{1.46}$ and $B_{1.69}$ for each of the 100 bootstrap replications. Within each bootstrap replication, images for each week were sampled separately and their weights computed using $B_{1.46}$ and $B_{1.69}$. The bootstrapped value of the raw calf index was then computed as described in the previous section.

No data are available for computing the SE of the 0.89 correction factor used in correcting the raw calf index to obtain the corrected percentage of calves. It was therefore treated as a constant in computing the SE of the corrected percentage by dividing the SE of the raw calf index by 0.89 to obtain $SE_{0.89}$. $SE_{0.89}$ is the SE of the corrected percentage for low-calf years.

For medium- and high-calf years, the year-to-year variability of the 1.046 factor, represented by the SD given above, must be incorporated to obtain the SE of the corrected percentage of calves. The usual approximate formula for estimating the variance of the product $1.046 \times R$, where R is the raw calf index for the year divided by 0.89, is (Goodman, 1960):

$$V(1.046 \times R) = 1.046^2 \times V(R) + R^2 \times V(1.046) + 2 \times 1.046 \times R \times \text{Covariance}(1.046, R)$$

where V denotes estimated variance. To assess the significance of the above covariance term, the correlation between (augmented calf index)/(raw calf index) and (raw calf index) for medium- and high-calf years was computed. This correlation was −0.6, and it was not significantly different from zero (P=0.173). Thus the covariance term in the above formula can be treated as zero. The negative sign of the correlation makes it unlikely that this will lead to $V(1.046 \times R)$ being negatively biased. $SE_{0.89}{}^2$ was used for $V(R)$ in the formula and 0.054^2 for $V(1.046)$. The square root of $V(1.046 \times R)$ estimates the SE of the percentage of calves in the population for a medium- or high-calf year.

Power analyses

Power analyses were conducted to evaluate the power to detect changes in calf production using the corrected calf index. Examination of the distribution of the corrected calf index suggested some pattern of high (>9%), medium (4%-7%) and low (<1%) years with gaps in between, not inconsistent with the observation by Rugh *et al.* (1992) that calving appears to increase every 3-4 years. While it is possible that sampling in future years will clarify such patterns, only nine years of data were available even when the incomplete 1987 and 1994 surveys were combined and treated as equivalent to an additional year. Therefore no attempt was made to incorporate patterns in the power analyses.

The distribution of available calf index values looks much more like a uniform distribution than a normal distribution, so parametric tests like the t-test are not appropriate. It seems reasonable for purposes of power calculations to model calf index values as a sample of size n=9 from a uniform distribution with lower limit 0 and upper limit θ, where θ is estimated by $(n+1)/n$ times the maximum corrected calf index value (Patel *et al.*, 1976, p.170). This estimate of θ is 11.6, and the mean of the corresponding uniform distribution is $\theta/2$=5.8 and the SD=3.35. This SD is quite close to that of the existing corrected calf index values, SD=3.75. It also seems reasonable to assume that if the average calf index value were reduced in the future, there would still be low-calf years with indices near zero, but values of the index in high-calf years would not be as high as at present. This can be modelled by assuming these values are drawn from a uniform distribution with a smaller upper limit.

An appropriate test for such a change in distribution of the calf index is the Mann-Whitney test (Breiman, 1973, p.292). If the existing calf index values are denoted by $x_1,\ldots,x_n$ and m is the number of calf index values $y_1,\ldots,y_m$ observed during the period with lower average value, then the Mann-Whitney test statistic U is the sum over the x_ι of the number of y_j that exceed x_ι. If the distributions of x_ι and y_ς are in fact the same, for $n \geq 9$ and $m \geq 9$, U is approximately normal with expected value $nm/2$ and variance $nm(n+m+1)/12$. Thus U can be standardised and compared to quantiles of a normal distribution with mean zero and variance one.

For this study, a one-sided test was appropriate as only if the y_j had a lower average value (i.e. U was small) would it be of concern. The null hypothesis (the x and y distributions are the same at the 10% level) was rejected if the standardised value of U was less than -1.28. Tests were done at the 10% rather than the 5% level to gain more power to detect a reduction in the calf index. Power was determined by simulating 1,000 samples in which the y distribution had a smaller θ than the x distribution (reductions of 40%, 50% and 60%) and either m=n=9, m=12 or m=18.

RESULTS

The proportion of the population that was estimated to have passed Point Barrow during each weekly period during each of the survey years is shown in Table 1. 1985 was excluded because of the unusual migration timing in that year (see the 1985 proportions in Table 3 and Koski *et al.* (2006)). The mean proportions over all four years in Table 1 were considered to be representative of the proportions during seasons with medium calf production. The mean proportions over high and lower calf years were assumed to be representative of the proportions passing in such years.

Table 2 shows numbers of photographs of calves and other whales (non calves) near Point Barrow during each of the weekly periods during 1985-86, 1989-92 and 2003-04. In each of these years, flights were made on 10 or more days from 14 May through 7 June, with several days representing each week. The incomplete 1987 and 1994 surveys had flights after 13 May on only 4 and 3 days, respectively, and one of the weeks was missed completely in each year. Table 2 includes all photographs, whether or not length data were available, because calves can be identified based on their colouration and morphology. The inclusion of unmeasured whales of all sizes resulted in larger samples for the calf index calculations.

Table 3 shows the percentages of calves during each weekly period after all corrections for differential detection of mother-calf pairs and increased numbers of photographs of mothers and yearlings or calves versus other whales. The survey proportions used in computing the calf index are also shown in Table 3. The raw calf index for each year, was calculated as

$$\Sigma \text{ Proportion}^{1} \times \% \text{ Calves}$$

for each weekly period and is shown in the right hand column. Table 4 also shows the raw calf index, with corrections that can be made to convert index values to % calves in the population, shown with its SE for each year.

The power to detect 40%, 50% and 60% reductions in the maximum of the corrected calf index distribution is shown in Table 5. Clearly there is little power to detect reductions of 40% or less in this maximum at any of the sample sizes compared; even with 18 years of samples after a 40% decline, power is only 68%. To have adequate power to detect a 50% reduction, 12 to 18 years of samples are needed. Additional baseline samples (i.e. before any reduction occurs) would increase n and therefore increase power.

DISCUSSION

The calf index developed in this paper provides a robust method of monitoring trends in calf production at a much lower cost than through ice-based or aerial surveys covering the entire spring migration. Furthermore, the calf index can become a direct estimate of the percentage of calves in the population by incorporating bias corrections for the few whales born before the surveys started and by accounting for calves that are born after their mothers pass Point Barrow. These estimates of calving rates could be used during periodic reviews of the status of B-C-B bowheads whales as they provide data to evaluate whether annual calving rates are within the range tested for the purposes of reviewing the B-C-B bowhead whale *SLA*. They also provide data for evaluating the effect of environmental variability on calving rates. When environmental variability is ignored, estimates of Maximum Sustainable Yield Rate (MSYR) could be substantially positively biased, which may mean that allowable harvest rates could be overestimated (IWC, 2009).

If photogrammetry studies are used to compute the calf index, adjustments should be made for the increased number of photographs of mother-calf pairs in comparison to other

Table 2

Numbers of images of calves and other whales photographed near Point Barrow, Alaska, during spring photography studies. All photographs are included whether or not length data are available. All images are classified as a calf or non-calf based on morphology.

	14-20 May			21-27 May			>27 May		
Year	Others	Calves	% Calves*	Others	Calves	% Calves	Others	Calves	% Calves
1985	564	0	0.0%	152	0	0.0%	311	22	6.6%
1986	80	16	16.7%	132	42	24.1%	57	37	39.4%
1989	88	5	5.4%	68	65	48.9%	37	36	49.3%
1990	104	12	10.3%	27	26	49.1%	32	22	40.7%
1991	93	37	28.5%	109	34	23.8%	16	9	36.0%
1992	114	0	0.0%	51	0	0.0%	37	18	32.7%
2003	39	0	0.0%	69	48	41.0%	149	94	38.7%
2004	176	97	35.5%	47	38	44.7%	281	63	18.3%
All years	**1,258**	**167**	**11.7%**	**655**	**253**	**27.9%**	**609**	**301**	**33.1%**

*Before corrections.

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[1] See Table 3 for a detailed description of ‘Proportion’.

Table 3

Calculation of the raw calf index as described in the methods using photography data from Table 2. The numbers from Table 2 (both calves and others) have been corrected for the higher probability of encountering a mother-calf pair (/1.69) and the tendency to take more photographs of mothers and calves than other whales (/1.46) when calculating the % calves during each weekly period.

		Weekly period							
		14-20 May		21-27 May		>27 May		Raw calf index	
Year	Calf production	Proportion*	% Calves	Proportion	% Calves	Proportion	% Calves	% Calves	SE
1985	Low	0.3850	0.00	0.1194	0.00	0.2464	2.96	0.73	0.20
1986	High	0.2386	8.42	0.1025	13.98	0.0734	30.35	5.67	0.79
1989	High	0.1944	2.37	0.0923	43.58	0.0798	48.34	8.34	0.82
1990	High	0.1944	4.78	0.0923	46.49	0.0798	32.73	7.83	0.91
1991	Medium	0.1463	17.43	0.0667	12.76	0.0598	25.49	4.93	0.89
1992	Low	0.0982	0.00	0.0412	0.00	0.0399	22.10	0.88	0.18
2003	Medium	0.1463	0.00	0.0667	34.15	0.0598	29.43	4.04	0.38
2004	High	0.1944	25.02	0.0923	35.49	0.0798	9.26	8.88	0.93
Mean of all years								**5.16**	

*The proportion of the migration is from aerial and ice-based visual and acoustic surveys. For years without an ice-based survey, the mean proportions of the highest two ice-based survey years in terms of percent calves seen (1986 and 2001) were used for the high calf production years, the mean of 1988 and 1993 for the low production years and the mean of all four of these years for the medium production years (Table 1). The 1985 ice-based survey proportions were used only for 1985 because the migration that year was unusually late (Koski *et al*., 2006). The characterisation of years without an ice-based survey as high, low or medium was based on first computing the raw calf index using the "medium" proportions and defining low as ≤2%, medium as 2%-5% and high as >5%.

Table 4

Raw calf indices for the years 1985-86, 1989-92 and 2003-04 and correction factors that can be applied to those indices to estimate the percentage of calves in the population. The <14 May correction is 1.046× for medium and high calf years; no correction was applied for low calf years. The correction for calves born east of Barrow is to divide by 0.89. The estimated percentage of calves and its SE are shown for each year.

	Raw calf index		Adjustment for calves		Corrected calf index	
Year	% Calves	SE	<14 May 1.046× or 1.000×	Born east of Barrow (/0.89)	% Calves	SE
1985	0.73	0.20	0.73	0.82	0.82	0.22
1986	5.67	0.79	5.93	6.37	6.66	0.99
1989	8.34	0.82	8.72	9.37	9.80	1.09
1990	7.83	0.91	8.19	8.80	9.20	1.17
1991	4.93	0.89	5.16	5.54	5.79	1.09
1992	0.88	0.18	0.88	0.99	0.99	0.20
2003	4.04	0.38	4.23	4.54	4.75	0.51
2004	8.88	0.93	9.29	9.98	10.44	1.22
Mean of all years	**5.16**		**5.39**	**5.80**	**6.06**	

Table 5

Power to detect various percent reductions in the maximum of the corrected calf index distribution with n=9 baseline samples and various sample sizes m for the index after the reduction in the maximum.

	Percent reduction		
m	40%	50%	60%
9	57%	70%	85%
12	62%	76%	87%
18	68%	82%	90%

whales as documented by Koski *et al*. (2006). In future analyses, the correction factor to account for increased effort to photograph mothers and calves in comparison to other whales should be calculated for each specific survey with adequate data. The value of 1.46 is based on a dataset that does not include 2003 or 2004 data.

If the calf index is calculated using aerial survey data, the index will be negatively biased; earlier studies have shown that some calves are missed during aerial surveys unless mothers with calves are circled for extended periods of time (Davis *et al*., 1983; Koski *et al*., 1993). With some circling of whales this bias can be minimised.

Although ice conditions near Point Barrow have been highly variable from year to year, the timing of the migration has been similar in all years of photogrammetry studies except 1985. Available evidence indicates a delayed migration in 1985 (Koski *et al*., 2006). Since the migration is size-structured (Angliss *et al*., 1995; Koski *et al*., 2006; Withrow and Angliss, 1992; 1994), length data from photographs collected during calf index surveys can be used to assess whether the migration timing was typical or unusual. If the timing were unusual, the length data could be used to adjust the index for the unusual timing in that season as was done by Koski *et al*. (2006) for the 1985 data.

Koski *et al*. (2006) noted that the proportion of the migration that passes Point Barrow late in the season (see Table 1) may have been underestimated during their and past studies, particularly in years with high calving success. The inclusion of different proportions of the migration for weekly periods, depending on whether the season was a low-, medium- or high-calf year, is a significant improvement over the average proportion used by Koski *et al.* (2006). During years with relatively low calf production, ~17.9% of the migration passed Point Barrow after 13 May but during high-calf years ~36.6% passed during that same period (Table 1). The procedure used by Koski *et al.* (2006) underestimated the percent calves in the population during medium- and high-calf years and overestimated the percent during low-calf years, but during low-calf years, the percentage of calves was so low that the mean value was underestimated. Further analyses of the 2003 and 2004 photogrammetry data may be useful in assessing the proportion of the migration that passed Point Barrow late in these seasons.

Monitoring of the percentage of calves in the B-C-B bowhead whale population using the calf index suggested above will permit detection of changes in reproductive success that may be used to warn of a possible change in the rate of increase or decrease in population size before it becomes detectable by a change in the population estimates. This information may be useful during periodic reviews of the status of B-C-B bowhead whales. Previous studies have found that the percentage of calves has varied widely from year to year (Angliss *et al.*, 1995; Koski *et al.*, 1993), so several years of surveys would be needed to cover the range of variation in calving that can be seen in Table 4.

Power analyses (Table 5) indicate that the power to detect a reduction in the maximum of the calf index distribution is low unless the reduction is large. Eighteen years of calf indices after a decline has occurred are required to have a 68% chance of detecting a 40% decline in the maximum of the calf index distribution. Nine years are adequate to detect a decline of 60% or more. In fact, if five years of calf index values after a decline of 60% were tested there would be a 78% chance of detecting that a decline had occurred. The low power to detect smaller declines is due more to the large year-to-year variability in the percentage of calves in the population than to the relatively small SE of the corrected percentages shown in Table 4. Power increases if additional years of data are collected before a decline in calf production occurs. Additional years of data would also aid in assessing whether the variability in % Calves is adequately modelled by the variability of a sample from the uniform distribution assumed in the power calculations. Although not all sources of variability have been captured in these calculations, we believe that the uncaptured variability would not have a significant impact on the calf index values that were calculated (Table 6).

At the population level, reproductive success in cetaceans appears to be influenced by many factors. The age structure of a population determines the number of mature females that are available to have calves. A growing population with many immature animals, such as the B-C-B bowhead whale population, would have a smaller proportion of mature females than a stable population. The age structure can also be influenced by whaling, predation or other sources of mortality. Changes in the age at first calving and the frequency of calving after whales become sexually mature can have marked effects on the percentage of calves in the population. Both are probably influenced by the body condition of individual whales. That is, whales with good body condition may become sexually mature at an earlier age (Gabriele *et al.*, 2007), and once sexually mature, they probably have calves at more frequent intervals than nutritionally stressed whales. There is strong evidence that in at least some cetaceans the adult females become nutritionally stressed following calving. For example, Pettis *et al.* (2004) found that female North Atlantic right whales (*Eubalaena glacialis*) were significantly thinner during calving years and the year after giving birth than the year before giving birth.

The availability of food has an obvious and direct effect on body condition and reproductive success as demonstrated by Perryman and Lynn (2002) and Perryman *et al.* (2002; 2004). Rice and Wolman (1971) noted seasonal differences in body mass of gray whales, and later Perryman and Lynn (2002) found a significant difference in the length/width ratios of southbound and northbound gray whales, indicating that two months of fasting in wintering areas resulted in measurable differences in body condition. Perryman *et al.* (2002; 2004) found a strong correlation between dates of retreat of sea ice in gray whale summer feeding areas and calf production. A longer feeding season resulted in higher calf production which was presumably related to gray whale mothers either feeding for longer or obtaining higher quality food during years with early ice retreat. The calf index studies that are recommended here for bowhead whales will not identify the cause of changes in reproductive success, but they will identify that they are occurring. Also, if photogrammetry data are collected to calculate the calf index, morphometric measurements from the photographs will provide information on the body condition of whales that can be useful for evaluating changes in calving rates.

If calf index surveys incorporated aerial photography, they would be a relatively economical method of obtaining additional data to refine and update B-C-B bowhead whale population parameters such as estimates of calving intervals (Miller *et al.*, 1992; Rugh *et al.*, 1992) and adult survival (Zeh *et al.*, 2002). Long-term photogrammetry studies of southern right whales (*E. australis*) have shown that by concentrating photographic effort on adult females, key reproductive and life-history parameters could be obtained. Payne *et al.* (1990) obtained estimates of survival, population growth, calving intervals and age of first calving for southern right whales, and with additional years of data Cooke *et al.* (2001) were able to improve the precision of earlier estimates. Best *et al.* (2001) estimated the same parameters using right whale photographs obtained along the south coast of Africa during a 28-year period.

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Table 6

Evaluation of factors that could affect calculation of the calf index and of whether variation that has not been quantified is likely to be consequential to use of the index for comparing year-to-year variation in the percentage of calves in the B-C-B bowhead whale stock.

Factors that could affect the calf index	Impact of the factor on index values	Has uncertainty been quantified?	Is unquantified uncertainty likely to be consequential?
Variability in proportion of population passing each week in low, medium and high calf years	Minor impact expected	No; few years with proportion data are available	No; believed to be much lower than variation between low, medium and high calf years
Variability of percentage of calves passing in each week in low, medium and high calf years	Major impact expected in medium and high calf years but data are collected during each survey	Yes; uncertainty is included in SE in Table 4	
Survey misses one or more days in a week	Little provided surveys conducted on 2-3 other days during the weekly period	Yes; included in SE in Table 4	
Encounter rates of mother-calf pairs vs others	Major impact before corrections but minor after corrections	Yes; 1.69 (SE=0.14) times as likely to encounter mother-calf pair as other whales; included in SE in Table 4	No; some minor variability remains due to effects of year-to-year variation in ice on encounter rates
Extra photographs of mother-calf pairs	Major before corrections but little after corrections; future surveys will correct for bias using survey-specific data	Yes; 1.46 (SE=0.17) times as many photos of mother-calf pairs as other whales; included in SE in Table 4	No
Lingering in study area	Minor	Partially accounted for in above correction	No; minimum impact on year-to-year comparisons for use of index, but may result in positive bias in estimates of % calves
Births before 14 May	Minor	Yes; 1.046 (SD=0.054); included in last SE column in Table 4	No; correction is small compared to year-to-year variation in % calves; better quantification possible with additional surveys
Calves born east of Barrow	Minor	No; summer surveys required in same year	No; little variability expected; late season calving is by primiparous females which are recruited at low rate; correction small compared to year-to-year variation in % calves

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REFERENCES

Angliss, R.P., Rugh, D.J., Withrow, D.E. and Hobbs, R.C. 1995. Evaluations of aerial photogrammetric length measurements of the Bering-Chukchi-Beaufort Seas stock of bowhead whales (*Balaena mysticetus*). *Rep. int. Whal. Commn* 45: 313-24.

Best, P.B., Brandão, A. and Butterworth, D.S. 2001. Demographic parameters of southern right whales off South Africa. *J. Cetacean Res. Manage. (special issue)* 2: 161-69.

Breiman, L. 1973. *Statistics: with a view towards applications*. Houghton Mifflin Company, Boston. 399pp.

Cooke, J.G., Rowntree, V.J. and Payne, R.S. 2001. Estimates of demographic parameters for southern right whales (*Eubalaena australis*) observed off Península Valdés, Argentina. *J. Cetacean Res. Manage. (special issue)* 2: 125-32.

Cooper, L.W., Ashjian, C.J., Smith, S.L., Codispoti, L.A., Grebmeier, J.M., Campbell, R.G. and Sherr, E.B. 2006. Rapid seasonal sea-ice retreat in the Arctic could be affecting Pacific walrus (*Odobenus romarus divergens*) recruitment. *Aquat. Mamm.* 32(1): 98-102.

Davis, R.A., Koski, W.R. and Miller, G.W. 1983. Preliminary assessment of the length-frequency distribution and gross annual reproductive rate of the western Arctic bowhead whale as determined with low-level aerial photography, with comments on life history. Paper SC/35/PS5 presented to the IWC Scientific Committee, June 1983, Brighton, UK (unpublished). i-ix+91pp+15 plates. [Paper available from the Office of this Journal].

Gabriele, C.M., Straley, J.M. and Neilson, J.L. 2007. Age at first calving of female humpback whales in southeastern Alaska. *Mar. Mammal Sci.* 23(1): 226-39.

George, J.C., Suydam, R.S., Philo, L.M., Albert, T.F., Zeh, J.E. and Carroll, G.M. 1995. Report of the spring 1993 census of bowhead whales, *Balaena mysticetus*, off Point Barrow, Alaska, with observations on the 1993 subsistence hunt of bowhead whales by Alaska eskimos. *Rep. int. Whal. Commn* 45: 371-84.

George, J.C., Suydam, R.S., Zeh, J. and Koski, W.R. 2004a. Estimated pregnancy rates of bowhead whales from examinations of landed whales. Paper SC/56/BRG10 presented to the IWC Scientific Committee, July 2004, Sorrento, Italy (unpublished). 7pp. [Paper available from the Office of this Journal].

George, J.C., Zeh, J., Suydam, R. and Clark, C. 2004b. Abundance and population trend (1978-2001) of western Arctic bowhead whales surveyed near Barrow, Alaska. *Mar. Mammal Sci.* 20(4): 755-73.

Goodman, L.A. 1960. On the exact variance of products. *J. Am. Stat. Assoc.* 55: 708-13.

International Whaling Commission. 2009. Report of the MSYR Workshop, 16-19 November 2007, National Marine Mammal Laboratory, Alaska Fisheries Science Center, Seattle, WA, USA. *J. Cetacean Res. Manage.* 11(Supplement): In press.

Koski, W.R., Davis, R.A., Miller, G.W. and Withrow, D.E. 1993. Reproduction. pp.239-74. *In*: Burns, J.J., Montague, J.J. and Cowles, C.J. (eds). *The Bowhead Whale. Special Publication No.2*. The Society for Marine Mammalogy, Lawrence, Kansas. 787pp.

Koski, W.R., Miller, G.W., Richardson, W.J. and Würsig, B. 2004. Bowhead whale (*Balaena mysticetus*) mothers and calves during spring migration in the Alaskan Beaufort Sea: Movements, behaviour and life history data. Paper SC/56/BRG27 presented to the IWC Scientific Committee, July 2004, Sorrento, Italy (unpublished). 31pp. [Paper available from the Office of this Journal].

Koski, W.R., Rugh, D.J., Punt, A.E. and Zeh, J. 2006. An approach to minimise bias in estimation of the length-frequency distribution of bowhead whales (*Balaena mysticetus*) from aerial photogrammetric data. *J. Cetacean Res. Manage.* 8(1): 45-54.

Miller, G.W., Davis, R.A., Koski, W.R., Crone, M.J., Rugh, D.J., Withrow, D.E. and Fraker, M.A. 1992. Calving intervals of bowhead whales – an analysis of photographic data. *Rep. int. Whal. Commn* 42: 501-06.

Patel, J.K., Kapadia, C.H. and Owen, D.B. 1976. *Handbook of Statistical Distributions*. Marcell Dekker, Inc., New York. 302pp.

Payne, R., Rowntree, V., Perkins, J.S., Cooke, J.G. and Lankester, K. 1990. Population size, trends and reproductive parameters of right whales (*Eubalaena australis*) off Peninsula Valdes, Argentina. *Rep. int. Whal. Commn (special issue)* 12: 271-78.

Perryman, W.L., Donahue, M.A., Perkins, P.C. and Reilly, S.B. 2002. Gray whale calf production 1994-2000: Are observed fluctuations related to changes in seasonal ice cover? *Mar. Mammal Sci.* 18(1): 121-44.

Perryman, W.L. and Lynn, M.S. 2002. Evaluation of nutritive condition and reproductive status of migrating gray whales (*Eschrichtius robustus*) based on analysis of photogrammetric data. *J. Cetacean Res. Manage.* 4(2): 155-64.

Perryman, W.L., Watters, G.M., Schwartz, L.K. and Rowlett, R.A. 2004. Preliminary results from shore-based surveys of northbound gray whale calves in 2003 and 2004, with a comparison to predicted numbers based on the distribution of seasonal ice. Paper SC/56/BRG43 presented to the IWC Scientific Committee, July 2004, Sorrento, Italy (unpublished). 7pp. [Paper available from the Office of this Journal].

Pettis, H.M., Rolland, R.M., Hamilton, P.K., Brault, S., Knowlton, A.R. and Kraus, S.D. 2004. Visual health assessment of North Atlantic right whales (*Eubalaena glacialis*) using photographs. *Can. J. Zool.* 82: 8-19.

Rice, D.W. and Wolman, A.A. 1971. *The Life History and Ecology of the Gray Whale (Eschrichtius robustus)*. American Society of Mammalogists, Special Publication No. 3, Stillwater, Oklahoma. viii+142pp.

Rugh, D.J., Miller, G.W., Withrow, D.E. and Koski, W.R. 1992. Calving intervals of bowhead whales established through photographic identifications. *J. Mammal.* 73(3): 487-90.

Stirling, I., Lunn, N.J. and Iacozza, J. 1999. Long-term trends in the population ecology of polar bears in western Hudson Bay in relation to climatic changes. *Arctic* 52(3): 294-306.

Stirling, I. and Parkinson, C.L. 2006. Possible effects of climate warming on selected populations of polar bears (*Ursus maritimus*) in the Canadian Arctic. *Arctic* 59(3): 261-75.

Withrow, D. and Angliss, R. 1992. Length frequency of bowhead whales from spring aerial photogrammetric surveys in 1985, 1986, 1989 and 1990. *Rep. int. Whal. Commn* 42: 463-67.

Withrow, D. and Angliss, R. 1994. Length frequency of the bowhead whale population from 1991 and 1992 spring aerial photogrammetric surveys. *Rep. int. Whal. Commn* 44: 343-46.

Zeh, J., Poole, D., Miller, G., Koski, W., Baraff, L. and Rugh, D. 2002. Survival of bowhead whales, *Balaena mysticetus*, estimated from 1981-98 photo-identification data. *Biometrics* 58: 832-40.

Zeh, J.E. and Punt, A.E. 2005. Updated 1978-2001 abundance estimates and their correlations for the Bering-Chuckchi-Beaufort Seas stock of bowhead whales. *J. Cetacean Res. Manage.* 7(2): 169-75.

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Essential and non-essential elements in the bowhead whale: epidermis-based predictions of blubber, kidney, liver and muscle tissue concentrations

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ABSTRACT

Assessment of element concentrations in wildlife must address both nutritional and toxicological considerations. The liver, epidermis, muscle and kidney of the bowhead whale are rich in some essential and non-essential elements. Blubber tends to have lower concentrations of these elements. Various cetaceans have been evaluated for these elements using a variety of sample sources (live and dead stranded whales, bycaught animals, remote and capture-release biopsy techniques, hunter killed whales etc). One constant shared by these approaches is the sampling of epidermis and adjacent dermis (blubber). In this study, the ability of elemental concentrations in bowhead whale epidermal samples to predict the corresponding elemental concentrations in blubber, kidney, liver and muscle is investigated. Epidermal concentrations had no predictive value for copper (Cu), manganese (Mn), lead (Pb), selenium (Se) or zinc (Zn) in any of the other tissues evaluated, except that the epidermal measurement provided an upper bound for blubber concentration of Cu, Mn, Se and Zn. Epidermal concentrations of the four other elements considered were predictive for some other tissues. Arsenic (As) concentrations could be predicted in kidney, liver and muscle but not blubber, although the preponderance of samples with concentrations below the minimum level reported (MLR, also known as 'detection limit') and the small sample sizes that resulted from their omission suggest that these data should be interpreted with caution. Epidermal concentrations of cadmium (Cd) were strongly predictive for blubber and weakly predictive for muscle concentrations. Epidermal concentrations of mercury (Hg) were weakly predictive of blubber, liver and muscle concentrations. Epidermal concentrations of magnesium (Mg) were strongly predictive in blubber, kidney and liver but only weakly predictive in muscle. Thus epidermal biopsy cannot predict elemental concentrations in four key tissues in bowhead whales in most cases. Cobalt (Co) and molybdenum (Mo) were not detected in any epidermal samples. This inability of epidermal element concentrations to reflect concentrations in internal tissues is likely true for other mysticetes and perhaps for cetaceans in general. At a minimum, before using epidermal biopsies to predict internal tissue concentrations of elements, researchers must establish that a sound scientific basis exists for doing so. Such proof must be specific to the elements, species and tissues in question as well as based upon statistically adequate sample sizes.

KEYWORDS: BOWHEAD WHALE; ELEMENTS; EPIDERMIS; HEAVY METALS; TISSUES; STATISTICS

INTRODUCTION

The bowhead whale (*Balaena mysticetus*) is a large mysticete found in the Arctic waters of the Bering, Chukchi and Beaufort Seas (B-C-B stock) that feeds on marine invertebrates (Lowry, 1993). Native subsistence whalers hunt this species under regulation by the International Whaling Commission (IWC), National Oceanographic and Atmospheric Administration (NOAA) Fisheries Service (NMFS) and the Alaska Eskimo Whaling Commission (AEWC). This hunt provides a valuable opportunity to study nutrients and contaminants in a large number of what probably are healthy cetaceans.

Element interactions in the bowhead whale have previously been the subject of limited studies (Dehn *et al.*, 2006; Woshner *et al.*, 2001b). This paper reports on the prediction of element concentrations in blubber, liver, kidney and muscle from measurements of the elements in epidermis. Reports from numerous investigators have addressed element concentrations in various matrices and species of cetaceans from around the globe (André *et al.*, 1991; Beck *et al.*, 1997; Becker *et al.*, 2000; Bustamante *et al.*, 2003; Decataldo *et al.*, 2004; Dehn *et al.*, 2006; Fossi *et al.*, 2004; Frodello *et al.*, 2000; Fujise *et al.*, 1988; Honda and Tatsukawa, 1983; Honda *et al.*, 1983; Kuehl and Haebler, 1995; Kuehl *et al.*, 1994; Kunito *et al.*, 2002; Law *et al.*, 1991; Mackey *et al.*, 2003; Marcovecchio *et al.*, 1990; Meador *et al.*, 1999; Monaci *et al.*, 1998; Nigro *et al.*, 2002; O'Hara *et al.*, 2003; Roditi-Elasar *et al.*, 2003; Stein *et al.*, 2003; Wagemann *et al.*, 1996; Woods and Van Vleet, 1996; Yang *et al.*, 2002).

Attempts to evaluate levels of contaminants (e.g. organochlorines and mercury) and nutrients (e.g. copper) in wildlife using non-lethal and/or minimally invasive procedures have met with varying degrees of success, depending upon the species, sampling design, endpoint measured, environmental/habitat conditions and matrix of interest. For example, the use of hair for assessing some essential elements (e.g. copper) and for detecting non-essential 'toxic' elements (e.g. mercury and arsenic) in various mammalian species is well established (Beckmen *et al.*, 2002; Born *et al.*, 1991; Flynn *et al.*, 1975; Flynn *et al.*, 1977; Frank *et al.*, 1994; Gogan *et al.*, 1989; Ikemoto *et al.*, 2004; O'Hara *et al.*, 2001; Underwood, 1977; Wiig *et al.*, 1999). Thus, the suggestion that epidermis may be useful for evaluating the status of essential and non-essential elements in the animal more holistically (blubber, muscle, kidney and liver) has some scientific precedent. Epidermal biopsies (and underlying blubber) from free ranging cetaceans have been obtained remotely (i.e. using 'darts') and via capture, followed by surgical biopsy and release of the animal (Fossi *et al.*, 2004; Hansen *et al.*, 2004; Ylitalo *et al.*, 2001). It is

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important to emphasise that cetacean 'skin' is a food item and may be a target organ of concern or monitoring tool for mercury intoxication (Gauthier *et al.*, 1998) and thus has merit as a sampled tissue regardless of the correlation of element concentrations or predictive capacity for other tissues that were tested in this study.

With respect to 'toxic' elements and xenobiotics in bowhead whales, there are global sources of contaminants in general (De Wit *et al.*, 2004; Woshner *et al.*, 2001b) and local activities of concern (Ford and Hasselbach, 2001; O'Hara *et al.*, 2003), including Red Dog Mine, a zinc/lead/silver mine (162°49'04"W 68° 04'11"N). The proximity of the mine, port and haul road to the coast has caused concern among local communities regarding potential contamination of the environment. Oil activities within and surrounding Prudhoe Bay, Alaska, also raise concerns related to mobilisation of heavy metals. Aspects of the environmental chemistry and bioavailability of toxic elements have been addressed for some regions of the Southern Beaufort Sea and rivers draining this area (Trefry *et al.*, 2003).

The suitability of epidermal biopsies were tested for their use in determining the essential and/or non-essential element status of bowhead whales by sampling five tissues (epidermis, blubber, liver, kidney and muscle) and evaluating whether animal-matched tissue concentrations of elements could be predicted from the epidermal sample. The accumulation of particular elements in marine mammal tissues varies with element and organ type, reflecting tissue-specific physiological mechanisms (Decataldo *et al.*, 2004; Woshner *et al.*, 2001a; Woshner *et al.*, 2001b). Thus it was hypothesised that, for elements exhibiting organ-specific bioaccumulation, epidermis is unlikely to serve as a good indicator of either general status or specific internal organ concentration.

MATERIALS AND METHODS

Field sampling

The field sampling methods used in this study have been previously described (O'Hara *et al.*, 1999) and some of the data used in this report, from 15 whales harvested in 1996-1997, have been published (Dehn *et al.*, 2006; Woshner *et al.*, 2001b). Table 1 provides the basic data on all 48 whales studied (data derived from Suydam *et al.*, 2004; Suydam *et al.*, 2003; Woshner *et al.*, 2001b). Full-thickness blubber cores and various tissues (epidermis, kidney, liver and muscle) from bowhead whales were provided by native subsistence hunters in Barrow, Alaska, USA. Samples were collected by staff at the Department of Wildlife Management with the permission of the Alaska Eskimo Whaling Commission (AEWC) and Barrow Whaling Captains Association (Barrow, Alaska, USA). Epidermal and blubber cores from approximately the same location on each whale (dorsal midline, 1 meter caudal to the blowhole) were collected. Life history information was recorded from each whale harvested (body length, sex, etc.), see Table 1. Relationships among these parameters with respect to various elements have been described previously by Bratton *et al.* (1997), Woshner *et al.* (2001b), and Dehn *et al.* (2006) and are not repeated here. Samples were temporarily stored at −20°C at the Arctic Research Facility (Barrow, Alaska, USA) and temperature was maintained during transport to Texas A&M University (College Station, TX) via provision of the US Marine Mammal Protection Act (Permit No. 782-1399 and 932-1489-05).

Table 1

Whale identification number (ID), date landed (dd/mm/yy), length (m) and sex of bowhead whales landed by Alaskan Eskimos during the 1996/97, and 2002/03 subsistence hunts evaluated in this study.

Whale ID	Date landed	Sex	Length (meters)
96B1	25/04/96	F	8.46
96B2	03/05/96	F	7.65
96B3	05/05/96	F	7.63
96B4	24/05/96	F	14.38
96B5	29/05//96	F	14.9
96B22	24/09/96	M	11.63
96B23	26/09/96	M	7.59
96B24	26/09/96	F	10.87
97B1	04/05/97	M	10
97B3	07/05/97	F	16.97
97B5	10/05/97	F	10.08
97B6	12/05/97	F	8.3
97B7	12/05/97	F	13.15
97B8	15/05/97	F	13.9
97B10	04/06/97	F	16.71
02B1	03/05/02	F	11.7
02B2	10/05/02	F	16.7
02B3	30/05/02	F	19.2
02B4	30/09/02	F	8.6
02B5	01/10/02	F	8.5
02B6	03/10/02	M	9.0
02B7	03/10/02	M	8.0
02B8	03/10/02	F	6.8
02B9	10/10/02	F	7.5
02B10	10/10/02	M	9.5
02B11	15/10/02	F	8.1
02B13	15/10/02	M	9.6
02B14	18/10/02	F	8.5
02B15	18/10/02	M	8.8
02B16	19/10/02	M	8.3
02B17	19/10/02	F	9.3
02B21	22/10/02	F	10.0
02B22	25/10/02	F	8.1
03B1	19/04/03	F	9.1
03B2	03/05/03	M	13.8
03B3	07/05/03	F	9.0
03B4	08/05/03	M	13.4
03B5	08/05/03	M	7.7
03B6	09/05/03	F	13.9
03B7	12/05/03	M	12.8
03B8	24/05/03	M	14.9
03B9	25/05/03	F	16.4
03B11	08/10/03	F	8.7
03B12	09/10/03	F	11.2
03B13	09/10/03	M	11.9
03B14	09/10/03	M	11.1
03B15	14/10/03	F	12.5
03B16	14/10/03	F	10.1

The first two numbers of the ID indicate the year landed; the letter the village where landed (B = Barrow); and the final number(s) indicate the sequence in which it was landed (1=first) for that calendar year. Sample size 1996=8; 1997=7; 2002=18; 2003=15. The lengths reported are taken from Suydam *et al.* (2003; 2004) and Woshner *et al.* (2001b).

Minerals and metals analysis

Upon receipt in the laboratory, sample integrity was evaluated and samples were immediately transferred to secure freezers for storage until processed. All tissues were stored at −60°C until analysis. Tissues were thawed, homogenised by chopping in plastic weigh boats and microwave digested as previously described (Woshner *et al.*, 2001b). Samples were run in sets of 20 along with standard reference materials, SRMs (bovine liver 1577b, Dogfish liver Dolt 2, and Dogfish muscle Dorm 2), a blank, a blank spike (Lab Control Sample-LCS), a sample duplicate for each sample type, and a sample spike for each sample type. Two SRMs were used per sample set with the intent to bracket the expected analyte levels in the tissues being considered. In general, each type of tissue was digested separately, with pooling of tissue types for digestion only carried out when less than 20 tissues of a given type were received. Following digestion, all samples and QA (quality assurance) samples were diluted to 20ml with 18meg ohm water, a final weight was taken and the samples were density corrected. Digestates were stored tightly sealed until analysis was complete. All analytical work was generally completed within a month after digestion. Table 2 summarises the procedures used in this study.

Elements were analysed by atomic absorption spectrophotometry (AAS) at Texas A&M University (TAMU) Trace Element Research Laboratory (TERL) as in Woshner *et al*. (2001b) for those samples collected in 1996-1997, employing a strict quality assurance/quality control protocol with appropriate standard reference materials, sample duplicates, blanks and spiked samples. The following elements were analysed: arsenic (As), cadmium (Cd), cobalt (Co), copper (Cu), mercury (Hg), magnesium (Mg), manganese (Mn), molybdenum (Mo), lead (Pb), selenium (Se) and zinc (Zn). Neither Co nor Mo was detected in any epidermal sample, so they are not considered further. The remaining elements were detected in more than half of the samples for at least two tissues. Co, As, Mg, Mn, Pb, and Se were analysed using a *Perkin-Elmer* (Norwalk, Connecticut, USA) model SIMAA 6000 graphite furnace atomic absorption spectrophotometer (GFAAS) equipped with an AS-60 autosampler and Zeeman background correction (Perkin-Elmer); Cd and Zn were determined using a *Perkin-Elmer* instrument model 306 flame AAS; total Hg was determined via cold vapor AAS (AAS-CVG) using a Thermo-Jarrell Ash (Franklin, Massachusetts, USA) model S-11 AAS with a *Thermo-Jarrell Ash* AVA-440 atomic vapor accessory. The minimum level reported (MLR, also known as 'detection limit') for Hg was 0.001 µg/g. For total Hg analysis (at the Texas Veterinary Diagnostic Laboratory, Amarillo, Texas USA), wet tissue samples (1996-1997) were weighed and transferred to 250ml quartz volumetric digestion tubes. Sample digestion and analysis followed Korsrud *et al*. (1985) with minor modifications as reported in Woshner *et al*. (2001b). See Bratton *et al*. (1997) and Woshner *et al*. (2001b) for details. The minimum level reported for all elements except Hg was 0.01µg/g.

For samples collected in 2002-2003, subsample preparation and digestion followed the method previously described by Woshner *et al*. (2001b) and the analyses is similar to that reported by Dehn *et al*. (2006). Total mercury was determined using a cold-vapor atomic absorption spectrometry (CVAAS) method with a *Cetac* 7500 QuickTrace Hg analyser. Hg^{2+} was converted to Hg^0 by reduction with $SnCl_2$, purged from the digested sample with a stream of argon gas, and swept into a thermally-stabilised absorption cell. Concentrations were determined by absorbance peak height using commercial calibration standards.

Inductively coupled plasma-mass spectroscopy (ICP-MS) is a hyphenated technique in which a high-temperature, radio frequency argon plasma provides ions that are measured by a mass-specific detector. TERL uses a *Perkin-Elmer/Sciex* DRC-2 ICP-MS instrument equipped with a quadrupole detector. This instrument also employs a dynamic reaction cell to remove molecular ion interferences. Digested samples were diluted to a final strength of 2% nitric acid. The aqueous samples were introduced to the plasma using a peristaltic pump, concentric nebuliser, and cyclonic spray chamber. Internal standards were added to all samples to compensate for viscosity differences and slight variations in instrument performance related to sample matrix effects. The instrument was calibrated using a blank and three external standards. Calibration was evaluated using both a low standard and an independent check standard (NIST SRM 1640). Data were collected in dual pulse/analog mode using the instrument's autolens feature to maximise sensitivity at each target mass.

Digested samples were diluted to 20ml with trace metal free water and run directly on a *Spectro* CirOS axial inductively coupled plasma optical emission spectrometer (ICP-OES) (Spectro AI, Fitchburg, MA) for Cu, Mg, Mn, and Zn. Additional aliquots of the digestates were then diluted further by a factor of ten and run on a *Perkin-Elmer/Sciex* DRC-2 ICP-MS (Perkin-Elmer, Norwalk, CT) for As, Cd, Co, Mo, and Pb. A separate aliquot was diluted ten-fold in 3N HCL and analysed for Se using a *PSA* Millennium HG- Atomic Fluorescence Spectrometer (AFS) system (PSA Analytical Deerfield Beach, FL). A final aliquot of the original digestate was diluted by a factor of five in 7% v/v HCL and analysed for Hg using a *Cetac* M7500 CVAAS system (Cetac Technologies, Omaha, NE).

QA was considered in compliance when recovery for SRMs, blank spikes, and sample spikes was +/-20% for minerals/metals that were very low and close to baseline levels and +/-10% for mineral/metals that were considerably above baseline levels. Duplications were considered acceptable when +/-10% and the analyte was significantly above the baseline. Blanks were considered acceptable if <0.0001 ppm.

Statistical analysis

Summary statistics were generated using *Microsoft* Excel (Microsoft Corporation, 1999) and S-PLUS (Venables and Ripley, 1999). Plots of element concentrations (µg/g wet weight) in blubber, kidney, liver and muscle tissues versus

Table 2

Summary of the procedures used in this study.

Years collected	Number of whales	Procedure	Elements*	Published
1996-97	15	Atomic absorption spectrophotometry (AAS)	Arsenic (As), cadmium (Cd), cobalt (Co), Copper (Cu), mercury (Hg), magnesium (Mg), manganese (Mn), molybdenum (Mo), lead (Pb), selenium (Se) and zinc (Zn)	Woshner *et al.* (2001b); Dehn *et al.* (2006)
2002-03	33	Hg via AAS Others via ICP (see next column)	Mercury via cold-vapour atomic absorption spectrometry (CVAAS). Inductively coupled plasma-mass spectrometry (ICP-MS). Perkin-Elmer/Sciex DRC-2 ICP-MS for As, Cd, Co, Mo and Pb. Using ICP - optical emission spectroscopy (ICP-OES) (Spectro AI, Fitchburg, MA) for Cu, Mg, Mn and Zn	This paper
Total	48			

the corresponding concentration in epidermal tissue (E), whale body length in meters (length) and sex of the whale were used to explore relationships. The plots indicated linear relationships, so simple linear regressions and multiple regressions with E, length and sex as potential predictors of concentrations in blubber, kidney, liver and muscle were used. Length was used as a surrogate for age, recognising that it is a poor surrogate, particularly for physically mature whales. However, ages of most of the sampled whales were unknown. Plots and regressions for each tissue only include whales in which both E and the concentration in that tissue ≥MLR. This could provide a misleading assessment of predictive power for those elements with some tissue concentrations <MLR in some samples (As, Cd, Hg, Mn and Pb). For elements with both E<MLR and concentrations <MLR in the tissue being predicted using E, cross-tabulations were calculated giving the number of whales with concentrations: (1) <MLR; (2) ≥MLR but less than the median concentration among all samples with concentrations ≥MLR; and (3) greater than that median concentration. Independence of row and column classifications was evaluated by Fisher's exact test. If the null hypothesis of independence is not rejected, this provides evidence against a strong association between E and the concentration in the other tissue. However, if the number of samples available for the test is small, failure to reject the null hypothesis may be due to a lack of power.

The best regression for each element in each tissue was chosen by minimising Akaike's Information Criterion (AIC) (Akaike, 1973) among regressions involving E, length and sex. A model with either too few or too many predictors has poor predictive ability. AIC is designed to identify the best predictive model, with neither poor predictive ability owing to omission of relevant predictors, nor excess variability due to inclusion of extraneous predictors. AIC penalises added predictors less severely than other selection criteria such as likelihood ratio tests (Venables and Ripley, 1999), so it sometimes selects unnecessary predictors. The main utility of the best regression result is to assess further whether E is a more useful predictor of the element's internal organ concentration than length and sex, which are much easier to measure.

Both the regression with E as the only predictor and the best regression were evaluated using R^2, the percentage of the variability in the concentration being predicted that is explained by the regression. The regression is characterised as having no predictive value if $R^2 \leq 35\%$, weakly predictive if R^2 is 36% to 55%, moderately predictive if R^2 is 56% to 75% and strongly predictive if $R^2 > 75\%$. However, these characterisations are sometimes tempered by patterns in the cross-tabulations described above or the results of the Fisher's exact tests.

RESULTS AND DISCUSSION

General results, with comparisons to other species

Of the elements evaluated in this study, Mg, Mn, Cu, Zn and Se are considered essential (Table 3), while As, Cd, Pb and Hg have no known function in mammals and are considered non-essential (Table 4) and are sometimes referred to as the 'toxic' elements. A basic mammalian need for an element was used to define 'essential', even if the element had not been specifically evaluated for cetaceans. This assumption may be somewhat inappropriate considering the many known morphologic and physiologic differences between cetaceans and terrestrial mammals. The non-essential elements important for toxicological assessment in the Arctic food chain include Cd, Hg and Pb (AMAP, 1998; 2002). All of the elements assayed in this study were below concentrations associated with toxic effects in domestic animals (Puls, 1994), although this extrapolation between terrestrial and marine mammals may be misleading (André *et al*., 1991; Beck *et al*., 1997; Bustamante *et al*., 2003; Decataldo *et al*., 2004; Frodello *et al*., 2000; Honda *et al*., 1983).

Compared to other species of northern Alaska, the bowhead whales used in this study had much lower tissue concentrations of Hg, in agreement with the reports of Dehn *et al*. (2006), Woshner *et al*. (2001b) and Bratton *et al*. (1997). It is well described that element-element interactions with length (age) exist, particularly for Hg and Se in marine mammals, especially odontocetes (Honda and Tatsukawa, 1983; Honda *et al*., 1983). Thus considering these interactions in a tissue specific manner by species for age (length) and sex is very important. The details of these relationships are not reviewed in this report since they have been documented elsewhere (note citations above).

Among marine mammals, Cd appears to be higher in species with an invertebrate-based diet (e.g. similar to walrus), and the Cd concentrations reported here are similar to concentrations previously reported for bowhead whales (Bratton *et al*., 1997; Dehn *et al*., 2006; Woshner *et al*., 2001a; Woshner *et al*., 2001b). Bowhead whales, like other mammalian species, have been shown to accumulate Cd with age in the liver (Honda and Tatsukawa, 1983; Honda *et al*., 1983) and particularly in the kidney, with variations in the rate of accumulation occurring by region (Aastrup *et al*., 2000; Cooper *et al*., 2000; Elkin and Bethke, 1995; Gamberg and Scheuhammer, 1994; Honda and Tatsukawa, 1983; Honda *et al*., 1983; Larter and Nagy, 2000; O'Hara *et al*., 2001; O'Hara *et al*., 2003; O'Hara *et al*., 1999; Woshner *et al*., 2001a; Woshner *et al*., 2001b).

For both Cd and As, over half the epidermal samples had E<MLR (Table 4), resulting in sample sizes <20 for the regression analyses. Although regression results are discussed for these elements, they are omitted from Table 5 for this reason. Blubber was less frequently sampled than the other tissues, resulting in sample sizes <20 for all elements. This is included in Table 5, but the small sample sizes mandate caution in interpreting blubber results.

Concentrations of essential elements

Magnesium

All 48 epidermal samples had concentrations of Mg above the MLR. The best single predictor of Mg in all four other tissues is E, which is weakly predictive for muscle but strongly predictive for the other three. The best regression for Mg, as determined by AIC, always includes E. In addition, length was also included for all tissues except blubber. In kidney, liver and muscle tissue, concentrations of Mg increase with E and decrease with length. The best regression for blubber, kidney and liver explains 83-90% of the variability in Mg in these tissues. Even the best regression for muscle is only moderately predictive, explaining 57% of the variability of Mg. Based on Puls (1994), the Mg status of mammals may best be assessed using other tissues (e.g. blood) and/or fluids (plasma, urine, etc.). The role of cetacean epidermis in Mg elemental dynamics and tissue tropism requires further investigation.

Manganese

Manganese was detected in fewer than half of the 2002/03 epidermal and blubber samples analysed using ICP-OES, while low Mn levels were detected in these tissues by AAS

Table 3

Summary statistics for essential elements for bowhead whales sampled in 1996/97 (analysed using AA*) and 2002/03 (analysed using ICP or AFS**) in epidermis, liver, kidney, muscle and blubber. All statistics are based on the *N* samples with concentrations ≥MLR***.

	Cu-AA	Cu-ICP	Mg-AA	Mg-ICP	Mn-AA	Mn-ICP	Se-AA	Se- AFS	Zn-AA	Zn-ICP
Epidermis										
Mean	0.53	0.34	521	172	0.056	0.075	0.75	0.64	15.2	12.5
SD	0.10	0.09	41	17	0.023	0.048	0.36	0.14	2.1	1.8
Minimum	0.37	0.22	448	136	0.030	0.037	0.14	0.39	11.1	9.9
Maximum	0.75	0.72	604	202	0.100	0.229	1.32	0.86	19.2	18.7
Geometric mean	0.52	0.33	520	171	0.053	0.066	0.64	0.63	15.0	12.3
Total samples	15	33	15	33	8	33	15	33	15	33
Liver										
Mean	11.02	4.91	298	123	2.07	1.24	1.98	1.07	39.3	34.5
SD	13.35	1.42	44	19	0.61	0.48	0.40	0.33	14.7	11.1
Minimum	2.53	3.08	220	91	1.39	0.45	1.39	0.50	19.7	23.6
Maximum	54.00	8.96	396	178	2.96	2.43	2.56	1.79	76.4	65.1
Geometric mean	7.33	4.74	295	122	1.99	1.15	1.95	1.02	37.0	33.0
Total samples	14	34	14	34	14	34	14	34	14	34
Kidney										
Mean	2.35	1.65	298	91	0.53	0.36	1.78	1.29	34.8	21.1
SD	0.69	0.26	108	10	0.18	0.08	0.40	0.27	9.8	8.4
Minimum	1.40	1.13	142	72	0.30	0.20	0.95	0.77	23.0	12.7
Maximum	3.29	2.29	480	132	0.87	0.55	2.32	2.04	56.3	57.2
Geometric mean	2.25	1.63	278	91	0.50	0.35	1.73	1.26	33.6	19.9
Total samples	14	33	14	33	14	33	14	33	14	33
Muscle										
Mean	0.90	0.57	468	232	0.17	0.12	0.14	0.20	51.6	36.3
SD	0.22	0.10	220	23	0.08	0.04	0.03	0.03	12.3	9.1
Minimum	0.53	0.36	203	180	0.07	0.05	0.08	0.13	33.2	24.7
Maximum	1.25	0.76	753	268	0.30	0.18	0.17	0.25	76.6	62.8
Geometric mean	0.87	0.56	416	231	0.15	0.11	0.14	0.19	50.3	35.4
Total samples	15	33	15	33	8	33	15	33	15	33
Blubber										
Mean	0.12	0.13	47.0	14.5	0.020	0.036	0.09	0.10	5.51	0.93
SD	0.04	0.02	11.1	3.2	0.007	NA	0.04	0.03	1.61	0.16
Minimum	0.06	0.10	33.0	9.4	0.010	0.036	0.05	0.06	3.85	0.71
Maximum	0.18	0.16	64.0	18.6	0.030	0.036	0.17	0.14	7.55	1.16
Geometric mean	0.12	0.13	46.0	14.2	0.019	0.036	0.08	0.10	5.32	0.92
Total samples	12	6	5	6	5	6	12	6	5	6

*AA = atomic absorption spectrophotometry (AAS). **ICP = inductively coupled plasma - mass spectroscopy (ICP-MS) or inductively coupled plasma - optical emission spectroscopy (ICP-OES), or Atomic Fluorescence Spectrometry (AFS). MLR = minimum level reported. ***All samples reported in this Table were > MLR, except Mn-ICP has 55% (18) and 83% (5) of epidermis and blubber <MLR, respectively.

(Woshner *et al.*, 2001b). Epidermal Mn is of no value as a predictor of Mn in any of the other four tissues. In no case is it chosen as a predictor by AIC. The mean (intercept) is the best predictor for kidney, liver and muscle. Although sex is weakly predictive for blubber, only six whales with Mn reported in both epidermal and blubber tissue were included in this analysis. A larger sample would be needed to determine whether sex is really a useful predictor of Mn in blubber.

In all 11 whales with both blubber and epidermal samples analysed, blubber concentration of Mn was lower than epidermal. This suggests that epidermal concentration could provide an upper bound for blubber concentration of Mn in bowheads with epidermis but not blubber sampled. However, Table 3 suggests that this would considerably overestimate blubber concentration.

Copper, Selenium and Zinc

Copper is an essential element reported to be at higher concentrations in foetal and neonatal bowhead whales that decreases with length (age) (Bratton *et al.*, 1997; Woshner *et al.*, 2001b) and Cu and Zn occur at similar concentrations in odontocetes (Decataldo *et al.*, 2004; Honda and Tatsukawa, 1983; Woods and Van Vleet, 1996). However, the Se concentration tends to be much higher in odontocetes (Kuehl and Haebler, 1995; Kuehl *et al.*, 1994; Mackey *et al.*, 2003). The best regressions for Cu in blubber, kidney and muscle in Table 5 support these reports.

Concentrations of Cu, Se and Zn were above the MLR in all epidermal samples. Nevertheless, E had no predictive value for concentrations of these elements in other tissues, despite the fact that AIC occasionally included E as a predictor for a given element-tissue combination. Among regression analyses for these three elements, even the best regression that included E (for Cu in muscle) accounted for only 25% of the variability (Table 5). However, as was the case for Mn, all blubber concentrations of Cu, Se and Zn were below the corresponding epidermal concentrations, so epidermal concentrations may constitute an upper bound for blubber concentrations with respect to these three elements.

Concentrations of non-essential elements

Cadmium

Cadmium occurs at lower concentrations in the epidermis than in the other tissues examined, with E<MLR in 24 (59%) of the 41 epidermal samples analysed (Table 4),

Table 4

Summary statistics for non-essential elements for bowhead whales sampled in 1996/97 (analysed using AA*) and 2002/03 (analysed using ICP**) in epidermis, liver, kidney, muscle and blubber. All statistics except the medians are based on the *N* samples with concentrations ≥MLR.

	As-AA	As-ICP	Cd-AA	Cd-ICP	Pb-AA	Pb-ICP	Hg-AA	Hg-AA#
Epidermis								
Mean	0.078	0.491	0.013	0.010	0.012	0.008	0.007	0.017
SD	0.049	0.091	0.006	0.009	0.005	0.003	0.004	0.010
Minimum	0.020	0.380	0.010	0.004	0.010	0.004	0.003	0.004
Maximum	0.160	0.660	0.020	0.039	0.020	0.016	0.014	0.037
Geometric mean	0.063	0.485	0.013	0.008	0.012	0.007	0.006	0.014
N ≥ MLR	15	7	3	14	4	19	7	29
N < MLR	0	26	5	19	4	14	1	4
Total samples	15	33	8	33	8	33	8	33
Median of total samples	0.070	<MLR	<MLR	<MLR	<MLR	0.006	0.005	0.016
Liver								
Mean	0.122	0.538	7.86	9.47	0.015	0.015	0.029	0.051
SD	0.029	0.146	9.16	11.14	0.007	0.007	0.015	0.039
Minimum	0.080	0.380	0.04	0.28	0.010	0.006	0.004	0.009
Maximum	0.160	0.820	30.50	42.20	0.030	0.030	0.052	0.194
Geometric mean	0.118	0.520	1.99	3.99	0.014	0.014	0.024	0.038
N ≥ MLR	13	13	14	34	11	34	14	34
N < MLR	1	21	0	0	3	0	0	0
Total samples	14	34	14	34	14	34	14	34
Median of total samples	0.120	<MLR	4.900	5.850	0.010	0.013	0.031	0.051
Kidney								
Mean	0.089	0.453	20.84	13.95	0.020	0.008	0.022	0.032
SD	0.071	0.055	22.15	15.01	0.017	0.003	0.012	0.032
Minimum	0.020	0.400	0.10	0.47	0.010	0.005	0.006	0.003
Maximum	0.240	0.510	62.18	70.20	0.040	0.015	0.050	0.180
Geometric mean	0.064	0.451	6.17	6.31	0.016	0.008	0.018	0.022
N ≥ MLR	14	3	14	33	3	21	14	33
N < MLR	0	30	0	0	11	12	0	0
Total samples	14	33	14	33	14	33	14	33
Median of total samples	0.050	<MLR	12.38	14.10	<MLR	0.005	0.022	0.029
Muscle								
Mean	0.029	0.608	0.100	0.044	NA	0.016	0.013	0.020
SD	0.015	0.187	0.116	0.057	NA	0.017	0.008	0.012
Minimum	0.010	0.410	0.010	0.007	NA	0.006	0.001	0.003
Maximum	0.050	0.830	0.300	0.212	NA	0.066	0.021	0.040
Geometric mean	0.025	0.584	0.057	0.026	NA	0.012	0.009	0.016
N ≥ MLR	8	5	5	22	0	15	8	33
N < MLR	0	28	3	11	8	18	0	0
Total samples	8	33	8	33	8	33	8	33
Median of total samples	0.030	<MLR	0.020	0.016	<MLR	<MLR	0.013	0.022
Blubber								
Mean	1.376	1.305	0.038	0.012	0.020	0.008	0.002	0.006
SD	0.355	0.366	0.017	0.002	0.007	0.003	0.001	0.001
Minimum	0.770	0.770	0.020	0.009	0.010	0.006	0.001	0.005
Maximum	1.920	1.770	0.060	0.015	0.030	0.012	0.003	0.008
Geometric mean	1.328	1.258	0.035	0.011	0.019	0.008	0.002	0.006
N ≥ MLR	12	6	4	5	5	4	3	5
N < MLR	0	0	1	1	0	2	2	1
Total samples	12	6	5	6	5	6	5	6
Median of total samples	1.430	1.325	0.030	0.011	0.020	0.006	0.001	0.006

As=arsenic; Cd=cadmium; Pb=lead; Hg=mercury; *AA=atomic absorption spectrophotometry (AAS); **ICP=inductively coupled plasma - mass spectroscopy (ICP-MS) or inductively coupled plasma - optical emission spectroscopy (ICP-OES); MLR=minimum level reported; NA=not available. #=2002/03 samples for Hg.

compromising prediction of Cd concentrations in other tissues using E. For E≥MLR for Cd (Table 5, Fig. 1), E was strongly predictive of blubber concentration and weakly predictive of muscle concentration, but had no predictive value for kidney or liver concentrations. Two of three whales with E<MLR also had blubber concentration <MLR, but the third had blubber concentration in the highest category. However, the sample sizes are too small to give statistically significant results. Fisher's exact test did not reject the null hypothesis of independence of epidermal and blubber Cd concentration levels, suggesting that the regression result for blubber should be interpreted with particular caution.

It is not surprising that E was a poor predictor for kidney and liver Cd concentration. These internal organs are well known to accumulate Cd with age and are rarely at concentrations <MLR (Bratton *et al.*, 1997; Roditi-Elasar *et al.*, 2003; Wagemann *et al.*, 1996; Woods and Van Vleet, 1996; Woshner *et al.*, 2001a; Woshner *et al.*, 2001b). The best regression for both of these organs had length as the

only predictor. However, although length was a strong predictor for liver concentration of Cd (R^2=81%), it had no predictive value for kidney concentration (R^2=18%). Fig. 1 shows why kidney Cd concentration cannot be predicted well. There are two whales of adult length with extremely high kidney concentrations of Cd; these whales may have been very old (possibly not well accounted for with length), accounting for the large amount of Cd they have accumulated in their kidneys.

Mercury

Only five epidermal samples had E<MLR (Table 4). An adequate number of samples were available for kidney, liver and muscle (Table 5). With a regression value of R^2=30%, E had no predictive value for kidney concentration of Hg, and it was only weakly predictive in the other tissues. Epidermal prediction of Hg concentration in internal tissues might prove more useful in toothed cetaceans that are known to accumulate much higher levels of Hg in liver, kidney, muscle and epidermis (André *et al*., 1991; Beck *et al*., 1997; Becker *et al*., 2000; Bustamante *et al*., 2003; Yang *et al*., 2002) than bowhead whales (Woshner *et al*., 2001b). The best regressions for bowhead whales, which increase R^2 slightly, all include E as a predictor and also include sex for blubber (females have higher Hg concentrations) and length for kidney, liver and muscle (longer whales have higher Hg concentrations). The best regressions are still only weakly predictive for Hg in kidney and liver and moderately predictive in blubber and muscle.

Lead

Eighteen (44%) of 41 epidermal samples analysed for Pb had E<MLR, resulting in small sample sizes for regression analyses. Table 5 indicates that epidermal Pb is of no value for predicting Pb in other tissues as $R^2 \leq 21\%$ for Pb. The hypothesis of independence of E and concentration in the other tissue is never rejected by Fisher's exact test. For blubber and liver, none of the potential predictors (E, length, sex) is judged by AIC to be useful for prediction. For kidney and muscle, $R^2 \leq 29\%$ even for the models chosen by AIC

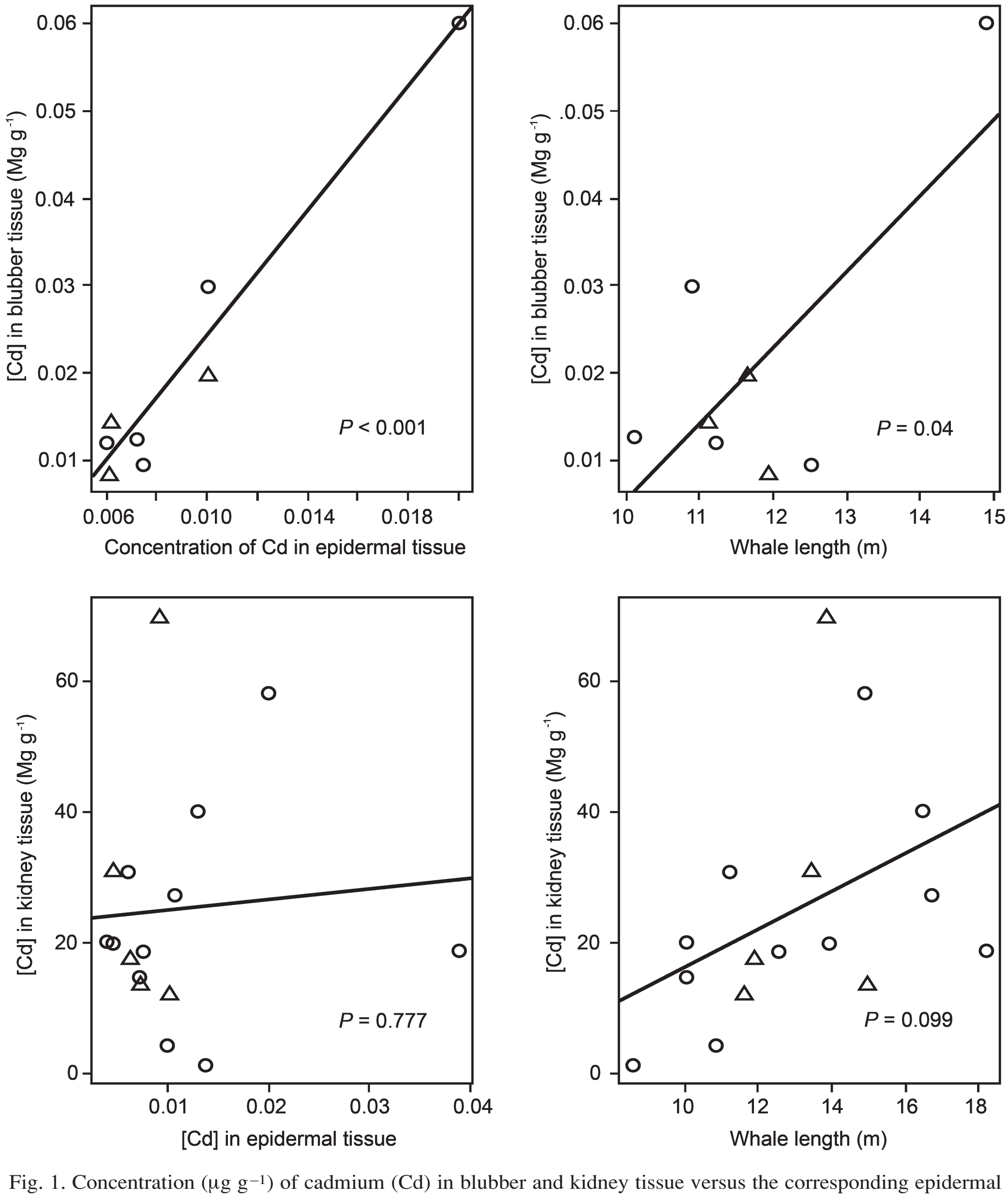

Fig. 1. Concentration (μg g^{-1}) of cadmium (Cd) in blubber and kidney tissue versus the corresponding epidermal concentrations and whale length. Males are denoted by triangles and females by circles. A least squares regression line with its *P*-value is shown on each plot.

Table 5

Evaluation of predictability of concentrations (µg/g wet weight) of elements in blubber, kidney, liver and muscle from the corresponding epidermal concentrations (E), whale length in meters (Length) and Sex (0 for males, 1 for females) in bowhead whales. Sample size is the number of whales with concentration ≥ MLR in both the epidermal sample and the other tissue sample; these are the whales on which the regression results for the element and tissue are based. The percentage of the variability of the element in the tissue explained by the regression is denoted by R^2. Standard errors (SE) of regression coefficients are given in parentheses after the coefficients. Best regression denotes the regression model chosen by Akaike's information criterion (AIC); NA for a coefficient means it was not selected by AIC. When AIC chose the mean (Intercept) as the best model, $R^2 =$ 0% is used to indicate that none of E, Length or Sex was useful for predicting concentration of the element in the tissue.

		Blubber	Kidney	Liver	Muscle
Mercury (Hg)	Sample size	8	35	36	36
Regression on E:	R^2	49%	30%	39%	55%
Coefficients:	Intercept (SE)	0.0005 (0.0019)	0.0085 (0.0079)	0.0179 (0.0088)	0.0076 (0.0023)
	E (SE)	0.3071 (0.1284)	1.6404 (0.4352)	2.2781 (0.4839)	0.8127 (0.1260)
Best regression:	R^2	70%	40%	54%	60%
Coefficients:	Intercept (SE)	-0.0008 (0.0017)	-0.0263 (0.0165)	-0.0324 (0.0174)	-0.0014 (0.0049)
	E (SE)	0.3213 (0.1085)	1.5838 (0.4089)	2.1958 (0.4289)	0.7979 (0.1205)
	Length (SE)	NA	0.0032 (0.0014)	0.0047 (0.0015)	0.0008 (0.0004)
	Sex (SE)	0.0021 (0.0011)	NA	NA	NA
Lead (Pb)					
	Sample size	7	15	22	8
Regression on E:	R^2	21%	10%	3%	6%
Coefficients:	Intercept (SE)	0.0045 (0.0081)	0.0069 (0.0017)	0.0138 (0.0031)	0.0049 (0.0136)
	E (SE)	0.8283 (0.7096)	0.2205 (0.1875)	0.2595 (0.3273)	0.8485 (1.3519)
Best regression:	R^2	0%	29%	0%	27%
Coefficients:	Intercept (SE)	0.0132 (0.0033)	0.0043 (0.0021)	0.0160 (0.0013)	0.0528 (0.0269)
	E (SE)	NA	0.3097 (0.1794)	NA	NA
	Length (SE)	NA	NA	NA	-0.0040 (0.0027)
	Sex (SE)	NA	0.0027 (0.0015)	NA	NA
Magnesium (Mg)					
	Sample size	11	46	47	47
Regression on E:	R^2	89%	78%	88%	52%
Coefficients:	Intercept (SE)	-2.438 (4.115)	-13.178 (15.407)	40.201 (8.690)	103.309 (33.955)
	E (SE)	0.095 (0.011)	0.600 (0.048)	0.487 (0.027)	0.717 (0.104)
Best regression:	R^2	89%	83%	90%	57%
Coefficients:	Intercept (SE)	-2.438 (4.115)	67.365 (27.330)	84.320 (15.792)	239.984 (64.499)
	E (SE)	0.095 (0.011)	0.622 (0.043)	0.499 (0.025)	0.744 (0.099)
	Length (SE)	NA	-7.903 (2.313)	-4.321 (1.339)	-13.140 (5.372)
	Sex (SE)	NA	NA	NA	NA
Manganese (Mn)					
	Sample size	6	22	23	23
Regression on E:	R^2	25%	<1%	2%	<1%
Coefficients:	Intercept (SE)	0.0097 (0.0117)	0.450 (0.066)	1.817 (0.296)	0.146 (0.023)
	E (SE)	0.1935 (0.1663)	0.363 (0.841)	-2.273 (3.738)	-0.007 (0.285)
Best regression:	R^2	52%	0%	0%	0%
Coefficients:	Intercept (SE)	0.0287 (0.0041)	0.474 (0.034)	1.662 (0.148)	0.145 (0.011)
	E (SE)	NA	NA	NA	NA
	Length (SE)	NA	NA	NA	NA
	Sex (SE)	-0.0120 (0.0057)	NA	NA	NA
Copper (Cu)					
	Sample size	18	46	47	47
Regression on E:	R^2	3%	3%	9%	15%
Coefficients:	Intercept (SE)	0.1064 (0.0311)	1.553 (0.262)	-0.370 (3.587)	0.4115 (0.0988)
	E (SE)	0.0417 (0.0626)	0.785 (0.628)	17.825 (8.667)	0.6498 (0.2351)
Best regression:	R^2	47%	15%	13%	25%
Coefficients:	Intercept (SE)	0.1331 (0.0277)	2.010 (0.313)	1.559 (3.736)	0.5966 (0.1209)
	E (SE)	NA	1.392 (0.648)	18.918 (8.556)	0.8444 (0.2371)
	Length (SE)	-0.0037 (0.0024)	-0.064 (0.027)	NA	-0.0240 (0.0099)
	Sex (SE)	0.0518 (0.0142)	NA	-3.578 (2.271)	NA
Selenium (Se)					
	Sample size	18	46	47	47
Regression on E:	R^2	3%	19%	21%	<1%
Coefficients:	Intercept (SE)	0.0758 (0.0264)	0.9651 (0.1561)	0.6228 (0.2179)	0.1738 (0.0169)
	E (SE)	0.0215 (0.0309)	0.7007 (0.2177)	1.0663 (0.3040)	0.0063 (0.0235)
Best regression:	R^2	0%	19%	30%	5%
Coefficients:	Intercept (SE)	0.0934 (0.0078)	0.9651 (0.1561)	0.2799 (0.2516)	0.1896 (0.0093)
	E (SE)	NA	0.7007 (0.2177)	NA	NA
	Length (SE)	NA	NA	0.0971 (0.0221)	NA
	Sex (SE)	NA	NA	NA	-0.0169 (0.0113)

Cont.

Table 5 cont.

		Blubber	Kidney	Liver	Muscle
Zinc (Zn)					
	Sample size	11	46	47	47
Regression on E:	R^2	5%	<1%	<1%	12%
	Coefficients:				
	Intercept (SE)	-0.305 (4.711)	20.387 (9.528)	42.472 (10.836)	15.813 (10.007)
	E (SE)	0.236 (0.330)	0.374 (0.706)	-0.497 (0.805)	1.862 (0.739)
Best regression:	R^2	19%	20%	35%	12%
Coefficients:	Intercept (SE)	-2.886 (4.182)	8.292 (5.369)	9.700 (5.566)	15.813 (10.007)
	E (SE)	NA	NA	NA	1.862 (0.739)
	Length (SE)	0.520 (0.363)	1.557 (0.471)	2.386 (0.489)	NA
	Sex (SE)	NA	NA	NA	NA

and E is included only in the model for kidney. This may be because means and standard deviations of Pb concentration are low in all tissues, with Pb undetectable in many samples (Table 4). Low Pb levels for many cetaceans have previously been reported (Dehn *et al*., 2006; Meador *et al*., 1999; Woshner *et al*., 2001b).

Arsenic

Arsenic was reported (Table 4) with E<MLR in 26 (54%) of the 48 epidermal samples because few whales in the 2002/03 dataset had concentrations high enough to be measured by ICP-MS. It was similarly low in all other tissues, except blubber. Comparing means between the two analytical techniques is inappropriate when greater than 50% of the samples are below detection; the difference in MLR is driving the difference in means by allowing more 1996/97 samples to have reported low concentrations and thus a lower reported mean.

Based on the 12 whales with E≥MLR and As also measured in blubber, none of the three predictor variables is of value as a predictor of As in blubber. When E≥MLR, E is the best single predictor of As in kidney, liver and muscle, explaining ≥79% of the variability in the concentration of As, with higher values of E associated with higher concentrations in those tissues. E is the only predictor of As in the kidney chosen by AIC. Length is added to E in the best regressions for liver and muscle chosen by AIC. The above regressions for those tissues are greatly influenced by the one (in the case of kidney and muscle) or two (in the case of liver) whales with concentrations of As high enough to be detected using ICP-MS; these concentrations are all higher than those in the AAS dataset. The relatively large number of samples with E<MLR but a concentration in kidney, liver or muscle at or above the median, or vice-versa, suggests that E might not be strongly predictive for these tissues. For example, there are 15 whales with both liver concentration and E<MLR, but 16 whales with E<MLR and high liver concentration or vice-versa. More samples with concentrations >MLR in all tissues are needed before firm conclusions can be drawn concerning the predictive power of epidermal As concentration for its concentration in other tissues.

CONCLUSIONS

Using concentrations of elements in epidermal tissue to predict corresponding elemental concentrations in other tissues (blubber, kidney, liver and muscle) does not appear to be a sound method based on our evaluation of bowhead whale samples from 1996, 1997, 2002 and 2003 (providing a sample size of 40 or more whales for all tissues except blubber). Epidermal concentration had no predictive value for Cu, Mn, Pb, Se or Zn in any of the other tissues evaluated. Epidermal concentrations of the four other elements considered were predictive for some other tissues. Arsenic could be predicted in kidney, liver and muscle, but not blubber, although the distribution of samples with concentrations below the MLR and the small sample sizes suggest that these results should be interpreted with caution. Epidermal concentrations of Cd were strongly predictive for blubber and weakly predictive for muscle concentrations. Epidermal concentrations of Hg were weakly predictive of blubber, liver and muscle concentrations. Epidermal concentrations of Mg were strongly predictive in blubber, kidney and liver but only weakly predictive in muscle. Thus, if investigators wish to develop an understanding of concentrations of essential and toxic elements in non-epidermal tissues, this cannot be accomplished via epidermal biopsy alone. One could monitor epidermis for its own sake (e.g. to assess whether it accumulates elements of toxicologic concern or could be a tissue affected by mineral deficiency) and might detect temporal or spatial trends. However, it has been shown here that epidermal biopsy cannot predict concentrations in four key tissues in bowhead whales in most cases. This ineffectiveness of epidermal element concentrations to reflect concentrations in internal tissues is likely true for other mysticetes and perhaps for cetaceans in general. At a minimum, before using epidermal biopsies to predict internal tissue concentrations of elements, researchers must establish that a sound scientific basis exists for doing so. Such proof must be specific to the elements, species and tissues in question as well as based upon statistically adequate sample sizes.

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REFERENCES

Aastrup, P., Riget, F., Dietz, R. and Asmund, G. 2000. Lead, zinc, cadmium, mercury, selenium and copper in Greenland caribou and reindeer (*Rangifer tarandus*). *Sci. Total Environ.* 245: 149-59.

Akaike, H. 1973. Information theory and an extension of the maximum likelihood principle. pp.267-81. *In*: Petran, B.N. and Csaáki, F. (eds). *International Symposium on Information Theory*. Akademia Kiado, Budapest, Hungary. 451pp.

Arctic Monitoring and Assessment Programme. 1998. *AMAP Assessment Report: Arctic Pollution Issues*. Arctic Monitoring and Assessment Programme (AMAP), Oslo, Norway. xii+859pp.

Arctic Monitoring and Assessment Programme. 2002. *Arctic Pollution 2002*, Oslo, Norway. 111pp.

André, J.M., Boudou, A. and Ribeyre, F. 1991. Mercury accumulation in Delphinidae. *Water Air Soil Pollut.* 56: 187-201.

Beck, K.M., Fair, P., McFee, W. and Wolf, D.L. 1997. Heavy metals in livers of bottlenose dolphins stranded along the South Carolina coast. *Mar. Poll. Bull.* 34: 734-39.

Becker, P.R., Krahn, M., Mackey, E.A., Demiralp, R., Schantz, M., Epstein, M.S., Donais, M.K., Porter, B.J., Muir, D.C.G. and Wise, S.A. 2000. Concentrations of polychlorinated biphenyls (PCBs), chlorinated pesticides, and heavy metals and other elements in tissues of belugas, *Delphinapterus leucas*, from Cook Inlet, Alaska. *Mar. Fish. Rev.* 62: 81-98.

Beckmen, K., Duffy, L.K., Zhang, X. and Pitcher, K.W. 2002. Mercury concentrations in the fur of Steller sea lions and nothern fur seals from Alaska. *Mar. Poll. Bull.* 44: 1130-35.

Born, E.W., Renzoni, A. and Dietz, R. 1991. Total mercury in hair of polar bears (*Ursus maritimus*) from Greenland and Svalbard. *Polar Res.* 9(2): 113-20.

Bratton, G., Flory, W., Spainhour, C.B. and Haubold, E.M. 1997. Assessment of selected heavy metals in liver, kidney, muscle, blubber and visceral fat of Eskimo harvested bowhead whales *Balaena mysticetus* from Alaska's north coast. Final report submitted to the North Slope Borough Dept. of Wildlife Management, Barrow, Alaska (unpublished). 233pp.

Bustamante, P., Garrigue, C., Breau, L., Caurant, F., Dabin, W., Greaves, J. and Dodemont, R. 2003. Trace elements in two odontocete species (*Kogia breviceps* and *Globicephala macrorhynchus*) stranded in New Caledonia (South Pacific). *Environ. Pollut.* 124: 263-71.

Cooper, L.W., Larsen, I.L., O'Hara, T.M., Dolvin, S., Woshner, V. and Cota, G.F. 2000. Radionuclide contaminant burdens in Arctic marine mammals harvested during subsistence hunting. *J. Arctic Inst. N. America* 53(2): 174-82.

De Wit, C.A., Fisk, A.T., Hobbs, K.E., Muir, D.C.G., Kallenborn, R., Krahn, M., Norstrom, R. and Skaare, J. 2004. Persistent organochlorine pollutants. *In*: De Wit, C.A., Fisk, A.T., Hobbs, K.E. and Muir, D.C.G. (eds). *Arctic Monitoring and Assessment Programme (AMAP) II*, Oslo, Norway.

Decataldo, A., Di Leo, A., Giandomenico, S. and Cardellicchio, N. 2004. Association of metals (mercury, cadmium and zinc) with metallothionein-like proteins in storage organs of stranded dolphins from the Mediterranean Sea (southern Italy). *J. Environ. Monit.* 6: 361-67.

Dehn, L.A., Follman, E., Rosa, C., Duffy, L.K., Thomas, D.L., Bratton, G.R., Taylor, R.J. and O'Hara, T.M. 2006. Stable isotope and trace element status of subsistence hunted bowhead (*Balaena mysticetus*) and beluga whales (*Delphinapterus leucas*) in Alaska and gray whales (*Eschrichtius robustus*) in Chukotka. *Mar. Poll. Bull.* 52: 301-19. [Available on web].

Elkin, B.T. and Bethke, R.W. 1995. Environmental contaminants in caribou in the Northwest Territories, Canada. *Sci. Total Environ.* 160/161: 307-21.

Flynn, A., Franzmann, A.W. and Arneson, P.D. 1975. Sequential hair shaft as an indicator of prior mineralization in the Alaskan moose. *J. Anim. Sci.* 41: 906-10.

Flynn, A., Franzmann, A.W., Arneson, P.D. and Oldemeyer, J.L. 1977. Indications of copper deficiency in a sub-population of Alaskan moose. *J. Nutr.* 107: 1182-89.

Ford, J. and Hasselbach, L. 2001. Heavy metals in mosses and soils on six transects along the Red Dog Mine haul road. Alaska National Park Service No. NPS/AR/NRTR-2001/38. [Available from: *www.nps.gov/akso*].

Fossi, M.C., Marsili, L., Lauriano, G., Fortuna, C., Canese, S., Ancora, S., Leonzio, C., Romeo, T., Merino, R., Abad, E. and Jimenez, B. 2004. Assessment of toxicological status of a SW Mediterranean segment population of striped dolphin (*Stenella coeruleoalba*) using skin biopsy. *Mar. Environ. Res.* 58(2-5): 269-74.

Frank, I.A., Galgan, V. and Petersson, L.R. 1994. Secondary copper deficiency, chromium deficiency and trace element imbalance in the moose: effect of anthropogenic activity. *Ambio* 23: 315-17.

Frodello, J.P., Romeo, M. and Viale, D. 2000. Distribution of mercury in the organs and tissues of five toothed whale species of the Mediterranean. *Environ. Pollut.* 108: 447-52.

Fujise, Y., Honda, K., Tatsukawa, R. and Mishima, S. 1988. Tissue distribution of heavy metals in Dall's porpoise in the northwestern Pacific. *Mar. Poll. Bull.* 19(5): 226-30.

Gamberg, M. and Scheuhammer, A.M. 1994. Cadmium in caribou and muskoxen from the Canadian Yukon and Northwest Territories. *Sci. Total Environ.* 143: 221-34.

Gauthier, J.M., Dubeau, H. and Rassart, E. 1998. Mercury-induced micronuclei in skin fibroblasts of beluga whales. *Environ. Toxicol. Chem.* 17(12): 2487-93.

Gogan, P.J.P., Jessup, D.A. and Akeson, M. 1989. Copper deficiency in tule elk at Point Reyes, California. *J. Range Manage.* 42: 233-38.

Hansen, L.J., Schwacke, L.H., Mitchum, G.B., Hohn, A.A., Wells, R.S., Zolman, E.S. and Fair, P.A. 2004. Geographic variation in polychlorinated biphenyls and organochlorine pesticide concentrations in the blubber of bottlenose dolphins from the US Atlantic coast. *Sci. Total Environ.* 319: 147-72.

Honda, K. and Tatsukawa, R. 1983. Distribution of cadmium and zinc in tissues and organs, and their age related changes in striped dolphins, *Stenella coeruleoalba*. *Arch. Environ. Contam. Toxicol.* 15: 543-50.

Honda, K., Tatsukawa, R., Itano, K., Miyazaki, N. and Fujiyama, T. 1983. Heavy metal concentrations in muscle, liver and kidney tissue of striped dolphin, *Stenella coeruleoalba*, and their variations with body length, weight, age and sex. *Agric. Biol. Chem.* 47(6): 1,219-28.

Ikemoto, T., Kunito, T., Watanabe, I., Yasunaga, G., Baba, N., Miyazaki, N., Petrov, E. and Tanabe, S. 2004. Comparison of trace element accumulation in Baikal seals (*Pusa sibirica*), Caspian seals (*Pusa caspica*) and northern fur seals (*Callorhinus ursinus*). *Environ. Pollut.* 127(1): 83-97.

Korsrud, G.O., Meldrum, J.B., Slaiisbury, C.D., Houlahan, B.J., Saschenbrecker, P.W. and Tittiger, F. 1985. Trace element levels in liver and kidney from cattle, swine and poultry slaughtered in Canada. *Can. J. Comp. Med.* 49: 159-63.

Kuehl, D.W. and Haebler, R. 1995. Organochlorine, organobromine, metal and selenium residues in bottlenose dolphins (*Tursiops truncatus*) collected during an unusual mortality event in the Gulf of Mexico. *Arch. Environ. Contam. Toxicol.* 28: 494-99.

Kuehl, D.W., Haebler, R. and Potter, C. 1994. Coplanar PCB and metal residues in dolphins from the US Atlantic coast including Atlantic bottlenose obtained during the 1987/88 mass mortality. *Chemosphere* 28: 1,245-53.

Kunito, T., Watanabe, I., Yasunaga, G., Fujise, Y. and Tanabe, S. 2002. Using trace elements in skin to discriminate the populations of minke whales in the southern hemisphere. *Mar. Environ. Res.* 53: 175-97.

Larter, N.C. and Nagy, J.A. 2000. A comparison of heavy metal levels in the kidneys of High Arctic and mainland caribou populations in the Northwest Territories of Canada. *Sci. Total Environ.* 246: 109-19.

Law, R.J., Fileman, C.F., Hopkins, A.D., Baker, J.R., Harwood, J., Jackson, D.B., Kennedy, S., Martin, A.R. and Morris, R.J. 1991. Concentrations of trace metals in the livers of marine mammals (seals, porpoises and dolphins) from waters around the British Isles. *Mar. Poll. Bull.* 22(4): 183-91.

Lowry, L. 1993. Foods and feeding ecology. pp.201-38. *In*: Burns, J.J., Montague, J.J. and Cowles, C.J. (eds). *The Bowhead Whale*. Society for Marine Mammalogy, Lawrence, Kansas. xxxvi+787.

Mackey, E.A., Oflaz, R.D., Epstein, M.S., Buehler, B., Porter, B.J., Rowles, T., Wise, S.A. and Becker, P.R. 2003. Elemental composition of liver and kidney tissues of rough-toothed dolphins (*Steno bredanensis*). *Arch. Environ. Contam. Toxicol.* 22: 523-32.

Marcovecchio, J.E., Moreno, V.J., Bastida, R.O., Gerpe, M.S. and Rodríguez, D.H. 1990. Tissue distribution of heavy metals in small cetaceans from the southwestern Atlantic Ocean. *Mar. Poll. Bull.* 21(6): 299-304.

Meador, J.P., Ernest, D.W., Hohn, A., Tilbury, K.L., Gorzelany, J., Worthy, G. and Stein, J.E. 1999. Comparison of elements in bottlenose dolphins stranded on the beaches of Texas and Florida in the Gulf of Mexico over a one-year period. *Arch. Environ. Contam. Toxicol.* 36: 87-98.

Microsoft Corporation. 1999. *Microsoft Excel 2000*. Microsoft Corporation, Redmond, WA.

Monaci, F., Borrell, A., Leonzio, C., Marsili, L. and Calzada, N. 1998. Trace elements in striped dolphins (*Stenella coeruleoalba*) from the western Mediterranean. *Environ. Pollut.* 99(1): 61-8.

Nigro, M., Campana, A., Lanzillotta, E. and Ferrara, R. 2002. Mercury exposure and eliminiation rates in captive bottlenose dolphins. *Mar. Poll. Bull.* 44: 1071-75.

O'Hara, T.M., Carroll, G., Barboza, P., Mueller, K., Blake, J.B., Woshner, V. and Willetto, C. 2001. Mineral and heavy metal status as related to a mortality event and poor recruitment in a moose population in Alaska. *J. Wildl. Dis.* 37(3): 509-22.

O'Hara, T.M., George, J.C., Blake, J., Burek, K., Carroll, G., Dau, J., Bennett, L., McCoy, C.P., Gerard, P. and Woshner, V. 2003. Investigation of heavy metals in a large mortality event in caribou of northern Alaska. *Arctic* 56(2): 125-35.

O'Hara, T.M., Krahn, M.M., Boyd, D., Becker, P.R. and Philo, M. 1999. Organochlorine contaminant levels in eskimo harvested bowhead whales of Arctic Alaska. *J. Wildl. Dis.* 35(4): 741-52.

Puls, R. 1994. *Mineral Levels in Animal Health: Diagnostic Data*. Sherpa International, Clearbrook, British Columbia, Canada.

Roditi-Elasar, M., Kerem, D., Hornung, H., Kress, N., Shohan-Frider, E., Goffman, O. and Spanier, E. 2003. Heavy metal levels in bottlenose and striped dolphins off the Mediterranean coast of Israel. *Mar. Poll. Bull.* 46: 491-521.

Stein, J.E., Tilbury, K.L., Meador, J.P., Gorzelany, J., Worthy, G. and Krahn, M. 2003. Ecotoxicological investigations of bottlenose dolphin (*Tursiops truncatus*) strandings: accumulation of persistent organic chemicals and metals. pp.458-88. *In*: Vos, J.G., Bossart, G.D., Fournier, D. and O'Shea, T.J. (eds). *Toxicology of Marine Mammals*. Taylor and Francis, New York.

Suydam, R., George, J.C., O'Hara, T.M., Hanns, C. and Sheffield, G. 2004. Subsistence harvest of bowhead whales (*Balaena mysticetus*) by Alaskan Eskimos during 2003. Paper SC/56/BRG11 presented to the IWC Scientific Committee, July 2004, Sorrento, Italy (unpublished). 5pp. [Paper available from the Office of this Journal].

Suydam, R., George, J.C., O'Hara, T.M. and Sheffield, G. 2003. Subsistence harvest of bowhead whales by Alaskan Eskimos during 2002. Paper SC/55/BRG5 presented to the IWC Scientific Committee, May 2003, Berlin (unpublished). 5pp. [Paper available from the Office of this Journal].

Trefry, J.H., Rember, R.D., Trocine, R.P. and Brown, J.S. 2003. Trace metals in sediments near offshore oil exploration and production sites in the Alaskan Arctic. *Environ. Geol.* 45(2): 149-60.

Underwood, E.J. 1977. *Trace Elements in Human and Animal Nutrition*. Academic Press, New York. 196pp.

Venables, W.N. and Ripley, B.D. 1999. *Modern Applied Statistics with S-Plus*. 3rd ed. Springer-Verlag Inc., New York. xi+501pp.

Wagemann, R., Innes, S. and Richard, P.R. 1996. Overview and regional and temporal differences of heavy metals in Arctic whales and ringed seals in the Canadian Arctic. *Sci. Total Environ.* 186: 41-66.

Wiig, Ø., Renzoni, A. and Gjertz, I. 1999. Levels of cadmium and mercury in the hair of Atlantic walruses (*Odobenus rosmarus rosmarus*) from Svalbard, Norway. *Polar Biol.* 21(5): 343-46.

Woods, C.M. and Van Vleet, E.S. 1996. Copper, cadmium and zinc in liver, kidney and muscle tissues of bottlenose dolphins (*Tursiops truncatus*) stranded in Florida. *Mar. Poll. Bull.* 32(12): 886-89.

Woshner, V.M., O'Hara, T.M., Bratton, G.R. and Beasley, V.R. 2001a. Concentrations and interactions of selected essential and non-essential elements in ringed seals and polar bears of Arctic Alaska. *J. Wildl. Dis.* 37(4): 711-21

Woshner, V.R., O'Hara, T.M., Bratton, G.R., Suydam, R.S. and Beasley, V.T. 2001b. Concentrations and interactions of selected essential and non-essential elements in bowhead and beluga whales of Arctic Alaska. *J. Wildl. Dis.* 37(4): 633-710.

Yang, Y., Kunito, T., Tanabe, S., Amano, M. and Miyazaki, N. 2002. Trace elements in skin of Dall's porpoises (*Phocoenoides dalli*) from the northern waters of Japan: an evaluation for utilization as non-lethal tracers. *Mar. Poll. Bull.* 45: 230-36.

Ylitalo, G.M., Matkin, C.O., Buzitis, J., Krahn, M.M., Jones, L.L., Rowles, T. and Stein, J.E. 2001. Influence of life-history parameters on organochlorine concentrations in free-ranging killer whales (*Orcinus orca*) from Prince William Sound, AK. *Sci. Total Environ.* 281: 183-203.

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Estimates of large whale abundance in West Greenland waters from an aerial survey in 2005

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ABSTRACT

An aerial line transect and cue counting survey of large whales in West Greenland was conducted in August and September 2005. The survey covered the area between Cape Farewell and Disko Island on the West Greenland coast out to the 200m depth contour. The surveyed area covered 163,574km^2 and a total of 246 sightings of 9 cetacean species were obtained. Abundance estimates were developed for humpback whales, *Megaptera novaeangliae* (21 sightings), fin whales, *Balaenoptera physalus* (78 sightings) and common minke whales, *B. acutorostrata* (42 sightings). The mean group size of humpback whales was 3.30 but groups as large as 95 animals were seen off effort. The mean group size of fin whales was 2.96 with groups as large as 50 seen. Common minke whale group size was 1.1 with only one sighting of a group of two whales. Humpback whales were found both in offshore and coastal areas of West Greenland with the exception of Store Hellefiske Bank and the Cape Farewell offshore area. The line transect abundance estimate of humpback whales was 1,218 (CV=0.56), uncorrected for submerged whales (availability bias) and whales that were available to be seen but were missed by the observers (perception bias). Fin whales were observed in all areas of the survey and the uncorrected line transect estimate was 1,660 (CV=0.38). When corrected for perception bias the estimates increases to 3,234 fin whales (CV=0.44). Common minke whales were found in almost equal densities in all strata except for the Cape Farewell offshore area, where none were seen. The cue-counting abundance estimate of common minke whales was 4,856 (CV=0.49) for West Greenland using a cue rate of 46.3 cues per hour (CV=0.11). If the estimate is corrected for perception bias the common minke whale abundance is estimated to be 10,792 whales (CV=0.59). Low coverage was attained in the northern area of West Greenland and this should cause an especially large negative bias for the estimates of fin whale and humpback whale abundance because this area is believed to have particularly large densities of these whales.

KEYWORDS: FIN WHALE; COMMON MINKE WHALE; HUMPBACK WHALE; SURVEY-AERIAL; SURVEY-VESSEL; NORTHERN HEMISPHERE; ABUNDANCE ESTIMATE; CUE COUNTING; DISTRIBUTION; *g*(0); SCHOOL SIZE

INTRODUCTION

Most estimates of abundance of large baleen whales, including common minke whales, *Balaenoptera acutorostrata*, fin whales, *B. physalus*, and humpback whales, *Megaptera novaeangliae*, in West Greenland waters are more than 10 years old. A series of aerial surveys of large baleen whales in West Greenland were conducted between 1983 and 1993 and abundance estimates were developed from cue counting techniques *(cf.* Hiby, 1985) in 1987/88 and in 1993 (Hiby *et al*., 1989; Larsen, 1995; Larsen *et al*., 1989). From these surveys, all conducted in July and August, fin whale abundance was estimated at 1,100 (95% confidence interval (CI) 520-2,100) in West Greenland in 1987/88 (IWC, 1992) and abundance of common minke whales was estimated at 3,266 in 1987/88 (95% CI 1,700-5,710 (IWC, 1990) and at 8,371 (95% CI 2,414-16,929) common minke whales in 1993 (Larsen, 1995).

Abundance of humpback whales in West Greenland was estimated from photo-ID surveys in July and August 1988-93, with a combined estimate over the five years of surveys of 360 humpback whales (95% CI 314-413) (Larsen and Hammond, 2004). A line transect analysis of the aerial survey in July and August 1993 resulted in an uncorrected estimate of 599 (95% CI 237-1,512) (Kingsley and Witting, 2001) and an aerial photographic survey in July through October 2002 and August through October 2004 provided an estimate of 400 humpback whales (CV=0.64) corrected for submergence about three quarter of the time.

In September 2005 a ship-based line transect survey was conducted in East and West Greenland covering the shelf areas out to the 200m depth contour (Heide-Jørgensen *et al*., 2007). Fin whales were most abundant in East Greenland with an estimate of 3,214 (95% CI 980-10,547) and a lower abundance of 1,980 (95% CI 913-4,296) was estimated for West Greenland. Humpback whales were found in both offshore and coastal areas of West Greenland and abundance was estimated at 1,306 (95% CI 570-2,989). They occurred in low numbers in East Greenland with abundance estimated at 347 (95% CI 48-2,515). Finally, common minke whale abundance was estimated at 1,848 (95% CI 197-17,348) for East Greenland and 4,479 (95% CI 1,760-11,394) for West Greenland. These abundance estimates are negatively biased due to incomplete survey coverage and lack of correction factors for availability and perception bias.

The lack of up-to-date information on the abundance of large cetaceans in West Greenland has made it difficult for the Scientific Committee of the International Whaling Committee (IWC) to provide advice on sustainable takes from especially common minke whales and fin whales in West Greenland (IWC, 2006). Given that the average annual removals during 1999-2004 of common minke whales and fin whales were 172 and 9, respectively, it seems prudent to update abundance estimates for these two species.

An aerial survey of large cetaceans was conducted in West Greenland in August-September 2005 and is reported on here. Abundance estimates were developed for fin whales, humpback whales and common minke whales and

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are presented here, with comparisons to the abundance estimates obtained during a ship based survey conducted simultaneously in 2005.

METHODS

Survey methods and design

The survey was conducted between 28 August and 23 September 2005. The survey platform was an Icelandic *Partenavia Observer P-68*, in which two observers were located in the rear seats each with bubble windows. An additional observer/flight leader was seated in the right front seat. Sightings and a log of the cruise track (recorded from the aircrafts GPS) were recorded on laptop computers. Declination angle to sightings was measured with Suunto inclinometers and lateral angle from the nose of the aircraft was estimated. No correction for the drift of the plane was applied. Sightings with time stamps were entered on dictaphones and on a computer-based voice recording system that also logged the positions of the plane. Target altitude and speed was 750 feet (229m) and 90kts (167km hr^{-1}), respectively. The survey was conducted in passing mode and large group sizes were only occasionally examined in closing mode. However, the initial group size was consistently used for the abundance estimations.

Cues were defined as the dorsal ridge breaking the surface for common minke whales and as a blow for fin and humpback whales. All cues were reported unless the group size was so large that reporting was impossible. Declination and lateral angles, as well as time for each cue, were recorded together with information on number of whales in the group and the visual cue of the sighting.

Survey conditions were recorded at the start of the transect lines and whenever a change in Beaufort sea state, horizontal visibility and glare occurred. The survey was designed to systematically cover the area between the coast of West Greenland and offshore (up to 100km) to the shelf break (i.e. the 200m depth contour). Transect lines were placed in an east-west direction except for south Greenland where they were placed in a north-south direction. The surveyed area was divided into six strata (Fig. 1) and southern strata were planned to be covered first.

Analytical methods

Humpback whales

Animal abundance was estimated by

$$\hat{N} = \frac{n}{2L}\hat{f}(0)\hat{E}[s]A$$

where n was the number of groups detected, L was the transect line length, $\hat{f}(0)$ was the intercept of the estimated probability density function of distances to detected groups, $\hat{E}[s]$ was estimated mean group size, and A was stratum area (see Buckland *et al*., 2001, for further details of estimation methods). Only effort and detections in sea states 4 and below were used in the analyses.

A regression of log group size against estimated detection probability was used to estimate mean group size and because of the small sample size, a single mean group size was estimated over all strata.

In addition alternative abundance estimates were calculated where small groups (<11 whales) were estimated using the above described line transect analysis and large groups (>10 whales) were estimated using a fixed strip width.

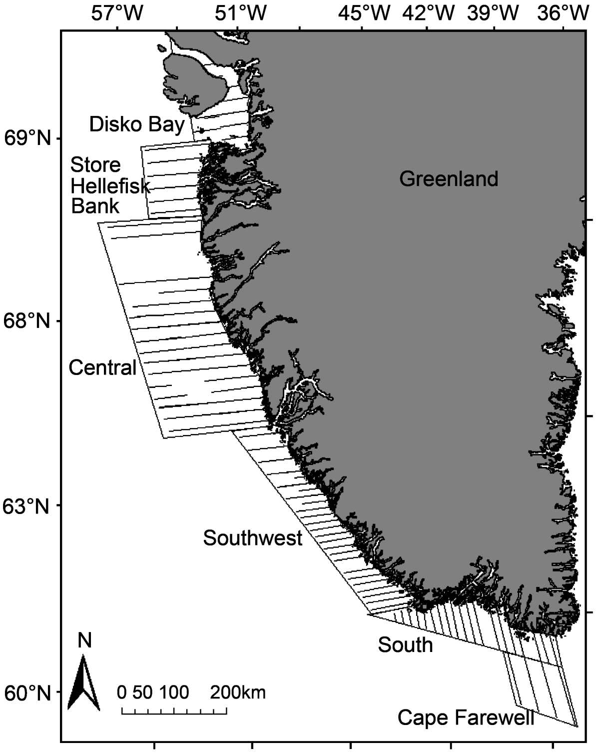

Fig. 1. Survey transect lines and delineation of strata for the aerial survey of large cetaceans in West Greenland in September 2005. The area of the strata was calculated as 12,312 km^2 for the Disko Bay strata, 15,669 km^2 for the Store Hellefiske Bank strata, 74,798km^2 for the central West Greenland strata, 29781 for the southwest Greenland strata, 11,523 km^2 for the Cape Farewell strata and 19,491km^2 for the South Greenland strata.

Fin whales

Fin whale abundance was also estimated using line transect methods. Only effort and detections in sea states 4 and below were used in the analyses. To reduce the influence of errors in the distance measurements the estimations were based on grouped distance data, using a regression of log school size on estimated detection probability to estimate mean group size. Because of small sample size, a single mean group size was estimated over all strata. Duplicates between right front and right rear observers of sightings were determined based on coincidence in timing, lateral angle and perpendicular distance.

Common minke whales

Standard cue-counting methods (assuming probability of detection at zero radial distance is 1) were used to estimate the abundance of common minke whales, as follows:

$$\hat{N} = \frac{n}{\varphi T\hat{\eta}}\hat{h}(0)\hat{E}[s]A$$

Here A is the survey area; n is the number of detected cues; T is the total time spent searching; $\varphi/(2\pi)$ is the fraction of a full circle searched (taken to be 0.5 here since the region ahead of abeam on both sides of the aircraft was searched); $\hat{h}(0)$ is the estimated slope of the probability density function of radial distances to detections, evaluated at distance zero; $\hat{\eta}$ is the estimated cue rate of animals (see Buckland *et al*., 2001, pp. 191-193 for further details). Only effort and detections in sea states 3 and below were used in the analysis.

Substantial random errors in measuring distance can lead to substantial positive bias (see Borchers *et al*., 2003), thus the data were examined for evidence of measurement error, and methods which take account of measurement errors were considered.

Although the sample size is small (only 4 duplicates from 32 sightings), the probability of detecting a cue at the closest distance was estimated and abundance was estimated using a 'point independence' method (Borchers *et al*., 2006) that does not assume certain detection at distance zero.

RESULTS

The survey covered the coast of West Greenland between northern Disko Island (70°45'N) south to Cape Farewell (60°N). Six strata were covered: Disko Bay, Store Hellefiske Bank, Central West Greenland, South West Greenland, South Greenland and an offshore Cape Farewell stratum (Fig. 1). All survey effort in Disko Bay and on Store Hellefiske Bank was completed before 12 September. After this, between 11 and 20 September, the survey was primarily concentrated in the southwest and south Greenland and after this effort was concentrated in the two strata in south Greenland. A total of 246 sightings were made during the survey. Species could not be determined for 54 sightings, but most of these were of unidentified dolphins (Table 1).

Distribution of sightings

Large baleen whale sightings were made in all strata (Figs 2a-d). Sightings of fin whales were heavily concentrated in the Central West Greenland strata in an offshore area at approximately 66°N 56°W, although additional sightings were made all along the West Greenland coast generally around the 200m depth contour (Fig. 2a). Sightings of humpback whales were also found at a high concentration off Central West Greenland, yet sightings of humpback whales in both the South West and South strata were made closer to the coast at depths of <100m (Fig. 2b). Common minke whale sightings were distributed along the entire coast and no apparent concentration areas were detected (Fig. 2c). Minke sightings were generally made at <200m depths. Sei whales were also mainly found in the same area where fin and humpback whales were found in large concentrations, although a few sei whales were seen outside of the high density region in Central West Greenland (Fig. 2d).

Large to medium sized toothed whales were also detected (Fig. 2d). Pilot whales (*Globicephala* spp.) were seen in all strata and sightings were generally far offshore beyond 400-600m depths. Two sightings of sperm whales occurred south of Cape Farewell in offshore waters. Several sightings of smaller toothed whales, particularly white-beaked dolphins (*Lagenorhynchus albirostris*) and Atlantic white-sided dolphins (*L. acutus*), were made. All sightings of these dolphins were concentrated in the South West and South strata and none were seen north of Nuuk (64°N). The many sightings of unidentified delphinoids (*n*=44) were in the same areas where the sightings of white-beaked dolphin and white-sided dolphins were made. Two unidentified small dolphins were seen in Disko Bay and these sightings were

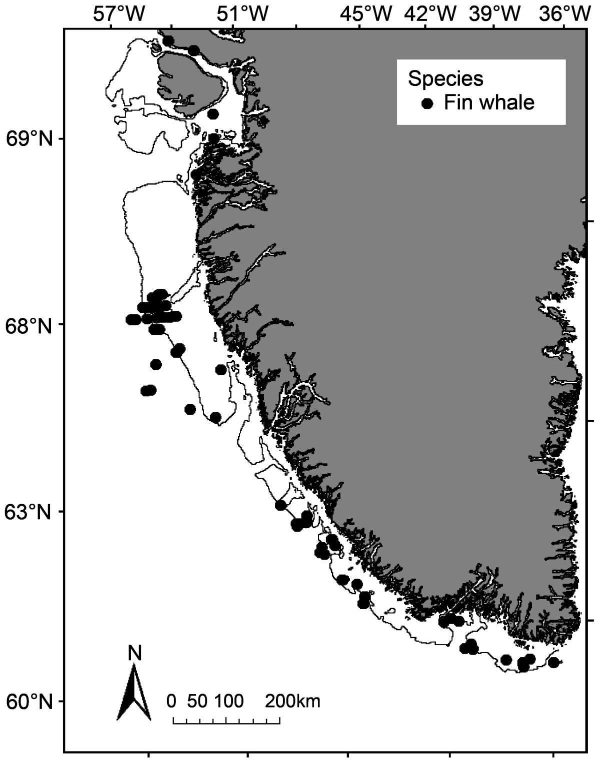

Fig. 2a. Sightings of fin whales during the aerial survey off West Greenland September 2005.

Table 1

The total numbers of observations of each of the different species of marine mammals observed during the survey. Observations are included from sea states and areas that are not included in the abundance estimations. Coefficients of variation are in brackets.

Species	Number of sightings	Number of individuals	Mean group size	Maximum group size	Minimum group size
Fin whale	78	231	2.96 (0.23)	50	1
Sei whale	4	13	3.30 (0.69)	10	1
Humpback whale	21	350	16.70 (0.35)	95	1
Sperm whale	2	2	1.00 (0)	1	1
Unidentified large whale	12	15	1.25 (0.14)	3	1
Minke whale	42	43	1.10 (0.02)	2	1
Pilot whale	10	181	18.20 (0.33)	50	1
Unidentified small whale	10	16	1.60 (0.27)	5	1
White-beaked dolphin	12	62	5.20 (0.25)	13	1
White-sided dolphin	3	27	9.00 (0.61)	20	3
Harbour porpoise	8	19	2.40 (0.26)	6	1
Unidentified dolphin	44	406	9.20 (0.15)	45	1

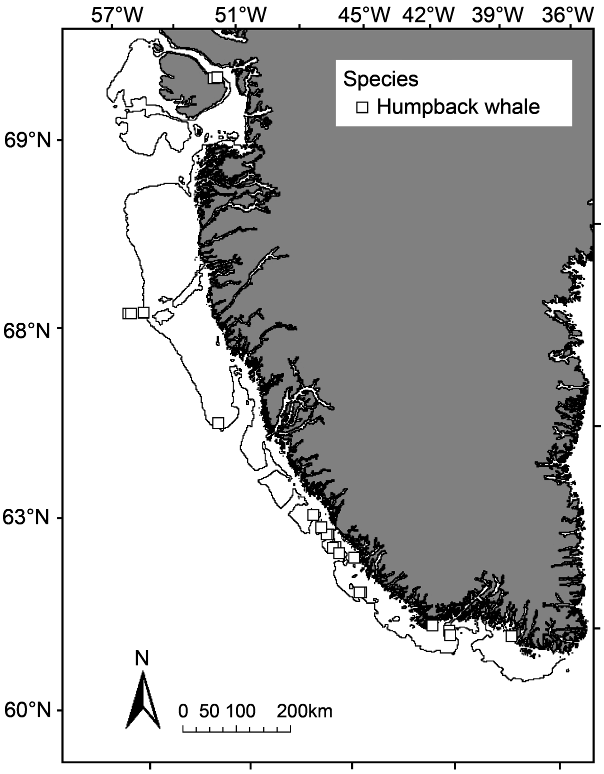

Fig. 2b. Sightings of humpback whales during the aerial survey off West Greenland September 2005.

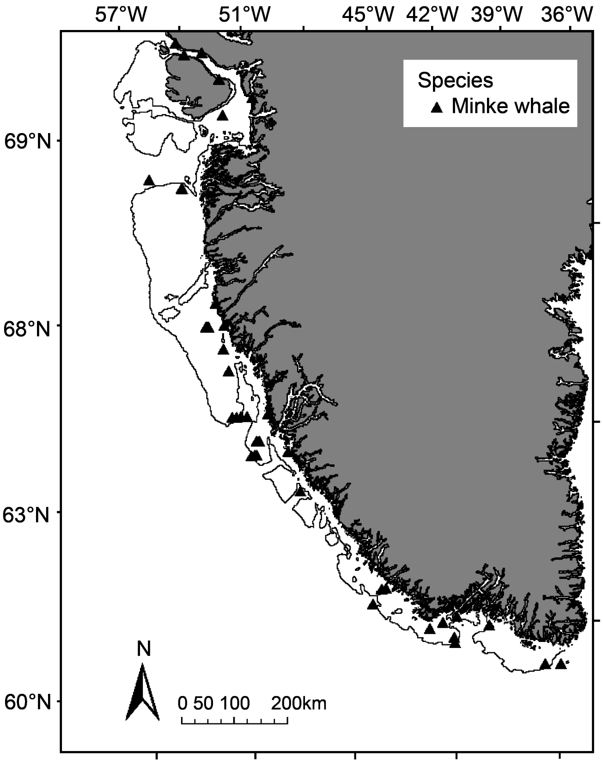

Fig. 2c. Sightings of common minke whales during the aerial survey off West Greenland September 2005.

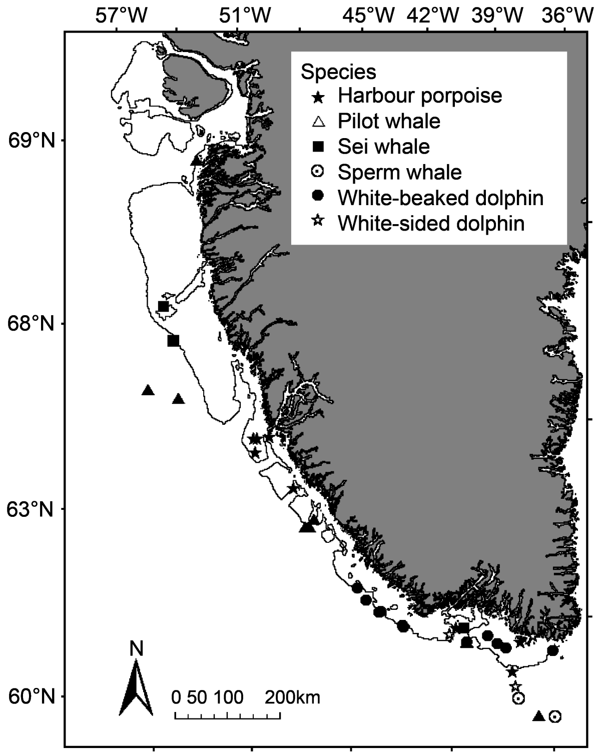

Fig. 2d. Sightings of sei whales, pilot whales, sperm whales, harbour porpoises, white-beaked and white-sided dolphin during the aerial survey off West Greenland September 2005.

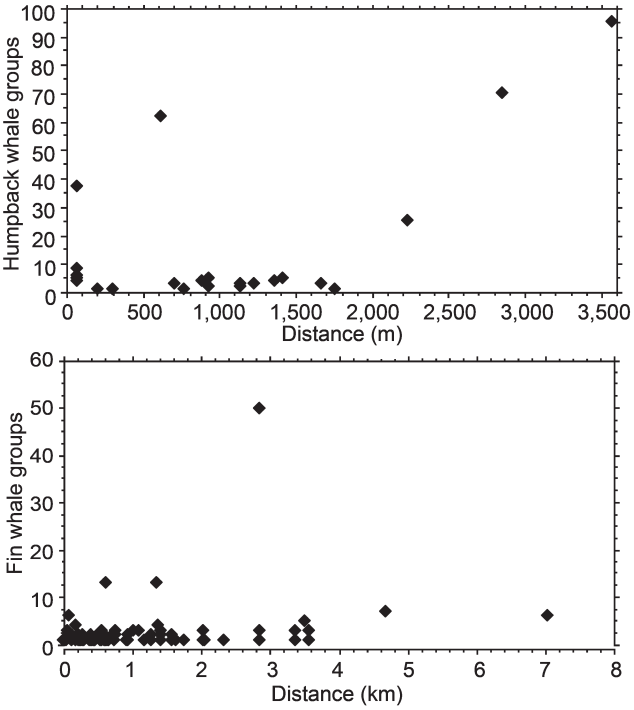

Fig. 3. Distribution of humpback whale (upper panel) and fin whale (lower panel) group sizes in relation to distance from trackline.

likely of harbour porpoises (*Phocoena phocoena*); additional sightings of this species were made south of Nuuk Fjord.

Humpback whale abundance estimates

Humpback whales were found predominantly in groups, and the size of the groups was often large; only 17% of detections were of single animals and 43% were of groups larger than five (Fig. 3). The frequent occurrence of humpback whales in large groups prevented the use of cue counting methods for abundance estimation, instead the abundance of humpback whales was analysed using standard line transect methods, assuming probability of detection on the line to be 1. There were no duplicate sightings of humpback whales so perception bias and measurement error could not be estimated.

Detection function and abundance estimates

Half-normal and hazard-rate detection functions were fitted to the grouped data. Sample size was lower than desirable for line transect surveys (only 22 groups out of 23 were within the truncation distance of 3km); this precluded stratifying for estimation of the detection function and *f*(0) and it precluded use of covariates in this estimation. Based on Akaike's Information Criterion (AIC), a half-normal detection function model with no adjustment terms was chosen (Fig. 4). The associated χ^2 goodness-of-fit statistic was not significant (p=0.63), indicating an adequate fit to the data.

Estimates of the key components of the line transect estimator are shown in Table 2, together with summaries of stratum areas, effort and estimated density and abundance. Total abundance was estimate to be 1,218 humpback whales (CV=0.57) with log-based 95% confidence interval (423; 3,508) and log-based 90% confidence interval (501; 2,960).

One problem with the humpback whale abundance analysis was the combination of both solitary whales and whales in large groups (>10) that could bias both the estimates of mean group size and the detection function in line transect analysis (Fig. 3). An alternative approach was to estimate the abundance based on small groups (<11 whales) and using the same line transect technique described above with a right truncation at 2.0km. Abundance based on large groups (>10 whales) was then estimated separately using strip census analyses with a fixed strip width of 3.6km. The combined estimate of the line transect and strip census analyses was 1,158 (CV=0.35) humpback whales (Table 3) and was thus not different from the results obtained from the line transect analysis of all group sizes.

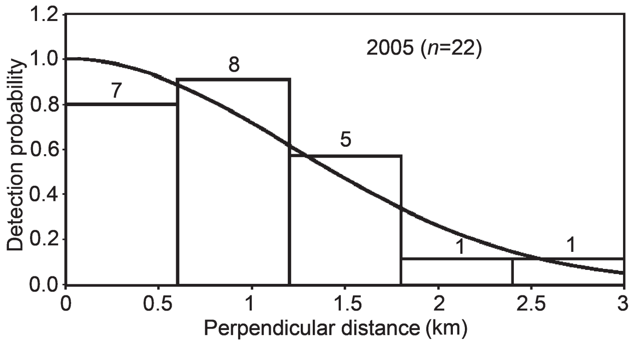

Fig. 4. Perpendicular distance histogram and fitted half-normal probability density function for humpback whale line transect data.

Fin whale abundance estimates

Fin whale group sizes were not as variable and large as for humpback whales; 61% of detections were of single whales, 17% were in groups of two and 9% were in groups of 5 or more (Fig. 3).

Measurement errors

Although the sample size was small, there appears to be little difference between the estimates of perpendicular distances from the two platforms at distances less than about 1.5km (Fig. 5). The level of distance 'binning' used in analysis (see Fig. 6) should make the line transect estimates of fin whale abundance insensitive to both the small errors at distances less than 1.5km and the more substantial errors at larger distances. The apparent lack of substantial errors at smaller distances (Figs 5 and 7) indicates that little, if anything, would be gained by incorporating a measurement error model in estimation. Estimating the measurement error process parameters from such a small sample size may add substantially to the variance of the resulting density and abundance estimates. Measurement errors were therefore dealt with only by using binned distance data in estimation.

Probability of detection at distance zero

Sightings from only the right side of the plane (where there were two independent observers) were used to estimate *g*(0). Conditional detection functions for each observer

Table 2

Humpback whale data summary and estimates. K is number of transects; a is area (km^2); L is transect length (km); n is number of groups detected within 3km; n/L is encounter rate (groups per 1,000km); $\hat{f}(0)$ is the intercept of the probability density function; $\hat{E}[s]$ is estimated mean group size; $\hat{D}$ is estimated animal density (animals per 1,000 km^2); $\hat{N}$ is estimated animal abundance. Coefficients of variation are in brackets.

Stratum	Area (km^2)	K	L (km)	n	n/L	$\hat{f}(0)$	$\hat{E}[s]$	$\hat{D}$	$\hat{N}$
Cape Farewell	11,523	4	293	0	0.0			0	0
Central West	74,798	30	1,958	4	2.04 (0.91)			5.63 (1.00)	421 (1.00)
Disko Bay	12,312	12	556	1	1.80 (1.78)	0.664	8.3	4.95 (1.82)	61 (1.82)
South Greenland	19,491	19	1,106	4	3.62 (0.46)	(0.12)	(0.38)	9.97 (0.62)	194 (0.62)
Store Hellefiske Bank	15,669	7	577	0	0			0	0
South West	29,781	31	1,968	12	6.61 (0.42)			18.2 (0.60)	542 (0.60)
Total	**163,574**							**19.1 (0.57)**	**1,218 (0.57)**

Table 3

Estimates of humpback whale abundance based on line transect analyses of groups <10 and strip census estimates of groups >10.

	Right truncation	n	N	CV	Mean group size	Expected group size
Strip census estimate of groups >10	3.6km	5	647	0.48	57.8	
Line transect abundance of groups < 10	2.0km	18	511	0.53	3.39	4.06
			N (sum)	CV	lower 95% CI	upper 95% CI
Combined estimate			1,158	0.35	595	2,255

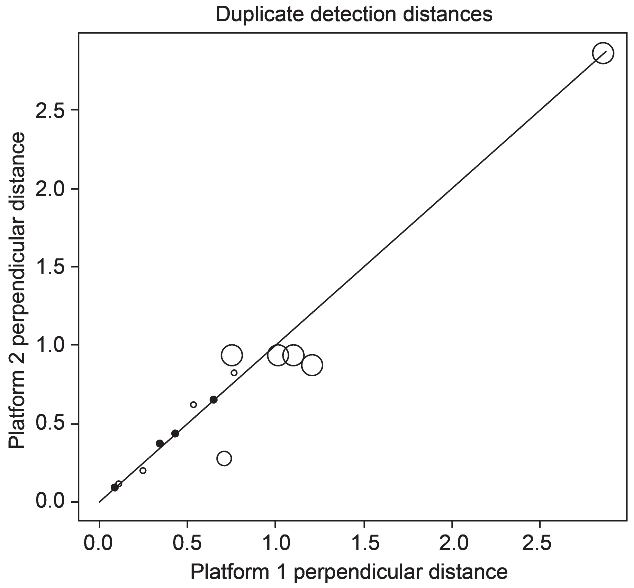

Fig. 5. Perpendicular distance estimates (in km) from duplicates (minke=solid dots, fin=circles; dots are proportional to group size (1, 2 or 3)). The line corresponds to platform 1 (front observer) and platform 2 (rear observer) estimated distances being equal.

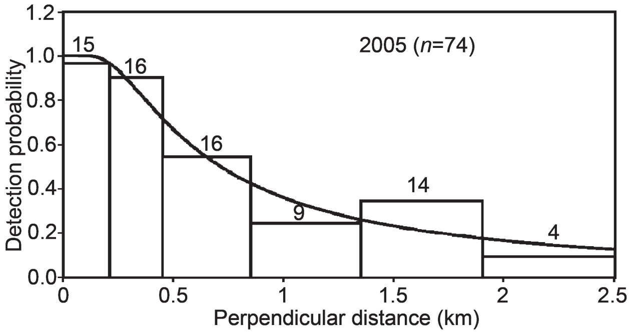

Fig. 6. Perpendicular distance histogram and fitted hazard rate probability density function for fin whale line transect data.

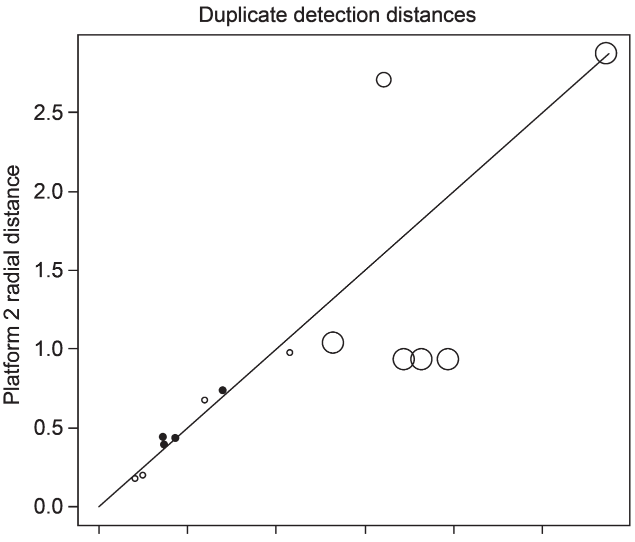

Fig. 7. Radial distance (in km) estimates from duplicates (minke=solid dots, fin=circles; dots are proportional to group size (1, 2 or 3)). The line corresponds to platform 1 (front observer) and platform 2 (rear observer) estimated distances being equal.

(conditional on detection by the other observer) were estimated using the iterative logistic regression, as implemented in *Distance* 5.0, release 2 (Thomas *et al.*, 2006). After truncating at 2.5km to remove an influential observation at 3km which led to conditional detection functions which increased slightly with distance, there remained 27 detections by the rear observer, 20 by the front observer and 6 duplicates. Fig. 8 shows the distribution of detections and duplicate proportions (proportion of each observer's detections which were seen by the other observer) as a function of distance, together with each observer's estimated conditional detection function (conditional on detection by the other observer). Models were selected using AIC and a model with radial distance and observer as explanatory variables was found to be best on this basis.

The probability of detecting a fin whale group on the trackline was estimated to be 0.34 (CV=0.29) for the rear observer, 0.26 (CV=0.32) for the front observer and 0.51 (CV=0.21) for both observers combined assuming that their probabilities are independent.

Detection function and abundance estimates

Truncation of perpendicular distances at 2.5km excluded 12% of detections (n= 84). Half-normal and hazard rate detection function forms were considered and a hazard rate function with no adjustment parameters was selected on the basis of AIC (Fig. 6). The associated χ^2 goodness-of-fit statistic was not significant (p=0.15), indicating an adequate fit to the data.

Estimates of the key components of the line transect estimator are shown in Table 4, together with summaries of stratum areas, effort and estimated density and abundance. Total fin whale abundance was estimated to be 1,660 animals (CV=0.38) and log-based 95% confidence interval (799; 3,450) and log-based 90% confidence interval (899; 3,066). The estimate corrected for $g(0)<1$, for both observers combined, was 3,234 animals (95% CI 1,412; 7,406, Table 4). This point estimate of abundance is likely negatively biased because $g(0)$ for the left side of the aircraft is likely to be lower than the combined $g(0)$ for the right side because the left side had only one observer.

An alternative approach that takes into account diving whales is the cue counting technique. Cue-counting methods were applied to estimate the abundance of solitary fin whales and to compare with line transect abundance of solitary fin whales. Using a cue rate of 50 cues per hour (Heide-Jørgensen and Simon, 2007), a cue counting abundance estimate of 8,889 (n=50, CV=0.68) solitary fin whales was achieved. This estimate is ~10 times bigger than a line transect estimate calculated solely for solitary fin whales (719, CV=0.40). The reason for this large difference is unclear; however, the detection function fitted to the observed radial distance distribution in the cue counting estimate showed a somewhat unrealistic rapid drop off close to the origin and cue counting estimates were not developed any further for fin whales.

Common minke whale abundance estimates

With the exception of one group of two whales, all common minke whale detections were of solitary animals and cue counting methods could be used for estimating abundance.

Measurement errors

The sample size of four common minke whale cues detected by both front and rear observers (minke duplicates) in the right side of plane was too small to estimate the distance

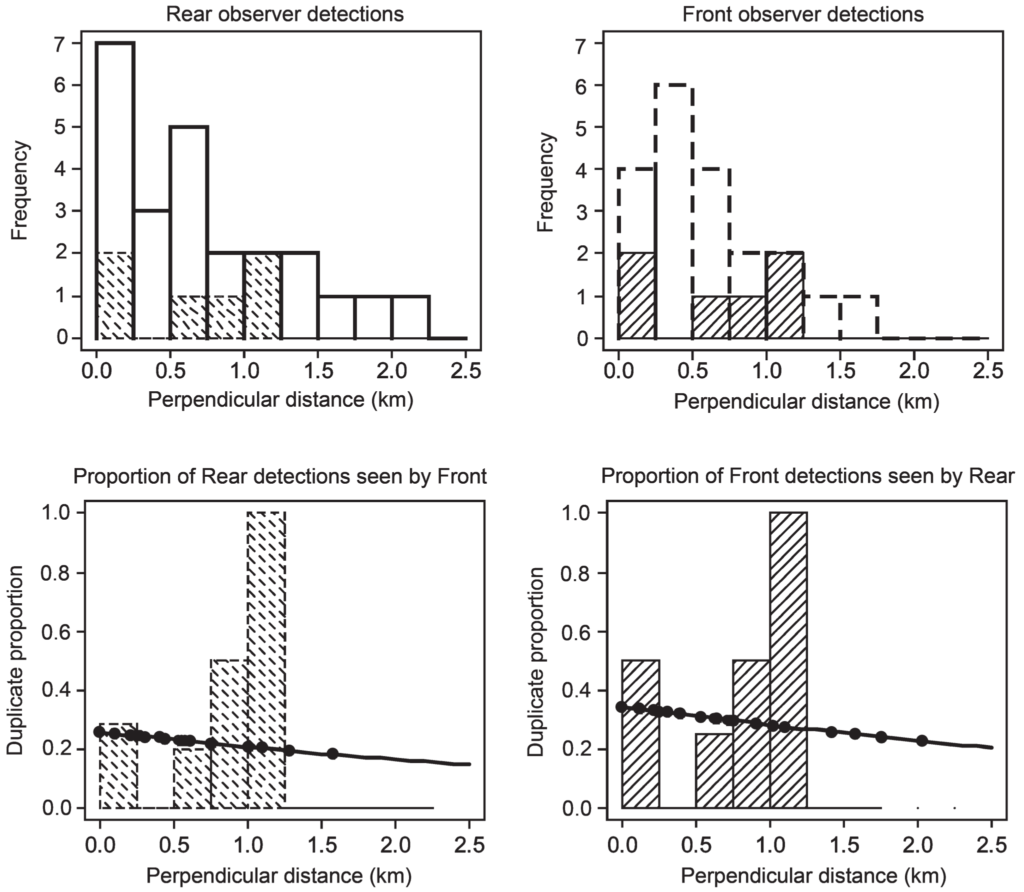

Fig. 8. Duplicate proportions and estimated conditional detection functions for fin whales. All data and estimates are for the right hand side of the aircraft only. The top row of plots shows the number of detections by each observer, with the numbers of these that were detected by the other observer (the duplicates) shaded. Bars with solid lines correspond to rear observer detections, bars with dashed lines correspond to front observer detections. The bottom row of plots shows the duplicate proportions, together with fitted detection function (smooth curve) and estimated detection probability for individual detections made by the observer in question.

Table 4

Fin whale data summary and estimates. K is number of transects; a is area (km^2); L is transect length (km); n is number of groups detected within 3km; n/L is encounter rate (groups per 1,000km); $\hat{f}(0)$ is the intercept of the probability density function; $\hat{E}[s]$ is estimated mean group size; $\hat{D}$ is estimated animal density (animals per 1,000 km^2); $\hat{N}$ is estimated animal abundance. Coefficients of variation are in brackets.

Stratum	Area (km^2)	K	L (km)	n	n/L	$\hat{f}(0)$	$\hat{E}[s]$	$\hat{D}$	$\hat{N}$
Cape Farewell	11,523	4	293	2	6.8 (2.09)	0.997 (0.22)	1.54 (0.12)	5.21 (2.10)	60 (2.10)
Central West	74,798	30	1,958	38	19.4 (0.41)			14.87 (0.47)	1,112 (0.47)
Disko Bay	12,312	12	556	1	1.80 (0.67)			1.38 (0.71)	17 (0.71)
South Greenland	19,491	19	1,106	17	15.4 (0.29)			11.78 (0.37)	230 (0.37)
Store Hellefiske Bank	15,669	6	577	6	10.4 (1.14)			7.96 (1.17)	125 (1.17)
Southwest Greenland	29,781	31	1,968	10	5.1 (0.28)			3.89 (0.37)	116 (0.37)
Total	163,574							10.15 (0.38)	1,660 (0.38)
Corrected for $g(0)<1$									3,234 (0.44)

measurement error process reliably. However, comparison of measurement of cues from both minke and fin whales suggest that the difference in measurement error between the two platforms within about 1.5km is negligible (Fig. 7) and no attempt was made to incorporate distance measurement error into the abundance estimation. It is not possible to estimate bias in estimating distance by either platform from these data.

Probability of detection at distance zero

Independent observer data were available only for the right side of the aircraft. These were used to estimate probability of detection at the closest radial distance used in analysis. As the front observer did not have a clear view of distance zero (because there was no bubble window in this position), and no detections were made within 0.2km of the aircraft, data were left-truncated at 0.2km before analysis. Fig. 9 shows

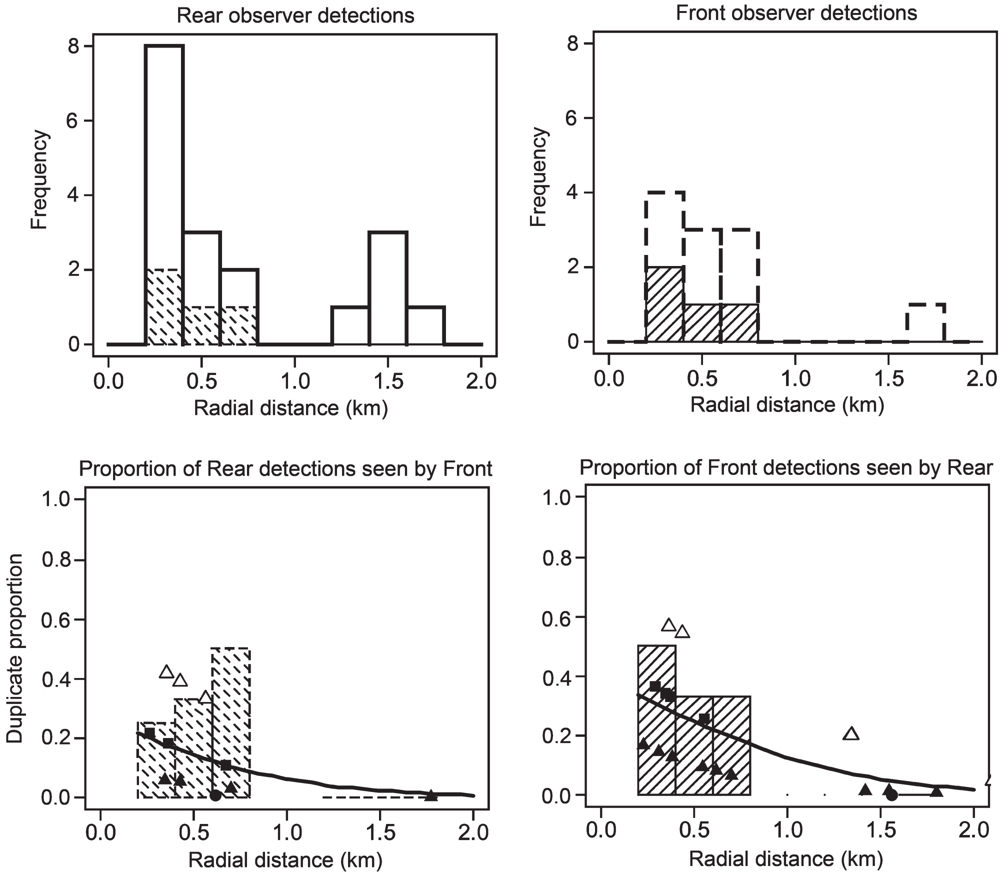

Fig. 9. Duplicate proportions and estimated conditional detection functions for common minke whales. All data and estimates are for the right hand side of the aircraft only. The top row of plots shows the number of detections by each observer, with the numbers of these that were detected by the other observer (the duplicates) shaded. Bars with solid lines correspond to rear observer detections, bars with dashed lines correspond to front observer detections. The bottom row of plots shows the duplicate proportions, together with fitted detection function (smooth curve) and estimated detection probability for individual detections made by the observer in question. Different Beaufort sea state for individual detections is indicated using different symbols: 0, 1, 2, and 3 are plotted using , , and respectively.

the duplicate proportions (proportion of each observer's detections which were seen by the other observer) as a function of distance, together with each observer's estimated conditional detection function (conditional on detection by the other observer). Conditional detection functions were estimated using the iterative logistic regression, as implemented in *Distance* 5.0, release 2 (Thomas *et al*., 2006). Models were selected using AIC and a model with radial distance, observer and Beaufort sea state as explanatory variables was found to be best on this basis.

The probability of detecting a cue at distance 0.2 km was estimated to be 0.36 (CV=0.39) for the rear observer, 0.22 (CV=0.42) for the front observer and 0.45 (CV=0.33) for both observers combined. As noted above, the sample size for this analysis was small (21 detections by the rear observer, 11 by the front observer, with 4 duplicates) and as a result, the reliability of these estimates is somewhat uncertain.

Detection function and abundance estimates

The slope of the probability density function $h(0)$ was estimated by fitting half-normal and hazard-rate functional forms to grouped radial distance data truncated at 1.6km. This led to seven detections (17% of the distances) being discarded. A hazard-rate detection function form with no adjustment terms was selected on the basis of AIC. The resulting detection function and fit of the pdf of radial distances to the observed radial distance distribution are shown in Figs 10 and 11. The associated χ^2 goodness-of-fit statistic was not significant (p=0.47), indicating an adequate fit to the data.

Estimates of the key components of the cue-counting estimator are shown in Table 5, together with summaries of stratum areas, effort and estimated density and abundance. Cue densities were converted to animal densities by dividing by an estimated cue rate of 46.3 cues per hour (CV=0.11) (Heide-Jørgensen and Simon, 2007). If detection

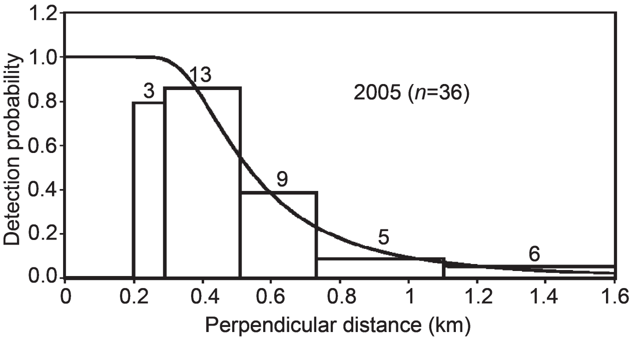

Fig. 10. Radial distance histogram and fitted hazard-rate detection function for common minke whale cue-counting data. (Note that the histogram bar heights have been scaled in inverse proportion to their mean radial distance, in order to place them on a comparable scale to the detection function curve.)

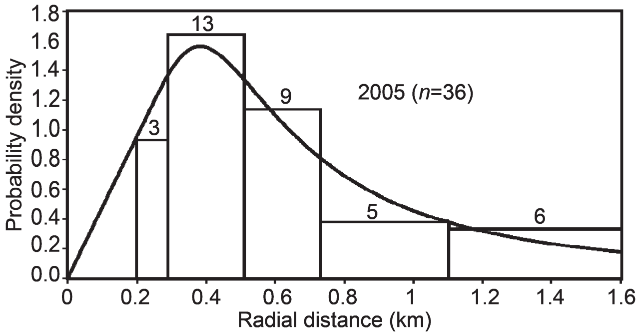

Fig. 11. Fit of the hazard-rate probability density function of radial distances to the observed radial distance distribution for common minke whale cue-counting data.

at distance 0.2km (called '$g(0)$' in the table) is assumed to be certain, total common minke whale abundance is estimated to be 4,856 animals (CV=0.49), log-based 95% CI=1,910-12,348 and log-based 90% CI=2,219-10,628. If detection at distance 0.2km is estimated as above, total common minke whale abundance is estimated to be 10,792 animals (CV=0.59), log-based 95% CI=3,594-32,407 and log-based 90% CI=4,289-27,156. In obtaining these estimates it is assumed that the observer on the left side of the aircraft has the same probability of detecting a cue at 0.2km as the two observers on the right side of the plane.

DISCUSSION

Due to inclement weather conditions the survey failed to cover areas west of Disko Island, the western part of the northern edge of Store Hellefiske Bank and a large part of the Central West Greenland strata. This lack of coverage, especially in the latter area, may cause a negative bias in the estimate of fin whale abundance in West Greenland, since large concentrations of fin whales are known to occur in this region. Supporting evidence for a negative bias is that the ship-based survey in September 2005 found large numbers of fin whales around 67°N, 57°W, the area not covered in the present survey. Furthermore locations from fin whales tracked by satellite as well as observations from Norwegian minke whalers indicate that fin whales occur in this area in conspicuous numbers (Heide-Jørgensen *et al*., 2007; Heide-Jørgensen *et al*., 2003). No survey coverage was attained in offshore areas (i.e. west of the 200m depth contour) south of 64°N and this may cause additional negative bias to the estimates of fin and common minke whale abundance in West Greenland.

The line transect estimate of humpback whale abundance in this study (1,218; 95% CI-423-3,508) was very similar to the estimate from a simultaneous ship-based survey (1,306; 95% CI-570-2,989) (Heide-Jørgensen *et al*., 2007). However, the estimate from the aerial survey is negatively biased because some animals will have been underwater and hence undetectable during passage of the plane and no corrections were made for whales missed by the observers. If estimates of the percentage of time humpback whales are visible from the air were available, this bias might be reduced substantially. Bannister and Hedley (2001) estimated the surface detection probabilities for aerial surveys of Southern Hemisphere humpback whales to range between 0.25 and 0.41. Satellite-linked time-depth recorders deployed on five humpback whales off Central West Greenland (Fyllas Bank) in June-July 2000 has shown that these whales spend between 29.7 and 43.6% of their time at the surface above 4m with an average of 36% (Dietz *et al*., 2002). If it is assumed that humpback whales can be seen at depths down to 4m the estimates will need to be multiplied by approximately three to account for the time the whales are visible (above a certain depth) to be seen by the observers. This would lead to a substantially larger abundance estimate of humpback whales in West Greenland.

Previously the abundance of humpback whales in West Greenland has been estimated to about 360 humpback whales (95% CI 314-413) for 1988-93 (Larsen and Hammond, 2004), 599 (95% CI=237-1,512) in 1993 (Kingsley and Witting, 2001) and 400 (CV=0.64) in 2002 and 2004 (Witting and Kingsley, 2005). The uncorrected aerial and the ship based surveys in 2005 both confirm that the current abundance of humpback whales in West Greenland is substantially larger than what was estimated in the surveys in the 1990s. This may be due to both a severe underestimation of abundance in previous surveys, growth in population size and/or increased affinity to the West Greenland feeding ground. The timing of the surveys in 2005 was one month later than the surveys conducted in the 1990s. Humpback whales arriving late on the West Greenland feeding ground could have contributed to the larger abundance estimates in 2005. The unprecedented observations of large groups of humpback whales (up to 95 individuals), often with a reddish defecation trailing behind, could be interpreted as an autumn feeding migration to West

Table 5

Minke whale data summary and estimates. K is number of transects; a is area (km^2); T is time spent searching (hours); n is number of cues detected within 1.6 km; n/T is encounter rate (cues per hour); $\hat{h}(0)$ is the slope of the density function; $\hat{D}$ is estimated animal density (animals per 10^6 km^2); $\hat{N}$ is estimated animal abundance. Coefficients of variation are in brackets. Estimated cue rate of $\hat{\eta}$ =46.3 cues per hour (CV=0.11) was used to convert cue density to whale density. Estimates in columns headed 'estimated $g(0)$' are those in columns headed '$g(0)$=1' divided by the estimated $g(0)$ of 0.45 (CV=0.33).

Stratum	Area (km^2)	K	T hour	n	n/T	$\hat{h}(0)$	$\hat{D}$	$\hat{N}$
Cape Farewell	11,523	3	1.26	0	0	4.77 (0.40)	0	0
Central West	74,798	27	11.47	12	1.047 (0.45)		34.35 (0.61)	2,569 (0.61)
Disko Bay	12,312	11	3.02	2	0.663 (0.45)		21.76 (0.61)	268 (0.61)
South Greenland	19,491	19	7.09	8	1.129 (0.38)		37.04 (0.56)	722 (0.56)
Store Hellefiske Bank	15,669	6	3.52	3	0.853 (0.55)		28.00 (0.69)	439 (0.69)
Southwest Greenland	29,781	29	11.38	10	0.879 (0.47)		28.84 (0.62)	859 (0.62)
Total	163,574						29.69 (0.49)	4,856 (0.49)
Corrected for $g(0)$<1							65.97 (0.59)	10,792 (0.59)

Greenland, but could also be the result of an aggregation of whales before the autumn migration out of Greenlandic waters.

Comparison of cue counting and line transect estimates for solitary fin whales resulted in a cue counting estimate that was ~10 times the line transect estimate. This suggests that the availability bias in line transect estimates may be large and that the fin whale abundance estimate presented here (based on a line transect analysis of all schools) may be substantially negatively biased. Circumstances made the cue counting estimate less attractive: the direction of the bias, if any, is unknown; the cue counting method can not deal with large group sizes; and the detection function showed an implausible drop near the origin.

The line transect estimate of fin whale abundance (1,660; 95% CI 799-3,450) was similar to the estimate obtained from a simultaneous ship-based survey (1,980; 95% CI 913-4,296). Both estimates are negatively biased to an unknown degree by incomplete coverage, lack of correction for submerged whales and especially for the aerial survey, by the lack of correction for whales missed by the observers. Correcting the aerial survey for perception bias increases the abundance estimate to 3,234 whales (95% CI 1,412-7,406). However, all three estimates confirm that the likely magnitude of the fin whale abundance off West Greenland in September is in the low thousands. The 1987/88 estimate of 1,100 (95% CI 520-2,100) fin whales in West Greenland (IWC, 1992) was a cue counting estimate and is therefore not directly comparable to the current abundance estimates. However, considering that the current but uncorrected estimates are larger than the earlier estimates corrected for availability bias (by the cue counting technique) it seems likely that the abundance of fin whales in West Greenland has increased. Additional evidence that fin whale abundance has increased in West Greenland comes from a simple comparison of encounter rates. About three times as many whales were seen (per unit effort) in the 2005 survey than in the 1987 survey. The later timing of the aerial survey in 2005 could be partially responsible by including fin whales arriving late on the West Greenland feeding ground. However, like humpback whales, fin whales were also seen in large groups of up to 50 whales. These group sizes were not seen on previous surveys, and could be interpreted as an autumn aggregation before the initiation of the southward migration.

The cue counting estimate of common minke whale abundance (4,856; 95% CI 1,910-12,348) was close to the estimate obtained from the simultaneous ship-based survey (4,479, 95% CI 1,760-11,394). The two estimates are however not directly comparable since the aerial survey estimate corrects for availability bias (cue counting technique) and the ship based survey estimate assumes that all common minke whales are at the surface to be seen during the passage of the survey platform. The cue counting common minke whale abundance estimate from this survey is also not significantly different from previous estimates from West Greenland, but when corrected for perception bias or $g(0)$ it is considerably larger than previous estimates, although not statistically different. The data that were used for estimating the perception bias were based on a small sample size from just one side of the plane and the estimate of $g(0)$ is similarly imprecise (CV=0.59). However, the few duplicate sightings between the front and rear observer indicate that a considerable number of common minke whales were not detected. In comparison with perception bias of other species of marine mammals in aerial surveys, common minke whales are clearly among the most difficult animals to detect and the low estimate of $g(0)$, i.e. the high estimated perception bias, determined in this study is not unexpected (Table 6). The $g(0)$ for the fin whales was unexpectedly low given their conspicuous large blows and body size. A possible explanation for the low fin whale detection is the fact that the survey was a multispecies survey where the detection might by negatively affected by the simultaneous recording of several species. Common minke whales are hard to detect because they are inconspicuous and spend a short time at the surface, but it could also be because of the rather demanding data collection from each cue of a whale. Finally the fact that the survey targets whales close to the plane (i.e. common minke whales) as well as those farther away (fin and humpback whales) might add to perception bias for common minke whales.

This study demonstrates the amount of data that can be obtained from an aerial survey effort of the shelf area off West Greenland in a year with reasonably good weather conditions. Other years in which surveys were attempted have had much more severe weather conditions and the timing of the present survey (late August and September) may have improved the likelihood of experiencing fair weather. The trade off is that the southward migration of baleen whales out of the Greenland shelf areas might already have started which also negatively affects the abundance estimates. Víkingsson and Heide-Jørgensen (2005) showed that some common minke whales tagged with satellite transmitters left the Icelandic shelf areas in mid September when they initiated their southbound migration.

This study has also brought to light the difficulties of applying the cue counting method to other species besides solitary common minke whales. Fin whales and humpback whales occur in groups and some of these groups are of up to 50 fin whales and 95 humpback whales. It is not a simple or practical task to count cues from tens of animals simultaneously and it becomes increasingly complicated with increasing whale pod size. Also, because there is a

Table 6

Estimates of fraction detected on the transect line for multispecies aerial surveys of marine mammals in West Greenland and characterization of the main features of the sighting process. GINR=Greenland Institute of Natural Resources.

Species	Survey platform	Mean pod size	Detection of cues	Perception bias	Estimation method	Ref.
Narwhal	Twin Otter	1.7	Dark but mostly in leads	0.86 (0.13)	Mark-recapture, full conditional independence	GINR
Beluga	Twin Otter	3.0	White moving groups	0.77 (0.10)	Mark-recapture, full conditional independence	GINR
Bowhead whale	Twin Otter	1	Big black body, blows, in leads	0.62 (0.19)	Mark-recapture, full conditional independence	GINR
Walrus	Twin Otter	1-2	Small brown body	0.51 (0.25)	Mark-recapture, full conditional independence	GINR
Fin whale	Partenavia	3.0	Large blows	0.51 (0.21)	Line transect, point conditional independence	This survey
Minke whale	Partenavia	1.1	Inconspicuous blows	0.45 (0.33)	Cue counting, point conditional independence	This survey

considerable range in fin whale group sizes, some of them large, the fin whale cue counting estimates will be fairly sensitive to whether or not animals in groups cue at the same rate as the observed individuals from which cue rate estimates were obtained.

The question remains if the cue counting method is the most efficient and accurate way to obtain abundance estimates of large cetaceans in West Greenland. Alternative methods include sight-resight methods applied to aerial line-transect survey (e.g. Innes *et al*., 2002) with correction for perception bias from double platform experiments and telemetry data on species specific surface times to correct for availability bias.

In summary, we believe that the abundance estimates presented in this study are definitely underestimates of the actual abundance of large whales in West Greenland because of incomplete coverage in presumed high density areas, no correction for perception bias in the case of humpback whales, lack of correction for availability bias for fin whales and humpback whales and sightings of unidentified large whales that were not included. Some whales may also have started their southbound autumn migration out of Greenland and were therefore not available to be counted during the survey.

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REFERENCES

Bannister, J.L. and Hedley, S.L. 2001. Southern Hemisphere group IV humpback whales: their status from recent aerial survey. *Mem. Queensl. Mus*. 47(2): 587-98.

Borchers, D.L., Lake, J.L., Southwell, C. and Paxton, C.G.M. 2006. Accommodating unmodelled heterogeneity in double-observer distance sampling surveys. *Biometrics* 62: 372-78.

Borchers, D.L., Pike, D., Gunnlaugsson, T. and Víkingsson, G.A. 2003. Analyses of the NASS 1987 and 2001 minke whale cue counting surveys taking account of distance estimation errors. Paper SC/55/NAM3 presented to the IWC Scientific Committee, May 2003, Berlin (unpublished). 33pp. [Paper available from the Office of this Journal].

Buckland, S.T., Anderson, D.R., Burnham, K.P., Laake, J.L., Borchers, D.L. and Thomas, L. 2001. *Introduction to Distance Sampling: Estimating Abundance of Biological Populations*. Oxford University Press, Oxford, UK. vi+xv+432pp.

Dietz, R., Teilmann, J., Heide-Jørgensen, M.P. and Jensen, M.V. 2002. Satellite tracking of humpback whales in West Greenland. *NERI Technical Report* 411(2002): 1-40. [Published by National Environmental Research Institute, Ministry of the Environment, Denmark].

Heide-Jørgensen, M.P. and Simon, M. 2007. A note on cue rates for common minke, fin and humpback whales off West Greenland. *J. Cetacean Res. Manage*. 9(3): 211-14.

Heide-Jørgensen, M.P., Simon, M.J. and Laidre, K.L. 2007. Estimates of large whale abundance in Greenland waters from a ship-based survey in 2005. *J. Cetacean Res. Manage* 9(2): 95-104.

Heide-Jørgensen, M.P., Witting, L. and Jensen, M.V. 2003. Inshore-offshore movements of two fin whales *Balaenoptera physalus* tracked by satellite off West Greenland. *J. Cetacean Res. Manage*. 5(3): 214-45.

Hiby, A.R. 1985. An approach to estimating population densities of great whales from sighting surveys. *IMA (Inst. Math. Appl.) J. Math. Appl. Med. Biol*. 2: 201-20.

Hiby, A.R., Ward, A. and Lovell, P. 1989. Analysis of the North Atlantic Sightings Survey 1987: aerial survey results. *Rep. int. Whal. Commn* 39: 447-55.

Innes, S., Heide-Jørgensen, M.P., Laake, J., Laidre, K.L., Cleator, H., Richard, P. and Stewart, R.E.A. 2002. Surveys of belugas and narwhals in the Canadian high Arctic in 1996. *NAMMCO Sci. Publ*. 4: 169-90.

International Whaling Commission. 1990. Report of the Scientific Committee. *Rep. int. Whal. Commn* 40:39-79.

International Whaling Commission. 1992. Report of the Comprehensive Assessment Special Meeting on North Atlantic Fin Whales, Reykjavík, 25 February-1 March 1991. *Rep. int. Whal. Commn* 42:595-644.

International Whaling Commission. 2006. Report of the Scientific Committee. Annex E. Report of the Standing Working Group (SWG) on the Development of an Aboriginal Whaling Management Procedure (AWMP). *J. Cetacean Res. Manage. (Suppl.)* 8:91-109.

Kingsley, M.C.S. and Witting, L. 2001. A preliminary analysis of aerial survey observations of humpback whales in Greenland waters. Paper SC/53/NAH23 presented to the IWC Scientific Committee, July 2001, London (unpublished). 51pp. [Paper available from the Office of this Journal].

Larsen, F. 1995. Abundance of minke and fin whales off West Greenland, 1993. *Rep. int. Whal. Commn* 45: 365-70.

Larsen, F. and Hammond, P.S. 2004. Distribution and abundance of West Greenland humpback whales *Megaptera novaeangliae*. *J. Zool., London*. 263: 343-58.

Larsen, F., Martin, A.R. and Nielsen, P.B. 1989. North Atlantic Sightings Survey 1987: report of the West Greenland aerial survey. *Rep. int. Whal. Commn* 39: 443-46.

Thomas, L., Laake, J.L., Strindberg, S., Marques, F.F.C., Buckland, S.T., Borchers, D.L., Anderson, D.R., Burnham, K.P., Hedley, S.L., Pollard, J.H., Bishop, J.R.B. and Marques, T.A. 2006. Distance 5.0. Release 1. Research Unit for Wildlife Population Assessment, University of St Andrews, UK. [Available from: *http://www.ruwpa.st-and.ac.uk/distance/*].

Víkingsson, G.A. and Heide-Jørgensen, M.P. 2005. A note on the movements of minke whales tracked by satellite in Icelandic waters in 2001-2004. Paper SC/57/O9 presented to the IWC Scientific Committee, June 2005, Ulsan, Korea (unpublished). 3pp. [Paper available from the Office of this Journal].

Witting, L. and Kingsley, M. 2005. Abundance of marine mammals off West Greenland, 2002-2004. Paper SC/57/AWMP3 presented to the IWC Scientific Committee, June 2005, Ulsan, Korea (unpublished). 13pp. [Paper available from the Office of this Journal].

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Behaviour of a social unit of sperm whales (*Physeter macrocephalus*) entangled in a driftnet off Capo Palinuro (Southern Tyrrhenian Sea, Italy)

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ABSTRACT

Driftnet fishing is notorious for being the major source of fatal entanglement of cetaceans and for its devastating impact on some pelagic species of the Mediterranean fauna. Of all the large cetaceans, the sperm whale (*Physeter macrocephalus*) is most affected by this fishing technique. On 9 August 2004, a group of five sperm whales, two adult females and three juvenile individuals, was found trapped in a driftnet 40 miles southwest off Capo Palinuro (Italy). Their tails were totally immobilised by the net and one animal was completely entangled. All the animals showed numerous lesions on their bodies. The group was freed by the Italian Coast Guard scuba-diving team during a two-day rescue operation.

This exceptional case of sperm whale disentanglement was a unique opportunity to study the group's acoustic and general behaviour during a particularly stressful event. Out of a total video/acoustic recording of 110 minutes, 91 were examined. During the rescue procedures, the whales' behaviour was described as open mouthed, sideways roll, agitation of fluke and pectoral fins, head rubbing, fluke contact (with head, flippers and back by the liberated animals) and defecation. As expected, the entangled individuals produced different patterns of clicks, identified as 'usual clicks', 'codas' and 'creaks'. Each pattern was associated with specific behaviour.

Despite international and national regulation banning fishing with driftnets in the Mediterranean Sea, driftnets continue to be used illegally in this sperm whale habitat, posing a constant threat to the species' survival in the region.

KEYWORDS: INCIDENTAL CATCHES; SPERM WHALE; DRIFTNET; MEDITERRANEAN SEA; BEHAVIOUR; NORTHERN HEMISPHERE

INTRODUCTION

On 9 August at 14.00, a social unit (sensu Whitehead, 2003) of five sperm whales (*Physeter macrocephalus*), two adult females and three juvenile individuals, was found entangled in a driftnet 40 miles southwest off Capo Palinuro (Southern Tyrrhenian Sea, Italy). Driftnets are large, floating nets made of a mesh of monofilament or multifilament line, generally deployed in open marine waters. They can be up to 50km long and hang vertically 20-30m from the surface. They are designed primarily to trap and entangle large fish such as tuna (*Thunnus* sp.) and swordfish (*Xiphias gladius*), however, left to drift freely, they indiscriminately trap and kill non-target large pelagic species such as whales, dolphins, sharks, turtles, rays and seabirds.

Large-scale pelagic driftnet fishing is of considerable international concern; the United Nations banned the use of large-scale driftnet operations on the open seas from 31 December 1992 and the European Union prohibited the use of driftnets of all sizes from the 1 January, 2002.

Driftnets were the main cause of fatal entanglements for cetaceans in the Mediterranean Sea, with serious consequences for some populations (Di Natale and Notarbartolo di Sciara, 1994; IWC, 1994). Between 1986 and 1990, 83% of all recorded cetacean strandings were attributed to fisheries by-catch, nearly all in driftnets (Cagnolaro and Notarbartolo di Sciara, 1992). At the peak of driftnet deployment, an annual by-catch of over 7,000 cetaceans was estimated for the Italian seas alone (Notarbartolo di Sciara, 1990).

Despite their illegal status, these nets are still in use in Italy (where both nets and vessels are usually called 'spadare') and continue to cause harm and/or the death of unknown numbers of protected species each year. Of the large cetaceans, the sperm whale is the most affected by this method of fishing (Lazaro and Martin, 1999; Notarbartolo di Sciara *et al*., 2004). Between 1986 and 2000, 64 sperm whales were killed in Italy alone as a result of entanglement in fishing gear (they showed injury or were stranded as a result entanglement); most, if not all, of these were attributable to driftnet bycatch (Reeves and Notarbartolo di Sciara, 2006).

The aim of this work is to describe the behaviour and acoustic vocalisations (clicks) of an entangled social unit of sperm whales during the rescue operation conducted by the Italian Coast Guard scuba-diving team.

Sperm whale clicks are sharp-onset, broadband, impulsive vocalisations with a frequency of between 5 and 25kHz (Madsen *et al*., 2002), arranged in various patterns (usual clicks, slow clicks, codas, creaks, etc.) and used in a variety of circumstances (Whitehead, 2003). Within sperm whale social groups, clicks are possibly representative of intimate interactions among its members and the exchange of codas is probably the most evident form of communication (Watkins and Schevill, 1977) aimed at social interaction. Hence, a detailed analysis of these sounds, emitted during the rescue procedures, was performed.

METHODS

A professional underwater camera was used to record the sperm whales' behaviour during the disentanglement process. Out of a total video/acoustic recording of 110 minutes, 91 were visually examined with the aim of

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analysing the animals' behaviour during the rescue actions. For the study, a short behavioural catalogue of seven activities – open mouthed, sideways roll, agitation of fluke and pectoral fins, head rubbing, fluke contact (with head, flippers and back by the liberated animals) and defecation – was established.

For the acoustical analysis, three categories were identified: 'usual clicks'; 'codas'; and 'creaks'.

'*Usual clicks*': a series composed of regularly spaced clicks lasting for several minutes. These have been interpreted as echolocation clicks, used for locating prey and orientation (Whitehead and Weilgart, 1990), but may also serve to keep widely dispersed foraging groups in contact (Andrè and Kamminga, 2000).

'*Codas*': distinctive stereotyped patterns of clicks (Watkins and Schevill, 1977) with different rhythms. Each rhythm defines a distinct coda type (Weilgart and Whitehead, 1997), these characterise diverse vocal clans within sperm whale populations. Coda repertoires are reported to be transmitted culturally within the sperm whale social unit (Rendell and Whitehead, 2003).

'*Creaks*': patterns of closely spaced clicks with inter click intervals (ICIs) ranging from 5 to 100ms and lasting from 0.1 to 45s. Creaks are thought to be produced by sperm whales investigating objects at close range (Mullins *et al*., 1988). In social context they have been called codacreaks (Weilgart, 1990), rapid clicks or chirrups (Goold, 1999). They have been described as social sounds (Gordon, 1987) but their exact function is still unknown.

Forty-five minutes of acoustic recordings were examined using the *Rainbow Click* software package (see Gillespie and Leaper, 1997; Jaquet *et al*., 2001; Leaper *et al*., 2000). Codas were then marked and outputs of the digitised sound data for each click in each coda were used for IPI (interpulse interval) analysis. A *MATLAB* routine written by Rendell and Whitehead (2003) was used to automatically analyse clicks by extracting the maximum value from the cepstrum, following Goold's (1996) method. Only codas for which IPI estimates were identical in 50% or more of the clicks were included.

RESULTS

The sperm whales were found with their tails totally immobilised by the net and one animal was completely entangled (Fig. 1). All the whales showed numerous lesions on their bodies; their flukes in particular appeared to have been seriously injured. The estimated lengths of the two adult females were 10-12m, while the younger animals (gender unknown) was 5-7m long.

On the first day the divers managed to free two of the trapped whales; an adult and a younger individual by severing the nylon netting with cutters. It took 65 minutes to free the entangled adult whale, which remained calm throughout the rescue procedures and subsequently stayed close by, frequently touching the other entangled members of the group on their heads, flanks and flukes and observing the divers whilst they released a juvenile animal. The younger whale, freed 45min later, was relatively agitated compared to the adult during the net cutting operations, vigorously moving its fluke and frequently opening its mouth. Both the freed whales remained nearby surveying the divers at work and repeatedly rubbing on their trapped schoolmates' flanks with their heads and stroking their entangled flukes. This physical interaction hindered the liberation of the other animals by effectively stopping the divers' work. At 18:50hr, the young whale gradually abandoned the rescue site and disappeared from the divers' view. At 20:00hr, the rescue operations were suspended, scheduled to recommence the next day at daybreak.

During the night, the whales were constantly monitored from the Coast Guard vessel by radar and night-vision equipment. The freed adult whale remained near the group almost all night, moving away just before sunrise. On 10 August, at 06:30hr, the divers resumed cutting through the netting, managing to liberate a second young whale at 08:15hr and at 08:30hr the remaining juvenile was cut free. Finally, the largest animal was disentangled at 08:50hr. Following release, this female lingered close to the divers for over an hour, moving slowly and accepting hand contact on her side.

The behaviour of the sperm whales during the rescue operations included several specific actions: open mouthed (29%); sideways roll (17%); agitation of fluke (21%) and pectoral fins (12%); head rubbing (9%; Fig. 2), fluke contact with head, flippers and back by the released animals (9%; Fig. 3); and defecation (3%). No threatening or other aggressive behaviour toward the divers was recorded.

As expected, the entangled individuals produced different patterns of clicks, identified as 'usual clicks', 'codas' and 'creaks'. Almost all of the sounds provided an estimated length of between 9.30 and 9.35m (Fig. 4), suggesting that they were produced by the same whale or by the two adults that were similar in size.

A coda frequency rate of 1.13 codas per minute was recorded, with a total number of 51 codas detected. About 88% lasted between 200 and 600ms. Only 10% exceeded 600ms in total duration and just 2% were shorter than 200ms (Fig. 5). The overall mean duration of the codas was 398ms (N=51, SD=133.4, range 195-813, mode 284, median 377).

Fig. 1. The entangled whales.

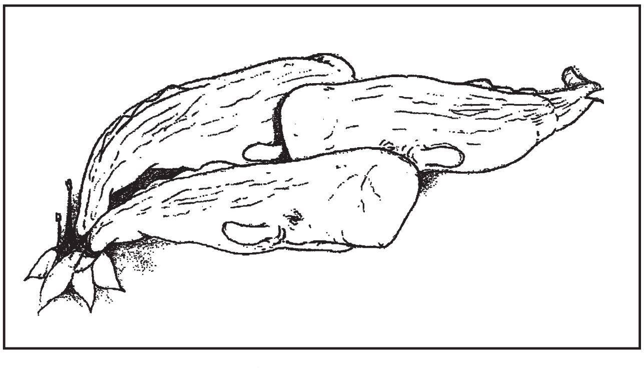

Fig. 2. Head rub.

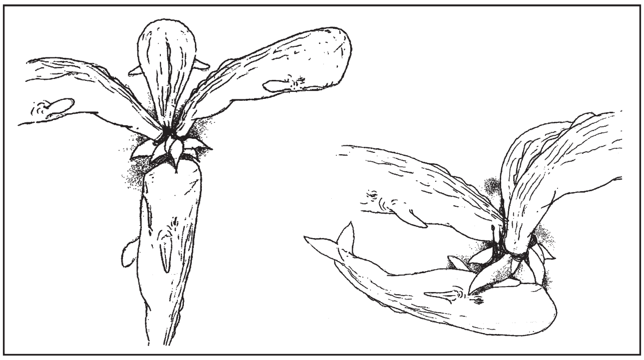

Fig. 3. Fluke touch.

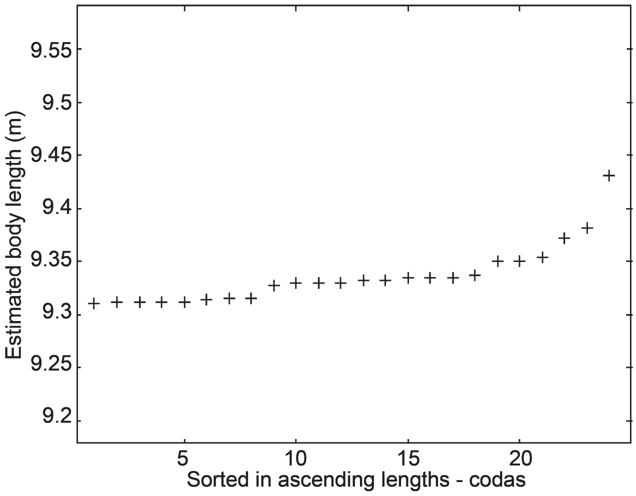

Fig. 4. Body length estimates from IPI.

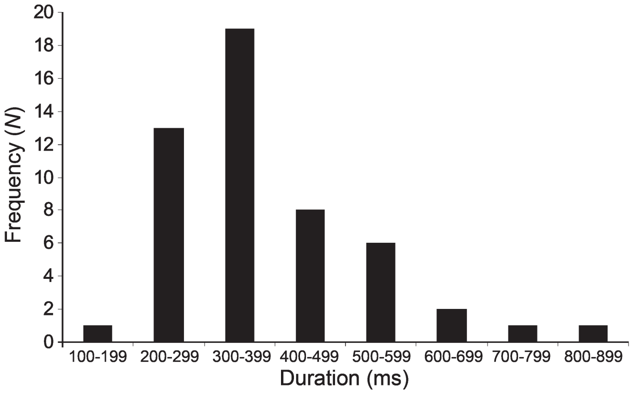

Fig. 5. Frequency distribution of codas duration.

Six coda types, containing 3-6 clicks, were catalogued and classified in accordance with Weilgart and Whitehead (1993). Two patterns of 3-click and 3+1-click codas were found to be the most common, constituting 80% of all codas recorded (Table 1). Codas were principally heard when the animals swished their flukes and during contact with other entangled tails.

Codacreaks analysis indicated that the frequency rate was 10.51min^{-1}, with a total number of 473 codacreaks detected. The number of clicks in codacreaks ranged from 3 to 45, with the modal value within the 20-30 clicks class (Fig. 6). This type constituted about 36% of the total, followed by the 10-20 type (30%). The overall mean duration of the codacreaks was 614ms (N=473, SD=302.8, range 43-1,706, median 663, mode 765), with 61% lasting between 400 and 900ms. Only 14% of the codacreaks had an overall duration of more than 900ms and 26% were shorter than 400ms (Fig. 7). From the behavioural point of view, codacreaks were associated with 'open mouthed' and 'sideways roll' displays, even if, like codas, they were heard when the animals swished their flukes.

Table 1

Coda types.

Type	*N*
2+1	2 (4%)
3R	23 (45%)
3+1	17 (33%)
4R	6 (12%)
4+1	1 (2%)
5+1	2 (4%)

DISCUSSION

'Head rubbing' and 'fluke contact' were the most obvious demonstrations of social behaviour showed by these animals. Female sperm whales are reported to cooperatively assist their offspring and other whales in dangerous situations, (Caldwell *et al*., 1966) and the members of a school seem to safeguard injured calves. This tendency was evident during this event, where the first freed adult female whale showed a higher number of 'fluke contact' displays than the younger individuals (even when liberated), clearly trying to comfort the animals still entangled in the net. Females and immature sperm whales socialising near the

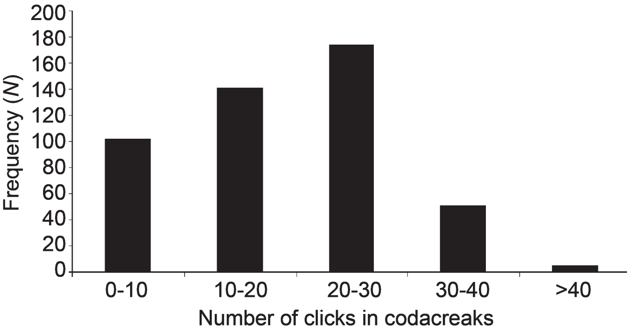

Fig. 6. Frequency distribution of clicks in codacreaks.

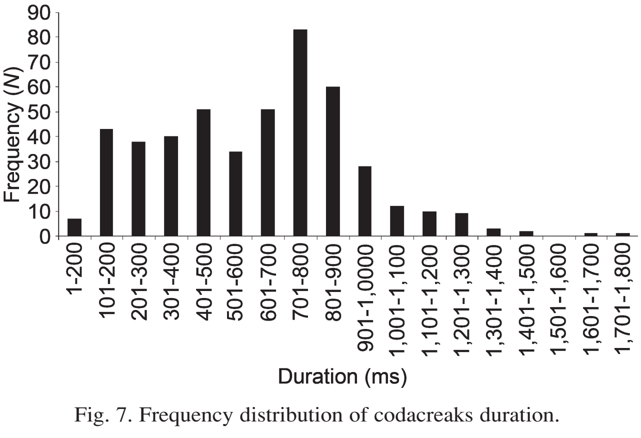

Fig. 7. Frequency distribution of codacreaks duration.

surface often touch and stroke one another with the jaw or flippers, actively maintaining physical contact with each other (Whitehead and Weilgart, 2000). In this case, physical contact appeared to be central to reassuring the entangled animals. An intense 'head rubbing' movement, performed primarily on the whales' sides without emitting any form of vocalisation, was also observed mutually between adults and juveniles. The lack of acoustic patterns associated with such contact seems to indicate the importance of touch to reinforce bonds between group members and demonstrates the significance of tactile signals as a direct form of support. As reported, the first disentangled female remained with the group for many hours after liberation, demonstrating this supportive behaviour towards individuals who may or may not have been related. Female sperm whales live in a social, ecological and physical environment where supportive behaviour may develop and be commonly practiced (Mesnick *et al*., 2003). Reinforcing social bonds through cooperation and association is adaptive behaviour and calf protection would seem to be the most likely primary functions of sociality among females (Whitehead and Weilgart, 1991).

The other notable behaviour observed, both in adult and immature individuals, was 'open mouthed'. This action was performed exclusively when the animals were trapped and was repeatedly associated with vocalisations. 'Open mouthed' displays are frequently reported in other odontocetes species during aggressive/agonistic bouts (Samuels and Gifford, 1997) or in stressful situations. It seems likely that this type of behaviour was accentuated during this traumatic experience; it may occur more frequently in stressful circumstances than under normal conditions.

'Sideways roll' and 'agitation of flukes and pectoral fins', correlated with vocalisations, were principally observed in, but not limited to, immature individuals. As sperm whales often roll along each others' bodies during interactive social sessions or roll onto a flank, with one of its fluke lobes out of the water, during prolonged periods of surface swimming (Whitehead, 2003). It is possible they behaved in this way, not only to try to free themselves from the net but also to facilitate visual observation (in this case, the divers cutting the net). Furthermore, the movements of flukes and flippers were often associated with the cutting procedures near the peduncle; this was possibly a reaction to pain caused by the net cutting into the numerous wounds and vocalisations were often heard. In female sperm whales there is a strong correlation between categories of visually observable behaviour and vocalisation types (Whitehead and Weilgart, 2000).

The recorded coda repertoire, i.e. the set of codas emitted by a set of whales in a particular circumstance (Whitehead, 2003), dominated by 3R and 3+1, is analogous to that recorded off the Balearic Islands (Nutthila, 2004) and in the Tyrrhenian Sea (Drouot, 2003), suggesting that these whales may belong to the same clan (sensu Whitehead, 2003). However, the complete recorded repertoire of the entangled whales, consisting of six different coda types, slightly differs from data reported by Drouot (2003) for the Tyrrhenian Sea and is in contrast with previous studies (Borsani and Pavan, 1994; Pavan *et al*., 2000).

Codas were principally heard when the animals swished their tails and during contact with entangled tails. This last finding is consistent with other observations, which report that an extensive coda repertoire is generally associated with cohesive groups near the surface and during exchanges with other whales (Whitehead and Weilgart, 1991). The acoustic results strongly suggest an interactive function of codas and codacreaks within the social group, underlining the link between their production, communication and sociality (Whitehead, 2003). It has been hypothesised that vocalisations may not only reflect the general 'disposition' of an animal but may also be indicative of moods and emotions. It cannot be ruled out that in such traumatic conditions, vocalisations serve to communicate emotions, since it has been suggested they may play a role in social interaction (Aureli, 1997) and could be adaptive, evolving in species where social bonding, group cohesion and mutual interactions favour the species' survival. Codas and codacreaks production may be related to levels of anxiety and possibly apparent dangers (they were higher during the initial phases of the rescue procedures) and seem to be emulative between animals. However, the echolocation function for close objects cannot be excluded.

In the Mediterranean Sea, driftnets are still a major threat to certain vulnerable pelagic species and, despite international and national regulation banning them from the region, numerous sperm whales have been found dead following entanglement in driftnets illegally set for swordfish. In the last three decades (from 1971 to 2004) the documented number of sperm whales found dead or entangled for Spain, France and Italy was collectively 229 and the true number is probably much higher (Reeves and Notarbartolo di Sciara, 2006).

The majority of whale strandings (recognisable from the characteristic wounds on the whales' bodies or the presence of net fragments) in Italy and Mediterranean Spain were caused by entanglement in high seas driftnets (Lazaro and Martin, 1999; Podestà and Magnaghi, 1989); deaths from this illegal activity persist today (ACCOBAMS, 2003; Tudela *et al*., 2003). While the true abundance of sperm whales in the Mediterranean Sea is unknown, most estimates suggest stock sizes in the hundreds rather than in the thousands (Reeves and Notarbartolo di Sciara, 2006). Given such low population numbers, there are major concerns over the impact of this type illegal fishing on this isolated population. Urgent management measures are clearly needed to monitor illegal fisheries and to protect cetaceans and other marine species, from the devastating effects of driftnet bycatch.

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REFERENCES

ACCOBAMS. 2003. Recommendation 2.2 from the Scientific Committee: On pelagic gillnets in the ACCOBAMS area. Adopted in Istanbul, 20-22 November. Accessible from *http://www.accobams.org/sc/index.htm*.

Andrè, M. and Kamminga, C. 2000. Rhythmic dimension in the echolocation clicks train of sperm whales: a possible function of identification and communication. *J. Mar. Biol. Ass. UK.* 80: 163-69.

Aureli, F. 1997. Post-conflict anxiety in non-human primates: the mediating role of emotion in conflict resolution. *Aggr. Behav.* 23: 315-28.

Borsani, J.F. and Pavan, G. 1994. Acoustics and aspects of sperm whale (*Physeter macrocephalus*) behaviour and ecology in the Mediterranean Sea. *It. J. Zool. (Suppl.)* 61: 79.

Cagnolaro, L. and Notarbartolo-di-Sciara, G. 1992. Research activities and conservation status of cetaceans in Italy. *Bull. Mus. Ist. Biol. Univ. Genova* 56-57: 53-85.

Caldwell, D.K., Caldwell, M.C. and Rice, D.W. 1966. Behavior of the sperm whale *Physeter catodon* L. pp.678-717. *In*: Norris, K.S. (eds). *Whales, Dolphins and Porpoises.* University of California Press, California. xv+789pp.

Di Natale, A. and Notarbartolo di Sciara, G. 1994. A review of the passive fishing nets and trap fisheries in the Mediterranean Sea and of the cetacean bycatch. *Rep. int. Whal. Commn (special issue)* 15: 189-202.

Drouot, V. 2003. Ecology of sperm whales (*Physeter macrocephalus*) in the Mediterranean Sea. PhD thesis, University of Wales, Bangor, UK. 338pp.

Gillespie, D. and Leaper, R. 1997. Detection of sperm whales (*Physeter macrocephalus*) clicks, and discrimination of individual vocalisations. *Eur. Res. Cet.* 10: 87-91.

Goold, J. 1996. Signal processing techniques for acoustic measurement of sperm whale body lengths. *J. Acoust. Soc. Am.* 100: 3431-41.

Goold, J.C. 1999. Behavioural and acoustic observations of sperm whales in Scapa Flow, Orkney Islands. *J. Mar. Biol. Assoc. UK* 79(3): 541-50.

Gordon, J.C.D. 1987. The behaviour and ecology of sperm whales off Sri Lanka. PhD dissertation, Darwin College, University of Cambridge. 347pp.

International Whaling Commission. 1994. Report of the Workshop on Mortality of Cetaceans in Passive Fishing Nets and Traps, 22-25 October 1990. *Rep. int. Whal. Commn (special issue)* 15:1-71.

Jaquet, N., Dawson, S.M. and Douglas, L. 2001. Vocal behaviour of male sperm whales: why do they click? *J. Acoust. Soc. Am.* 109: 2254-59.

Lazaro, F. and Martin, V. 1999. Sperm whales and drifting nets in the Mediterranean Sea: the example of the Balearic Islands. *Eur. Res. Cet.* 13: 118.

Leaper, R., Gillespie, D. and Papastavrou, V. 2000. Results of passive acoustic surveys for odontocetes in the Southern Ocean. *J. Cetacean Res. Manage.* 2(3): 187-96.

Madsen, P.T., Wahlberg, M. and Møle, B. 2002. Male sperm whale (*Physeter macrocephalus*) acoustics in a high latitude habitat: implications for echolocation and communication. *Behav. Ecol. Sociobiol.* 53: 31-41.

Mesnick, S.L., Evans, K., Taylor, B.L., Hyde, J., Escorza-Trevino, S. and Dizon, A. 2003. Sperm whale social structure: why it takes a village to raise a child. pp.170-74. *In*: de Wall, F.B.M. and Tyack, P. (eds). *Animal Social Complexity: Intelligence, Culture and Individualized Societies.* Harvard University Press, Cambridge.

Mullins, J., Whitehead, H. and Weilgart, L.S. 1988. Behaviour and vocalizations of two single sperm whales, *Physeter macrocephalus*, off Nova Scotia. *Can. J. Fish. Aquat. Sci.* 45(10): 1736-43.

Notarbartolo di Sciara, G. 1990. A note on the cetacean incidental catch in the Italian driftnet swordfish fishery, 1986-1988. *Rep. int. Whal. Commn* 40: 459-60.

Notarbartolo di Sciara, G., Bearzi, G., Canadas, A. and Frantzis, A. 2004. High mortality of sperm whales in the north-western Mediterranean, 1971-2003. Paper SC/56/BC10 presented to the IWC Scientific Committee, July 2004, Sorrento, Italy (unpublished). 3pp. [Paper available from the Office of this Journal].

Nutthila, H.K. 2004. Photo-identification and coda repertoire of sperm whales (*Physter macrocephalus*) in the Balearic Sea. PhD thesis, University of Wales, Bangor. 101pp.

Pavan, G., Hayward, T.J., Borsani, J.F., Priano, M., Manghi, M., Fossati, C. and Gordon, J. 2000. Time patterns of sperm whale codas recorded in the Mediterranean Sea 1985-1996. *J. Acoust. Soc. Am.* 107(6): 3487-95.

Podestà, M. and Magnaghi, L. 1989. Unusual number of cetacean bycatches in the Ligurian Sea. *Eur. Res. Cet.* 3: 67-70.

Reeves, R. and Notarbartolo di Sciara, G. 2006. *The status and distribution of cetaceans in the Black Sea and Mediterranean Sea – Workshop report – Monaco 5-7 March 2006.* IUCN Centre for Mediterranean Cooperation, Malaga, Spain. 137pp.

Rendell, L. and Whitehead, H. 2003. Vocal clans in sperm whales (*Physeter macrocephalus*). *Proc. R. Soc. Lond. Ser. B.* 270: 225-31.

Samuels, A. and Gifford, T. 1997. A quantitative assessment of dominance relations among bottlenose dolphins. *Mar. Mammal Sci.* 13(1): 70-99.

Tudela, S., Guglielmi, P., El Anadalossi, M., Kai Kai, A. and Maynou, F. 2003. Biodiversity impact of the Moroccan driftnet fleet operating in the Alboran Sea (SW Mediterranean) – a case study of the harmful effects inflicted by current IUU large-scale driftnet fleets in the Mediterranean on protected and vulnerable species. *WWF Mediterranean Progamme*: 78pp.

Watkins, W.A. and Schevill, W.E. 1977. Sperm whale codas. *J. Acoust. Soc. Am.* 62: 1485-90. [+ phonograph record].

Weilgart, L. 1990. Vocalizations of the sperm whale (*Physeter macrocephalus*) off the Galapagos Islands as related to behavioural and circumstantial variables. PhD thesis, Dalhousie University, Halifax, Nova Scotia.

Weilgart, L. and Whitehead, H. 1993. Coda communication by sperm whales (*Physeter macrocephalus*) off the Galapagos Islands. *Can. J. Zool.* 71(4): 744-52.

Weilgart, L. and Whitehead, H. 1997. Group-specific dialects and geographical variation in coda repertoire in South Pacific sperm whales. *Behav. Ecol. Sociobiol.* 40: 277-85.

Whitehead, H. 2003. *Sperm Whales: Social Evolution in the Ocean.* University of Chicago Press, Chicago. 464pp.

Whitehead, H. and Weilgart, L. 1990. Click rates from sperm whales. *J. Acoust. Soc. Am.* 87(4): 1798-806.

Whitehead, H. and Weilgart, L. 1991. Pattern of visually observable behaviour and vocalization in groups of female sperm whales. *Behaviour* 118(3-4): 275-96.

Whitehead, H. and Weilgart, L. 2000. The sperm whale: social females and roving males. pp.154-72. *In*: Mann, J., Connor, R.C., Tyack, P. and Whitehead, H. (eds). *Cetacean Societies: Field Studies of Dolphins and Whales.* University of Chicago Press, Chicago. 433pp.

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Distribution and density estimates of cetaceans along the mid-Atlantic Ridge during summer 2004

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ABSTRACT

During 4 June-2 July 2004, the Norwegian R/V *G.O. Sars* conducted a multi-disciplinary survey along the mid-Atlantic Ridge (MAR) from the Reykjanes Ridge to north of the Azores. This provided the first systematic survey information on MAR cetacean populations. Using naked eye or 7×50 hand-held binoculars, observers searched in a 140° arc centred along the ships' heading. Eleven cetacean species and 10 other taxonomic groups were identified along 2,321km of transect effort. The sei whale (*Balaenoptera borealis*) and sperm whale (*Physeter macrocephalus*) were the most commonly sighted species (53 and 48 sightings, respectively). There were 12 sightings of the fin whale (*B. physalus*). There were 26, 13 and 12 sightings, respectively of the common dolphin (*Delphinus delphis*), pilot whale (*Globicephala* sp.) and striped dolphin (*Stenella coeruleoalba*). Density estimates of species ranged from 0.018 to 0.238 animals km^{-2}. The precision of the estimates (CV) was low, ranging from 40% to 61%. Species distribution varied north to south; the highest aggregations of baleen whales were sighted at the Charlie Gibbs Fracture Zone (CGFZ). Sperm whales were also observed at the CGFZ as well as north of this area. Pilot whales and Atlantic white-sided dolphins (*Lagenorhynchus acutus*) were sighted mainly in the cold (5-16°C) and less saline (34.6-35.8‰) water masses along the Reykjanes Ridge. Conversely, common dolphins and striped dolphins were most commonly sighted south of the CGFZ in areas with warmer (12-22°C) and more saline (34.8-36.7‰) surface water temperatures.

KEYWORDS: ATLANTIC OCEAN; NORTHERN HEMISPHERE; DISTRIBUTION; SURVEY-VESSEL; ABUNDANCE ESTIMATE; SPERM WHALE; SEI WHALE; COMMON DOLPHIN; FIN WHALE; PILOT WHALE; STRIPED DOLPHIN; ATLANTIC WHITE-SIDED DOLPHIN

INTRODUCTION

Under the Census of Marine Life initiative, the mid-Atlantic Ridge Ecology Program (MAR-ECO) was initiated in 2003 (Bergstad *et al*., 2008; Wenneck *et al*., 2008). One principal goal of the program is to obtain quantitative data on the abundance and distribution of marine species inhabiting the mid-oceanic North Atlantic (Bergstad and Godø, 2002; Decker and O'Dor, 2002; O'Dor, 2003).

Knowledge of cetacean species inhabiting the Mid-Atlantic Ridge (MAR) and adjacent waters has come from historical whaling data (Clark, 1887; Reeves *et al*., 2004), anecdotal reports from fishermen (G. Vikingsson, pers. comm.), sighting surveys off Iceland (Sigurjónsson *et al*., 1991; Sigurjónsson *et al*., 1989), fishery observer data (Morato *et al*., 2008) and more recently from marine mammal observer sightings made in June 2003 aboard the Russian R/V *Akademik Mstislav Keldysh* (NMFS, NEFSC, unpubl. data). Recent acoustic studies (Mellinger and Clark, 2003; Nieukirk *et al*., 2004) have recorded baleen whale vocalisations near the MAR. These findings indicate that the MAR is an important cetacean habitat.

Various studies conducted worldwide have shown strong correlations between cetacean distribution and physiographic and oceanographic features and biological productivity (Ballance and Pitman, 1998; Baumgartner, 1997; Cañadas *et al*., 2002; Davis *et al*., 1998; Griffin, 1999; Hui, 1985; Kiszka *et al*., 2007; Moore *et al*., 2002; Reilly and Fiedler, 1994; Tynan, 1997; Tynan *et al*., 2005; Waring *et al*., 2001). The MAR is a region of high biodiversity and bio-productivity (Felley *et al*., 2008; Fock *et al*., 2004; Fossen *et al*., 2008; Gaard *et al*., 2008; Hareide and Garnes, 2001; Sigurjónsson *et al*., 1991; Vinogradov, 2005) and supports several important fisheries for deep-water species such as redfish (*Sebastes* spp.), Greenland halibut (*Reinhardtius hippoglossoides*) (Hareide and Garnes, 2001) and blue whiting (*Micromesistius poutassou*) (Gerber, 1993). Some of these species have been documented in odontocete stomachs sampled from adjacent regions (Desportes and Mouritsen, 1993; Roe, 1969; Sigurjónsson and Víkingsson, 1995). Zooplankton biomass and production particularly of the marine copepod (*Calanus finmarchicus*) were found to be highest in the area close to the Sub-Polar Front (SPF) and within the Charlie-Gibbs Fracture Zone [CGFZ] (Gaard *et al*., 2008; Gislason *et al*., 2008). The Boreoatlantic gonate squid (*Gonatus fabricii*) was the dominant cephalopod species found in the northern part of the MAR north of CGFZ (M. Vecchione, pers. comm., NMFS, National Systematics Laboratory, Washington, DC).

This paper provides information on cetacean distribution and density from the first systematic survey conducted along the entire northern mid-Atlantic Ridge.

METHODS

Study area

The MAR is a tectonic spreading zone between the Eurasian and American plates, running from Iceland in the North to the Azores in the South (Rossby, 1996); (Fig. 1). The area is characterised by rough bottom, hydrothermal activity, seamounts and other topographical features. The CGFZ is the deepest feature associated with the MAR, descending to around 4,500m at its deepest point (*http://www.mar-eco.no/*). The MAR has an important influence on the circulation of the North Atlantic, partly separating waters of

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the eastern and western basins (Rossby, 1996; Sy, 1988). There is flow of surface, intermediate and deep water between the basins through the CGFZ at 53°N (Bower *et al.*, 2002; Rossby, 1996). The dominating water masses of the region are the North Atlantic Deep Water (which is formed by mixing of the overflowing water masses from the Norwegian and Greenland seas with the Labrador Sea Water), the low-saline intermediate depth Labrador Sea Water and the northeastwards flowing high-saline surface mode North Atlantic Current (i.e. one of the major branches of the Gulf Stream), which at the CGFZ marks the SPF as it turns eastwards as 2-4 major branches (Bower *et al.*, 2002; Rossby, 1996; Sy *et al.*, 1992).

Survey design and data collection

During 4 June – 2 July 2004, the Norwegian R/V *G.O. Sars* conducted a single transect (3,016km) multidisciplinary survey along the MAR from the Reykjanes Ridge to north of the Azores (Fig. 1). To investigate potential cetacean habitats, the ship track was designed to cross as many seamounts and rises as possible when steaming between 20 oceanographic sampling stations. The vessel transited the trackline 24hr day^{-1}, except at some multi-day sampling sites (e.g. CGFZ) (Wenneck *et al.*, 2008). Vessel speed ranged from 9.0 to 12.9kt during transects, but slowed when approaching sampling (e.g. CTD, trawl) stations.

Data were collected between stations by 1-3 observers located on the ship's flying bridge at an eye height of 15.5m above sea level, during daylight hours (0400-2300), weather conditions permitting (i.e. Beaufort ≤5 and no rain or fog). Three observers worked overlapping shifts. Generally two observers were sighting simultaneously, but one extra observer assisted when passing high-density areas. In areas of low densities (or in association with meals), a single observer generally was on watch. The survey was conducted in passing mode (i.e. the vessel did not close with sightings).

Each observer searched for cetaceans and seabirds in a 140° arc centred along the trackline. When two observers were on duty, one observer searched by naked eye aided by 7×50 hand-held binoculars to identify possible sightings; the second observer searched using 7×50 hand-held binoculars. Observers recorded sightings and effort data onto data sheets. Sighting data included: time; species; group size; number of calves; radial distance; bearing; swim direction; behaviour and association with seabirds. Calibration of distance measurements was made by regularly using calipers with distance markings from 100m to 2,000m. Effort and environmental data included: transect number; date; time; course; speed; observer position and environmental variables (e.g. weather, cloud cover, wind direction Beaufort sea state, visibility, swell size, sea surface temperature, glare (severity and angle). Vessel sensor data

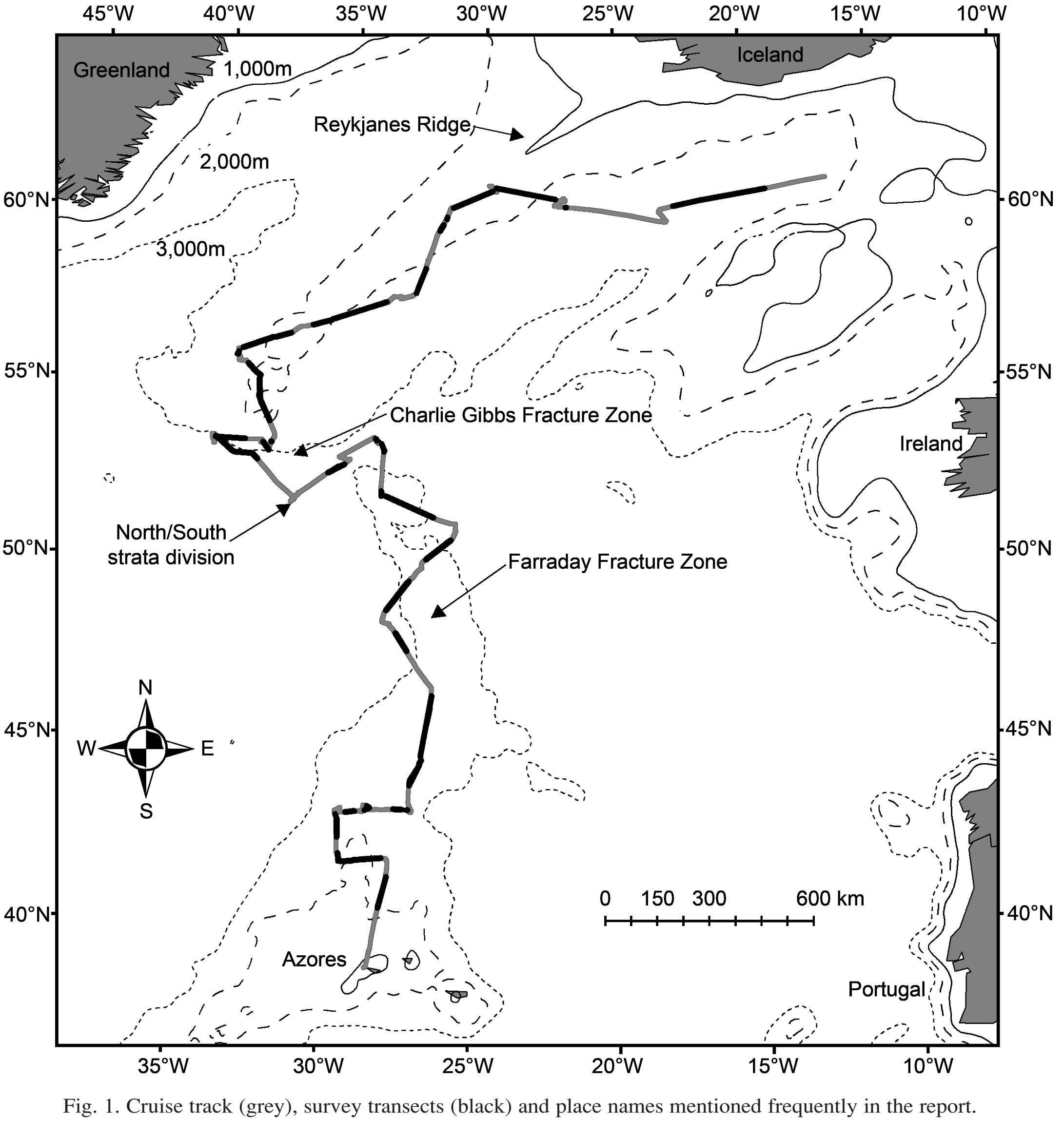

Fig. 1. Cruise track (grey), survey transects (black) and place names mentioned frequently in the report.

(e.g. latitude, longitude, speed, wind direction and speed, etc.) were downloaded from the ship's computer system on a daily basis.

Analytical methods

All on-effort data were included in the analysis, where transect effort was both parallel and perpendicular to the north/south orientation of the MAR. Because of the strong thermal gradient north and south of the CGFZ (Bower *et al*., 2002; Rossby, 1996), the survey area was post-stratified into two strata: North and South.

Density was estimated for each species or taxonomic group and each strata with line-transect methods using the program *DISTANCE* 4.1 (Buckland *et al*., 2001; Thomas *et al*., 2003). The parameter $g(0)$ was not estimated, and so was assumed to be 1 (Buckland *et al*., 2001), i.e. all animals on the trackline were assumed to be seen. The variances of the densities were estimated as 4.1, using the empirical option.

Transect length was based on the distance (km) of on-effort searching between consecutive stations. The perpendicular distance of each sighting was estimated using radial distance and bearing measurements to the sighting. Since the vessel transited a 'single line', stratum area was set to zero. Sample sizes for sei whales, *Balaenoptera borealis,* (n=53) and sperm whales, *Physeter macrocephalus*, (n=48) were sufficient to estimate the effective half-strip width (*ESW*) (Table 1; Figs 2 and 3). Since the number of common dolphin or striped dolphin sightings were insufficient to estimate *ESW*, they were pooled with other 'unidentified small dolphins' (Table 2; Fig. 4). This pooling was appropriate since the two identified species have similar sighting characteristics and they were the only small dephinidae recorded in the southern strata.

Data modelling and analysis followed protocol recommended by Buckland *et al*. (2001). Each data set was modelled with and without covariates using the hazard-rate and half-normal key functions, and the cosine and simple polynomial series expansions. The right-hand truncation values were based on visual inspection of initial model runs. Expected group size by stratum was estimated based on regression of log group size against $g(y)$. The best group size estimate was the regression based group size if the regression was significant (P-value <0.15), otherwise the average group size was used. Encounter rate and density of each taxonomic category were estimated for each 'stratum', and the model option to estimate the variance of the encounter rate analytically was selected. The best model for each category was selected based Akaike's Information Criteria (AIC). For each model the following covariates were investigated: sea surface temperature (SST); group size; and Beaufort sea state.

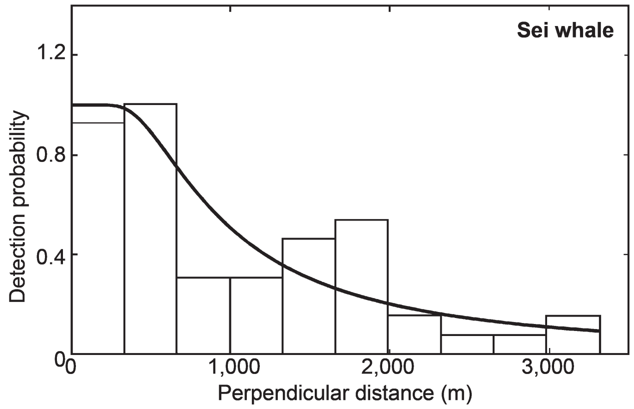

Fig. 2. Hazard-rate key model fit to sei whale perpendicular distance.

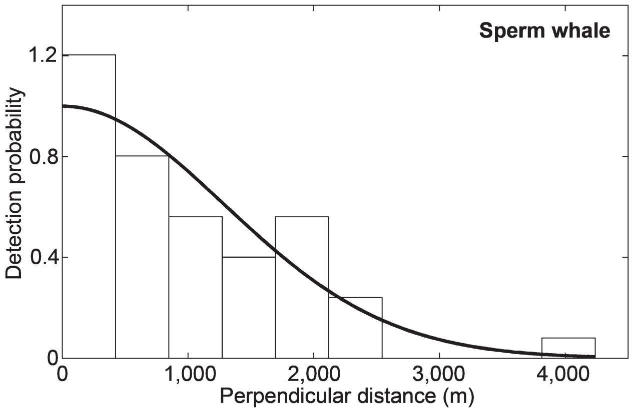

Fig. 3. Half-normal key model fit to sperm whale perpendicular distance.

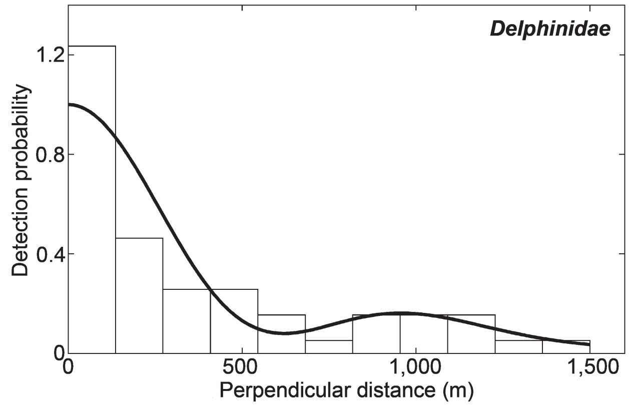

Fig. 4. Half-normal key model fit to delphinidae (common dolphin, striped dolphin, common/striped dolphin, and unknown dolphin in the southern strata) perpendicular distance.

Table 1

Estimate of $f(0)$ for each species or species group sighted ≥ 40 times along the MAR during 4 June – 2 July 2004; n = number of sightings after truncation; *ESW* = effective half-strip width, = $1/f(0)$.

Species/species group	n	Truncation (m)	*ESW* (m)	$f(0)$	%CV
Sei whale	52	3,000	1,282.7	0.0008	26.84
Sperm whale	48	4,200	1,646.4	0.0006	8.64
Small delphinidae *	58	1,500	406.8	0.0024	10.60

*Species include: common dolphin, striped dolphin, common/striped dolphin, and unidentified dolphin (southern strata).

RESULTS

Effort and weather

Effort was distributed along the entire length (3,016 km) of the cruise track from the Reykjanes Ridge to north of the Azores (Fig. 1). Of the total cruise track, 1,741km (57.8%) was in the northern stratum and 1,275km (42.2%) in the southern stratum. The total on-effort trackline was 2,321km, of which 1,274km (54.9%) was north and 1,047km (45.1%) south of the CGFZ.

The overall weather conditions were highly varied, being influenced by cyclonic systems, with a mean wind speed of 9.9ms^{-1} (Beaufort 5) and up to 8m wave height. Flat sea

Table 2

Number of on-effort sightings (*n*), mean group size (S) and range thereof (G), sighting rate (*n*/L=animals/km) with %CV, and density (D=animals/km^2) with %CV, of cetaceans sighted along the MAR, north and south of the Charlie Gibbs Fracture Zone during 4 June - 2 July 2004.

	North							South						
Species/species group	*n*	S	G	*n*/L	%CV	D	%CV	*n*	S	G	*n*/L	%CV	D	%CV
Sei whale	53	1.42	1-4	0.076	38.54	0.018	47.32	-	-	-	-	-	-	-
Sperm whale	40	1.89	1-15	0.038	32.69	0.042	40.06	8	1.6	1-3	0.04	56.5	0.036	60.53
Blue whale	-	-	-	-	-	-	-	4	1	1	0.007	63.21	-	-
Fin whale	5	1	1	0.006	77.27	-	-	7	1.71	1-2	0.012	93.2	-	-
Fin/sei whale	5	1.2	1-2	0.006	77.27	-	-	-	-	-	-	-	-	-
Fin/sperm whale	1	1	1	0.001	74.55	-	-	-	-	-	-	-	-	-
Sei/Bryde's whale	-	-	-	-	-	-	-	1	1	1	0.002	68.92	-	-
Humpback whale	1	2	2	0.001	84.6	-	-	-	-	-	-	-	-	-
Unidentified large baleen whales	7	1	1	0.007	40.9	-	-	-	-	-	-	-	-	-
Unidentified large whales	6	1	1	0.009	35.47	-	-	4	1	1	0.007	42.1	-	-
Minke whale	1	1	1	0.001	84.61	-	-	-	-	-	-	-	-	-
Unidentified beaked whales	6	1.33	1-3	0.009	34.07	-	-	2	3	1-5	0.004	68.92	-	-
Killer whale	1	5	5	0.001	85.62	-	-	-	-	-	-	-	-	-
Long-finned/short-finned pilot whales	9	11.44	1-40	0.013	33.77	-	-	4	25.76	3-60	0.007	55.69	-	-
Atlantic white-sided dolphin	7	14.71	3-60	0.01	34.47	-	-	-	-	-	-	-	-	-
White-beaked dolphin	3	3	1-5	0.004	111.89	-	-	-	-	-	-	-	-	-
Unidentified small whales	-	-	-	-	-	-	-	1	1	1	0.002	68.92	-	-
Common* dolphin	-	-	-	-	-	-	-	26	9.15	1-30	0.046	37.24	0.238	45.23
Striped dolphin*	-	-	-	-	-	-	-	12	9.69	3-25	0.021	35.43	0.122	45.54
Common/striped dolphin*	-	-	-	-	-	-	-	14	9.08	1-20	0.025	34.42	-	-
Unidentified* dolphin	1	100	100	0.001	84.61	-	-	8	3.43	2-5	0.014	68.92	-	-

*Species used in Delphinidae distance analysis, excluding unidentified dolphin (North).

conditions only occurred during short periods of time; 32.5% of the effort (km) was in Beaufort 2 or less, while 67.5% was in Beaufort 3 or more.

The proportion of search effort (km) conducted by an observer team comprised of one, two or three individuals, respectively, was 21.7%, 44.0% and 35.3%.

Most search effort (km) (65.7%) occurred at depths between 2,000m and 4,000m, with relatively little search effort at depths less than 1,000m (5.5%) and greater than 4,000m (0.6%).

Sightings and abundance

Two hundred and thirty-seven on-effort sightings were grouped into 21 categories based on species identification (Table 2). Fourteen species were recognised; the most commonly sighted species were sei whales (53); sperm whales (48), common dolphins, *Delphinus delphis*; (26) and striped dolphins, *Stenella coeruleoalba*; (12). Sperm whales were the large whales most commonly detected in both strata (Table 2). Among the smaller cetaceans, pilot whales (*Globicephala* sp.) and Atlantic white-sided dolphins (*Lagenorhynchus acutus*) were the most common species in the northern stratum, while common dolphins and striped dolphins were the most common in the southern stratum. Mean group sizes were ≤ 2 for all large and medium sized whales (Table 2). For delphinids, excluding a single sighting of 100 unidentified dolphins, mean group sizes ranged from 3 to 26.

Sighting rates of species ranged from 0.001 to 0.076 animals km^{-1}, and the precision of the estimates (CV) was low-ranging from 33% to 112% (Table 2).

The hazard-rate key function was the best model for the sei whale data, whereas, the half-normal key function with a series expansion was best for the delphinidae and sperm whale data sets (Figs 3-5). The AICs were nearly identical when the covariate SST were examined in the sei whale and sperm whale models, thus the more parsimonious model without covariates was used. None of the covariates improved the model selected for the delphinidae. Estimates of *f*(0) ranged from 0.0006 for sperm whales to 0.0022 for delphinidae (Table 1). Density estimates of species ranged from 0.018 to 0.238 animals km^{-2}, and the precision of the estimates (CV) was low-ranging from 40% to 61% (Table 2).

Cetacean distribution and behavioural observations

Distribution summaries exclude off-effort sightings, thus there are some differences with delphinidae data presented in Doksæter *et al*. (2008). Six species of baleen whales: blue whale (*Balaenoptera musculus*), fin whale (*B. physalus*), humpback whale (*Megaptera novaeangliae*), sei whale, Bryde's whale (*B. edeni*) and common minke whale (*B. acutorostrata*) were sighted during the survey (Table 2).

A total of 53 sightings were made of 85 sei whales. All sei whales were observed north of the CGFZ region (Fig. 5), near the frontal area just north and southwest of the CGFZ, where 80 sei whales were sighted. This area was a local zone of maximum surface temperature and salinity. In general, sei whales were at the slopes of seamounts and rises and were in waters varying from 1,160m to 4,500m deep (Fig. 5). The whales were often observed feeding and in areas where zooplankton (calanoids) were sampled. A wide range of size classes was observed and most groups contained 2-5 animals, although schools of up to 10 animals were observed.

Two sightings of single blue whales were made just south of the Faraday Fracture Zone [FFZ] (49°30'N-31°00'W) and one sighting of one blue whale was made approximately 100km further south (Fig. 6). Another sighting of a possible blue whale was also made in the Faraday region. The Faraday region was characterised by krill patches and fin whales were seen feeding on these patches (see below). All observations of blue whales were made in areas with depths between 2,200m and 2,800m.

Twelve sightings of 20 fin whales were made. The fin whale sightings consisted of one animal at the Reykjanes Ridge, seven animals north of the CGFZ, and 12 animals in the southern part of the MAR (Table 2; Fig. 6). In the

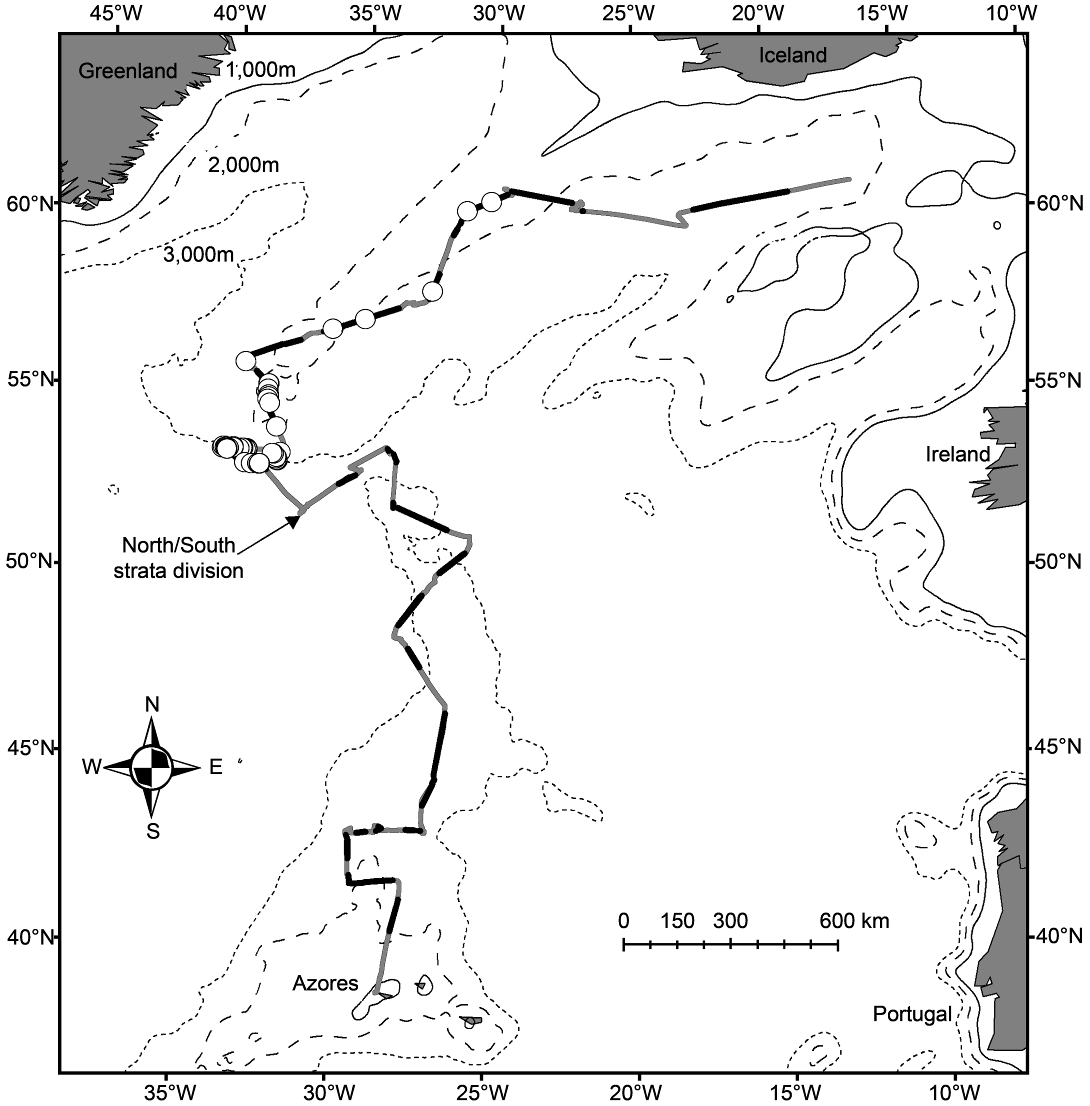

Fig. 5. Distribution of on-effort sightings of sei whale during R/V *G.O. Sars* survey.

Reykjanes region, several unidentified large rorquals may have been fin whales. The animals in the CGFZ and in the southern part of the MAR were frequently observed feeding, and a wide range of size classes were seen. In the FFZ, three fin whales were sighted feeding on krill patches. The animals were seen in waters with depths varying between 1,760m to 4,470m.

A possible Bryde's whale was recorded in the southern part of the study area (Fig. 6), where the surface temperature was warmer than 20.5°C. The species was identified by its size, surface behaviour and dorsal fin, though the dorsal ribs on the head were not seen (Jefferson *et al*., 1993).

One sighting of two humpback whales was recorded just north of the CGFZ (Fig. 6). One animal was recorded feeding, and an attempt was made to attach a satellite transmitter to it.

One minke whale was observed in the CGFZ in waters of 2,900m depth (Fig. 6).

A total of 48 sightings were made of 83 sperm whales. School sizes varied from 1-15 animals (Fig. 7). Animals were seen along the entire length of the MAR, with a notable concentration north of the CGFZ and smaller concentrations in the southern region. The area at the CGFZ coincided with a frontal region with local maximum surface temperature and salinity gradients. Unlike the sei whales, sperm whales were usually seen at the tops of the seamounts and rises and did not generally occur over the slopes. Sperm whales were recorded over depths varying from 800m to 3,500m, where the highest mean sighting rate was over areas shallower than 2,000m.

Eight sightings of 14 beaked whales (*Mesoplodon* spp.) were made in the southern part of the Reykjanes Ridge to the southern part of the MAR (Fig. 8). Observation conditions were generally sub-optimal for effective sightings of beaked whales, and species identification was virtually impossible.

A total of 206 long/short-finned pilot whales (*G. melas*/*macrorhynchus*) in 13 schools were recorded, mainly in the cold (5-16°C) and less saline (34.6-35.8‰) water masses (Doksaeter *et al*., 2008) along the Reykjanes Ridge (Fig. 8). Most animals are identified as *G. melas*, but *G. macrorhynchus* cannot be ruled out for animals seen south of the CGFZ region. School size varied between 1 and 60 animals and sightings were recorded over depths from 1,500m to 3,900m.

One school of five killer whales (*Orcinus orca*) was observed in the southern part of the Reykjanes Ridge (Fig. 8).

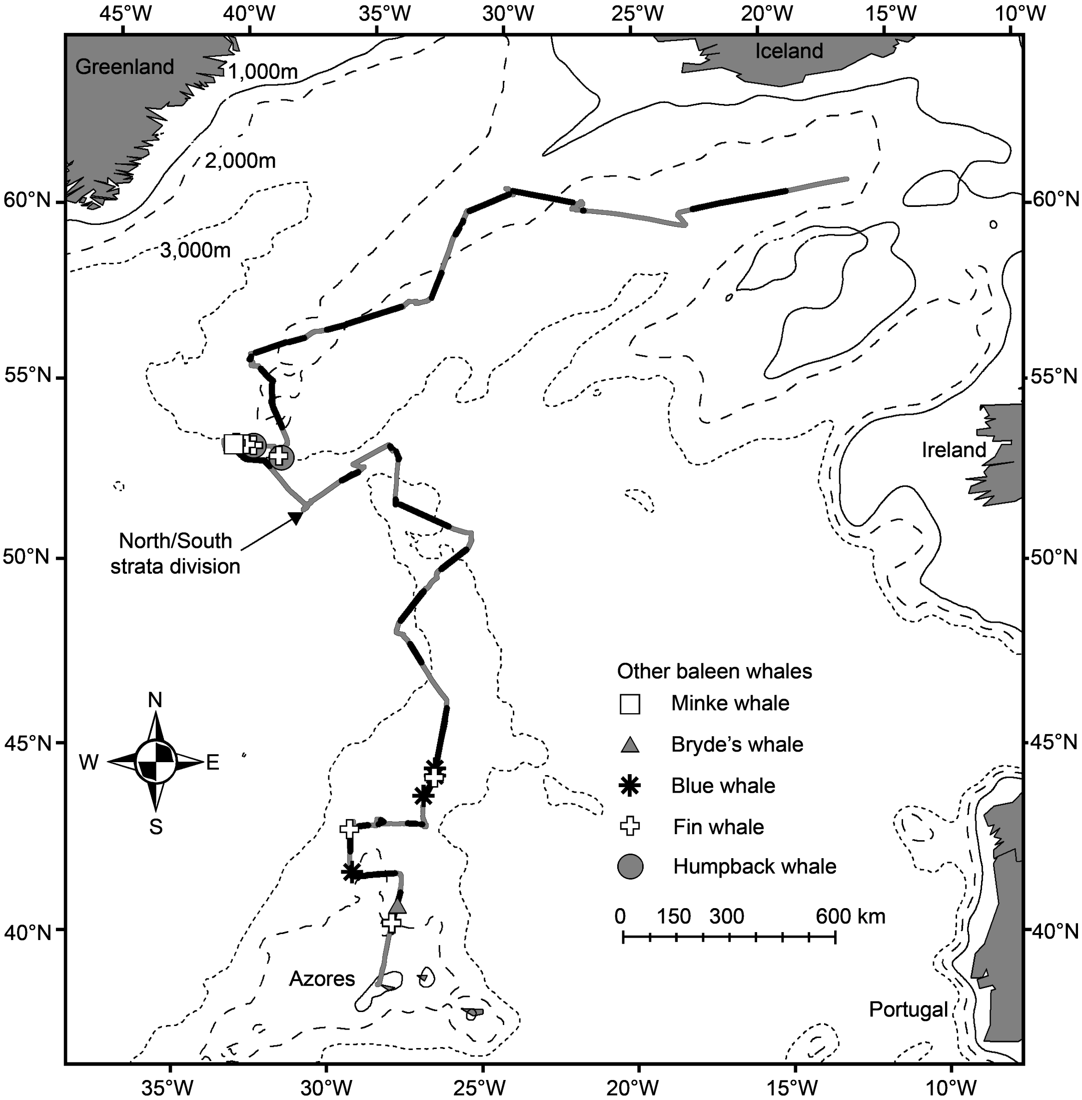

Fig. 6. Distribution of on-effort sightings of other baleen whales during R/V *G.O. Sars* survey.

Atlantic white-sided dolphins were sighted along and north of the CGFZ (Fig. 8) and observed only in the cold (5-16°C) and less-saline (34.6-35.8‰) water masses (Doksaeter *et al*., 2008). A total of 103 animals were observed in seven schools. The dolphins were sighted in areas with water depths between 1,200m and 2,400m, and one of the schools was also accompanied by pilot whales.

Three schools of 11 white-beaked dolphins (*L. albirostris*) were observed over the central part of the Reykjanes Ridge (Fig. 8).

Common dolphins were only observed south of the SPF in the CGFZ (Fig. 9) in areas with warmer (>14°C) and more-saline (34.8-36.7‰) water masses (Doksaeter *et al*., 2008). A total of 272 animals were observed in 26 schools. The animals were sighted in areas with water depths between 1,600m and 2,800m, and one of the schools was mixed with striped dolphins. In some cases, Cory's shearwater (*Calonectris diomedea*) were associated with the dolphins.

Striped dolphins shared a latitudinal trend in distribution with common dolphins (Fig. 9), although relatively more striped dolphins were sighted when surface water was warmer than 18°C (Doksaeter *et al*., 2008). A total of 86 animals were observed in 12 schools. The dolphins were sighted in areas with water depths between 2,100m and 2,500m, and one of the schools was mixed with common dolphins. In some cases, Cory's shearwater were associated with the dolphins.

DISCUSSION

Cetacean distribution and abundance along the MAR have not been previously reported, although North Atlantic Sighting Surveys (NASS) in 1989 covered some of the present study area between the CGFZ and Iceland (Sigurjónsson *et al*., 1991). The 1989 NASS survey, historical whaling information, acoustic recordings, cetacean studies in adjacent areas, and opportunistic sightings all suggested that seasonally the MAR was an important cetacean habitat (Nieukirk *et al*., 2004; Reeves *et al*., 2004; Sigurjónsson *et al*., 1991). For example, the aggregation of sei whales at and just north of the CGFZ in 2004 overlaps spatially with the observations of the July-August 1989 NASS survey, when large numbers of sei whales were recorded in the region (Sigurjónsson *et al*., 1991; Skov *et al*., 2008).

Species diversity and habitat associations along the north-south gradient of the RV *G.O. Sars* survey track are similar to those seen in other oceanographic regions influenced by complex bathymetry and strong frontal features

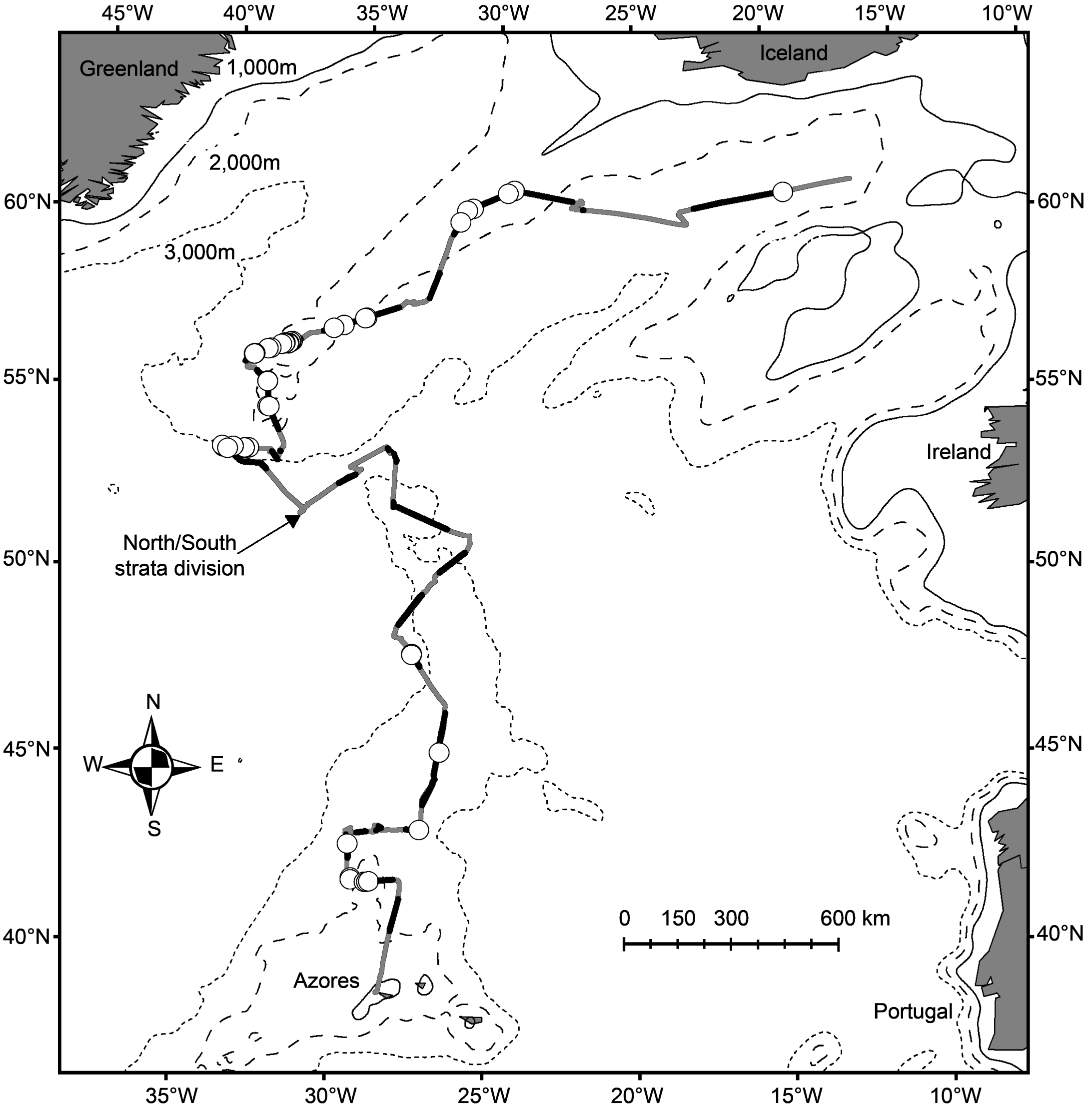

Fig. 7. Distribution of on-effort sightings of sperm whale during R/V *G.O. Sars* survey.

(Baumgartner, 1997; Davis *et al*., 1998; Kenney and Winn, 1987; Kiszka *et al*., 2007; Mullin and Fulling, 2004; Reilly and Fiedler, 1994; Smith and Whitehead, 1993; Tynan, 1997; Waring *et al*., 2001).

Sei whales were most common over the slopes of seamounts and rises in waters with depths between 1,500m and 3,000m, while sperm whales were common in waters shallower than 2,000m. Dolphins, however, were widespread over all categories of water depth, but showed marked inter-specific differences in relation to surface temperatures with almost allopatric distributions of white-beaked/Atlantic white-sided dolphins and common/striped dolphin around the 14°C isotherm. The distinct use of 'shallows' and 'slopes' by sperm and sei whales, respectively, was evident when passing over seamounts in the CGFZ (Skov *et al*., 2008), with sperm whales being found mainly over the top of the ridge and sei whales mainly over the slopes. Analyses of potential prey associations have not been completed. However, calanoids were abundant at stations in the CGFZ coinciding with concentrations of sei whales (Gislason *et al*., 2008; Skov *et al*., 2008). This implies that the CGFZ may be a 'hotspot' for sei whales along the MAR. Likewise, sightings of sperm whales and catches of the squid (*Gonatus* spp.) co-occurred in the northern part of the MAR. *Gonatus* spp. is an important prey item for sperm whales in northern Atlantic waters (Bjørke, 2001; Christensen *et al*., 1992; Clarke *et al*., 1993).

The density estimates are negatively biased due to operational constraints, environmental conditions, few number of observers, and the assumption that cetaceans on the trackline are detected with certainty (i.e. $g(0)=1$). Sea state, group size and animal characteristics are known to affect perception bias (e.g. Mullin and Fulling, 2004). In addition, searching was conducted by naked eye or using low-powered hand-held binoculars, as opposed to high-powered binoculars used in some other multi-disciplinary surveys (Moore *et al*., 2002; Tynan *et al*., 2005); these may have assisted with species identification and school size estimates but would only have improved abundance estimates if used to assist in experiments to determine $g(0)$. Multi-disciplinary surveys mean that the vessel could not be diverted to identify species or to improve group size counts. These operational constraints likely impaired the ability of observers to identify some species (Mullin and Fulling, 2004). Conversely, the trackline covered high relief areas, which may have biased samples (Buckland *et al*., 2001) to high-density areas. High relief features are known to influence oceanographic processes that concentrate prey

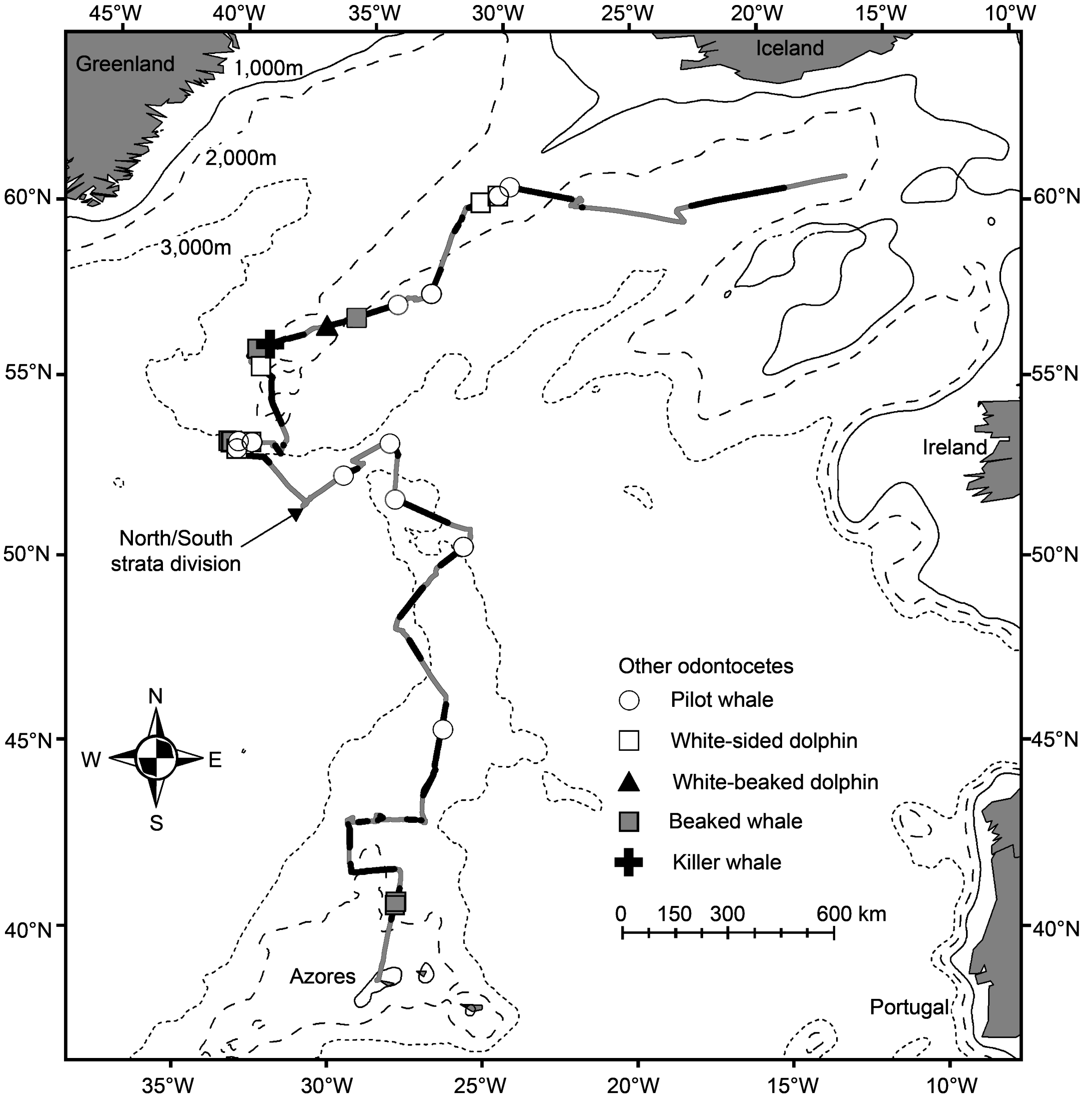

Fig. 8. Distribution of on-effort sightings of killer whale, beaked whale, pilot whale, Atlantic white-sided dolphin and white-beaked dolphin during R/V *G.O. Sars* survey.

(Ballance and Pitman, 1998; Baumgartner, 1997; Hui, 1985; Kenney and Winn, 1987; Moore *et al*., 2002; Tynan *et al*., 2005). Further, the high CVs are attributable to aforementioned concerns and large variations in the sighting rates due to the well-known patchy distribution of cetaceans. The perpendicular distributions for sei whales and dolphins (Figs 3 and 4), also raise concerns regarding animal avoidance and rounded distance estimation.

Sighting rates derived from this survey are not comparable to values reported for dedicated shipboard cetacean surveys conducted in other regions, or other multi-disciplinary surveys where searching was conducted using high power binoculars. Further, the RV *G.O. Sars* values are substantially lower than rates obtained from a long-term platform of opportunity survey in the Bay of Biscay (Kiszka *et al*., 2007), where observers also searched using naked-eye or 7×50 binoculars.

The *G.O. Sars* survey provided a snapshot of the cetacean community along the northern portion of the MAR in early summer. Despite the overall low encounter rates and density estimates, the survey identified a presumed foraging hotspot for sei whales around the Charlie Gibbs Fracture Zone. Future MAR-ECO multidisciplinary studies may provide additional data to designate the CGFZ as an important seasonal feeding habitat (i.e. similar to the Great South Channel off the coast of Massachusetts for North Atlantic right whales (*Eubalaena glacialis*) and sei whales). The spatial distribution of sperm whales also suggests that the MAR is an important oceanic habitat for this species. A more comprehensive line-transect survey and fine-scale habitat sampling will be required to further delineate cetacean distribution and habitat use, and to obtain more precise density estimates. Furthermore, biopsy sampling will be important for understanding the stock structure of cetaceans utilising the MAR boundary between the eastern and western North Atlantic, and whether this is a large whale migration corridor between sub-tropical/tropical breeding grounds and boreal feeding habitats.

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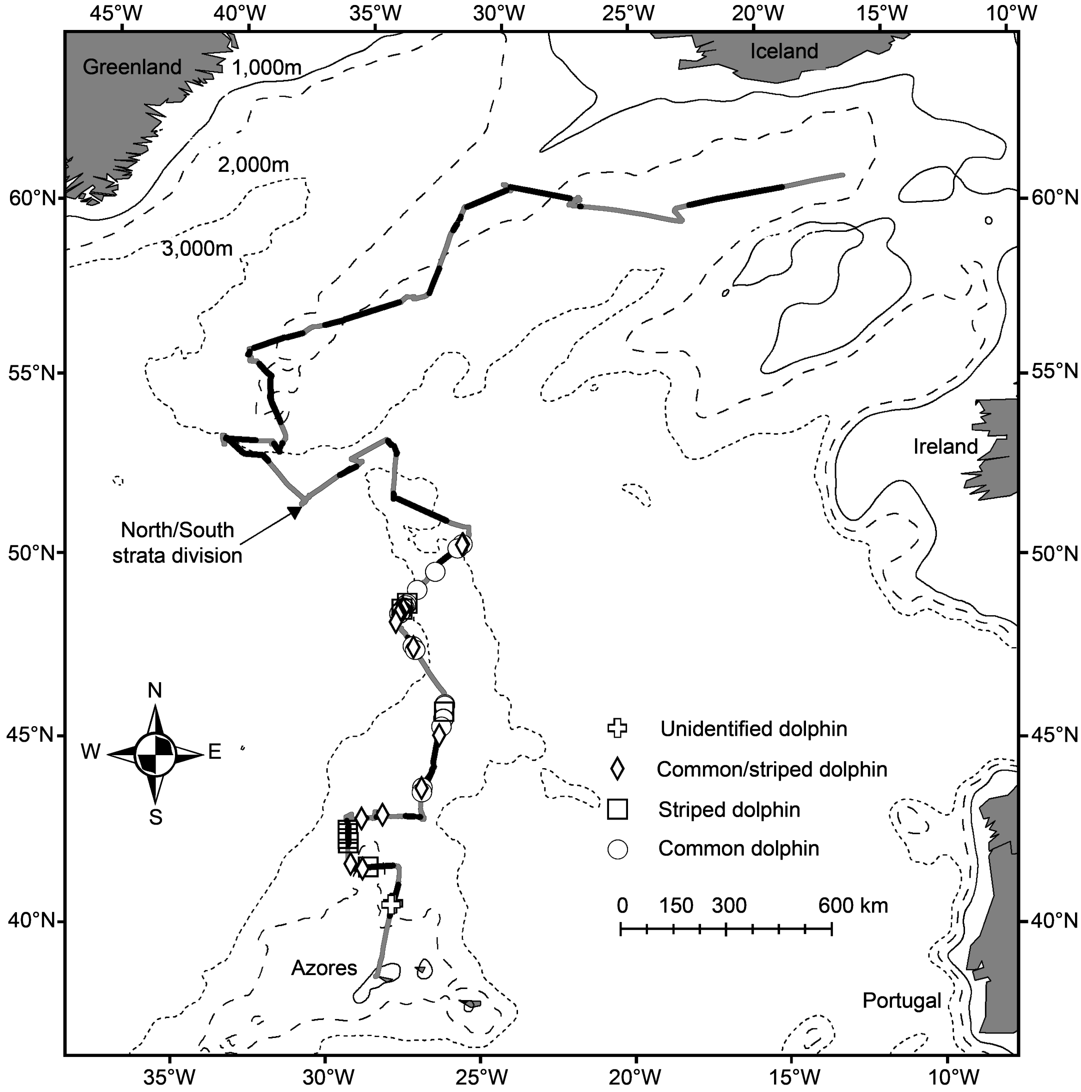

Fig. 9. Distribution of on-effort sightings of common dolphin, striped dolphin, common/striped dolphins, and southern strata unidentified dolphins during R/V *G.O. Sars* survey.

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REFERENCES

Ballance, L.T. and Pitman, R.L. 1998. Cetaceans of the Western Tropical Indian Ocean: distribution, relative abundance, and comparisons with cetacean communities of two other tropical ecosystems. *Mar. Mammal Sci.* 14(3): 429-59.

Baumgartner, M.F. 1997. The distribution of Risso's dolphin (*Grampus griseus*) with respect to the physiography of the northern Gulf of Mexico. *Mar. Mammal Sci.* 13(4): 614-38.

Bergstad, O.A., Falkenburg, T., Asstthorsson, O.S., Byrkjedal, I., Gebruk, A.V., Piatkowski, U., Priede, I.G., Santos, R.S., Vecchione, M., Lorance, P. and Gordon, J.D.M. 2008. Towards improved understanding of the diversity and abundance patterns of the mid-ocean ridge macro- and megafauna. *Deep-Sea Res. II* 55: 1-5.

Bergstad, O.A. and Godø, O.R. 2002. The pilot project 'patterns and processes of the ecosystems of the northern mid-Atlantic': aims, strategy and status. *Oceanol. Acta.* 25(5): 219-26.

Bjørke, H. 2001. Predators of the squid *Gonatus fabricii* (Lichtenstein) in the Norwegian Sea. *Fish. Res.* 52: 113-20.

Bower, A.S., Le Cann, B., Rossby, T., Zenk, W., Gould, J., Speer, K., Richardson, P.L., Prater, M.D. and Zhang, H.M. 2002. Directly measured mid-depth circulation in the northeastern North Atlantic Ocean. *Nature* 419: 603-07.

Buckland, S.T., Anderson, D.R., Burnham, K.P., Laake, J.L., Borchers, D.L. and Thomas, L. 2001. *Introduction to Distance Sampling: Estimating Abundance of Biological Populations.* Oxford University Press, Oxford, UK. vi+xv+432pp.

Cañadas, A., Sagarminaga, R. and García-Tiscar, S. 2002. Cetacean distribution related with depth and slope in the Mediterranean waters off southern Spain. *Deep-Sea Res. I* 49(11): 2053-73.

Christensen, I., Haug, T. and Øien, N. 1992. A review of feeding and reproduction in large baleen whales (*Mysticeti*) and sperm whales *Physeter macrocephalus* in Norwegian and adjacent waters. *Fauna Norv. Ser. A* 13: 39-48.

Clark, A.H. 1887. History and present condition of the fishery. pp.3-218. *In*: Goode, G.B. (eds). *The Fisheries and Fishery Industries of the United States. Section V. History and methods of the fisheries. Vol. II.* Gov. Print. Off., Washington DC.

Clarke, M.R., Martins, H.R. and Pascoe, P. 1993. The diet of sperm whales (*Physeter macrocephalus* Linnaeus 1758) off the Azores. *Philos. Trans. R. Soc. Lond. B. (Biol. Sci.)* 339(1287): 67-82.

Davis, R.W., Fargion, G.S., May, N., Leming, T.D., Baumgartner, M., Evans, W.E., Hansen, L.J. and Mullin, K. 1998. Physical habitat of cetaceans along the continental slope in the north-central and western gulf of Mexico. *Mar. Mammal Sci.* 14(3): 490-507.

Decker, C.J. and O'Dor, R.K. 2002. A census of marine life. Special issue. *Oceanol. Acta*. 25: 179-284.

Desportes, G. and Mouritsen, R. 1993. Preliminary results on the diet of long-finned pilot whales off the Faroe Islands. *Rep. int. Whal. Commn (special issue)* 14: 305-24.

Doksaeter, L., Olsen, E., Nøttestad, L. and Fernö, A. 2008. Distribution and feeding ecology of dolphins along the Mid-Atlantic Ridge between Iceland and the Azores. *Deep-Sea Res. II* 55: 243-53.

Felley, J.D., Vecchione, M. and Wilson, R.R.J. 2008. Small-scale distribution of deep-sea demersal nekton and other megafauna in the Charlie-Gibbs Fracture Zone of the Mid-Atlantic Ridge. *Deep-Sea Res. II* 55: 153-60.

Fock, H.O., Pusch, C. and Ehrich, S. 2004. Structure of deep-sea pelagic fish assemblages in relation to the Mid-Atlantic Ridge (45 degree-50 degree N). *Deep-Sea Res. I* 51(7): 953-78.

Fossen, I., Cotton, C.F., Bergstad, O.A. and Dyb, J.E. 2008. Species composition and distribution patterns of fishes captured by longlines on the Mid-Atlantic Ridge. *Deep-Sea Res. II* 55: 203-17.

Gaard, E., Gislason, A., Falkenhaug, T., Musaeva, E.I., Vereshchaka, A. and Vinogradov, G. 2008. Horizontal and vertical distribution of mesozooplankton composition and abundance on the Mid-Atlantic Ridge in June 2004. *Deep-Sea Res. II* 55: 59-71.

Gerber, E.M. 1993. Some data on the distribution and biology of the blue whiting, *Micromesistius poutassou*, at the Mid-Atlantic Ridge. *J. Ichthyol*. 33: 26-34.

Gislason, A., Gaard, E., Debes, H. and Falkenburg, T. 2008. Abundance, feeding and reproduction of *Calanus finmarchius* in the Irminger Sea and on the northern Mid-Atlantic Ridge in June. *Deep-Sea Res. II* 55: 72-82.

Griffin, R.B. 1999. Sperm whale distributions and community ecology associated with a warm-core ring off Georges Bank. *Mar. Mamm. Sci*. 15: 33-51.

Hareide, N.R. and Garnes, G. 2001. The distribution and catch rates of deep water fish along the Mid-Atlantic Ridge from 43 to 61°N. *Fish. Res*. 51: 297-310.

Hui, C.A. 1985. Underseas topography and the comparative distributions of two pelagic cetaceans. *Fish. Bull*. 83: 472-75.

Jefferson, T.A., Leatherwood, S. and Webber, M.A. 1993. *FAO Species Identification Guide. Marine Mammals of the World*. FAO, Rome. 320pp.

Kenney, R.D. and Winn, H.E. 1987. Cetacean biomass densities near submarine canyons compared to adjacent shelf/slope areas. *Cont. Shelf Res*. 7: 107-14.

Kiszka, J., Macleod, K., van Canneyt, O., Walker, D. and Ridous, V. 2007. Distribution, encounter rates, and habitat characteristics of toothed cetaceans in the Bay of Biscay and adjacent waters from platform-of-opportunity data. *ICES J. Mar. Sci*. 64: 1033-43.

Mellinger, D.K. and Clark, C.W. 2003. Blue whale (*Balaenoptera musculus*) sounds from the North Atlantic. *J. Acoust. Soc. Am*. 114(2): 1108-19.

Moore, S.E., Waite, J.M., Friday, N.A. and Honkalehto, T. 2002. Cetacean distribution and relative abundance on the cenral-eastern and the southeastern Bering Sea shelf with reference to oceanographic domains. *Prog. Oceanogr*. 55: 249-61.

Morato, T., Varkey, D.A., Damaso, C., Machete, M., Santos, M., Prieto, R., Santos, R.S. and Pitcher, T.J. 2008. Evidence of a seamount effect on aggregating visitors. *Mar. Ecol. Prog. Ser*. 357: 23-32.

Mullin, K.D. and Fulling, G.L. 2004. Abundance of cetaceans in the oceanic northern Gulf of Mexico, 1996-2001. *Mar. Mammal Sci*. 20: 787-807.

Nieukirk, S.L., Stafford, K.M., Mellinger, D.K., Dziak, R.P. and Fox, C.G. 2004. Low-frequency whale and seismic airgun sounds recorded in the mid-Atlantic. *J. Acoust. Soc. Am*. 115(4): 1832-43.

O'Dor, R.K. 2003. *The unknown ocean: baseline report of the Census of Marine Life Program*. Consortium for Oceanographic Research and Education, Washington, DC. Available at: *http://www.coml.org/baseline/*.

Reeves, R.R., Smith, T.D., Josephson, E.A., Clapham, P.J. and Woolmer, G. 2004. Historical observations of humpback and blue whales in the North Atlantic Ocean: clues to migratory routes and possibly additional feeding grounds. *Mar. Mammal Sci*. 20(4): 774-86.

Reilly, S.B. and Fiedler, P.C. 1994. Inter-annual variability of dolphin habitats in the eastern tropical Pacific. 1. Research vessel surveys, 1986-1990. *Fish. Bull*. 92(2): 434-50.

Roe, H.S.J. 1969. The food and feeding habits of the sperm whale (*Physeter catodon* L.) taken off the west coast of Iceland. *J. Cons. Int. Explor. Mer* 33(1): 93-102.

Rossby, T. 1996. The North Atlantic Current and surrounding waters: at the crossroads. *Rev. Geophys*. 34(4): 463-81.

Sigurjónsson, J., Gunnlaugsson, T., Ensor, P., Newcomer, M. and Víkingsson, G. 1991. North Atlantic Sightings Survey 1989 (NASS-89): shipboard surveys in Icelandic and adjacent waters July-August 1989. *Rep. int. Whal. Commn* 41: 559-72.

Sigurjónsson, J., Gunnlaugsson, T. and Payne, M. 1989. NASS-87: Shipboard sightings surveys in Icelandic and adjacent waters June-July 1987. *Rep. int. Whal. Commn* 39: 395-409.

Sigurjónsson, J. and Víkingsson, G.A. 1995. Seasonal abundance of and estimated food consumption by cetaceans in Icelandic and adjacent waters. *J. Northwest Atl. Fish. Sci*. 22: 271-87.

Skov, H., Gunnlaugsson, T., Budgell, P., Horne, J.K., Nøttestad, L., Olsen, E., Søiland, H., Vikingsson, G. and Waring, G. 2008. Small-scale spatial variability of sperm and sei whales in relation to oceanographic and topographic features along the Mid-Atlantic Ridge. *Deep-Sea Res. II* 55: 254-68.

Smith, S.C. and Whitehead, H. 1993. Variations in the feeding success and behaviour of Galápagos sperm whales (*Physeter macrocephalus*) as they relate to oceanographic conditions. *Can. J. Zool*. 71: 1991-96.

Sy, A. 1988. Investigation of large-scale circulation patterns in the central North Atlantic: the North Atlantic Current, the Azores Current, and the Mediterranean Water Plume in the area of the Mid-Atlantic Ridge. *Deep-Sea Res. I* 35: 383-413.

Sy, A., Schauer, U. and Meincke, J. 1992. The North Atlantic Current and its associated hydrographic structures above and eastwards of the Mid-Atlantic Ridge. *Deep-Sea Res. I* 39: 825-53.

Thomas, L., Laake, J.L., Strindberg, S., Marques, F.F.C., Buckland, S.T., Borchers, D.L., Anderson, D.R., Burnham, K.P., Hedley, S.L., Pollard, J.H. and Bishop, J.R.B. 2003. *Distance 4.1. Release 2*. Research Unit for Wildlife Population Assessment, University of St. Andrews, UK. [Available from *www.ruwpa.st-and.ac.uk/distance/*].

Tynan, C. 1997. Cetacean distributions and oceanographic features near the Kerguelan Plateau. *Geophys. Res. Lett*. 24(22): 2793-96.

Tynan, C.T., Ainley, D.G., Barth, J.A., Cowles, T.J., Pierce, S.D. and Spear, L.B. 2005. Cetacean distributions relative to ocean processes in the northern California Current System. *Deep-Sea Res. I* 52: 145-67.

Vinogradov, G.M. 2005. Vertical distribution of macroplankton at the Charlie-Gibbs Fracture Zone (North Atlantic), as observed from the manned submersible 'Mir-1'. *Mar. Biol*. 146: 325-31.

Waring, G.T., Hamazaki, T., Sheenan, D., Wood, G. and Baker, S. 2001. Characterization of beaked whale (Ziphiidae) and sperm whale (*Physeter macrocephalus*) summer habitat in shelf-edge and deeper waters off the northeast US. *Mar. Mammal Sci*. 17(4): 703-17.

Wenneck, T., de L., Falkenbaug, T. and Bergstad, O.A. 2008. Strategies, methods, and technologies adopted on the R.V. *G.O. Sars* MAR-ECO expedition to the Mid-Atlantic Ridge in 2004. *Deep-Sea Res. II* 55: 6-28.

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Click train patterns of free-ranging harbour porpoises acquired using T-PODs may be useful as indicators of their behaviour

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ABSTRACT

Harbour porpoise signals consist of directional, high frequency stereotypic clicks which can be logged using T-PODs. Variation in interclick intervals (ICIs) can be used to distinguish different acoustic behaviours. So far, studies on ICI variation are mostly descriptive and the behavioural context in which certain click train patterns are emitted is poorly understood.

In this study, the behaviour of free-ranging porpoises was quantified by using typical ICI patterns known from the literature. These were recorded using two T-PODs deployed at a wind farm site (Nysted, Denmark) between 14 June and 12 July 2005 and during the entanglement of a porpoise calf in a gillnet (Clayoquot Sound Canada). It was possible to distinguish between feeding, approach behaviour and communication and known ICI patterns associated with these behaviours were used to categorise acoustic data.

During feeding typical click trains start with long ICIs (30-70ms) and end with ICIs down to about 2ms. In a transition phase ICIs rapidly decrease. Click trains attributed to feeding were found in the wind farm data at a rate of $6.3d^{-1}$ (n=174) with a patchy distribution. We found 20 to 74s long click train sequences with ICIs gradually decreasing from a median of 72ms (range 34 to 143ms) down to 5ms at a rate of $1.6day^{-1}$ (n=45). This was interpreted as approach behaviour, in which the animal was acoustically 'locked on' to a reflective structure. Communication signals are built up of click trains with very short ICIs (<7.7ms). During the entanglement of a porpoise calf, three different call types were determined at a rate of $8.9min^{-1}$ (n=89). One call with variable duration (100 to 890ms) and relatively stable ICIs as low as 3.6ms resembled 'distress calls' described by Amundin (1991b). Another call type with durations from 780 to 830ms and ICIs ranging from 3.0 to 10 ms and thus different with respect to ICI curve progression was found only three times. These had a U-shaped ICI curve, similar to an 'alarm' or 'fright' call described by Busnel and Dziedzic (1966). A third and previously unreported call is characterised by a long call duration (up to 1,270ms) and sometimes oscillating ICIs with an initial decrease from about 9ms to around 7ms and an increase towards the end.

The data presented suggest that the T-POD is a promising tool for behavioural studies. It is possible to recognise certain acoustic behavioural categories described in the literature, but it is important to look at the temporal context with other vocalisations in T-POD data, such as ICIs of preceding click trains.

KEYWORDS: COMMUNICATION; ECHOLOCATION; FEEDING, FOOD/PREY; BIOSONAR; HARBOUR PORPOISE; ACOUSTICS; NORTHERN HEMISPHERE

DEFINITIONS

To describe the nature of click series, some authors use the term 'pulse repetition frequency' (PRF, given in Hz or clicks per second) while others relate to 'interclick intervals' (ICIs) or 'click intervals' (in ms), meaning the time elapsed between the peaks of the envelopes of two consecutive clicks (Madsen *et al*., 2005). Interclick intervals are the reciprocal of pulse repetition frequency. The term ICI is used throughout this paper. When necessary, pulse repetition frequency is converted into ICI.

Some authors use the term 'click train' only for click series with certain ICIs (e.g. Verboom and Kastelein, 1995), while most others use it for any series of clicks regardless of their ICI (*cf*. Au, 1993). In this study, the term click train is used for any series of clicks separated by gradually or cyclically changing ICIs suggesting a unit during an echolocation event or a communication signal. Click trains may be separated from others by distinctly longer intervals. If these are emitted in a certain behavioural context such as approach behaviour a number of click trains form a 'click train sequence'.

INTRODUCTION

Harbour porpoises emit stereotypic acoustic click signals to navigate and communicate under water (Amundin, 1991b; Au, 1993). The acoustic patterns vary with behaviour (Amundin, 1991b), but determining the behaviour associated with specific acoustic patterns is difficult as visual observations are logistically challenging and can rarely be conducted simultaneously with the recording of acoustic data. High-frequency click train data can be acquired via T-PODs, and this static acoustic monitoring instrument is commonly used to record the presence or absence of harbour porpoises (Carstensen *et al*., 2006; Tougaard *et al*., 2006). This paper proposes that the data recorded with T-PODs may also be used to examine specific click trains or click train sequences to illuminate porpoise behaviour. It is hypothesised that typical sequence patterns can be found regularly within T-POD data and can be used as indicators for certain types of behaviour. This study reviews existing information and uses data recorded by T-PODs to identify typical patterns in click train data.

Harbour porpoises emit narrowband pulses with distinct peaks at frequencies between 110 and 160kHz, mainly around 130kHz, and a typical duration of 75 to 150μs (e.g. Amundin, 1991b; Kamminga and Wiersma, 1981; Verboom and Kastelein, 1997; Villadsgaard *et al*., 2007). For a 3yr old individual, the average 3dB bandwidth of the peak was 16.4kHz (Au *et al*., 1999). For juveniles, the peak frequency is higher and the bandwidth narrower than for adults (Au *et al*., 1999; Goodson and Datta, 1995; Goodson *et al*., 1995; Goodson and Sturtivant, 1995). The −3dB beam width (a measure for the directionality of the echolocation beam) in the horizontal and the vertical plane was 16.5° (Au *et al*.,

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1999). Peak to peak source levels (SL) ranged from 133-172dB re 1μPa @1m for captive harbour porpoises (Au *et al*., 1999; Goodson *et al*., 1995) and 175-205dB re 1μPa @1m for free-ranging harbour porpoises (Villadsgaard *et al*., 2007). The latter translates into a maximum energy level for an echolocating harbour porpoise of 150 dB re 1μPa^2 s @1m (Villadsgaard *et al*., 2007).

The ultrasonic echolocation signal was first described independently by Dubrovskii *et al.* (1971) and Møhl and Andersen (1973). In some early studies (e.g. Amundin, 1991b; Busnel and Dziedzic, 1967; Schevill *et al*., 1969), a narrowband low-frequency component of harbour porpoise vocalisations was used for the analysis of click train patterns. Since the latter seems to be part of the same sound production event (Amundin, 1991a) and may be a byproduct of tissue generated ultrasonic clicks data from these studies were applied to our findings.

High-frequency narrow-band click trains of harbour porpoises can be logged with T-PODs which are self-contained, anchored click detectors that record the time and duration of each ultrasound click to 10μs resolution. Harbour porpoise clicks are identified by the comparison of the outputs of two bandpass filters with different centre frequencies. When the set ratio between the target filter and the reference filter output is exceeded, the T-POD logs the start and end times of a sound. This ratio makes it possible to exclude noise clicks as well as clicks from other odontocetes. Custom made software analyses the T-POD data to identify characteristic harbour porpoise click trains using an algorithm which defines the regularity of ICIs within the train.

Signal-to-noise ratio (SNR), transducer sensitivity, sound radiation and directional properties of the sonar beam limit the detection range of a T-POD. A directivity related effect of click intensity is often obvious in T-POD data, even though received intensity of the clicks is only recorded indirectly through click duration (Fig. 1). In biosonar recordings of free-ranging porpoises, Goodson and Sturtivant (1995) described a similar sharp fading and strong reappearing of the signal intensity in an almost regular pattern, producing the effect of a series of very short click trains as fragments of longer trains. They suggested that porpoises were scanning a small sector ahead of their path by body or head movements. Such scanning movements during echolocation are known from captive animals (Akamatsu *et al*., 1992).

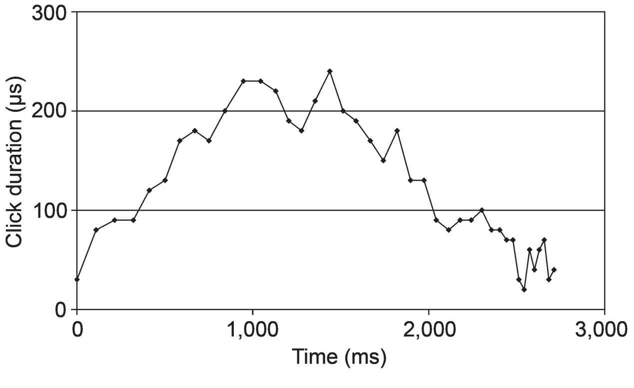

Fig. 1. Artefact related to the directivity of the echolocation beam of harbour porpoises as recorded by a T-POD. The changes in signal intensity at the receiver are expressed indirectly by a corresponding variation in click duration.

Given the SL mentioned above, under ideal conditions harbour porpoise vocalisations can be recorded by a T-POD over 300 to 400m away (Tougaard *et al*., 2006; Villadsgaard *et al*., 2007). Matching theodolite and T-POD data resulted in an effective detection distance of T-PODs between 86 and 107m (Culik and Koschinski, 2004; Tougaard *et al*., 2006); (T-POD v. 1 and 3) with detection probability decreasing rapidly at greater distance. T-PODs are often employed in habitat use studies where factors describing porpoise activity are limited to porpoise presence or absence (Tougaard *et al*., 2006).

Since harbour porpoise clicks are remarkably stereotypic (Au *et al*., 1999; Villadsgaard *et al*., 2007), a key factor in different acoustic behaviour seems to be the high variation in ICI. Studies on harbour porpoise vocalisations with respect to ICI variation are mostly descriptive (e.g. Verboom and Kastelein, 1995; 1997). The behavioural context in which certain click train patterns are emitted has so far only been addressed in captive studies (e.g. Amundin, 1991b; Busnel and Dziedzic, 1967; Nakamura *et al*., 1998; Verfuss *et al*., 2005). Knowledge on how harbour porpoises utilise their biosonar in the wild is thus limited.

Generally, harbour porpoises send out the next click within an echolocation click train after reception of the echo of the previous click, thus ensuring that the echo is not disturbed by subsequent clicks. ICIs are thus greater than the two-way transit time (TWT) of the sound between animal and target. The difference between TWT and ICI, called ‘lag time’, varied between 14 and 36ms in different studies (Au *et al*., 1999; Verfuss *et al*., 2005). As a consequence, animals would delimit the distance they inspect acoustically at a certain range behind expected targets when locked on a target. The use of different ICIs of animals observing floating objects in a pool and navigating around ropes may simply express such differences in focal distance above which porpoises adjust their ICIs (Kastelein *et al*., 1995).

If the animal is locked on a clearly identified target, the ICI is generally rather stable in the decrease during an approach (Akamatsu *et al*., 2007; Akamatsu *et al*., 2005; Verfuss *et al*., 2005). Sometimes porpoises increased ICIs suddenly after gradually decreasing intervals, indicating a switch from a close target to another target further away. The use of prominent features on the seabed or in the water column as navigation aid by free-ranging porpoises and the approach to prey are possible explanations. An acceleration indicated by a steeper slope of decreasing ICIs sometimes followed by a sudden decrease in swim speed at the end may indicate approach to prey (Akamatsu *et al*., 2005 for *Neophocaena phocaenoides*). If not locked on the target, the ICI most often varies, possibly indicating that the animal is exploring the existence of anticipated targets at different distances. Then a lag time cannot be specified.

Short ICIs around 2ms with no or a very short lag time (cf. Au, 1993) are commonly found for harbour porpoises when observing an object at close range (Verboom and Kastelein, 1995), closely inspecting a hydrophone (Amundin, pers. obs.), when inspecting the sea floor at close range during a foraging activity called ‘bottom grubbing’ (Lockyer *et al*., 2001) or during hand-feeding of dead fish in an enclosure (Busnel and Dziedzic, 1967; Schevill *et al*., 1969). A typical echolocation pattern found by Busnel and Dziedzic (1967) and Schevill *et al.* (1969) which can be used to describe foraging behaviour is presented in Fig. 2. It is characterised by click trains beginning with relatively long ICIs and ending with very short ones (still being longer than the TWT to the fish).

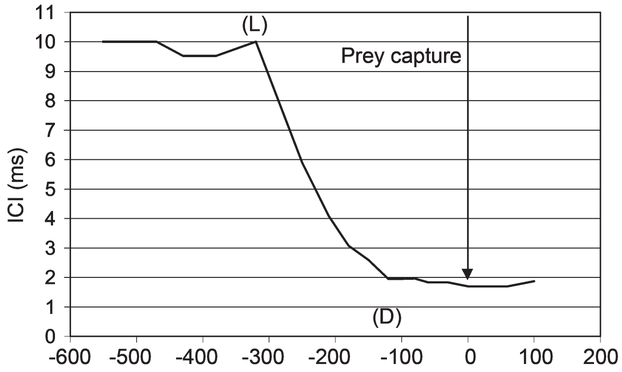

Fig. 2. Harbour porpoise interclick intervals immediately before and during prey capture when hand-fed in a pool (redrawn from Busnel and Dziedzic, 1967). (L) indicates the 'localisation point', about 20 to 40cm from prey, (D) indicates the 'decision point', about 5cm from the prey.

In the initial phase, harbour porpoises used ICIs between 5.2 and 15.6ms (mean 8.6ms, *n*=27). At a 'localisation point' (*L*), 11-37cm (mean 28.4cm) from the prey, ICIs decreased rapidly. The end of this transition phase was marked by the 'decision point' (*D*) (0-11cm mean 5.8cm from the fish, *n*=26). In the terminal phase animals used relatively stable ICIs with mean values of 2.1ms during which the prey was captured. Such 'buzzes' are also known from free-ranging porpoises during foraging (Chappell and Gordon, 1993). Very short ICIs may be necessary in the terminal phase to avoid losing moving prey as the time it takes a prey to leave the acoustic beam is proportional to the distance from the porpoise.

Like echolocation, harbour porpoise communication signals are exclusively built up of click trains (Amundin, 1991b). The message conveyed may be dependent on the social and ecological context in which they are emitted. During social communication harbour porpoises seem to use click trains with very short intervals consistently below 7.7ms (Amundin, 1991b; Busnel and Dziedzic, 1966; Nakamura *et al*., 1998). Amundin (1991b) recorded a variety of social signals, mostly 'threat' and 'distress' calls. His sonagrams and click repetition rate graphs were based either on the low or the high-frequency component of porpoise clicks. The much stronger high-frequency component seems to carry the information because the range within which a porpoise is able to detect the signal will always be larger than that of the low-frequency component (Hansen *et al*., 2008). In some cases, porpoises turned their rostrum towards the addressee (Amundin, 1991b; Nakamura *et al*., 1998), indicating that the high frequency directional sound is purposefully used. In these cases high-intensity signals with very short ICIs may cause a painful hearing sensation providing 'discomfort' in the addressee ('acoustic box on the ear'; (Amundin, 1991b)) especially in the light of recent findings of source levels up to 205dB re 1μPa@1m (Villadsgaard *et al*., 2007).

The communication calls described by Amundin (1991b) are presented in some detail in Table 1 and Figs. 3-6. Data were acquired via high-frequency[1] (251 calls) and low-frequency (15 calls) recording equipment[2]. The ICIs of the low-frequency calls were derived from the harmonic interval in the sonagrams (cf. Watkins, 1967). Table 1 further shows the characteristics of communication calls recorded by Busnel and Dziedzic (1966) and Nakamura *et al*. (1998).

This study presents examples of certain vocalisation patterns expressed in two T-POD data sets from Nysted, Denmark and Clayoquot Sound, Canada, and compares these with patterns described above in order to explore whether behaviour of wild porpoises can be inferred from acoustic patterns recorded via T-POD.

METHODS

Data files were acquired by T-PODs (Chelonia Ltd, UK) versions 1 and 4. T-POD1 (version 4, nr. 458) was chosen at random from 20 T-PODs which logged harbour porpoise clicks within the Danish Baltic Sea wind farm 'Nysted' (54°34.2'N, 11°40.02'E) between 14 June and 12 July 2005. The distance to the nearest wind power generator was 148m. T-POD1 was positioned 1.5m above the bottom at a water depth of 6m. Since this data set represents a long time period it was assumed that a number of different behaviours may have occurred in the vicinity and typical signals been picked up by the T-POD. Due to the large size of the data set from T-POD1 only obvious click train patterns, such as feeding and approach behaviour were searched for. Click trains were classified as feeding behaviour if they showed a rapid decline of intervals to less than 10ms, preceded by an initial phase with much longer intervals (e.g. Busnel and Dziedzic, 1967). Click trains were classified as approach behaviour if they showed a gradual decrease in ICIs over a period of many seconds (Verfuss *et al*., 2005).

T-POD2 (version 1, nr. 68) recorded data associated with a single incident of a porpoise calf becoming entangled in a gillnet panel positioned in up to 30m deep water in Clayoquot Sound/Canada (49°11'N, 125°46.5'W) (Koschinski *et al*., 2006). Data from T-POD2 were searched for communication sounds because they could be matched with visual observations of behaviour during this incident. A period of 10min was searched from the collision and entanglement of the calf in the net panel. The calf's mother collided with the net just before the calf, but did not become entangled. She swam around the net until the calf was released. Entanglement took place about 20m from the T-POD and 1m below the surface. The T-POD was suspended at the net panel 4.5m below the surface. Click trains were classified as communications if they showed relatively regular intervals below 10ms, and did not show a marked decline in the beginning.

Data were processed and displayed using the custom made *TPOD.exe* software v. 7.41. This program uses an algorithm determined empirically to identify click trains based on the regularity of the train. The algorithm takes variation between consecutive ICIs into account and can identify click trains in which ICIs increase or decrease by 38%. Based on the ICI variation *TPOD.exe* assigns each identified click train one of four levels of confidence, ranging from high probability trains ('CET HI') to very doubtful trains ('..??..'). The software can also display the raw data using the display setting 'cluster', also containing clicks which are not classified in trains, e. g. clicks very close together such as echoes or multi-path duplicates. During train classification usually only the first of these duplicates is processed. However, sometimes multi-path duplicates have to be removed manually even from classified click trains. In a quiet environment, it is often useful to have a look at doubtful and very doubtful click

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[1] B&K 8103 hydrophone fastened to the study animals' melon via suction cup, or hand held to the surface of the melon, custom made preamplifier, B&K 2607 measuring amplifier, Krohn Hite 3322 filter, Lyrec TR-47 instrumentation recorder at 60 ips

[2] LC32 hydrophone suspended in the centre of a 41m^2, 1m-deep pool, custom made preamplifier, B&K 2607 measuring amplifier, Krohn Hite 3322 filter, Nagra IV-D tape recorder at 15 ips.

Table 1

Communicative call types noted by different authors (A: Amundin 1991b, B: Busnel and Dziedzic 1966, N: Nakamura *et al.* 1998).

Call type	Duration	ICIs	Observed behaviour
'Distress calls' (A)	Varying duration (100ms to >1s long)	Rather evenly spaced clicks with intervals of between 2 and 3ms. Some click trains showed a slight increase of intervals followed by a prominent decrease before reaching the steady level (Figs. 3a and b). Sometimes grouped into click train sequences or 'phrases' of several calls	In situations when animals experienced discomfort, e.g. 1-2 yr old animals, just retrieved from pond nets, in the first few days after being installed in captivity, possibly thereby separated from their mothers, also during transport in a stretcher
'Fear from removal from familiar surroundings'/ 'alarm or fright calls' (B)	400ms to 1.55s	4 to 7.7ms	Signals emitted when animals were newly introduced into a pool
'Signal of pain' (A)	200ms followed by another 300ms long call	First call: decreasing click intervals of 1.7 to 1.2ms, second call: modulating intervals between 1.4 and 1.7ms (Fig. 4)	Only one signal recorded when an animal accidentally was inflicted pain
'Sideward turn threat call' (A)	200ms	Starting at 2.5ms decreasing steeply to 1.4 – 1ms (Fig. 5a)	Agonistic behaviour between subadult males during which the aggressive porpoise quickly turns its head and hence its sonar beam towards the head of the other
'Push threat call' (A)	Over 1 to 1.5s	1.3ms with a (sometimes sharp) decrease in the beginning and an increase at the end, sometimes grouped into click train sequences or 'phrases' of several calls (Fig. 5b)	Agonistic behaviour between subadult males during which an aggressive male chased after another at full speed
Trains during 'snouting behaviour' (N)	Cannot be extracted from paper written in Japanese	Mean=3.7ms, SD=1.7ms	'Snouting' - assumingly agonistic behaviour found in males and females
'Signal of dominance' (A)	Sequence of calls with a duration of 50 to 100ms	0.8ms (Fig. 6)	During food competition situations
'S-display sound' (A)	Total duration of sometimes >10s	A click train with very long intervals (>100ms) interrupted by bursts of somewhat shorter intervals (about 40ms)	Subadult males during sexual display

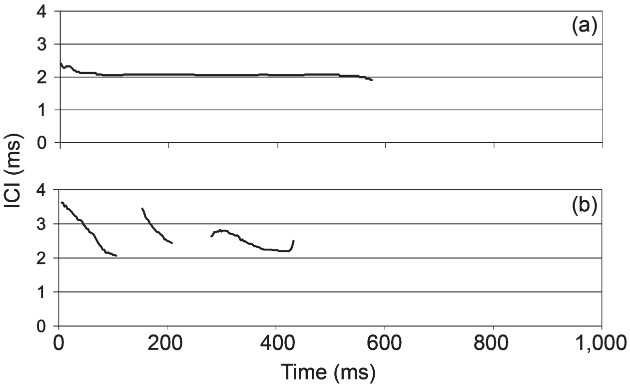

Fig. 3 Examples of long (a) and short (b) 'distress calls' as recorded by Amundin (1991b) using high-frequency equipment during situations in which animals experienced discomfort (e.g. when juveniles were separated from their mothers).

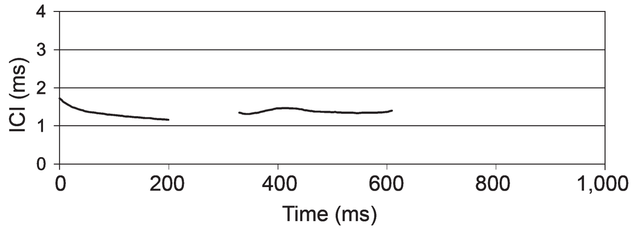

Fig. 4 'Signal of pain' as recorded as low-frequency pulsed call by Soren Andersen (in Amundin, 1991b) when an animal experienced pain.

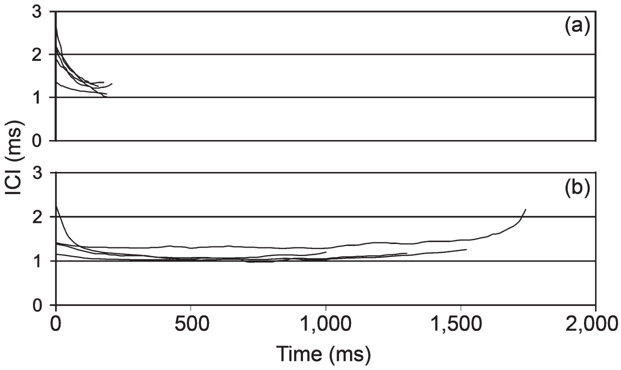

Fig. 5 Calls produced during agonistic behaviour recorded as low-frequency pulsed calls by Amundin (1991b). Several 'Sideward turn threat calls' plotted on top of each other (a). These calls were recorded when an aggressive porpoise turned its rostrum and thus the high frequency sound beam towards the head of another individual by quickly turning sideward with the anterior part of the body; the other animal reacted by avoidance. Several 'push threat calls' plotted on top of each other (b). These calls were heard when an aggressive animal chased after another at full speed, often making contact by nodding with its rostrum against the other's back.

trains. Thomsen *et al.* (2005) were able to show in an experiment with captive harbour porpoises that 41% of porpoise click trains were classified as doubtful trains. In order not to lose valuable information these should be carefully investigated. The category chosen depends on field conditions such as noise.

A manual search for click train patterns described in the literature in T-POD data was undertaken. By switching between the settings '..??..' and 'cluster', all four levels of

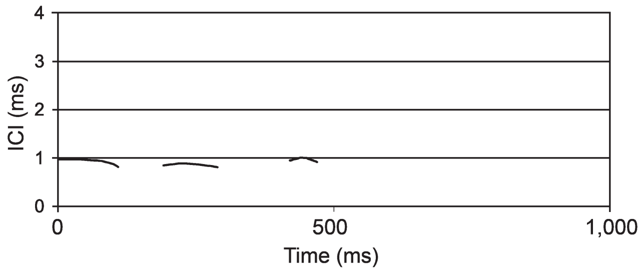

Fig. 6 'Signal of dominance', recorded as low-frequency pulsed call by Soren Andersen (in Amundin, 1991b). This type of signal was recorded in a food competition situation where an adult female intimidated younger males and thereby got access to hand-fed fish.

confidence and neighbouring clicks unclassified by the algorithm were searched in order to avoid clicks within click trains being lost due to processing by the algorithm.

To account for multi-path clicks in the ICI distribution clicks with ICIs below 1ms were omitted and ICIs recalculated. Multi-path propagation of sound waves may result in double clicks due to different delays arriving at the T-POD along different paths, e.g. by reflections from structures such as nearby deployment gear or water surface.

RESULTS

Inter-click interval distribution

ICIs within very doubtful click trains from T-POD1 showed a wide distribution, with 79% of ICIs between 2 and 50ms (Fig. 7). ICIs from T-POD2 were mostly below 10ms (92%, Fig. 7). Although clicks with intervals below 1ms were removed, the data used to produce Fig. 7 may still have contained some multi-path intervals between 1 and 2ms.

Feeding

A total of 174 click trains were found associated with feeding at a rate of 6.3day^{-1} in the T-POD1 data. However, the distribution of feeding-like click trains was very patchy (Fig. 8). For example, 53 of the 174 observed trains occurred within 81min, and another 19 within 113min (0.5% of the recorded time). In all cases where initial, transition and terminal phases were present, these were classified as different trains by the *TPOD.exe* software, most often as different levels of confidence. Some parts of the click trains were not detected by the algorithm of the software and hence only found by manually searching the raw data.

The mean interval from which the transition phase started was 26.7ms (SD=12.7, *n*=174). Fig. 9 shows an example with an initial phase with ICIs oscillating between 30 and 70ms and rapidly decreasing ICIs from about 40 to 2ms marking the transition to the terminal phase which is characterised by the buzz with ICIs of 2-3ms (*cf*. Busnel and Dziedzic, 1967). At the end, in some click trains an increase to longer ICIs could be found.

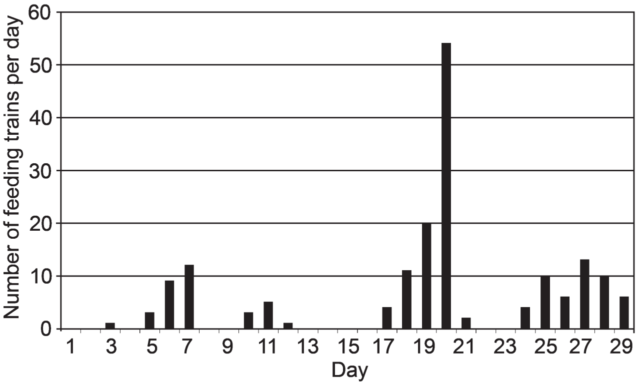

Fig. 8. Number of observed feeding-like click trains per day in T-POD1 data.

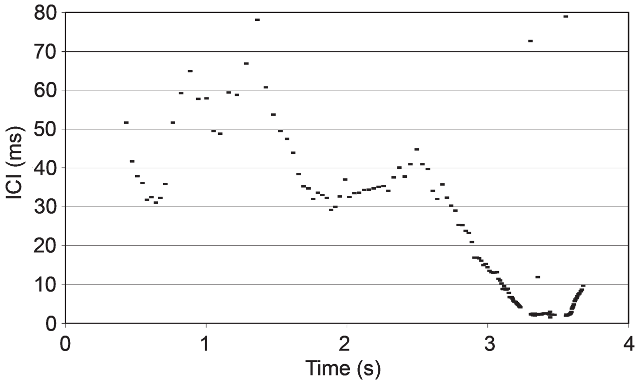

Fig. 9. Click train of presumably echolocating porpoise during prey capture as recorded by T-POD1 in the wind farm area of Nysted (display setting: 'cluster').

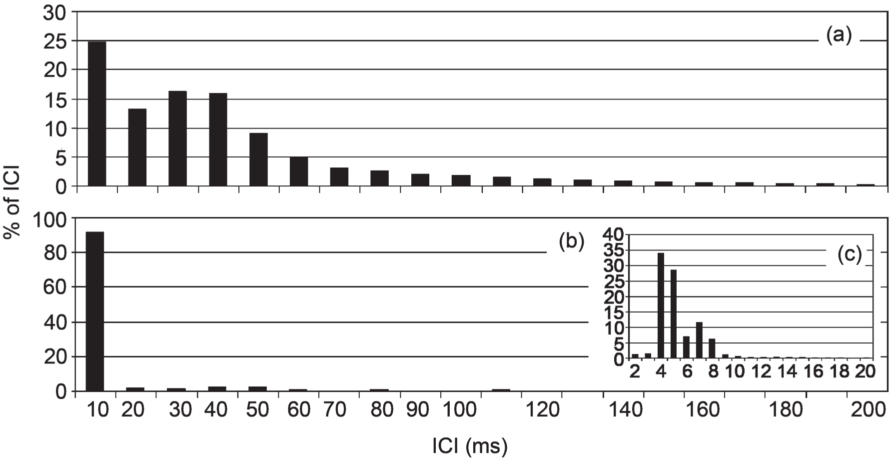

Fig. 7. Distribution of interclick intervals classified as '..??..' (in 10ms classes, inset c in 1ms classes) within a 27.52d period in a Danish wind farm, (a: T-POD1 data; *n*=138,558 ICIs) and within a 10 minute period after entangling of porpoise calf in a gillnet (b and c: T-POD2 data, *n*=4,200 ICIs). Intervals counted from 2 to 200ms, multi-path clicks with intervals below 1ms were removed.

Approach behaviour

A total of 45 click train sequences were found associated with approaches to a target at a rate of 1.6 day^{-1} in the T-POD1 data. In a randomly chosen subset of the data, click train sequences were 20-74s long (median=32s, *n*=19) and two examples of this are shown in Fig. 10. The difference between them is the ICI at the end of the sequence which decreases to 30ms in Fig. 10a, whereas the example shown in Fig. 10b ends with ICIs at around 5ms.

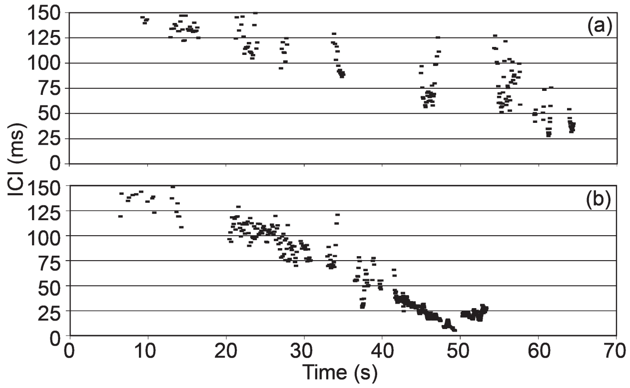

Fig. 10. Acoustic approach behaviour as logged by T-POD1 in the wind farm area of Nysted starting with highest ICIs of 120ms and ending with ICIs of down to 30ms (a) and 5ms (b) (click train category: '..??..').

Communication

A total of 89 click trains were found associated with communication in the T-POD2 data at a rate of 8.9min^{-1}. Some click trains were truncated. There were two dominating ICIs, between 4 and 5ms, and around 7ms (Fig. 7). Click trains with consistently very short ICIs (<2ms) such as in 'threat calls' and 'signal of pain' or 'signal of dominance' (sensu Amundin, 1991b) were not found within the data set.

Figs 11 and 12 show examples of three different types of click trains and click train sequences from the T-POD2 data. Calls similar to those in the sequence shown in Fig. 11a were found throughout the data set and are characterised by ICIs as low as 3.6ms and a flat ICI curve progression and thus are similar to 'distress calls' described by Amundin (1991b); (Fig. 3b). The call duration is variable in the data set (range <100 to 890ms). Twelve out of 66 of these calls appeared to be truncated.

Fig. 11b shows a sequence of two long calls with similar ICIs (ranging 3.0-10ms) and relatively long durations of 780 and 830ms, respectively. The distinct U-shape with respect to ICIs, seen only in three calls within the first minute after entanglement, is a prominent feature of this call type.

The click trains shown in Fig. 12 consist of longer ICIs (5.7-11.2ms). These calls, up to 1,270ms long, were found 17 times in the data set. Thirteen of these seem to be truncated, which may be related to directionality of the echolocation beam. This call type occurred only in the first 2.5min of the data set.

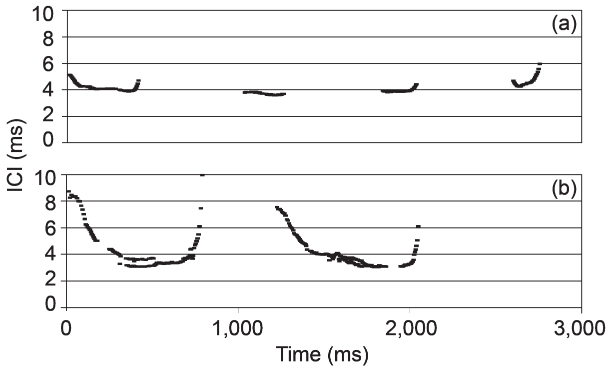

Fig. 11. Sequences recorded by a T-POD in Clayoquot Sound, Canada, as part of T-POD2 data; display setting: 'cluster'). (a) Sequence of four short calls with a duration of 195 to 395ms and minimum intervals of 3.6ms resembling 'distress calls' (cf. Amundin, 1991b) (Fig. 3); (b) sequence of two long calls with a duration of 780 and 830ms and minimum intervals of 3.0ms. In contrast to (a), these show a distinct u-shape. The double traces around 400ms and 1.6s on the time axis are probably caused by multi-path propagation from the sea bed, or the surface (N. Tregenza, pers. comm.).

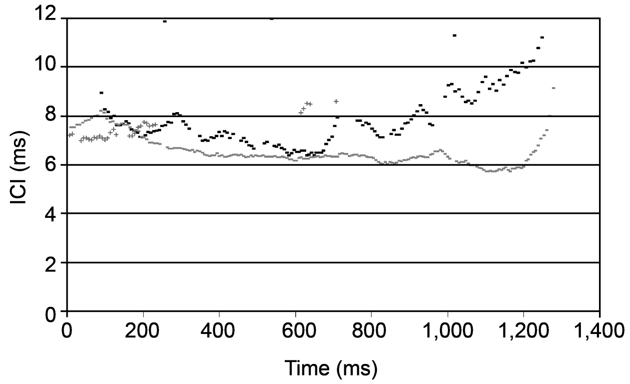

Fig. 12. Previously unreported possible communication sounds found within the first 2.5min of T-POD2 data. Calls plotted on top of each other. ICIs are longer than in the calls shown in Figs 11a and b. Calls plotted in black show a distinct oscillation whereas the call plotted in grey is characterised by a flat curve progression. '+' symbols mark a truncated call. All sequences were recorded by a T-POD in Clayoquot Sound, Canada, as part of T-POD2 data; display setting: 'cluster').

DISCUSSION

Interclick interval distribution

ICIs in harbour porpoises click trains are highly variable. The distribution of ICIs can indicate the occurrence of certain acoustic behaviours associated with communication or feeding which contain short ICIs. T-POD2 data contains 92% of ICIs <10ms because T-POD2 almost exclusively recorded communication behaviour. In free-ranging, travelling harbour porpoises, Petersen (2007) found ICIs between 61 and 70ms to be most common, and only <2% of intervals were shorter than 30ms within the analysed range of <10ms to 300ms (*n*=2,993 ICIs). Villadsgaard *et al.* (2007) reported dominating ICIs between 41 and 50ms and no intervals below 30ms (*n*=822 ICIs). Both studies found much fewer ICIs <30ms compared to our T-POD1 data which comprised 60% of ICIs within these classes. In the study by Petersen (2007) porpoises passing through a shallow area at Fyns Hoved (Denmark) were recorded using a click detector. Animals were typically not engaged in foraging, although occasional buzzes were heard and may have been recorded from animals further away. Recording was manually begun when porpoise clicks were heard. The chance of recording the occasionally heard buzzes was thus low. Villadsgaard *et al.* (2007) recorded harbour porpoise clicks at three different locations in inner Danish waters. Animals from Little Belt were less shy and were more intense in foraging compared to the other areas Aarhus Bay and Bogense where presumably more animals were involved in travelling behaviour. However, the recording equipment in their study was not set to detect the weaker feeding buzzes since porpoises adjust their SL to lower range during the final phase of a feeding train (Magnus Wahlberg, pers. comm.).

U-shaped click trains

Click trains with U-shaped ICI curve progression can be found during feeding (Fig. 9), communication (Fig. 11b) and during approach behaviour (Fig. 10) when choosing another time domain (the time axis would have to be stretched). Verboom and Kastelein (1995) describe a tendency in a captive animal to start with a certain ICI, decrease intervals and increase them again. There may be different explanations for U-shapes in separate behavioural categories. U-shaped click trains may reflect a pre-adjustment to an unknown or expected range in the initial phase during foraging or during travelling. In communication, it is more likely that this interval pattern belongs to the signal and may carry part of the information since the ICIs in such signals do not refer to a certain range and morphological reasons can be ruled out. As shown in Figs 4, 5 and 6 porpoises are able to produce very short ICIs at once without 'tuning' in.

Echolocation during feeding

ICI patterns attributed to feeding were found 174 times in the T-POD1 data (e.g. Fig. 9). The long ICIs during the initial phase, the short transition and the terminal phase with short ICIs are similar to those observed by Busnel and Dziedzic (1967); Fig. 2. However, ICIs during the initial phase were markedly longer in T-POD1 data (transition starting from a mean of 26.7ms) compared to mean intervals of 8.6ms reported by Busnel and Dziedzic for captive harbour porpoises. The high variability of ICIs in the initial phase may reflect a more variable search range in free-ranging animals compared to hand-feeding in a pool. The lower value in the captive animals is probably due to the limited search range of only 7m and the fact that dead fish is easier to catch than moving live prey. ICI oscillations shown in Fig. 9 indicate that animals explore a range of distances ahead of them before locking on a target in the beginning of the transition phase. In contrast to the data presented here, the possible foraging related data of a free-ranging harbour porpoise equipped with an acoustic tag only show gradually decreasing ICIs and lack typical terminal buzzes (Akamatsu *et al*., 2007). This may be explained by the low sensitivity of the laterally attached hydrophone and buzzes adjusted to a lower SL for short detection ranges in the terminal phase of feeding trains. While the acoustic pattern recorded for harbour porpoises is similar to presumably foraging free-ranging spinner dolphins, *Stenella longirostris,* (Lammers *et al*., 2004; Lammers *et al*., 2003), it remains unknown how free-ranging harbour porpoises operate their biosonar during prey capture.

Approach behaviour

Sequences built up of click trains with gradually decreasing lowest ICIs starting at a median of 72ms (range 34 to 143ms) indicate approaches to a target (Fig. 10). These ICIs translate into an acoustically inspected distance of 54m (range 25.5 to 107.3m). The most common ICIs found by Petersen (2007) and Villadsgaard *et al.* (2007) point to most often inspected distances of 45.8 to 52.5m and 30.8 to 37.5m, respectively. Thus, these data fall within the range of inspection distances reported in other studies.

The performance of biosonar with respect to range is more dependent on the target strength (TS) than only the TWT. The TS of a T-POD in side aspect can be calculated as TS = −1.3dB[3] (Urick, 1983). The resulting prominent echo is much stronger than from a prey sized fish (TS = −35 to −38db in Klinowska *et al*., 1992; Urick, 1983). Since the auditory system typically processes acoustic information by detecting acoustic energy, the energy flux density in the echo is the appropriate parameter to determine (Kastelein *et al*., 1999; Villadsgaard *et al*., 2007). Assuming a maximum source energy level of an echolocating harbour porpoise of 150 dB re 1µPa^2 s @1m (Villadsgaard *et al*., 2007), the T-POD housing may be detected at a range of 310 to 350m under the most favourable conditions (assuming 20logR spreading loss, detection threshold 22.4 to 27.4 dB re 1µPa^2 s (Kastelein *et al*., 1999), absorption coefficient 0.035dBm^{-1}). This is above the maximum inspected distances indicated by the ICI in this study.

It is therefore realistic to assume that during the recording of approach behaviour in some cases the animals may have been locked on the T-POD. Within the wind farm, the foundations produce even stronger echoes and may in some cases have attracted even more attention. It can be speculated that due to the (aspect dependent) strong echo created by the T-POD, porpoises may either use it as a navigation aid or regard it as interesting and investigate it. If porpoises are not directed towards the T-POD, the approach phase will be cut off at higher ICIs when the T-POD becomes off-axis (Fig. 10a). In Fig. 10b, with much shorter ICIs at the end, porpoises may have been locked on the T-POD and investigated the T-POD closely using decreasing ICIs as short as 5ms – similar to investigation of objects in a pool (Verboom and Kastelein, 1995). It is therefore possible that the presence of a T-POD distracts harbour porpoises or alters their behaviour. This needs to be considered in behavioural studies using T-PODs.

Communication

Click trains used during social communication show consistently very short intervals. In bottlenose dolphins, these communicative click trains appear to have a more prominent <20kHz frequency component than echolocation trains (Blomqvist, 2004). Such differences are not seen in harbour porpoises (Hansen *et al*., 2008). For this species, communicative signals cannot be defined by the duration of intervals alone, as porpoises use similarly short ICIs during prey capture and close investigation of objects. We propose that communication sounds can be distinguished by the absence of immediately preceding ICIs distinctly longer than 10ms and a transition with rapidly decreasing intervals (such as in click trains used during foraging, Figs 2 and 9) and a gradual decrease in ICI over many seconds (typical for approach behaviour, Fig. 10). However, in some cases isolated fish catching buzzes may occur when porpoises are not orientated towards the T-POD during their search and then suddenly turn towards it, e.g. bottom grubbing porpoises (cf. Lockyer *et al*., 2001) searching for benthic fish standing vertically above the bottom and chasing after fish that leave their bottom shelter to escape.

Within communication behaviour, it is also difficult to distinguish between different categories (Table 1) from T-POD data alone. Differences between certain communication signals are the duration of sequences, ICI and ICI curve progression. Further, the formation of sequences of a number of similar calls may be meaningful. However, there is substantial variability within communication signals. For example, Nakamura *et al.*

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[3] $TS_{cylinder}$=10log(radius×length^2/2×wavelength).

(1998) described threat calls during agonistic 'snouting' behaviour with ICIs much longer than in threat calls described by Amundin (1991b); (*cf.* Table 1, Figs 5 and 6).

Vocalisation patterns with similar and consistently short ICIs are found throughout T-POD2 data. It is thought that these are not fragments of other sequences during other behaviours such as 'feeding' or 'observation of objects', because such behaviours did not occur in this short and clearly defined incident. As sequences were obtained during entanglement of a porpoise calf in a gillnet, 'signals of pain' and 'distress calls' were expected, however no click train sequences similar to the 'signal of pain' were found. As the 'signal of pain' has been recorded only once (Amundin, 1991b) before it is proposed that porpoises may have different vocalisations to express pain.

Patterns found in T-POD2 data do not unequivocally match with categories from earlier studies. While the click train duration is similar to that described by Amundin (1991b) for distress calls, the ICIs are generally longer and seem to be more variable. It was not possible to determine which of the calls were produced by the mother vs. the calf. It is possible that the two dominating ICIs reflect calls from the mother and the calf, respectively, and represent individual variability in ICI patterns.

It is hypothesised that the calls in T-POD2 data represent three different call types with specific meanings. The first call type (Fig. 11a) with short ICIs down to 3.6ms, a varying duration between 100 and 890ms and flat curve progression probably represents 'distress calls' similar to those recorded by Amundin (1991b). Amundin (1991b) found variable (duration 100 to 1,000ms) 'distress calls' in juveniles and sub-adults up to two years of age that had been separated from their mothers during entrapment in pond nets. Thus these calls have been interpreted as having been produced by the entangled calf when it was separated from its mother.

Another call (Fig. 11b) was different with respect to ICI and curve progression. This call with a distinctly U-shaped curve and with ICIs as low as 3.0ms and a duration of 780 to 830ms is very similar to the 'fear from removal from familiar surroundings (alarm) or fright' call (Table 1) with respect to duration, ICI and interval pattern (see fig. 48 in Busnel and Dziedzic, 1966). In their study, ICIs within an approximately 800ms long call decrease at the beginning and increase at the end of the call and therefore also show a characteristic U-shape. We speculate that this call may have been produced by the adult female since there are hints in Busnel and Dziedzic's study that the three females which produced this call were adults. Thus, this rarely seen call may represent an adult signal.

The third and previously undescribed call type seen in T-POD2 data is shown in Fig. 12. Typical features are the much longer ICIs (around 7ms) decreasing from 8-9ms in the beginning and increasing towards the end of the call (sometimes with oscillations) and a long duration of up to 1,270ms. It is hypothesised that this call was produced by the adult female indicated by the higher rate of truncated calls in T-POD data compared to the 'distress calls'. Truncation may have been caused by the directivity of echolocation of the moving female in connection with the static deployment of the T-POD.

T-PODs as a tool for comparative behavioural studies

This study shows that certain click sequences from T-POD data have a potential link to the behavioural categories described above. Hence, the T-POD is a promising tool for comparative behavioural studies using passive acoustic monitoring. The ICI alone is not enough to differentiate between categories. Moreover, when trying to recognise certain acoustic behavioural categories in T-POD data sets, it is important to look at the temporal context with other vocalisations such as preceding intervals or click trains. For example, the end of an approach (Fig. 10b) sometimes looks very similar to the terminal phase during presumed feeding (Fig. 9), but both are preceded by typical sequences which allow their categorisation. The buzz in echolocation during feeding may also be similar to communication calls such as 'distress' or 'alarm or fright' calls. Again, echolocation during prey capture can be distinguished from social or communication signals by their two phases with distinct ICIs and transitions.

A problem with T-POD data is that frequently only fragments of click trains are logged due to the static deployment of the T-POD and the narrow echolocation beam of harbour porpoise biosonar. These fragments can be erroneously assigned to different categories even though they belong to the same click train. Further, click trains of different individuals may overlap, rendering classification of an individual's click train difficult. During feeding, the initial phase, the transition and the terminal phase are often classified as different click trains by the T-POD software because the relative change in ICIs differs between the phases. This makes it difficult to search for certain behaviours using automatic data processing. Given the large amount of data recorded by static acoustic monitoring devices, an automatic search routine for potentially meaningful sequences is desirable. In order to deduct useful information on porpoise behaviour from T-POD data it is crucial to understand the classification algorithm of automatic pattern detection software. Therefore developers of classification software should be encouraged to communicate the details of algorithms used and to implement settings that can be defined by users to enable a more flexible classification scheme. Further work should concentrate on developing algorithms that identify behavioural categories from raw data automatically.

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REFERENCES

Akamatsu, T., Hatakeyama, Y., Kojima, T. and Soeda, H. 1992. The rate with which a harbor porpoise used echolocation at night. pp.299-315. *In*: Thomas, J. (eds). *Marine Mammal Sensory Systems*. Plenum Press, New York.

Akamatsu, T., Teilmann, J., Miller, L.A., Tougaard, J., Dietz, R., Wang, D., Wang, K., Siebert, U. and Naito, Y. 2007. Comparison of echolocation behaviour between coastal and riverine porpoises. *Deep-Sea Res. II* 54: 290-97.

Akamatsu, T., Wang, D., Wang, K. and Naito, Y. 2005. Biosonar behaviour of free-ranging porpoises. *Proc. Royal Soc. B* 272: 797-801.

Amundin, M. 1991a. Helium effects on the click frequency spectrum of the harbour porpoise, *Phocoena phocoena*. *J. Acoust. Soc. Am.* 90(1): 53-59.

Amundin, M. 1991b. Sound production in odontocetes with emphasis on the harbour porpoise. PhD thesis, Stockholm University, Stockholm. 144pp

Au, W., Kastelein, R., Rippe, T. and Schooneman, N. 1999. Transmission beam pattern and echolation signals of a harbor porpoise (*Phocoena phocoena*). *J. Acoust. Soc. Am.* 106(6): 3699-705.

Au, W.W.L. 1993. *The Sonar of Dolphins*. Springer-Verlag, New York. 277pp.

Blomqvist, C. 2004. Directional aggressive pulse sounds in the bottlenose dolphin (*Tursiops truncatus*): technical aspects and social implications. PhD thesis. University of Linkoping, Sweden.

Busnel, R.G. and Dziedzic, A. 1966. Acoustic signals of the pilot whale *Globicephala melaena* and of the porpoises *Delphinus delphis* and *Phocoena phocoena*. pp.607-46. *In*: Norris, K.S. (eds). *Whales, Dolphins and Porpoises*. University of California Press, Berkeley, California, USA.

Busnel, R.G. and Dziedzic, A. 1967. Resultats metrologiques experimentaux de l'echolocation chez le *Phocoena phocoena* et leur comparison avec ceux de certaines chauves-souris. pp.307-35. *In*: Busnel, R.G. (eds). *Animal Sonar Systems, Biology and Bionics*. Laboratoire de Physiologie Acoustique, Jouy-en-Josas, France. 1,135pp. [In French].

Carstensen, J., Henricksen, O.D. and Teilmann, J. 2006. Impacts of offshore wind farm construction on harbour porpoises: acoustic monitoring of echolocation activity using porpoise detectors (T-PODs). *Mar. Ecol. Prog. Ser.* 321: 295-308.

Chappell, O. and Gordon, J. 1993. Investigations of harbour porpoise vocalisations. *Eur. Res. Cet.* 7(Inverness, Scotland, 18-21 February 1993): 49-52.

Culik, B.M. and Koschinski, S. 2004. *Zeit ist Leben – Schweinswale gewinnen kostbare Reaktionszeit durch reflektive Netze*. WWF Germany, Frankfurt, Germany. 46pp. [In German].

Dubrovskii, N.A., Krasnov, P.S. and Titov, A.A. 1971. On the emission of echolocation signals by the Azov Sea harbor porpoise. *Soviet Physics – Acoustics* 16(4): 444-47.

Goodson, A.D. and Datta, S. 1995. Investigating the sonar signals of the harbour porpoise. *J. Acoustical Soc. India* 23.

Goodson, A.D., Kastelein, R.A. and Sturtivant, C.R. 1995. Source levels and echolocation signal characteristics of juvenile harbour porpoises (*Phocoena phocoena*) in a pool. pp.41-53. *In*: Nachtigall, P.E., Lein, J., Au, W.W.L. and Read, A.J. (eds). *Harbour Porpoises – Laboratory Studies to Reduce Bycatch*. De Spil Publishers, Woerden, the Netherlands. 168pp.

Goodson, A.D. and Sturtivant, C. 1995. Sonar characteristics of the harbour porpoise; source levels and spectrum. *ICES J. Mar. Sci.* 53: 465-72.

Hansen, M., Wahlberg, M. and Madsen, P.T. 2008. Low-frequency components in harbour porpoise (*Phocoena phocoena*) clicks: communication signal, by-products, or artifacts? *J. Acoust. Soc. Am.* 124(6): 5,059-68.

Kamminga, C. and Wiersma, H. 1981. Investigations of cetacean sonar II. Acoustical similarities and differences in odontocete sonar signals. *Aquat. Mamm.* 8(2): 41-62.

Kastelein, R.A., Au, W.W.L., Rippe, H.T. and Schooneman, N.M. 1999. Target detection by an echolocating harbor porpoise (*Phocoena phocoena*). *J. Acoust. Soc. Am.* 105: 2493-98.

Kastelein, R.A., de Haan, D. and Staal, C. 1995. Behaviour of harbour porpoises (*Phocoena phocoena*) in response to ropes. pp.69-90. *In*: Nachtigall, P.E., Lien, J., Au, W.W.L. and Read, A.J. (eds). *Harbour Porpoises – Laboratory Studies to Reduce Bycatch*. De Spil Publishers, Woerden, The Netherlands. 168pp.

Klinowska, M., Goodson, D. and Bloom, P. 1992. *Progress in the development of efficient warning devices to prevent the entrapment of cetaceans (dolphins, porpoises and whales) in fishing nets*. ICES CM Marine Mammals Committee. 14pp.

Koschinski, S., Culik, B.M., Trippel, E.A. and Ginzkey, L. 2006. Behavioural reactions of free-ranging habour porpoises *Phocoena phocoena* encountering standard nylon and BaSO4 mesh gillnets and warning sound. *Mar. Ecol. Prog. Ser.* 313: 285-94.

Lammers, M.O., Au, W.W.L., Aubauer, R. and Nachtigall, P.E. 2004. A comparative analysis of the pulsed emissions of free-ranging Hawaiian spinner dolphins (*Stenella longirostris*). pp.414-19. *In*: Thomas, J.A., Moss, C.F. and Vater, M. (eds). *Echolocation in Bats and Dolphins*. University of Chicago Press, Chicago and London.

Lammers, M.O., Au, W.W.L. and Herzing, D.L. 2003. The broadband social acoustic signalling behavior of spinner and spotted dolphins. *J. Acoust. Soc. Am.* 114: 1629.

Lockyer, C., Amundin, M., Desportes, G. and Goodson, A.D. 2001. The tail of EPIC. Final report of EPIC, Elimination of Harbour Porpoise Incidental Catches. EU Project DG XIV 97/0006. 249pp.

Madsen, P.T., Johnson, M., Aguilar de Soto, N., Zimmer, W.M.X. and Tyack, P. 2005. Biosonar performance of foraging beaked whales (*Mesoplodon densirostris*). *J. Exp. Biol.* 208: 181-94.

Møhl, B. and Andersen, S. 1973. Echolocation: high-frequency component in the click of the harbour porpoise (*Phocoena phocoena* L.). *J. Acoust. Soc. Am.* 54: 1,368-1,72.

Nakamura, K., Akamatsu, T. and Shimazaki, K. 1998. Threat clicks of captive harbour porpoises, *Phocoena phocoena*. *Bull. Fac. Fish. Hakkaido Univ.*: 91-105.

Petersen, N.K. 2007. Acoustic behaviour of wild harbour porpoises (*Phocoena phocoena*) exposed to an interactive pinger. MSc thesis. Animal Behaviour Group, Biological Institute, University of Copenhagen, Copenhagen. 79pp.

Schevill, W.E., Watkins, W.A. and Ray, C. 1969. Click structure in the porpoise, *Phocoena phocoena*. *J. Mammal.* 50(4): 721-28.

Thomsen, F., Van Elk, N., Brock, V. and Piper, W. 2005. On the performance of automated porpoise click-detectors in experiments with captive harbour porpoises (*Phocoena phocoena*) (L.). *J. Acoust. Soc. Am.* 118: 37-40.

Tougaard, J., Rosager Poulsen, L., Amundin, M., Larsen, F., Rye, J. and Teilmann, J. 2006. Detection function of T-PODS and estimation of porpoise densities. *ECS Newsletter* 46(Special Issue – proceedings of the workshop on static acoustic monitoring of cetaceans, 20th Annual Meeting of the European Cetacean Society, Gdynia, Poland, 2 April 2006): 14pp.

Urick, R.J. 1983. *Principles of Underwater Sound*. McGraw Hill, New York, USA. 423pp.

Verboom, W.C. and Kastelein, R.A. 1995. Acoustic signals by harbour porpoises (*Phocoena phocoena*). pp.1-39. *In*: Nachtigall, P.E., Lien, J., Au, W.W.L. and Read, A.J. (eds). *Harbour Porpoises – Laboratory Studies to Reduce Bycatch*. De Spil Publishers, Woerden, The Netherlands. 168pp.

Verboom, W.C. and Kastelein, R.A. 1997. Structure of harbour porpoise (*Phocoena phocoena*) click train signals. pp.343-63. *In*: Read, A.J., Wiepkema, P.R. and Nachtigall, P.E. (eds). *The Biology of the Harbour Porpoise*. De Spil Publishers, Woerden, The Netherlands.

Verfuss, U.K., Miller, L.A. and Schnitzier, H.U. 2005. Spatial orientation in echolocating harbour porpoises (*Phocoena phocoena*). *J. Exp. Biol.* 208: 3385-94.

Villadsgaard, A., Wahlberg, M. and Tougaard, J. 2007. Echolocation signals of wild harbour porpoises, *Phocoena phocoena*. *J. Exp. Biol.* 210: 56-64.

Watkins, W.A. 1967. The harmonic interval: fact or artifact in spectral analysis of pulse trains. *Mar. Bioacoust.* 2: 15-43.

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Seasonal abundance and distribution patterns of common bottlenose dolphins (*Tursiops truncatus*) near St. Joseph Bay, Florida, USA

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ABSTRACT

Three unusual mortalities events involving bottlenose dolphins (*Tursiops truncatus* Montagu 1821) occurred along Florida's northern Gulf of Mexico coast between 1999 and 2006. The causes of these events, in which over 300 bottlenose dolphins are known to have died, are still under investigation. The impact of these mortality events cannot be fully evaluated, because little prior information on bottlenose dolphin abundance and distribution patterns exist in this region. Thus, the goals of this study were to estimate seasonal abundance, develop site-fidelity indices, and describe distribution patterns of bottlenose dolphins in St. Joseph Bay, Gulf County, Florida, USA. This study site was chosen because it was impacted by all three unusual mortality events and was the geographic focus of the 2004 event. Mark-recapture photo-identification surveys were conducted across multiple seasons from February 2005 through July 2007. Site-fidelity indices were calculated for each identifiable dolphin based upon all photo-ID efforts undertaken in the area. Distribution patterns were investigated by short-term (12-94 days) radio-tracking of tagged individuals across seasons (April-July, n=9; July-October, n=15). Mark-recapture closed and robust abundance estimates, as well as site-fidelity indices suggest that St. Joseph Bay supports a resident community of 78-152 bottlenose dolphins. During spring and autumn, this region experiences an influx of dolphins, as demonstrated by closed and robust abundance estimates of 313-410 and 237-340, respectively. These results are supported by the distribution patterns of radio-tagged individuals. Individuals tagged in summer tended to stay within or near St. Joseph Bay, whereas two individuals tagged in spring ranged more than 40km from the study site. This study provides the first detailed examination of bottlenose dolphin abundance and distribution patterns for this region of the northern Gulf coast of Florida. These results suggest that unusual mortality events probably had, and will in the future have, seasonally variable effects on bottlenose dolphins in St. Joseph Bay. Future mortality events that occur during the summer and winter in St. Joseph Bay may predominantly affect resident individuals, while those that occur during the spring and autumn will probably affect both residents and seasonal visitors.

KEYWORDS: BOTTLENOSE DOLPHIN; ABUNDANCE ESTIMATE; MARK-RECAPTURE; SITE- FIDELITY; PHOTO-ID; RADIO-TAGGING; NORTH AMERICA

INTRODUCTION

Our ability to assess the impacts of natural and anthropogenic catastrophic events on populations of bottlenose dolphins, *Tursiops truncatus* Montagu (1821), suffers from a general lack of baseline information on stock structure and abundance in many areas (McLellan *et al*., 2002; Wells *et al*., 2004). For example, between 1999 and 2006 along Florida's northern Gulf of Mexico coast, bottlenose dolphins experienced three large scale mortality events, resulting in over 300 bottlenose dolphin deaths (NMFS, 2004; Waring *et al*., 2007). These events were defined as 'Unusual Mortality Events' (UMEs) because of their distinct dissimilarity to normal stranding patterns in this region (1972 Marine Mammal Protection Act + 1992 Amendments). Although the causes of these events are still under investigation, they may have been spatially and temporally correlated with blooms of *Karenia brevis*, the dinoflagellate known to cause red tide harmful algal blooms (HABS) in Florida (NMFS, 2004). However, the impact of these UMEs cannot be fully evaluated because the structure and size of bottlenose dolphin stocks in the northern Gulf of Mexico are not well understood (Waring *et al*., 2007).

In the United States, all marine mammals are protected under the Marine Mammal Protection Act (MMPA), which is jointly administered by the National Marine Fisheries Service under the National Oceanic and Atmospheric Administration (NOAA Fisheries Service), and the United States Fish and Wildlife Service. Specifically for bottlenose dolphins, stock assessments are conducted and conservation plans are implemented as necessary by NOAA Fisheries Service. Currently, stocks of bottlenose dolphins that inhabit each bay and estuary in the northern Gulf region are defined and managed as separate estuarine communities, largely based on geographical features rather than on empirical data on ranging patterns or genetics (Waring *et al*., 2007). A community is a group of resident animals that share home ranges, display similar genetic features, and interact more frequently with each other than with dolphins in adjacent waters (Wells *et al*., 1987). In addition, NOAA identifies eastern, northern, and western stocks of coastal bottlenose dolphins within the Gulf of Mexico (Waring *et al*., 2007). The coastal waters are defined as shoreline and bay boundaries to the 20m isobath (Waring *et al*., 2007). Thus, there is potential geographic overlap of coastal and estuarine bottlenose dolphins.

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Long-term resident communities of bottlenose dolphins, as well as dolphin groups that display seasonal movements have been identified along the Texas coastline (Bräger, 1993; Fertl, 1994; Gruber, 1981; Irwin and Würsig, 2004; Lynn and Würsig, 2002; Maze and Würsig, 1999; Shane, 1977; Weller, 1998) and within Mississippi Sound (Hubard *et al*., 2004). Relatively stable, long-term resident communities of bottlenose dolphins have also been identified in Sarasota Bay, Florida (Irvine *et al*., 1981; Wells, 1986; Wells *et al*., 1987) and in the adjacent large estuaries of Charlotte Harbor (Wells *et al*., 1997) and Tampa Bay (Wells, 1986). Long range movements of coastal bottlenose dolphins have been observed in the 'western' Gulf stock, along the coast of Texas (Beier, 2001; Lynn and Würsig, 2002). Both 'eastern' coastal and estuarine bottlenose dolphin stocks have been identified within the coastal waters of Tampa Bay, Sarasota Bay, and Charlotte Harbour (Fazioli *et al*., 2006). Currently, community structure and seasonal movements of bottlenose dolphins along the northern Gulf coast of Florida are unknown.

Identifying stocks, estimating the number of individuals belonging to those stocks, and determining individuals' distribution patterns are necessary steps for establishing effective management plans (Macdonald *et al*., 1979; Taylor and Gerrodette, 1993; Westgate and Read, 1998). Systematic surveys and mark-recapture methods utilising photographically-identified individuals have yielded insights into patterns of bottlenose dolphin abundance and site-fidelity in other geographic regions (e.g. Barco *et al*., 1999; Maze and Würsig, 1999; Read *et al*., 2003; Seber, 1982; Shane, 1980; 1990a; 1990b; Torres *et al*., 2005; Wells, 1986; Wells, 1994; Williams *et al*., 1993; Wilson *et al*., 1999; Würsig and Würsig, 1977). Radio-tracking of individuals has provided insight into cetacean short-term distribution patterns (e.g. Evans, 1971; Perrin, 1975; Leatherwood and Evans, 1979; Norris and Dohl, 1980; Irvine *et al*. 1981; Read and Gaskin, 1985; Watkins *et al*. 1999).

The goals of this study were to utilise mark-recapture photo-identification (ID) surveys and radio-tracking of individuals to provide baseline data on the abundance and distribution patterns of bottlenose dolphins in St. Joseph Bay, Gulf County, Florida, USA. This study site was chosen because it was impacted by all three UMEs, and was the geographic focus of the 2004 mortality event. These techniques were used to: (1) provide accurate, seasonal estimates of bottlenose dolphin abundance in the St. Joseph Bay region; (2) identify the level of site-fidelity expressed by individual animals on a seasonal and interannual scale; and (3) determine distribution patterns of individuals across seasons. Photo-ID surveys were conducted over three years to generate seasonal abundance estimates. Multiple, independent photo-ID surveys of dolphins in the St. Joseph Bay region were used to calculate site-fidelity indices. Radio-tracking of individual bottlenose dolphins near St. Joseph Bay was used to identify distribution patterns across two seasonal transitions.

METHODS

Mark-recapture photo-identification surveys

The mark-recapture survey area included the Gulf of Mexico waters from Cape San Blas northwest to and including Crooked Island Sound and St. Joseph Bay (Fig. 1). The survey design used both line and contour transects to cover the entire region (Fig. 1). St. Joseph Bay was divided into 18 east-west line transects, spaced 1km apart. In regions where water depth was less than 1m (i.e. southern St. Joseph Bay and Crooked Island Sound), contour transects along the 1m isobath were used to survey the area. Contour transects are line transects that follow a particular geographic feature such as bathymetry or coastline. Contour transects that followed the coastline were used to cover the Gulf regions, extending from Cape San Blas northwest to the entrance of Crooked Island Sound, at distances of 0.5km and 1.5km from shore. Transects were followed with the assistance of a GPS unit.

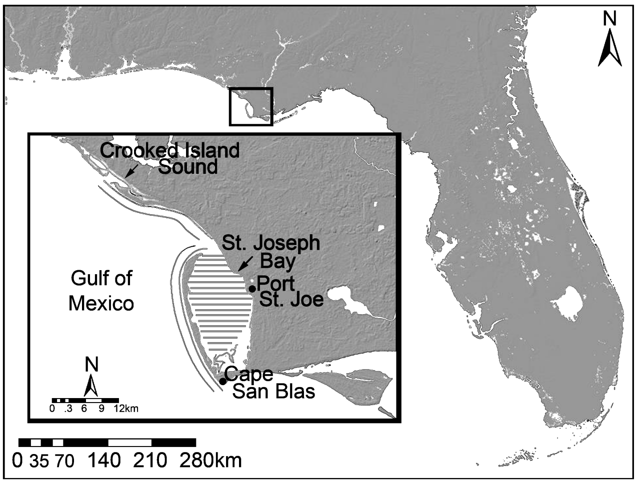

Fig. 1. St. Joseph Bay mark-recapture photo-ID survey region, including survey track lines.

Mark-recapture surveys were conducted across multiple seasons, including February/March, April, May and July 2005; February and September/October 2006 and June/July 2007. All transects were covered in a Beaufort Sea State of 3 or less for each survey, but the order of coverage was determined by random selection. All transects were also completed in as short a period of time as possible to meet the assumption of a closed population. Each mark-recapture survey was completed on average in 4.1 ±0.8 SD days, and the mark and recapture periods were separated by 1.2 ± 0.4 SD days on average.

A sighting was recorded when any dolphin was encountered. The total number of animals, numbers of calves including young-of-the-year and environmental data including salinity, water temperature, cloud cover, Beaufort Sea State, depth and geographic location were recorded for each sighting. Digital photographs were obtained of all individuals using a Nikon D-100 camera with 70-300m lens and downloaded onto a laptop computer in the lab. Dorsal fin images were cropped (*ACDSee* 7.0, ACD Systems, British Columbia, Canada) and graded on both distinctiveness of the dorsal fin and photographic quality, following the methods of Urian *et al.* (1999) and reviewed in Read *et al.* (2003) and Wilson *et al.* (1999). The distinctiveness rating (D1-D3) focused primarily on the notches along the trailing edge of the dorsal fin. Dolphins were given a D1 rating if their fin features were distinctive and most were still observable even in poor quality photos. A D2 rating was given to individuals with intermediate features (at least two distinguishing fin characteristics). D3 animals were those with few to no distinguishing characteristics. The photographic quality rating (Q1-Q3) focused on clarity, contrast, and angle of the fin to the photographer. A Q1 rating was given to a dorsal fin picture that was in perfect focus and that filled the entire field of the image. A Q2 rating was given when the image was still sharply focused but the fin occupied a smaller portion of the image. Q3 photos were those in which only a portion of a fin was included in the image or when the fin was not in sufficient focus. Two judges scored each image, one graded distinctiveness (BCB) and the other graded quality (SMN).

Using the quality and distinctive grades for images, a catalogue of fins was compiled (e.g. Urian *et al*., 1999). Q1-D1 and Q1-D2 photos were automatically added to the catalogue. Q2-D1 and Q2-D2 fins were not added until the fin was sighted twice, which ensured that lesser quality images were not added to the catalogue until they were proved matchable. Q3 images were not used for analysis. D3 images were used to help clarify the number of non-distinctive or clean individuals in a sighting.

In this study, a mark was considered a photograph of an individual dolphin's dorsal fin (Read *et al*., 2003; Urian *et al*., 1999; Wells *et al*., 1996; Williams *et al*., 1993; Wilson *et al*., 1999). A ratio of distinctive to non-distinctive ('clean') dolphins photographed in every sighting was calculated to estimate the proportion of marked versus unmarked animals during each survey season. This ratio is referred to as the distinctiveness rate.

Mark-recapture data analysis

When photographic mark-recapture methods are used to study bottlenose dolphin populations, the four assumptions of the closed, mark-recapture model (Seber, 1982) can be reasonably met if the sampling period is short, marks are not lost on recapture, and full survey coverage of the area allows for capture homogeneity (Read *et al*., 2003). The applicability of these assumptions was reviewed in Read *et al*. (2003) in their study of bottlenose dolphin abundance along North Carolina estuaries.

There are a number of closed and robust models that can be used to estimate population abundance (Thompson *et al*., 1998). The Chapman modification of the Lincoln-Petersen model, which assumptions require that of a closed population, was first applied to the data gathered during this study (Chapman, 1951). The data were then analysed using nine different closed and robust models that relaxed one or more of the closed population assumptions in the computer programs *MARK* and *CAPTURE* (Rexstad and Burnham, 1992; White *et al*., 1982). Model suitability was determined by having: (1) the lowest Akaike's Information Criterion (AIC) values (Burnham and Anderson, 1992); and (2) model parameters thought to be most representative of bottlenose dolphins along the northern Gulf coast of Florida (i.e. capture probabilities varying over time during and between survey periods, see results below). The two models that best fitted these requirements were the closed model (M_{th}) (Burnham and Overton, 1978; 1979; Darroch, 1958) and the robust 'Markovian Emigration' model (M_t) (Kendall *et al*., 1997).

The first model selected was the Chapman modification of the Lincoln-Petersen model (Chapman, 1951; Seber, 1982; Thompson *et al*., 1998). For each survey period, the sighting histories for all individuals were divided into two separate sampling occasions, the mark (n_1) and the recapture (n_2), where (n) equals the number of individuals identified during each sampling period. The total number of individuals seen during both mark and recapture equals (m_2). The abundance estimate (N_c), variance (var N_c), and standard error (SE) of the Chapman modification to the Lincoln-Petersen model were calculated as (Chapman, 1951):

$$N_c = \frac{(n_1+1)(n_2+1)}{(m_2+1)} - 1 \tag{1}$$

$$\text{var}\, N_c = \frac{(n_1+1)(n_2+1)(n_1-m_2)(n_2-m2)}{(m_2+1)^2(m_2+2)} \tag{2}$$

$$\text{SE} = \sqrt{\text{var}\, N_c} \tag{3}$$

The closed population model M_{th} was used because it allows animals to have different capture probabilities due to demographic variations, such as age or sex (model M_{h}) and it permits capture probabilities to vary by sample period (model M_{t}) (Burnham and Overton, 1978; 1979; Darroch, 1958; reviewed in Otis *et al*., 1978). This model is useful because it generates an abundance estimate while relaxing the assumption that all animals have equal capture probabilities. However, as the number of assumptions is reduced, variance in abundance estimates is increased (Thompson *et al*., 1998).

The robust design model (Pollock, 1982) uses characteristics of closed population abundance estimates and open population survival/emigration estimates (Kendall *et al*., 1997; reviewed in Pine *et al*., 2003; Pollock, 1982; Thompson *et al*., 1998). This approach permits abundance estimates to be determined during multiple, short term periods within a closed population model (M_{t}) and uses the Jolly-Seber open population model to estimate survivorship, emigration rates, and capture-recapture probabilities between the short term survey periods (reviewed in Pine *et al*., 2003; Pollock, 1982). The robust design model selected for this study was the 'Markovian Emigration' model, which permits unequal emigration and immigration rates across survey periods (Kendall *et al*., 1997). This model assumes that an animal 'remembers' that is has left the study area, and returns based on a time-dependent function (reviewed in Pine *et al*., 2003).

Abundance estimates from the closed (M_{th}) and robust 'Markovian Emigration' population models were based solely on the number of distinctive animals sighted during a survey period. The total population size (distinctive and non-distinctive individuals) was estimated as:

$$\tilde{N}_{\text{total}} = \tilde{N} / \Theta \tag{4}$$

where $\tilde{N}_{\text{total}}$=estimated total population size, $\tilde{N}$=mark-recapture estimate of distinctive individuals, and Θ=estimated proportion of distinctive individuals in each survey period (Read *et al*., 2003; Wilson *et al*., 1999).

Photo-identification site-fidelity indices

All photo-ID efforts within the survey region were used to calculate site-fidelity indices. These efforts began in April 2004, with a preliminary study to obtain genetic samples through biopsy darting. All photo-ID effort thus included the mark-recapture surveys, biopsy sampling, and radio tracking (see methods below). These efforts totalled 145 days over 15 months from April 2004 through July 2007.

To define a site-fidelity index for individual dolphins in the St. Joseph Bay region, the total number of sightings of each catalogued animal was determined. Then, for each mark-recapture photo-ID survey period, each observed individual was placed into one of five bins, based upon the total number of times it was sighted. The optimum bin size for each survey period was determined as:

$$BINSIZE = \frac{2*(IQR)}{\sqrt[3]{n}} \qquad (5)$$

where IQR=the interquartile range of the number of sightings, and n=the total number of animals sighted. This estimator has been found to generate histograms that reliably represent the underlying density distribution of the data (Freedman and Diaconis, 1981). In this study, for each survey period, bin sizes were determined to be: (1) 1-8 sightings; (2) 9-17 sightings; (3) 18-26 sightings; (4) 27-35 sightings; and (5) 36 or greater sightings. These bins were used as the site fidelity index. A single factor analysis of variance (ANOVA) was used to test for differences in site-fidelity indices among seasons.

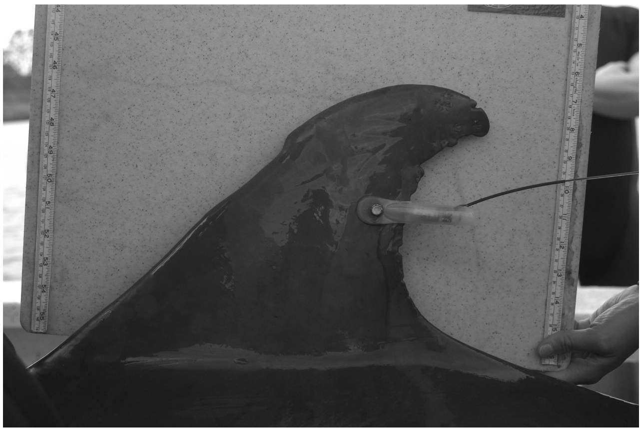

Fig. 2. Photograph of the dorsal fin of a temporarily captured and released bottlenose dolphin with radio transmitter mounted within bullet tag (Photo by S. Hofmann).

Distribution patterns of radio-tagged individuals

In April 2005 and July 2006, NOAA in collaboration with Chicago Zoological Society's Sarasota Dolphin Research Program and other partners, conducted bottlenose dolphin health assessment studies in the St. Joseph Bay region. The two goals of these studies were to: (1) carry out a detailed health examination of surviving bottlenose dolphins from the area impacted by the UMEs; and (2) deploy radio transmitters on bottlenose dolphins to obtain information on short-term movements. Only data from the second goal are presented here. Bottlenose dolphins in and around St. Joseph Bay, Florida were temporarily captured and restrained using practices similar to those implemented by the Sarasota Dolphin Research Program (Wells *et al*., 2004). Each individual was freeze-branded on the dorsal fin and/or body with a letter ('X') and two digit number ('01, 02, 03' etc.). Even numbers were given to males and odd numbers to females.

Twenty-three individuals across both health assessments were fitted with radio transmitters; one of these individuals was tagged in both years (April-July, n=9; July-October, n=15). The VHF radio transmitter (MM130, Backmount Transmitter, Advanced Telemetry Systems, Inc., Isanti, MN) was mounted in a modified plastic casing with a one-hole attachment, known as a bullet tag (Trac Pac, Ft. Walton Beach, FL). Prior to tag attachment, the dorsal fin was cleaned with ethanol and a chlorohexiderm scrub, and at the tag attachment point, a local anaesthetic (lidocaine 2% with epinephrine) was administered. The hole for tag attachment was made near the dorsal fin's trailing edge using a sterile 5mm biopsy punch. The tag was attached to the dorsal fin using a ¼" Delrin pin, threaded for ½" on each end, with non-stainless steel (corrodible) nuts on each side of the dorsal fin (Fig. 2). The VHF transmitters were tested prior to the health monitoring events and at sea level had a range of approximately 7-8km. The VHF transmitters were received over a 15km distance from an aircraft.

Radio-tracking was conducted using vessel, vehicle, and/or plane with the highest priority of visually locating each radio tagged dolphin daily (Fig. 3). Vessel tracking covered approximately 90km of coastline daily. When weather conditions were too poor to track by vessel (Beaufort Sea State >3), animal locations were triangulated from a land-based vehicle which covered approximately 150km of coastline per day. Since there were no prior data on dolphin movement patterns in this region, it was important to ascertain if individuals were leaving the areas covered by vessel or vehicle. Six aerial surveys covering over 270km per day were flown during the 2005 tracking period in a Cessna O-2A 'Skymaster'. To cover both estuarine and coastal waters, the aircraft stayed approximately 2km offshore of the coastline.

Radio-tracking of individuals ceased due to one of three conditions: the animal was sighted without its radio tag; the animal was sighted with its radio tag but the tag was not transmitting; or weather/logistical constraints did not permit continued tracking. During the 2005 tracking period, numerous hurricanes in the region prevented tracking after day 94. During the 2006 tracking period, only 2 tags remained functional after 75 days. The expense of remaining in the region to wait out the storm season outweighed the benefit of remaining to track the last two animals.

For each individual, the minimum number of tag transmission days was calculated. Ideally, this number was obtained by sighting an individual either without its radio tag attached, or with the radio tag still attached but non-functional, the day after a sighting of that animal with a functional tag. However, in most cases an individual was not observed the day after the last known transmission date. For these individuals an estimated final transmission date was calculated by counting the number of days between the last sighting with a functional tag and first sighting without a functional tag and dividing by two.

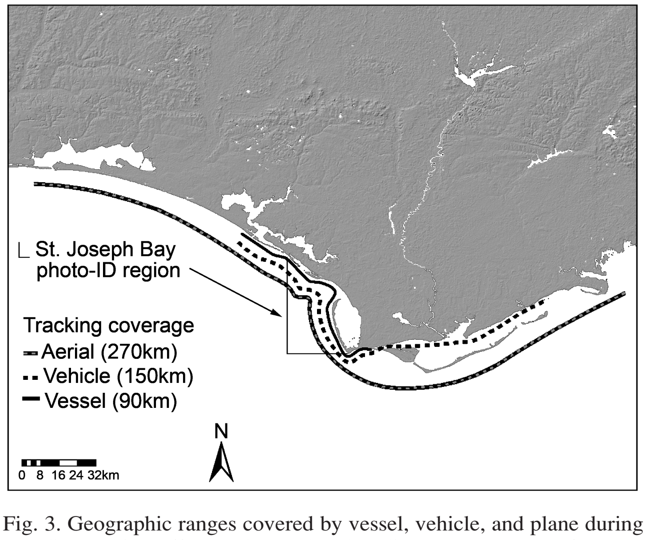

Fig. 3. Geographic ranges covered by vessel, vehicle, and plane during radio-tracking efforts. The 'L' bracket displays the range of the St. Joseph Bay photo-ID region.

Locations for all radio-tagged individuals were determined by visual identification via vessel, triangulation from shore, or maximum signal strength via aerial tracking. All locations for each individual were plotted in *ArcMap* 9.2 (ESRI, Redlands, CA). The distribution pattern of a radio-tagged dolphin was defined as the maximum distance travelled along a shoreline between its farthest northwest and southeast tracking locations during each radio-tracking period. This linear method was selected over conventional home range analyses because it is a more conservative description of an individual's movement patterns and it better describes the study's temporal conditions and the nature of the animals' movements. The dolphins moved through a very narrow strip of coastline, such that measures of area are not as meaningful as linear measurements of range. In this study, the radio tracking was short-term (maximally 94 days; range 11-94 days) and although aerial and vehicle tracking extended the tracking coverage, complete distribution patterns may not have been obtained. Home range, the area that an individual conducts its normal activities such as resting, foraging, mating, and caring for young, is a term that has been applied to periods of time that encompass a greater percentage of an individual's life (Burt, 1943).

RESULTS

Mark-recapture abundance estimates

From April 2004 through July 2007, 313 individual bottlenose dolphins were identified in the St. Joseph Bay study region. The discovery curve of new individuals increased steeply until May 2005 and much more gradually thereafter (Fig. 4). The largest number of identifiable individuals was sighted in May 2005, including 129 previously identified and 73 newly identified individuals.

The number of identifiable dolphins directly counted during a photo-ID survey ranged from 45 to 202 (Table 1). The mean rate of distinctiveness across all seasons was 0.79±0.09 SD. The number of identifiable individuals was divided by the distinctiveness rate to estimate the total number of individuals (marked and unmarked) observed during each survey period (Table 1).

Closed population models (Lincoln-Petersen and M_{th}) were used to estimate dolphin abundance during each survey period (Fig. 5). Both models, respectively, estimated the highest abundances in May 2005 (313, 410) followed closely by April 2005 (240, 282) and September/October 2006 (237, 337). The lowest abundances occurred in June/July 2007 (84, 78), July 2005 (104, 105) and February 2006 (113, 105). The robust 'Markovian Emigration' model also estimated dolphin abundance to be highest in spring and autumn and lowest in summer and winter (Fig. 5). The lowest abundance estimates for the robust model were February 2006 (122) followed by July 2005 (131).

Photo-identification site-fidelity

For each survey period, each identified individual was placed into one of five sighting bins (i.e. site-fidelity indices) representing the total number of times that individual was sighted across all photo-ID efforts. To determine whether site-fidelity indices varied among seasons, histograms were plotted for each season using corresponding survey periods; spring (May 2005), summer (June/July 2007), autumn (September/October 2006) and winter (February 2006) (Figs 6a-6d). During May 2005 and September/October 2006, greater than 50% of the individuals were sighted only 1-8 times. In contrast, during June/July 2007 and February 2006, over 50% of the individuals were sighted 9-26 times. Site-fidelity indices differed significantly across seasons in the St. Joseph Bay region (*df*=3, *p*=1.62E-08, *F* =13.83).

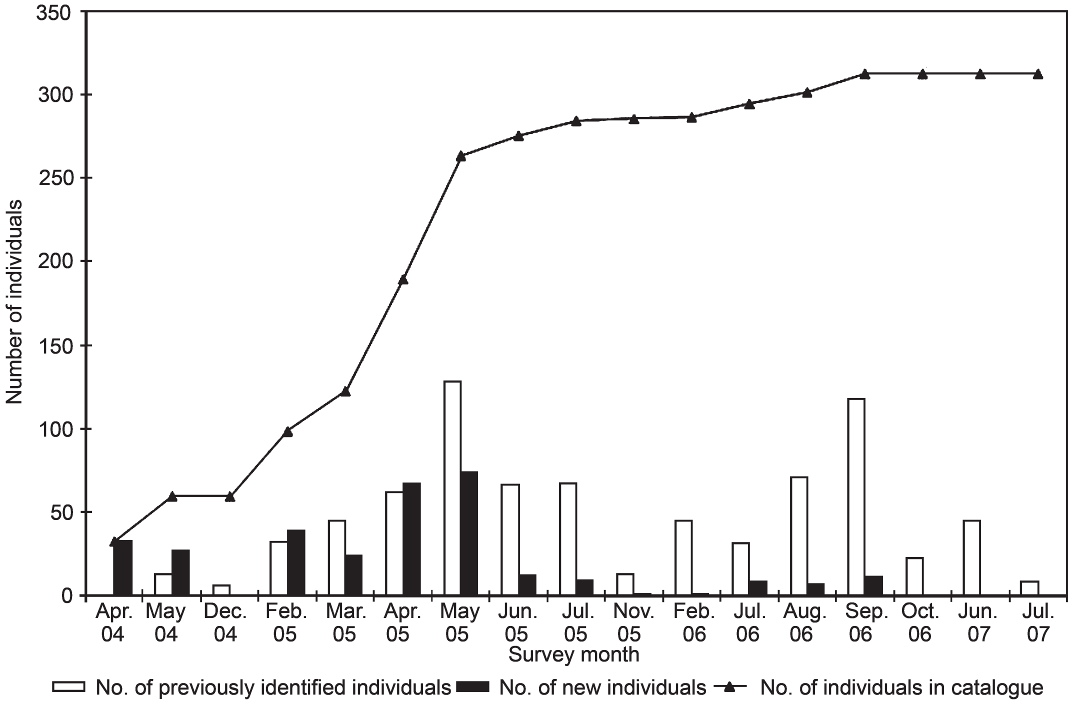

Fig. 4. Number of individuals sighted during all photo-ID efforts and discovery curve for bottlenose dolphins in the St. Joseph Bay region.

Table 1

Number of identified individuals sighted, distinctiveness rate, and estimate of total number of dolphins present during each mark-recapture survey season from photo-identification counts.

Field season	Feb./Mar 2005	Apr. 2005	May 2005	Jul. 2005	Feb. 2006	Sep./Oct. 2006	Jun./Jul. 2007
Number of identified (distinctively marked) dolphins sighted	122	144	202	83	47	176	45
Mark/distinctiveness rate	0.88	0.79	0.85	0.85	0.68	0.84	0.67
Estimate of total marked + unmarked dolphins	139	183	238	98	69	210	70

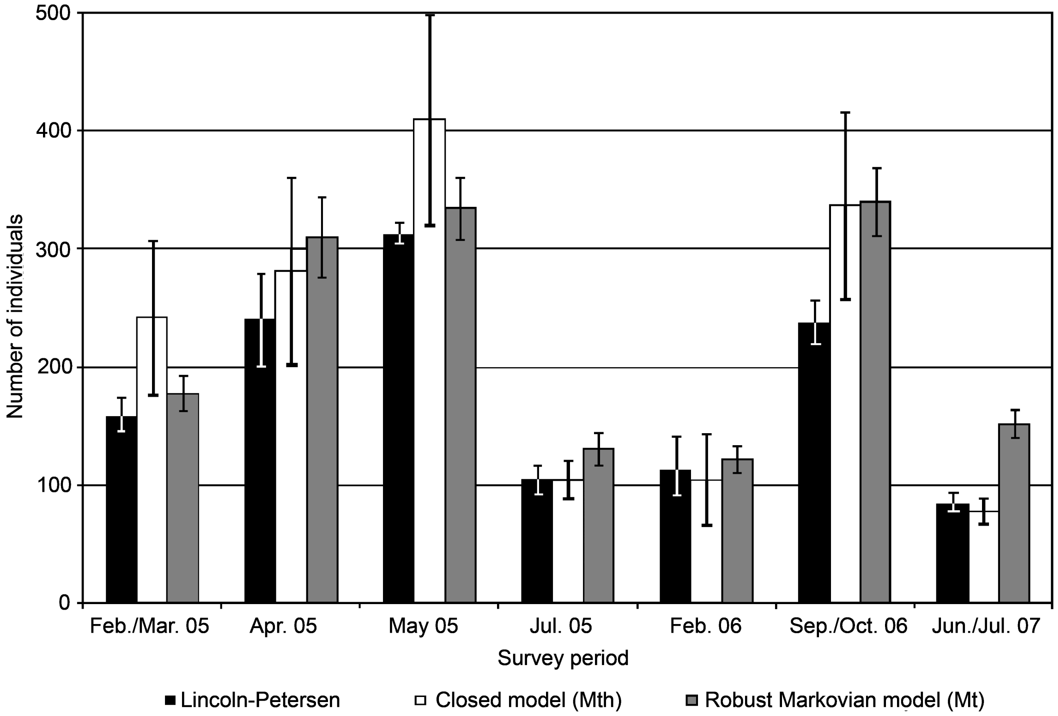

Fig. 5. Population size (± S.E.) estimated using closed (Lincoln-Petersen, M_{th}) and robust (Markovian Emigration) models for each survey period.

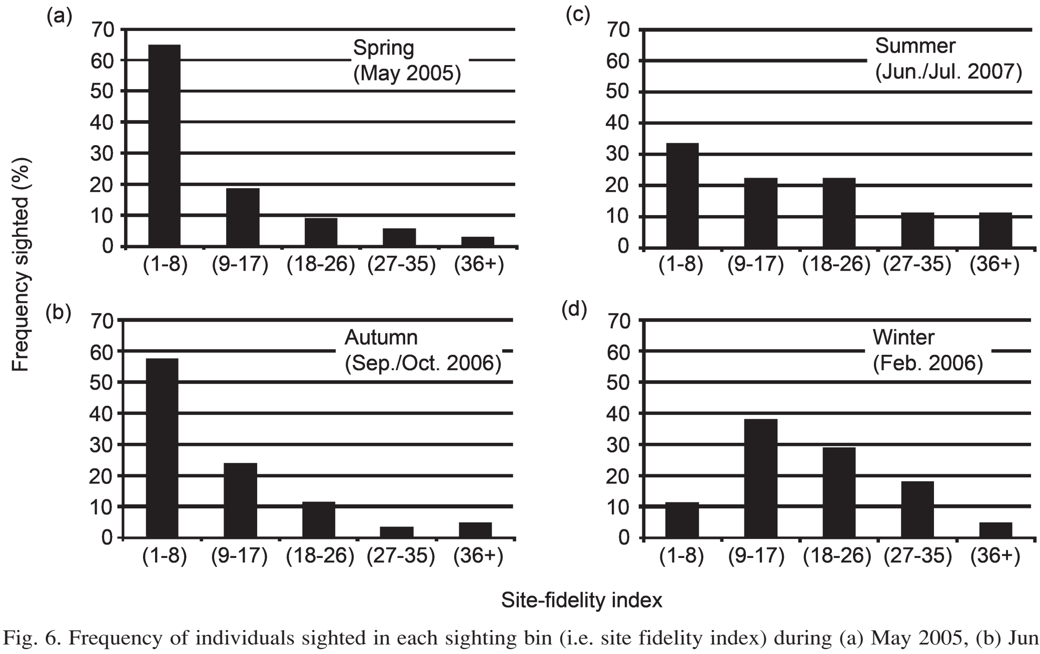

Fig. 6. Frequency of individuals sighted in each sighting bin (i.e. site fidelity index) during (a) May 2005, (b) June/July 2007, (c) September/October 2006 and (d) February 2006.

Distribution patterns

Twenty-three individual dolphins, eleven females (one female was tagged in both years) and twelve males, were radio-tagged during 2005 April 18-28 and 2006 July 17-28 (Table 2). In 2005, the average number of tag transmission days and number of fixed locations were higher than in 2006 (Table 2), but individuals with longer transmission periods and more fixed locations did not necessarily have larger distributional ranges.

In 2005, when tagging occurred in spring, two of the tagged dolphins (X09 and X13) travelled over 70km from their capture locations, and were infrequently seen within the survey region after their initial capture date (Fig. 7a). Two other individuals (X03and X08) had ranges that partially included the St. Joseph Bay photo-ID survey region (Fig. 7b). In contrast, dolphins X04 and X05 displayed relatively small maximal distances travelled and their ranges were completely within the St. Joseph Bay photo-ID survey region (Fig. 7c). In 2006, when tagging occurred in summer, only two dolphins (X23 and X29), ranged outside of the St. Joseph Bay photo-ID region but even these two were seen routinely within this area (Fig. 8a). The other eleven tagged dolphins were always located within the St. Joseph Bay survey region (Fig. 8b).

Five radio tagged individuals [X01, X02, and X11 (2005); X15 and X18 (2006)] were excluded from the radio tracking results described above. Dolphins X01 and X02 were exclusively observed begging for food from vessels in a small area just outside of the St. Joseph Bay region and all of their sightings during the radio-tracking period were restricted to this region. Because these individuals' distributions appeared to be strongly influenced by human activity, they were excluded from the analysis. Dolphin X11, an adult female, was radio tracked for 21 days before tag transmission ceased. During this period, her body condition deteriorated rapidly, she developed widespread skin lesions and her surfacings became progressively more lethargic. Because of this individual's decline in health, and eventual disappearance from the broader survey region, her tracking record was considered anomalous and was excluded. In 2006, dolphin X15 was resighted once post-capture, and dolphin X18 was monitored for only eight days post-capture, until tag transmissions ceased. For these reasons there were insufficient data to include dolphins X15 and X18 in the general analyses.

DISCUSSION

The goals of this study were to estimate bottlenose dolphin abundance, identify site-fidelity indices, and determine distribution patterns across seasons in a geographic region recently affected by several Unusual Mortality Events. Irrespective of how they were estimated, whether from direct counts of dolphins from photo-ID surveys, or from closed or robust population models, dolphin abundance varied across survey periods (Fig. 5). Abundance estimates increased between February/March 2005 and May 2005 survey periods. Between May and July 2005, abundance estimates decreased, and were low in February 2006 as well as June/July 2007. Abundance estimates were elevated again during September/October 2006. These data strongly suggest that in spring and autumn there is a movement of dolphins into the St. Joseph Bay region. These seasonally variable abundance estimates are similar to patterns seen for coastal bottlenose dolphins in other study sites within the western (Bräger, 1993; Fertl, 1994; Henningsen, 1991) and northern (Hubard *et al*., 2004) Gulf of Mexico.

Abundance estimates determined from the robust 'Markovian Emigration' model yielded seasonal patterns of abundance estimates similar to those of the closed population models (Fig. 5). Because this model allows for immigration and emigration rates to vary between survey periods, and for heterogeneity in capture probabilities within survey periods, the robust 'Markovian Emigration' model appears to best represent dolphin abundance in the St. Joseph Bay region. The radio-tracking results support this conclusion, because while some individuals (e.g. X05) were located consistently within the St. Joseph Bay region for the

Table 2

Tracking summaries for individual dolphins radio-tagged during 2005 and 2006. Linear distance of coastline represents maximum distance travelled along a shoreline between an individual's farthest northwest and southeast tracking locations.

Dolphin	Sex	Radio tagging date	Date of last radio signal	Min. no. days transmitting	No. of fixed locations	Linear distance of coastline (km)
2005						
X04	M	19 Apr.	08 Jul.	83	52	43
X03	F	20 Apr.	03 May	14	7	38
X05	F	20 Apr.	17 Jul.	91	44	42
X08	M	25 Apr.	25 Jul.	94	45	57
X09	F	25 Apr.	05 Jul.	74	23	105
X13	F	28 Apr.	05 Jul.	69	5	68
			Mean ± S.D.:	**71 ± 29**	**29 ± 21**	**59 ± 25**
2006						
X05	F	19 Jul.	17 Sep.	61	34	44
X10	M	19 Jul.	18 Aug.	30	26	44
X12	M	19 Jul.	02 Aug.	15	15	44
X06	M	20 Jul.	30 Jul.	11	11	44
X14	M	20 Jul.	10 Aug.	22	16	24
X16	M	20 Jul.	05 Aug.	17	14	12
X23	F	21 Jul.	01 Aug.	12	12	56
X25	F	25 Jul.	01 Oct.	75	37	50
X27	F	25 Jul.	01 Oct.	75	37	50
X20	M	27 Jul.	17 Sep.	61	23	53
X22	M	28 Jul.	01 Oct.	75	37	15
X24	M	28 Jul.	27 Aug.	29	10	43
X29	F	28 Jul.	26 Aug.	30	17	51
			Mean ± S.D.:	**35 ± 27**	**22 ± 11**	**40 ± 14**

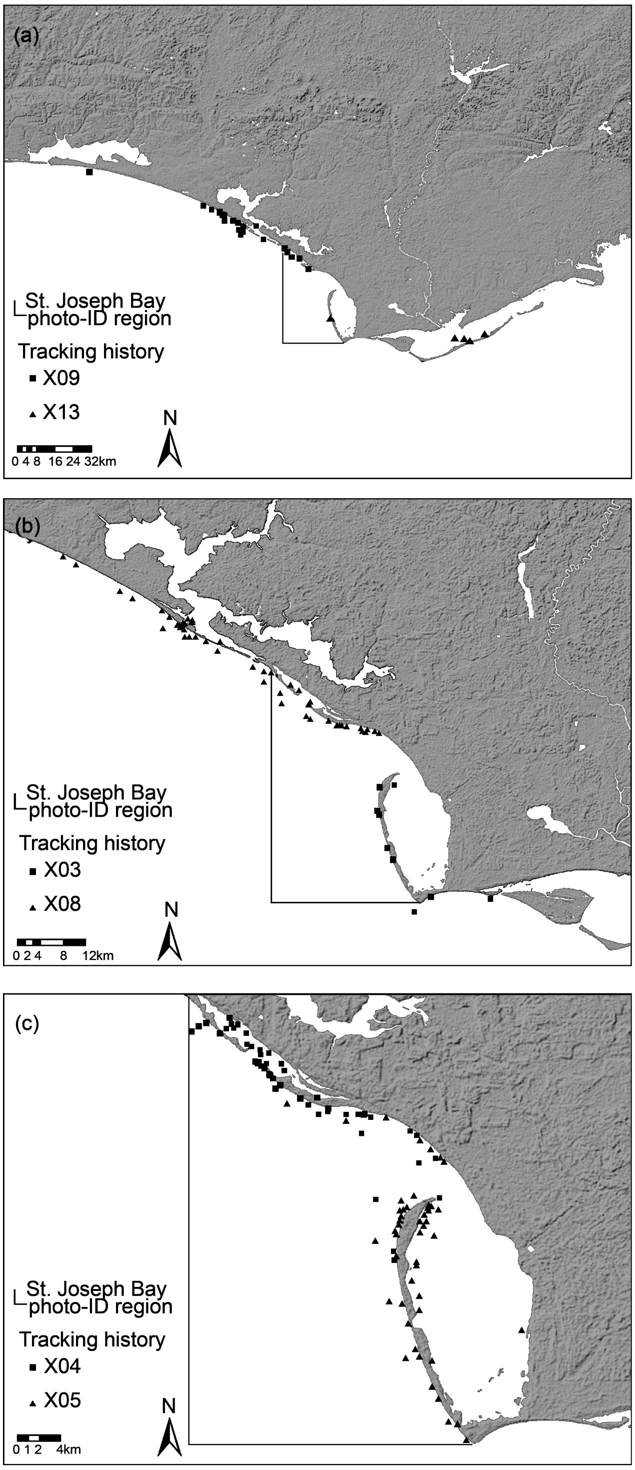

Fig. 7. Fixed locations of individually radio-tagged dolphins, during April-July 2005, whose distributions (a) extended outside, (b) partially overlapped, or (c) were completely within the St. Joseph Bay photo-ID region. The 'L' bracket displays the range of the St. Joseph Bay photo-ID region.

entirety of the study, other individuals (e.g. X09 and X13) clearly moved away from the region, and thus violated the assumptions of a closed population.

Individual sighting history data, which are temporally correlated with the abundance estimates, provide insight into site-fidelity patterns in the St. Joseph Bay region. In spring, when dolphin abundance estimates were highest, the percentage of individuals with the lowest site-fidelity index (1-8 sightings) was also highest (Fig. 6a). In contrast, in winter and summer, when abundance estimates were lowest, the majority of individuals sighted were those with moderate (9-17 sightings) to high (18-26 sightings) site-fidelity indices (Figs 6b and 6d). During autumn, the percentage of individuals with the lowest site-fidelity index (1-8 sightings) was again elevated as overall abundance within the survey region increased (Fig. 6c). These results suggest that during spring and autumn, when dolphin abundances are highest, the majority of dolphins sighted are visitors to the St. Joseph Bay region. In contrast, bottlenose dolphins seen in the winter and summer months are more likely to be sighted year-round.

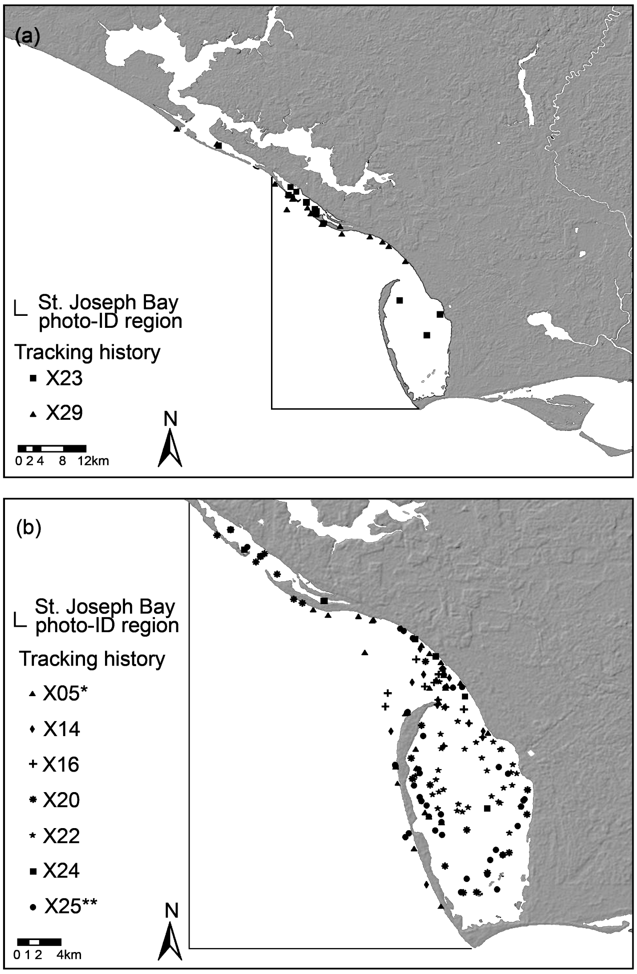

Fig. 8. Fixed locations of individually radio-tagged dolphins, during July-October 2006, whose distributions (a) partially overlapped, or (c) were completely within the St. Joseph Bay photo-ID region. The 'L' bracket displays the range of the St. Joseph Bay photo-ID region. *X05, X06, X10, and X12 had identical distribution patterns; **X25 and X27 had identical distribution patterns (X27 was a dependent calf of X25).

These combined results would predict that at least some individuals radio-tagged in spring may have different movement patterns than those radio-tagged in summer, and this was indeed the case. Two individuals (X09 and X13) tagged in April 2005, ranged the farthest of all radio-tagged dolphins, with ranges extending largely outside of the St. Joseph Bay region. These results suggest that individuals sighted only in spring may have extended movement patterns both to the southeast and northwest of St. Joseph Bay. As would be predicted if there were year-round residents, though, some radio-tagged individuals displayed distributions that were completely within the St. Joseph Bay region (Fig. 7c). X05, a female captured and radio-tagged across seasons, for example, was located only within the focal, photo-ID study region.

In contrast, during July 2006, 11 of 13 radio-tagged individuals were sighted only within the St. Joseph Bay region. The two individuals who were sighted outside the focal study region still had the majority of their sightings (87-91%) within this region. These results suggest many individuals sighted in summer likely remain within the area for the entire season.

Estuarine bottlenose dolphin communities that have been studied in other regions tend to include between 60 and 150 individuals (Hubard *et al*., 2004; Wells, 1991; Williams *et al*., 1993; Wilson *et al*., 1999). The estimated size of the bottlenose dolphin community in Sarasota Bay, Florida, ranges between about 120 and 180 individuals (Wells, 2003, unpublished data). In the St. Joseph Bay region, during winter and summer, when the majority of dolphins display moderate to high site-fidelity indices, the robust 'Markovian' model estimates abundance at between 122 and 152 individuals. These results suggest that individuals sighted during winter and summer months may form a St. Joseph Bay estuarine dolphin community.

Coastal bottlenose dolphin stocks within other regions of the Gulf of Mexico have extended ranges (Beier, 2001; Lynn and Würsig, 2002) as well as geographic overlap with estuarine bottlenose dolphin communities (Fazioli *et al*., 2006). During spring and autumn, abundance estimates in the St. Joseph Bay region are two to three times higher than in summer and winter, and individuals sighted tend to have lower site-fidelity indices. Two individuals (X09, X13) radio-tagged in spring had distribution patterns extending over 70km from their capture locations. These two dolphins moved in opposite directions away from St. Joseph Bay after their initial capture, suggesting that there are likely multiple movement patterns that occur in spring and autumn. Whether this is a normal, long-term pattern for dolphins in this region, or if it is influenced by changes in dolphin abundance and density as a result of a series of UMEs is also unknown.

The data from this study are the first to describe seasonal abundance estimates, site-fidelity indices, and distribution patterns for bottlenose dolphins along Florida's northern Gulf of Mexico coast. The absence of such baseline data, prior to the UMEs, limits our understanding of the impacts of these events on bottlenose dolphins in the region at this time. However, several hypotheses can be generated about their potential impacts based upon the results of this study. The 2004 UME will be the focus of this discussion.

The 2004 UME may have had the greatest local impact on the St. Joseph Bay region, as 70% (75/107) of the mortalities occurred within or just outside St. Joseph Bay (NMFS, 2004). If this mortality event impacted only dolphins from the hypothesised St. Joseph Bay resident estuarine community, it would have reduced this group by at least 33-38%. Thus, in the years following this UME, we would hypothesise that higher birth rates and survivorship would be observed in the St. Joseph Bay dolphins, relative to other stable estuarine communities, as density-dependent responses to losses. In addition, there could be a potential increase in the number of visiting dolphins that are invading or staying within the St. Joseph Bay area. This could be tested through continuation of seasonal, mark-recapture, photo-ID surveys in the St. Joseph Bay region to determine if the changes in abundance, survivorship, and site-fidelity were indicative of a localized UME in the region.

An alternative hypothesis is that the 2004 UME, which occurred during March-April, a time of year when local abundance within the region is high, also affected seasonal visitors (Fig. 5). Thus, resident individuals of the St. Joseph Bay region, seasonal visitors, or both may have been impacted. If true, we would hypothesise a relatively reduced impact on the local St. Joseph Bay population and, perhaps, an elevated impact on the seasonal visitors travelling into the region. Continued short-term radio-tracking, targeting the St. Joseph Bay seasonal visitors, would provide insight into distribution patterns of these individuals. Extended mark-recapture, photo-ID surveys, targeting a broader geographic area along the northern Gulf coast of Florida could provide insights into changes in demographics and abundance of these seasonally transient bottlenose dolphins.

In summary, the results of this study demonstrate that the abundance of bottlenose dolphins in the St. Joseph Bay region varies seasonally. Dolphin abundance increases during the spring and autumn, and the majority of individuals sighted during these periods are those with low site-fidelity. In contrast, during the winter and summer, abundance estimates are lower and individuals demonstrate higher site-fidelity. These results suggest that the St. Joseph Bay region may have a resident community of dolphins (122-152 individuals) as well as seasonal visitors in spring and autumn, which may be part of the 'northern Gulf of Mexico' coastal stock.

NOAA Fisheries Service currently manages bottlenose dolphins along Gulf of Mexico estuaries as individual communities (Waring *et al*., 2007). Coastal bottlenose dolphins are managed as three separate stocks based on geographic location (Waring *et al*., 2007). This study supports the hypothesis of a resident, estuarine community in the St. Joseph Bay region that is seasonally visited by members of a potential coastal migratory stock. Future research is necessary to determine if these findings are consistent across other regions along the northern Gulf coast. It would be valuable, for example, to carry out systematic surveys, similar to the mark-recapture surveys conducted in this study, along other regions of the northern Gulf coast. Such efforts are currently underway in nearby Apalachicola Bay and St. Andrew's Bay (Tyson, 2008); T. Bouveroux, pers. comm. Ongoing analyses of genetic samples from biopsy darting of live individuals as well as samples from stranded animals will also provide additional insight into community/stock structure in the northern Gulf of Mexico, as they have elsewhere (Sellas *et al*., 2005; Torres *et al*., 2003). Continuation of mark-recapture photo-ID surveys in the St. Joseph Bay region is crucial to identify whether the seasonal fluctuations in abundance are an artifact of new animals filling in the gaps left by resident mortality, or a coastal migratory stock travelling through the region. Identifying the direct factors (foraging, reproductive, etc.) that cue seasonal abundance increases in the St. Joseph Bay region would also provide a better understanding of community structure of coastal bottlenose dolphins along the northern Gulf coast. All of these data are required to understand the impacts of future natural and/or anthropogenic catastrophic events on bottlenose dolphins in a region that seems unusually susceptible to such events.

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REFERENCES

Barco, S.G., Swingle, W.M., McLellan, W.A., Harris, R.N. and Pabst, D.A. 1999. Local abundance and distribution of bottlenose dolphins (*Tursiops truncatus*) in the nearshore waters of Virginia Beach, Virginia. *Mar. Mammal Sci*. 15(2): 394-408.

Beier, A.G. 2001. Occurrence, distribution, and movements of outer coastline bottlenose dolphins off Galveston, Texas. MSc thesis. College Station, Texas A&M University. 97pp.

Bräger, S. 1993. Diurnal and seasonal behaviour patterns of bottlenose dolphins (*Tursiops truncatus*). *Mar. Mammal Sci*. 9: 434-40.

Burnham, K.P. and Anderson, D.R. 1992. Data-based selection of an appropriate biological model: the key to the modern data analysis. pp.16-30. *In*: McCullough, D.R. and Barret, R.H. (eds). *Wildlife 2001: Populations*. Elsevier Science Publishers, London.

Burnham, K.P. and Overton, W.S. 1978. Estimation of the size of a closed population when capture probabilities vary among animals. *Biometrika* 65: 625-33.

Burnham, K.P. and Overton, W.S. 1979. Robust estimation of population when capture probabilities vary among animals. *Ecology* 60: 927-36.

Burt, W.H. 1943. Territoriality and home range concepts as applied to mammals. *J. Mammal*. 30: 346-52.

Chapman, D.G. 1951. Some properties of the hypergeometric distribution with applications to zoological censuses. *Univ. Calif. Publ. Statist*. 1: 131-60.

Darroch, J.N. 1958. The multiple-recapture census. I: Estimation of a closed population. *Biometrika* 45: 343-59.

Fazioli, K.L., Hofmann, S. and Wells, R.S. 2006. Use of Gulf of Mexico coastal waters by distinct assemblages of bottlenose dolphins (*Tursiops truncatus*). *Aquat. Mamm*. 32: 212-22.

Fertl, D. 1994. Occurrence patterns and behavior of bottlenose dolphins (*Tursiops truncatus*) in the Galveston ship channel, Texas. *Texas J. Sci*. 46(4): 299-317.

Freedman, D. and Diaconis, P. 1981. On the histogram as a density estimator: L2 theory. *Probab. Theory Rel*. 57: 453-76.

Gruber, J.A. 1981. Ecology of the Atlantic bottlenose dolphin *Tursiops truncatus* in the Pass Cavalla area of Matagorda Bay. Master's thesis. Texas A&M University. 182pp.

Henningsen, T. 1991. Zur Verbreitung und Okologie des Grossen Tummlers (*Tursiops truncatus*) in Galveston, Texas. Diploma. Christian-Albrechts Universitat zu Kiel. 80pp.

Hubard, C.W., Maze-Foley, K., Mullin, K.D. and Schroeder, W.W. 2004. Seasonal abundance and site fidelity of bottlenose dolphins (*Tursiops truncatus*) in Mississippi Sound. *Aquat. Mamm*. 30: 299-310.

Irvine, A.B., Scott, M.D., Wells, R.S. and Kaufmann, J.H. 1981. Movements and activities of the Atlantic bottlenose dolphin, *Tursiops truncatus*, near Sarasota, Florida. *Fish. Bull*. 79(4): 671-88.

Irwin, L.J. and Würsig, B. 2004. A small resident community of bottlenose dolphins, *Tursiops truncatus*, in Texas: monitoring recommendations. *Gulf of Mexico Science* 22: 13-21.

Kendall, W.L., Nichols, J.D. and Hines, J.E. 1997. Estimating temporary emigration using capture-recapture data with Pollock's robust design. *Ecology* 78: 563-78.

Lynn, S.K. and Würsig, B. 2002. Summer movement patterns of bottlenose dolphins in a Texas bay. *Gulf of Mexico Science* 20: 25-37.

Macdonald, D.W., Ball, F.G. and Hough, N.G. 1979. The evaluation of home range size and configuration using radio tracking data. pp.405-24. *In*: Amlaner, C.J. and Macdonald, D.W. (eds). *A Handbook on Biotelemetry and Radio Tracking*. Pergamon Press, Oxford. 804pp.

Maze, K.S. and Würsig, B. 1999. Bottlenose dolphins of San Luis Pass, Texas: occurrence patterns, site fidelity, and habitat use. *Aquat. Mamm*. 25(2): 91-103.

McLellan, W.A., Friedlander, A.S., Mead, J.G., Potter, C.W. and Pabst, D.A. 2002. Analysing 25 years of bottlenose dolphin (*Tursiops truncatus*) strandings along the Atlantic coast of the USA: do historic records support the coastal migratory stock hypothesis? *J. Cetacean Res. Manage*. 4(3): 297-304.

NMFS. 2004. Interim report on the bottlenose dolphin (*Tursiops truncatus*) unusual mortality even along the panhandle of Florida. 36pp. [Available from: NMFS, Southeast Fisheries Science Center, 75 Virginia Beach Dr., Miami, FL 33149 and at *http://www.nmfs.noaa.gov/pr/health/mmume/event2004.htm*].

Otis, D.L., Burnham, K.P., White, G.C. and Anderson, D.R. 1978. Statistical inference from capture data on closed animal populations. *Wildl. Monogr*. 62: 1-135.

Pine, W.E., Pollock, K.H., Hightower, J.E., Kwak, T.J. and Rice, J.A. 2003. A review of tagging methods for estimating fish population size and components of mortality. *Fisheries* 28: 10-23.

Pollock, K.H. 1982. A capture-recapture design robust to unequal probability of capture. *J. Wildl. Manage*. 46: 757-60.

Read, A.J., Urian, K.W., Wilson, B. and Waples, D.M. 2003. Abundance of bottlenose dolphins in the bays, sounds and esturies of North Carolina. *Mar. Mammal Sci*. 19(1): 59-73.

Rexstad, E.A. and Burnham, K.P. 1992. *User's Guide for Interactive Program CAPTURE*. Colorado Coop. Fish and Wildl. Res. Unit, Colorado State University, Fort Collins. 29pp.

Seber, G.A.F. 1982. *The Estimation of Animal Abundance and Related Parameters*. 2nd ed. Charles Griffin and Company Ltd., London. i-xvii+654pp.

Sellas, A.B., Wells, R.S. and Rosel, P.E. 2005. Mitochondrial and nuclear DNA analyses reveal fine scale geographic structure in bottlenose dolphins (*Tursiops truncatus*) in the Gulf of Mexico. *Conserv. Genet*. 6: 715-28.

Shane, S. 1977. The population biology of the Atlantic bottlenose dolphin *Tursiops truncatus* in the Arkansas Pass area of Texas. MSc thesis. College Station,Texas A&M University. 238pp.

Shane, S.H. 1980. Occurrence, movements and distribution of bottlenose dolphins, *Tursiops truncatus*, in southern Texas. *Fish. Bull*. 78: 593-601.

Shane, S.H. 1990a. Behavior and ecology of the bottlenose dolphin at Sanibel Island, Florida. pp.245-66. *In*: Leatherwood, S. and Reeves, R.R. (eds). *The Bottlenose Dolphin*. Academic Press Inc, San Diego. 653pp.

Shane, S.H. 1990b. Comparison of bottlenose dolphin behavior in Texas and Florida, with a critique of methods for studying dolphin behavior. pp.541-58. *In*: Leatherwood, S. and Reeves, R.R. (eds). *The Bottlenose Dolphin*. Academic Press, Inc, San Diego, CA.

Taylor, B.L. and Gerrodette, T. 1993. The uses of statistical power in conservation biology: the vaquita and northern spotted owl. *Conserv. Biol*. 7(3): 489-500.

Thompson, W.L., White, G.C. and Gowan, C. 1998. *Monitoring Vertebrate Populations*. Academic Press, San Diego. 365pp.

Torres, L.G., McLellan, W.A., Meagher, E. and Pabst, D.A. 2005. Seasonal distribution and relative abundance of bottlenose dolphins, *Tursiops truncatus*, along the US mid-Atlantic coast. *J. Cetacean Res. Manage*. 7(2): 153-62.

Torres, L.G., Rosel, P.E., D'Agrosa, C. and Read, A.J. 2003. Improving management of overlapping bottlenose dolphin ecotypes through spatial analysis and genetics. *Mar. Mammal Sci*. 19(3): 502-14.

Tyson, R. *Abundance of bottlenose dolphins (Tursiops truncatus) in the Big Bend of Florida, St. Vincent Sound to Alligator Harbor* 2008 [cited. MSc thesis. Florida State University, Tallahassee. xxpp.

Urian, K., Hohn, A.A. and Hansen, L.J. 1999. Status of the photo-identification catalog of coastal bottlenose dolphins of the western North Atlantic. Report of a workshop of catalog contributors. *NOAA Technical Memorandum NMFS-SEFSC* 425: 22pp. [Available from: *www.nmfs.gov*].

Waring, G.T., Josephson, E., Fairfield-Walsh, C.P. and Maze-Foley, K. 2007. US Atlantic and Gulf of Mexico marine mammal stock assessments – 2007. *NOAA Tech. Mem*. NMFS-NE-194: 453pp. [Available at: *http://www.nefsc.noaa.gov/nefsc/publications/tm/tm194*].

Weller, D.W. 1998. Global and regional variation in the biology and behaviour of bottlenose dolphins. PhD thesis. Texas A&M University, College Station. 142pp.

Wells, R.S. 1986. Population structure of bottlenose dolphins: behavioural studies along the central west coast of Florida. NMFS Tech. Report 45-WCNF-5-00366 (unpublished). 70pp.

Wells, R.S. 1991. The role of long-term study in understanding the social structure of a bottlenose dolphin community. pp.199-205. *In*: Pryor, K. and Norris, K.S. (eds). *Dolphin Societies, Discoveries and Puzzles*. University of California Press, Berkeley, California. 397pp.

Wells, R.S. 1994. Determination of bottlenose dolphin stock discreteness: application of a combined behavioural and genetic approach. pp.16-20. *In*: Wang, K.R., Payne, P.M. and Thayer, V.G. (eds). *Coastal stock(s) of Atlantic bottlenose dolphin: status review and management. Proceedings and recommendations from a workshop held in Beaufort, NC, 13-14 September 1993*. NOAA Technical Memorandum NMFS-OPR-4. 120pp.

Wells, R.S. 2003. Dolphin social complexity: lessons from long-term study and life history. pp.32-56. *In*: de Waal, F.B.M. and Tyack, P.L. (eds). *Animal Social Complexity: Intelligence, Culture, and Individualised Societies*. Harvard University Press, Cambridge, MA. 640pp.

Wells, R.S., Bassos, M.K., Urian, K.W., Shane, S.H., Owen, E.C.G., Weiss, C.F., Carr, W.J. and Scott, M.D. 1997. Low-level monitoring of bottlenose dolphins, *Tursiops truncatus*, in Pine Island Sound, Florida: 1996. Final Contract Report to National Marine Fisheries Service, Southeast Fisheries Science Center, Miami, FL. Contract No. 40-WCNF601958. 86pp. [Available from: *www.nmfs.gov*].

Wells, R.S., Rhinehart, H.L., Hansen, L.J., Sweeney, J.C., Townsend, F.I., Stone, R., Casper, D., Scott, M.D., Hohn, A.A., Rowles, T.K. and Howard, L. 2004. Bottlenose dolphins as marine ecosystem sentinels: developing a health monitoring system. *EcoHealth* 1(3): 246-54.

Wells, R.S., Scott, M.D. and Irvine, A.B. 1987. The social structure of free-ranging bottlenose dolphins. pp.247-306. *In*: Genoways, H. (eds). *Current Mammalogy*. Plenum Press, New York. 519pp.

Wells, R.S., Urian, K.W., Read, A.J., Bassos, M.K., Carr, W.J. and Scott, M.D. 1996. Low-level monitoring of bottlenose dolphins, *Tursiops truncatus*, in Tampa Bay, Florida: 1988-1993. *NOAA Tech. Mem*. NMFS-SEFSC-385: 25pp. [Available from: *www.nmfs.gov*].

Westgate, A.J. and Read, A.J. 1998. Applications of new technology to the conservation of small cetaceans. *Mar. Technol. Soc. J*. 32: 70-81.

White, G.C., Anderson, D.R., Burnham, K.P. and Otis, D.L. 1982. Capture-recapture and removal methods for sampling closed populations. *Biometrics* 39: 1122-23.

Williams, J.A., Dawson, S.M. and Slooten, E. 1993. Abundance and distribution of bottlenose dolphins (*Tursiops truncatus*) in Doubtful Sound, New Zealand. *Can. J. Zool*. 71: 2080-88.

Wilson, B., Hammond, P.S. and Thompson, P.M. 1999. Estimating size and assessing trends in a coastal bottlenose dolphin population. *Ecol. Appl*. 9: 288-300.

Würsig, B. and Würsig, M. 1977. The photographic determination of group size, composition, and stability of coastal porpoises (*Tursiops truncatus*). *Science* 198: 755-56.

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Age estimates for female eastern and whitebelly spinner dolphins (*Stenella longirostris*) incidentally killed in the eastern tropical Pacific tuna purse-seine fishery from 1973-82

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ABSTRACT

Age was estimated from teeth for 1,267 female eastern spinner dolphins (*Stenella longirostris orientalis*) and 1,071 female whitebelly spinner dolphins (*S. longirostris*) incidentally killed in the eastern tropical Pacific yellowfin tuna purse-seine fishery between 1973 and 1982. The final age assigned to each specimen was the mean of two readers' age estimates made independently and without knowledge of the corresponding biological data for each specimen. The oldest eastern spinner dolphin was estimated to be 24.5 years and the oldest whitebelly spinner dolphin was 26 years. Age bias plots revealed nonlinear systematic bias between readers while a measure of overall precision, coefficient of variation (CV), indicated equivalent difficulty in estimating age for each population. The age frequency distributions generated in this study document the age structure of dolphins sampled from the observed incidental kill, which will facilitate further assessments of the impact of the fishery on these dolphins.

KEYWORDS: SPINNER DOLPHIN; PACIFIC OCEAN; PURSE-SEINES; INCIDENTAL CATCHES; AGE DETERMINATION; AGE DISTRIBUTION

INTRODUCTION

Eastern spinner dolphins (*Stenella longirostris orientalis*) and whitebelly spinner dolphins, a hybrid form of spinner dolphin (*S. longirostris*), have been incidentally killed in the yellowfin tuna (*Thunnus albacares*) purse-seine fishery that operates in the eastern tropical Pacific (ETP) for more than four decades (Perrin, 1969). These two forms are managed as separate populations in the region. Using estimates of the incidental kill and population abundance, the eastern spinner dolphin population was estimated to be at approximately 44% of its pre-exploitation size of 1,100,000 to 1,956,000 dolphins in 1988 (Wade, 1993) and is listed as 'depleted' under the US Marine Mammal Protection Act[1]. The whitebelly spinner dolphin population is incidentally killed less frequently and was estimated to be between 58% and 72% of its pre-exploitation size of 400,000 to 500,000 dolphins in 1979 (Smith, 1983). Recent evidence suggests that these two dolphin populations are not recovering as expected, despite greatly reduced mortality levels of <1,000 dolphins per year since 1993 (Gerrodette and Forcada, 2005; IATTC, 2004; Reilly *et al*., 2005a; Reilly *et al*., 2005b).

Since the 1970s, research on spinner dolphins and other ETP dolphin populations incidentally taken during purse-seine fishing activities has been conducted in order to better understand the dynamics of their populations and the impacts of the fishery on them. Included in that research were biological studies to characterise the age and sex selectivity of the fishery kill and to quantify vital rates for estimating the reproductive potential of the populations.

For this research, fishery observers working aboard purse-seine fishing vessels collected biological samples from more than 4,000 eastern and whitebelly spinner dolphins incidentally killed in the ETP tuna fishery since 1968. Two studies conducted in the late seventies and the mid-eighties estimated age for 250 female eastern spinner dolphin (Perrin and Henderson, 1984; Perrin *et al*., 1977) and 232 female whitebelly spinner dolphin (Perrin and Henderson, 1984) specimens collected through 1978 to study growth and reproductive patterns in these populations. In these studies, one reader counted tooth growth layer groups (GLGs) for each specimen and several models of GLG deposition rate were explored. Age frequency distributions were not presented in these studies because samples were selected to describe age-specific growth patterns and not to describe the age structure of the incidental kill (Perrin and Henderson, 1984).

Following these two studies and calibration of GLG deposition in captive Hawaiian spinner dolphins, *S. longirostris* (Myrick *et al*., 1984), a study was conducted to document the age structure of the incidental kill of females for the two spinner dolphin populations by estimating age for a larger dataset collected over a longer time series. The results of this study are presented here. The analyses employed quantify the bias and precision in age estimation by two independent readers for the female eastern and whitebelly spinner dolphins and generate an age frequency distribution for the dolphins incidentally killed in the fishery between 1973 and 1982 for each population.

MATERIALS AND METHODS

Biological data collected

In 1968, the National Marine Fisheries Service (NMFS) began collecting mortality and biological data from dolphins incidentally killed during fishing operations (Perrin *et al*., 1976). Beginning in October 1972, biological data collection procedures were standardised, and the sampling scheme that selectively collected large, female specimens was replaced by a less-selective sampling scheme that sampled the first available dead dolphins brought aboard. In 1979, the Inter-American Tropical Tuna Commission (IATTC) joined the NMFS in placing observers aboard US-registered vessels and collecting life history data from incidentally killed dolphins. Instructions and protocols for data collection were the same for NMFS and IATTC observers.

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[1] Federal Register Vol. 58, No. 164, August 26, 1993 (58 FR 45066).

The biological data collected by observers included the species, stock, total body length and sex of all cetaceans incidentally killed and brought aboard the vessel along with the date, geographic location and a tally of the total number (examined and unexamined) of dolphins killed in the set (Myrick *et al*., 1986; Perrin *et al*., 1976; Perrin and Oliver, 1982). Reproductive organs and a section of the middle of the lower left jaw containing teeth were collected and preserved in formalin from as many specimens as possible.

Potential bias in the analyses was reduced by only using data from specimens collected after October 1972, which is when observers stopped selecting large female dolphins to sample and started collecting samples from dolphins in the order they were brought aboard. The data set includes 1,267 female eastern spinner dolphins and 1,071 female whitebelly spinner dolphins that were incidentally killed in 991 purse-seine sets between 1973 and 1982 (Table 1). Specimens were collected throughout the range of each form of spinner dolphin in the ETP (Fig. 1).

Age estimation

Multiple age estimates of a specimen permit the precision in interpreting GLGs to be quantified. Results from a prior ageing study of spotted dolphins (*S. attenuata*), which are closely related to spinner dolphins (LeDuc *et al*., 1999), found inter-reader variation to be notably greater than intra-reader variation (Reilly *et al*., 1983). Thus, the study design for this experiment specified that two readers would age each specimen once to minimise workload and to allow quantification of the more important contributor to ageing variation, inter-reader precision.

Samples were randomly selected from all female specimens incidentally killed between 1973 and 1982. A tooth was removed from the jaw section of each specimen, decalcified, thin sectioned, hematoxilyn-stained and mounted on microscope slides for ageing (Hohn and Hankins, 1983; Myrick Jr *et al*., 1983). Two readers (hereinafter referred to as readers A and B) with experience ageing *Stenella* spp. estimated age by counting GLGs in the dentine of prepared tooth sections without knowledge of the specimen's accompanying biological data (e.g. population, total body length, state of maturity) or any prior age estimates. Neither of these readers had estimated ages for the two prior eastern and whitebelly spinner studies. The GLGs identified in eastern and whitebelly spinner dolphin teeth were interpreted as annual events based on conclusions from a calibration experiment conducted with captive Hawaiian spinner dolphins exposed to the seasonal variability of the subtropics because they were kept in outdoor pens (Myrick *et al*., 1984). For each specimen, readers independently scored the same tooth recording their best estimate of age to the nearest 0.1 year for the first three GLGs and to the nearest integer thereafter, their confidence in the estimate, and the quality of the tooth sections read. If a reader did not feel confident in their first reading because the quality of the preparation was poor, another tooth was prepared and used by both readers to estimate age of that specimen. When more than one age estimate was made by a reader for a given specimen, the estimate with the highest confidence rating was chosen as the reader's best age estimate. The final age assigned to each specimen was the mean of the two readers' best estimates, which is referred to as the 'assigned' age. The interval between successive readings varied from days to months, and the age estimates were generated over a three year time period, from 1983 to 1985.

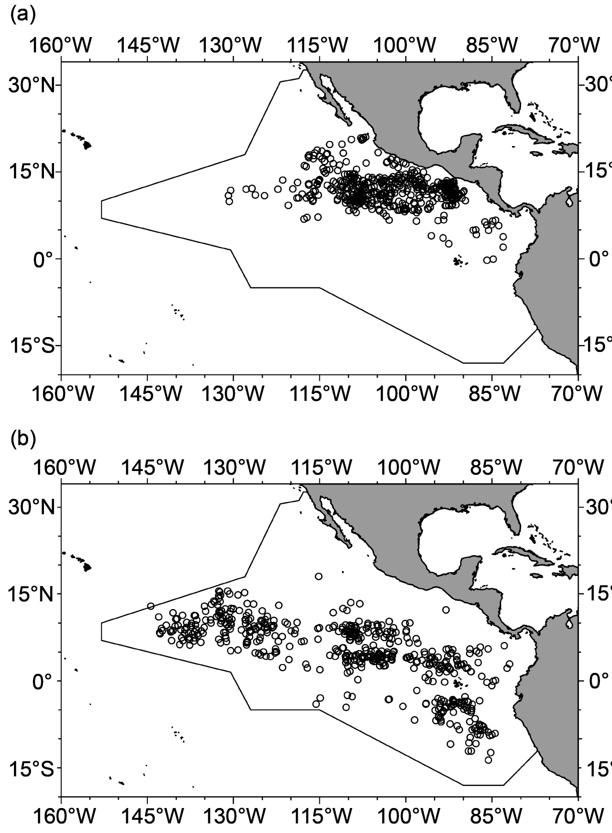

Fig. 1. Locations where each aged (a) female eastern spinner dolphin specimen (*n*=1,267) and (b) female whitebelly spinner dolphin specimen (*n*=1,071) were collected. The dolphins were sampled in the eastern tropical Pacific yellowfin tuna purse-seine fishery between 1973 and 1982. The boundary line shown marks the study area used to estimate species abundance for all *Stenella* sp. impacted by the purse-seine fishery (Wade and Gerrodette, 1993).

Age selectivity of the incidental kill

Dolphin schools may segregate by age or sex and certain age classes may have a higher probability of becoming entangled in a purse-seine net, which could result in non-random sampling and collection of data that is not representative of the population. Previous analyses of data on spotted dolphins incidentally killed in the ETP tuna purse-seine fishery have shown that the age structure of the kill was not independent of the total kill size (Barlow, 1985). Rather, low kill sets contained relatively higher numbers of young spotted dolphins than presumably less selective large kill sets. To test for age selectivity in the spinner dolphins data, the method of Barlow (1985) was followed and used a

Table 1

Number of aged female eastern spinner dolphin and whitebelly spinner dolphin specimens sampled in the eastern tropical Pacific yellowfin tuna purse-seine fishery by year collected.

	1973	1974	1975	1976	1977	1978	1979	1980	1981	1982	Total
Eastern	248	306	290	79	114	55	76	33	33	33	1,267
Whitebelly	74	36	168	264	195	94	54	39	69	78	1,071

contingency table to test the null hypothesis that age frequency (binned into 0-1, 1-2, and 2+ yr) was independent of the size of the total kill[2] (1-10, 11-20, 21-30, 30+ dolphins). Power was calculated by first calculating the effect size index, *w*, where

$$w = \sqrt{\frac{\chi^2}{N}}$$

and *N* is the total sample size (Cohen, 1988). Using the effect size index, total sample size, degrees of freedom, and significance level, power may be found in tables.

Bias and precision in age determinations

Systematic differences in inter-reader age estimates were assessed by interpreting age bias plots, which have been demonstrated to be more appropriate for detecting both linear and nonlinear bias patterns than other methods, including parametric and nonparametric matched-pair tests, regression analysis, analysis of variance, and age difference plots (Campana *et al*., 1995). Age bias plots depict the ages estimated by one reader, grouped into categories, against the means of the other reader's estimates for the same specimens within a category. Bias between two readers is detected by visually comparing the observed line to a 1:1 equivalence line. A 1:1 expected correspondence in age estimates made by the readers would be expected when readers use the same model of GLG deposition and no reader bias exists. The reader chosen for the abscissa is arbitrary. Reproducibility of age determinations was evaluated by use of the coefficient of variation, CV (Campana *et al*., 1995; Chang, 1982). CV can be expressed as

$$\mathrm{CV}_j = 100 \times \frac{\sqrt{\sum_{i=1}^{R} \frac{\left(X_{ij} - X_j\right)^2}{R-1}}}{X_j}$$

where R is the number of times each specimen is aged, X_{ij} is the i^{th} age determination of the j^{th} specimen, and X_j is the mean age of the j^{th} specimen. A mean CV was calculated for each age class as well as averaged over all specimens.

Age distributions

Given the potential sampling biases due to fishery activities and the removal of a large portion of both populations by the fishery in the more than ten years prior to and during the collection of specimens, one would not expect the populations to have stable age distributions. However, comparisons of age distributions generated in this study to stable age distributions provide a reference for characterising the age selectivity of the sampled incidental kill and comparing the populations. No empirical data are available to generate age distributions for the populations before they were exploited by the purse-seine fishery, but there is also no evidence that suggest the populations were previously exploited. Therefore, expected stable age distributions were compared to the observed age distributions. The stable age distributions were generated using an estimate of longevity derived from the results of this study together with age-specific fecundity and survival schedules based on published reproductive data (Perrin and Henderson, 1984) and methods for estimating survival rates (Barlow and Boveng, 1991). Kolmogorov-Smirnov (K-S) tests comparing the observed and expected age distributions illustrate potential under- and over-representations of age classes.

Comparison to prior studies

In two prior studies that estimated age for eastern spinner dolphins, Perrin *et al*. (1977) analysed specimens collected from 1968 to 1975, and Perrin and Henderson (1984) analysed specimens collected from 1968 to 1978. All aged specimens that were common to these earlier studies and to this study were selected for comparison (*n*=207). Although both prior studies analysed several models of GLG deposition rates, their final GLG count for each specimen was interpreted as the best estimate of age for the specimen. An age bias plot and age frequency distribution was generated to compare estimates between the studies.

RESULTS

Age selectivity of the incidental kill

A count of the total number of dolphins killed in the purse-seine sets in which the dolphins aged in the study were collected was available for 99.8% of the eastern spinner specimens and 100% of the whitebelly spinner specimens. The total number of dolphins killed in a set ranged from 1-624 for sets containing eastern spinner dolphins and 1-738 for sets containing whitebelly spinner dolphins. The null hypothesis that kill size per set and specimen age were independent variables could not be rejected for either eastern spinner (chi-square, P=0.17, power=0.82) or whitebelly spinner (chi-square, P=0.87, power=0.70) dolphins, and therefore all available data were used in further analyses.

Bias and precision in age determinations

The maximum age estimated for eastern spinner dolphins by reader A and B was 25 and 28yr, respectively, while the maximum assigned age was 24.5yr. For whitebelly spinner dolphins, the maximum age estimated by readers A and B was 30yr and 26yr, respectively, with a maximum assigned age of 26yr. The mean age of the oldest 5% of specimens was 20.0yr (SE=0.2) for eastern spinner dolphins and 19.3yr (SE=0.2) for whitebelly spinner dolphins.

Age bias plots for both populations (Fig. 2) indicated nonlinear systematic differences between readers. Variance in age estimation increased with specimen age for both populations. CV tended to increase with age and mean values between populations were similar (Table 2). Imprecision for the 0-1 year old age class was substantially greater relative to other age groups; however, this is understandable because the complexity in estimating fractions of a year would cause small differences between readers that translated into large values for CV especially considering that the mean values for the age class were less than unity.

Age distributions

The observed age frequency distribution for eastern spinner dolphins was significantly different from a stable age distribution (K-S test, $P<0.001$) and contained notably fewer 0-1 year-olds and more 1-3 year-olds than a stable distribution (Fig. 3). The observed age frequency distribution for whitebelly spinner dolphins was also significantly different from a stable age distribution (K-S test, $P<0.001$) and contained fewer 0-4 and 6-7 year-olds and a greater number of 7-15 year-olds than a stable distribution (Fig. 3).

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[2] Total kill refers to the number of all dolphin species killed in a set.

Table 2

Number of specimens and age estimation coefficients of variation (CV) by age class for female eastern spinner and whitebelly spinner dolphins. The mean CVs for all age classes are weighted by sample size.

Age class	*n*		CV	
	Eastern	Whitebelly	Eastern	Whitebelly
0	43	31	35.6	56.6
1	150	71	9.0	7.0
2	109	52	8.5	6.7
3	90	58	10.7	8.5
4	88	68	9.2	8.2
5	65	52	9.7	10.8
6	53	44	10.1	11.9
7	64	68	9.6	11.8
8	62	82	9.3	9.5
9	61	67	11.8	10.7
10	46	81	9.8	10.3
11	62	83	11.1	11.0
12	62	63	10.2	8.9
13	60	59	12.5	14.7
14	53	50	11.1	12.0
15	55	44	11.6	10.4
16	51	34	13.3	12.5
17	24	20	16.9	11.2
18	20	18	16.8	12.6
19	21	11	10.3	15.6
20	11	6	11.1	4.3
21	8	6	8.4	20.5
22	2	0	14.4	
23	5	1	11.1	6.1
24	2	1	2.9	0.0
25	0	0		
26	0	1		21.8
27		0		
$\sum$	1,267	1,071		
$\bar{x}$			11.3	11.7

Comparison to prior studies

There were 207 specimens of eastern spinner dolphins aged in this study that were also aged in previous studies (Perrin and Henderson, 1984; Perrin *et al*., 1977). An age bias plot comparing age estimates indicated a systematic difference for the older specimens (Fig. 4). The age frequency distribution generated from eastern spinner dolphin specimens in the two previous studies was significantly different from this study's age distribution for the same specimens (K-S test, $P<0.001$). Original data used by Perrin and Henderson (1984) could only be obtained for nine whitebelly spinner dolphin specimens and therefore a between study comparison was not possible for this population.

DISCUSSION

The results of this study characterise the age selectivity for female eastern and whitebelly spinner dolphins killed in the ETP tuna purse-seine fishery from 1973 to 1982. Dolphins from all age groups were sampled with the oldest eastern spinner dolphin specimen estimated to be 24.5 years old and the oldest whitebelly spinner dolphin to be 26 years. No significant reader bias was detected except for the oldest specimens, for which sample size was small, but because the 'true' age of specimens is unknown, the assigned age is considered the best estimate of age for each specimen. Precision was comparable between populations and calves were underrepresented relative to a stable age distribution in both populations.

Fishery bias

Analyses of age data for stocks of spotted dolphins incidentally killed in the fishery have shown that the total number of dolphins killed in a set affects the observed age structure of that set's kill (Barlow, 1985; Perrin and Oliver, 1982). Samples from small-kill sets (<40 dolphins) of spotted dolphins were found to have proportionately more calves than larger kill sets. Contrary to spotted dolphins, a significant effect of the kill-size of a set on the proportion of young (0-2 years old) spinner dolphins was not found.

Variation in the age and sex composition of dolphin schools, and those subsequently encircled during fishing operations, was another potential source of bias in the subset of dolphins sampled. Evidence of segregation by age or breeding condition has not been consistent between *Stenella* spp. studied. No evidence was found of school segregation for spotted dolphins in the ETP (Perrin *et al*., 1976). Conversely, three types of striped dolphin (*S. coeruleoalba*) schools have been reported in the waters off Japan: juvenile; adult; and mixed (Miyazaki and Nishiwaki, 1978). More recently, length information from aerial photogrammetry of striped dolphins in the ETP indicated segregation based on size analogous to that found in the western Pacific (Perryman and Lynn, 1994). Earlier preliminary research of ETP spinner dolphins suggests schooling by age and sex, with small schools more likely to be composed of immature males, females or adult males (Perrin and Gilpatrick, 1994). However, it was not possible to determine how representative the sample of dolphins associated with tuna was compared to the whole population.

Age validation

The importance of validating the process, or model, used to estimate age has been well documented (Beamish and McFarlane, 1983; Campana, 2001; Campana *et al*., 1995; Kimura and Lyons, 1991) and is only possible when mark-recapture studies can be conducted or known-age dolphins are available (Power *et al*., 2006). Neither are possible or available for pelagic dolphins. The absence of a reference collection of known age samples, meant that it was not possible to measure reader accuracy or analyse the ageing process to identify reader drift over the three years during which ages were estimated.

The ageing model used was based on the results of a calibration experiment of captive Hawaiian spinner dolphins that concluded GLGs were deposited annually; however, annual GLG formation was not verified for the entire age range (Myrick *et al*., 1984). The model chosen in this study for ageing spinner dolphins was considered the best available; the calibration study involved dolphins of the same species and available data suggest that the application of calibration study results from captive dolphins to wild populations is valid (Hohn, 1990; Myrick *et al*., 1984).

For this study, age acceptance criteria were not implemented. That is, readers did not re-evaluate or discuss specimens whose estimated ages varied beyond some set limit. While this avoided the potential for choosing inappropriate acceptance criteria and subsequent bias in age estimates and derived parameters (Marriott and Mapstone, 2006), it resulted in several instances for which readers' estimates for a particular specimen varied by many years (Table 3a and 3b).

Reader bias and precision

Age bias plots indicated nonlinear systematic differences between readers for both eastern and whitebelly spinner dolphins. Except for the very oldest dolphins (with small

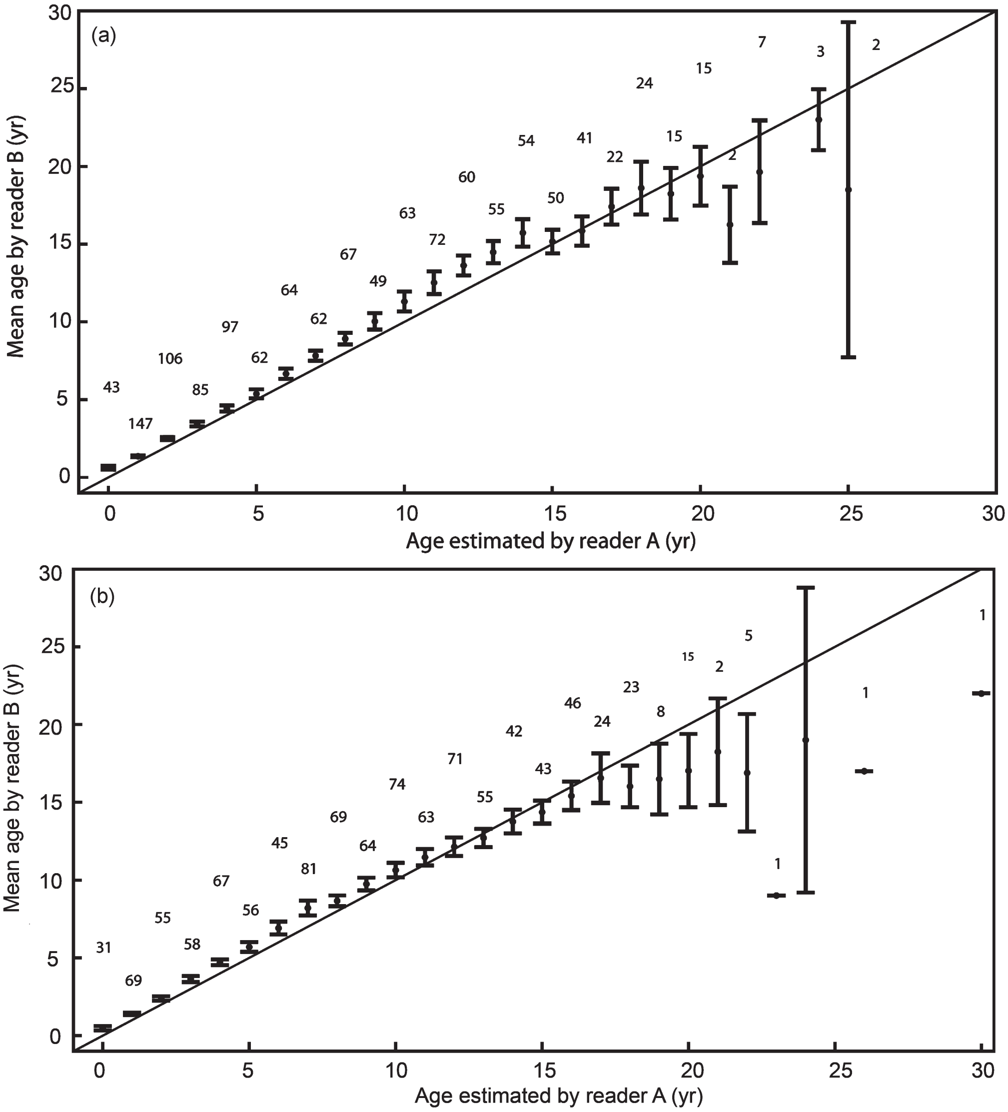

Fig. 2. Age bias plots for pairwise comparison between two readers of aged (a) female eastern spinner dolphin (n=1,267) and (b) female whitebelly spinner dolphin (n=1,071) specimens sampled in the eastern tropical Pacific yellowfin tuna purse-seine fishery between 1973 and 1982. Reader A estimates are grouped into one year age categories. Error bars are the 95% confidence interval of the means of reader B age estimates. Sample size for each age group is given above the error bar. The solid line is the expected 1:1 correspondence for both readers' age estimates assuming no bias.

sample sizes), these patterns showed a bias of no more than one year, suggesting that these results are not practically significant considering the lifespan of these dolphins. The offset from the 1:1 correspondence line for the younger dolphins might be partially explained by differences between readers in interpreting the first GLG, which can be particularly difficult. Hohn (1990) and Hohn *et al*. (1989) noted that the prominence of accessory layers produced during the first and second year in particular which may cause misidentification of GLGs and subsequently bias age estimates upwards. As a dolphin matures, GLGs tend to become compact, irregular and possibly indiscernible (Myrick Jr *et al*., 1983) leading to increased inter-reader variation. In addition, the greater number of accessory layers may cause disparity as well.

The CV indicated that the level of difficulty in interpreting age structures is similar for the two populations. Although Akin (1988) reported differing tooth morphology with the average whitebelly spinner tooth being longer and wider than the average eastern spinner dolphin tooth, these differences did not translate into more consistent identification of GLGs in whitebelly spinner dolphins compared to eastern spinner dolphins as the CV was not appreciably different between populations.

Values of overall CV for eastern and whitebelly spinner dolphins (~11%) were lower than those reported by Reilly *et al*. (1983) for incidentally killed ETP spotted dolphins (CV=16%). These differences in CV may reflect improved ageing techniques or variation in GLG deposition patterns and the ability to identify and interpret GLGs between the *Stenella* species. Additionally, the experimental design for the studies differed. In the spotted dolphin study, each tooth was read three times by two readers and overall CV was presumably calculated based on all estimates and therefore incorporated both inter- and intra-reader variability. They found inter-reader differences to be much larger than intra-reader differences. For this study of spinner dolphins, each reader estimated age for each specimen only once, therefore the estimates of CV only reflect inter-reader variation.

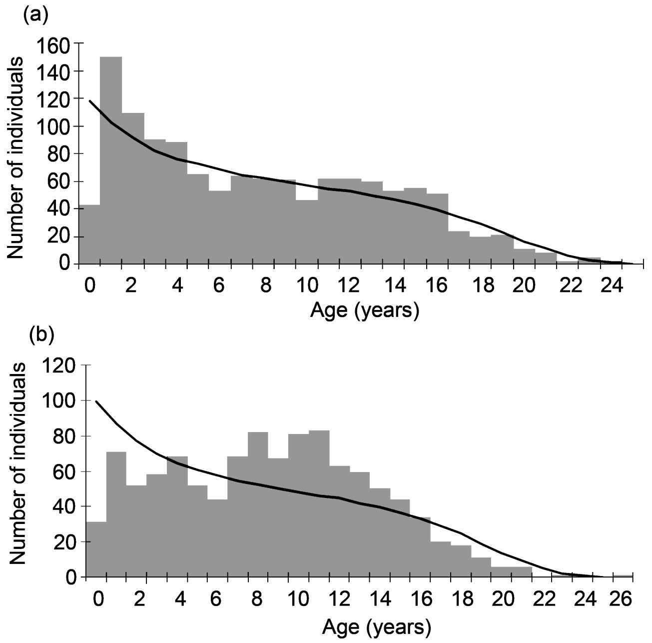

Fig. 3. Age frequency distribution of (a) female eastern spinner (*n*=1,267) and (b) female whitebelly spinner dolphins (*n*=1,071) sampled in the eastern tropical Pacific yellowfin tuna purse-seine fishery between 1973 and 1982. The solid line represents a stable age distribution for a population with a sample size equivalent to that studied here.

Age distributions

The observed age distributions for eastern and whitebelly spinner dolphins were found to be significantly different from stable age distributions. This comparison characterises the apparent age selectivity of the incidental kill of these dolphins in the yellowfin tuna purse-seine fishery. The age selectivity of the fishery kill in the years prior to sampling and its effect on the populations is unknown, and therefore whether the observed age distributions captures the underlying age distribution of the populations could not be determined.

In the observed age distributions for both eastern and whitebelly spinner dolphins, 0-1 yr olds were under-represented for all years combined as well as when the observed age distributions were examined by year, except for whitebelly spinner dolphins in 1977. The dearth of specimens in the first age class is observed every year for both populations and suggests there is bias in either sampling of the incidental kill or ageing methodology. Archer *et al*. (2001; 2004) proposed several hypotheses of how mothers and nursing calves may become separated during purse-seine fishing and are therefore less likely to be caught in the nets. For example, cows with calves may not be able to keep up with the portion of the school being chased and therefore, may not be set on, killed and sampled. The extent to which this may occur is unknown. This could explain the observed under-representation of calves in the age distributions of spinner dolphins.

Another contributing factor, more so for eastern spinner dolphins than whitebelly spinner dolphins, is the lesser extent to which teeth were collected from very young dolphins killed and brought aboard tuna vessels. Although teeth were not necessarily collected from every dolphin, total length was recorded. In this study length information in conjunction with estimates of average length at one year reported by Perrin and Henderson (1984) were used to partition the data into two length categories. The percentage of teeth collected from dolphins estimated to be in the ≤ 1 yr old age class was less than that collected from dolphins estimated to be in the >1 year old age class for both eastern spinner dolphins (70% and 84%, respectively) and whitebelly spinner dolphins (79% and 81%, respectively). However, even if teeth from calves were collected in the same proportions as dolphins in the older age classes, which translated to an additional 47 eastern spinner dolphin and 6 whitebelly spinner dolphin specimens being collected, the <1 yr old age class would still be under-represented. Therefore, it can be concluded that some of the mechanisms proposed by Archer *et al.* (2001; 2004) to be affecting spotted dolphin sampling from this fishery are likely to be acting for spinner dolphins.

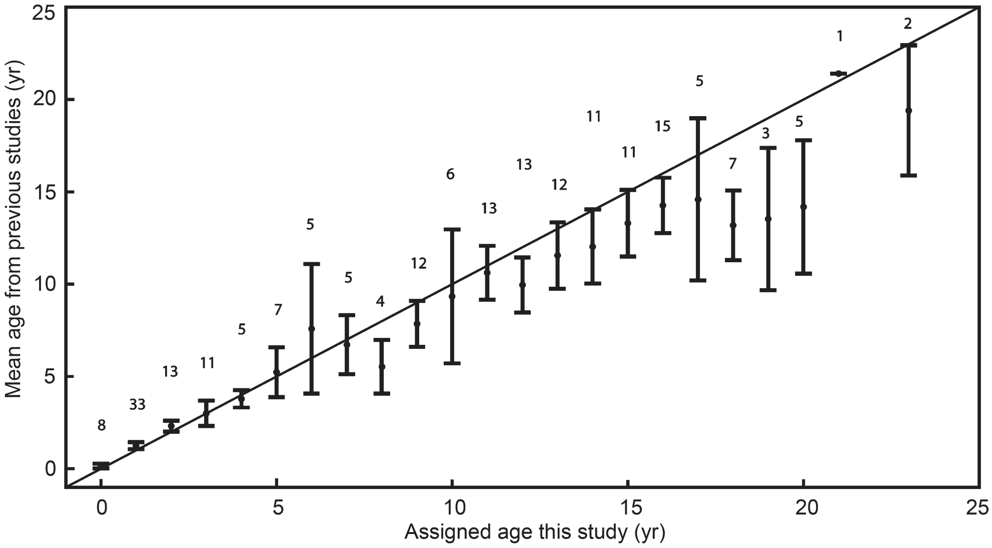

Fig. 4. Age bias plot for pair-wise comparison of female eastern spinner dolphins (*n*=207) from this study and previous studies (Perrin and Henderson, 1984; Perrin *et al*., 1977). Estimates from this study are grouped into one year age categories. Error bars are the 95% confidence interval of the means of prior studies' age estimates. Sample size for each age group is given above the error bar. The solid line is the expected 1:1 correspondence for both readers' age estimates.

Table 3a

Age frequency tables for female eastern spinner dolphin and (b) female whitebelly spinner dolphin specimens sampled in the eastern tropical Pacific yellowfin tuna purse-seine fishery between 1973 and 1982 and aged in this study.

Reader B age (yrs)	Reader A age (yrs)																													
	0	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	Total
0	27	1																												28
1	15	132	5																											152
2	1	14	73	13																										101
3			25	45	20	2																								92
4			3	20	45	14	3	1																						86
5				7	23	30	11	2	2																					75
6					5	10	21	5	2	1	1	1																		46
7					4	3	18	21	10	3	3	1					1													64
8						1	2	22	18	11	4	5	1			1			1											66
9						2	8	5	14	7	10	2	1																	49
10							1	4	12	10	9	10	2	2	1	1														52
11								2	6	7	11	10	6	3	3	4	3				1									56
12									2	5	9	16	11	10	5															58
13										3	7	4	13	10	6	6	4	2	1	1	1		1			1				60
14									1	1	4	10	10	8	10	7	6		2	3	1		1							64
15										1		3	8	6	4	9	5	3	1	1		1								42
16											2	3	3	6	6	10	6	6	2											44
17												1		2	4	6	7	4	2			1								27
18											3	1	1	2	4	2	2		2	1	2									20
19												1	2	2	2	1	1	1	1	2	1		1							15
20												2	1	2	3	1	5	3	6	3	1		1							28
21												2		2	2				2	2	2									12
22													1		3	1		2	1	1	4				2					15
23															1	1		1	1	1	2		1							8
24																	1						2			1				4
25																									1					1
26																			1											1
27																														0
28																			1											1
Total	43	147	106	85	97	62	64	62	67	49	63	72	60	55	54	50	41	22	24	15	15	2	7	0	3	2	0	0	0	1,267

Table 3b

Age frequency tables for female whitebelly spinner dolphin specimens sampled in the eastern tropical Pacific yellowfin tuna purse-seine fishery between 1973 and 1982 and aged in this study.

Reader B age (yrs)	Reader A age (yrs)																															
	0	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	Total
0	23																															23
1	8	61	4																													73
2		8	41	2																												51
3			8	33	3																											44
4			2	19	34	11	2	1																								69
5				2	21	23	8	4		1	1																					60
6				2	8	10	11	10	6																							47
7					1	9	9	19	9	3	4	1	1																			56
8						1	11	22	23	15	8	2	3				1				1											87
9						1	2	13	16	18	6	6	4	6	2		1		1		1			1								78
10						1	2	5	7	10	21	17	8	3	1		3	1														79
11								3	7	5	12	14	19	7	5	7			1		1											81
12								1	1	8	9	8	14	16	6	2	2	2	1				1									71
13								1		3	9	4	7	5	8	7	4	4	2													54
14								1		1	1	4	4	9	7	9	6	2	2	4					1							51
15											1	6	4	3	5	7	8	2	3	1	1		1									42
16											2		3	3	2	6	6	1	4		3	1	1									32
17													2	2	2	2	6	3	2		1		1				1					22
18															3	2	2	3	3		1											14
19												1	1	1			1	1	1	1												7
20								1									2	2	2	1	1	1										10
21															1		3	1			3											8
22													1				1			1	1										1	5
23																					1											1
24																1			1				1		1							4
25																		1														1
26																		1														1
27																																0
28																																0
29																																0
30																																0
Total	31	69	55	58	67	56	45	81	69	64	74	63	71	55	42	43	46	24	23	8	15	2	5	1	2	0	1	0	0	0	1	1,071

Comparison to prior studies

Refinement of tooth processing, ageing techniques and reader experience between previous studies and this study were most likely responsible for the different age estimates made for the same specimens. Ages estimated in this study followed procedures outlined by Myrick *et al*. (1986) who considered their methodology improved over earlier studies of *Stenella spp*. for two reasons: (1) new tooth preparation methods improved GLG resolution; and (2) a study of captive Hawaiian spinner dolphins (Myrick *et al*., 1984) was used to calibrate a model of GLG deposition. Improvements in methodology and the calibration study occurred after the earlier studies and benefited this study by improving understanding of GLG deposition patterns.

Differences in age estimates for eastern spinner dolphins between this study and earlier studies by Perrin *et al*. (1977) and Perrin and Henderson (1984) were detected in both the age bias plot and by statistical tests. Bias patterns appeared to be close to linear and variance was relatively large, even for younger age groups. The differences in age estimation are probably due to the ageing model being improved and refined between the earlier studies and the one described here. The discrepancy in age estimates suggests that revision of the age-specific reproductive rate estimates reported in earlier studies (Perrin and Henderson, 1984; Perrin *et al*., 1977) may be warranted using the age estimates generated in this study.

CONCLUSIONS

This study has improved on earlier ageing studies of spinner dolphins through the calibration of GLG deposition rates in the Hawaiian spinner dolphin, the use of a larger sample size and employing two readers to estimate age to capture inter-reader variation in age estimation. The age structure presented here is the best available for eastern and whitebelly spinner dolphins incidentally killed in the ETP yellowfin purse-seine fishery. This large data set documenting the age structure of the incidental kill includes specimens with additional biological data collected and will benefit future studies of these populations and assessing the impacts of the fishery on them.

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REFERENCES

Akin, P.A. 1988. Geographic variation in tooth morphology and dentinal patterns in the spinner dolphin, *Stenella longirostris*. *Mar. Mammal Sci*. 4(2): 132-40.

Archer, F., Gerrodette, T., Dizon, A., Abella, K. and Southern, S. 2001. Unobserved kill of nursing dolphin calves in a tuna purse-seine fishery. *Mar. Mammal Sci*. 17(3): 540-54.

Archer, F.I. and Robertson, K.M. 2004. Age and length at weaning and development of diet of pantropical spotted dolphins, *Stenella attenuata* from the eastern tropical Pacific. *Mar. Mammal Sci*. 20(2): 232-45.

Barlow, J. 1985. Variability, trends, and biases in reproductive rates in spotted dolphins, *Stenella attenuata*. *Fish. Bull*. 83(4): 657-69.

Barlow, J. and Boveng, P. 1991. Modelling age-specific mortality for marine mammal populations. *Mar. Mammal Sci*. 7(1): 50-65.

Beamish, R.J. and McFarlane, G.A. 1983. The forgotten requirement for age validation in fisheries biology. *Trans. Am. Fish. Soc*. 112(6): 735-43.

Campana, S.E. 2001. Accuracy, precision and quality control in age determination, including a review of the use and abuse of age validation methods. *J. Fish. Biol*. 59(2): 197-242.

Campana, S.E., Annand, M.C. and McMillan, J.I. 1995. Graphical and statistical methods for determining the consistency of age determinations. *Trans. Am. Fish. Soc*. 124(1): 131-38.

Chang, W.Y.B. 1982. A statistical method for evaluating the reproducibility of age determination. *Can. J. Fish. Aquat. Sci*. 39: 1208-10.

Cohen, J. 1988. *Statistical Power Analysis for The Behavioural Sciences*. Lawrence Erlbaum Associates, Inc., Hillsdale, NJ. 567pp.

Gerrodette, T. and Forcada, J. 2005. Non-recovery of two spotted and spinner dolphin populations in the eastern tropical Pacific Ocean. *Mar. Ecol. Prog. Ser*. 291: 1-21.

Hohn, A. and Hankins, R.J. 1983. Documentation of tooth-reading records and age-date files for the northern offshore spotted dolphin. *NOAA Administrative Report* LJ-83-19: 71pp. [Available from: NMFS, La Jolla, CA 92037].

Hohn, A.A. 1990. Reading between the lines: An analysis of age estimation in dolphins. pp.575-86. *In*: Leatherwood, S. and Reeves, R.R. (eds). *The Bottlenose Dolphin*. Academic Press, San Diego, CA. 653pp.

Hohn, A.A., Scott, M.D., Wells, R.S., Sweeney, J.C. and Irvine, A.B. 1989. Growth layers in teeth from known-age, free-ranging bottlenose dolphins. *Mar. Mammal Sci*. 5(4): 315-42.

IATTC. 2004. *Annual Report of the Inter-American Tropical Tuna Commission, 2003*. Inter-American Tropical Tuna Commission, La Jolla, California.

Kimura, D.K. and Lyons, J.J. 1991. Between-reader bias and variability in the age-determination process. *Fish. Bull*. 89(1): 53-60.

LeDuc, R.G., Perrin, W.F. and Dizon, A.E. 1999. Phylogenetic relationships among the delphinid cetaceans based on full cytochrome b sequences. *Mar. Mammal Sci*. 15(3): 619-48.

Marriott, R.J. and Mapstone, B.D. 2006. Consequences of inappropriate criteria for accepting age estimates from otoliths, with a case study for a long-lived tropical reef fish. *Can. J. Fish. Aquat. Sci*. 63(10): 2259-74.

Miyazaki, N. and Nishiwaki, M. 1978. School structure of the striped dolphin off the Pacific coast of Japan. *Sci. Rep. Whales Res. Inst., Tokyo* 30: 65-116.

Myrick, A.C., Hohn, A.A., Barlow, J. and Sloan, P.A. 1986. Reproductive biology of female spotted dolphins, *Stenella attenuata*, from the eastern tropical Pacific. *Fish. Bull*. 84(2): 247-59.

Myrick, A.C., Shallenbeger, E.W., Kang, I. and MacKay, D.B. 1984. Calibration of dental layers in seven captive Hawiian spinner dolphins, *Stenella longirostris*, based on tetracycline labeling. *Fish. Bull*. 82(1): 207-25.

Myrick Jr, A.C., Hohn, A.A., Sloan, P.A., Kimura, M. and Stanley, D.D. 1983. Estimating age of spotted and spinner dolphins (*Stenella attenuata* and *Stenella longirostris*) from teeth. *NOAA Tech. Rep., NMFS SWFC* 30: 12pp. [Available from: NMFS, La Jolla, CA 92037].

Perrin, W.F. 1969. Using porpoise to catch tuna. *World Fish*. 18(6): 42-45.

Perrin, W.F., Coe, J.M. and Zweifel, J.R. 1976. Growth and reproduction of the spotted porpoise, *Stenella attenuata*, in the offshore eastern tropical Pacific. *Fish. Bull*. 74(2): 229-69.

Perrin, W.F. and Gilpatrick, J.W., Jr. 1994. Spinner dolphin, *Stenella longirostris* (Gray, 1828). pp.99-128. *In*: Ridgway, S.H. and Harrison, R. (eds). *Handbook of Marine Mammals. Vol. 5. The First Book of Dolphins*. Academic Press, London and San Diego. 416pp.

Perrin, W.F. and Henderson, J.R. 1984. Growth and reproductive rates in two populations of spinner dolphins, *Stenella longirostris*, with different histories of exploitation. *Rep. int. Whal. Commn (special issue)* 6: 417-30.

Perrin, W.F., Holts, D.B. and Miller, R.B. 1977. Growth and reproduction of the eastern spinner dolphin, a geographical form of *Stenella longirostris* in the eastern tropical Pacific. *Fish. Bull*. 75(4): 725-50.

Perrin, W.F. and Oliver, C.W. 1982. Time/area distribution and composition of the incidental kill of dolphins and small whales in the U.S. purse-seine fishery for tuna in the eastern tropical Pacific, 1979-80. *Rep. int. Whal. Commn* 32: 429-44.

Perryman, W.L. and Lynn, M.S. 1994. Examination of stock and school structure of striped dolphin (*Stenella coeruleoalba*) in the Eastern Pacific from aerial photogrammetry. *Fish. Bull.* 92(1): 122-31.

Power, G.R., King, P.A., Kelly, C.J., McGrath, D., Mullins, E. and Gullaksen, O. 2006. Precision and bias in age determination of blue whiting, *Micromesistius poutassou* (Risso, 1810), within and between age-readers. *Fish. Res.* 80(2-3): 312-21.

Reilly, S.B., Donahue, M.A., Gerrodette, T., Forney, K.A., Wade, P.R., Ballance, L.T., Fielder, P.C., Dizon, A., Perryman, W.L., Archer, F. and Edwards, E.F. 2005a. Preliminary report to Congress under the International Dolphin Conservation Program Act of 1997. *NOAA Technical Memorandum NMFS* NOAA-TM-NMFS-SWFSC-371: 39pp.

Reilly, S.B., Donahue, M.A., Gerrodette, T., Forney, K.A., Wade, P.R., Ballance, L.T., Forcada, J., Fielder, P.C., Dizon, A., Perryman, W.L., Archer, F. and Edwards, E.F. 2005b. Report of the scientific research program under the International Dolphin Conservation Program Act. *NOAA Technical Memorandum NMFS* NOAA-TM-NMFS-SWFSC-372: 100pp.

Reilly, S.B., Hohn, A. and Myrick Jr, A.C. 1983. Precision of age determination of northern offshore spotted dolphins. *NOAA Technical Memorandum NMFS* NOAA-TM-NMFS-SWFC-35: 27pp.

Smith, T.D. 1983. Changes in size of three dolphin (*Stenella* spp.) populations in the eastern tropical Pacific. *Fish. Bull.* 81(1): 1-14.

Wade, P.R. 1993. Estimation of historical population size of the eastern stock of spinner dolphin (*Stenella longirostris orientalis*). *Fish. Bull.* 91(4): 775-87.

Wade, P.R. and Gerrodette, T. 1993. Estimates of cetacean abundance and distribution in the eastern tropical Pacific. *Rep. int. Whal. Commn* 43: 477-93.

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A note on the use of dolphins as bait in the artisanal fisheries off Bahía Solano, Chocó, Colombia

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ABSTRACT

Dolphin hunting for fishing bait in Bahía Solano, Chocó, Colombia, was evaluated during eight months, between July 2005 and April 2006. Interviews were conducted with 122 fishermen (18.2% of the registered fishermen in the zone), who cover at most 890km^2 when fishing (approximately 2.3% of the Pacific Territorial Sea of Colombia), and data obtained from landings at a fishing company. Only fishermen using longlines (37.3%) confirmed using dolphins as bait. It was not possible to obtain additional information about date, specific location or dolphin species, but the most probable captured species were common bottlenose dolphin and pantropical spotted dolphin. Nine dolphins were killed during the study period (1.1 dolphins/month) and extrapolating these numbers to all fishermen using longlines in the region (250), 24 dolphins might have been taken during the study period (3 dolphins/month). Fish species caught using dolphin bait include Pacific bearded brotula, groupers and smooth-hound.

KEYWORDS: PANTROPICAL SPOTTED DOLPHIN; BOTTLENOSE DOLPHIN; PACIFIC OCEAN; SOUTH AMERICA; DIRECT CAPTURE; FISHERIES; PURSE-SEINES; GILLNETS; TRAWLS

INTRODUCTION

Bahía Solano (06°04'-06°40'N, 77°25'-77°30'W) is a rural municipality that contains about 6,900 people. It is located in the province of Chocó on the north Pacific coast of Colombia, South America and includes the villages of El Valle (06°06'N, 77°25'W), Cupica (06°20'N, 77°25'W) and Ciudad Mutis (06°14'N, 77°24'W); the latter is the main town and a port for cargo boats trading provisions, materials, timber and for passenger transportation. The National Natural Park (PNN) Utría (06°02'N, 77°20''W') is one of the most important marine protected areas on the Pacific coast of Colombia (Fig. 1).

The two most common species of dolphins off Bahía Solano are common bottlenose dolphins (*Tursiops truncatus*) and pantropical spotted dolphins (*Stenella attenuata*), but little is known about their ecology and population status in Colombia (Avila *et al*., 2008; García *et al*., 2006). In the PNN Utría there are small groups of less than 10 common bottlenose dolphins that frequent protected zones, remaining close to shore, while the pantropical spotted dolphins move in larger groups with an average of 45 individuals, usually associated with open areas further offshore (Suárez, 1994). In Cupica Bay, common bottlenose dolphins are usually found within four miles from shore, in groups of 2-200 animals, feeding or travelling. Conversely, pantropical spotted dolphins are frequently seen more than four miles from shore, travelling (Avila *et al*., 2008).

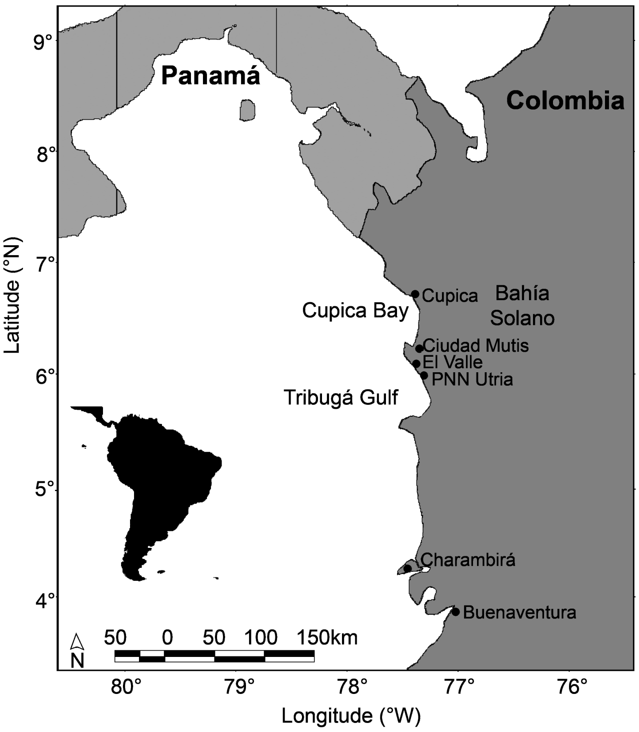

Fig. 1. Study area: Bahía Solano, localised in the northwestern section of Colombia in the department of Chocó, between PNN Utría and Cupica town.

The main economic activities of Bahía Solano include artisanal fisheries, agriculture and timber extraction (Matallana, 1999). There is also much tourism in this region, which is focusing on trekking, sport fishing, diving and humpback whalewatching; there is no focussed dolphin watching. Artisanal fisheries products are purchased by five main fish trading companies in Bahía Solano and then sold to companies in the main inland cities. There are 670 active fishermen, who are registered with the Bahía Solano Port Authority (H.J. Quesada, pers. comm.). These fishermen cover at most 890km^2 when fishing, approximately 2.3% of the Pacific Territorial Sea of Colombia. Artisanal fishermen here use 15-30ft long fibreglass or wooden boats and six main fishing techniques: (1) hand lines with a weight and one or several baited hooks from boat; (2) trawling behind the boat or canoe, using a line and either bait or artificial lures; (3) gillnets 20-100m long and 3-5m high that are fixed at both ends with a weight and a marking buoy – these nets are usually left in the water for 5-10 hours; (4) harpoons used by divers; (5) cast nets, or circular nets with lead

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weights that trap fish in the water column while the net is falling; and (6) bottom longlines, the main line containing 500-3,000 baited hooks that are approximately 1.5m apart. Different baits are used for each fishing technique, including fish, crustaceans, squids and artificial fishing lures (Tobón, 2004), and at times dolphin parts. The government does not prohibit killing dolphins, but a license is required (Presidencia de la República, 1974). However, killing dolphins is not culturally acceptable and the Colombian Institute for Agriculture, ICA (previously the Colombian Institute for Rural Development, INCODER) discourages the practice.

With the objective of evaluating the practice of hunting dolphins for bait off Bahía Solano, Chocó, Colombia, data were collected on 246 days over eight months, 1 July-24 November 2005 and 11 January-19 April 2006. Interviews were conducted and observations made when fishermen unloaded their catch at a fish trade company in Ciudad Mutis. The fish trade company is the second most important company in the region. Identities of the company and fishermen were kept anonymous. Usually, fishermen sell their entire catch to one company. One hundred and twenty two fishermen (18.2% of all registered fishermen in the area) were interviewed. Ninety-four fishermen (37.3%) used longlines, 68 (27.0%) used hand lines, 66 (26.2%) trolling, 15 (5.9%) cast nets, 8 (3.2%) harpoons, and one (0.4%) gillnets. Most fish were caught using hand lines (5,881.0kg of fish) and longlines (2,8790.3kg), following by trolling (4,505.5kg), harpoon (591.0kg), cast net (528.0kg) and gillnet (70.5kg). The species with most significant landings in terms of weight in Bahía Solano were the Pacific bearded brotula (*Brotula clarckae*) (45.0%), groupers (*Epinephelus acanthistius, E. cifuentesi*) (10.3%) and smooth-hound (*Mustelus lunulatus*) (10.1%). Only fishermen using longlines confirmed using dolphins (locally known as 'bufeos') as bait.

Usually, longlines are set 7-18km off the coast between PNN Utría and Cupica, towns that are separated by 52km. For longline fishing, fibreglass or wood boats and 15-40hp outboard engines are used. The crew consists of 3-5 fishermen and the total load of these boats is 1-2 tons including crew, engine and catch. During a fishing bout, the long line is set an average of one time. The best time and place to set a longline depends on environmental factors such as tide and moon phase. Fish caught with longlines include brotulas (33.3%), groupers (33.3%), smooth-hounds (28.6%) and triple tails (*Lobotes pacificus*) (4.8%). The main bait used for longline fishing is sardine (*Cetengraulis mysticetus*) from March to July, complemented by mullets (*Mugil cephalus*) and bigeye scad (*Selar crumenophthalmus*) during the last quarter of the moon, and occasionally herring (*Opisthonema medirastre*) and squid (*Lolliguncula panamensis*) when trawling boats are in the area. As alternative bait, fishermen use smooth-hounds (*Mustelus lunulatus*) and eels, which can result in a catch of 75-152kg of fish. Although many longline fishermen admitted hunting dolphins, they were reluctant to identify the species or to let us see the dolphin carcasses. For longline fishermen, three (3.2%) stated that they hunted dolphins when possible, 12 (12.8%) hunted dolphins occasionally, when no other bait was available, and 34 (36.2%) stated that they never hunted dolphins. The remaining 45 (47.8%) longline fishermen provided no information on this topic.

Based on information collected during interviews, a minimum of nine dolphins were killed during this study (1.1 dolphin/month). However, this is probably an underestimate due to the unreliability of interview data (Lien *et al*., 1994). If these numbers are used to estimate number of dolphins killed by all 250 longline fishermen in the region, it can be estimated that at least 24 dolphins could have been killed during this study (3 dolphins/month). It was not possible to collect information about the dates and locations of dolphin captures, or the dolphin species involved. Based on fishermen's descriptions and relative abundance (Avila *et al*., 2008; García *et al*., 2006; Suárez, 1994), the most probable species used for bait were common bottlenose dolphins and pantropical spotted dolphins. Fishermen might occasionally harpoon striped dolphins (*S. coeruleoalba*), since Mora and Muñoz (1994) found a specimen that appeared to have marks on it. To hunt a dolphin, fishermen approach a group, or wait until dolphins approach the boat and harpoon them. Fishermen said they sometimes use bait, e.g. yellowfin tuna (*Thunnus albacares*) or sardines (*Cetengraulis mysticetus*), to attract the dolphins. Fishermen stated that the best bait for certain fish species, like smooth-hound, is dolphin.

Mora and Muñoz (1994) found that fishermen prefer to hunt pantropical spotted dolphins, since they are less hardy than common bottlenose dolphins, which may live for up to six hours after harpooning. They also found that fishermen prefer to focus on mother-calf pairs, since they are inseparable even when hunted. By focusing on mother-calf pairs, fishermen can hunt two dolphins simultaneously.

This study provides the first quantitative evidence of the minimum number of dolphins that are used as bait in the Colombian Pacific. The killing of dolphins for use as fishing bait occurs in the Colombian Pacific, in spite of social and governmental disapproval. There is also evidence that this practice occurs in the Colombian Caribbean (C. García, pers. obs.). In the Colombian Pacific, the killing of dolphins for bait appears to have begun around 1970, becoming common probably towards 1990 (Fernández, 1975; Prieto, 1990). In Bahía Solano, dolphin killing appears to mainly occur when traditional bait (i.e. fish and squid) is not available.

It is difficult to extrapolate this study to other regions of the Colombian Pacific coast, since practices and beliefs are not homogeneous. For example, informal dialogue with approximately 15 fishermen in El Valle suggest that dolphin hunts are not common there (J.G. Soler, pers. comm.). Conversely, in Charambirá, Chocó (04°17'N, 77°30'W) dolphin hunts are common and licenses to hunt dolphins have been illegally sold since 1995 (see Figs 2 and 3; V. Puentes, pers. comm.). Mora and Muñoz (1994) conducted a series of interviews between the southern coast of Chocó (Charambirá) and Nariño (La Vigía, 02°37'N and 78°20'W) in 27 communities, and found that dolphins are used as bait for about 3% of longline fishing boats. Mora and Muñoz (1994) found that some industrial longline vessels also hunt dolphins, especially during the first half of the year and in the northern region of the Colombian Pacific. Industrial vessels usually take 10-20 dolphins in one hunt. Staff of the former INPA (National Institute of Fisheries and Aquaculture), confirmed to the authors that in the 1980s, they harpooned dolphins to use as bait in government shark fisheries research cruises.

The IUCN (International Union for the Conservation of Nature) has classified the common bottlenose dolphin and pantropical spotted dolphin as 'Least Concern'[1]. However, these classifications are for the species worldwide and do not take into account that at least four stocks of the coastal

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[1] *www.redlist.org*.

Figs 2 and 3. Killing a dolphin for bait in Charambirá, Chocó (04°17'N, 77°30'W), in 1995.

pantropical spotted dolphins have been identified in the Eastern Tropical Pacific (Escorza-Treviño *et al*., 2005). These stocks may face different risks. In Colombia, both species are considered to be in the 'Near Threatened' category (Rodríguez-Mahecha *et al*., 2006). In the Colombian Pacific Exclusive Economic Zone (EEZ) (329,492km^2), the estimated population sizes are 3,548-14,493 common bottlenose dolphins and 1,755-8,820 pantropical spotted dolphins, the latter for the oceanic and coastal populations combined (Gerrodette and Palacios, 1996). However, there are no studies available regarding the status of coastal pantropical spotted dolphin populations, or their risks in the Colombian Pacific.

It is not possible at this time to estimate how dolphin hunting (minimum 1.1 dolphin/month) might affect long-term population viability, since population parameters for dolphins in this region are unknown. The preference for hunting mother-calf pairs could potentially influence the reproductive success of dolphins and alter their social structures.

Further research is necessary, including a determination of direct takes of dolphins in other fishing communities along the Pacific coast of Colombia, and other causes of mortality such as bycatch. The use of methods such as onboard observers on fishing boats would allow the identification of dolphin species. It would also allow for the collection of reliable data on interactions between fisheries and marine mammals. Research on the population dynamics and abundance of common bottlenose and pantropical spotted dolphins is also needed. Abundance data would allow a baseline to be established from which the possible effects of fisheries interactions could be estimated. It would also allow monitoring of their populations over the long term. Information from interviews is not completely reliable and thus the data in this note represent minimum numbers of direct takes of dolphins. However, these numbers provide an important starting point for further research.

The use of dolphins as bait, and in some cases for human consumption, is widespread (e.g. Alfaro-Shigueto *et al*., 2008; Crespo *et al*., 1994; Félix and Samaniego, 1994; Goodall *et al*., 1988; IWC, 1994; Northridge, 1984; Reeves and Leatherwood, 1994; Romero *et al*., 1997; Sánchez-Criollo *et al*., 2007; Vidal, 1992; Zavala-González *et al*., 1994). In some places fisheries that occasional hunted dolphins in the past have rapidly increased their take due to the perceived effectiveness of using dolphins for bait (e.g. Alfaro-Shigueto *et al*., 2008; Sánchez-Criollo *et al*., 2007; Trujillo and Gómez, 2005). Even if the current dolphin take does not have population level impacts, it has the potential to increase, as fishing resources diminish through overexploitation. Thus, we suggest that mariculture techniques to produce bait be explored, to supply bait for fishermen demand. We also recommend implementing an environmental education programme. Finally, sustainable tourism, including dolphin-watching, may have a lesser impact and would facilitate conservation on a regional level.

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REFERENCES

Alfaro-Shigueto, J., Mangel, J.C. and Van Waerebeek, K. 2008. Small cetacean captures and CPUE estimates in artisanal fisheries operating from a port in northern Perú, 2005-2007. Paper SC/60/SM19 presented to the IWC Scientific Committee, June 2008, Santiago, Chile (unpublished). 13pp. [Paper available from the Office of this Journal].

Avila, I.C., Alvarez-Vargas, F. and Parra-Vidal, A. 2008. Una aproximación a la presencia de mamíferos marinos en el Chocó, Pacífico Colombiano. Abstract Bie 138. Memoirs of the Seminario Nacional de Ciencia y Tecnología del Mar, May 20-23 2008, San Andrés, Colombia. p.169. [In Spanish].

Crespo, E.A., Corcuera, J.F. and López Cazorla, A. 1994. Interactions between marine mammals and fisheries in some coastal fishing areas of Argentina. *Rep. int. Whal. Commn (special issue)* 15: 269-81.

Escorza-Treviño, S., Archer, F.I., Rosales, M., Lang, A. and Dizon, A.E. 2005. Genetic differentiation and intraspecific structure of Eastern Tropical Pacific pantropical spotted dolphins, *Stenella attenuata*, revealed by DNA analyses. *Conserv. Genet*. 6(4): 587-600.

Félix, F. and Samaniego, J. 1994. Incidental catches of small cetaceans in the artisanal fisheries of Ecuador. *Rep. int. Whal. Commn (special issue)* 15: 475-80.

Fernández, P. 1975. Estudio biológico y pesquero de algunas especies de tiburones del Pacífico colombiano. BSc thesis. Universidad Jorge Tadeo Lozano, Bogotá, Colombia.154pp. [In Spanish].

García, C., Soler, G.A., Avila, I.C. and Bessudo, S. 2006. Observaciones preliminares de la presencia y distribución estacional de Mamíferos Marinos del Pacífico colombiano. Memories Primera Reunión Internacional sobre el Estudio de los Mamíferos Acuáticos SOMEMMA-SOLAMAC, November 5-9 2006, Mérida, México. p.123. [In Spanish].

Gerrodette, T. and Palacios, D.M. 1996. Estimates of cetacean abundance in EEZ waters of the eastern tropical Pacific. *SWFSC Admin. Rep. No.* LJ-96-10: 28pp. [In English and Spanish].

Goodall, R.N.P., Galeazzi, A.R. and Lichter, A.A. 1988. Exploitation of small cetaceans off Argentina 1979-1986. *Rep. int. Whal. Commn* 38: 407-10.

International Whaling Commission. 1994. Report of the Workshop on Mortality of Cetaceans in Passive Fishing Nets and Traps, 22-25 October 1990. *Rep. int. Whal. Commn (special issue)* 15:1-71.

Lien, J., Stenson, G.B., Carver, S. and Chardine, J. 1994. How many did you catch? The effect of methodology on bycatch reports obtained from fishermen. *Rep. int. Whal. Commn (special issue)* 15: 535-40.

Matallana, M. 1999. *Documento Proyecto Utría Regional PUR: Sociedad Economía y Territorio*. Fundación Natura. 34pp. [Available from *www.natura.org.co*].

Mora, D. and Muñoz, M. 1994. Registro y análisis de las muertes y varamientos de mamíferos marinos en al Pacífico colombiano, Universidad Nacional de Colombia, Bogotá, Colombia. 205pp. [In Spanish].

Northridge, S.P. 1984. World review of interactions between marine mammals and fisheries. *FAO Fish. Rep.* 251: 190pp.

Presidencia de la República. 1974. Código de Recursos Naturales Decreto 2811 del 18 diciembre de 1974.

Prieto, M. 1990. Estudio preliminar en la interacción de la pesca artesanal con los cetáceos costeros del Pacífico colombiano. Final report no. 699, INDERENA (Instituto Nacional de los Recursos Naturales Renovables y del Ambiente), División de Pesca Artesanal, Bogotá, Colombia. 10pp. [In Spanish].

Reeves, R.R. and Leatherwood, S. 1994. *Dolphins, Porpoises, and Whales: 1994-1998 Action Plan for the Conservation of Cetaceans*. IUCN, Gland, Switzerland. 92pp.

Rodríguez-Mahecha, J.V., Alberico, M., Trujillo, F. and Jorgenson, J. 2006. *Libro rojo de los mamíferos de Colombia. Serie libros rojos de especies amenazadas de Colombia*. Conservación Internacional Colombia, Instituto de Ciencias Naturales, Universidad Nacional de Colombia, Ministerio del Medio Ambiente, Bogotá, Colombia. 433pp. [In Spanish].

Romero, A., Agudo, A.I. and Green, S.M. 1997. Exploitation of cetaceans in Venezuela. *Rep. int. Whal. Commn* 47: 735-46.

Sánchez-Criollo, L., Briceño-Reina, Y., Bolaños-Jiménez, J., Hernández-Rangél, J. and Burmúdez-Villapol, L. 2007. Interacciones antrópicas como causas del incremento en la mortalidad y varamientos de cetáceos en al estado Zulia, Venezuela. p.210. Memories VII Congreso Venezolano de Ecología, November 5-9, 2007, Ciudad Guayana, Venezuela. [In Spanish].

Suárez, M. 1994. Aspectos ecológicos y del comportamiento de *Tursiops truncatus* y *Stenella attenuata* en el Parque Natural de Utría Chocó, Colombia. BSc thesis. Universidad Nacional, Bogotá, Colombia. 105pp. [In Spanish].

Tobón, A. 2004. Evaluación de la pesca artesanal sobre los recursos ícticos del Parque Nacional Natural Utría. Unpublished final report. 25pp. [Available from the author].

Trujillo, F. and Gómez, C. 2005. Pesca de mota *Calophysus macropterus* en el Amazonas utilizando delfines como carnada. Capitulo 1. Unpublished report, Fundación Omacha – Corpoamazonia. 28pp. [In Spanish. Available from the author].

Vidal, O. 1992. Los mamíferos marinos del Océano Pacífico sudeste (Panamá, Colombia, Ecuador, Perú y Chile): diagnóstico regional. *Informes y Estudios del Programa de Mares Regionales del PNUMA* 142: 26pp. [In Spanish].

Zavala-González, A., Urban-Ramirez, J. and Esquivel-Macías, C. 1994. A note on artisanal fisheries interactions with small cetaceans in México. *Rep. int. Whal. Commn (special issue)* 15: 235-37.

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