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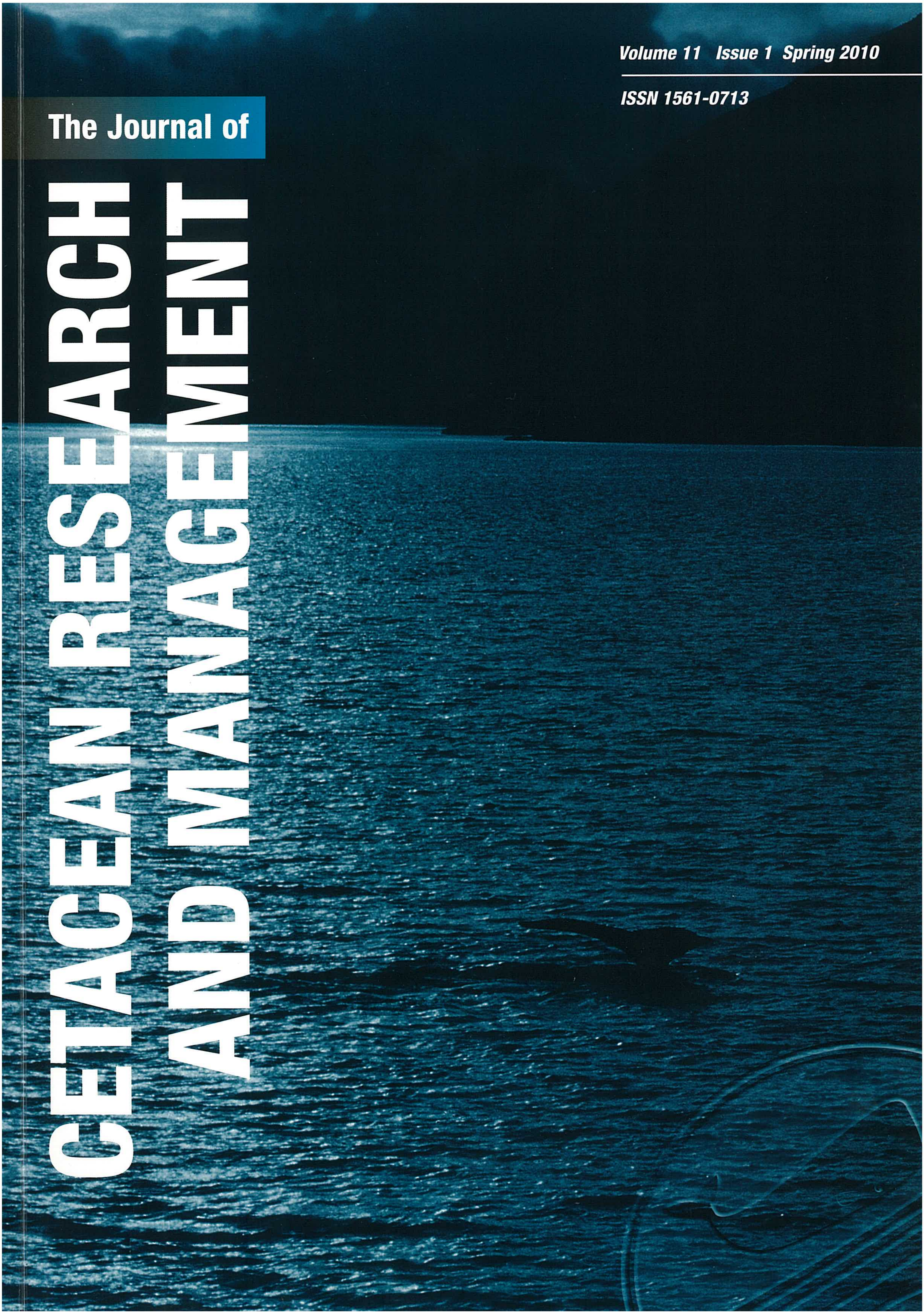

Contents

Editorial

Welcome to this the first issue of the eleventh volume of the *Journal of Cetacean Research and Management*. This volume contains nine papers covering a range of conservation and management issues. We have unfortunately had a series of problems with respect to getting the Journal published due to internal problems at the printers we have used for many years. Sadly, after attempts to secure further investment, they are no longer trading. We are now dealing with a different company and the Journal should once again appear promptly.

The impact of ship strikes on cetaceans, and thus potentially on cetacean populations, is an issue of increasing concern. Quantifying the extent of ship strike mortality is difficult for a number of reasons including the fact that with large fast vessels, collisions often go unnoticed and thus unreported. The paper by Williams and O'Hara uses spatial modelling and GIS visualisation techniques to provide spatial risk maps for fin, humpback and killer whales in British Columbia. Such an approach is valuable for determining priorities for mitigation measures, for example, instigating shipping lanes.

Studies of bowhead whales in the Bering-Chukcki-Beaufort (B-C-B) Seas are of great importance since IWC management advice using the *Bowhead Strike Limit Algorithm* is required for the aboriginal subsistence hunt from this population. Information on stock structure and abundance is vital to providing advice on safe catch limits and there are two relevant papers in this issue. Givens *et al.* provide information on the factors that influence aerial line transect detection of B-C-B whales, which has the potential to improve understanding and accuracy of future surveys in the area. Sadykova and Schweder present information on the inter-annual migration ranks of B-C-B bowhead whales passing Barrow in the spring. This migration occurs around the mating season and has important implications for genetic interchange and stock structure.

Photo-identification remains an invaluable and widely applicable tool for studying cetacean populations, providing *inter alia* information on abundance, stock structure, migration and population biology. There are several papers, from as many countries, employing the technique in this issue. Poncelet *et al.* present a comprehensive study of killer whale population dynamics in the Indian Ocean, spanning 1977-2002. Minton *et al.* present important evidence of a discrete Arabian Sea population of humpback whales. O'Brien *et al.* draw on the data contained in a number of existing photo-identification catalogues to find possible long-distance matching of bottlenose dolphins around the Irish coast. Da Silva and Tiburcio use Empirical Bayesian methods to improve estimation of the size of a closed population using photo-identification data.

Interactions between cetaceans and fisheries are important for a number of reasons. Data on consumption is of importance for ecosystem modelling. Cetaceans are commonly the top predators in their ecosystems and their interactions with the targets of commercial fisheries are of great interest. The paper by Laran *et al.* examines information on densities of both cetaceans and their prey species in the Ligurian Sea and considers estimates of consumption and prey composition for different species.

The Journal strongly encourages the publication of results from previously little studied areas. In this issue it is pleased to publish a comprehensive review of marine mammal records from Iran. Despite its 1,700km coastline, very few records of marine mammals off Iran exist. Braulik *et al.* compile marine mammal records from numerous sources in Iran including skeletal remains, photographs, videos and strandings data. As well as bringing all this information together, the threats to marine mammals in the area are also reviewed.

I would like to draw your attention to the *Guide for Authors* included at the end of this issue. Please read these carefully before submitting manuscripts. Not following the guidelines may result in considerable delay in the consideration of your manuscript!

Finally I would like to thank Andrea Cooke for stepping up to take on many of Helen Coulson's duties, who is now on maternity leave.

G.P. Donovan
Editor

Modelling ship strike risk to fin, humpback and killer whales in British Columbia, Canada

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ABSTRACT

Many cetacean species are susceptible to mortality or serious injury from vessel collisions. Spatially explicit assessments of risk per whale can help identify potential problem areas to guide appropriate mitigation measures. Canada's Pacific waters host high cetacean densities and intense maritime traffic, and the issue of vessel collisions has taken on a high priority in British Columbia (BC) recently due to several major industrial development applications. Spatially-explicit statistical modelling and Geographic Information System (GIS) visualisation techniques identified areas of overlap between shipping activity and waters used by humpback, fin and killer whales. Areas of highest risk were far removed from areas with highest concentrations of people, suggesting that many beach-cast carcasses could go undetected. With few exceptions, high-risk areas were found in geographic bottlenecks, such as narrow straits and passageways. Port expansion and a proposed pipeline for carrying oil from Alberta to BC's north coast (with associated oil tanker traffic) would increase ship strike risk for all three species. The risk assessments illustrate where ship strikes are most likely to occur, but cannot estimate how many strikes occur. Propeller wounds on live killer whales are relatively common in the region, and fatal collisions have been reported in BC for all three species. Procedures were used to estimate potential mortality limits in accordance with a wide range of quantitative management objectives from jurisdictions around the world. While the extent of under-reporting of ship strikes has not been evaluated, the few known cases of collisions involving fin whales suggest that mortality due to ship strike for this species may already be approaching or even exceeding mortality limits under the most risk-averse management objectives. It is hoped that these risk maps may inform environmental impact assessments of marine traffic because it will be easier to plan new shipping lanes so that they avoid high-density areas for whales than it will be to move the lanes after they become entrenched.

KEYWORDS: SHIP STRIKE; CONSERVATION; SPATIAL MODELLING; REGULATIONS; ABUNDANCE ESTIMATE; MANAGEMENT OBJECTIVES; RISK ASSESSMENT; NORTHERN HEMISPHERE; FIN WHALE; HUMPBACK WHALE: KILLER WHALE

INTRODUCTION

Collisions with vessels cause serious injury and mortality in many cetacean species. Quantifying the population-level extent of ship strike mortality, however, is notoriously difficult; collisions are frequently unnoticed, and consequently go unreported (Laist *et al.*, 2001; Panigada *et al.*, 2007; Vanderlaan and Taggart, 2007). Ship strikes can jeopardise the viability of small populations (Fujiwara and Caswell, 2001), and the importance of the topic is reflected in its appearance in the terms of reference of both the Scientific and Conservation Committees of the International Whaling Commission (IWC).

Important areas for research include developing methods for quantifying ship strike mortality, assessment of the effects of such mortality at the population level and the development of appropriate mitigation measures. A valuable exercise to inform the estimation of the potential size of the problem and the identification of mitigation measures, involves spatially explicit risk assessment. Underlying this premise is a common-sense view that minimising spatial overlap between ships and whales is the best way to minimise ship strike risk. Although spatial overlap between ships and whales is not equivalent to collision risk, spatial overlap is obviously a prerequisite for ship strikes.

Canada's Pacific waters host high densities of cetaceans (Williams and Thomas, 2007) as well as intense maritime traffic (O'Hara and Morgan, 2006), but there has been little effort towards estimating cetacean mortality due to ship strikes. There is reason to believe that in British Columbia (BC) this issue has taken on greater urgency in recent years as considerable industrial development is occurring throughout coastal BC, including *inter alia*: major port expansions for Prince Rupert and Delta superport; a planned pipeline terminal for accepting condensate and dispensing crude oil to and from the Alberta tarsands oil fields, with associated petroleum tanker traffic; and potential offshore oil and gas exploration and production in Hecate Strait and Queen Charlotte Sound (Fig. 1). All of these developments would result in a considerable increase in shipping traffic and consequently an increase in the risk of whales being struck. Within Canada, there is a growing recognition of the need to assess the extent of cetacean mortality associated with human activities and to mitigate impacts where feasible. Canada has not specified a uniform set of quantitative management objectives to protect marine mammal stocks from anthropogenic mortality, but methods that take into account uncertainty in population vital rates and abundance estimates have been proposed to estimate potential limits to anthropogenic mortality of Canadian marine mammal stocks (Johnston *et al.*, 2000; Williams *et al.*, 2008). It is unclear what level of ship strike mortality would constitute a sufficiently large fraction of a cetacean population to warrant legislative management action in Canada.

Risk assessment is needed especially for humpback (*Megaptera novaeangliae*) and fin whales (*Balaenoptera physalus*), and for the small killer whale (*Orcinus orca*) populations found in the region. Commercial whaling in British Columbia (BC) brought baleen whale populations

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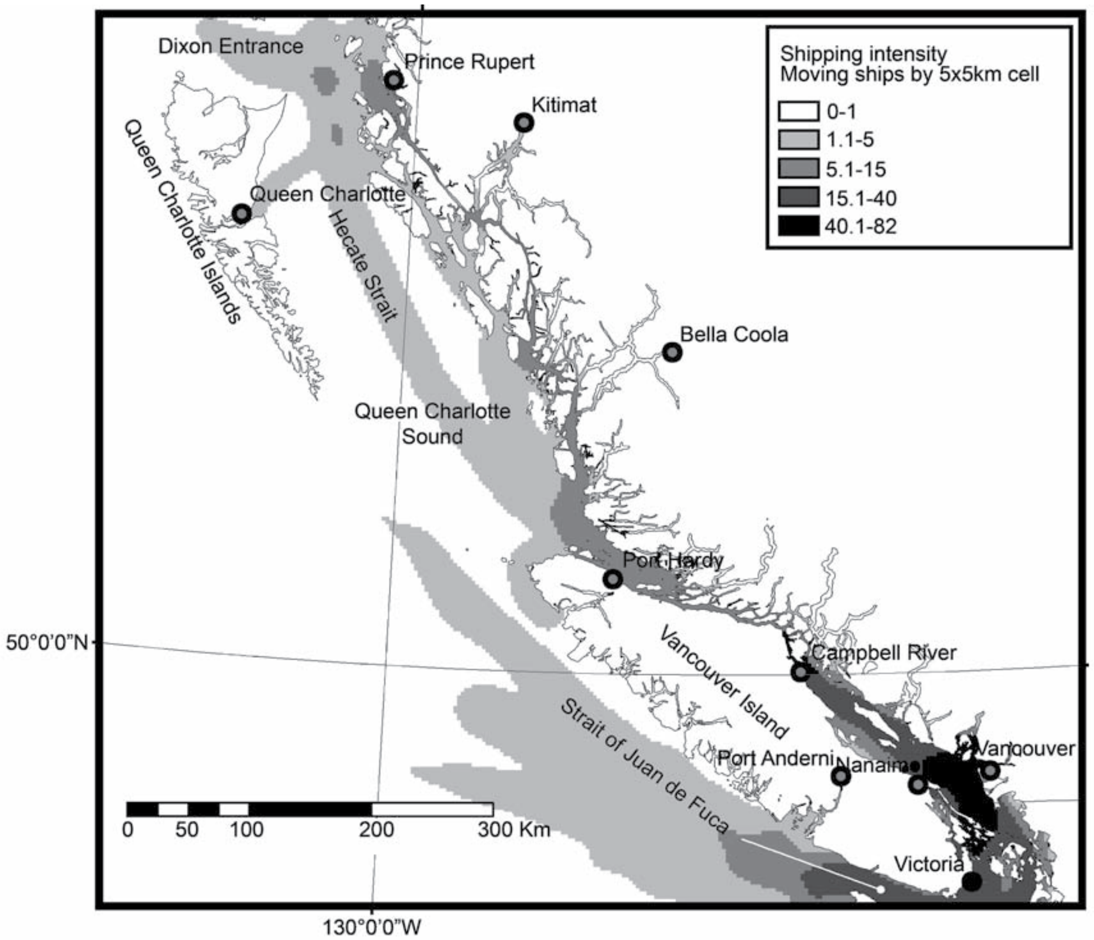

Fig. 1. Marine traffic vessel intensity (number of movements per grid cell) along the coast of BC for June, July and August, 2003.

well below historic levels of abundance (Government of Canada, 2006). In Canadian regulatory frameworks, ship strikes have been identified as important factors in the humpback, blue (*B. musculus*), fin and sei (*B. borealis*) whale recovery plans (Government of Canada, 2006), and for both resident and transient ecotypes of killer whales (Fisheries and Oceans Canada, 2007; 2008). Humpback, gray (*Eschrichtius robustus*) and fin whales have occasionally been reported to be struck by ships transiting the 'Inside Passage' (Douglas *et al*., 2008), which refers to the series of inland and protected waterways used by ships transiting between Johnstone Strait (northern Vancouver Island) and Prince Rupert (Fig. 1).

In this paper, results from a spatially-explicit risk assessment that identifies areas of overlap between whales and shipping activity in BC coastal waters are reported. This assessment is based on data from a recent systematic survey of Inside Passage waters of BC that yielded estimates of distribution and abundance for six cetacean species (Williams and Thomas, 2007). The assessment also includes shipping activity based on compiled and summarised information made available by the Canadian Coast Guard (CCG) that tracks ship movements through their Exclusive Economic Zone (O'Hara and Morgan, 2006). A secondary goal was to use existing abundance estimates to assess potential mortality limits for three cetacean species. Finally, the frequency of vessel collisions and propeller strikes are reported (based on scars seen in photographs of living animals) that have been reported in the region in the primary and grey literature. This minimum estimate of known vessel collisions is used to assess, qualitatively, the plausibility that ship strikes could be causing mortality that exceeds potential mortality limits calculated for BC waters according to procedures that have been used in other regions.

METHODS

Whale abundance and density surface fitting

Whale distribution data

Whale data used in the analyses were collected from a systematic line transect survey designed (Thomas *et al*., 2007) and conducted (Williams and Thomas, 2007) in BC coastal waters in the summers (June-August) of 2004 and 2005. The survey was conducted using 20m boats and covered coastal waters (out to approximately 80 n.miles) between the BC-Washington and BC-Alaska borders. Methodology and conventional distance sampling abundance estimates have been reported previously for several cetacean species from these surveys (Williams and Thomas, 2007; 2009). Additional data were also collected in August 2006, but funding limitations only allowed about half of the planned tracklines to be surveyed. As a result, potential mortality limits were estimated using the analytic abundance and variance estimates previously reported from the design-unbiased survey, i.e. data collected during the 2004 and 2005 field seasons (Williams and Thomas, 2007). However, data collected in 2006 were included in model-based, density surface fitting models (see below) for distribution maps to inform the risk analyses, in order to benefit from increased numbers of sightings for fitting the density surface model. For the case of northern resident killer whales, in which every individual is known from annual censuses conducted by Fisheries and Oceans Canada (Ford *et al*., 2000), known abundance with zero variance was used to estimate mortality limits rather than using abundance estimates from the survey data; although the conventional distance sampling abundance estimates agree well with the known population size (Williams and Thomas, 2009). For humpback and fin whales, abundance refers to the average number of whales in the study area at the time of the surveys, rather than biological population size, because the fraction of the stock(s) using BC waters in summer is unknown.

Whale density surface fitting

Animal density was modelled using the density surface modelling engine in *Distance 6.0 Beta 5* (Thomas *et al*., 2006) following the four-stage approach outlined by Thomas *et al.* (2006): (1) fitting a detection function; (2) estimating whale abundance in each segment as a function of spatial covariates; (3) using the descriptive model to predict whale density throughout the study region; and (4) producing variance estimates. Candidate forms for the detection function were the hazard-rate and half-normal models (Buckland *et al*., 2001). Model selection was guided by Akaike's Information Criterion (AIC) and goodness of fit statistics. Trackline detection probability was assumed to be certain (i.e. $g(0)$ was assumed to be 1). The log of school size, $\ln(s)$, was regressed on the estimated detection probability at the perpendicular distance for each school. The predicted value of $\ln(s)$ at zero distance (where detection probability was assumed to be 1) was then back-transformed to provide the required estimate.

Effort and sightings data were modelled using the 'count' method (Hedley *et al*., 1999; Williams *et al*., 2006), which has been packaged into the Density Surface Modelling (DSM) engine in *Distance* (Thomas *et al*., 2006). Tracklines were divided into segments approximately 1 n.mile in length. Depth of the midpoint of the segment was estimated by overlaying the tracklines on a bathymetry grid in *ArcView 3.2*. The saturated DSM model was of the general form:

$$N \sim s(longitude, latitude) + s(depth) - offset$$

The DSM engine in *Distance* models abundance of whales in each segment using generalised additive models, using thin-plate regression splines (s) by calling the mgcv package in programme *R* (Wood, 2006). This saturated model was used unless a term was not significant at $p<0.05$, or if AIC favoured replacing the bivariate locational spline ($s_{\text{longitude, latitude}}$) with two one-dimensional smooths.

A gridded dataset was created, containing a value in every grid cell for each explanatory variable in the model. A square grid size of 2 n.miles on a side (i.e. 4 n.miles^2) was chosen for prediction. Values for the explanatory variables (latitude, longitude and depth) were calculated using the value at the midpoint of each grid square. The prediction grid data were passed to the selected model for each species in *Distance*, which called the predict.gam function in mgcv. The output of the model was an estimate of the predicted number of whale schools in each grid cell, based on each cell's latitude, longitude, depth and area. Animal abundance was calculated by multiplying the predicted density in each cell by expected school size from the size-bias regression in the detection function modelling step (Buckland *et al*., 2001) and by the area of each cell, and taking the sum of all values in the grid. The prediction grid was defined by the same shapefile as that used for designing the original survey (Thomas *et al*., 2007), so the model prediction only interpolated density between tracklines and did not involve extrapolation beyond the survey region.

Shipping movement data

The Canadian and US Coast Guards monitor ship traffic using radio communication, radar detection and an Automatic Identification System (AIS). The only AIS data used for this study were collected by the US Coast Guard in the transboundary waters of the Strait of Juan de Fuca. The Canadian Coast Guard (CCG) documents ship position approximately every 4 minutes with ship-identification (registered name and Lloyd's registry number), flag-state (country of registry), ship-type and size. Included in this database are ships over 20m in length, and ships engaged in towing or pushing any vessel or object more than 20m (other than fishing gear) that had a combined length of more than 45m. The database does not include vessels towing or pushing inside a log-booming ground, pleasure yachts <30m, or fishing vessels <24m and 150 tonnes gross, which are not required to report to the CCG.

Shipping movement analyses were based on shipping information for the calendar year 2003 as provided by the CCG (Pacific Region). The first complete year of data archived by the CCG (Pacific Region) was 2003, and these data were assumed to be representative of ship movement patterns off the BC coast for all years considered in this study (2004-06). To minimise computer processing time for the analyses, observations were reduced to one uniquely identifiable ship observation per hour per cell in a grid of 5×5km cells using data manipulation procedures in *SAS* (Cary, North Carolina: *SAS v9.3*). Ship identification was based on vessel name, call-sign and Lloyd's registry number. Shipping data were removed when ship movement between cells was not indicated (i.e. ensuring that data were from moving ships only). Finally, for each grid cell, data were summarised by calculating total number of uniquely identifiable ship observations ('Proc Tabulate': *SAS v9.3*), and these totals were used as an index of ship intensity throughout our study area (Fig. 1). This index of ship intensity is a minimum estimate of actual ship movements because a number of ships were not clearly identified in the dataset (i.e. ships tracked by radar were not always identified), and in regions where radar was not available some ships passing through Canadian waters were not tracked because they were not always required to call in (i.e. they were not destined for a Canadian port).

Mapping relative ship strike risk

A ship strike risk layer was created by multiplying the predicted whale density estimates at each grid point with the nearest value of shipping intensity. The resulting surface layers were explored for potential hotspots of elevated risk of ship strike for all three species of whales studied. These surfaces were created to quantify risk spatially, in relative terms within species, and no attempt was made to compare vulnerability to ship strike across species.

Shipping movement patterns, predicted whale density estimates, and relative ship-strike grids were mapped using Inverse Distance Weighting (IDW) ArcGIS v9.3 (ESRI 2002), which is an interpolation technique that estimates focal cell or point values by averaging values for neighbouring cells or points. Average values were calculated using a fixed minimum number of neighbour-values and variable radius. The effect of distance of neighbour cell on the estimated average value of the focal cell is affected by distance of the neighbouring cell from the focal cell. Categories of gray-shading in the mapping were defined using 'Natural Breaks' or 'Jenks' method in ArcGIS 9.3.

Potential mortality limits

Canada does not use a generic set of quantitative objectives to calculate allowable annual anthropogenic mortality to marine mammal stocks. Consequently, a range of conservation objectives were considered that have been specified in various national and international frameworks (Wade *et al*., 2008; Williams *et al*., 2008). As an illustrative example, the Potential Biological Removal (PBR) calculations under the US Marine Mammal Protection Act were conducted using the default guidelines for assessing marine mammal stocks in US waters (Wade and Angliss, 1997), and are described as follows:

$$PBR - N_{min} x0.5(R_{max})xF$$

Where R_{max} is defined as the maximum theoretical or estimated net productivity rate (default value for cetaceans=0.04), *F* as the recovery factor, set to 0.5 for these stocks as recommended for depleted stocks and N_{min} as the 20th percentile of a log-normal distribution surrounding an abundance estimate:

$$N_{min} = N / e^{(0.842x(\ln(1+CV(N)^2))^{1/2})}$$

where, *N* is the abundance estimate and *CV*(*N*) is the coefficient of variation of the abundance estimate.

This first step toward estimating potential mortality limits is tentative because information is lacking for fin and humpback whales on stock definition and stock boundaries, and because this study lacks information for all three species on the proportion of the stock found in the study area in summer months. Applying mortality limits such as those estimated by PBR to a small area (more specifically to the average number of animals within an area), rather than to a biological population is a conservative approach. Lack of information on seasonal patterns in distribution and abundance is a weakness that will affect the estimates of risk (i.e. exposure to ships), but this is a precautionary first step and is the best that can be done with the existing information.

A review of US and Canadian status reports and grey literature was conducted to produce minimum estimates of known cases of ship strike and propeller wounds. Note that current mortality data are presented from scattered records reported throughout the year, but abundance, mortality limits, distribution and risk analyses are restricted to a summer, three-month period. Despite this temporal mismatch, there is no information available on seasonal variability in abundance of these species in the region. Consequently, the methods use all available information and, by including information on known mortality events from outside the summer season, err on the side of being precautionary.

RESULTS

Whale abundance and density surface fitting

Whale distribution, abundance and potential mortality limits

Previously reported abundance estimates for fin and killer whales suffered due to a lack of sightings (Williams and Thomas, 2007; 2009). Including the effort and sightings data from 2006 improved the fit of the detection function for both fin and killer whales. Although model-based abundance estimates that incorporated the additional data collected in 2006 had little effect on the point estimates of abundance for any of the three species, analytic abundance and variance estimates were used for estimating potential mortality limits due to known problems with reliability of variance estimates from model-based abundance estimators (Hedley *et al*., 1999; Williams *et al*., 2006). Abundance estimates and associated CVs used in the analyses are shown in Table 1. A comparison of six assessments of potential limits to annual anthropogenic mortality of fin, humpback and northern resident killer whales are presented in Table 1.

The highest density regions predicted for fin whales (Fig. 2) were found in Dixon Entrance and off the southern end of Queen Charlotte Islands. Fin whale density in mainland inlets was generally low, with one exception on the central coast. The highest-density regions for humpback whales were qualitatively similar to those of fin whales (Dixon Entrance and off the southern end of Queen Charlotte Islands), but humpback whale density in mainland inlets was much higher than it was for fin whales. For northern resident killer whales, the highest density region was Johnstone Strait, however, additional high-density areas were found in central coast waters.

Table 1

A comparison of mortality limits estimated for three cetacean species using six conservation objectives used in international conservation and management frameworks (after Wade *et al*. 2008).

		Fin whale	Humpback whale	Killer whale
Abundance		496	1,313	235
% CV		45.8	27.5	0
N_{min} (20th percentile)		332.3	1,024.9	235
Conservation approach:	**Formula:**			
IWC Scientific Committee[1]	2% of N_{best}	9.9	26.3	4.7
ASCOBANS 'unacceptable'	1.7% of N_{best}	8.4	22.3	4
ASCOBANS 'precautionary'	1% of N_{best}	5	13.1	2.4
PBR 'no bias or uncertainty'	1/2 R_{max} * N_{min} * 1.0	6.6	20.5	4.7
PBR 'robust'	1/2 R_{max} * N_{min} * 0.5	3.3	10.2	2.4
New Zealand MALFIRM	1/2 R_{max} * N_{min} * 0.15	1	3.1	0.7

[1] The IWC Scientific Committee cautions that bycatch levels >2% of the best abundance estimate are unacceptable, and that takes of 1% of N_{best} (i.e. the same criteria as those used by ASCOBANS) warrant close attention (IWC, 1996, p.89).

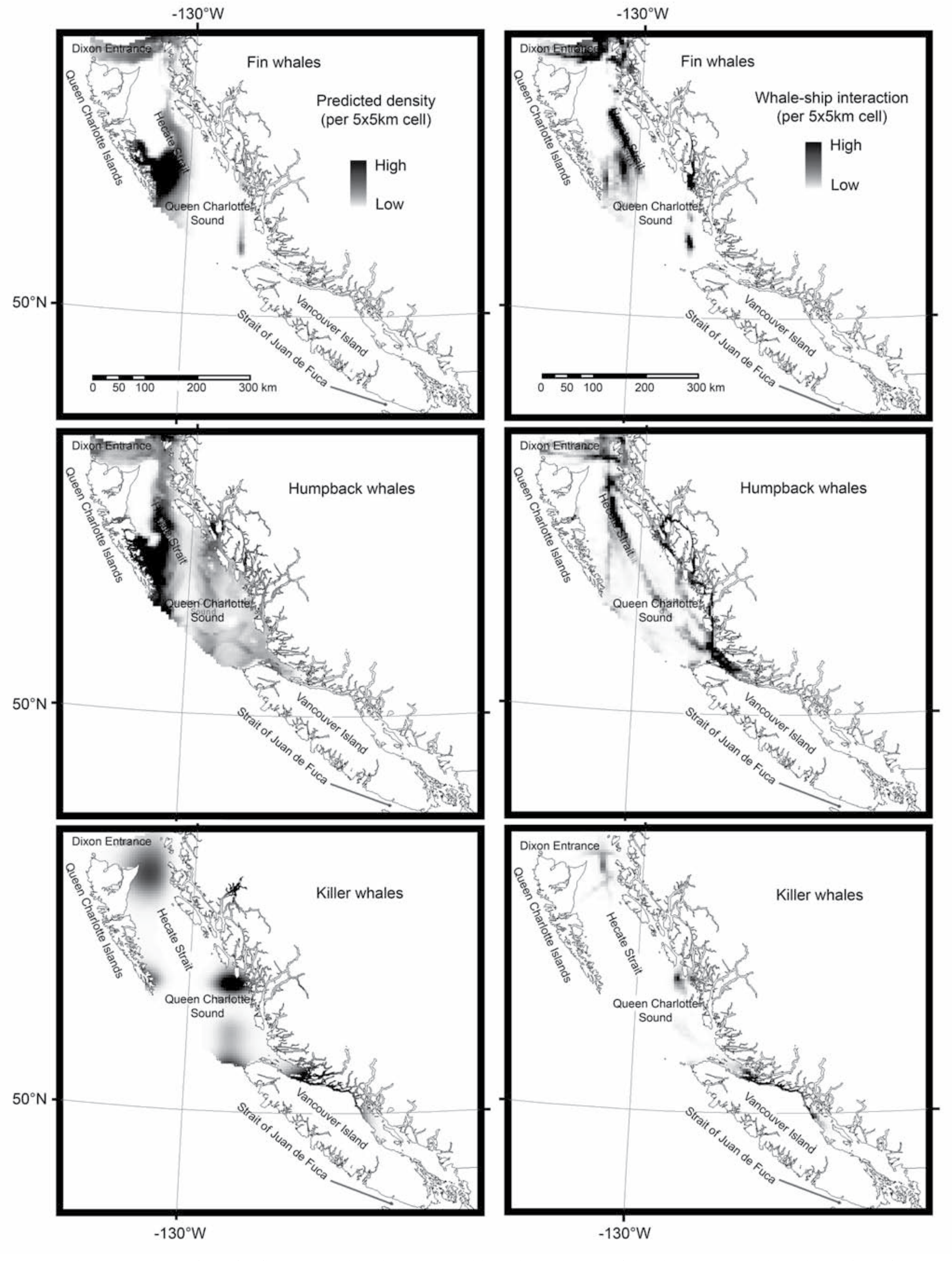

Fig. 2. Density surfaces for fin, humpback and northern resident killer whales (left-hand column), and intensity surfaces for whale-ship interactions (right-hand column) for fin, humpback and killer whales on the right (whale density x marine traffic vessel intensity: see Methods). Whale densities (numbers per grid cell) range from 0-5 for fin whales, 0-4 for humpback whales, and 0-1 for killer whales. Whale-ship interactions scale from 0-224 (fin whales), 0-841 (humpback whales), and 0-1,279 (killer whales).

Table 2

Known ship strikes affecting BC cetacean species, with summaries of events compiled from killer whale recovery strategies (Canada and the US), humpback and fin whale status reports (COSEWIC) (Douglas *et al*., 2008; Jensen and Silber, 2004), the newsletter of Vancouver Aquarium's BC Cetacean Sightings Network (*http://www.vanaqua.org*), and personal observations from Jackie Hildering (whalewatch naturalist working in Johnstone and Queen Charlotte Straits).

Year	Species	ID	Location	Fate of animal
1999	Fin whale	UNK	British Columbia (BC)	Fatal
2002	Fin whale	UNK	Puget Sound, Washington (WA)	Fatal
2002	Fin whale	UNK	Puget Sound, WA	Fatal
2002	Fin whale	UNK	Puget Sound, WA	Fatal
2002	Fin whale	UNK	Puget Sound, WA	Fatal
2004	Fin whale	UNK	West coast Vancouver Island (VI) BC	Fatal
2006	Fin whale	UNK	Northwest inland waters WA	Fatal
2006	Fin whale	UNK	Puget Sound, WA	Fatal
2004	Humpback whale	UNK	West coast WA	Fatal
2006	Humpback whale	UNK	Knight Inlet, BC	Uncertain
2006	Humpback whale	UNK	Swiftsure Bank (west coast VI, BC)	Uncertain
2006	Humpback whale	BCX0022 calf	Johnstone Strait, BC	Seen injured and disappeared
2006	Humpback whale	BCY0177	Johnstone Strait, BC	Serious injury
1995	Killer whale (NR)	UNK	British Columbia	Non-fatal injury
2005	Killer whale (NR)	A60	Johnstone Strait, BC	Non-fatal strike
2006	Killer whale (NR)	A82	Campbell River, BC	Injured and died following year
2006	Killer whale (NR)	C21	Prince Rupert, BC	Fatal
2006	Killer whale (NR)	A59	Campbell River, BC	Non-fatal strike (calf A82 injured)
2006	Killer whale (NR)	G39	Johnstone Strait, BC	Serious injury
2007	Killer whale (offshore)	UNK	Johnstone Strait, BC	Serious injury (dorsal cut off)
1998	Killer whale (SR)	UNK	Haro Strait, BC	Non-fatal strike
2006	Killer whale (SR)	L98	Nootka Sound (west coast VI, BC)	Fatal
2005	Killer whale (SR)	UNK	Haro Strait, BC	Non-fatal strike

Ship strike risk

Areas of relatively high risk of ship strikes for fin whales were found in Dixon Entrance (off northern Queen Charlotte Islands), and two areas coincidental with elevated shipping movement patterns in Hecate Strait, and at the entrance to one inlet system on the central coast (Fig. 2). Areas of relatively high risk of ship strikes for humpback whales were roughly similar to those for fin whales, but also occurred in Queen Charlotte Strait, Hecate Strait, and several inlet systems along the central coast. For killer whales, the region of highest ship strike risk was constrained to Johnstone Strait, where risk was estimated to be about an order of magnitude higher than anywhere else along the coast.

Minimum estimates of mortality and serious injury due to ship strikes

Evidence of injuries and mortalities due to vessel collisions is presented in Table 2. The number of cases reported for each species probably does not represent relative frequency of collisions, because killer whales are better studied in the region than the other two species. Similarly, much of the available information on collisions comes from Washington State, while the abundance estimates for assessing mortality limits apply only to BC waters.

DISCUSSION

This study presents an objective and quantitative framework for identifying areas of elevated risk of ship strike for whales based on existing data on whale distribution and shipping traffic intensity. A pattern emerges that is consistent among the three species of whales (humpback, fin and killer), whereby areas with the highest relative risk (i.e. risk of ship strike within species) are found in 'bottlenecks'; regions where whale and boat densities are both concentrated (Fig. 2). Ship strike risk to killer whales is highest in Johnstone Strait, and for humpback whales, the Queen Charlotte and Johnstone Straits (northeast of Vancouver Island) and the narrow passages of the central coast are relatively high-risk areas for both species. Although the waters off southern Queen Charlotte Islands host the highest densities of fin whales, risk of ship strike is relatively low because of the low levels of shipping traffic there; the highest relative risk areas are found in Dixon Entrance where ship traffic is more concentrated.

While the risk assessments can predict where ship strikes are most likely to occur, they cannot predict how many strikes are actually occurring. One technical development that will assist these ongoing efforts is a more consistent use of the AIS system coastwide. While AIS coverage in BC is currently sparse, the system is expected to come into widespread use in the near future. At that point, the risk metric could be recalculated in absolute, rather than relative units. Efforts will still stall, however, at the point of evaluating whether current mortality rates can be deemed acceptable. A considerable hurdle for setting mortality limits is the inability to state Canada's current management objectives in quantitative terms and whether quantitative objectives will be based on N_{best} or N_{min} (i.e. the degree of uncertainty that will be tolerated). In BC, this is especially problematic for fin whales because of the large uncertainty associated with existing abundance estimates (Williams and Thomas, 2007). For the two baleen whale species, limits for an area, rather than a population, have been calculated because it is currently unknown what fraction of the populations was likely to be in the study area at the time of the survey, which will differ among species. In a related way, ship strike mortality may apply to killer whales year-round in this region but only for a limited period for the other species. Until information on stock boundaries and seasonal patterns in abundance becomes available, the range of mortality limits presented are necessarily simplistic, but a useful starting point for discussion. Based on objectives from the different management approaches reviewed (Table 1), potential limits to anthropogenic mortality would vary by an order of magnitude for both fin and humpback whales (Table 1). Regardless of the management approach and objectives that Canada eventually specifies, mortality limits will be relatively low for these species, both because populations are small and uncertainty in abundance estimates is large (Table 1).

It remains to be seen whether ship strikes are causing mortality rates that exceed all but the most precautionary limits to anthropogenic mortality, but a cursory review of the primary and grey literature reveals that ship strikes are far more common in the region than expected.

Estimating ship-strike mortality

Fin whales

Many British Columbians first became aware of the threat that ship strikes pose to fin whales in June 1999, when a cruise ship arrived in the port of Vancouver with a fin whale carcass draped over its bulbous bow. Although mortality rate estimates based on anecdotal information received through self-reporting and compiled in an informal monitoring scheme (Table 2; average of one animal per year in BC-Washington waters) are no doubt much lower than total mortality rates, estimated rates would still be high enough to trigger management action in other jurisdictions (e.g. New Zealand; Table 1). Nevertheless, high priority must be placed on identifying the degree to which under-reporting of ship strikes is occurring for this species. Existing abundance estimates for fin whales are accompanied by such large CVs (Williams and Thomas, 2007) that only the most catastrophic population declines problems would be detected. This lack of robust abundance estimates, coupled with an apparent propensity for fin whales to be struck by ships (Douglas *et al*., 2008; Laist *et al*., 2001), suggests that understanding ship-strike impacts on fin whales should be a priority for future work (Panigada *et al*., 2008).

Humpback whales

Collisions with humpback whales are reported frequently enough to raise concern. Three of the five reported collisions (Table 2) occurred in the 'high-risk area', which may reflect a true tendency for ship strikes to occur in areas where humpback whales aggregate and where shipping may intensify in narrow coastal passageways (i.e. 'bottlenecks'). Alternatively, it could reflect simply the high probability that whalewatchers, researchers and naturalists will detect and report such events because they too would be drawn to places where whales aggregate. One pattern seen in these sparse data is a tendency for humpback whale collisions to result in an uncertain fate of the animal. A priority is thus to ensure that additional resources are allocated to allow long-term monitoring of struck individual animals to assess post-strike survivorship. However, it is clear that under-reporting would have to be severe for annual mortality to be approaching anything but the most precautionary conservation objectives for this species. It is possible that 10-20 (Table 1) humpback whales could be killed each year by ships in BC and this level of mortality could go unnoticed or unreported, but existing data do not allow the plausibility of this scenario to be evaluated.

Killer whales

The number of collisions reported between resident killer whales and vessels was surprising given the attention paid in BC to whalewatching guidelines. However, resident killer whales are censused in most years by Fisheries and Oceans (DFO) Canada researchers (Ford *et al*., 2000) and heavily scrutinised by commercial whalewatchers, making it less likely that vessel strikes go unreported for killer whales than for fin or humpback whales. The small size and highly social nature of BC killer whale populations means that these populations are unable to absorb anything beyond very low levels of anthropogenic mortality (Table 1; Williams and Lusseau, 2006). Any limit to anthropogenic mortality established for these small populations would be low, regardless of the conservation approach (Table 1) and the minimum mortality or serious injury rates due to vessel collisions based on anecdotal information and self-reporting approach or exceed these limits already. Fortunately, BC killer whale populations are very well studied, and variation in mortality resulting from ship strikes would be detectable, provided that DFO's Cetacean Research Program and the Center for Whale Research (Washington State) have adequate resources to continue their long-term monitoring study of resident killer whales. However, clearly attributing a proportion of mortality to ship-strikes, or any anthropogenic cause, remains an obstacle for conservation efforts. For this reason, increasing the recovery and necropsy rates of killer whale carcasses is a priority for future research supporting the conservation of this species (Raverty and Gaydos, 2004).

Utility of the approach

The approach described here represents an early attempt to overlay whale and shipping density to calculate the spatial distribution of relative risk, which has been identified by the IWC Scientific Committee as an important step in understanding ship strikes. The approach adopted, namely to use GAM-based spatial models to estimate whale distribution (Hedley *et al*., 1999; Williams *et al*., 2006) and overlay spatially explicit data on marine vessel traffic intensity, provides a reasonable, quantitative and objective method to identify areas in which animals are particularly vulnerable to human activities. There is also value in reporting a range of mortality limits, when conservation objectives are not framed in easily quantifiable terms (Wade *et al*., 2008). For example, one of the motivations for this study was to assess the likely impacts on whales resulting from the expansion of the Port of Prince Rupert to accommodate increased bulk and container shipping. Given that most of the traffic is expected to travel in an east-west direction, this port development might lead to greater risk to fin whales than humpback or killer whales. On the other hand, fin, humpback and killer whales would all be impacted by the construction of a pipeline to Kitimat (Fig. 1) and the concomitant rise in petroleum tanker traffic in narrow passages along the central coast (Fig. 1: the coastal mainland north of Port Hardy and south of Prince Rupert). Given the difficulty in adequately monitoring oil pollution in most regions of BC, shipping intensity is one of the best available proxy indices for ship-source oil pollution (O'Hara and Morgan, 2006). In the same way, movement patterns for large vessels will probably also serve as a proxy for catastrophic oil spill risk. In August 2007, a barge loaded with a fuel truck and other equipment tipped over in the area identified to be the area of highest risk for interactions between killer whales and ships (Fig. 2). The accident spilled approximately 10,000L of diesel fuel and a similar volume of other hydrocarbons. It was estimated that approximately 25% of the northern resident killer whale population was seen in the vicinity of the spill and may have been exposed to fuel (Williams *et al*., 2009).

Quantitative risk assessments such as those presented here can be useful for identifying areas of overlap between intense or high-risk human activities and relatively large fractions of wildlife populations. This framework might be useful for evaluating various least-cost scenarios to plan new shipping routes that minimise threat to whales while also minimising disruption to industry. It would certainly be easier to consider whale distribution early in the planning stages before environmental impact assessments are completed, permits attained, business/operation plans are developed and infrastructure is built. There is a need for research to inform policy as soon as possible, before shipping traffic patterns become established, because once entrenched and integrated into business plans, shipping routes become difficult to modify. For humpback and killer whales, several channels along the Inside Passage emerge from the analyses as candidates for places where ships might be requested to travel at low speed, or to avoid altogether where feasible. Future risk assessments along these lines can inform management of protected areas and lead to efficient resource allocation for emergency preparation and response measures. If there is an accident, the industry responsible for the accident will likely benefit from such emergency preparation as this will lead to a more efficient response.

As Canadian management objectives for marine mammal stocks are being developed and articulated in quantitative terms (Hammill and Stenson, 2007; Johnston *et al*., 2000; Williams *et al*., 2008), it is time to assess the population-level consequences of ship strikes and non-fishery mortality in similarly quantitative terms. Fisheries and Oceans Canada is developing a regional marine mammal response network to respond to cetacean strandings, particularly for those species that are listed under Canada's Species at Risk Act. The spatial statistical modelling methods presented here provide a useful, visual tool for managers to identify potential problem areas, to manage shipping activities accordingly in as efficient a manner as possible, to allocate funds in priority regions for research, for identifying priority beaches to monitor for carcass detection and possible recovery and to mitigate impacts wherever possible.

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Factors that influence aerial line transect detection of Bering-Chukchi-Beaufort Seas bowhead whales

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ABSTRACT

This paper presents a rich, complex dataset including 25 years of aerial line transect surveys for bowhead whales in the Bering, Chukchi and Beaufort Seas, for which a distance detection function was estimated. The analysis was limited to the autumn migratory period and to the portions of the Beaufort and Chukchi Seas occupied by bowhead whales during this period. The primary purpose of the work was to improve the understanding of what factors significantly affect detection. Comprehensive model selection efforts based on the AIC identified useful predictors. Results showed that Beaufort Sea state, ocean depth, inter-sighting waiting distance and year were among the factors affecting detections. For example, increased depth and long wait distances between sightings were both associated with narrower effective strip widths. Some of the results can be interpreted as evidence for a relationship between detection probabilities and whale behaviour. The complexity of the overall dataset required substantial data organisation and offered many alternative analysis approaches, but the results were fairly consistent across such choices. Notwithstanding successful estimation of the detection function, the data present substantial challenges to standard abundance estimation using line transect methods.

KEYWORDS: ARCTIC; NORTHERN HEMISPHERE; BOWHEAD WHALE; BERING SEA; CHUKCHI SEA; BEAUFORT SEA; SURVEY-AERIAL; MODELLING

INTRODUCTION

In June 1978, a proposed oil and gas lease sale in the Beaufort Sea prompted the US Bureau of Land Management and subsequently the Minerals Management Service (MMS) to study the possible effects of industrial activity on the marine and coastal environment in this region. In response, from 1979-2007 annual aerial surveys of marine mammals were conducted in the Bering, Chukchi, and Beaufort Seas (B-C-B). These aerial surveys were named the Bowhead Whale Annual Survey Program (BWASP) and were carried out by the MMS, the Naval Ocean Systems Center and affiliated MMS contractors. Particular interest focused on the spatio-temporal distribution of bowhead whales (*Balaena mysticetus*) and the effects - if any - of industrial activity on this distribution. The primary types of industrial activities of concern included the exploration and development of petroleum resources, including seismic exploration. Industry impacts would have important implications for resource conservation and utilisation as well as for industrial regulation. The B-C-B bowhead whale population is utilised by native Inupiat and Yupik communities in northern and western Alaska, who conduct limited aboriginal hunting to satisfy subsistence and cultural needs as permitted by the International Whaling Commission. Bowhead whale avoidance of industrial activity could reduce availability of whales to the hunters and require villagers to venture greater distances at greater personal risk in order to hunt.

During the period of the surveys, the abundance of B-C-B bowhead whales has at least tripled from point estimates of 2,264 (with a 'range of uncertainty' of 1,082) in 1978 (Braham *et al*., 1979) to 10,470 (95% confidence interval 8,100 to 13,500) in 2001 (George *et al*., 2004). Even if bowhead whales avoided sites of industrial activity, counts of whales at such sites might increase over time merely due to increased total abundance. Therefore, indices of relative abundance would better detect spatio-temporal changes in migratory patterns in response to the growth of industrial activity in various locations over time. Although modelling the bowhead migration over time will be a key element of upcoming efforts to gauge potential industry impacts or other migratory changes, the goal here is more modest: to estimate an appropriate detection function for these surveys to better understand the impact of possible covariates on detection.

There are several reasons for this limited focus. The BWASP data have been statistically analysed only rarely and merit greater study. Organising the BWASP data for this analysis was in itself an enormous task and documenting this effort will aid future work while providing a common corrected database for analysis. Second, there are presently opportunities to improve the BWASP protocol. The results presented here can inform this process by identifying changes to survey design and more focused choice of covariates, thereby enabling a more efficient and effective survey. For example, there is discussion of how block randomisation is critical and how longitude and whale behaviour are vastly more important than sky and ice conditions in fall surveys. Finally, the detection function estimation presented here could serve as a component of a more sophisticated ongoing effort to build a spatio-temporal characterisation of the bowhead migration using methods similar to those of Hedley and Buckland (2004) and Hedley *et al.* (2004). Such modelling is beyond the scope of this study but it requires the careful estimation of a detection function and its dependence on covariates described here.

The multiple covariate distance sampling analysis used in this paper has proved useful in other situations where important covariates (Marques and Buckland, 2003; Marques *et al*., 2006) must be accounted for. In such cases, resorting to the pooling robustness notion of Buckland *et al.* (2001) - which would generally argue against fitting covariate effects in detection functions - can be a less useful approach. Reliance on pooling robustness is more relevant when estimating (relative) abundance, in which case integration over extra variation due to possible covariates is sensible.

Several authors have previously analysed subsets of the BWASP data. For example, Manly *et al.* (2007) analysed the 1996-98 BWASP data to explore how human activities

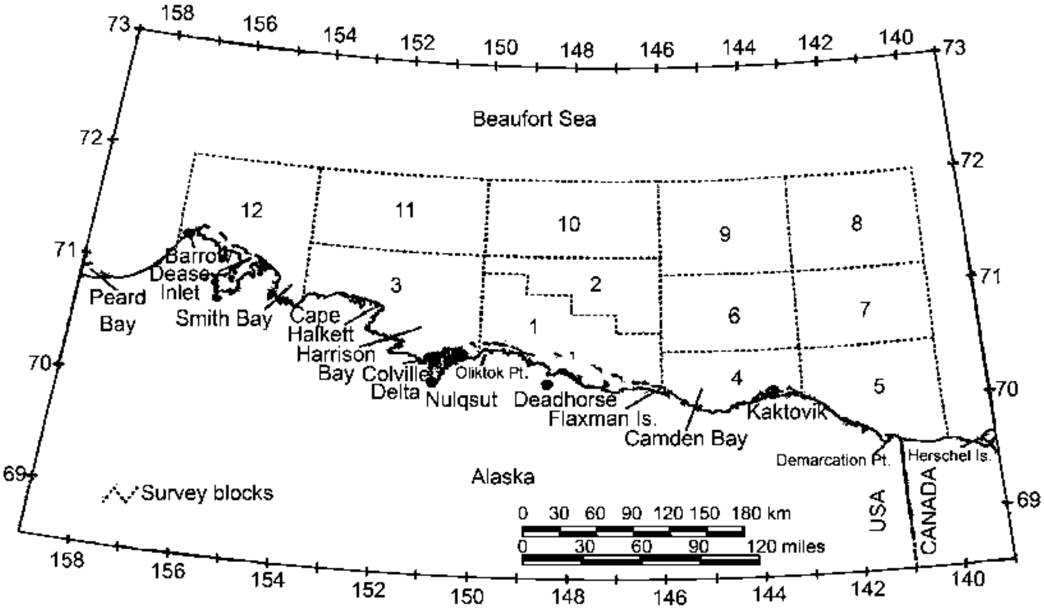

Fig. 1. Map of BWASP survey blocks [Monnett and Treacy, (2005), used with permission].

affected bowhead distribution. In their preliminary study based on these three years of data, the authors binned the transects into 5km long sampling units and used Poisson regression models to infer that there is evidence that seismic activity is associated with reduced numbers of observed bowhead whales. They also investigated whether whale swimming direction was impacted by marine seismic activity and found some evidence that it was. Schick and Urban (2000) found that bowhead whale distribution patterns were correlated with distance to oil drilling rigs. Treacy *et al.* (2006) investigated the effect of annual variation in ice distribution on bowhead migration patterns in the BWASP data, finding significant evidence that bowhead whales tend to migrate further offshore during heavy ice years compared to years with moderate or light ice.

Detailed description of BWASP survey methods is given by Treacy (2002) and Monnett and Treacy (2005). The analysis presented here was limited to 1982-2006, as equipment and protocol differences before then clearly render the earlier data incomparable. Survey methods were comparable from year to year thereafter. The 2000 survey described below illustrates key details of the protocol.

Survey methods

The surveys were conducted mainly in autumn between 140°W and 157°W and south of 72°N. Fig. 1 shows that the survey area was subdivided into 12 blocks. All survey flights began from Deadhorse, Alaska. There is no specification of a maximum sea state beyond which flights were cancelled; flights were conducted 'weather permitting'. For a given survey block, a random transect grid was determined by dividing the block into 30-minute of longitude sections. Minute marks along both the northern and southern edges of each partition were randomly chosen and connected with straight lines to create transect legs. This procedure was repeated for all 30-minute sections within the survey block. Northern and southern transect ends were connected alternately to form a flight path, and the start and end points were connected to Deadhorse. Fig. 2 shows a typical flight pattern.

During the 1982-2006 period, each year included between 23 and 93 flights. During each survey season, the pattern of block coverage was chosen opportunistically based on prevailing weather, a desire to investigate regions of potential industrial impact and sometimes on suspected regions of greater whale abundance. East of 154°W, two-week spatio-temporal coverage was disproportionately targeted towards areas of suspected higher relative abundance as inferred from past surveys (1979-86). Consequently, survey coverage yielded proportionally greater effort in near-shore regions and therefore increased total sightings by focusing on the primary migration corridor.

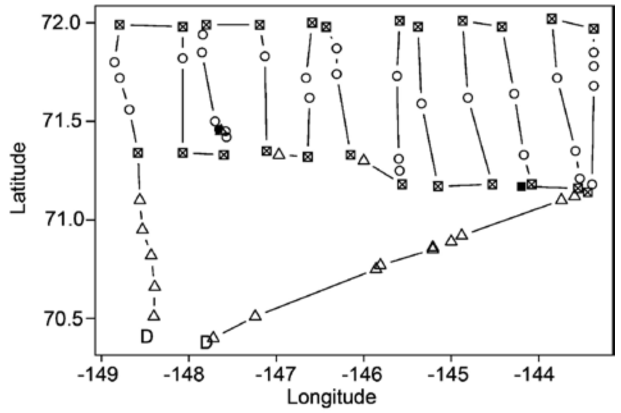

Fig. 2. Example flight path. Deadheads are 'D'. Points on search, connect, and transect are triangles, squares and circles, respectively. In these cases, hollow shapes are records with no sightings and solid shapes had sightings. Squares with 'X' in them are transition points to/from on-connect segments.

The partially opportunistic survey scheme violates one of the key assumptions of distance sampling analysis: that the transect lines should be randomly placed with respect to the distribution of animals (Buckland *et al*., 2001). It is important to emphasise, however, that concern about non-random block selection is mitigated here because no estimate of relative abundance will be produced; the interpretation of covariates that are associated with whale sightings here is in the context of the sampling design.

Surveys used a *de Havilland Twin Otter Series* 300 aircraft equipped with two medium-size bubble windows behind the cabin bulkhead and one on the aft starboard side.

These enabled complete trackline viewing and the pilot and co-pilot seats provided good viewing forward and to the sides. Sighting distances were measured orthogonal from the transect line abeam of the plane, and computed from altitude and hand-held clinometer readings. The nominal flight altitude was 458m (1,500ft). Observers and pilots communicated using a common communication system. Data were recorded on a laptop computer connected to a *Garmin III* Global Positioning System with external antenna, using a customised data-entry system.

Observers on the port side included the primary observer, positioned at a bubble window affording a view from the trackline below the aircraft to the horizon, the pilot, and an occasional secondary observer or visitor at an aft flat window. On the starboard side at a bubble window sat a data recorder-observer who partially focused on guarding the trackline, and a team leader at an aft bubble window. The co-pilot was also starboard.

Focus was limited to the area shown in Fig. 1 and to the period from August 28 to October 23, which encompasses the vast majority of the autumn bowhead migration in the survey area while excluding most summer residents (to the extent they may exist). Occasionally, a portion of a flight extended beyond the boundaries of the survey region. Therefore, a flight was deemed to be within the study area if no more than 10% of the positions recorded during that flight were outside the area. Only a few flights were eliminated on this basis.

For analysis, each single flight was broken into discrete portions, or segments, defined as a period of flight between two recorded events such as a sighting or incidental record of plane location taken during a lull. Each data record corresponds to the start or end of one segment. There are many more data records than sightings because additional data were recorded between sightings, as described below.

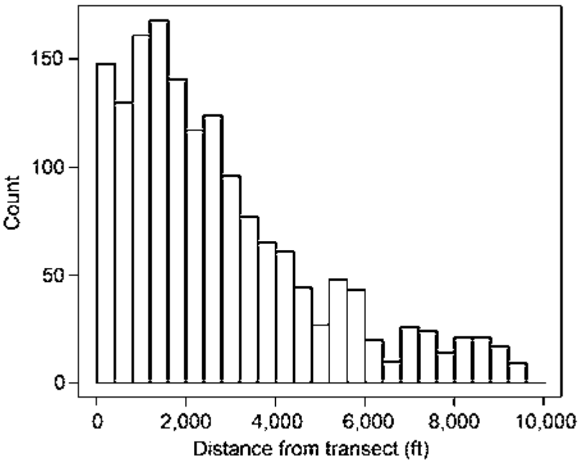

Fig. 3. Histogram of on-transect sighting distances (ft).

Flight segments to and from Deadhorse were denoted 'on-search', except that all flight portions over land were denoted as 'deadhead'. Segments on transect legs were denoted 'on-transect', with segments on connective legs between transects denoted 'on-connect'. Sightings during such legs were labelled as 'sighting-on-transect' and 'sighting-on-connect' (referred to below as 'sot' and 'soc'). Transect legs began and ended with 'start-transect' and 'end-transect' (referred to below as 'st' and 'et'). Occasionally, a possible cue or tentative sighting of some animal was detected. To investigate, a 'divert-transect' event was recorded, and the flight continued 'on-search' until the plane began 'resume-transect'. During on-search effort, the goal was to confirm or refute that the possible sighting was a bowhead whale. These on-search periods were generally characterised by a

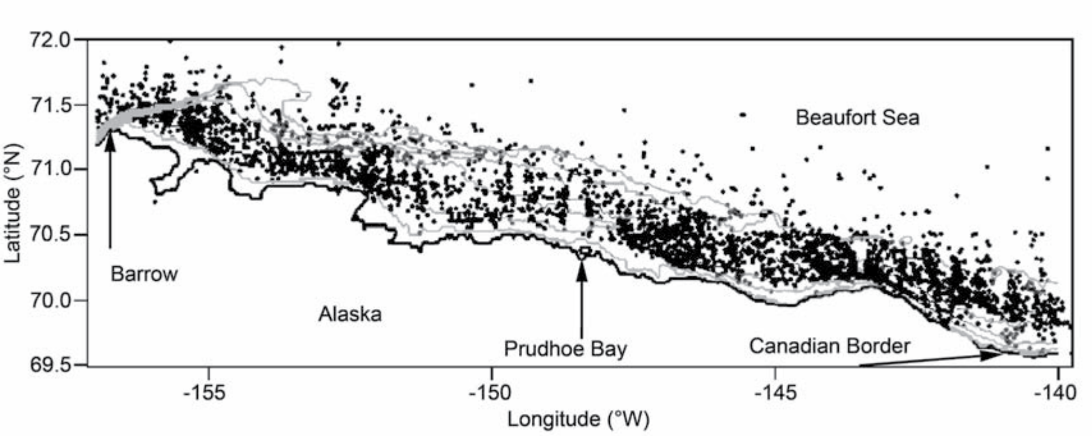

Fig. 4. All bowhead sightings. Contours of depth from 5m to 65m in increments of 10m are shown with light grey lines.

Table 1

Key covariates in the BWASP dataset. Counts of missing values are among only bowhead whale sightings not excluded for other reasons described in the text.

Observed variable	Levels	Number missing for bowhead whale sightings
Beaufort Sea State	B0,...,B8	15
Visibility on side of plane corresponding to sighting (km)	0, <1, 1-2, 2-3, 3-5, 5-10, unlimited	1
Sky condition	clear, overcast, partly cloudy	500
Percent ice (ICE)	0-100	0
Year since 1982 (YEAR)	0-24	0
Day (DAY)	Aug. 28-Oct. 23	0

limited period of circling. If at any time during the on-search period additional whales were sighted, they were recorded as 'sightings-on-search'. Perpendicular distances to on-search sightings were measured in the same manner as on-transect sightings, to the extent possible. Aside from sightings, records of location were recorded at 'point-on-transect', 'point-on-connect', and 'point-on-search' at convenient times between sightings (referred to below as 'pot', 'poc' and 'pos', respectively). Sightings of species were treated aside from bowhead whales as points on segments rather than sightings on segments. Rare circumstances required 'abort-flight' events. A histogram of on-transect sighting distances is shown in Fig. 3. Fig. 4 shows all bowhead whale sightings in the dataset.

MATERIALS AND METHODS

The raw dataset contained 1,187 flights consisting of 84,543 records including 4,469 bowhead sightings and over 750,000km of total flight distance. The number of bowhead whales per sighting (cluster size) was initially ignored in the analysis because the distribution of cluster sizes was extremely skewed. Although whale behaviour likely has important implications for detection, it was not explicitly included in estimation of detection probabilities because the key behaviour, feeding, was only observed in 2.8% of cases. For each sighting (and frequently for other types of records during the flight), a variety of covariates were recorded. Key covariates are listed in Table 1. It is important to note that the 'visibility' variable describes the atmosphere, not some informal combination of atmosphere, sea conditions and other factors. Ice coverage and visibility were judged subjectively. English units are used on occasion for covariates for consistency with the original data records.

A variety of data coding errors and omissions were detected during the analysis. Out of the 84,543 records, there were 4,816 corrections to sea states, 37,757 corrections to visibilities, 3 corrections to ice coverage, and 1 event type correction, mostly due to inconsistent data coding. Twelve missing visibility entries were imputed when visibilities were discernable from long sequences of identical entries in temporal windows surrounding the missing entry. Finally, 78 event types were altered to the most sensible alternative because the original entry was not sensible. For example, a sighting-on-transect (sot) entry would be changed to sighting-on-connect (soc) if it occurred in the sequence st-pot-pot-pot-et-poc-poc-**sot**-poc-poc-poc-st-pot-pot-et.

Of the available flights in this corrected dataset, 786 flights were retained for being within the time and space limitations described above. The data for these flights comprised 50,463 records after deleting 1,712 records with failed or missing clinometer readings and 91 repeat sightings. Among these data, there were 2,786 bowhead whale sightings comprising 1,695 observations on-transect, 1,000 on-search and 91 on-connect.

From these raw data, a variety of additional covariates were constructed (Table 2). Sea-state and visibility were categorised. The categorisation of Beaufort Sea state was intended to bin sea-states into glassy, intermediate, and choppy conditions and is hereafter labelled BSS. Visibility categories (VIS) were constructed to provide sufficient bin counts and to maximise between-bin differences in detection probabilities. Later, for the purposes of averaging, the 'unlimited' category was treated as 20km. Available GIS data (NOAA, 2008) were used to determine the water depth (DEPTH) at each sighting. Preliminary comparisons of the effects of water depth and offshore distance indicated that depth was a more effective covariate. These two variables are very highly correlated due to the bathymetry of the region, where depth contours closely match the shoreline except along the west edge of the survey region in the Barrow Canyon. In addition to providing slightly better predictive power, depth may also be the more ecologically sensible covariate (see Discussion).

To investigate spatial patterns, an idealised shoreline was created, which is a straight line from Point Barrow to the point on the coast at the Canadian border. Given this definition, the distance along this idealised shoreline (DAS) was calculated for each sighting. Due to the shape of the northern Alaska coastline (Fig. 1), DAS correlates strongly with longitude. This variable was standardised so that the distance from Barrow to Canada was approximately three standard deviations, with smaller values indicating greater proximity to Barrow.

Many of the additional covariates pertain to sums or averages accumulated along the flight path, not only at sightings but also for most other segments along the flight path. The 'waiting distance' (WAIT) was defined to be the total distance along the flight path from the previous sighting (or from the start of the survey) until the present sighting. Covariates were averaged over this wait, reflecting the possibility that conditions associated with a sighting may be better summarised by typical conditions while awaiting the detection rather than specifically at the moment of detection. One justification for this approach is that it reduces variability when measurement of conditions includes a notable white noise component. The approach is also useful when covariate observations at the moment of detection are missing.

Covariate averages were computed as follows (e.g. Fig. 5). Each waiting distance comprises a collection of one or more shorter segments determined by records of point-on-transect, etc., as described above. A covariate average over a waiting distance was defined to be the segment length-weighted average of the covariate values over all non-

Table 2

Additional covariates created for analysis, including those averaged or summed over waiting distances.

Computed variables	Method of calculation
Categorical sea state (BSS)	Low (B0-B1), Medium (B2-B3), and High (B4 and above)
Categorical visibility (VIS)	Low (≤ 5), High (>5)
Raw Beaufort Sea state average	Average of values from 0 to 8
Categorical BSS average	Average of values of 1, 2 or 3
Raw visibility average	Average of midpoints of original visibility intervals
Categorical visibility average	Average of VIS
Raw ice coverage average	Average of values from 0% to 100%
Waiting distance until sighting, std. units (WAIT)	Accumulated as described in text
Location of sighting along idealized shoreline, std. units (DAS)	See text

missing data along the segment. Specifically, for a given flight, let *n* denote the number of segments within a flight, determined by records at points $p_0,...,p_n$. Denote the between-point segment lengths $l_1,...,l_n$. Let the covariate x_i be measured at some or all of the points. Then let the indicator z_i equal 1 if x_i is observed and 0 if it is missing, so that x_i contributes to the average only when z_i=1. Finally, let integers s_j⌊ {1,...,*n*} index sightings and locations so that $s_j=k$ if the *j*th sighting occurs at p_k. The weighted average covariate value corresponding to the *j*th sighting is given by

$$\overline{x}_{s_j} = \frac{z_{s_{j-1}} x_{s_{j-1}} l_{s_{j-1}+1} + \left\{\sum_{i=s_{j-1}+1}^{s_j} z_i x_i \left(l_i + l_{i+1}\right)\right\}}{z_{s_{j-1}} l_{s_{j-1}+1} + \sum_{i=s_{j-1}+1}^{s_j} z_i \left(l_i + l_{i+1}\right)}$$

for *j*=1,...,*b*, where s_0=0, the number of bowhead sightings on the flight is *b* ≥1, and l_{s_j+1} must exist since no flight ends with a sighting. Furthermore, the above discussion over-simplifies the definition of the z_i: there are reasons aside from missing data when x_i should not contribute to the waiting period. For example, any single segment from deadhead to abort-flight should not count in the average.

When the covariate *x* is categorical with levels 1,...,*M*, analogous expressions can be defined for the weighted average level (averaging level values) and for the weighted average proportion of the waiting period spent in level *m* (averaging binary indicators of state). The former approach is not sensible unless the levels are at least ordered.

The analysis was based on only the on-transect sightings. The *DISTANCE* program (Thomas *et al*., 2006) was used to fit parametric models for detection functions with covariates. For example, a detection function based on an underlying hazard function model (see below) can take the form

$$g(y) \quad 1 \quad \exp\{\ (y/s)^{\alpha}\}$$

where

$$s = \beta_0 \exp\left\{\sum_{i=1}^{c} \beta_i X_i\right\}$$

and the X_i denote covariates 1,...,*c*. The parameters of this model are α and β_i for *i*=0,...*c*.

Initial model selection was conducted by incorporating each covariate listed in Tables 1 and 2 in a separate model for estimation of the detection function, using *DISTANCE 5.0* (Thomas *et al*., 2006). Half-normal (with possible Hermite expansions) and hazard function (with possible polynomial expansions) models were investigated. On the basis of Akaike's information criterion (AIC) and log likelihood comparisons between models using the alternative versions of the same covariate, a preferred version or binning of each covariate was selected. These covariates have been assigned capitalised labels in Tables 1 and 2, namely BSS, VIS, ICE, WAIT, DAS, DEPTH, DAY, and YEAR. Sky condition was never found to provide any useful information and is hereafter ignored. The distribution of depths at sighting locations was extremely skewed, with a heavy tail to the right. Concern about the influence of this skew led to consideration of using log(depth). After experimentation, it was determined that a more reliable approach was to eliminate the 2.6% of sightings at depths exceeding 200 feet (61m).

With these data and covariates, model choice was made using a forward selection strategy with AIC (Burnham and Anderson, 1998) as the comparison metric, stopping when no additional variable reduced AIC by at least 2.0 units. This model selection exercise was conducted independently for two choices of data truncation. For the first choice, observations with distances exceeding 5,280 feet (1,609m) were excluded, roughly corresponding to the distance at which a preliminary estimated detection function equalled 0.15. For the second choice, observations with distances exceeding 9,500 feet (2,896m) were excluded, closely corresponding to 95th percentile of distances. Both strategies are among those offered by Buckland *et al.* (2001).

Table 3

Results from stepwise AIC model selection. For truncation at 9,500 feet, there was an inconsequential tie.

Model	ΔAIC
Truncation at 5,280 feet	
BSS +WAIT+YEAR+DEPTH	0.0
BSS+WAIT+YEAR	2.2
BSS+WAIT	5.6
BSS	9.5
NULL	15.2
Truncation at 9,500 feet	
WAIT+DEPTH+DAS+YEAR	0.0
WAIT+DEPTH+DAS	2.5
WAIT+DEPTH	7.6
WAIT+DAS	7.6
WAIT	11.6
NULL	20.8

RESULTS AND DISCUSSION

Model choice

Initial model fitting showed that the normal model was always worse than the hazard model. Therefore model selection was limited to the hazard model for the detection function. Although polynomial covariate terms were not considered in the model, polynomial expansions to the hazard model were investigated. These usually did not improve AIC, therefore model selection was also limited to models with no series expansion terms.

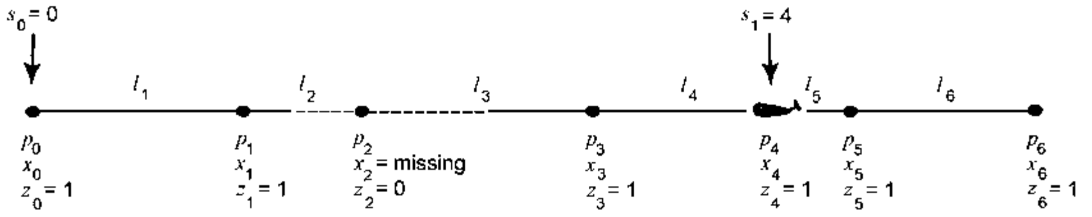

Fig. 5. Illustration of segment-weighted averaging for the first sighting on a transect. At point p_4 a bowhead was sighted. The covariate values x_1, x_3 and x_4 contribute (in proportion to their respective surrounding segment lengths) to the average covariate value during the wait until the sighting (at the fourth point here). The value at x_2 cannot contribute because it is missing.

Table 3 shows the model selection results for the datasets with distance truncations at 5,280 and 9,500 feet, respectively, using the simple hazard model. Aside from the null model, models constituting steps in a logical progression of nested models leading to the best model and having improvements of at least 2.0 AIC units are shown.

Having identified good models, the question of cluster size effects was revisited. To compensate for the extremely skewed distribution of this covariate, cluster size was separated into three categories: 1 whale; 2 whales; and at least 3 whales. The addition of this variable raised AIC, indicating an inferior model fit adjusted for the increased number of parameters. Thus, contrary to expectations, cluster size did not affect the detection function. This may reflect the fact that most sightings occurred in good sea states and good visibility conditions with little sea ice. However, since the distribution of cluster sizes is highly positively skewed, there may be too few data to obtain a reliable estimate of cluster size effects, particularly since the comparative impact of large cluster sizes is likely most severe at extreme distances but sighting distances were truncated at 5,280 feet for analysis.

The on-connect and on-search data were not used in the main on-transect analyses. The protocol employed during on-connect survey effort was similar to that for on-transect except that some observers may rest. There are 66 additional on-connect sightings with no relevant missing covariates. Fitting a model identical to the best one shown in Table 3 but including the on-connect data yielded a similar estimate of the detection function found in our chosen model, and the average effective strip width was decreased by less than one percent. Notwithstanding this result, future survey protocol could be improved by clearly articulating the goal for on-connect effort. Ideally, on-connect effort should be identical to on-transect effort and the protocol should reflect this goal.

The protocol for on-search survey effort was qualitatively different than for either other survey mode. However, a histogram of on-search distances is virtually indistinguishable from on-transect distances. The same model identification and fitting strategy as above was experimented with, applying it only to the on-search data truncated at 5,280 feet. In this case, only DAS influenced detection. Recall that on-search effort is triggered by the sighting or suspected sighting of a whale. Therefore, variables that assess sighting conditions (such as BSS, ICE, VIS) and variables that reflect relative density (such as WAIT and YEAR) should no longer matter. The importance of DAS for on-search data probably relates again to whale behaviour: feeding and clustering in the eastern Beaufort as opposed to swimming further westward. Of course, the on-search analysis cannot be considered reliable due to its survey protocol.

Model results and diagnostics

Table 4 provides the parameter estimates for the two models discussed above. Hereafter the model using distance truncation at 5,280 feet is focused on. This model should be less sensitive to the right tail of the distance distribution, thereby likely providing a better fit to the bulk of the data.

The average effective strip half-widths (ESW) were 3,635 feet (1,108m) and 4,246 feet (1,300m) for the small and large truncation distances, respectively, with CVs of less than two percent.

Buckland *et al.* (2004) describe several goodness-of-fit model diagnostics. A quantile-quantile plot showed good correspondence between observed and fitted cdfs, except that the observed data include some zero distances, as would be due to heaping or rounding. The model need not be adjusted in this case (Buckland *et al*., 2004). The cosine-weighted Cramer-von Mises test provided no evidence of a poor fit ($p>0.15$). Informal examination of graphs of the model fit also identified no severe problems.

Interpretation and discussion

For BSS, we found that glassy sea state (B0-B1) reduced the effective strip width compared to when sea state is merely good (B2-B3). This is counterintuitive because one would expect greater ease of detecting distant whales when conditions are excellent. However, for white whales (*Delphinapterus leucas*) DeMaster *et al.* (2000) found no convincing relationship between BSS and ESW. It is suspected that the finding presented here may partially reflect observer behaviour. Despite the intended survey protocol, observers may have favoured nearby effort during excellent conditions because sightings were comparatively easy. Nevertheless, other past studies of bowhead whales (Cosens *et al*., 1997) and other cetaceans (e.g. Kingsley and Reeves, 1998) have found that sightings per unit effort were reduced in poorer sea states.

An alternative explanation for the BSS finding is that the binning of sea state categories may not have been the best choice. To investigate this, a different binning of BSS was considered, namely low (B0,B1,B2) and high (BSS≥3). Such a binning separates unbroken surfaces from surfaces with some breaking crests. The model was re-fitted using this binary BSS pooling and found virtually no effect for BSS. Although this represents a weakening of the primary BSS finding, it still fails to indicate a reduction in ESW as sea states deteriorate. Perhaps one could infer that when sea states are poor, sightings are so difficult that it doesn't much matter how nearby you look.

It is also difficult to disentangle a BSS effect from potential effects of location and behaviour. There is a strong relationship between BSS and sighting location. The median sighting location during excellent sea states (B0-B1) is 69% further eastward than during good (B2-B3) states. In addition, whales sighted in the eastern Beaufort tend to be feeding (particularly before the peak migration), whereas whales in the western Beaufort and eastern Chukchi are migrating (see Fig. 6). The median cluster sizes for diving, swimming, and feeding whales are 1, 1, and 5, respectively.

DEPTH is another influential term in the models. The ESW narrows with increasing depth. Whales sighted at locations having large sea depths generally are swimming quickly as they migrate westward at high latitudes with little clustering. Feeding whales tend to be in shallow water (see

Table 4

Parameter estimates (standard errors) for selected models.

Truncation	DEPTH	WAIT	YEAR	BSS (low)	BSS (high)	DAS	β_0	α
5,280	-0.0023	-0.090	-0.015	-0.22	0.47	NA	4,358	2.52
	(0.0012)	(0.043)	(0.006)	(0.09)	(0.92)		(63)	(0.91)
9,500	-0.0030	-0.118	-0.011	NA	NA	0.073	3,999	2.13
	(0.0012)	(0.043)	(0.006)			(0.067)	(53)	(0.75)

Fig. 6). If distant whales are more difficult to detect unless they spend relatively more time near the surface and/or if lone whales are more difficult to detect at large distances than are clusters, then the observed inverse correlation between ESW and depth would be expected.

Next the effect of WAIT was considered. Fitting an adjustment term for WAIT is the continuous analogue to stratifying the analysis by encounter rate as described by Buckland *et al.* (2001). It was found that long waits between sightings are associated with reduced ESW. One explanation for this may be that long waits are associated with poor sighting conditions, during which periods of effort might tend to be focused closer to the plane. More importantly, long waits clearly serve as a proxy for all sorts of unmeasured variables that effect sighting probability. Although the BWASP dataset contains data on several such variables, many other factors (known and unknown) probably impact detection probabilities as well. WAIT is effectively an indirect measure of such effects. It should be emphasised that WAIT is not a factor that can be controlled by the surveyors. However, one implication of the finding is that it may be useful to stratify data by encounter rate when analysing bowhead whale aerial survey data.

The results in Table 2 for the model with truncation at 9,500 feet show that the only covariate substitution in the alternative models is the exchange of BSS for DAS. As discussed above, there is a strong positive correlation between increasing DAS and improved sea states. These two variables act as partial surrogates for each other. Furthermore, the presence of DAS in the model explains why calendar day is not selected in the modelling. Recall the spatio-temporal nature of the migration. Early in the autumn season, when weather tends to be better, the whales are mostly in the eastern portion of the survey region and sightings predominate there. Later in the autumn as the weather degrades, the whales (and sightings) are mostly in the west. Although these correlations involve DAY too, we believe that the position along shore is a superior indicator of the location of whales during the migration because the day-to-day timing of the migration exhibits substantial inter-annual variability.

Increasing YEAR decreases the ESW. George *et al.* (2004) have estimated that the bowhead whale population abundance has increased dramatically over the BWASP survey period. Thus the results presented here confirm again that encounter rate affects the detection function.

Due to serious concerns about the survey design and features of the data, a reliable estimate of total abundance cannot be obtained from the BWASP data. Nevertheless, a crude reality check based on these results is not alarming. For the year 2000 on-transect data only, there were 46 sightings over a survey region of 1.185e+12 ft^2. Effort was strongly imbalanced in 2000, so the analysis was stratified into two regions: one with sparse effort and one with heavy effort. Across both regions the total transect length was about 3.485e+7ft and the average effective strip width was taken to be the estimate for the model with distance truncation at 5,280 feet. These results yielded uncorrected abundance estimates of 63 and 141 whales for the sparse and dense regions, respectively. Krutzikowsky and Mate (2000) provide estimates of correction factors for availability due to bowhead whale diving behaviour. They estimate that bowhead whales are sufficiently near the surface to be available for visual detection from the airplane 11.1% of the time. Heide-Jørgensen *et al.* (2007) offer a perception bias correction factor of 0.48. The mean cluster size in the data presented here is 2.04. Adjusting for all these correction factors yields a crude estimate of total abundance of 7,836 whales. One notable source of downward bias in this estimate is that it ignores 38 additional whales seen on-connect and on-search with comparatively little extra survey effort. For 2001, a reliable abundance estimate is 10,470 with 95% confidence interval (8,100-13,500); see George *et al.* (2004).

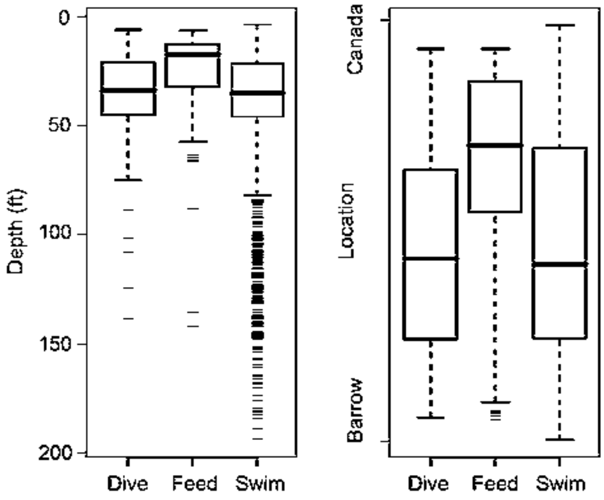

Fig. 6. Boxplots of depth and location of sightings split by whale behaviour.

Although the BWASP data constitute one of the longest and richest time series of data regarding bowhead whales, they also present serious challenges for analysis and interpretation. Most notably, the block coverage was not wholly random with respect to the distribution of animals, although transects within blocks were random. Non-random block selection can bias estimates of relative density. However bias in estimation of the detection function should be reduced if detection probabilities are independent of location and adequate covariate sampling is maintained. The transect locations also changed every season. Although this might be important for a monitoring programme, it is not necessary for estimation of absolute or relative abundance, nor for the detection function estimation we present here.

The spatio-temporal variation in whale presence, survey coverage, and whale behaviour (and hence availability) presents another challenge for analysis. Adjustment for short-term and long-term changes in encounter rates merits consideration. Stratification by encounter rate can be implemented in the survey design, or in *post hoc* analysis. In general, stratification can be carried out on the basis of encounter rates and/or covariates shown to influence the detection function. For the model fit to data truncated at 5,280 feet, the only covariate available for stratification during the survey would be depth. Such stratification could be particularly effective because whale presence is extremely strongly (negatively) correlated with depth.

Over the 25 year period of surveys, many aspects of the survey effort and region must have changed: migration patterns may have systematically evolved over time; weather conditions may have changed, and ice coverage has clearly decreased over the period despite substantial interannual variation; observers have changed, along with equipment. Such variations raise the question of whether a single detection function can reasonably be fitted to data collected over such a long period.

Despite the above difficulties, several other important distance sampling assumptions listed by Buckland *et al.* (2001) appear quite reasonable for this dataset. Compared to the scale of transect strip widths, animals are detected at their initial locations for all practical purposes. There is probably little response to the aircraft: for example Patenaude *et al.* (2002) estimated that only 2.2% of bowhead whales reacted to overflights of a *Twin Otter* aircraft and that the vast majority of these occurred at flight altitudes not exceeding 182m. In the BWASP data, the target flight altitude was 458m and only 2% of on-transect sightings occurred at less than 182m. Clinometer readings should be reliable, except that there was heaping on 5° increments (variation in altitudes meant that no heaping was seen for distances). There are some distance outliers when clinometer readings were very small, but these were eliminated during the data truncation phase. Finally, a shoulder in the histogram of sighting distances is clearly seen near zero (Fig. 2), providing a better basis for estimation of the detection function.

Considering the results overall, it appears that the detection function depends notably on whale behaviour. When information on behaviour is sparse or lacking, it appears that variables related to space and time can be used as surrogates, as long as information about spatio-temporal patterns of behaviour is available. Annual surveys like BWASP are likely to continue in the near future, providing even greater opportunity to improve understanding of bowhead whale detection, distribution, behaviour and migration in the region.

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Migration ranks for bowhead whales (*Balaena mysticetus*) at Barrow in spring

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ABSTRACT

In a series of aerial photographic surveys of bowhead whales migrating past Barrow in Alaska in the spring, 40 individuals were captured in more than one year. To study individual-specific persistency in migratory pattern, the relative ranks of the captures of these whales among all captures that year were analysed. Controlling for body length and the presence of calves, the correlation of relative ranks in individuals captured multiple times was found not to be significantly different from zero (p-value=0.78).

KEYWORDS: BOWHEAD WHALE; MARK-RECAPTURE; MIGRATION; MODELLING; PHOTO-ID; SURVEY – AERIAL; BERING SEA; BEAUFORT SEA; CHUKCHI SEA; NORTHERN HEMISPHERE

INTRODUCTION

Bowhead whales in the Bering-Chukchi-Beaufort Seas migrate in the spring north and eastwards past Barrow, Alaska, but to what degree does an individual keep its temporal rank in the migration from year to year? This question is interesting from a behavioural point of view. Behaviour is of interest in itself, and is also of concern for abundance estimation and other studies. Schweder *et al.* (2009) used results from the present paper when estimating abundance and demographic parameters from aerial photographic surveys of bowhead whales.

The spring migration happens during or shortly after the mating season, so bowhead whales have an opportunity for genetic interchange across most of the population if there is little temporal stratification in the ranking of whales through the migration. The question above is therefore also of interest when investigating possible structure in the bowhead whale population in the Bering-Chukchi-Beaufort Seas.

The calendar time of the migratory season varies from year to year (Rugh *et al.*, 2008). The calendar day of capture is therefore not directly useful, and the relative rank of a capture within the captures made in the respective year was used. Provided the surveys were timed similarly relative to the migratory season, the relative ranks are invariant to temporal shifts in the migratory season. Mothers with calves, and also most large whales without calves, are known to migrate relatively late (Angliss *et al.*, 1995; Nerini *et al.*, 1984; Rugh, 1990). This paper measures the effects on relative rank of these covariates, both within all captures and within the recaptures.

A mixed effects linear model was used with normally distributed individual effects, and with fixed effects for length, being associated with a calf and for differences in years between recapture and capture. The response variable is the logistic transform of the relative rank (rank divided by number of captures in the survey plus one).

METHODS

The data are summarised in Tables 1 and 2 and Figs 1 and 2. They were obtained through systematic aerial photographic surveys during the spring migration at Barrow, Alaska (Rugh *et al.*, 2008). The length measurements were obtained from the photographic images when possible. When duplicate images have been obtained for a whale, the average value of lengths was considered as a length value for this whale. The mean measured length of the 1,782 captures in the subset where length is recorded is 12.03m and among the 40 recaptured individuals where length is recorded is 13.88m.

To investigate possible persistence over the years in relative rank within individuals, the ranks of the 40 individual whales that were photographically captured in more than one year were examined. The matching protocol was stringent to avoid false positive matches (Rugh *et al.*, 1998; Schweder *et al.*, 2009) and it was assumed that the recorded recaptures were real. There may have been, however, unrecognised recaptures because many bowhead whales were not marked uniquely enough to be consistently recognised in aerial photographs. The relative ranks at capture and recapture are shown in Fig. 2.

Among the 40 whales, 38 were seen in two years, and two whales were seen in three different years, making 42 recognised between-year recaptures. When length was recorded for both capture and recapture its mean was used for both captures. This was done to reduce the effect of measurement errors (9 of 28 whales had a smaller recorded

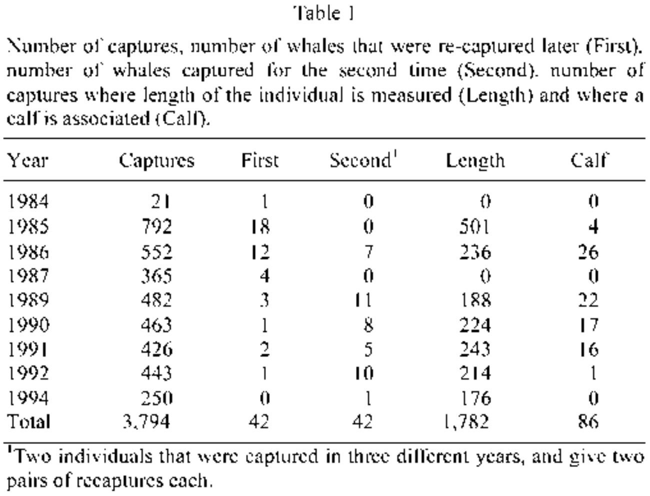

Table 1

Number of captures, number of whales that were re-captured later (First), number of whales captured for the second time (Second), number of captures where length of the individual is measured (Length) and where a calf is associated (Calf).

Year	Captures	First	Second[1]	Length	Calf
1984	21	1	0	0	0
1985	792	18	0	501	4
1986	552	12	7	236	26
1987	365	4	0	0	0
1989	482	3	11	188	22
1990	463	1	8	224	17
1991	426	2	5	243	16
1992	443	1	10	214	1
1994	250	0	1	176	0
Total	3,794	42	42	1,782	86

[1] Two individuals that were captured in three different years, and give two pairs of recaptures each.

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Table 2

Bowhead whales resighted during the spring migration past Point Barrow, Alaska. Whale numbers are as defined in the database. Date at capture (Sighting 1), date at recapture (Sighting 2), length at capture (Length 1) and length at recapture (Length 2) are given.

Whale no.	Sighting 1	Length 1	Sighting 2	Length 2
1058	18/05/1985	13.46	13/05/1986	12.88
1184	07/05/1987	N/A	23/04/1992	15.17
1880	08/05/1991	13.59	13/05/1992	N/A
1890	08/05/1984	N/A	23/04/1992	13.37
1921	02/05/1985	10.15	05/05/1990	10.55
1937	11/05/1985	13.23	27/04/1992	13.36
2024	14/05/1985	10.37	12/05/1986	N/A
2037	17/05/1985	14.97	29/05/1986	15.17
2200	22/05/1985	16.31	26/05/1991	16.16
2217	23/05/1985	14.63	10/05/1991	14.49
2246	26/05/1985	13.39	06/05/1989	14.05
2247	26/05/1985	13.38	17/05/1989	N/A
2291	27/05/1985	13.50	18/05/1989	N/A
2312	29/05/1985	14.59	19/05/1990	13.71
2347	31/05/1985	14.56	11/05/1986	14.67
2371	01/06/1985	15.05	26/05/1992	15.46
2374	01/06/1985	13.88	29/05/1986 [1]	14.29
2384	02/06/1985	12.97	15/05/1989	14.01
2392	02/06/1985	14.45	22/05/1986	13.97
2392	22/05/1986	13.97	18/05/1989 [2]	14.66
2403	02/06/1985	14.34	19/05/1986	13.98
2428	06/06/1985	16.70	27/05/1989	16.01
3963	11/05/1986	9.80	14/05/1992	11.26
4020	11/05/1986	13.33	06/05/1989	13.79
5149	09/05/1992	13.57	25/05/1994	14.45
7946	06/05/1986	12.99	03/05/1989	13.60
8002	11/05/1986	13.44	10/05/1991	14.17
8015	11/05/1986	13.51	02/06/1990 [1]	13.80
8026	11/05/1986	N/A	16/05/1992	13.71
8033	11/05/1986	14.60	19/05/1990	14.72
8090	14/05/1986	N/A	19/04/1989	12.84
8135	22/05/1986	13.65	21/04/1989	13.05
8142	22/05/1986	13.78	19/05/1990	13.34
8250	04/05/1987	N/A	11/05/1990	14.56
8288	08/05/1987	N/A	25/05/1991 [1]	16.03
8312	18/05/1987	N/A	11/05/1990	13.76
8622	19/05/1986	13.55	26/05/1989 [1]	13.94
8744	20/04/1989	12.61	13/05/1992	13.56
8824	25/04/1989	12.75	14/05/1992	14.57
9304	31/05/1989	N/A	29/05/1990	14.18
9304	29/05/1990	N/A	10/05/1991 [1, 2]	14.95
10573	11/05/1991	14.68	26/05/1992	15.26

[1] Accompanied by a calf. [2] Third resighting.

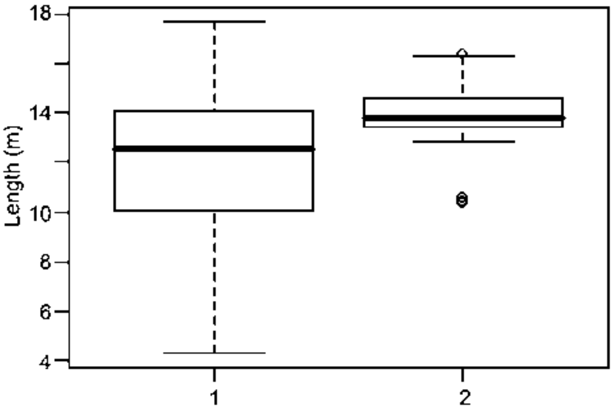

Fig. 1. Boxplot of length data for all captures (1) and for captures with recaptures (2).

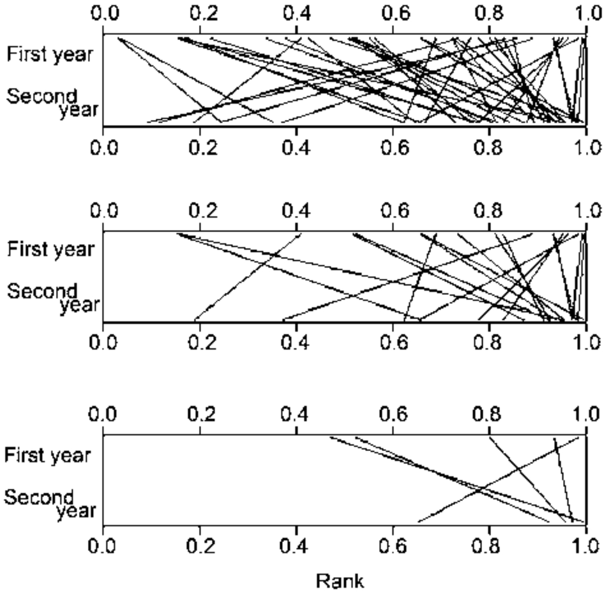

Fig. 2. The relative ranks at capture (first year) and recapture (second year) for all whales (top); for large whales (length more than average 13.88m) (middle); and for whales with calves (the whales were seen with calves only in the second year) (bottom).

length at recapture than at capture). When length for one capture or recapture was not recorded, the recorded capture or recapture length of that individual was imputed. Any bias introduced by this was small since bowhead whales grow slowly (Angliss *et al*., 1995; Koski *et al*., 2006), particularly after sexual maturity.

In addition to body length, an indicator covariate for being associated with a calf and also the difference in years between recapture and capture were used in a logistic mixed regression of the relative ranks of recaptures which is denoted 'time'. Large whales are known to be late migrants. The covariate time was introduced to see whether migration tends to be later the older the whale is when controlling for length.

Logistic mixed model

Years is denoted by y and recaptured whales by i. A logistic mixed model was considered with three whale-specific covariates denoted as 'calf', 'length' as explained above, and 'time'. The latter is zero at capture and the number of years from capture to recapture. Length was measured in meters, but with mean length for all length-measured individuals subtracted. The response of whale i in year y

$$\mathrm{rank}_{iy} = \frac{r_{iy}}{n_y + 1}$$

where r_{iy} is the sequence number of the capture among the n_y captures that year.

For recaptured individuals the model is:

$$\ln\left(\frac{\mathrm{rank}_{iy}}{1-\mathrm{rank}_{iy}}\right) - \beta_0 - \beta_c \cdot \mathrm{calf}_{iy} + \beta_l \cdot \mathrm{length}_{iy} + \beta_t \cdot \mathrm{time}_{iy} + \xi_i + \varepsilon_{iy}. \quad (1)$$

where β_0, β_c, β_l and β_t are regression coefficients, ξ_i is a whale-specific random variable that represents the degree of consistency with which whale i positions itself in the migration sequence in different years, and ε_{iy} is a residual term. The clusters, i.e. the data referring to individual whales, are assumed independent.

The random individual effects and the residual terms are assumed to be independent and normally distributed with mean zero, and with $\mathrm{Var}(\xi_i) \equiv \sigma^2$ and $\mathrm{Var}(\varepsilon_i) \equiv \theta^2$.

Dependence between any two responses, rank_{iy} and $\mathrm{rank}_{i\hat{y}}$, for the same whale captured in years y and $\hat{y}$ respectively can be expressed by the correlation between the logistic transforms

$$\rho \equiv \mathrm{Cor}(\ln(\frac{\mathrm{rank}_{iy}}{1-\mathrm{rank}_{iy}}), \ln(\frac{\mathrm{rank}_{iy'}}{1-\mathrm{rank}_{iy'}})) = \frac{\sigma^2}{\theta^2+\sigma^2}. \qquad (2)$$

Large individuals, and also mothers with calf, are known to be late migrants (Angliss *et al*., 1995; Koski *et al*., 2006; Nerini *et al*., 1984; Rugh, 1990). How much they delay their migration in terms of relative rank was measured by the logistic regression effects of the covariates calf and length on the relative migration rank for all the 1,782 captures for the subset of the data where length is measured. Here the fact that 42 of the captures were known recaptures was discarded, and model (1) was used, but with covariate time and random individual effect ξ_i excluded. The index *i* now runs over all the captures.

A quadratic version of the model was also fitted to the capture-recapture data,

$$\begin{aligned}\ln(\frac{\mathrm{rank}_{iy}}{1-\mathrm{rank}_{iy}}) &= \beta_0 + \beta_c \cdot \mathrm{calf}_{iy} + \beta_l \cdot \mathrm{length}_{iy} + \beta_t \cdot \mathrm{time}_{iy} \\ &+ \beta_{ll} \cdot \mathrm{length}_{iy}^2 + \beta_{tt} \cdot \mathrm{time}_{iy}^2 + \beta_{cl} \cdot \mathrm{calf}_{iy} \cdot \mathrm{length}_{iy} \\ &+ \beta_{ct} \cdot \mathrm{calf}_{iy} \cdot \mathrm{time}_{iy} + \beta_{lt} \cdot \mathrm{length}_{iy} \cdot \mathrm{time}_{iy} + \xi_i + \varepsilon_{iy}. \qquad (3)\end{aligned}$$

This model was also used for all the 1,782 captures, but with covariate time (and the linked parameters to that covariate) and random individual effect ξ_i excluded.

To investigate the power of testing for positive correlation, a small simulation study has been carried out. Ranks for all the capture-recaptures were simulated using the logistic mixed model (1), with covariates as observed and with regression coefficients, random individual effects variance and residual variance as estimated. The model was fitted to the simulated ranks and observed data exactly as it was fitted to the observed data. A one-sided likelihood ratio test was performed to calculate *p*-values for each of 1,000 replicates. Finally, a generalised linear model (GLM) on the logistic scale was applied to obtain a power curve for testing the null hypothesis of $\rho = 0$. Additional repeated simulations were carried out for $\sigma = 1.69$ ($\rho = 0.5$) and $\sigma = 5.1$ ($\rho = 0.9$) to get maximum likelihood estimates for the logistic mixed model with simulated ranks. In addition, simulated results were used to estimate a confidence curve and obtain a confidence interval for ρ as in Schweder *et al*. (2009).

Table 3

Maximum likelihood estimates and standard errors (in parenthesis) for all captures where length of the individual is measured and for captures with recaptures.

	All captures *n*–1,782	Captures with recaptures *n*–42[1]
β_0	0.17 (0.04)	1.01 (0.24)
β_c	2.16 (0.19)	1.55 (0.79)
β_l	0.26 (0.02)	0.53 (0.15)
β_t		0.04 (0.08)
σ		2.3e-06 (0.01)
θ	1.65 (0.03)	1.69 (0.13)
- log likelihood	1,784.94	86.10

[1] The 2 whales captured in 3 different years were regarded as 4 cases of recaptures.

RESULTS

The model was fitted by way of the computer package *AD Model Builder* (Otter Research, 2004). Maximum likelihood estimates and standard errors based on the Hessian of the log likelihood are given in Table 3 for the simple logistic regression and the mixed model (1).

The correlation coefficient between ranks (2) is estimated to be 1.9e-12, and is not significantly different from zero (*p*-value 0.78). Simulation results estimated ρ to be 0.00 with 95% confidence interval (0.00, 0.35). The confidence curve is given in Fig. 3 (right).

The estimated intercept is higher when only captures with recaptures are considered (Table 3). This reflects that well marked whales tend to be long and thus late migrants. Association with a calf and being of a long length have both a significant effect of delaying the migration relative to the other migrants (*p*-value 0.00, all captures), while the time has no significant effect on the migration rank (Table 3).

Adding quadratic terms, as in (3), did not improve the fit appreciably for the capture-recapture data. The improvement in log likelihood was only 2.11 units on 5 degrees of freedom. There is thus no evidence for interaction or quadratic effects of covariates. For the capture data of size 1,782 the likelihood was improved significantly (22.67 units), but only the quadratic length term β_{ll} is significant.

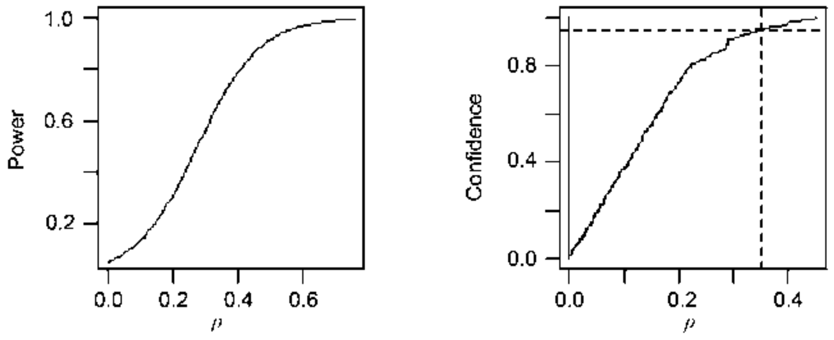

Fig. 3. Power curve of testing for positive temporal correlation in relative ranks within individuals at significance level 0.05 (left) and confidence curve for ρ (right). The horizontal line represents confidence 0.95. The vertical lines indicate 95% confidence interval.

DISCUSSION

To illustrate the regression results, the effect of having a calf associated was explored. Based on all captures, the intercept was estimated to be 0.17, and the effect of having a calf was estimated to be 2.16. An individual of average length without a calf thus has a predicted relative rank of exp(0.17) / (1 + exp(0.17)) = 0.54, while the predicted relative migration rank would be exp(2.16 + 0.17) / (1 + exp(2.16 + 0.17)) = 0.91 if it was associated with a calf. Recall that average length (12.03m) was subtracted from the observed length. The effects on calf and length on relative migration rank are highly statistically significant in the total capture data and in the capture-recapture data the effect of length is strongly significant. The effect of being associated with a calf is only of borderline significance here, but note that there were only five cases of capture-recaptures in which a calf was associated (Fig. 2).

It is important to note that these results are valid when surveys are assumed to cover the migration periods in a consistent pattern. However, if the first few surveys were performed early in the migration and the last few surveys were only able to cover the latter part of the migration, the relative ranks would be measured differently. In this case, an artefact would be observed that indicates a tendency of the recaptures to appear later in the migration than the captures, even when there is no such pattern in the true ranks. Fortunately, except for 1984, 1986, 1987 and 1994, the surveys covered the migration periods consistently (Koski *et al.*, 2006). Since only captures for which length of the individual was measured were considered, the surveys in 1984 and 1987 were excluded automatically. Elimination of 1986 and 1994 produced nearly the same results (β_c, β_l and θ were estimated as 2.18, 0.28 and 1.68 respectively). Elimination of these four years, when only captures with recaptures were considered, produced similar results for the parameters β_l, β_t, θ and σ (0.96, 0.07, 1.61 and 1.4e-06 respectively), while the estimate for β_c was different (-1.34). This result is not surprising since four records with calves were removed from the five-records database.

Although the capture-recapture sample size was small, the power of detecting migratory patterns was still reasonable. The power of testing $H_0 : \rho = 0$ at level 0.05 was about 50% when $\rho = 0.23$. Figs 3 and 4 illustrate the power of testing for positive correlation. Fig. 2 and the confidence curve shown on Fig. 3 (right) give additional support to the finding of a low intra-whale correlation in relative rank.

To assess the quality of the linear model, it was used as a predictive tool. First the model was applied only to 1985 and the maximum likelihood estimates obtained from this fit were applied to the year 1986 to obtain predicted ranks and residuals. The model was then fitted to both years 1985 and 1986 to yield predicted ranks for 1989 (years are not consecutive, Table 1), etc. Finally, the model was fitted to all the years 1985-1992 to obtain predicted ranks for 1994. The maximum likelihood estimates based on the sequentially cumulated data used to find predicted ranks, are found in Table 4. It is reassuring that these estimates vary little and hardly show any trends. Predicted ranks, residuals and normal-probability plot of the sequential residuals are found in Fig. 5.

Table 4

Maximum likelihood estimates based on increasing subsets of the data.

Subset	85	85-86	85-89	85-90	85-91	85-92
β_0	0.18	0.12	0.15	0.13	0.11	0.16
β_c	3.31	2.05	2.19	2.38	2.19	2.16
β_l	0.2	0.22	0.25	0.26	0.26	0.27
n	501	737	925	1,149	1,392	1,606

Except for the well-known systematic effect of large whales, and also the late migration of cows with calves, age is not found to significantly affect the migration rank. The main result is however that individual whales appear not to have any persistency from year to year in their relative rank when passing Barrow in the spring migration. In the limited capture-recapture data the estimated intra-whale correlation in relative rank, when controlling for covariates, is indeed small and not statistically significant. The power of testing for positive correlation at a significance level 5% is about 50% when $\rho = 2.8$.

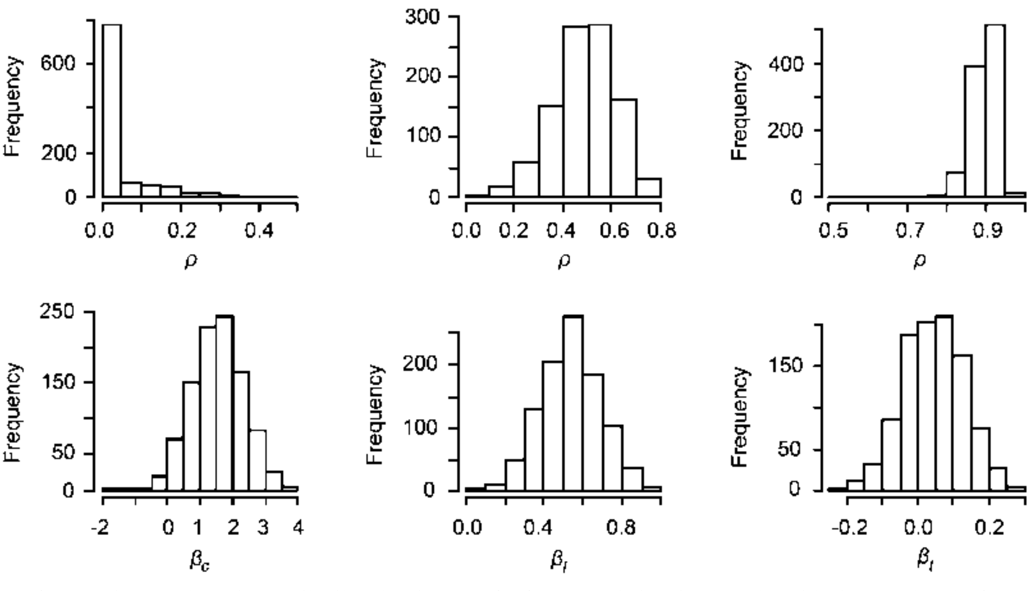

Fig. 4. Histograms of 1,000 simulated maximum likelihood estimates of ρ for the logistic mixed model with simulated ranks for ρ assumed to be: 0.0 (top left); 0.5 (top middle); 0.9 (top right) and for parameters: β_c (true value 1.55, bottom left); β_l (true value 0.53, bottom middle); β_t (true value 0.04, bottom right) for the assumed value of $\rho = 0.0$.

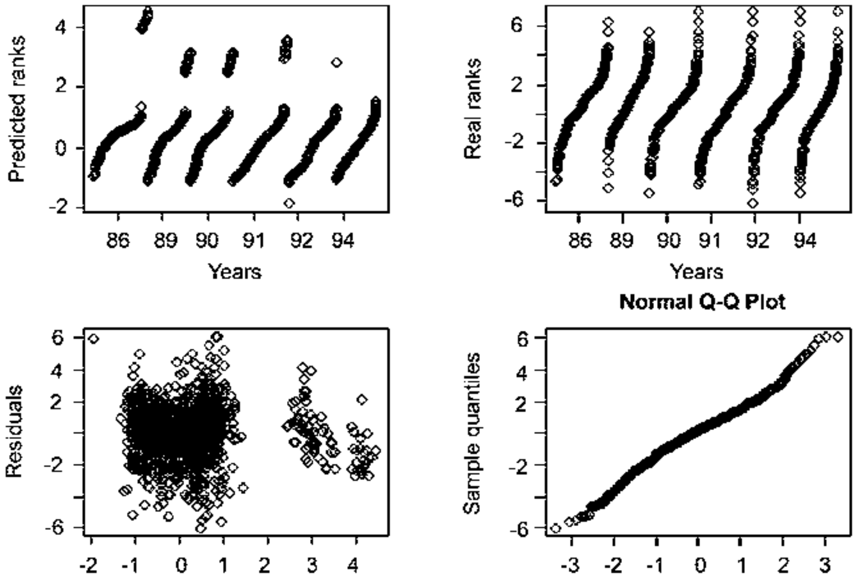

Fig. 5. Predicted ranks (sorted) versus years (top left); real ranks (sorted) versus years (top right); predicted ranks versus residuals for all years (bottom left); normal-probability plot of residuals for all years (bottom right).

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Empirical Bayes estimation of the size of a closed population using photo-identification data

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ABSTRACT

Photo-ID data are broadly used for estimating animal abundance using capture-recapture models. Animals that do not possess either natural or acquired marks sufficient to allow re-identification are called unmarked, and when a substantial part of the population is composed of such individuals, the classical models described in the literature do not apply. In this paper an Empirical Bayes capture-recapture analysis for dealing with the estimation of the capture probabilities and the estimation of abundance N for populations that include unmarked individuals is presented. Using a Gibbs sampling approach, Monte Carlo estimates for the posterior distribution of N were obtained. The Empirical Bayes approach was found to improve precision in the estimation of N compared to the results obtained using other Bayesian methods. Additionally, when the population included a very large number of unmarked individuals, inferences for N obtained using the Empirical Bayes approach were definitely superior to those obtained using any of the vague beta priors tested. The methodology was applied to bowhead whale data for the 1985 and 1986 photo-ID surveys.

KEYWORDS: BOWHEAD WHALE; ABUNDANCE ESTIMATE; PHOTO-ID; EMPIRICAL BAYES; MODELLING; BERING SEA; CHUKCHI SEA; BEAUFORT SEA

INTRODUCTION

The bowhead whale, *Balaena mysticetus*, was once the target of commercial whaling (for oil and baleen) and was severely depleted by commercial whalers up to the beginning of the 20th century (Bockstoce and Burns, 1993); the Bering-Chukchi-Beaufort Seas stock[1] (sometimes referred to as the western Arctic stock) was primarily hunted between 1848 and 1914, after which such activity declined due to the reduction in availability of whales and the advent of petroleum goods (Bockstoce and Botkin, 1983). This species is listed as endangered under the US Endangered Species Act and is protected from commercial whaling by the International Whaling Commission (IWC). Limited whaling for subsistence is allowed by the IWC for native groups in Northern Alaska (USA) and the west coast of Chukotka (Russian Federation) with catch limits being set within sustainable levels determined by the IWC Scientific Committee using the simulation-tested '*Bowhead Strike Limit Algorithm*' (IWC, 2003, pp. 18-23).

Abundance and trend information for the Bering-Chukchi-Beaufort seas stock has been obtained from ice-based censuses carried out during the spring migration past Point Barrow, Alaska (Raftery *et al.*, 1995; Raftery and Zeh, 1998). George *et al.* (2004) used a method that consisted of computing abundance estimates from estimates (*N4*) of the number of whales that passed within the 4km visual range of the observation 'perch' from which the whales are counted, the estimated proportions *P4* of the whales that passed within this range and the estimated standard errors (SE) of *N4* and *P4*. Their 2001 abundance estimate was 10,470 (SE=1,351) with 95% confidence interval of 8,100-13,500. Zeh and Punt (2005) estimated that the annual rate of increase (ROI) of the Western Arctic bowhead whale population from 1978 to 2001 was 3.4% (95% CI 1.7%-5%) indicating a population in steady recovery even with the subsistence harvest.

An independent method of estimating *inter alia* abundance and trend information is the use of mark-recapture data (Hammond *et al.*, 1990). The bowhead whale is totally black, except for white pigmentation on the chin and tail in some animals. Some individuals have natural markings that make their re-identification possible through comparison of photographs taken at different times. Others, besides their natural markings, may have acquired marks (scars) as a result of wounds, attack, etc.

A study by da Silva *et al.* (2000) examined aerial photographs of the bowhead whale suitable for identification of individuals using their natural markings that have been collected in Bering, Chukchi and Beaufort Seas since 1976. Most of the photographs have been collected by LGL Ltd. (LGL), the National Marine Mammal Laboratory (NMML) and the Cascadia Research Collective (CRC). The photos are housed at LGL and NMML.

Capture-recapture methods based on photo-identification data (hereafter photo-ID data) are widely used for estimating abundance of marine mammals and other species. Instead of artificially tagging the captured individuals, the natural and acquired marks of the photographed ones are used to build the matrix of their capture histories that is used in most capture-recapture estimation processes.

Animals whose extent of marks does not allow re-identification are called *unmarked*. Those individuals are *uncatchable* in the sense that they cannot be recognised. This violates a basic assumption of most capture-recapture models which requires that every animal in the population be uniquely identifiable.

In choosing the modelling most adequate for the data in this study, a choice between closed or open capture-recapture models had to be made (e.g. Hammond, 1986).

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[1] The most recent review of stock structure and movements can be found in IWC (2007; 2008a; 2008b).

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The first option requires that the time span that is considered in the analysis is small enough to prevent the occurrence of substantial demographic changes in the population. In this study closed population models are used.

Recent studies that have used mark-recapture data to estimate bowhead whale abundance (da Silva *et al.*, 2000; Koski *et al.*, 2008) have obtained results that are in accordance with those from the census data referred to above.

Solving the problem of estimating animal abundance in the presence of unmarked individuals was first attempted by Seber (1982, p.72). Working with bottlenose dolphin photo-ID data, Williams *et al.* (1993) used Seber's approach for obtaining an abundance estimate of that population. Da Silva (1999) and da Silva *et al.* (2000) developed frequentist models allowing for heterogeneity in capture probabilities. The inferences were dealt with using parametric bootstrap methods. The methodology was applied to real and simulated bowhead whale photo-ID data. Their results were in good agreement with those obtained by Raftery and Zeh (1998) and Raftery *et al.* (1995), who used bowhead whale ice-based census data. Schweder (2003) developed alternative methodology to that of da Silva (1999) and da Silva *et al.* (2000). He applied his methods to the same bowhead whale photo-ID data used by those authors and obtained bowhead whale population inferences largely in agreement with those obtained by them.

Bayesian estimation of population sizes *(N)* of demographically closed populations often depend upon the estimation of nuisance parameters such as capture probabilities at different occasions. Vague beta priors are usually assigned to those nuisance parameters in order to describe their posterior distributions. Using bowhead whale simulated data, da-Silva *et al.* (2003) observed that some choices of vague beta priors may cause substantial biases in the estimated values of *N*. For a variety of problems the pitfall of using vague priors is, according to Bernardo and Smith (1995, p.298) that 'every prior specification has *some* informative posterior or predictive implications'. One approach to deal with this problem is to estimate the hyperparameters of the prior beta distributions using an Empirical Bayes analysis.

Huggins (2002) proposed an Empirical Bayes analysis for estimating animal abundance for the case of heterogeneous capture probabilities. In this paper, an Empirical Bayes analysis for estimating the size of an animal population including unmarked individuals with capture probabilities varying according to the sampling occasions is presented. A Gibbs sampling algorithm was considered in order to obtain Monte Carlo estimates for the posterior distribution of *N* using both vague and Empirical Bayes defined priors for the nuisance parameters.

NOTATION

The photo-ID data available for capture-recapture estimation of animal abundance consists of the capture histories of the *naturally marked* individuals and some summary statistics related to the photos of an individual taken over the sampling occasions. In order to avoid biases caused by re-identification errors, only good quality photos were used in the analysis. All good quality photos of the photographed individuals were used. However, only individuals who possessed an acceptable extent of natural marks comprise what is termed the population of the '*marked individuals*'. A *capture* means that a good quality photograph of a whale was taken and, if a whale presented a non negligible extent of natural marks, it was considered *marked*. The notation below was used throughout.

N^u : the total number of unmarked whales in the population.

N^m : the total number of marked whales in the population.

$N = N^m + N^u$: the total number of whales.

X_j^m : the number of good photos of marked whales at occasion j, $j = 1, \ldots, t$, where good photos are those for which the identification of the whales is possible.

X_j^u : the number of good photos of unmarked whales at occasion j.

The total number of good photos at occasion j: $X_j = X_j^m + X_j^u$.

n_j : the total number of marked whales captured at time j.

r : the number of different marked whales captured over the experiment.

ω : any subset of $\{1, \ldots, t\}$.

u_ω : the number of marked whales with history ω.

$$n_j = \sum_{\omega \supset \{j\}} u_\omega \text{ and } r = \sum_{\omega} u_\omega$$

$p = (p_1, \ldots, p_t)$ where p_j is the capture probability at time j.

A LIKELIHOOD BASED ON GOOD PHOTOGRAPHS

In da-Silva *et al.* (2003), the relationship between N^m and N^u due to $N = N^m + N^u$ was expressed in terms of

$$\Delta = \log\left(\frac{N^u}{N^m}\right), \tag{1}$$

which represents the log of the unknown fraction of the population sizes of unmarked to marked individuals in the population. Therefore the estimated size of the whole population was given by

$$\hat{N} = \hat{N}^m\left(1 + exp\left(\hat{\Delta}\right)\right).$$

The parameters N^m and Δ were estimated using a Bayesian procedure involving a conditional likelihood of $\theta = (\Delta, p, N^m)$ given the total number of good photos at each of the sampling occasions, $\{X_j\}$. The likelihood consists of a combination of Darroch's model (Darroch, 1958) and a binomial model as follows,

$$\begin{aligned}
&L\left(\Delta, p, N^m\right) \\
&= Pr\left(\{u_\omega\}, \{X_j^m\} \mid \{X_j\}, \Delta, p, N^m\right) \\
&= Pr\left(\{u_\omega\} \mid \{X_j^m\}, \{X_j\}, \Delta, p, N^m\right) \\
&\qquad Pr\left(\{X_j^m\} \mid \{X_j\}, \Delta, p, N^m\right) \\
&= Pr\left(\{u_\omega\} \mid p, N^m\right) Pr\left(\{X_j^m\} \mid \{X_j\}, \Delta\right) \\
&\propto \frac{N^m!}{\left(N^m - r\right)!} \prod_{j=1}^{t} p_j^{n_j} \left(1 - p_j\right)^{N^m - n_j} \\
&\quad \times \left[\frac{1}{1 + e^\Delta}\right]^{\sum_{j=1}^{t} X_j^m} \left[\frac{e^\Delta}{1 + e^\Delta}\right]^{\sum_{j=1}^{t} X_j^u}
\end{aligned} \tag{2}$$

Notice that $Pr\ (\{u_\omega\} \mid p, N^m)$ accounts for the marked part of the population and is related to Darroch's model, which is completely described in terms of the set of random variables $\{u_\omega\}$ (along with the appropriate parameters p and N^m, only). Thus, the knowledge about $\{X_j\}$ and $\{X^m_j\}$ is irrelevant, justifying them to be dropped. In the expression $Pr\ (\{X^m_i\} \mid \{X_j\}, \Delta)$, a binomial distribution can be seen, which incorporates, through the number of good photos of unmarked individuals, the information about the unmarked part of the population. The absence of parameters p and N^m, shows that they are clearly not important in describing such a part of the model. Using vague beta priors for the capture probabilities and the adaptive rejection sampling method (ARS) by Gilks and Wild (1992) for drawing values from the full conditional posterior distribution of Δ, da-Silva *et al.* (2003) estimated N for real and simulated bowhead whale data. In that work, the full conditional posterior distributions of N and $\{p_j\}$ were standard, and could be sampled without any difficulty. An alternative way (the Gibbs sampling algorithm) to obtain Monte Carlo estimates of the posterior distribution of N is presented below.

GIBBS SAMPLING FOR ESTIMATING *N*

In this section, alternative methods to the ones proposed by da-Silva *et al.* (2003) are described for drawing samples from the joint posterior distribution of $\theta = (N^m, \{p_j\}, \Delta)$.

The Gibbs sampling is essentially a special case of the Metropolis-Hastings algorithm (Hastings, 1970; Metropolis *et al.*, 1953); which generates a Markov chain by sampling from full conditional distributions. Each iteration cycle of the Gibbs sampler gives an updated vector of the estimated values of θ. Each coordinate of is sampled conditionally to the values of the other components. For a very large number of Gibbs sampling cycles, the sampled values of θ are from the joint posterior distribution. The joint posterior is our target distribution.

Let $\theta = (\theta_1,\dots,\theta_k)$ be a k dimensional vector of unknowns, D a vector of observed data and $P\ (\theta \mid D)$ be the corresponding joint posterior distribution. Let $P\ (\theta_j \mid D, \theta_{-j})$ be the full conditional distribution of θ_j, and θ_{-j} denote the vector θ with θ_j removed. The following scheme illustrates the Gibbs sampling method for generating samples from $P\ (\theta \mid D)$,

(1) Choose starting values $\theta_1^{(0)},\dots,\theta_k^{(0)}$;

(2) Sample $\theta_1^{(j+1)}$ from $p\left(\theta_1 \mid \theta_2^{(j)},\dots,\theta_k^{(j)}, D\right)$;

(3) Sample $\theta_2^{(j+1)}$ from $p\left(\theta_2 \mid \theta_1^{(j+1)}, \theta_3^{(j)} \dots, \theta_k^{(j)}, D\right)$;

. . .

(4) Sample $\theta_k^{(j+1)}$ from $p\left(\theta_k \mid \theta_1^{(j+1)}, \theta_2^{(j+1)} \dots, \theta_{k-1}^{(j+1)}, D\right)$;

(5) Repeat step 2 thousands of times.

An extensive discussion of the Gibbs sampler can be found in Gelman *et al.* (1995).

Returning to the whale problem, since N is expressed as a function of Δ and N^m, its full conditional posterior distribution is estimated through the estimated values of those quantities. Expression (2) can be rewritten in terms of

$$\varphi = \frac{1}{1+e^\Delta}$$

Such reparameterisation allows an easy to sample full conditional posterior distribution to be described for φ. Since

$$\Delta = \log\left(\frac{1-\varphi}{\varphi}\right),$$

for each updated value of φ the corresponding updated value of Δ can be obtained.

The following prior distributions are considered:

$p_j \sim beta(a,b)$, $j=1,\dots,t$;

$\phi \sim beta(c,d)$;

$\pi(N^m) \propto 1/N^m$, i.e. the Jeffreys' prior (see Gelman *et al.*, 1995).

The values a, b, c and d are hyperparameters are discussed later.

Considering prior independence among the parameters, the joint prior distribution is described by

$$\pi(\theta) = \pi(N^m, p, \varphi) = \pi(N^m)\pi(p)\pi(\varphi).$$

Thus, the corresponding joint posterior distribution of $\theta = (N^m, p, \varphi)$ is

$$\pi\left(\varphi, \mathrm{p}, N^m \mid \{u_\omega\}, \{X^m_j\}, \{X_j\}\right) \propto L\left(\varphi, p, N^m\right) \pi(\varphi)\pi(p)\pi(N^m) \tag{3}$$

The Gibbs procedure for generating samples from the joint posterior distribution of

$$\theta = \left(N^m, \{p_j\}, \phi\right)$$

consists of drawing the θ values through the following sequence of draws:

$$\varphi \mid \{X^m_j\}, \{X_j\} \sim Beta\left(\sum_{j=1}^{t} X^m_j + c; \sum_{j=1}^{t} X_j - X^m_j + d\right); \tag{4}$$

$$N^m \mid p, r \sim Negative-Binomial\left(r, 1-\prod_{j=1}^{t}\left(1-p_j\right)\right); \tag{5}$$

$$p_j \mid N^m, n_j \sim Beta\left(n_j + a, N^m - n_j + b\right). \tag{6}$$

Expressions (4) to (6) represent the full posterior distributions of ϕ, N^m and p_j, respectively. The distributions in (4) and (6) are easily obtained. Expression (5) is obtained when, in expression (3), we consider only the terms involving N^m:

$$\pi\ (N^m \mid p, r) \propto \frac{N^m!}{(N^m-r)!}\prod_{j=1}^{t} p_j^{n_j}(1-p_j)^{N-n_j} \times \frac{1}{N^m}$$

$$\propto \frac{(N^m-1)!}{(N^m-r)!}\prod_{j=1}^{t} p_j^{n_j}(1-p_j)^{N^m-n_j} \propto \frac{(N^m-1)!}{(N^m-r)!}\prod_{j=1}^{t}(1-p_j)^{N^m} = \frac{(N^m-1)!}{(N^m-r)!}\left[\prod_{j=1}^{t}(1-p_j)\right]^{N^m}$$

$$\propto \frac{(N^m-1)!(r-1)!}{((N^m-1)-(r-1))!(r-1)!}\phi^{N^m} \propto \binom{N^m-1}{r-1}\phi^{N^m}$$

$$\propto \binom{N^m-1}{r-1}(1-\phi)^r \phi^{N^m-r} = \binom{N^m-1}{r-1}\eta^r(1-\eta)^{N^m-r}$$

where $\phi = \left[\prod_{j=1}^{t}(1-p_j)\right]$ and $\eta = 1-\prod_{j=1}^{t}(1-p_j)$.

Therefore, the full conditional of N^m is Negative-binomial with parameters r and η.

The values *a, b, c* and *d* of the hyperparameters are either fixed in order to define vague priors for the $\{p_j\}$ and φ, or estimated using an Empirical Bayes approach. This is discussed below.

AN EMPIRICAL BAYES APPROACH

In da-Silva *et al.* (2003), the vague priors *beta*(0, 0), *beta*(0.5, 0.5), and *beta*(1, 1) for the capture probabilities were considered in a simulation study aiming to assess the sensitivity of the inferences for *N* to the choices of the beta hyperparameters (*a, b*).

For inferences about *N*, the authors concluded that beta prior (0,0) causes positive bias while beta prior (1,1) causes negative bias. Vague beta prior (0.5, 0.5) seemed to be the best choice for the bowhead whale data.

Inferences for *N* can possibly be improved with better choices of (*a, b*). In that sense consider an iterative Empirical Bayes approach which consists of describing a marginal distribution of a given random variable which is parameterised by *a* and *b* so that estimation of these two parameters is possible.

The approach used in this consisted of: (1) finding the joint distribution of $(\{n_j\} \mid N^m, a, b)$; (2) given initial guesses for *a* and *b,* obtaining a temporary estimate of N^m using a Bayesian procedure; (3) given such an estimated value of N^m, estimating *a* and *b* via maximum likelihood; (4) repeating steps (2) and (3) until convergence of the estimates of *a* and *b*; and (5) using the final estimated values of *a* and *b*, running, one more time, the Bayesian procedure in order to estimate N^m, ϕ (and then Δ) and *N*, using the expression $\hat{N} = \hat{N}^m\left(1+exp\left(\hat{\Delta}\right)\right)$.

FINDING THE JOINT DISTRIBUTION OF $\left(\{n_j\} \mid N^m, a, b\right)$

Consider a population with N_* individuals and a model where capture probabilities vary only due to temporal effects. For the bowhead whales, let $N_* = N^m$. Also, let p_j be the capture probability at sampling occasion *j* for individual *i*, $i = 1,\ldots, N_*$ and $j = 1,\ldots, t$, and let n_j be the sample size at sampling occasion *j*, with

$$n_j \mid N_*, p_j, a, b \sim binomial\left(N_*, p_j\right);$$

$$p_j \mid a,b \sim beta\left(a,b\right).$$

In order to find a distribution for n_j given N_*, *a* and *b*, i.e., $P\left(n_j \mid N_*, a, b\right)$, $P\left(n_j, p_j \mid N_*, a, b\right)$, is integrated with respect to p_j:

$$P\left(n_j \mid N_*, a, b\right) = \int_0^1 p\left(n_j, p_j \mid N_*, a, b\right) dp_j = \int_0^1 P\left(n_j, p_j \mid N_*, a, b\right) \mathrm{P}\left(p_j \mid a, b\right) dp_j$$

$$= \binom{N_*}{n_j} \frac{\Gamma(a+b)}{\Gamma(a)\Gamma(b)} \frac{\Gamma(N_*+b-n_j)\Gamma(n_j+a)}{\Gamma(N_*+a+b)}$$

$$= \binom{N_*}{n_j} \frac{B(n_j+a, N_*-n_j+b)}{B(a,b)} \tag{7}$$

The right-hand side of expression (7) describes the parametric form of a binomial-beta distribution with parameters *a*, *b* and N_* for variable n_j (see Bernardo and Smith, 1995, p.117). Let $\Psi = \left(N_*, a, b\right)$ and $L\left(\Psi\right)$ be the likelihood associated to Ψ. Note that the n_js are independent and N_* fixed, so that

$$L(\Psi) = \prod_{j=1}^{t} P(n_j \mid N_*, a, b)$$

$$= \prod_{j=1}^{t} \int_0^1 p(n_j, p_j \mid N_*, a, b)\, dp_j$$

$$= \prod_{j=1}^{t} \binom{N_*}{n_j} \frac{B(n_j+a, N_*-n_j+b)}{B(a,b)} \tag{8}$$

ITERATIVE APPROACH TO ESTIMATE *a* AND *b*

(1) Initially consider $a^{(o)} = a$ and $b^{(o)} = b$, where *a* and *b* are the parameters of a vague beta prior.

(2) Using $a^{(k-1)}$ and $b^{(k-1)}$ and the Gibbs sampling discussed earlier, obtain $\hat{N}_*^{(k)}$, for the estimated value of N_*. Here we use a point estimate for N_* represented by the average of the MCMC draws from the conditional posterior distribution N_*.

(3) Replace $\hat{N}_*^{(k)}$ in equation (8) and obtain the maximum likelihood estimates $\hat{a}^{(k)}$, and $\hat{b}^{(k)}$.

(4) For $k = 1,\ldots$ return to step 2 until convergence of *a* and *b*.

Below some analyses resulting from the application of the methods discussed in the previous sections to simulated data are presented.

SENSITIVITY OF THE INFERENCES FOR *N*

The sensitivity of the inferences for *N* to choices of the beta priors is described in this section. The same bowhead whale simulated datasets analysed by da-Silva *et al.* (2003) were used.

Da Silva *et al.* (2000) generated bowhead whale data considering a total of four sampling occasions in the simulation and two intra-year occasions (spring and summer) in 1985 and 1986. For the intra-year occasions the population was considered closed. However, inter-year additions and deletions were allowed for. The authors worked with five scenarios (cases) for varying values of total population size, capture probabilities and population size of unmarked individuals. For each of the cases the authors generated 500 four occasion capture-recapture samples, in order to make possible to evaluate bias and uncertainty in the estimated values produced by the models they proposed.

In this study, only 4 of the 5 cases in da Silva *et al.* (2000) are presented. For all the cases a fixed population size of 1,186 marked individuals was considered whereas the size of the unmarked population varied from moderate to high. Capture probabilities were set as low or high. For the simulated data, the population sizes for the years of 1985 and 1986 were fixed as 6,649 and 6,820, respectively. Such values were obtained using the most likely trajectory from the Bayesian synthesis analysis by Raftery *et al.* (1995). The value 1,186 for the population size of marked whales was derived by fixing in about 82% the fraction of the unmarked whales in the hypothetical population when the average population size is 6,734. This percentage matched the fraction of good photographs of unmarked whales to the total number of good photos. For more details about the simulated data see da Silva (1999).

For brevity consider the events: S = small capture probabilities, U = high number of unmarked individuals in the population, where the complementary event of E is $\bar{E}$. The four cases are the following: *Case* 1 = $\left(S,\bar{U}\right)$, *Case* 2 = $\left(\bar{S},\bar{U}\right)$, *Case* 3 = $\left(\bar{S},U\right)$, *Case* 4 = $\left(S,U\right)$. Case 2 represents the most optimistic scenario where capture probabilities are high and the number of unmarked individuals is moderate. Case 4 represents the most pessimistic one, with low capture probabilities and high number of unmarked individuals.

For the Gibbs sampling approach for estimating N discussed earlier,

$$\varphi = \frac{1}{1+e^{\Delta}}, \text{ with } \varphi \sim beta\ (c,\ d)$$

was defined. It is important to evaluate whether or not inferences about N are sensitive not only to the choices of the values a and b of the beta prior for the capture probabilities, but also to choices of the values of c and d.

For each capture-recapture sample (data in this study) from a given case, the corresponding Bayesian point estimate of N^m was based on the average value (considering the quadratic loss) of 1,600 MCMC pseudo-independent draws from the full conditional posterior of N^m (see expression (5)), obtained from 20,000 MCMC such draws, having the first 4,000 ones discarded (burn-in period) and using thinning of 10 observations. The convergence of the MCMC procedure was verified by the convergence diagnosis techniques of Gelman and Rubin (1992), Heidelberger and Welch (1983) and Geweke (1992), which is available in the software CODA (*http://www.mrc-bsu.cam.ac.uk/bugs/classic/coda04/readme.shtml*).

Considering the Bayesian approach via Gibbs sampling, for each Case and their corresponding 500 capture-recapture generated samples (the data), the corresponding 500 Bayesian estimates of N^m were obtained. Some descriptive analyses were performed in order to evaluate bias and uncertainty of the inferences using the proposed methodology (see Table 1). As can be observed from Table 1, the inferences about N are sensitive to the choices of the hyperparameters a and b for the p_js, but not to the choices of the hyperparameters c and d for φ. Therefore, any choice of the beta priors (*beta*(0, 0), *beta*(1, 1) or *beta*(0.5, 0.5)) for φ works equally well, i.e. none cause any remarkable bias in the estimated values of N. In general it was noticed that the hyperparameters a=1/2 and b= 1/2 for the p_js, produced smaller biases in the estimation of N.

Considering the Empirical Bayes methodology described earlier, it can be seen from Table 2 (and also Table 1) for Cases 1 and 2, that the Empirical Bayes methodology did not improve the estimates with respect to either bias or uncertainty, compared to the Bayes estimation approach using the Gibbs sampling. For Cases 3 and 4, the Empirical Bayes approach using the estimates for (a,b) yielded small biases (Table 2, lines 3 and 4), whereas the Bayes method (via Gibbs sampling), even for the best choice of vague prior for the p^js, (a,b)= (1/2,1/2) (see second half of Table 1) had negative biases which were greater in magnitude.

ANALYSIS USING BOWHEAD WHALE DATA

The bowhead whale photo-ID data was obtained by aerial surveys off Barrow, Alaska. Such data consists of capture histories for four sampling occasions (spring 1985, summer 1985, spring 1986, and summer 1986).

Of the 1,677 records in the data set, only 229 belong to marked individuals and, of those, only 16 were captured more than once. This gives an idea of how sparse the bowhead whale data are. For more details about the bowhead whale data see da Silva *et al.* (2000). These data were processed (see Table 3) in order to obtain the data needed in models (4) to (6) among others.

Table 1

Summary statistics for estimated values of N based on 500 bowhead whale simulated samples, using the Gibbs sampling approach and different values of a and b and c and d. The events, S = small capture probabilities, U = High number of unmarked individuals in the population (where the complementary event of E is $\bar{E}$) describe the cases. Cases 1 and 2 are the ones with few while Cases 3 and 4 are the ones with high numbers of unmarked individuals.

	Parameters						
Case	a	b	c	d	Mean	Bias	SD
1 $\left(S,\bar{U}\right)$	0.0	0.0	0.0	0.0	6,845	113	773
			0.5	0.5	6,843	111	772
			1.0	1.0	6,842	110	771
	0.5	0.5	0.0	0.0	6,695	-37	730
			0.5	0.5	6,693	-40	729
			1.0	1.0	6,691	-41	729
	1.0	1.0	0.0	0.0	6,552	-179	693
			0.5	0.5	6,550	-182	692
			1.0	1.0	6,548	-184	692
2 $\left(\bar{S},\bar{U}\right)$	0.0	0.0	0.0	0.0	6,746	12	360
			0.5	0.5	6,745	11	360
			1.0	1.0	6,745	11	355
	0.5	0.5	0.0	0.0	6,721	-13	356
			0.5	0.5	6,720	-14	356
			1.0	1.0	6,720	-15	352
	1.0	1.0	0.0	0.0	6,697	-37	352
			0.5	0.5	6,696	-38	352
			1.0	1.0	6,695	-39	353
3 $\left(\bar{S},U\right)$	0.0	0.0	0.0	0.0	13,574	106	1,711
			0.5	0.5	13,569	101	1,711
			1.0	1.0	13,563	95	1,711
	0.5	0.5	0.0	0.0	13,276	-192	1,616
			0.5	0.5	13,270	-198	1,617
			1.0	1.0	13,264	-204	1,615
	1.0	1.0	0.0	0.0	12,995	-473	1,530
			0.5	0.5	12,989	-479	1,531
			1.0	1.0	12,981	-487	1,529
4 $\left(S,U\right)$	0.0	0.0	0.0	0.0	14,716	1,248	4,931
			0.5	0.5	14,702	1,234	4,922
			1.0	1.0	14,685	1,217	4,908
	0.5	0.5	0.0	0.0	13,058	-410	3,532
			0.5	0.5	13,046	-422	3,528
			1.0	1.0	13,035	-433	3,529
	1.0	1.0	0.0	0.0	11,817	-1,651	2,736
			0.5	0.5	11,808	-1,660	2,734
			1.0	1.0	11,797	-1,671	2,728

Table 2

Summary statistics (mean and bias) for the estimated values of N based on the empirical Bayes method with 500 bowhead whale 1985 and 1986 surveys simulated data from each Case (and the corresponding $\bar{a}$ and $\bar{b}$ - average values of a and b based on the 500 mentioned data). Each N estimated according to the posterior mean based on 1,600 MCMC draws and different values of a and b. The events, S = small capture probabilities, U = High number of unmarked individuals in the population (where the complementary event of E is $\bar{E}$) describe the cases. Cases 1 and 2 are the ones with few while Cases 3 and 4 are the ones with high numbers of unmarked individuals.

Case	$\bar{a}$	$\bar{b}$	Mean	Bias	SD
1- $\left(S,\bar{U}\right)$	6.1	68.8	6,761	108	763
2- $\left(\bar{S},\bar{U}\right)$	5.5	28.4	6,744	23	362
3- $\left(\bar{S},U\right)$	6.1	68.6	13,392	103	1,702
4- $\left(S,U\right)$	6.4	143.7	13,025	384	3,919

Table 3

Bowhead whale data from photo-ID surveys in the spring 1985, summer 1985, spring 1986, and summer 1986. The statistics in column 1 are the ones needed for the models in this article.

Occasions	Spring 1985	Summer 1985	Spring 1986	Summer 1986
n_j	87	56	76	26
X_j^m	166	115	126	37
X_j^u	609	704	382	255

Table 4

Inferences for *N* based on bowhead whale data – Empirical Bayes estimates and Gibbs sampling. Data from photo-ID data in the spring 1985, summer 1985, spring 1986, and summer 1986.

a	*b*	$\hat{N}$	CV	Credible intervals (95%)
Empirical Bayes				
5.9	107.7	6,340	0.162	(4,544; 8,595)
Gibbs sampling				
0.0	0.0	6,690	0.261	(4,360; 10,200)
0.5	0.5	6,150	0.248	(3,970; 9,610)
1.0	1.0	5,700	0.215	(3,760; 8,500)

All images taken in the photographic surveys were submitted to screening and classified using the scoring system developed by Rugh *et al.* (1998). All images were scored on the basis of their *quality* and *identifiability*.

The result of the application of the methods discussed above are summarised in Table 4.

According to the conclusions above for Cases 3 and 4 (representing a large number of unmarked individuals in the population), the inferences for *N* using the estimated (*a,b*) present very small biases. Those biases are even smaller than those obtained using the vague *beta*(0.5,0.5). Da-Silva *et al.* (2003) estimated that the fraction N^u / N of unmarked individuals in the population to be around 0.815, i.e. the majority of the individuals in the population do not possess any natural marks that could be used to uniquely identify the individuals. Therefore, for the actual bowhead whale data, the best choice for the hyperparameters *a* and *b* is obtained when using the Empirical Bayes approach.

When compared to the estimates obtained by Raftery and Zeh (1998) - 6,039 (SE=1,915) and 7,734 (SE=1,450) for 1985 and 1986 respectively - and with the 1985 and 1986 estimates of 6,649 and 6,820 (excluding calves) from the Bayesian synthesis analysis of Raftery *et al.* (1995), the inferences for *N* obtained with the Empirical Bayes approach (see first line of Table 4), yields smaller estimated standard deviation than those other approaches. However, it is not at all clear whether this is because the Empirical Bayes is truly a more precise estimator or because the estimate of SE produced by the Empirical Bayes approach is downwardly biased.

CONCLUSION

The present paper considered Bayesian approaches for estimation of the size *N* of animal populations considering that: (1) the data are from a photo-ID capture-recapture experiment; (2) capture probabilities vary only due to temporal effects; and (3) part of the population is unmarked. Da-Silva *et al.* (2003) concluded that, for such setting, the corresponding Bayesian analysis for *N* is sensitive to the choices of vague beta priors for the capture probabilities. A Gibbs sampling approach was suggested for the estimation of *N*. The objective was to define a quantity that represents the log of the unknown fraction of the population sizes of unmarked to marked individuals. As a function of that it was possible to define the probability of occurrence of a good photograph of a marked individual. Additionally, a reparameterisation of such probability allowed further simplification of the Gibbs sampling procedure.

Performance of the proposed methods was evaluated through a simulation study involving bowhead whale data generated under four different scenarios (the same as used by da-Silva *et al.*, 2003). An Empirical Bayes analysis was proposed as an attempt to diminish the biases in the inferences for *N* caused by sensitivity to the prior specifications of the capture probabilities. The conclusions are given below.

(1) The use of the Empirical Bayes approach yields either smaller or comparable biases for the estimated values of *N* compared to the biases observed using the *beta*(0.5,0.5) prior (the one that conducted to the smaller biases for the Bayes estimation via Gibbs sampling).

(2) The Empirical Bayes approach apparently also improves precision in the estimation *N* as revealed by the comparison of CVs in Table 4 (however, it is possible that such estimated standard deviation are downwardly biased).

(3) When the population includes a very large number of unmarked individuals, inferences for *N* obtained using the Empirical Bayes approach are definitely superior to the Bayes approach (via Gibbs sampling) using any of the vague beta priors.

Some observations and concerns about possible violations in the model assumptions are addressed below.

(1) *Possible changes in markings*. Only photographs in which the mid-back region of the whales was of good quality, i.e. classified as 2- or better, were used in the analyses so that whales with identifying marks in that region would be recognised when they were photographed on more than one sampling occasion. (*Quality* is scored on a five-point scale (1+, 1-, 2+, 2-, 3) indicating how much of the area is visible: 1+ represents the highest and 3 the lowest quality. A whale must also be at least moderately marked on the mid-back to be treated as marked in the analyses. The scoring system developed by Rugh *et al.* (1998) is stringent enough to ensure that a whale categorised as marked on one occasion will be recognised if photographed again on a subsequent occasion. Miller *et al.* (1992) argues that it is unlikely that large scars disappear. However, small marks may be disguised by new marks, and they are also more likely than large marks or groups of marks to be obscured in a photograph).(*Identifiability* is scored as H+, H-, M+, M-, U+, U-, with highly (H) and moderately (M) and unmarked (U) whales).

(2) *Closed population assumption*. In the analyses performed data were used from two different years (photo-ID data from spring 1985, summer 1985, spring 1986 and summer 1986). The closed population assumption does not strictly apply since whales are born and die between samples. However, bowhead whales have high survival rates (George *et al.*, 1999) and low fecundity rates (Miller *et al.*, 1992), which implies that the population is not expected to suffer considerable demographic changes and the closed population assumption to be reasonably acceptable. George *et al.* (2004) discuss the population trend of Western Arctic bowhead whales from 1978 to 2001. Their estimate of annual rate of increase of the population in such period is 3.4%. So the estimates presented here may be somewhat negatively biased.

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Seasonal estimates of densities and predation rates of cetaceans in the Ligurian Sea, northwestern Mediterranean Sea: an initial examination

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ABSTRACT

The Ligurian Sea is one of the most attractive areas for cetaceans in the Mediterranean Sea, and is now included in a Marine Protected Area, the Pelagos Sanctuary. Despite a lower species diversity than in other parts of the world, because of their abundance, cetaceans are thought to represent significant consumers in this ecosystem. Surveys were conducted within the Pelagos Sanctuary from 2001 to 2004. Densities of five species: striped dolphin (*Stenella coeruleoalba*); fin whale (*Balaenoptera physalus*); sperm whale (*Physeter macrocephalus*); long-finned pilot whale (*Globicephala melas*); and Risso's dolphin (*Grampus griseus*), were estimated and converted to biomass. Total biomass density of cetaceans in the Ligurian Sea was estimated as 93kg km^{-2} (CV=28%) in winter (October to March) and 509kg km^{-2} (CV=16%) in summer (April to September). Daily predation rates by cetaceans were estimated as 2.9kg km^{-2} d^{-1} in winter, increasing to 10.4kg km^{-2} d^{-1} in summer, corresponding to a total annual ingestion of 2.4t km^{-2} y^{-1}. The annual primary production required for cetaceans was estimated to be 12.6gC m^{-2} y^{-1}, corresponding to 6-15% of the net primary production known for this area. Estimated cetacean predation on fish was similar to reported fisheries landings, nevertheless, management of artisanal fisheries and accurate quantification of the resources they exploit will be necessary for the responsible management of fisheries in this Mediterranean Marine Protected Area.

KEYWORDS: INDEX OF ABUNDANCE; NUTRITION; FOOD/PREY; SANCTUARIES; FEEDING GROUNDS; SURVEY - VESSEL; SURVEY – ACOUSTIC; STRIPED DOLPHIN; FIN WHALE; SPERM WHALE; LONG-FINNED PILOT WHALE; RISSO'S DOLPHIN; MEDITERRANEAN SEA; NORTHERN HEMISPHERE

INTRODUCTION

Marine mammals often play key roles within marine ecosystems, consequently their abundance and their distribution can have important effects on the structure and function of some ecosystems (Bowen, 1997; Estes *et al*., 2006). Nevertheless their role as top predators needs to be characterised and quantified in order to better understand their habitat use and identify the possible impacts of human activities. All cetaceans are carnivores and in many marine ecosystems they are among the top predators (Bowen, 1997; Trites, 2002). Their diet includes a wide variety of prey species from small crustaceans up to large squid (Barros and Clarke, 2002). They have a few predators of their own; these include large sharks, a small number of other cetaceans and humans. Given their large body sizes and relatively high metabolic rates, cetaceans can represent significant consumers in marine ecosystems.

Concerns about the interactions of fisheries with marine mammals in the Mediterranean Sea are probably as old as the first human attempts to catch fish with a net (Bearzi, 2002). In the Mediterranean, most commercial fish stocks are considered overexploited (Farrugio *et al*., 1993). This adds some degree of urgency to a need for estimates of cetacean consumption. Cetaceans may be affected by fisheries even when their prey species are not target species of commercial fisheries because of linkages though the food web (Trites *et al*., 1997). In addition, since 2002, the Ligurian Sea, located in the northwestern Mediterranean Sea, has been designated as a Marine Protected Area (MPA), called the Pelagos Sanctuary (Fig. 1).

In summer, the Ligurian Sea attracts large numbers of cetaceans (Forcada *et al*., 1996; Forcada and Hammond, 1998; Gannier, 2005), in particular striped dolphins (*Stenella coeruleoalba*) and fin whales (*Balaenoptera physalus*). In addition, six other species are known to inhabit this area: sperm whales (*Physeter macrocephalus*); Cuvier's beaked whales (*Ziphius cavirostris*); long-finned pilot whales (*Globicephala melas*); Risso's dolphins (*Grampus griseus*); bottlenose dolphins (*Tursiops truncatus*); and more rarely short-beaked common dolphins (*Delphinus delphis*). Summer densities have previously been reported for striped dolphins (Forcada and Hammond, 1998; Gannier, 1998) and fin whales (Forcada *et al*., 1996; Gannier, 1997), however those for other species and seasons have not been published yet.

For the Mediterranean Sea, the only previous estimates of cetacean prey consumption were by Viale (1985). This author estimated roughly the number of individuals for north of 40°N latitude from opportunistic surveys conducted on oceanographic vessels between 1972 and 1982. It was assumed that strip transect methodology could be considered and the effective strip half-width used was taken from other studies. With additional survey data to allow estimation of cetacean densities throughout the year, accurate estimates of consumption rates are now possible.

A single-species approach to estimating consumption rates or trophic relationships beginning from population size has a number of limitations when dealing with multiple species, especially in terms of ecological requirements of species that vary widely in body size. In this paper, an attempt was made to estimate annual prey consumption rates by cetaceans in the Ligurian Sea, and their overall trophic impacts as measured by primary production required to support that consumption. It has been assumed that cetaceans use the habitat for feeding purposes, as for the majority of species, feeding activity was observed or acoustically verified several times during surveys, except for pilot whales, which are known to feed at night (Baird *et al*., 2002).

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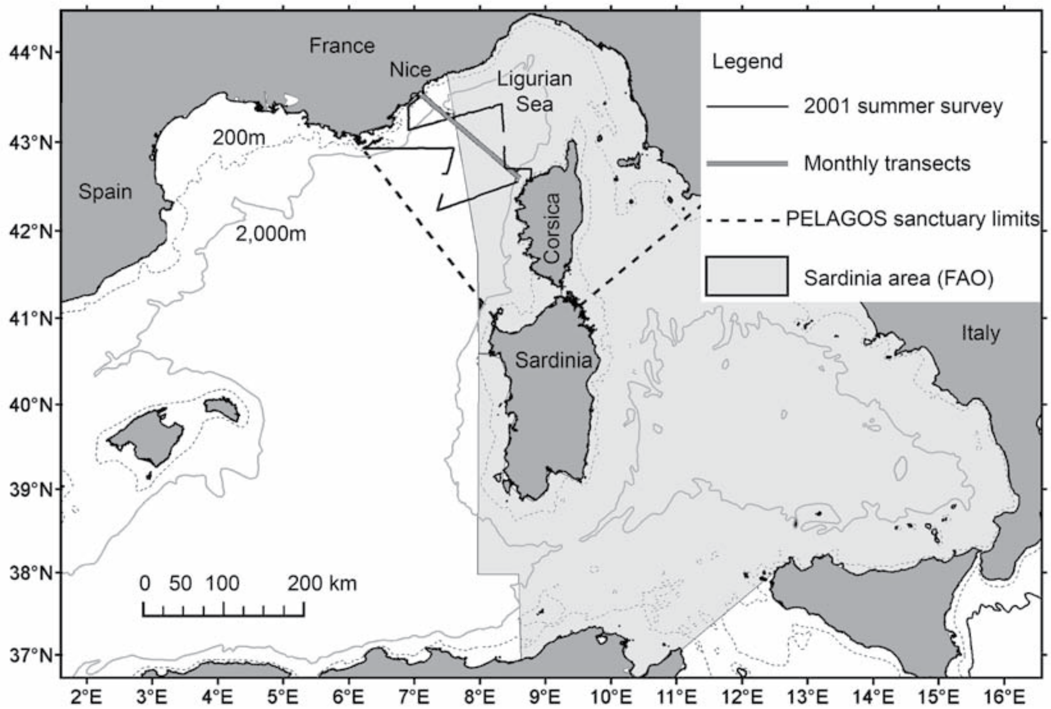

Fig. 1. Study area with transect locations (black and grey lines), PELAGOS Sanctuary borders (dashed lines) and Sardinia area (FAO).

MATERIALS AND METHODS

The Ligurian Sea is located north of the western Mediterranean basin (Fig. 1). This region includes large areas of deep water (>2,000m), with a narrow continental shelf. It is characterised by a frontal system, which provides a high level of primary production, peaking in March-April (Jacques *et al*., 1973; Nival *et al*., 1975). The Pelagos Sanctuary includes 87,500km^2, but the estimates used in this study only pertain to the northernmost portion (Fig. 1). In the absence of seasonal surveys of the whole MPA, cetacean density was estimated from transects conducted only in its northern part. It must be noted that environmental conditions in the corridor do not represent those of the entire MPA and that some cetaceans (e.g. fin whales) are known to aggregate near the northern frontal region in summer. Nevertheless it was considered that even rough estimates of biomass, densities and predation could be useful in term of management. For all estimates, the year was divided into two equal periods, April-September and October-March, which are referred to as 'summer' and 'winter' respectively, for convenience.

Density estimates

Data were collected between February 2001 and February 2004 from 30 dedicated line-transect surveys, conducted monthly along the same 160km track between the French mainland and Corsica (Fig. 1) and part of the return transect. The standard sampling design was to survey from France to Corsica at a speed of about 22km h^{-1} (12knots). In this analysis only effort conducted between 18km h^{-1} and 23km h^{-1} under sea conditions of Beaufort 3 or lower was considered. The return trip on the next day followed a parallel transect offset 11km north-east from the southbound track. A shorter (74km) section of the northbound transect was surveyed at lower speeds (13km h^{-1}) to try to estimate the probability of seeing a whale on the trackline, $g(0)$, for the most common species. Only sections of the northbound transect conducted at 18-23km h^{-1}, before and after the lower-speed segment, were included in the analysis. There was one additional survey conducted in summer 2001 within the same general area in the sanctuary (Gannier, 2006) (Fig. 1). All surveys were conducted with the same dedicated platform, a 13m vessel powered by two 350HP inboard engines, and a consistent crew. Three experienced observers, seated with their eyes 4m above the water surface, searched the forward sector (-90° to +90° relative to the bow) with the naked eye and were rotated every hour (see Laran and Drouot-Dulau, 2007).

The survey data were grouped by six-month seasons across the three years of sampling and analysed applying standard line-transect methods (Buckland *et al*., 2001). Transects selected for analysis varied from 10 to 158km (mean=81.7km) depending the length of segment conducted with good sighting conditions. The effective strip half-width (*esw*) was estimated for each species using *Distance 5.0* (Thomas *et al*., 2006); as the numbers of sightings were too low to reliably estimate *esw* for Risso's dolphins and pilot whales, additional detections of the same species, recorded in the northwestern Mediterranean Sea from the same platform were included. For fin whales and striped dolphins, sightings were truncated prior to analysis to exclude 5% of the groups detected at the largest distances following Buckland *et al*. (2001). The density of species *i* during period *j* (in individuals per km^2) was estimated by:

$$D_{ij} = \frac{n_{ij} \; s_{ij}}{2 \; L_j \; esw} \qquad (1)$$

where s_{ij} is the mean school size of species *i* during period *j*; n_{ij} is the number of primary sightings (after truncation) of species *i* during period *j* and L_j is the total transect length (km) surveyed during period *j*. The variance of *D* was estimated using *Distance 5.0*, by the delta method (Buckland *et al*., 2001). Replicate transects weighted by transect length were considered to estimate $\mathrm{var}(\underset{\sim}{n})$. The annual variance or groups of species variances were estimated as the sum of variances of the different components (Buckland *et al*., 2001).

For sperm whales, a strip-transect method was applied to combined visual and acoustic detections. Two-minute recording sessions (with the vessel propeller de-clutched) were performed, each 18.5km of the southbound transect, with a monaural hydrophone (Magrec, HP 60MT). As the exact number of whales could not be reliably determined when more than three whales were vocally active in the area, three was the maximum school size allocated by acoustic sampling alone (Gannier *et al*., 2002). Two consecutive positive stations or a positive station following/preceding a sighting were considered as distinct whales when the recorded click-level index was equal or greater than 3 (on a scale varying from 0 to 5; see Laran and Drouot-Dulau, 2007). As sperm whales do not usually produce regular clicks at the surface (Drouot *et al*., 2004), the school size of each sighting was estimated by combining visual and acoustic information. With the same monaural hydrophone, Gannier *et al*. (2002) observed a click-level index of 0 for a sperm whale located at 14.8km and a level of 2 at 9.4km; from their results it is estimated that whales were heard up to 13km away (see fig. 3, plot for mono-hydrophone, in Gannier *et al*. 2002). Therefore an arbitrary distance of 13km was assumed to be acoustically scanned on each side of the transect line (equivalent to *esw*), considering the detection capability of the hydrophone. The calculation of sperm whale density was equivalent to Eqn. (1).

Biomass and prey consumption

Biomass densities for each species were estimated by multiplying calculated densities by average body mass (W in kg). The mean body mass values, for males and females separately, were taken from Trites and Pauly (1998) except for species where independent evidence suggested that individuals in the Mediterranean tended to be smaller than elsewhere in the world. In those cases, maximum lengths from the Mediterranean were used in the regression models from Trites and Pauly (1998) to compute mean weights for males and females. Maximum body lengths for Mediterranean specimens came from the long-term stranding database and were provided by F. Dhermain (Groupe d'Etude des Cétacés de Méditerranée) and O. Van Canneyt (CRMM - University of La Rochelle). For each species the male and female means were averaged with the sex ratio assumed to be 50%, except for the strongly dimorphic species (sperm whale and pilot whale), where the sex ratio was assumed to be 40% male and 60% female (following Barlow *et al*., 2008; Trites and Pauly, 1998). The CV of the biomass density estimate was assumed to be the same as that of the corresponding density, as no information on maximum length variability was available. Cumulative biomass densities for all odontocetes and total cetaceans were computed by summing the estimates for the individual species, and cumulative CV's were computed by summing the individual variances (following Buckland *et al*., 2001).

A variety of methods exist for estimating the consumption rates of cetaceans (see review by Leaper and Lavigne, 2007). Sergeant (1969), extrapolating from feeding rates of captive odontocetes ranging in size from harbour porpoises to killer whales, proposed that feeding rates of free-living cetaceans could be computed as a percentage of body weight, ranging from 3.5-4% in larger animals to 10-12% in the smallest individuals, but he did not fit a mathematical model. The available mathematical models are generally of two types: computing ingestion rate as a function of body weight; or computing metabolic rate as a function of body weight and scaling upward to ingestion rate for assimilation efficiency and activity. Innes *et al*. (1987) proposed that daily ration (R, in kg d^{-1}) could be estimated from body weight (W, in kg) by:

$$R_1 = 0.123\ W^{0.8} \tag{2}$$

Trites *et al*. (1997) modified that model by adjusting the multiplier slightly downward in an attempt to account for the difference between ingestion for growth and ingestion for maintenance:

$$R_2 = 0.1\ W^{0.8} \tag{3}$$

Kenney *et al*. (1997) used the model of Kleiber (1975) to estimate basal metabolic rate (BMR, in kcal d^{-1}):

$$BMR = 70\ W^{0.75} \tag{4}$$

and then applied a scaling factor to account for assimilation efficiency and activity:

$$R_3 = \frac{2.5\,BMR}{E} \tag{5}$$

where E is the energy density of the prey consumed, assumed to be 1,000kcal kg^{-1} for fish and crustaceans (Clarke and Prince, 1980; Sissenwine *et al*., 1984) and 830kcal kg^{-1} for squid (Croxall and Prince, 1982). Sigurjónsson and Víkingsson (1997) used Lockyer's (1981) model for near-basal metabolic rate:

$$M = 110\ W^{0.783} \tag{6}$$

which they then scaled upwards for 80% assimilation efficiency and a 1.5× activity factor. Incorporating the energy-to-biomass conversion, their model becomes:

$$R_4 = \frac{206.25\,W^{0.783}}{E} \tag{7}$$

All four models were used to estimate the daily rations of cetaceans ranging in size from 30kg to 100t (i.e. harbour porpoise to blue whale), presuming the same diet at 1,000kcal kg^{-1} (Fig. 2). The Sigurjónsson and Víkingsson (1997) method resulted in the highest estimates across the entire range, and the Trites *et al*. (1997) method generated the lowest values at all but the very largest body weights. The Innes *et al*. (1987) and Kenney *et al*. (1997) methods produced intermediate values, with the latter differing in slope. Barlow *et al*. (2008) tested an even broader range of consumption models, and settled on the same one used by Kenney *et al*. (1997). They also concluded that the same model using 3.0 as a multiplier rather than 2.5 (Fig. 2) and

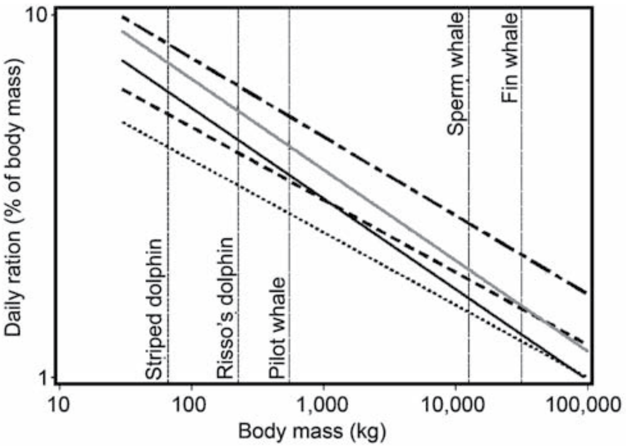

Fig. 2. Estimates of daily ration (as a percentage of body mass) from body mass for cetaceans from 30kg (e.g. an average male harbour porpoise) to 100 tonnes (e.g. a blue whale) from four different models: Trites *et al*. (1997) (dotted line); Kenney *et al*. (1997) (solid black line); Innes *et al*. (1987) (dashed line); and Sigurjónsson and Víkingsson (1997) (alternating long and short dashes). The solid grey line represents the Kenney *et al*. (1997) model using an activity multiplier of 3.0 instead of 2.5.

Table 1

Survey effort and on-effort total sightings after truncation (and number of individuals) collected between February 2001 and February 2004.

Seasonal period	No. of surveys	Effort (km)	Fin whale	Sperm* whale	Pilot whale	Risso's dolphin	Striped dolphin	Total
April-September	19	3,967	77 (126)	19 (29)	6 (171)	4 (39)	169 (3,520)	275
October-March	12	2,235	8 (9)	8 (24)	0	6 (68)	74 (959)	96
Total	31	6,202	85 (135)	27 (53)	6 (171)	10 (107)	243 (4,478)	371

*Both visual sightings and acoustic detections are included for sperm whales.

the Innes *et al.* (1987) model were also plausible. Similarly, the Kenney *et al.* (1997) model has been used for the principal analyses reported in this paper.

Consumption rates were estimated using Eqns (4) and (5), and partitioned into three prey categories: fish; cephalopod; and zooplankton (crustaceans). In the absence of knowledge on variation of the ingestion rate, the CVs were propagated from biomass densities estimates through to the consumption estimates, whilst aware that the CV value would be underestimated by an unknown and maybe important amount. For the group of species, the sum of variances of the different components were estimated. The estimated percentages of each species' diet comprising the three categories were based upon previous reviews (Kenney *et al.*, 1985; Kenney *et al.*, 1997; Pauly *et al.*, 1998) as modified by literature and data specific to the Mediterranean Sea. The food of fin whales in summer was assumed to be 100% crustaceans, as the euphausiid *Meganyctiphanes norvegica* is considered as its only food resource (Astruc, 2005; Orsi Relini and Giordano, 1992). Since fin whales are present in the Mediterranean Sea in winter and there is evidence of winter feeding, at least close to Sicily (Canese *et al.*, 2006), no scaling factor was applied to increase summer feeding rate to account for winter fasting. Based on information for other areas (Lockyer, 2007; Sigurjónsson and Víkingsson, 1997; Viale, 1985), it was assumed that during winter, fin whales feed mainly on euphausiids (90%) but occasionally on fish when available (10%). For sperm whales, there have been reports on two stomach contents from the Mediterranean Sea (Astruc, 2005; Roberts, 2003); both included only cephalopods, mainly *Histioteuthis bonnellii*. However, to account for possible consumption of fish, as is reported in the Atlantic Ocean (Clarke *et al.*, 1993), it was assumed that 90% of the diet is cephalopods and 10% is fish. For pilot whales and Risso's dolphins, based on a small sample in the Mediterranean Sea (Astruc, 2005; Orsi Relini and Garibaldi, 1992) and the earlier reviews, diets of 95% cephalopods and 5% fish were assumed. The food of striped dolphins in the Ligurian Sea is comprised of 49.3% fish, 49.7% cephalopods and 1% crustaceans (Würtz and Marrale, 1993).

The daily prey consumption rate for each species in each six-month season (in kg km^{-2} d^{-1}) was then estimated by multiplying seasonal density by daily ration. Seasonal consumption was calculated by multiplying daily rates by the number of days in each six-month period (182.5), and the annual consumption rate per species (Q, in kg km^{-2} y^{-1}) was then the sum of the winter and summer values, with the variance calculated as the sum of the seasonal variances.

Primary production required

The role of cetaceans within the food web of their ecosystem was also examined by estimating the proportion of net primary production required to sustain the prey that they consumed. This was estimated using a constant transfer efficiency of 10% between successive trophic levels, *TL* (Pauly and Christensen, 1995). The primary production required (PPR$_p$, gC m^{-2} y^{-1}) to support consumption of any prey type *p* was calculated from consumption of that prey (Q_p) using a factor 10^k, with *k* being the number of trophic steps between phytoplankton (*TL* = 1) and the given prey category:

$$PPR_p = \frac{(Q_p \cdot E_p) \times 10^{(TL-1)}}{13.3 kcal\ gC^{-1} \times 10^6 m^2\ km^{-2}} \quad (8)$$

where E_p is the energy density of the prey. *TL* is the trophic level of the prey category and assumed to be 2.2 for crustaceans, 3.2 for cephalopods, and 3.0 for fish (Pauly and Christensen, 1995). The terms in the denominator convert from energy to carbon units (Platt, 1969) and from km^2 to m^2. The primary production required was then compared to total net primary production as reported in the literature.

Comparison with fisheries

Annual global capture production estimates were extracted with *FishStat Plus*[1] and the time series of the Food and Agriculture Organisation of the United Nations (FAO), available from the area. Results were averaged from 2000 to 2005 for two different areas: (1) the total Mediterranean Sea plus Black Sea global dataset of Capture Production (1950-2006); (2) total fishery production (1950-2006) considering commercial, industrial, recreational captures and aquaculture and other kinds of fish farming (FAO, 2008); and (3) the Sardinia region alone (Tyrrhenian Sea to east of Sardinia and Corsica; Fig. 1) extracted from GFCM (Mediterranean and Black Sea) Capture Production (1970-2005) (FAO, 2008). Total fisheries production values were converted to rates by dividing by the respective surface area. Surface area for the Mediterranean and Black Sea is 2,966,000km^2 (Aubouin and Durand-Delga, 2002). Surface area for the Sardinia region was estimated with *ArcView 9.2* as 288,750km^2.

RESULTS

Density, biomass and prey consumption

During these surveys, 371 sightings (or acoustic detections in the case of sperm whales) were recorded (Table 1). Five cetacean species were recorded on-effort. Striped dolphins were the most frequently observed (*n*=243 sightings), followed by fin whales (85), sperm whales (27), Risso's dolphins (10) and finally pilot whales (6), the only species that was encountered in summer only. Total survey effort was 2,235km during October-March and 3,967km during April-September.

Striped dolphin

An *esw* of 489m (CV=8.4%) was estimated for striped dolphins using a hazard-rate model without adjustment, after truncation at 1,400m. Mean school size was 19.9

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[1] http://www.fao.org/fishery/statistics/programme/3,1,2/en

Table 2

Mean body masses (*W*, in kg) for males, females, and both sexes averaged, for five cetacean species in the Ligurian Sea, and mean daily ration per individual (kg d^{-1}, and as % of body mass in parentheses) estimated from four different models: (1) Innes *et al.* (1987); (2) Trites *et al.* (1997); (3) Kenney *et al.* (1997); (4) Sigurjónsson and Víkingsson (1997). Model 3 (in bold) was selected for use in the analysis reported in this paper. Mean body masses were taken from Trites and Pauly (1998) or estimated using their regression models from maximum lengths (L_{max}, in cm) from Mediterranean specimens (F. Dhermain, GECEM and O. Van Canneyt, CRMM - University of La Rochelle, pers. comm.).

	L_{max}		*W*			Daily ration			
Species	♂	♀	♂	♀	Mean	(1)	(2)	(3)	(4)
Fin whale	2,000	2,000	31,429	30,832	31,131	484 (1.6)	393 (1.3)	**410 (1.3)**	680 (2.2)
Sperm whale	1,500	na	16,083	10,098	12,492	233 (1.9)	189 (1.5)	**244 (2.0)**	393 (3.1)
Pilot whale	600	500	689	450	546	19.0 (3.5)	15.5 (2.8)	**23.6 (4.3)**	34.2 (6.3)
Risso's dolphin	na	na	236	211	224	9.3 (4.2)	7.6 (3.4)	**12.1 (5.4)**	17.0 (7.6)
Striped dolphin	227	225	68	65	66	3.5 (5.3)	2.9 (4.3)	**4.4 (6.7)**	6.0 (9.1)

(CV=9.4%) in April-September and 10.9 (CV=13.5%) in October-March. The maximum density was observed in April-September with 0.87 individuals km^{-2} (CV=15.2%). The density in winter was somewhat less than half of the summer density at 0.37 (CV=21.7%), with a significant difference (Z-test=3.23, $p<0.005$).

Maximum lengths of stranded striped dolphins from the Mediterranean were 227cm for males and 225cm for females (from 406 males and 327 females; F. Dhermain, GECEM and O. Van Canneyt, CRMM - University of La Rochelle, pers. comm.). The average weights computed from the Trites and Pauly (1998) regressions were 68kg and 65kg, respectively, and the average for the species was 66kg (Table 2).

The seasonal biomass densities were 57.6kg km^{-2} (CV=15.2%) in April-September and 24.5kg km^{-2} (CV=21.7%) in October-March (Fig. 3). The average daily ration for a striped dolphin was estimated from the four different models to range from 2.9 to 6.0kg d^{-1} (4.3-9.1% of body mass, Table 2), with 4.4kg d^{-1} estimated from Kenney *et al*. (1997) model. The striped dolphin annual consumption rate was estimated to be 999kg km^{-2} y^{-1} (CV=17.7%): 492kg of fish; 497kg of cephalopods; and 10kg of crustaceans (Table 3).

Risso's dolphin

Risso's dolphin sightings were truncated at 600m and an *esw* of 430m (CV=8.9%) was estimated using a half-normal model. Mean school size was 9.8 (CV=43.2%) in April-September and 11.3 (CV=41.2%) in October-March. These results lead to an extrapolated winter density of 0.035 individuals km^{-2} (CV=58.2%), decreasing to 0.011 (CV=58.9%) during summer. Risso's dolphins were the only species with a substantially higher density in winter than in summer, differing by a factor of about three, but with no significant difference due to large CVs (Z-test=1.10, $p>0.30$).

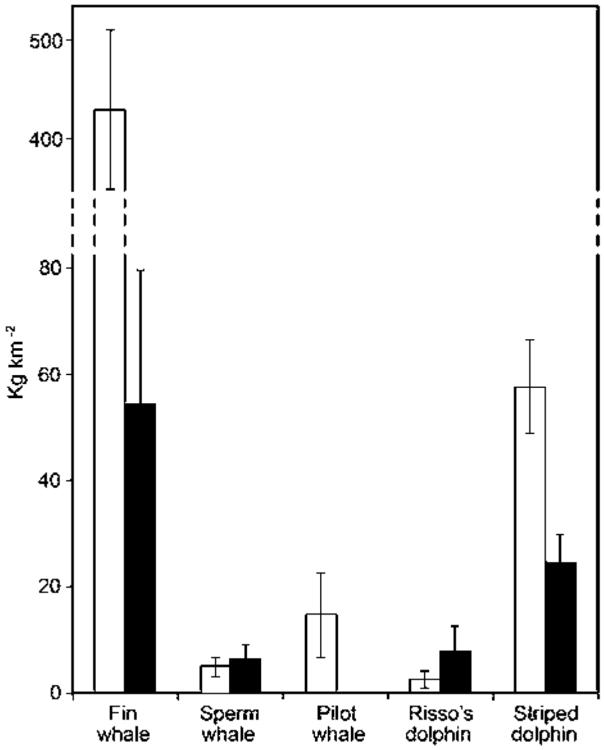

Fig. 3. Estimated biomass density (in kg km^{-2}) for each species for April-September (open bars) and October-March (filled bars) periods. Error bars represent the standard errors.

Table 3

Seasonal (kg km^{-2} d^{-1}) and annual (kg km^{-2} y^{-1}) estimates of consumption of three categories of prey by five species of cetaceans in the Ligurian Sea.

		Season		
Species	Prey	Apr.-Sep.	Mar.-Oct.	Annual
Sperm whale	Fish	0.01	0.01	4
	Cephalopods	0.09	0.12	37
Pilot whale	Fish	0.03	0.00	6
	Cephalopods	0.60	0.00	110
Risso's dolphin	Fish	0.01	0.02	5
	Cephalopods	0.13	0.41	98
Striped dolphin	Fish	1.89	0.80	492
	Cephalopods	1.91	0.81	497
	Crustaceans	0.04	0.02	10
All odontocetes	Fish	1.94	0.84	507
	Cephalopods	2.73	1.33	742
	Crustaceans	0.04	0.02	10
Fin whale	Fish	0.00	0.07	13
	Crustaceans	5.66	0.65	1,150
All species	Fish	1.94	0.91	521
	Cephalopods	2.73	1.33	742
	Crustaceans	5.69	0.66	1,160
	Total	10.4	2.9	2,422

Maximum lengths of Risso's dolphin from the French Mediterranean stranding network differed by only 20cm from the global values of 380cm for males and 360cm for females reported by Trites and Pauly (1998) and were based on small sample sizes ($n<20$ for both males and females). Therefore average weights were used for males and females as in Trites and Pauly (1998); 236kg and 211kg, respectively. The average for the species was 224kg (Table 2).

The seasonal biomass densities were 7.9kg km^{-2} (CV=58.2%) in October-March and 2.6kg km^{-2} (CV=58.9%) in April-September (Fig. 3). The average daily ration for Risso's dolphin was estimated to range from 7.6 to 17.0kg d^{-1} (3.4-7.6% of body mass, Table 2). From the selected model (Kenney *et al*., 1997) a value of 12.1kg d^{-1} was obtained. The annual consumption rate was estimated to be 103kg km^{-2} (CV=65.3%): 5kg of fish; and 98kg of cephalopods (Table 3).

Pilot whale

Most of the sightings of pilot whales occurred at perpendicular distances of less than 800m; therefore a uniform model was adopted, considering that all animals were detected up to 800m from the transect. The species was encountered in summer only, with a mean school size of 28.4 (CV=28.0%). The density was estimated as 0.027 individuals km^{-2} (CV=49.1%).

Maximum lengths of Mediterranean pilot whales were 600cm from 31 males and undetermined individuals and 500cm from 20 females (F. Dhermain, GECEM and O. Van Canneyt, CRMM - University of La Rochelle, pers. comm.). The average weights computed from the Trites and Pauly (1998) regressions were 689kg and 451kg, respectively, and the average for the species was 546kg (Table 2).

The summer biomass density was 14.7kg km^{-2} (CV=49.1%) (Fig. 3). The average daily ration for pilot whales was estimated from the four models to range from 15.5 to 34.2kg d^{-1} (2.8-6.3% of body mass, Table 2), with an estimate from the selected model of 23.6kg d^{-1}. The annual consumption rate was estimated to be 116kg km^{-2} (CV=69.4%): 110kg of cephalopods; and 6kg of fish (Table 3).

Sperm whale

Sperm whale visual sightings and distinct acoustic sequences represented a total of 27 encounters, including 20 detected only acoustically and 7 using both methods. Mean school size was 1.5 (CV=10.5%) in summer and 3.0 (CV=29.6%) in winter. Their extrapolated density varied between 3.9×10^{-4} individuals km^{2} (CV=39.1%) in April-September and 5.2×10^{-4} (CV=38.6%) in October-March, the smallest seasonal difference of any of the five species, with no significant difference (Z-test=0.52, $p>0.60$).

The maximum length of sperm whales stranded along the French Mediterranean coast was 15m from 18 males and undetermined individuals (F. Dhermain, GECEM and O. Van Canneyt, CRMM - University of La Rochelle, pers. comm.). This length was also greater than 30 length estimates based on inter-pulse interval measurements from acoustic recordings in the northwestern Mediterranean Sea (Drouot *et al*., 2004). The average male weight computed from the Trites and Pauly (1998) regression was 16.1t. As only one female length was available, the average female weight of 10.1t reported by Trites and Pauly (1998) was used. The average for the species was 12.5t (Table 2).

The seasonal biomass densities were 4.9kg km^{-2} (CV=39.1%) and 6.6kg km^{-2} (CV=38.6%), in April-September and October-March respectively (Fig. 3). The average daily ration for sperm whales was estimated to range from 189 to 393kg d^{-1} (1.5-3.1% of body mass, Table 2). The daily ration estimated from Kenney *et al*. (1997) model was 244kg d^{-1}. The annual consumption rate was estimated to be 41kg km^{-2} (CV=39.2%): 37kg of cephalopods; and 4kg of fish (Table 3).

Fin whale

An *esw* of 1,152m (CV=10.3%) was estimated for fin whales, using a hazard-rate model without adjustment and after truncation at 2,000m. Mean school size was 1.6 (CV=8.1%) in April-September and 1.1 (CV=11.1%) in October-March. The maximum density was observed in summer with 0.014 individuals km^{-2} (CV=19.2%), against 0.002 (CV=46.3%) in winter. The 8-fold difference between seasonal densities was the highest of any of the four species that were present in both seasons and was significant (Z-test=4.35, $p<0.0001$).

The maximum length of Mediterranean fin whales was 20m, with no clear difference between males and females (from 68 stranded individuals; F. Dhermain, GECEM and O. Van Canneyt, CRMM - University of La Rochelle, pers. comm.). The average weights computed from the Trites and Pauly (1998) regressions were 31.4t for males and 30.8t for females, and the average for the species was 31.1t (Table 2).

The seasonal biomass densities correspond to 429kg km^{-2} (CV=19.2%) in April-September and 54kg km^{-2} (CV=46.3%) in October-March (Fig. 3). The average daily ration for a fin whale was estimated to range from 393 to 680kg d^{-1} (1.3-2.2% of body mass; Table 2) and computed to be 410kg d^{-1} from the selected model. The annual consumption rate was estimated to be 1,163kg km^{-2} (CV=25.2%): 1,150kg of crustaceans; and 13kg of fish (Table 3).

All cetacean species

For all odontocetes combined, the biomass densities varied between 38.9kg km^{-2} (CV=19.2%) in winter and 79.8kg km^{-2} (CV=14.5%) in summer. The total cetacean biomass densities were 93.4kg km^{-2} (CV=28.2%) in winter and 509.0kg km^{-2} (CV=16.3%) in summer. These seasonal values were significantly different (Z-test=4.9, $p<0.0001$).

The combined daily food consumption of all cetaceans was estimated to be 2.9kg km^{-2} d^{-1} (CV=28.2%) in winter (Table 3), dominated by cephalopods (45.9%), followed by fish (31.3%) and crustaceans (22.8%). In summer, daily consumption increased to 10.4kg km^{-2} d^{-1} (CV=16.3%), strongly dominated by crustaceans (54.9%) and followed by cephalopods (26.3%) and fish (18.7%). The seasonal difference in prey types is driven by the different densities of fin whales. Annual food requirement represents 2.4t km^{-2} (CV=20%) (Table 3, Fig. 4).

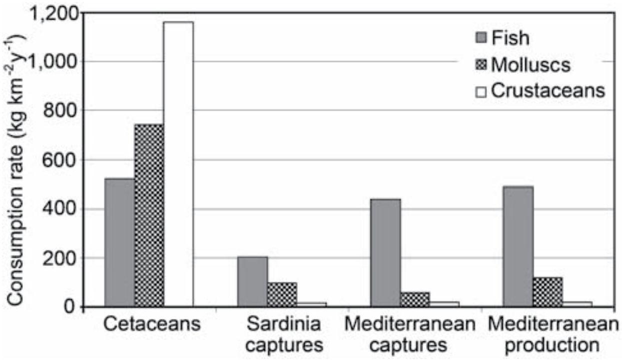

Fig. 4. Annual consumption rate (kg km^{-2} y^{-1}) by cetaceans in the Ligurian Sea compared to 2000-2005 average fishery landings and production reported for Sardinia (FAO area 1.3) and the entire Mediterranean and Black Sea.

Compared to reported fishery landings from either the whole Mediterranean Sea or only the Sardinia region, cetacean predation rates on crustaceans and molluscs are much larger than fishery harvest rates (Fig. 4). Competition for molluscs between cetaceans and humans is even lower than apparent from the data because most of the species consumed by teuthophageous odontocetes, particularly large ones (Astruc, 2005), are not commercial species. Cetacean consumption of fish is much closer to fish (including sharks) harvest rates reported for the Sardinia area (202kg km^{-2}) or for the entire Mediterranean and Black Sea (437kg km^{-2} or 487 considering aquaculture).

Primary production required

The primary production required to support total prey consumption by cetaceans was estimated to be 12.6gC m^{-2} y^{-1}. In the Ligurian Sea, the mean primary production has been estimated at 165gC m^{-2} y^{-1}, from SeaWiFS remotely sensed imagery from 1998 to 2001 (Bosc *et al*., 2004). *PPR* for cetaceans is 7.6% of that value. Total annual productivity estimates from *in situ* ^{14}C methods have varied from 86 to 226gC m^{-2} y^{-1} (Marty and Chiavérini, 1999), of which the primary production requirement for cetaceans represents between 5.6 and 14.7%.

DISCUSSION

This study estimates for the first time the seasonal variability of density and biomass of cetaceans in the Ligurian Sea, as well as their rates of prey consumption and trophic effects. Although the results are sensitive to many input parameters and assumptions, these results allow basic comparisons in order of magnitude with reported fishery landings and phytoplankton production. A recent document from the European Community (COM, 2003) concluded that despite an increase of the fishing effort in the Mediterranean Sea overall production and rates have been steadily decreased compared to the past. The approach allows better quantification of the trophic importance of cetaceans in the area and their fish demand than has been available in the past.

Density

Both seasonal sampling periods were covered by more than 2,000km of survey effort, including at least 12 surveys over the 4 years. The estimated densities for the two most common species, striped dolphin and fin whale, should be considered as reliable, which is supported by CVs of <22% except for fin whales in winter. The estimate of summer fin whale density (0.014 individuals km^{-2}; CV=19.2%) is in agreement with previous results, which vary from 0.015 individuals km^{-2} (CV=15.9%; Gannier, 1997) in the Liguro-Provençal area to 0.024 individuals km^{-2} (CV=27.0%; Forcada *et al*., 1996; Gannier, 1997) in the western Mediterranean Sea. Fin whale density in the Ligurian Sea is also similar to other regions of the North Atlantic, with 0.021 individuals km^{-2} to 0.053 (Buckland *et al*., 1992; Kenney *et al*., 1985) Previous estimates of the summer density of striped dolphins in the area ranged between 0.30 individuals km^{-2} (CV=35%) and 0.75 (Forcada and Hammond, 1998; Gannier, 2006), with the minimum estimated just after an epizootic mortality event. The estimate of 0.87 individuals per km^{-2} (CV=15.2%) in April-September period is in agreement, considering that previous estimates were conducted in July and/or August, while in the data set used in this study surveys were also carried out in September, which corresponds to the maximum occurrence of striped dolphins in the area (Laran and Drouot-Dulau, 2007). In the central Spanish Mediterranean Sea, a maximum seasonal abundance of 0.60 individuals per km^{-2} (CV=26.0%) was recorded in Autumn (Gómez de Segura *et al*., 2006) – this is a well-known productivity area (e.g. Cañadas and Hammond, 2006). These estimates are higher than the maximum density estimate for any sampling stratum in the northwest Atlantic (0.37 individuals per km^{-2}; Kenney *et al*., 1985) or for small delphinids in the Bay of Biscay (0.55 individuals per km^{-2}, CV=29%; Certain *et al*., 2008), however both studies were based on aerial surveys and for the northwest Atlantic a much higher proportion of small delphinid sightings was not identified to species. In addition, striped dolphins in the northwest Atlantic are known to be most abundant in waters of the continental slope and farther offshore (Waring *et al*., 2008), but the surveys reported by Kenney *et al*. (1985) were almost entirely inshore of the shelf break.

The estimated densities for the less common species (sperm whales, pilot whales and Risso's dolphins) must be considered with some caution, and the CVs are substantially larger in most cases. For sperm whales, the annual encounter rate of individuals was estimated to be 0.012 individuals km^{-1} (CV=55.0%), close to previous values; 0.006 individuals per km (CV=44.0%; Gannier, 2006) or 0.007 (CV=21.7%; Gannier *et al*., 2002) estimated in the same area. The estimated densities of 5.2×10^{-4} individuals km^{-2} (CV=38.6%) in winter and 3.9×10^{-4} (CV=39.1%) in summer obtained in this study could only be compared with the rough estimate of 10×10^{-4} by Gannier (1995), which considered visual sightings only. The wide arbitrary distance (13km), on both sides of the transect, to account for hydrophone efficiency may have led to an underestimate of sperm whale density and is a factor that must be better quantified for future work. For Risso's dolphins, the few existing estimates vary over the year from 0.015 individuals km^{-2} (CV=60.6%) for the central Spanish Mediterranean (Gómez de Segura *et al*., 2006) to 0.021 (CV=37.1%) for the northwestern Mediterranean Sea (Gannier, 1995). An estimated annual average of 0.023 individuals km^{-2} (CV=65.3%) was obtained in this study, which is similar. There was a strong seasonal variation, with winter density three times summer density, showing the migratory behaviour of Risso's dolphin in the area. For pilot whales, the obtained sighting rate of 0.043 individuals km^{-1} (CV=49.1%) between April and September is quite low when compared to the value of 0.14 whales km^{-1} (CV=69.3%) obtained in the area in July-August 2001 (Gannier, 2006). However the latter result was based on only a single sighting, and both estimates have large variances. The estimated summer density (0.027 individuals km^{-2}; CV=49.1%) is almost identical to the 0.028 (CV=62.3%) value computed from the results of Gannier (1995).

Biomass and food consumption

Prior to the first dedicated surveys for cetaceans in the Mediterranean Sea in the 1990s, biomasses of the eight most common species were roughly estimated for the area between 40°N and European coasts (300,000km^2) (table 13 in Viale, 1985). Interestingly, beginning from mean body mass estimates that varied substantially from the values used in this study and approximate numbers of animals in the area (with no clear details available on those estimates), the author calculated a total cetacean biomass of 86,950t, representing a biomass density of 290kg km^{-2}, very close to the estimate obtained in this study (300kg km^{-2}). In addition, Viale (1985) estimated fish consumption of 58,100t, corresponding to 194kg km^{-2}, while a value of 522 kg km^{-2} was obtained in this study. For cephalopods her results corresponded to 763kg km^{-2}, and for macro- and microzooplankton, 1,100kg km^{-2}, while estimates of 739 and 1,160kg km^{-2} respectively were obtained here. Since the methods and input parameters were completely independent, this level of agreement is somewhat encouraging. The better-supported estimates obtained through this study, using better density values, also identify variations between warm and cold seasons.

Comparisons with different studies and locations

The Mediterranean Sea, a semi-enclosed sea, has a lower cetacean diversity than many other areas. Along the US western coast, for example, about twenty cetacean species are observed in the Californian Current ecosystem (Barlow *et al*., 2008). Thirty-five species of cetaceans are known to occur along the eastern coast of the US (Waring *et al.*, 2008). Estimates of biomass densities and prey consumption rates allow for more informative comparisons with other areas than is possible using only species abundances or densities. The estimate of annual average biomass density obtained in this study (301kg km^{-2}) is intermediate between 143kg km^{-2} for marine mammals in the entire Pacific Ocean (Trites *et al.*, 1997) and 729kg km^{-2} for cetaceans only in the northeastern US continental shelf system (Kenney *et al.*, 1997). During summer and autumn, Barlow *et al.* (2008) estimated a value of 282kg km^{-2} for cetacean biomass density in the California current ecosystem, with a proportion of Balaenopteridae (70%) similar to the observations noted in this paper. Seasonal variability was somewhat stronger in the Ligurian Sea than in the NE US shelf; the results detailed here differ by a factor of five between six-month winter and summer seasons, while Kenney *et al.* (1997) reported a maximum ratio of 3.8 between winter and spring. In agreement with the results of the study presented here and those of Barlow *et al.* (2008), Kenney *et al.* (1997) showed a cetacean community dominated by balaenopterids, at 72-78% of the total standing stock, but their dominance continued through all four seasons of the year.

The point estimate of food intake by cetaceans (2.4t km^{-2} y^{-1} in this study) is much greater than results for northern European seas, ranging between 0.25t km^{-2} y^{-1} in Atlantic waters to 0.75 around Spitsbergen and in polar waters (Joiris, 1992; 1996; 2000). Prey consumption estimates from the studies discussed immediately above, as expected, follow the same order as the estimates of biomass density. Barlow *et al.* (2008) reported consumption of 1.5-2.4t km^{-2} y^{-1} in the California current, the most similar value to that of this study; the minimum was 0.84t km^{-2} y^{-1} in Pacific Ocean (Trites *et al.*, 1997) and the maximum was 6.7t km^{-2} y^{-1} on the northeastern US continental shelf (Kenney *et al.*, 1997). Estimates of fish consumption by marine mammals vary from 0.10t km^{-2} y^{-1} in the North Sea to 5.4t km^{-2} on Georges Bank (Bax, 1991), and the point estimate obtained here of 0.48t km^{-2} y^{-1} of fish consumed corresponds to the lower end of that range. Kenney *et al.* (1997) estimated fish consumption to be an order of magnitude higher at 4.6t km^{-2} y^{-1} because the diet of fin, humpback and minke whales off the northeastern US is primarily fish rather than crustaceans.

World fishery catch rates vary between 10 and 22.2t km^{-2} y^{-1} (from oligotrophic open-ocean systems to highly productive upwellings) representing 1.8-35% of the total net primary production (Pauly and Christensen, 1995). Compared with commercial fisheries, the point estimate of the relative proportion of fish consumed by marine mammals represents some 2% of the fisheries in the North Sea (Bax, 1991), 167% in the Barents Sea (Bax, 1991) and 171% in the northeastern US shelf (Kenney *et al.*, 1997). About 150% was estimated for herring only in the Gulf of Maine (Overholtz and Link, 2006). In the Ligurian Sea, the point estimate of the proportion of fish consumed by cetaceans represents 257% of the reported fishery if only the Sardinia area is considered and 107% compared to global production of fisheries (i.e. catches and aquaculture combined) from the entire Mediterranean Sea. Since a large proportion of the fish harvested remains unrecorded, relative percentages of cetacean consumption should probably be reduced compared to actual catches. In the Pacific Ocean, Trites *et al.* (1997) estimated that fisheries target only 35% of the prey items sought by marine mammals. However this ratio could vary between predator species; for example 70% of the total prey species of striped and Risso's dolphins in the Mediterranean are commercial species (Würtz *et al.*, 1992).

The primary production required for cetaceans was estimated as 20-30gC m^{-2} y^{-1} in the Pacific Ocean (Trites *et al.*, 1997), 31.4gC m^{-2} y^{-1} in the California Current ecosystem (Barlow *et al.*, 2008) and 47.5gC m^{-2} y^{-1} in the northeastern US shelf ecosystem (Kenney *et al.*, 1997), all higher than the estimate of 12.6 obtained here. The mathematical model used to estimate *PPR* (Eqn. 8) includes a power function, so the *PPR* estimates are especially sensitive to the trophic level of the prey species and the most difficult result to compare between ecosystems. Following Barlow *et al.* (2008), who conducted sensitivity analysis in a similar study in the California area, the main effect on approximation of result is the energy transfer across the food web.

Potential sources of variability and error

In the area used in this study, further investigation is necessary to derive more reliable density estimates for less common species such as sperm whales, pilot whales and Risso's dolphins, in addition to the rarer or coastal species that were not sampled at all during the surveys. In addition, there is a negative bias caused by not considering $g(0)$. For the fin whale, no decrease in detection probability on the line was recorded between fast and reduced-speed sampling (22 and 13km h^{-1}), in contrast with the striped dolphin for which a decrease of 12% was estimated at 22km h^{-1} (Laran, 2005). Therefore there was probably an underestimation of striped dolphin density. For the sperm whale, acoustic sampling allowed detection of clicks during almost all their dive durations (Mullins *et al.*, 1988), but the efficiency of the hydrophone likely varies with water column conditions, instead of remaining constant at the arbitrary sampling width of 13km. In addition, the sampling protocol allowed monthly effort to be maintained during three years, but was not suited to estimation of cetacean abundance in the entire Pelagos Sanctuary. Additional field campaigns over broader areas of the Sanctuary, dedicated to abundance estimation, should be carried out in summer and winter to obtain accurate estimates.

Previous studies of this type (Kenney *et al.*, 1985; Kenney *et al.*, 1997; Sigurjónsson and Víkingsson, 1997; Trites and Pauly, 1998) generally have relied on relatively imprecise estimates of body mass available from the literature as the starting point for bioenergetic models. Kenney *et al.* (1985) had reliable data from their own study area for only one species, using a set of photogrammetric length measurements of fin whales and a published weight-length equation to derive a mean weight for the study region. Trites and Pauly (1998) have assisted researchers developing marine mammal energetic models by presenting estimates of average body weights for all species, although they did not provide estimates of variability. Finally, using maximum lengths observed within a particular area, when available, enables the modelling results to better represent the local or regional system. Large datasets of body weights from a particular region would allow direct estimation of mean weights and variability, although it becomes more difficult with increasing body size and there are concerns over bias if the data are obtained from strandings.

Another important source of uncertainty in the results is prey consumption rate. The mean daily rations estimated as percentages of an individual's body mass (1.3-6.7% using the selected model and 1.3-9.1% across all four models) are consistent with general approximations of 3 to 5% for marine mammals (Trites, 2003). The model used here was intermediate in value, and was the model proposed by Barlow *et al.* (2008) to be the most realistic. Fin whale daily intake has been estimated as 1.3-3.3% of body mass from various methods (Lockyer, 1981; 2007), but the estimates generally are based on very low or no feeding during winter and higher rates in summer to compensate. The rate of 1.3% obtained during the study described here represents the lower end of the range, but increased feeding in summer to account for lower consumption during winter was not considered. Although fin whales have been observed feeding in winter in the Mediterranean (Canese *et al*., 2006), it is believed that they feed very little or not at all and therefore must increase their summer feeding rate.

For many marine mammal species, Pauly *et al*. (1998) estimated proportions of their diets comprised of eight different prey categories (benthic invertebrates, large zooplankton, small squid, large squid, small pelagic fishes, mesopelagic fishes, miscellaneous fishes and higher invertebrates). However their estimates represent worldwide averages, do not includes estimates of variability and are themselves based on relatively sparse data. Additional detailed information on diet composition specific to the Ligurian Sea is required to improve consumption estimates for individual prey categories and to better assess variability. For pilot whales and Risso's dolphins only a few results are available for the Mediterranean Sea, and we recognise that our conclusions could vary greatly based on new and better information. Striped dolphins feed on a variety of pelagic and benthopelagic fish and squid (Archer, 2002). Pauly *et al*. (1998) described their diet as 5% benthic invertebrates, 20% small squid, 15% large squid, 5% small pelagics, 30% mesopelagics and 25% miscellaneous or 60% fish, 35% squid and 5% invertebrates, as compared with the values used in this study of 49.3% fish, 49.7% squid and 1% crustaceans. In the Ligurian Sea they exploit many mid-water species (Würtz and Marrale, 1993). The few winter samples analysed from the Ligurian Sea suggest that they may feed at times in winter on cephalopods alone (G. Astruc and D. Agati, pers. comm.). The stable-isotope analyses developed for several species in the area could also help to better quantify and refine cetacean diets and interannual variability in diet, and stable-isotope studies on particular prey species would enable more precise estimates of the trophic levels of prey for *PPR* calculations. Meanwhile accurate estimate of numerous parameters in the area and better quantification of their variability is important to better quantify CVs associated with cetacean consumption estimated in the area.

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Population dynamics of killer whales (*Orcinus orca*) in the Crozet Archipelago, southern Indian Ocean: a mark-recapture study from 1977 to 2002

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ABSTRACT

Population size and annual survival probabilities for the killer whales (*Orcinus orca*) inhabiting the inshore waters of Possession Island, Crozet Archipelago, southern Indian Ocean, were estimated through mark-recapture modelling. Capture histories were generated from a set of photographs taken under a photo-identification protocol and a set of photographs taken opportunistically, between 1964 and 2002. Photographs were selected according to their intrinsic quality and the degree of natural marking of individuals. Under those conditions, only well-marked individuals were considered as 'marked' from a capture-recapture perspective. The purpose of this double selection was to minimise identification errors and reduce the heterogeneity of capture probabilities. Abundance estimates were derived from the M_{th} sequential model for closed populations and adjusted for the proportion of well-marked individuals in the study population and for the number of photo-identified individuals. Under this framework, estimates of 98 (95% CI 70-156) individuals in 1988-89, and 37 (95% CI 32-62) individuals in 1998-2000 are proposed. After a weighted model averaging, the Cormack-Jolly-Seber models with the strongest support from the data produced low survival probability estimates, decreasing from 0.935 (95% CI 0.817-0.979) to 0.895 (95% CI 0.746-0.961) for males, and from 0.942 (95% CI 0.844-0.980) to 0.901 (95% CI 0.742-0.966) for females over the period 1977-2002. A Jolly-Seber model was used as a 'second opinion' model. It confirmed the worrying status of the population with a constant survival probability estimated at 0.89 (95% CI 0.84-0.93) and a constant rate of increase (applying to the well-marked fraction of the population) estimated at 0.94 (95% CI 0.90-0.99) for the period 1987-2000. This rate of increase is consistent with the abundance estimates presented here. Possible violations of the underlying model assumptions were investigated and it was concluded that the abundance estimates for the period 1988-89 and the CJS survival estimates should be the most reliable results. It is feared that the killer whales around Possession Island are in sharp decline, as may be true for the whole Crozet Archipelago. The effect of low prey stocks and lethal interactions with fisheries as the most likely causes of this decline are discussed.

KEYWORDS: KILLER WHALE; INDIAN OCEAN; PHOTO-ID; MARK-RECAPTURE; ABUNDANCE; SURVIVAL; FISHERIES

INTRODUCTION

Top predators are dependent upon an extensive set of trophic links within the marine food web. Consequently, they are directly or indirectly affected by human activities and changes in environmental conditions such as climatic and subsequent habitat changes (Barbraud and Weimerskirch, 2001), concentration of pollutants in the food web (Ylitalo *et al*., 2001), interactions with fisheries (Lewison *et al*., 2004), or depletion of prey stocks. Top predators are thus conveying a range of information on the marine environment and are often considered as biological indicators of the changes in their ecosystems (Boyd *et al*., 2006; Sergio *et al*., 2005).

Around the southern Indian Ocean Subantarctic islands, the killer whale (*Orcinus orca*) can be considered as a biological indicator of choice because of its eclectic diet (elephant seals, penguins, cetaceans, fish; Guinet, 1991). The first documented sighting in the Crozet Islands occurred in 1825 (Lesquin, 1840) and in the 1970s the first studies focused on their behaviour (Voisin, 1976). The first demographic parameters were estimated by Guinet (1991), who pointed out a low fecundity and a decrease in the number of individuals observed from the coasts of Possession Island (one of the main islands in the archipelago). This paper focuses on these individuals, whose status is still unknown from a population biology point of view. However, for the sake of simplicity, they are hereafter referred to as a 'population'.

Initially developed to model physical recaptures and derive population parameters, capture-recapture models are now widely applied to capture histories generated from photographic observations (Hammond, 1986; Karanth and Nichols, 1998). Since part of the Crozet population can be reliably identified from natural marks (Guinet, 1991), mark-recapture models were used to estimate some population parameters (annual adult survival probabilities, population size and population growth rate).

Today, only northeastern Pacific resident killer whales have been studied using advanced population dynamics methods leading notably in survival estimates (Olesiuk *et al*., 1990). The results presented have been compared to the parameters of this, at least at that time, healthy growing population.

METHODS

The photographic collection

A pool of photographs taken between 1964 and 2002 by land-based observers from various places along the shore of Possession Island (46°25'S, 51°40'E) in the Crozet Archipelago was used for this study. Most photographs were taken according to a protocol aiming at getting the completely exposed dorsal fins of all the individuals surfacing in the study area with the best possible magnification. The rest of the photographs were taken opportunistically without any special protocol.

Selection and analysis of photographs

The photographs were given a 'Q' (quality) value between 0 and 3. Q=3 when individuals were very well represented with fully visible dorsal fins on close-up and when the shooting angle was 90°. Q=2 when dorsal fins were fully visible, but not on close-up or with an angle slightly different from 90°. Q=1 when dorsal fins were partially visible on exploitable photographs. Q=0 for unusable

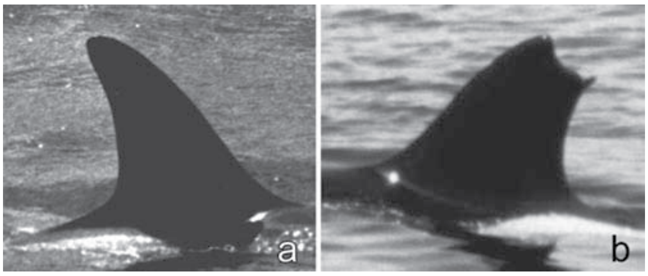

Fig. 1. a. Individual without any significant natural mark ('*M*' quality value = 0; photo C. Guinet). b. Individual with a significant natural mark (amputation; '*M*' quality value = 2; photo E. Fernandez).

photographs (e.g. subject blurred or too far, shooting angle very different from 90°).

The whales were identified by the natural marks on their dorsal fins (Bigg, 1982). A photo-identification catalogue was created and each occurrence of identified whales was recorded in a database with date and location details to produce sighting histories.

The quality of marking of each photographed whale was given an '*M*' quality value between 0 and 2. M=0 for individuals with dorsal fins bearing no significant mark (Fig. 1a). M=1 for individuals with dorsal fins bearing temporary marks (e.g. scars, desquamation), non symmetric marks, or marks that are hardly visible on photograph with $Q \geq 2$. M=2 for well-marked physically mature individuals with dorsal fins bearing symmetric marks that are assumed to remain unchanged, or almost unchanged, for the study duration (e.g. notches, amputations, Fig. 1b) and that are easily visible on photographs with $Q \geq 2$.

Estimating demographic parameters

Only photographs with $Q \geq 2$ of individuals with M=2 were considered. Thus, only well-marked individuals were considered as 'marked' from a capture-recapture perspective. This double selection aimed at minimising identification errors and reducing the influence of the quality of natural marks on capture probabilities, in other words, reducing the heterogeneity in capture probabilities (Hammond, 1986).

Abundance

The best documented periods of the study were focussed on, i.e. 1988-89 (Table 1) and 1998-2000 (Table 2), to estimate the number of killer whales frequenting the coasts of Possession Island. Among the classical sequential mark-recapture models for closed populations (Otis *et al.*, 1978; Pollock *et al.*, 1990), model M_{th} was chosen for the consistency of its underlying assumptions with the study conditions. These assumptions are: (1) the population is closed demographically (no deaths or births) and geographically (no emigration or immigration) for the duration of the study; (2) all marks are correctly read and recorded on each capture occasion; (3) marks are not lost nor overlooked; (4) individual capture probabilities are heterogeneous; and (5) capture probabilities can vary with time.

The closure assumption could not be tested because the data were too sparse for the closure tests of Otis *et al.* (1978) and Stanley and Kenneth (1999). The possible violations of this assumption and their consequences are discussed later. Assumptions (2) and (3) were considered to be fulfilled thanks to the selection procedure used for photographs and marks. A model with assumptions (4) and (5) was needed because many parameters affected capture probabilities during the study (behavioural heterogeneity among individuals, diversity of natural marks, photographers and capture sites, varying effort of observation, etc.).

As the photographic material was initially intended for simple photo-identification analyses, the sampling occasions were not planned 'by the rule book' for mark-recapture modelling. Therefore capture occasions were defined *a posteriori* in such a way that the time intervals between them were supposedly long enough (at least two months) to allow mixing between individuals.

For choosing among the various estimators for model M_{th}, Chao *et al.* (1992) recommend examining the sample coverage (C) defined as 'the proportion of the total individual capture probabilities of the captured animals' and the coefficient of variation of individual capture probabilities (γ, a measure of the heterogeneity mentioned in assumption (iv)). $\hat{C}$ can be estimated by the mean of estimators $\hat{C}_1$ and $\hat{C}_2$ (see Chao *et al.*, 1992 for details):

$$\hat{C} = 1 - \frac{f_1 - f_2/(t-1)}{\sum_{k=1}^{t} kf_k}$$

where f_k is the number of animals captured k times in t samples. $\hat{\gamma}^2$, the estimation of the square of γ, and the abundance were estimated by the program *CAPTURE* (Otis *et al.*, 1978).

Since only well-marked individuals (with M=2) were regarded as 'marked' in the analyses, the models estimated the abundance of this fraction of the population ($\hat{N}$). To estimate the abundance of the whole population, the proportion of well-marked individuals was estimated, denoted θ, in the population. This proportion was estimated for the periods 1987-90 (corresponding to 1988-89 plus two years of extension in order to increase the sample size) and 1998-2000. For each period, photographs were selected with $Q \geq 2$, taken according to the protocol and showing at least two individuals to avoid over-representation of well-marked animals. Standard errors were estimated using the binomial theory of probability.

The size of the whole population (N') was estimated by adjusting $\hat{N}$ for $\hat{\theta}$ with $\hat{N}' = \hat{N} / \hat{\theta}$.

To maintain the asymmetry in the confidence interval of computed by *CAPTURE* (has a non-normal distribution so *CAPTURE* assumes a log-normal distribution or exploits the likelihood principle), the limits of this interval were adjusted for the coefficient of variation (CV) of $\hat{\theta}$, according to formulas derived from Whitehead *et al.* (1997):

$$\text{l.b.}(\hat{N}') = \frac{\hat{N}}{\hat{\theta}} \cdot \left(1 - 2 \cdot \sqrt{\left(\frac{\hat{N} - \text{l.b.}(\hat{N})}{2 \cdot \hat{N}} \right)^2 + \text{CV}(\hat{\theta})^2} \right)$$

$$\text{u.b.}(\hat{N}') = \frac{\hat{N}}{\hat{\theta}} \cdot \left(1 + 2 \cdot \sqrt{\left(\frac{\text{u.b.}(\hat{N}) - \hat{N}}{2 \cdot \hat{N}} \right)^2 + \text{CV}(\hat{\theta})^2} \right)$$

where l.b.(X) and u.b.(X) are respectively the lower and upper bounds of the 95% confidence interval of the variable X.

Analysis of the apparent annual survival and rate of increase of the population

The annual capture-recapture data (see Tables 1, 2 and 3) were analysed with the Cormack (1964), Jolly (1965) and Seber (1965) model (referred to as the 'CJS model' hereafter) to estimate the apparent survival probabilities and the capture probabilities for adults (physically mature individuals) over the study period. The underlying assumptions for this model are: (1) capture probabilities (p) are homogeneous among marked individuals at each occasion *t*; (2) survival probabilities (Φ) are homogeneous among marked animals between each occasion; (3) marks are not lost nor overlooked; (4) capture occasions are short in comparison to the time interval between successive occasions; (5) emigration is permanent; and (6) animals are independent regarding capturability and survival (Williams *et al.*, 2002).

Table 1

Capture-recapture summary statistics for the period 1988-89. *i* is the capture occasion number, C_j the number of individuals captured at occasion *j*, R_j the number of individuals recaptured among C_j, N_j the number of newly captured individuals during occasion *j* and M_j the cumulated number of marked individuals in the population at the end of occasion *j*.

j	Date	Effort	C_j	R_j	N_j	M_j
1	April 11 1988	6	3	0	3	3
2	November-December 1988	102	14	0	14	17
3	November-December 1989	57	19	11	8	25

Table 2

Capture-recapture summary statistics for the period 1998-2000. *j* is the capture occasion number, C_j the number of individuals captured at occasion *j*, R_j the number of individuals recaptured among C_j, N_j the number of newly captured individuals during occasion *j* and M_j the cumulated number of marked individuals in the population at the end of occasion *j*.

j	Date	Effort	C_j	R_j	N_j	M_j
1	April 1998	1	1	0	1	1
2	November-December 1998	141	13	0	13	14
3	December 1999-January 2000	40	3	3	0	14
4	April 15 2000	2	2	2	0	14
5	June 21-29 2000	26	3	3	0	14
6	October-December 2000	175	11	10	1	15

Table 3

Capture-recapture summary statistics for the period 1977-2002. *j* is the capture occasion number, C_j the number of individuals captured at occasion *j*, R_j the number of individuals recaptured among C_j, N_j the number of newly captured individuals during occasion *j* and M_j the cumulated number of marked individuals in the population at the end of occasion *j*.

i	Year	Effort	C_j	R_j	N_j	M_j
1	1977	44	2	0	2	2
2	1978	2	1	1	0	2
3	1979	3	1	0	1	3
4	1980	60	5	1	4	7
5	1981	8	1	1	0	7
6	1982	27	1	1	0	7
7	1984	3	1	0	1	8
8	1985	40	4	2	2	10
9	1986	38	1	1	0	10
10	1987	443	9	3	6	16
11	1988	399	17	10	7	23
12	1989	321	19	13	6	29
13	1990	26	2	2	0	29
14	1993	1	1	1	0	29
15	1996	108	4	3	1	30
16	1997	7	3	3	0	30
17	1998	402	14	10	4	34
18	1999	90	3	3	0	34
19	2000	796	12	11	1	35
20	2001	10	1	1	0	35
21	2002	61	6	6	0	35

In the standard parameterisation of the CJS model, denoted $[\Phi_t\, p_t]$, time is regarded as a source of variation in Φ and p. More general variants of this model allow the consideration of extra sources that are regarded alone or combined, with or without interaction (see Lebreton *et al.*, 1992 for details). The effect of time (t) and sex (s) on parameters Φ and p were studied with the general starting model $[\Phi_{s*t}\, p_{s*t}]$. The notation s*t, represents the cumulated effect of time and sex and their interaction on the considered parameter. The notation s+t represents the additive model without interaction.

Assumptions (3) and (4) were considered met thanks to the study design. Assumption (6) could not be met; the consequences of this violation will be discussed at the end of the study. The goodness-of-fit of the starting model $[\Phi_{s*t}\, p_{s*t}]$ for the remaining assumptions was tested with the program *U-CARE* (Choquet *et al.*, 2003). Variants of this model were fitted in two steps, first focusing on the modelling of capture probabilities with increasing constraints while keeping the full variability in survival probabilities. The annual photographic effort was used as a covariate to test the hypothesis of an effort-dependent capture probability (notation p_{effort}). The best model from the first step to model survival probabilities was then used. Survival probabilities were progressively constrained and tested for a trend over the study period (denoted Φ_{trend}) as well as the influence of the beginning of Patagonian toothfish (*Dissostichus eleginoides*) poaching in 1996 (denoted Φ_{poaching}).

To compare the survival estimations produced by the CJS models to another source of estimation, a set of Jolly-Seber models was fitted with the Pradel-λ parameterisation (hereafter referred to as 'JS models'; Pradel, 1996). Jolly-Seber models have an extra assumption compared to CJS models; unmarked animals in the population have the same probability of capture as marked animals in the population. This assumption was considered to be met (well-marked photo-identified individuals have the same probability of capture as well-marked individuals that have not been photo-identified yet). A sex effect could not be included in the JS candidate models because our data were too sparse to allow goodness-of-fit testing. Consequently, the starting model was the fully time dependant model $[\Phi_t\, p_t\, \lambda_t]$, where λ denotes the apparent rate of increase of the adult population. The goodness-of-fit of this starting model was tested with the program *JOLLY* (Pollock *et al.*, 1990). All possible candidate models were designed to include a trend over time on Φ and λ, and the effects of the photographic effort on p. λ is the sum of Φ and the apparent fecundity, which is small compared to Φ in large-mammal populations, especially in the study population (Guinet, 1991). As Φ is approximately equal to λ, models were designed with the same effects on these parameters. Due to the complexity of the JS models compared to the small size of the data set, the candidate models were applied only to the years with high photographic effort (i.e. 1987, 1988, 1989, 1998, 1999 and 2000) to avoid numerical convergence problems in the computing process.

The selection among CJS and JS model sets was achieved following the information-theoretic approach (Burnham and Anderson, 2002). The Akaike's information criterion adjusted to the size of the sample (AIC_c) was used to measure the parsimony of candidate models (Hurvich and Tsai, 1989). Differences of AIC_c (ΔAIC_c) were used to measure the plausibility of a given model compared to the model with the lowest AIC_c. In the case of selection uncertainty, i.e. when several models had $\Delta\text{AIC}_c < 2$ (Burnham and Anderson, 2002), a model averaging was performed with the best candidate models. This procedure yields a weighted average of the estimates produced by these models, using Akaike weights (w_i, a normalised measure of the relative support for model *i* in a set of models; Burnham and Anderson, 2002). All computations (model fitting, parameter estimation, AIC_c and w_i computation and model averaging) were carried out using the program *MARK* (White and Burnham, 1999).

RESULTS

Photo-identification

A total of 2,329 photographs were examined, including 1,812 taken according to the photo-identification protocol and 517 opportunistically. There were on average 1.26 individuals per photograph (2,930 killer whales were represented on the photographs). Each representation of a whale was treated as a photograph. The following totals were obtained for each 'Quality' category: Q = 0 (498 photographs); Q = 1 (582 photographs); Q = 2 (1,612 photographs); and Q = 3 (238).

All values of Q and M confounded, 70 different killer whales were photo-identified in the study area for the period 1988-89, and 32 for the period 1998-2000. These values represent minimum abundance estimates. Photographic effort for 1964-2002 is illustrated in Fig. 2.

Opportunistic photographs were of significant importance in our study. For the two abundance analyses (periods 1988-89 and 1998-2000) and for the survival analysis (period 1977-2002), respectively 16.2%, 5.7% and 31.5% of the captures were opportunistic.

Estimation of the number of individuals frequenting the coast of Possession Island

For the period 1988-89, the estimated sample coverage was high ($\hat{C}$= 0.76) and the estimated heterogeneity in individual capture probabilities was low ($\hat{\gamma}$ = 0.24). With $\hat{C}$>50% and $\hat{\gamma}$ <0.4, Chao *et al.* (1992) recommend using Darroch's estimator (Darroch, 1958) for model M_t instead of their estimator for model M_{th} (it performs better with this level of heterogeneity). Thus, under model M_{th} and with Darroch's estimator, the estimated number of the well-marked individuals was $\hat{N}$ = 30 (95%CI 25-42) for the period. After adjustment for $\hat{\theta}_{87\text{–}90}$ =30.6% (sample size: 49, SE 6.6%), the estimated total number of individuals was $\hat{N}'$=98 (95% CI 53-156). If the number of photo-identified whales for the period is considered as the lower bound of the confidence interval, the 95% CI can be crudely adjusted to [70, 156].

For the period 1998-2000, the estimated sample coverage was very high ($\hat{C}$ = 0.92) and a high level of heterogeneity in individual capture probabilities was detected ($\hat{\gamma}$=0.43). With >50% and $0.4 \leq \hat{\gamma} < 0.8$, Chao *et al.* (1992) recommend using their estimator for model M_{th}. Under these conditions, the estimated number of the well-marked individuals was $\hat{N}$=17 (95% CI 16-28) for the period. After adjustment for $\hat{\theta}_{98\text{–}00}$ =45.9% (sample size: 98, SE 5.0%), the estimated total number of killer whales was $\hat{N}'$=37 (95% CI 29-62). If the number of photo-identified whales for the period is considered as the lower bound of the confidence interval, the 95% CI can be crudely adjusted to [32, 62].

From these two abundance estimates, the corresponding geometric rate of increase of the population is $(37/98)^{1/10}$=0.907. The associated standard error estimated with the Delta method (Oehlert, 1992) is 0.027, hence a 95% confidence interval (assuming a Normal distribution) of [0.854, 0.961].

Analysis of apparent survival and rate of increase of the population

The overall goodness-of-fit test did not detect any significant lack of fit to the CJS starting model [$\Phi_{t*s}\ p_{t*s}$] (see Table 4). However, most component tests for males could not be carried out due to sparse data. Possible violations of the model assumptions are discussed later. Table 5 summarises the details of the candidate CJS models fitted to the observed data. Starting from model 1, capture probabilities were constrained in models 2 to 6. Model 6 [$\Phi_{s*t}\ p_{effort}$] had the highest empirical support from the data with the lowest AIC_c to this point. Models 6 to 16 were pursued, constraining survival probabilities. Finally, having the lowest AIC_c, model 10 [$\Phi\ p_{effort}$] was designated as the most adequate model to the data. However models 9 [$\Phi_s\ p_{effort}$], 13 [$\Phi_{trend}\ p_{effort}$] and 16 [$\Phi_{poaching96}\ p_{effort}$] had also strong empirical support from the data, with ΔAIC_c-values < 2 (Burnham and Anderson, 2002). The evidence ratios of these models ranged from 1.3 to 2.2, indicating a likely high uncertainty on the selection of the best model. To account for this uncertainty, a weighted model averaging was performed over models 9, 10, 13 and 16 to obtain survival probability estimates that

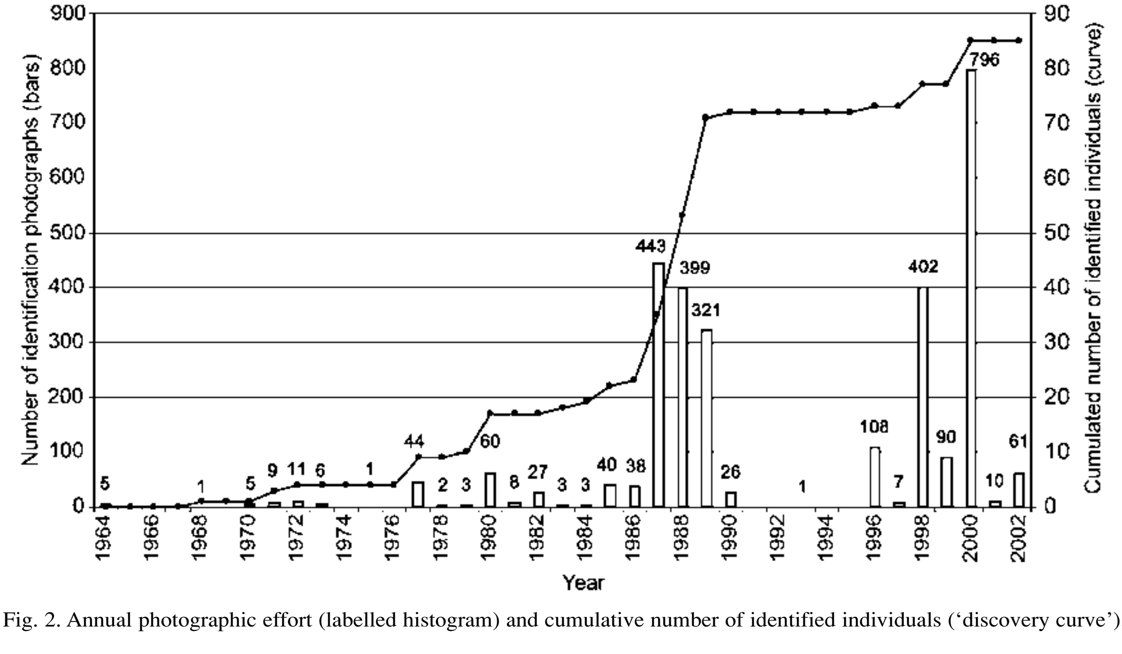

Fig. 2. Annual photographic effort (labelled histogram) and cumulative number of identified individuals ('discovery curve').

are unconditional to any model or sample. The estimated apparent survival probabilities decreased between 1977 and 2002, from 0.935 (95%CI 0.817-0.979) to 0.895 (95%CI 0.746-0.961) for males, and from 0.942 (95%CI 0.844-0.980) to 0.901 (95%CI 0.742-0.966) for females (Fig. 3).

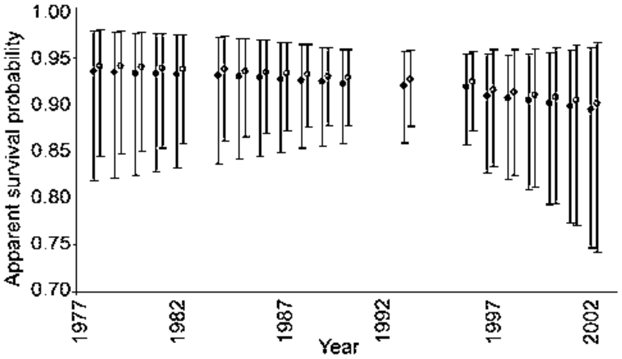

Fig. 3. Unconditional estimates of survival probabilities for male and female killer whales, obtained from a weighted model averaging procedure over the most adequate fitted models (error bars represent the 95% confidence intervals). ● = male; ○ = female.

Under the JS model framework, the goodness-of-fit test did not detect any significant lack of fit to the data for the starting model [$\Phi_t\ p_t\ \lambda_t$] ($\chi^2_1 = 0.780$, $P = 0.377$). However, due to sparse data again, most component tests could not be carried out. Possible violations of the model assumptions are discussed later. For the most adequate models in the set of candidate models, most parameters were not estimable: the program *MARK* returned invalid estimates of Φ and λ (i.e. with standard errors tending to 0). The next most adequate model producing valid estimates was the model [$\Phi\ p_t\ \lambda$]. Under this model, Φ was constant and estimated at 0.894 (95% CI 0.835-0.934) for the period 1987-2000. The rate of increase (applying to the well-marked fraction of the population) was estimated 0.940 (95% CI 0.895-0.987) for this period.

DISCUSSION

Due to the sparseness of the data, the classical tests aiming at investigating the validity of the underlying assumptions could not be undertaken for the models used. Consequently, in the first part of this discussion, the possible violations and their consequences are reviewed.

Possible violations of the closure assumption while estimating abundance

Mortality, births, permanent migrations, temporary emigration and transience are the modalities of violation of the closure assumption.

Regarding mortality, had some deaths occurred during the assessment periods, they are expected to be rare since the sampling periods were short (1.75 and 2.75 years) relative to the life expectancy of an adult individual. Moreover, these hypothetical deaths would have occurred during the longest period, i.e. 1998-2000, which is the period with the lowest estimated survival.

Since the observed fecundity rate was extremely low (of the order of 0.02 neonates per year per killer whale over one-year old; Poncelet, unpublished), the recruitment of juveniles into the adult study population was probably negligible.

Since 1997, fishery controllers have been conducting a photo-identification programme on killer whales observed off the Crozet Islands and interacting with fishing vessels. An analysis of over 1,600 opportunistic photographs taken in this area indicated that eight killer whales, initially identified along the coasts of Possession Island, temporarily joined other individuals offshore. In 2004, these eight whales were still occurring mainly in the coastal waters (Guinet, unpublished data). In addition, none of the easily identifiable individuals initially photo-identified offshore have ever been observed in the coastal waters of Possession Island. These facts highlight the existence of temporary emigrations out of the study area and support the hypothesis that permanent migrations and transience are non-existent or anecdotal in this coastal killer whale population. The social cohesion in this population of killer whales (Guinet, 1991) is another argument against permanent emigration. Temporary emigration episodes were most probably short relative to the time intervals (at least 2 months, Tables 1 and 2) separating capture occasions. It therefore seems reasonable to assume that temporary emigration movements can be considered as random for our sampling scheme.

Table 4

Results of the goodness-of-fit tests for the CJS starting model [$\Phi_{t*s}\ p_{t*s}$].

Test	Chi-square value	*df*	*p*-value
Males			
TEST 2.*Ct*	-	-	-
TEST 2.*Cl*	0.000	1	1.000
TEST 3.*SR*	0.455	1	0.884
TEST 3.*Sm*	0.000	2	1.000
Females			
TEST 2.*Ct*	4.327	9	0.889
TEST 2.*Cl*	1.872	7	0.967
TEST 3.*SR*	1.162	4	0.844
TEST 3.*Sm*	0.000	4	1.000
Both sexes			
Overall test	7.816	28	1.000

Based on the above, the following violations may have occurred during the study: temporary emigration for both assessment periods, plus mortality for the period 1998-2000. Consequently, and also because the sample size was larger for the period 1988-1989, the abundance estimate for 1988-89 appears to be the most reliable.

According to Kendall (1999), whichever closed model is selected, temporary emigration with random movements result in accurate but less precise estimations. If mortality occurred during the study, then the estimates presented here would be upwardly biased.

Possible violations of the model assumptions while estimating survival

Selection of high quality photographs and well-marked individuals was undertaken to reduce the heterogeneity of capture probabilities generated by the photo-identification process. Nevertheless, some level of heterogeneity must persist due to the existence of opportunistic sightings in the samples and to the behavioural variability among individuals. The bias induced by such heterogeneity is negligible when capture probabilities are high enough (Carothers, 1973), and in this respect Buckland (1990) recommends to plan at least 10 capture occasions and to achieve a minimum capture probability of *ca.* 0.2. With 20 capture occasions and an average capture probability of 0.343 from the CJS survival analysis, the above recommendations have been met and thus the residual heterogeneity should not significantly bias survival estimates. With regards to the JS analysis, the

Table 5

Candidate Cormack-Jolly-Seber models for killer whales occurring in inshore waters of Possession Island from 1977 to 2002. ΔAIC_c indicate the AIC_c difference with the most parsimonious model, ER is the evidence ratios and NP indicates the number of parameters in each model.

No.	Model	AIC_c	ΔAIC_c	w_i	ER	NP	Deviance
Modelling capture probabilities							
1	$\Phi_{s*t}\,p_{s*t}$	967.328	723.353	0.000	-	74	124.292
2	$\Phi_{s*t}\,p_{s+t}$	487.201	243.226	0.000	-	57	136.636
3	$\Phi_{s*t}\,p_{t}$	475.874	231.899	0.000	-	56	139.380
4	$\Phi_{s*t}\,p_{s}$	406.120	162.145	0.000	-	40	219.712
5	$\Phi_{s*t}\,p$	403.175	159.200	0.000	-	39	223.081
6	$\Phi_{s*t}\,p_{effort}$	351.967	107.992	0.000	-	40	165.559
Modelling survival probabilities							
6	$\Phi_{s*t}\,p_{effort}$	351.967	107.992	0.000	-	40	165.559
7	$\Phi_{s+t}\,p_{effort}$	287.534	43.559	0.000	-	23	183.205
8	$\Phi_{t}\,p_{effort}$	280.674	36.700	0.000	-	21	183.380
9	$\Phi_{s}\,p_{effort}$	245.314	1.339	0.143	1.953	4	194.760
10	$\Phi\,p_{effort}$	243.975	0.000	0.280	1.000	3	195.608
11	$\Phi_{s*trend}\,p_{effort}$	247.783	3.808	0.042	6.711	6	192.700
12	$\Phi_{s+trend}\,p_{effort}$	246.058	2.084	0.099	2.834	5	193.267
13	$\Phi_{trend}\,p_{effort}$	244.424	0.449	0.224	1.251	4	193.870
14	$\Phi_{s*poaching96}\,p_{effort}$	248.670	4.695	0.027	10.457	6	193.587
15	$\Phi_{s+poaching96}\,p_{effort}$	247.038	3.063	0.060	4.626	5	194.246
16	$\Phi_{poaching96}\,p_{effort}$	245.571	1.596	0.126	2.222	4	195.017

number of capture occasions was only six, but the estimated capture probabilities were high (≥ 0.698) suggesting that survival estimates should not be substantially biased.

As stated previously, temporary emigration from the study site has been documented. Emigration episodes are believed to be short compared to the intervals between capture occasions, and temporary emigration movements can thus be considered as random for the sampling scheme. In this context, survival estimates are assumed to be unbiased (Burnham, 1993) although their precision is reduced. As also stated previously, transience is considered non-existent or anecdotal in the study population.

Effect of social grouping

Social grouping results in non-random associations of individuals that violate the (often implicit) assumption of independence of capture histories underlying mark-recapture models. Although this should not result in biased estimates, the precision may be overestimated in an extent depending on the fluidity of the associations and the proportion of the population captured at each sampling occasion (Anderson *et al.*, 1995; Wilson *et al.*, 1999).

Identity of the study animals

In addition to respecting the underlying assumptions of the models, it is imperative to clearly define the population under study (Cormack, 2001). The abundance analysis is based on observations conducted in the very inshore waters of Possession Island. Consequently, the estimates only describe what are referred to as 'Possession killer whales' hereafter. Considering the temporary emigration of Possession killer whales to offshore waters, an area that is predominantly exploited by individuals that have never been observed along the coasts of Possession Island, Possession killer whales must be regarded as as a fraction of a group of individuals whose home range is unknown.

The killer whale is widely distributed in the Indian Ocean (Leatherwood *et al.*, 1991), inhabiting the waters of Prince Edward, Kerguelen, Amsterdam and St-Paul Islands among others. In the north-eastern Pacific, two very distant populations in terms of phylogeny and behaviour live in sympatry (Barrett-Lennard, 2000). Such a segregation has not been suggested in the Indian Ocean yet. The high mobility of the species, 2,400km (Matkin *et al.*, 1999) or perhaps even 4,000km (Visser, 1999), raises the question of which status should be granted to the individuals observed in Crozet Islands. No mixing with well known Marion Island individuals (Prince Edward Islands; Keith *et al.*, 2001), located a thousand kilometres away from Crozet Islands, has been documented as yet (Guinet, unpublished data). In addition, no type B or C individuals (Pitman and Ensor, 2003) have been observed in the Crozet Islands. If there is no gene flow between Crozet killer whales and other adjacent groups, they could be regarded as a distinct population.

A declining concentration?

The estimates of the number of Possession killer whales suggest a sharp decline of the order of 60% between 1988 and 2000, although the slight overlap in the confidence intervals does not entirely rule out the possibility of stable numbers. This decline was previously suggested by Guinet (1991) for the period 1987-1990. Other results also support the decline hypothesis; abundance estimates and the JS model yielded similar growth rates that are substantially lower than one for the period 1987-2000.

The abundance estimates are strongly bound to the estimates of the proportion of well-marked individuals in the population. Although many precautions were taken to estimate this proportion as precisely as possible with the available data, the sensible difference (about +15%) in this proportion between 1987-1990 and 1998-2000 could result from a difference in the implementation of the photo-ID protocol or be the consequence of the violent interactions between poachers and killer whales in the latter period.

The apparent survival estimated from the CJS models for well-marked individuals, which were mostly mature during the study according to their size, decreased approximately from 0.94 in 1977 to 0.90 in 2002 (it should be emphasised that the JS model produced consistent estimates for the period 1987-2000). When compared to other well-studied killer whale populations such as the so-called 'residents' of the coastal waters British Columbia and Washington State (which had survival rates of 0.961 and 0.989 in males and mature females respectively for the period 1973-87); Olesiuk *et al.*, 1990), the apparent survival rate of the Crozet killer whales was strikingly low, both sexes having similar survival rates and undergoing a similar declining rate.

As stated previously, the social cohesion of Possession killer whale groups makes the dispersion hypothesis highly unlikely as an explanation for the decrease in their numbers, and supports the hypothesis of a high mortality. It is feared that these killer whales, which have developed a unique culture of hunting and social interactions transmitted to the young individuals by the most skilled females (Guinet and Bouvier, 1995) are disappearing. The scarcity of their prey in the region is a possible cause. The elephant seal population in the Crozet Islands declined by 70% from 1970 to 1990, falling to its lowest documented numbers until 1997 (Guinet *et al*., 1999). The whaling industry exploited large-whale populations in the south-western Indian Ocean (among other areas) until 1979 (IWC, 1983) and again may have impacted the local killer whales by lowering the abundance of some of their prey species. In addition to these possible causes which would have long term consequences, more recently, Patagonian toothfish (*Dissostichus eleginoides*) poachers were a new immediate threat to killer whales. Witnesses reported that they use explosives to repel killer whales that come to the longlines to feed on the hooked fishes. As suggested in our modelling approach, these sometimes lethal interactions may increase the decline of Possession killer whales, some of which are known to take part in these interactions.

The population status of both Possession killer whales and Crozet killer whales are of concern. Unfortunately there are insufficient data regarding strictly offshore individuals to describe their demography and feeding ecology. Research is needed to investigate a potential segregation in the diet of inshore and offshore killer whales. In order to better understand the ecology of this top predator in the region, complementary observations throughout the archipelago, and if possible, from adjacent archipelagos, either by increased information from fishery controllers or by running a specific research programme, are needed. The use of satellite tags and activity recorders can yield important information about movements, feeding areas and prey types. Finally, collection of DNA samples from killer whales in the Indian and Antarctic Oceans would increase the understanding of their population biology and help to define priorities for the conservation of populations.

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Marine mammal records from Iran

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ABSTRACT

Iran has 1,700km of coastline that borders the Persian Gulf and the Arabian Sea in the northwest Indian Ocean. Apart from a handful of records, almost nothing is known about which marine mammal species occur in Iranian waters. This review was conducted to fill this information gap. A total of 127 marine mammal records of 14 species were compiled from Iranian coastal waters. Ninety-nine were from the Persian Gulf, 26 from the Gulf of Oman and 2 were of unknown location. Records of finless porpoise (*Neophocaena phocaenoides*) (25), Indo-Pacific humpback dolphin (*Sousa chinensis*) (24) and Indo-Pacific bottlenose dolphin (*Tursiops aduncus*) (22) were by far the most numerous, a probable reflection of their inshore distribution and local abundance. Other species recorded were long-beaked common dolphin (*Delphinus capensis tropicalis*), rough-toothed dolphin (*Steno bredanensis*), striped dolphin (*Stenella coeruleoalba*), spinner dolphin (*Stenella longirostris*), Risso's dolphin (*Grampus griseus*), false killer whale (*Pseudorca crassidens),* sperm whale (*Physeter macrocephalus*) and dugong (*Dugong dugon*). Records of 26 mysticetes were compiled, 10 of which were tentatively identified as Bryde's whales (*Balaenoptera edeni*), 1 possible fin whale (*Balaenoptera physalus*), 3 humpback whales (*Megaptera novaeangliae*) and the remainder were not identified to species. The largest threat to small cetaceans in Iran is likely to be incidental capture in fishing gear. Nine finless porpoises were recorded as bycatch and this and other coastal species may be declining due to unsustainable mortality rates. Some of the world's busiest shipping lanes pass through Iranian waters and ship strikes are likely to be the largest threat to mysticetes in the area.

KEYWORDS: DISTRIBUTION; NORTHERN HEMISPHERE; INDIAN OCEAN; IRAN; SIRENIA; STRANDINGS; CONSERVATION; PERSIAN GULF; FINLESS PORPOISE; INDO-PACIFIC HUMPBACK DOLPHIN; LONG-BEAKED COMMON DOLPHIN; ROUGH-TOOTHED DOLPHIN; STRIPED DOLPHIN; SPINNER DOLPHIN; RISSO'S DOLPHIN; FALSE KILLER WHALE; SPERM WHALE; BRYDE'S WHALES; FIN WHALE; HUMPBACK WHALE.

INTRODUCTION

The southern coast of the Islamic Republic of Iran is 1,700km in length, and is bordered to the east by Pakistan and to the west by Iraq (Fig. 1). There are four coastal provinces, from west to east: Khuzestan, Bushehr, Hormozgan, and Sistan and Baluchistan. The marine environment of Iran includes two very different habitats; the Persian Gulf, a warm, hyper-saline, shallow and enclosed sea and the Gulf of Oman, a relatively more exposed and deep component of the Arabian Sea in the northwest Indian Ocean. The Persian Gulf is connected to the Gulf of Oman by the Straits of Hormoz, a channel approximately 50km wide and 100m deep at its narrowest point (Fig 1). Qeshm Island, 120km long and up to 30km wide, is the largest island in the Gulf and is separated from the Iranian coast by the narrow Khurran Straits. The Hara Protected Area lies on the north coast of Qeshm Island encompassing 100,000ha of mangrove and inter-tidal channels (see Fig. 2b). Established in 1972, it is the largest marine protected area in Iran.

In Iranian waters of the Persian Gulf, extensive shallow areas less than 25m deep exist adjacent to Iraq and around Qeshm Island. Water enters the enclosed Persian Gulf through the Hormoz Straits and a density and wind driven counter-clockwise current flows northwest along the Iranian coast and then southeast along the Arabian coast with a turnover time that ranges from 3 to 5.5 years (Sheppard, 1993). As a consequence of the extreme aridity and high summer temperatures (up to 48ºC) in the region, evaporation exceeds freshwater input tenfold creating extremely high salinity, commonly measured at 40-50ppt and up to 70ppt in shallow, enclosed bays in the southeast (Sheppard, 1993) and highly variable sea surface temperatures between 12ºC and 35ºC (ROPME, 2003). The harsh environment of the Persian Gulf, combined with its recent geologic origin, have created biological communities characterised by low species richness and moderate to low primary productivity compared to the Arabian Sea (Price, 2002; Sheppard, 1993). In contrast, the Gulf of Oman exhibits characteristics typical of pelagic ecosystems having lower and less variable temperature and salinity, greater depth (>2,000m), and higher productivity and species richness (Reynolds, 1993; ROPME, 2003; Subba-Rao and Al-Yamani, 1998).

Important fisheries for *Penaeid* shrimp, grouper, jack fish and Spanish mackerel, exist in the Persian Gulf (Price *et al.*, 1993) and for large pelagics, especially tuna, and small pelagics, such as sardines and anchovies, in the Gulf of Oman (FAO, 2005). Iran has the largest fishing fleet and reports the largest landings in the region, however the fisheries sector contributes only 0.23% to the GDP of this rich nation (FAO, 2005). Purse seine fisheries for tuna in the Indian Ocean have been expanding, and in 2003 Iran landed 11,830t, 12% of western Indian Ocean tuna catches (FAO, 2005).

The Persian Gulf is far from pristine; it is one of the world's busiest shipping lanes, with approximately 25,000-35,000 oil tankers carrying about 60% of the world's oil passing through the Strait of Hormoz each year (UNEP, 1999). It has experienced three major wars: Iran-Iraq (1980-88), Gulf War (1991) and Iraq (2003), the world's largest oil spill (1 million tonnes of crude) in 1991; and multiple other large spills

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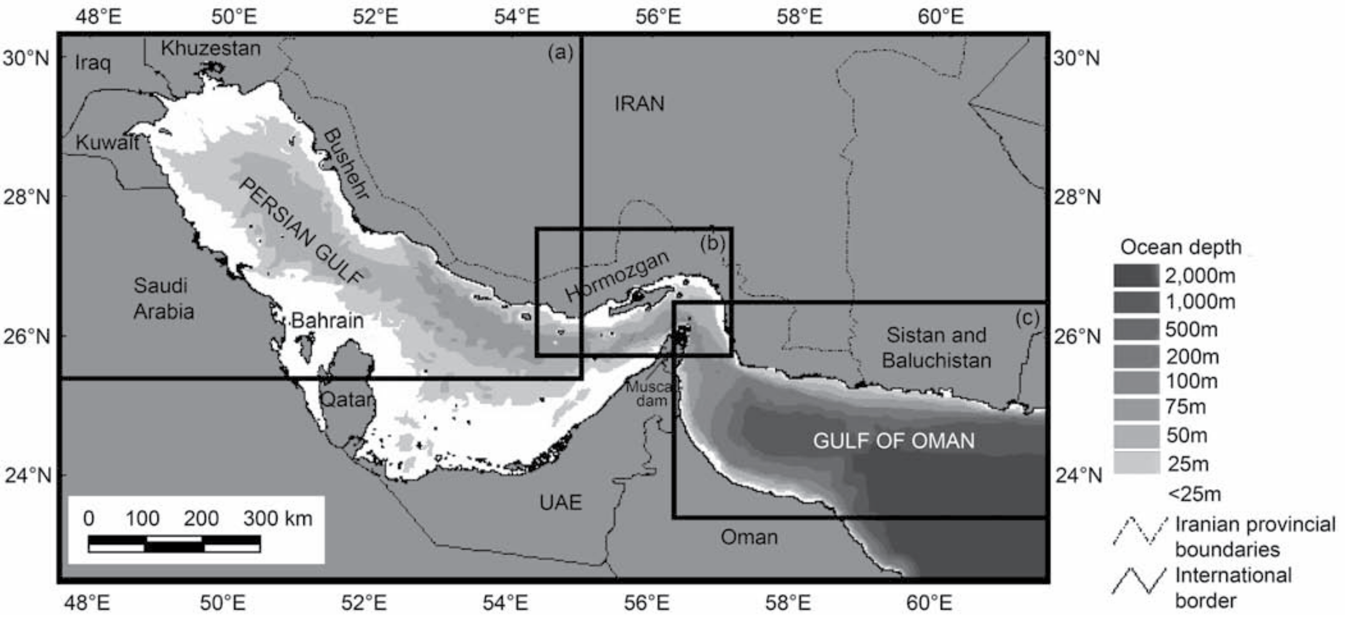

Fig. 1. Iran, the Persian Gulf and Gulf of Oman (English spelling of Farsi names are taken from those used on maps produced by the Gita Shenasi Cartographic and Geographic Institute, Tehran, Iran). For (a), (b) and (c) see Fig. 2

including the Nowruz spill in 1983 (Gerges, 1993; Price *et al.*, 1994; ROPME, 2003). As a result of normal oil extraction and transport it has been estimated that in a ten year period 1.5 million tonnes of oil are released into the Persian Gulf (Michel *et al.*, 1986). The World Conservation Monitoring Centre (WCMC, 1991) suggested that the Persian Gulf is the most oil polluted marine area in the world.

There have been at least two mass mortalities of cetaceans in the southern Persian Gulf: the first, in 1986 involved 520 cetaceans (comprising six from Iran) and was tentatively linked to a red tide event (Baldwin *et al.*, 1999; ROPME, 1986; Subba-Rao and Al-Yamani, 1998), the second, in 1991 around the time of the Gulf War oil spill, involved 71 dolphins and the cause was not determined (Preen, 2004; Robineau, 1998). Between 1986 and 1999, Preen (2004) recorded a 71% decline in cetacean abundance along the coast of the United Arab Emirates (UAE) in the Persian Gulf.

Almost nothing is known about the marine mammal species that inhabit the coastal waters of Iran other than a handful of records published in local journals, and the Iranian coastline is among the least studied marine areas in the world (Price *et al.*, 1994). This review was conducted to fill this information gap with the hope that it will stimulate future studies and conservation of the marine mammal fauna of Iran.

METHODS

From 17 November to 10 December 2005, marine mammal records were compiled during visits to universities, natural history museums, Department of Environment (DoE) offices, Iranian Fisheries Research Organisation (IFRO) centres and various wildlife non-governmental organisations (NGOs) in Tehran, Bushehr city, Kish Island, Bandar Abbas, Qeshm Island and Chabahar city. Security constraints restricted access to Khuzestan Province adjacent to Iraq and to the Pakistan border areas and time constraints limited the number of visits to smaller cities on the coast. Fewer marine mammal records from these areas reflect the lack of ‘effort’ rather than marine mammal abundance.

Cetacean skeletal remains are stored in a number of natural history museums in Tehran and in towns along the coast. Specimens were photographed and identification was made based on external and cranial morphology and tooth counts. Records were also compiled by the authors from good quality photographs or video recordings of marine mammal sightings and strandings. From January 2006 onwards, an informal stranding network was established and new strandings data were opportunistically collected and systematically collated. Records were compiled from published references in English and English translations of references in Farsi.

RECORDS

A total of 127 marine mammal records of 14 species were compiled from Iranian coastal waters of the Persian Gulf and Gulf of Oman. Ninety-nine were from the Persian Gulf, 26 from the Gulf of Oman and 2 were of unknown location. The largest numbers of records were from Qeshm Island (39) and Bushehr Provinces (32), which is probably because there are active marine biologists working in these locations. Records of finless porpoises, *Neophocaena phocaenoides* (25), Indo-Pacific humpback dolphins, *Sousa chinensis* (24) and Indo-Pacific bottlenose dolphins, *Tursiops aduncus* (22) were by far the most numerous, a probable reflection of their inshore distribution and local abundance. Other species recorded were long-beaked common dolphins (*Delphinus capensis tropicalis*), rough-toothed dolphins (*Steno bredanensis),* striped dolphins (*Stenella coeruleoalba*), spinner dolphins (*Stenella longirostris*), Risso’s dolphins *(Grampus griseus),* false killer whales (*Pseudorca crassidens),* sperm whales *(Physeter macrocephalus)* and dugongs (*Dugong dugon).* Records of 26 mysticetes were compiled, 10 of which were tentatively identified as Bryde’s whales (*Balaenoptera edeni*), 1 as a possible fin whale (*Balaenoptera physalus*), 3 as humpback whales (*Megaptera novaeangliae)* and the remainder were not identified to the species level. Some individuals stranded and the skeleton was then collected, these are counted as a single record (see several mysticete records in Table 1). The location of each record has been plotted, using GPS data when available or described locations if they were relatively precise, on Fig. 2a (Southwest Iran coast), Fig. 2b (Qeshm Island and Hormozgan) or Fig. 2c (Gulf of Oman), and records are compiled in Table 1. The following is a description of Iranian marine mammal records by species and location.

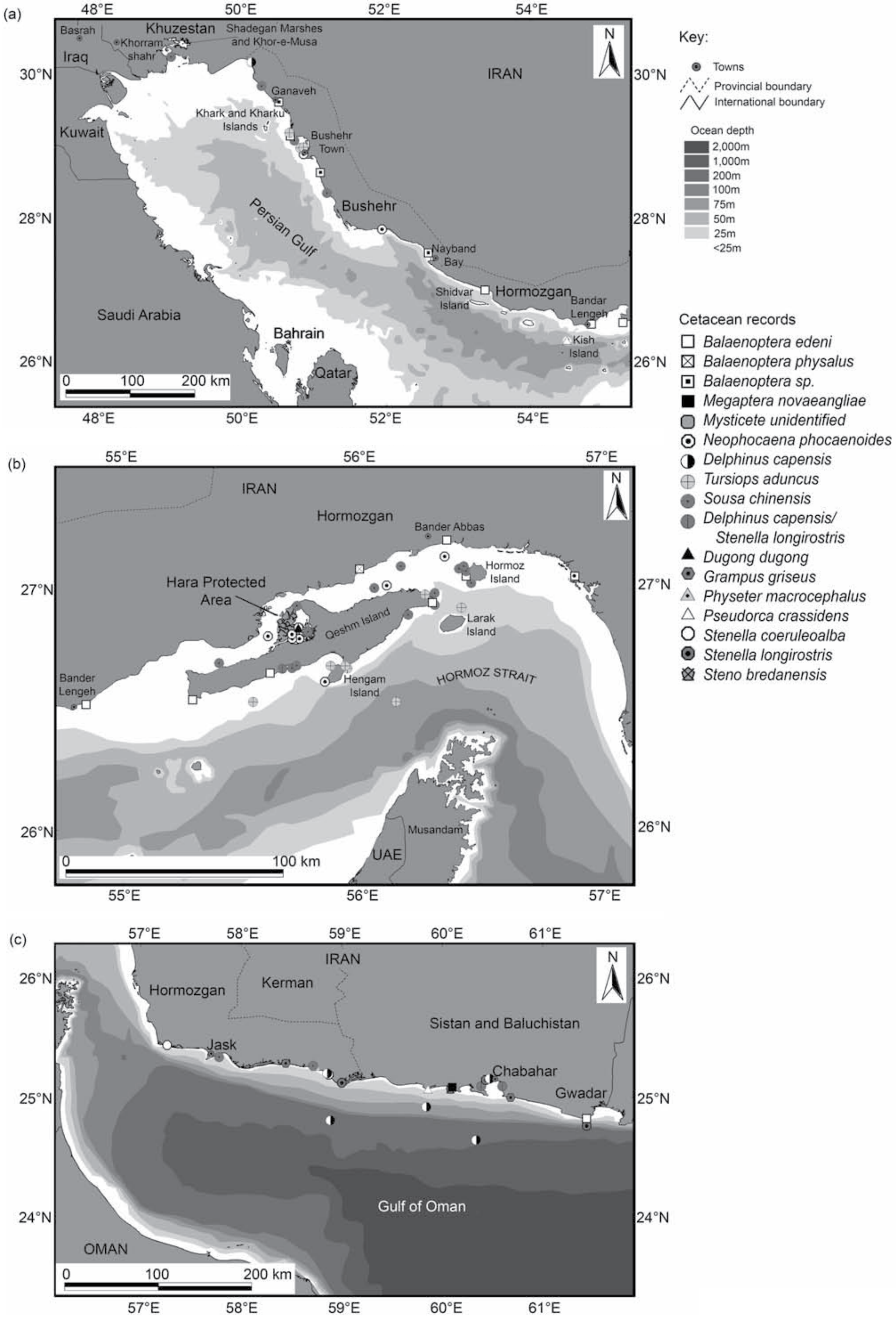

Fig. 2. Location of marine mammal records along: (a) the southwest coast of Iran; (b) in the vicinity of Hormozgan and Qeshm Island; and (c) in the Gulf of Oman, Iran.

Table 1

Records of marine mammals in Iran.

No.	Species	Type	Province	Location	Date	Notes	Source
Odontocetes							
4	*Tursiops aduncus*	Skull	Sistan/Baluchistan	IFRO, Chabahar	17/12/99	-	This paper
6	*Tursiops aduncus*	Skull/skeleton	Bushehr	Museum of Natural History, Tehran	-	-	This paper
14	*Tursiops aduncus*	Skull	Bushehr	IFRO Office, Bushehr city	1995	-	This paper
15	*Tursiops aduncus*	Skull	Bushehr	IFRO Office, Bushehr city	1995	-	This paper
16	*Tursiops aduncus*	Skull	Bushehr	IFRO Office, Bushehr city	1995	-	This paper
31	*Tursiops aduncus*	Stranding	Bushehr	Near Bushehr city	1995	-	This paper
34	*Tursiops aduncus*	Stranding	Bushehr	North of Bushehr city port	1994	-	This paper
42	*Tursiops aduncus*	Stranding	Bushehr	Bushehr city	1997	Animal had been skinned	This paper
43	*Tursiops aduncus*	Sighting	Qeshm	Between Qeshm and Hengam Isl.	2005	Group of 10-20	This paper
48	*Tursiops aduncus*	Skull	Hormozgan	IFRO Office, Bandar Abbas	-	-	This paper
49	*Tursiops aduncus*	Stranding	Qeshm	South coast of Qeshm Island	2003	-	This paper
57	*Tursiops aduncus*	Skull	Qeshm	GeoPark Museum, Qeshm Island	-	-	This paper
58	*Tursiops aduncus*	Skull	Qeshm	GeoPark Museum, Qeshm Island	-	-	This paper
61	*Tursiops aduncus*	Sighting	Qeshm	Between Qeshm and Hengam Isl.	10/02/06	-	This paper
68	*Tursiops aduncus*	Skull/skeleton	Qeshm	Hormuz Island, Stored in the Stuttgart museum	Jan. 1973	-	This paper
92	*Tursiops aduncus*	Sighting	Qeshm	Between Hormoz and Larak Islands	23/01/73	10-12 animals	Pilleri and Gihr (1973-74)
93	*Tursiops aduncus*	Sighting	Qeshm	Between Qeshm and Hengam Isl.	24/01/73	5 animals	As above
94	*Tursiops aduncus*	Sighting	Qeshm	Southeast of Qeshm Island	26/01/73	Small group	As above
95	*Tursiops aduncus*	Sighting	Offshore	10nm south of Qeshm Island, 26°31.9'N; 56°7.8'E	04/08/06	8-12 animals	This paper
104	*Tursiops aduncus*	Stranding	Bushehr	Rood-e-Kolmeh Creek, 15km S of Bushehr Port, 29°10.8'N; 50°38.8'E	24/06/07	-	This paper
115	*Tursiops aduncus*	Sighting	Offshore	Strait of Hormoz	08/07/84	Several small groups 75m deep	Weitkowitz (1992)
122	*Tursiops aduncus*	Stranding	Qeshm	N Qeshm Island. 26°58.5'N; 56°15.0'E	01/11/07	-	This paper
7	*Sousa chinensis*	Skull/skeleton	Hormozgan	From Bandar Abbas. Stored at Uni of Tehran Zoological Museum	1974	-	This paper
21	*Sousa chinensis*	Sighting	Hormozgan	East of Jask Port	1995	-	This paper
22	*Sousa chinensis*	Sighting	Bushehr	Behrekan Bay	May 2003	-	This paper
25	*Sousa chinensis*	Sighting	Khuzestan	Musa Creek, 30°14'N; 49°E	Mar. 1995	-	Anon. (1995a)
30	*Sousa chinensis*	Sighting	Bushehr	Close to Bushehr town, 29°4.0'N; 50°43.0'E	29/11/05	1 mature male	This paper
45	*Sousa chinensis*	Sighting	Hormozgan	Near Hormoz Island	-	-	This paper
50	*Sousa chinensis*	Sighting	Qeshm	Salakh, south Qeshm Island	16/01/05	6+ animals	This paper
51	*Sousa chinensis*	Sighting	Qeshm	Berkeh Kalaf, south Qeshm Island	27/07/05	10+ animals	This paper
56	*Sousa chinensis*	Skull	Qeshm	GeoPark Museum, Qeshm Island	-	-	This paper
60	*Sousa chinensis*	Sighting	Qeshm	Zaitoon Park, south of Qeshm town	25/04/06	25 animals	This paper
80	*Sousa chinensis*	Sighting	Khuzestan or Bushehr	Near shore	22-29/09/91	7 individuals photo-id'd	Henningsen and Constantine (1992)
81	*Sousa chinensis*	Sighting	Qeshm	NW of Qeshm Island in Clarence Strait	27/01/73	1 animal	Pilleri and Gihr (1973-74)
82	*Sousa chinensis*	Sighting	Hormozgan	West tip of Hormoz Island	22/01/73	1 animal	As above
83	*Sousa chinensis*	Sighting	Hormozgan	800m SW of Hormoz Island	23/01/73	12-15 animals	As above
84	*Sousa chinensis*	Sighting	Qeshm	1 mile N of Dargahan, N of Qeshm Island	29/01/73	Large group	As above
85	*Sousa chinensis*	Sighting	Qeshm	Near Qeshm town	29/01/73	2 animals	As above
86	*Sousa chinensis*	Sighting	Hormozgan	South of Hormoz Island	30/01/73	16 animals	As above
87	*Sousa chinensis*	Sighting	Qeshm	Hara Protected Area, Qeshm Island. 26°49.1'N; 55°45.9'E	29/01/00	1 animal	Keijl and van der Have (2002)
88	*Sousa chinensis*	Sighting	Qeshm	Hara Protected Area, Qeshm Island, 26°55.6'N; 55°43.3'E	29/01/00	1 animal	As above
89	*Sousa chinensis*	Sighting	Qeshm	Salakh, south Qeshm Island	Jul.2006	-	This paper
103	*Sousa chinensis*	Sighting	Qeshm	Between Bandar Abbas and Qeshm Island	May 2007	-	This paper
106	*Sousa chinensis*	Stranding	Bushehr	Leilatein Creek, north Bushehr coast, 29°49.8'N; 50°15.6'E	Oct. 2003	Neonate	This paper

Cont.

No.	Species	Type	Province	Location	Date	Notes	Source
Odontocetes cont.							
123	*Sousa chinensis*	Stranding	Hormozgan	East of Jask, 25°34.5'N; 58°47.6'E	Dec. 2008	-	This paper
129	*Sousa chinensis*	Sighting	Khuzestan	Khor-e-Musa	11-14/02/54	-	Mörzer-Bruyns (1960)
12	*Neophocaena phocaenoides*	Skull	Bushehr	IFRO office museum, Bushehr	-	-	This paper
18	*N. phocaenoides*	Stranding	Bushehr	Stuffed, displayed in Aquarium shop	-	-	This paper
39	*N. phocaenoides*	Stranding	Bushehr	Bushehr port, 28°52.8'N; 50°50.4'E	27/11/02	115cm	Anon. (2003a)
40	*N. phocaenoides*	Sighting	Qeshm	Hara Protected Area, Qeshm Island, 26°47.2'N; 55°43.0'E	06/12/05	12 animals	This paper
41	*N. phocaenoides*	Stranding	Bushehr	Bushehr town	Mar. 1998	Bycatch, 145cm	Anon. (1998)
46	*N. phocaenoides*	Stranding	Hormozgan	Bandar Abbas near IFRO office	Feb. 1995	Bycatch. 147cm long	Anon. (1995b)
52	*N. phocaenoides*	Stranding	Qeshm	Hara Protected Area, Qeshm Island	27/01/03	Bycatch	This paper
54	*N. phocaenoides*	Sighting	Qeshm	Hara Protected Area, Qeshm Island, 26°48.5'N; 55°41.9'E	06/12/05	4 animals	This paper
62	*N. phocaenoides*	Stranding	Bushehr	Flukes displayed in aquarium shop, Bushehr town	-	Bycatch	This paper
63	*N. phocaenoides*	Stranding	Bushehr	Flukes displayed in aquarium shop, Bushehr town	-	Bycatch	This paper
64	*N. phocaenoides*	Stranding	Bushehr	Flukes displayed in aquarium shop, Bushehr town	-	Bycatch	This paper
70	*N. phocaenoides*	Sighting	Qeshm	Hara Protected Area, Qeshm Island	28/01/73	2 animals	Pilleri and Gihr (1973-74)
71	*N. phocaenoides*	Sighting	Qeshm	N of Qeshm Island, near Dargahan	29/01/73	3 animals	As above
72	*N. phocaenoides*	Sighting	Sistan/Baluchistan	Chabahar	Winter 1971	-	Roberts (1977)
73	*N. phocaenoides*	Sighting	Khuzestan	Khorramshahr	1980s	-	Etemad (1985)
74	*N. phocaenoides*	Sighting	Qeshm	Hara Protected Area, Qeshm Island, 26°50.2'N; 55°43.6'E	24/01/00	2 animals	Keijl and van der Have (2002)
75	*N. phocaenoides*	Sighting	Khuzestan	Khorramshahr	-	-	Anon. (1998)
76	*N. phocaenoides*	Sighting	Bushehr	Bandar Dayer	Mar. 1995	-	Anon. (1995b)
77	*N. phocaenoides*	Stranding	Qeshm	Hara Protected Area, Karwasta, Qeshm Island	20/01/07	Bycatch	This paper
78	*N. phocaenoides*	Sighting	Khuzestan/Bushehr	S Khuzestan/N Bushehr Province	23-29/09/91	4 animals; 1km from shore	Henningsen and Constantine (1992)
79	*N. phocaenoides*	Sighting	Khuzestan/Bushehr	S Khuzestan/N Bushehr Province	23-29/09/91	3 animals; 1km from shore	As above
90	*N. phocaenoides*	Stranding	Bushehr	Near Bushehr City, 28°56.7'N 50°50.5'E	Mar. 2007	3 animals	This paper
91	*N. phocaenoides*	Stranding	Qeshm	South Hengam Island, 26°36.8'N 55°52.2'E	16/03/07	-	This paper
96	*N. phocaenoides*	Sighting	Qeshm	Hara Protected Area, Qeshm Island	21/01/07	Caught in fishing net, released live	This paper
118	*N. phocaenoides*	Stranding	Hormozgan	East of Jask, 25°30.0'N; 58°55.7'E	23/11/07	152cm	This paper
28	*Delphinus cf tropicalis*	Stranding	Sistan/Baluchistan	Near Chabahar harbour	Early 2000s	-	This paper
55	*Delphinus cf tropicalis*	Skull	Qeshm	GeoPark Museum, Qeshm Island	-	-	This paper
97	*Delphinus cf tropicalis*	Sighting	Khuzestan/Bushehr	S Khuzestan/N Bushehr Province	22-30/09/91	12 animals	Henningsen and Constantine (1992)
98	*Delphinus cf tropicalis*	Sighting	Sistan/Baluchistan	Southwest of Chabahar	Early 1970s	-	Pilleri and Gihr (1973-74)
99	*Delphinus cf tropicalis*	Sighting	Sistan/Baluchistan	Southwest of Chabahar	Early 1970s	-	As above
100	*Delphinus cf tropicalis*	Sighting	Sistan/Baluchistan	Southwest of Chabahar	Early 1970s	-	As above
119	*Delphinus cf tropicalis*	Stranding	Hormozgan	East of Jask, 25°30.2'N; 58°55.7'E	23/11/07	147cm.	This paper
125	*Delphinus cf tropicalis*	Stranding	Bushehr	Ameri Port	28/02/08	203cm, M, bycatch	This paper
126	*Delphinus cf tropicalis*	Stranding	Bushehr	Ameri Port	28/02/08	186cm, F, bycatch	This paper
127	*Delphinus cf tropicalis*	Stranding	Bushehr	Near Bushehr city, 28°56.7'N; 50°50.5'E	06/11/07	177cm, bycatch.	This paper
9	*Stenella longirostris*	Skull	Not known	Zoological Museum, Uni. of Tehran	-	-	This paper
20	*Stenella longirostris*	Stranding	Sistan/Baluchistan	Near Chabahar Harbour	Dec. 2005	-	This paper
111	*Stenella longirostris*	Mass stranding	Hormozgan	Kalirak village, east of Jask, 25°24.7'N; 59°4.1'E	20/09/07	79 animals over 13km	This paper
120	*Stenella longirostris*	Sighting	Sistan/Baluchistan	10nm SW of Gwatar	Nov. 2007	27-32 animals	This paper
53	*Stenella longirostris/ Delphinus cf tropicalis*	Stranding	Qeshm	Near Kargah jetty, 26°39.9'N; 55°39.6'E	27/03/03	-	This paper
65	*S. longirostris/ Delphinus cf tropicalis*	Stuffed	Qeshm	GeoPark Museum, Qeshm Island	-	-	This paper
112	*S. longirostris/ Delphinus cf tropicalis*	Stranding	Sistan/Baluchistan	Ramin 10km east of Chabahar	08/10/07	3 animals	This paper

Cont.

No.	Species	Type	Province	Location	Date	Notes	Source
Odontocetes cont.							
113	*S. longirostris/ Delphinus cf tropicalis*[a]	Stranding	Sistan/Baluchistan	5km west of Chabahar	09/10/07	-	This paper
114	*Stenella coeruleoalba*[a]	Mass stranding	Hormozgan	Kangan Bay, 25°46.3'N; 57°23.3'E	24/10/07	73 animals live stranded	This paper
117	*Stenella coeruleoalba*	Skull	Hormozgan	DoE office in Jask	01/09/04	-	This paper
3	*Steno bredanensis*[a]	Skull	Sistan/Baluchistan	Stored at IFRO office Chabahar. Found in Gourdim, SW of Chabahar	11/09/97	-	This paper
26	*Grampus griseus*[a]	Stranding	Sistan/Baluchistan	Chabahar Bay	2002	-	This paper
107	*Grampus griseus*[a]	Stranding	Sistan/Baluchistan	Near Zarabad village, between Jask and Konarak	1991	-	This paper
2	*Pseudorca crassidens*[a]	Skull	Sistan/Baluchistan	Stored at IFRO. Chabahar. Stranded Tang, SW of Chabahar	22/10/93	-	This paper
8	*Pseudorca crassidens*	Skull	Qeshm	Zoological Museum. Uni of Tehran	-	-	This paper
116	*Pseudorca crassidens*[a]	Skull	Hormozgan	Kish Island, stored with local resident	Approx. 1997	-	This paper
109	*Physeter macrocephalus*[a]	Stranding	Hormozgan	Abd coast east of Jask, 25°34.5'N; 58°47.8'E. Stored in GeoPark Museum, Qeshm Island	Jun. 2007	One jaw in Jask DoE office	This paper
Mysticetes							
10	*Balaenoptera physalus*[a]*	Stranding, skull and skeleton	Hormozgan	30km south of Bandar Abbas. Stored in Zoological Museum, Uni of Tehran	Apr. 1971	-	Baloutch (1972)
1	*Balaenoptera edeni*[a]*	Skeleton, skull	Sistan/Baluchistan	Stored IFRO office. Chabahar. Found Pasabandar, 120km E of Chabahar	Pre-1997	-	This paper
29	*Balaenoptera edeni**	Skull	Bushehr	IFRO office, Bushehr	-	Partial skull, possibly other half of No.13	This paper
44	*Balaenoptera edeni*[a]*	Stranding, skull and skeleton	Hormozgan	Found floating near Hormoz Island. Skeleton with EPA on Hormoz Isl.	23/04/04	-	This paper
59	*Balaenoptera edeni*[a]	Skull, skeleton	Qeshm	GeoPark Museum, Qeshm	-	-	This paper
66	*Balaenoptera edeni*[a]	Skull	Qeshm	Found near Salakh. now stored in GeoPark Museum, Qeshm	Spring 2006	Found with skull #67	This paper
69	*Balaenoptera edeni*[a]	Skull, skeleton	Qeshm	South tip Qeshm Island. Atlas and vertebrae in Stuttgart museum	Jan. 1973	-	Pilleri and Gihr (1973-74)
105	*Balaenoptera edeni*[a]*	Stranding	Hormozgan	Bandar Lengeh, 26°31.2'N; 54°51.0'E	04/07/07	13m long, gashes on body	This paper
108	*Balaenoptera edeni*[a]	Stranding	Hormozgan	Bandar Abbas	19/08/07	Gashes on head	This paper
110	*Balaenoptera edeni*[a]*	Live stranding	Qeshm	Qeshm Town, 26°56.4'N; 56°16.8'E	21/09/07	Young animal. 4m long	This paper
121	*Balaenoptera edeni*[a]*	Stranding	Hormozgan	3km W of Mogham Port, 350km W of Bandar Abbas. 26°59.7'N; 53°22.3'E	Late Nov. 07	13.6m	This paper
5	*Balaenoptera* sp.	Skeleton	Not known	Museum of Natural History, Tehran	-	-	This paper
11	*Balaenoptera* sp.[a]	Skeleton	Hormozgan	From Minab Kolahi port. Stored in Uni of Tehran Zoological Museum	1980s	-	This paper
17	*Balaenoptera* sp.	Skeleton	Bushehr	Aquarium shop, Bushehr city	-	-	This paper
32	*Balaenoptera* sp.[a]	Stranding	Bushehr	Nayband Bay	1996	-	This paper
35	*Balaenoptera* sp.[a]	Stranding	Bushehr	Near Ganaveh Port	1999	-	This paper
36	*Balaenoptera* sp.[a]	Skull	Bushehr	Ameri Port	1993	Juvenile	This paper
37	*Balaenoptera* sp.[a]	Stranding	Bushehr	Helle River Estuary. N Bushehr town	2004	-	This paper
38	*Balaenoptera* sp.	Stranding	Bushehr	Not known	-	-	This paper
128	*Balaenoptera* sp.	Stranding	Bushehr	Not known	Mar. 2008	-	This paper
23	*Megaptera novaeangliae*	Sighting	Sistan/Baluchistan	Near Chabahar	Sep. 2004	Mother-calf	This paper
24	*M. novaeangliae*	Stranding	Sistan/Baluchistan	Not Known	Dec. 2003	-	This paper
27	*M. novaeangliae*[a]	Stranding	Sistan/Baluchistan	Pozm, 50km west of Chabahar	Oct. 2004	-	This paper
13	Unidentified mysticete	Skull	Bushehr	IFRO Office, Bushehr	-	Partial skull, possibly other half of No.29	This paper
47	Unidentified mysticete	Skeleton, skull	Hormozgan	EPA Office, Bandar Abbas.	-	-	This paper
67	Unidentified mysticete[a]	Skull	Qeshm	Found near Salakh. Stored in the GeoPark Museum, Qeshm Island	Spring 2006	Possibly very young *B. edeni* found with No.66	This paper
Sirenia							
101	*Dugong dugon*[a]	Sighting	Qeshm	Hara Protected Area, Qeshm Island, 26°50.2'N; 55°43.6'E	29/01/00		Keijl and van der Have (2002)
102	*Dugong dugon*	Sighting	Qeshm	Hara Protected Area, Qeshm Island	01/11/00	3 animals	Green (2000)

*Identification requires confirmation. [a] Location displayed on map.

Odontocetes

Indo-Pacific bottlenose dolphin (Tursiops aduncus)

The Indo-Pacific bottlenose dolphin occurs throughout the Indian Ocean including the Persian Gulf and Gulf of Oman where it is considered sympatric with the common bottlenose dolphin, *T. truncatus*. Genetic analysis of bottlenose dolphins sampled in deep oceanic waters off Oman indicated that they were common bottlenose dolphins (Ballance and Pitman, 1998) but most other authors in the region referred to all bottlenose dolphin records as Indo-Pacific bottlenose dolphins (Preen, 2004; Robineau, 1998; Robineau and Fiquet, 1996). Skulls from the Iranian coast of the Persian Gulf showed the convex pre-maxillaries in lateral view, high tooth counts and distance between the tip of rostrum to the apex of the premaxillary convexity (TPC)/condylobasal length (CBL) ascribed to the Indo-Pacific bottlenose dolphin (Robineau, 1998; Robineau and Fiquet, 1996; Ross, 1977; 1984; Wang *et al.*, 2000). Given this, all bottlenose dolphin records in Iran are referred to here as Indo-Pacific bottlenose dolphins. It is possible that more detailed investigations, especially in the Gulf of Oman, may also reveal the presence of common bottlenose dolphins in Iran.

Twenty-two records of Indo-Pacific bottlenose dolphins were compiled from Iranian coastal waters; 1 record was from the Gulf of Oman, 2 from the Straits of Hormoz and 19 were in the Persian Gulf. There were 6 strandings, 7 sightings and the skeletal remains of 9 animals stored in museums.

PERSIAN GULF

Bottlenose dolphins are widely distributed throughout the Persian Gulf and are the most commonly recorded cetacean (Al-Robaae, 1974; Baldwin *et al.*, 1999; Gallagher, 1991a; Preen, 2004; Robineau, 1998). In the southern Gulf bottlenose dolphins are found in deeper water than Indo-Pacific humpback dolphins; 29% of groups seen by Preen (2004) and almost all of those seen by Henningsen and Constantine (1992) were in water greater than 10m deep. Indo-Pacific bottlenose dolphins are also common and widespread in Iranian waters of the Persian Gulf. Four Indo-Pacific bottlenose dolphins have been recorded stranded near to Bushehr port, the skulls of three individuals are stored in the IFRO office in Bushehr city and a skull and skeleton reportedly from Bushehr is stored at the Museum of Natural History in Tehran. On the 19 January 1973 while taking off from Bandar Lengeh airport Pilleri and Gihr (1973-74) sighted a scattered group of dolphins 200m from the coast that they identified as probably *Tursiops* sp. Given the distant view and possibility of confusion with other dolphin species this sighting should be treated as unconfirmed.

The majority of Indo-Pacific bottlenose dolphin records in Iranian waters occur around Qeshm Island, particularly of small groups in the narrow channel between Hengam Island and Qeshm Island. It is unclear if this is a high density area or if frequent sightings are due to the accessible ocean viewpoint nearby. Indo-Pacific bottlenose dolphins have been sighted near to Larak Island, along the southeast coast of Qeshm Island (Pilleri and Gihr, 1973-74), in the Straits of Hormoz approximately 10 n.miles south of Qeshm in water 70m deep and in the Straits (unknown location) in water approximately 75m deep (Weitkowitz, 1992). Two Indo-Pacific bottlenose dolphin skulls are stored in the GeoPark Museum on Qeshm Island, and a skull from Qeshm is stored in the Stuttgart Natural History Museum, Germany.

GULF OF OMAN

The only record indicating the presence of *Tursiops* sp. in Iranian waters of the Gulf of Oman is a skull stored in the IFRO office in Chabahar (Table 1). *Tursiops* sp. are commonly sighted along the Oman coast of the Gulf of Oman (Ballance and Pitman, 1998; Collins *et al.*, 2002) and it is likely that despite the lack of records they are also common in Iranian waters.

Indo-Pacific humpback dolphin (Sousa chinensis)

The taxonomy of the Genus *Sousa* is unresolved despite several recent morphological and molecular genetic studies (Jefferson and Van Waerebeek, 2004; Rosenbaum *et al.*, 2002). Humpback dolphins in Iran are primarily grey, possess prominent dorsal humps and morphologically conform to the description of *Sousa plumbea* (Ross *et al.*, 1994). To remain in line with current scientific consensus and until the taxonomic status of *S. plumbea* is resolved all records of *Sousa* sp. and *Sotalia* sp. in Iran are treated as *Sousa chinensis*.

Indo-Pacific humpback dolphins occur in shallow, nearshore waters, generally less than 20m deep and in many parts of their worldwide range occur near large river mouths. Water depth is probably the main factor limiting their offshore distribution (Jefferson and Karczmarski, 2001). They have been recorded as a common resident in shallow areas from all countries that border the Persian Gulf (Baldwin *et al.*, 2004; Preen, 2004; Robineau, 1998; Weitkowitz, 1992). The majority of sightings are of one to 20 individuals, although unusually large groups of up to 100 have also been seen (Baldwin *et al.*, 2004).

For this study, 24 records of humpback dolphins in Iranian waters were compiled; 22 from the Persian Gulf and 2 from the Gulf of Oman. These comprised 20 sightings, 2 skeletal records and 2 strandings.

PERSIAN GULF

The majority of Iranian Indo-Pacific humpback dolphin records (18) are from Qeshm Island and Hormozgan Province in the Persian Gulf. There are several records from the Iraqi coast very close to the Iranian border: a group (reported as *Stenella malayana* and *Sotalia lentiginosa*) was seen near Fao (Al-Robaae, 1974); one individual (reported as *S. lentiginosa*) was captured by fishermen in the Khor-Al-Zubair River (Al-Robaae, 1970); they were reported from the Shatt Al-Arab, Iraq (close to the Iranian border) in April 1958 (Mörzer Bruyns, 1960), and in Musa Creek near to Khorramshahr in February 1954 (Mörzer-Bruyns, 1971; Mörzer Bruyns, 1960). Examination of published photographs of a sighting reported as common dolphins (*Delphinus delphis*) in Musa Creek, Khuzestan revealed they were clearly Indo-Pacific humpback dolphins (Anon., 1995a). In 1992 seven individuals were photo-identified in coastal Iranian waters of either Khuzestan or Bushehr Province (Henningsen and Constantine, 1992). A single, large, Indo-Pacific humpback dolphin was sighted near Bushehr city on 1 December 2005 and a neonate was stranded in the same area in October 2003. Further south, a group of Indo-Pacific humpback dolphins was sighted near Bahrekan Bay in May 2003. Etemad (1985) cited a report by Murray, 1884, that humpback dolphins were found at Bandar-Lengeh port in Hormozgan. The original reference could not be traced and the presence of humpback dolphins in this area is unconfirmed.

In January 1973, Pilleri and Gihr circumnavigated Qeshm and Hormoz Islands and reported at least six sightings of Indo-Pacific humpback dolphin, three north of Qeshm Island and three south and west of Hormoz Island (Pilleri and Gihr, 1973-74). Reported group sizes were between 1 and 16 individuals and included sightings of calves and juveniles and observations of acrobatic behaviour. There were two sightings of humpback dolphins within the mangrove channels of Hara Protected Area on 29 January 2000 (Keijl and van der Have, 2002) and there have been recent sightings south of Qeshm Island, south of Qeshm town, between Qeshm and Bandar Abbas and near Hormoz Island (Table 1). The skeleton of a humpback dolphin stranded near Bandar Abbas in 1974 is deposited in the Zoological Museum at the University of Tehran and the skull of a different individual is in the GeoPark Museum on Qeshm Island.

The records show that Indo-Pacific humpback dolphin sightings occur throughout the year and the presence of calves in recorded sightings indicate that there is a breeding resident population in Iranian waters of the Persian Gulf. Given the affinity of this species for shallow estuarine water a relatively large population could be expected in the shallow, low salinity waters near Iraq. There are relatively few Indo-Pacific humpback dolphin records from this area, probably due to the long-term instability and sensitivity of this border region restricting human access for surveys.

GULF OF OMAN

There are two records of Indo-Pacific humpback dolphins in Iranian waters of the Gulf of Oman: a photograph of a single animal taken in 1995 just east of Jask, Hormozgan; and one animal stranded between Jask and Chabahar in December 2008. Humpback dolphins have not been recorded in Omani waters of the Gulf of Oman and there is thought to be an hiatus in distribution between those in the southern Persian Gulf and those in the Arabian Sea (Baldwin *et al.*, 2004). It is not clear from the limited records whether there is a continuous distribution of humpback dolphins along the Iranian coast to Pakistan.

Finless porpoise (Neophocaena phocaenoides)

Pilleri and Gihr (1972) showed the probable global geographic distribution of finless porpoises to include the entire coastline of Iran, however, until this present study there has been insufficient published data to substantiate this. Finless porpoises in Iranian waters are the Indian Ocean subspecies *N. p. phocaenoides* (Reeves *et al.*, 1997). Throughout their range finless porpoises inhabit shallow coastal waters, and inshore, partially enclosed, water bodies (Reeves *et al.*, 1997). For this study, 25 records of finless porpoises were compiled; 23 were from the Persian Gulf and 2 from the Gulf of Oman. These comprised 12 strandings, 12 sightings and the skeletal remains of one individual.

PERSIAN GULF

The finless porpoise has been listed as an uncommon breeding resident in the Persian Gulf (De Boer *et al.*, 2003). In general it appears to be rare but widespread throughout the south and west of the Gulf (Anon., 1995b; Collins *et al.*, 2005; Gallagher, 1991a; Preen, 2004; Robineau and Fiquet, 1996). It has not been recorded further east than Jebel Ali, Dubai in the UAE (Baldwin *et al.*, 1998; Collins *et al.*, 2005).

In contrast, records suggest that finless porpoises are common in Iranian waters of the Persian Gulf. There are several records from the northwest Persian Gulf in estuaries in Khuzestan, Iran and in nearby Iraq; two porpoise groups were sighted near the mouth of the Shatt al-Arab close to the Iraq border (Al-Robaae, 1975) and porpoises have been recorded near Khorramshahr where they sometimes enter the larger rivers and shallow water (Anon., 1998; 2003d; Etemad, 1985). Two groups of porpoises, one of 3 individuals and one of 4, were sighted about 1km from shore in waters less than 10m deep in northern Iran (Henningsen and Constantine, 1992).

The majority of the finless porpoise records in Iran are of stranded or incidentally captured animals from the vicinity of Bushehr city. One porpoise was reported as bycatch in a gillnet near Bushehr in March 1998 (Anon., 1998). A second individual, 115cm in length, was stranded on the western shores of Bushehr port on 27 November 2002 (Anon., 2003d). An aquarium shop in Bushehr city has a stuffed finless porpoise and the tail flukes of three other porpoises on display. These animals were reportedly fisheries bycatch and were purchased from fishermen.

In the Hara Protected Area on Qeshm Island, over a 30 year period there have been repeated sightings of finless porpoise groups in virtually the same location within channels flowing between the mangroves (Table 1; Fig. 2b). In January 1973, Pilleri and Gihr (1973-74) recorded two finless porpoises in the Protected Area. Two individuals were seen on 24 January 2000 (Keijl and van der Have, 2002) and during a survey conducted by two of the authors on 6 December 2005 two groups were sighted, one of 4 individuals and the other a best estimate of 12 (high 16, low 10) was recorded. Despite being a Protected Area, fishing with gillnets still occurs and porpoises with signs of gillnet entanglement were stranded during 2004 and 2007 and a porpoise was captured and released alive in January 2007 (Table 1). Outside of the Protected Area, porpoises have been recorded along the north coast of Qeshm Island (Pilleri and Gihr, 1973-74). One individual was stranded on Hengam Island in March 2007 and an animal measuring 147cm in length was killed in a gillnet between Hormoz Island and Bandar Abbas in 1995 (Anon., 1995b).

There are two areas of apparent porpoise concentration in Iran, one north of Qeshm Island and the other at the head of the Persian Gulf. The only evidence that there may be a continuous distribution between these areas is a report of a sighting (unclear whether stranded or alive) in March 1995 at Bandar-e-Dayer in Bushehr Province (Anon., 1995b).

GULF OF OMAN

There are only two records of finless porpoises from anywhere in the Gulf of Oman (excluding Pakistan) and these are both from the Iranian coast. A stranded porpoise was found on 23 November 2007 east of Jask and there was one ‘almost certain’ sighting in Chabahar, Iran in the winter of 1971 (Collins *et al.*, 2005; Roberts, 1977). Finless porpoises have been recorded along the coast of Pakistan, including from Gwadar adjacent to the Iranian border (Roberts, 1997) and it seems likely that they are distributed more widely along the Iran-Pakistan coast.

A seasonal movement of animals inshore during the winter and offshore during the summer has been noted in several parts of this species’ range including Pakistan (Pilleri and Gihr, 1972; Roberts, 1997) and Hong Kong (Jefferson and Braulik, 1999). It is interesting to note that all records of finless porpoise in Iran, for which a date is available, were made during the winter, between November and March. It is unclear whether this is due to the extreme high summer temperatures limiting fieldwork and speeding decomposition of strandings, or because seasonal inshore movement of populations renders them more prone to bycatch and more accessible for sightings during the winter months.

A large proportion of Iranian finless porpoise records are of stranded or bycaught animals which suggests that incidental mortality in coastal fishing gear may be unsustainable especially if, as the records indicate, the populations are small and localised.

Long-beaked common dolphin (Delphinus capensis tropicalis)

Delphinus delphis, D. capensis and *D.c. tropicalis* have been reported in the region (Jefferson and Van Waerebeek, 2002; Perrin, 2002). Most recent authors have attributed all *Delphinus* sp. records in the Gulf of Oman and Persian Gulf to the very long-beaked form *D.c. tropicalis* and it is possible to clearly differentiate this subspecies in the field (Ballance and Pitman, 1998; Robineau, 1998; Robineau and Fiquet, 1996). All skulls examined in Iran were identified as *D.c. tropicalis* based on very high tooth counts.

The common dolphin is the cetacean species cited most frequently by Iranian authors as occurring in Iranian waters (Anon., 1995a; Firouz, 2005; Harrington, 1977; Humphrey and Kharom, 1995; Ziaie, 1996), however many of the records refer to mis-identified sightings or skeletal remains. There are just 10 positive records: 5 from the Persian Gulf and 5 from the Gulf of Oman.

PERSIAN GULF

Long-beaked common dolphins have been frequently recorded in the south of the Persian Gulf, especially off the coast of Saudi Arabia and UAE. During surveys near Abu Ali Island in Saudi Arabia, common dolphins were the most frequently encountered species accounting for 75% of all individuals sighted (Robineau, 1998; Robineau and Fiquet, 1996). *Delphinus* sp. were not sighted at all during comprehensive aerial surveys of the entire southern Persian Gulf coastline and it was suggested that they may be more abundant closer to the Iranian coast where water is deeper (Preen, 2004).

In Iranian waters of the Persian Gulf, one group of 12 common dolphins were recorded in offshore waters in the northwest (Henningsen and Constantine, 1992). No specific location for this sighting was given, but the survey track indicates that the sighting must have been SSW of either Bushehr city, or Ganaveh. A young bycaught animal stranded near Bushehr city in November 2007, and two animals, a 203cm male (Fig. 3) and 186cm female, were bycaught near Ameri, Bushehr in February 2008 (Table 1). A *D.c. tropicalis* skull is stored at the GeoPark Museum on Qeshm Island.

Fig. 3. Long-beaked common dolphin, *D. c. tropicalis,* stranded near Bushehr. The extremely long rostrum, high tooth count, flipper to jaw stripe and hourglass pattern on the flanks are diagnostic. Photo: courtesy Fatemeh Mohsenizadeh.

GULF OF OMAN

D.c. tropicalis is widely distributed and abundant off the Oman and UAE coast of the Gulf of Oman where they are often seen in mixed groups with spinner dolphins, sometimes in association with yellowfin tuna, *Thunnus albacares* (Baldwin *et al*., 1999). Pilleri and Gihr (1973-74) reported three sightings of common dolphins in deep waters off the Iranian coast and there have been two strandings documented (Table 1).

Spinner dolphin (Stenella longirostris)

Spinner dolphins are known to occur in both the Persian Gulf and Gulf of Oman, and it is likely their range includes deeper waters of Iran. Van Waerebeek *et al.* (1999) concluded that spinner dolphins in the Gulf of Oman should be treated as a discrete population morphologically distinct from other spinner dolphin subspecies. Spinner dolphins in Oman have cranial morphometrics similar to *S.l. orientalis* from the east Pacific, but external features quite different from these. Two colour morphs have been described: a common tripartite pantropical form and another smaller, atypical bipartite form which is less common.

PERSIAN GULF

Spinner dolphins are present, but relatively uncommon, in the Persian Gulf. Records are limited to several skulls found on an island near Abu Dhabi, UAE and reports of sightings near Dubai (Baldwin *et al*., 1998; Preen, 2004; Robineau, 1998). Mörzer Bruyns (1971) observed concentrations of thousands either side of the Straits of Hormoz. It is likely that spinner dolphins occur in deeper waters of the Iranian Persian Gulf although there are no confirmed records at present.

GULF OF OMAN

The spinner dolphin is abundant in Oman, where groups of more than 1,500 have been seen (Van Waerebeek *et al*., 1999). They often occur in mixed groups with *Delphinus* sp., occasionally with pantropical spotted dolphins (*S. attenuata*) and associate with yellowfin tuna (Baldwin *et al*., 1998; Collins *et al*., 2002). A spinner dolphin was stranded 50m from Chabahar fishing port in December 2005 and a group was videoed 10 n.miles southwest of Gwadar on the Pakistan-Iran border. Large groups of small unidentified dolphins are regularly observed off the coast of Sistan and Baluchistan and it is possible that these may be groups of spinner dolphins. On the 20 September 2007, the partially decomposed carcasses of 79 spinner dolphins were stranded along 13km of coast, 125km east of Jask. A retrospective investigation concluded that the most likely cause of death was fishing activities (Braulik *et al*., In press). It is probable that spinner dolphins are common off the Iranian coast of the Gulf of Oman and may be represented by the morphologically distinct Oman form.

Spinner dolphin (Stenella longirostris)/*long-beaked common dolphin* (D.c. tropicalis) *records*

Four dolphin records were identified as either spinner dolphins or long-beaked common dolphins (Table 1) but identification could not be further refined based on available evidence (photographs of badly decomposed animals). There are two records of spinner dolphin/long-beaked common dolphin strandings near to Chabahar, one stranding from the south of Qeshm Island and a stuffed animal in the GeoPark Museum on Qeshm Island (that has not been examined in detail).

Striped dolphins (Stenella coeruleoalba)
Striped dolphins are rare in the Gulf of Oman and have never been recorded in the Persian Gulf (Alling, 1986; Baldwin *et al.*, 1999; Ballance and Pitman, 1998). There was a live mass stranding of 73 striped dolphins on 24 October 2007, 60km west of Jask. The stranded group appeared to have become trapped in an estuarine area with complex sandbanks and shallows. What caused this locally uncommon, pelagic species to enter such atypical habitat could not be determined (Braulik *et al.*, In press). A striped dolphin skull from a different stranding (reported to be in the same vicinity), is in the DoE office in Jask.

Rough-toothed dolphin (Steno bredanensis)
The complete skull of a mature rough-toothed dolphin is stored at the IFRO office in Chabahar (Fig. 4). This is the first, and only, record of this species in Iran. This species has not been recorded in Pakistan but it has been recorded (both sightings and strandings) a hand-ful of times in Omani waters of the Gulf of Oman (Ballance and Pitman, 1998; Van Waerebeek *et al.*, 1999; Oman Whale and Dolphin Research Group, unpublished data). There is no evidence of rough-toothed dolphin occurrence in the Persian Gulf and it is unlikely that this is suitable habitat for this deep water species (Robineau, 1998).

Fig. 4. Skull of rough-toothed dolphin, stored in the IFRO museum in Chabahar. The skull was identified based on the large orbit, number of teeth and the ridge at the ventral side of the frontals.

Risso's dolphin (Grampus griseus)
Risso's dolphin is a pelagic species that is relatively common seaward of the continental shelf in the northern Indian Ocean, including the Gulf of Oman and Arabian Sea (Baldwin *et al.*, 1998; Kruse *et al.*, 1991). Most Iranian authors list Risso's dolphin as present in Iran (Darrehshori *et al.*, 1996; Firouz, 2005; Ziaie, 1996), though no details are provided. Risso's dolphins are common in Omani waters of the Gulf of Oman (Baldwin *et al.*, 1998; Ballance and Pitman, 1998; Gallagher, 1991a; Kruse *et al.*, 1991) and are probably relatively common in Iranian waters. There are two stranding records of this species, one near to Chabahar (see Fig. 5) and one east of Jask (Table 1; Fig. 2c). The shallow water of the Persian Gulf is unlikely to be suitable habitat for Risso's dolphins and its presence there is unconfirmed and considered unlikely.

Melon-headed whale (Peponocephala electra)
Knowledge of this species in the northwest Indian Ocean is very limited and although there is a well documented record from Hallaniyah, Oman, there are no confirmed sightings in the Persian Gulf or Gulf of Oman (Baldwin *et al.*, 1999; Van Waerebeek *et al.*, 1999). The ease of confusion with other species means that reports of sighted melon-headed whales along the Makran Coast and Indus Delta in Pakistan (Roberts, 1997) should be treated as unconfirmed. Melon-headed whales have not been recorded in Iran.

Fig. 5. Stranded Risso's dolphin, close to Chabahar. This species is identified based on the white patch on the chest, white lips, blunt head, dark colouration with white scarring and tall falcate dorsal fin. Photo: courtesy Teymour Aminrad.

False killer whale (Pseudorca crassidens)
The false killer whale is believed to be relatively abundant in pelagic equatorial regions of the Indian Ocean (Leatherwood *et al.*, 1991) and it is uncommonly reported in waters of both the Persian Gulf and Gulf of Oman (Al-Robaae, 1971b; Baldwin *et al.*, 1998; Baldwin *et al.*, 1999; Mörzer-Bruyns, 1971; Mörzer Bruyns, 1969; Robineau, 1998; Weitkowitz, 1992). The presence of false killer whales in the Persian Gulf of Iran is confirmed by the presence of a skull found on Qeshm Island now stored at the Zoological Museum at the University of Tehran and a skull found on Kish Island stored with a local resident. Mörzer-Bruyns (1971) reported observing immature false killer whales in February in the Persian Gulf in water 36-47m deep.

Records suggest that the false killer whale is a breeding resident in the Gulf of Oman (Baldwin *et al.*, 1999; Leatherwood *et al.*, 1991). A sighting reported by Leatherwood *et al.* (1991) at 25.85ºN 59.85ºE is incorrectly located 30 miles inland in Iran, however the sighting itself may still be valid. One false killer whale skull stored at IFRO in Chabahar (Fig. 6), and collected from the nearby coast, suggest it is present in Iranian waters of the Gulf of Oman.

Fig. 6. Skull of a false killer whale. Nine round tooth sockets arranged along full length of rostrum, wide premaxilla bones and deep antorbital notches aided the identification of this specimen.

Killer whale (Orcinus orca)
The geographic location of six killer whales reportedly seen in the Persian Gulf corresponds to approximately 38km inland of Bandar Abbas, Iran (Leatherwood *et al.*, 1991) and therefore occurrence of this species in Iranian waters of the Persian Gulf is unsubstantiated. There have been numerous killer whale sightings in Oman (Baldwin *et al.*, 1999, Oman Whale and Dolphin Research Group, unpublished data); and in the Persian Gulf off UAE (Baldwin, pers. comm.) and although this species has not been recorded in Iranian waters of the Gulf of Oman it may be an uncommon visitor.

Sperm whale (Physeter macrocephalus)
Sperm whales have not been recorded and are not expected to occur in the Persian Gulf. There are many records of sperm whales in deep water in the Gulf of Oman where they are resident (Alling, 1986; Baldwin *et al.*, 1999; Ballance and Pitman, 1998; Gallagher, 1991b; Gore *et al.*, 2007). The first sperm whale record for Iran was a stranding in June 2007 near to Jask.

Other odontocetes
Other odontocetes that have been recorded in the region and may occur in Iranian waters are the pantropical spotted dolphin (*Stenella attenuata*), pygmy killer whale (*Feresa attenuata*), dwarf sperm whale (*Kogia sima*), pilot whale (*Globicephala macrorynchus*) and Cuvier's beaked whale (*Ziphius cavirostris*) (Alling, 1986; Baldwin *et al.*, 1999; Ballance and Pitman, 1998; Gallagher, 1991b; Harwood, 1980).

Mysticetes

Reports of baleen whale sightings in Iran are rare and there is no quantitative information on their distribution or abundance. It was reported by Daanehkaar (1998) that whales can be observed near to the Iranian coastline at Nayband Bay and Bandar Lengeh harbour where there is deep water close to the land and whales are apparently also infrequently seen in waters off Bandar Abbas and Qeshm Island (Firouz, 2005).

Twenty-six baleen whale records were compiled, 9 from Bushehr Province in the northwest of the Persian Gulf, 12 from Hormozgan and Qeshm Island, 4 from Sistan and Baluchistan and 1 of unknown origin. There are 13 records of skeletal material, 12 strandings and video of one sighting. In some cases it was not possible to obtain a definite species identification from photographs of strandings or from examination of bones. If identification was not possible records have been included as *Balaenoptera* sp. or the identification was treated as tentative (Table 1), pending confirmation using molecular analysis of bone or tissue samples.

Blue whale (Balaenoptera musculus)
Blue whales are reported by Iranian authors to occur in Iran (Etemad, 1985; Harrington, 1977; Humphrey and Kharom, 1995; Ziaie, 1996), however, no supporting data are provided and no evidence for the occurrence of this species in Iran has been found in this study. Given its shallow nature (<100m deep) Iranian waters of the Persian Gulf are unlikely to be frequented by blue whales and there is only one unconfirmed record from elsewhere in the Gulf; a stranding in Kuwait in 1963 (Al-Robaae, 1971a; Robineau, 1998). Blue whales have been sighted on several occasions in the Sultanate of Oman (Baldwin *et al.*, 1999) and it is possible that they also occur in Iranian waters of the Gulf of Oman.

Fin whale (Balaenoptera physalus)
There are several published but unconfirmed fin whale strandings and sightings from the Persian Gulf (Al-Robaae, 1982; Baldwin *et al.*, 1999; de Silva, 1987; Robineau, 1998). Firouz (2005) reported that fin whales are occasionally seen near Bandar Abbas and Qeshm Island in Iran, however large pods of as many as 100 individuals reported in Iranian waters by Humphrey and Kharom (1995) seem unlikely. There is one unconfirmed Iranian record of this species; a fin whale measuring 19m in length was stranded 30km south of Bandar Abbas in April 1971 (Baloutch, 1972). The skeleton is now displayed in the Zoological Museum of the University of Tehran. All the above records are unconfirmed and Baldwin (2003) was unable to find any substantiated evidence of fin whale occurrence in the Arabian region and suggests that they are unlikely to occur.

Bryde's whale (Balaenoptera edeni) *and Omura's whale* (Balaenoptera omurai)
The identity and number of species of Bryde's whales worldwide is currently uncertain (Perrin and Brownell, 2007). A new species, Omura's whale (*B. omurai*) was described in 2003 (Wada *et al.*, 2003) and there is believed to be a smaller inshore form of Bryde's whale from Asia (*B. edeni*) and a 'normal' larger offshore form (*B. brydei*) as well as the possibility of other intermediate forms (Ballance *et al.*, 2001; Perrin *et al.*, 2007; Rice, 1998). Perrin and Brownell (2007) recommended that *B. edeni* be used provisionally for the Bryde's whale complex until the taxonomy of the group is resolved. Bryde's whales are probably relatively common in Iranian waters although it is unclear at present which form or forms are represented.

Ten records of Bryde's whales in Iranian waters were compiled: 5 skeletal remains and 5 strandings. Nine records are from the Persian Gulf and there is a single record from Iranian waters of the Gulf of Oman.

Persian Gulf: There are multiple records of Bryde's whales from the Persian Gulf and this species is the most common mysticete in the area (Al-Robaae, 1969; Baldwin *et al.*, 1999; Robineau, 1998; Robineau and Fiquet, 1996). The remains of a Bryde's whale were found on the southern tip of Qeshm Island in 1973; the atlas and three vertebrae are now stored in the Stuttgart Museum (Pilleri and Gihr, 1973-74). The skull of a young Bryde's whale found on the south coast of Qeshm Island in spring 2006 and a skeleton tentatively identified as a Bryde's whale are both stored at the GeoPark Museum on Qeshm Island. In 2004 a Bryde's whale carcass found floating between Qeshm and Hormoz Islands was towed to Hormoz Island where the skeleton is now preserved by the Environmental Protection Authority. In 2007 there were four Bryde's whale strandings in Iranian waters of the Persian Gulf (Table 1).

Gulf of Oman: A skeleton identified as a Bryde's whale is at the IFRO office in Chabahar. It is believed to have stranded on the nearby coast and confirms the presence of this species in Iranian waters of the Gulf of Oman.

Sei whale (Balaenoptera borealis)
The occurrence of sei whales in the Arabian region is uncertain and their identification may be confused with Bryde's whales. There are unconfirmed sightings in the Gulf of Oman (Baldwin *et al.*, 1999) but a review of records led Baldwin (2003) to conclude that their presence in Arabia be unlikely. There is no evidence of their occurrence in Iran.

Common minke whale (Balaenoptera acutorostrata)
Minke whale sightings in the middle east were reported by Baldwin *et al.* (1999). However a later re-examination of records led to the conclusion there are no confirmed records of this species in the Arabian region (Baldwin, 2003). There is no evidence of their occurrence in Iranian waters.

Humpback whale (Megaptera novaeangliae)
Humpback whales are listed as occurring in Iran in almost all national mammal reviews and checklists (Etemad, 1985; Firouz, 2005; Harrington, 1977; Humphrey and Kharom, 1995; Ziaie, 1996), but these records appear to be based on many *Balaenoptera* sp. skeletons that have been misidentified as humpback whales. There are no known records of this species from Iranian waters of the Persian Gulf but there are two records from nearby Iraq (Al-Robaae, 1974; Gervais, 1883).

A resident, non-migratory population of humpback whales occurs in the Arabian Sea and Gulf of Oman. Highly productive upwelling along the coast of Oman ensures sufficient food to allow whales to remain in the region throughout the year (Minton *et al.*, In press; Papastavrou and Van Waerebeek, 1997; Reeves *et al.*, 1991; Whitehead, 1985). The greatest recorded concentrations of animals are from southern Oman, near to Masirah and the Halaniyat Islands, but there are also records, primarily of young animals, from the Gulf of Oman as far west as UAE (Baldwin *et al.*, 1999; Mikhalev, 1997; Minton *et al.*, In press). In this study three definite records of humpback whales were compiled; two strandings and one sighting, all from the Sistan and Baluchistan coast in the Gulf of Oman. A mother-calf pair was recorded close to the Chabahar coast in September 2004, a humpback whale stranded near Pozm in October 2004 and another stranded near Chabahar in December 2003. These individuals are presumably part of the Arabian Sea population. Surveys to evaluate the seasonal distribution and abundance of humpback whales in Iran and subsequent comparison of identified individuals with those from Oman would be valuable to understanding more about this resident population which is classified by the International Union for Conservation of Nature (IUCN) as 'endangered' (Minton *et al.*, 2008).

Sirenia

Dugong (Dugong dugon)
The world's second largest dugong population occurs in the southern margins of the Persian Gulf in the coastal waters of Bahrain, UAE, Qatar and Saudi Arabia (Marsh *et al.*, 2002). Abundance was estimated as 5,840 ± 903 and the largest aggregation ever recorded, numbering an estimated 674 animals, was found between Bahrain and Qatar in the winter of 1985/86 (Preen, 2004). Dugong typically inhabit shallow tropical and subtropical waters with a mean sea surface temperature of 23ºC or greater and avoid prolonged exposure to water temperatures of less than 18ºC. It was therefore suggested that the temperature regime and bathymetry in Iran (except for north Qeshm Island) would be unsuitable to support significant numbers of this species and Iran has not been recorded as a dugong range state (Marsh *et al.*, 2002; Preen, 2004).

There have been anecdotal reports of dugong sightings in Gwadar near the Pakistan border and a reported, but unconfirmed, sighting of two individuals in the Mond River estuary (approximately 100km south of Bushehr city) (Firouz, 2005). There have been two definite sightings of dugongs in the mangroves of the Hara Protected Area north of Qeshm Island. Keijl and van der Have (2002) reported that 'a single individual was seen briefly in a rather narrow and muddy creek about 15m wide on 29 January 2000. It surfaced about 5m from the boat and then dived. When it surfaced the broad flattened snout was seen, and when it subsequently dived the tailstock and V-shaped flukes were seen very clearly'. Green (2000) also described a sighting of three dugongs in the Hara Protected Area on 1 November 2000.

These records show that dugong have occurred in Iran, but it is unclear whether these individuals indicate the presence of a resident population in Iranian waters or whether they were vagrants that dispersed from the southern Persian Gulf population. In Australia dugongs regularly move distances of 40-100km and some individuals have been shown to undertake long distance movements of at least 600km across deep oceanic water, so dispersal 300km across the relatively shallow Persian Gulf is quite feasible (Marsh *et al.*, 2002).

THREATS FACING MARINE MAMMALS IN IRAN

Incidental capture in fishing gear

The largest threat to cetaceans in Iran is likely to be incidental capture in fishing gear. The country has the largest fishing fleet in the region and uses techniques such as fixed and drift gillnets known to cause mortality of cetaceans elsewhere in the world (FAO, 2005; 2007; Gosliner, 1999; Jefferson and Curry, 1994; Perrin *et al.*, 1994). There are nine records of finless porpoise and three of common dolphin incidental mortality in fishing gear in Iran. The nearshore distribution of finless porpoise places them in close proximity to intensively fished areas and losses are likely to have a greater impact on small and localised populations which appear to occur along the Iranian coast.

Shipping traffic

The Straits of Hormoz and Bandar Abbas region include major shipping lanes and 30% of the world's oil tankers pass through these areas annually (ROPME, 2003). In 2007, two Bryde's whales were stranded bearing gashes from propellers. Although it is not clear whether these occurred before or after death, cetaceans in the shipping lanes and entrance to the Persian Gulf are undoubtedly at risk of collision with vessels.

Oil pollution

The continual input of oil into the marine environment from natural seepage and routine oil extraction and transportation activities (estimated at 1.2 million barrels/year; ROPME, 2003) could have a chronic effect on marine mammal health. There is also always a risk of new catastrophic oil spills. In most cases cetaceans would be expected to avoid a spill and the greatest impact on them is likely to be indirect effects on prey availability, or the health effects of consuming prey contaminated by petroleum residues (Geraci *et al.*, 1999).

Chemical pollution

The Shadegan Marshes Ramsar site located on the Iran-Iraq border at the head of the Persian Gulf has been placed on the Montreux Record since 1993 due to chemical pollution from the Iran-Iraq war (RAMSAR, 2009). Finless porpoise and humpback dolphins have been sighted in this area and populations of these animals may have been impacted (either positively or negatively) by the wars and may also be affected by the chemical pollution.

Harmful algal blooms

Harmful algal blooms (HABs), often associated with seasonal upwelling, occur frequently in the Persian Gulf and Gulf of Oman and have caused mass mortality of fish and other marine organisms. A HAB was tentatively linked to the mass mortality of at least 520 marine mammals in the Persian Gulf in 1986 (Anon., 1994; 2003a; 2003b; 2003c; ROPME, 1986; Subba-Rao and Al-Yamani, 1998).

Coastal development

In the UAE and other states along the south of the Persian Gulf extensive coastal development including construction of new islands for housing complexes and resorts, causeway construction and dredging have severely degraded the marine environment and caused loss of seagrass beds and fish spawning sites (Jameson *et al.*, 1995). In the UAE, demersal fish stocks have declined dramatically, in some instances to 5% of 1978 levels, due to a combination of overfishing and destruction of demersal fish spawning sites by extensive coastal development (FAO, 2003). At present the coastal regions of Iran are less developed than those of southern Persian Gulf states, however, several resort islands such as Kish (Fig. 2a) are developing rapidly. Unless there are controls placed on coastal development in Iran, it is likely to proceed along similar unsustainable lines as states such as the UAE potentially causing declines in fisheries resources, degradation of marine habitats and negative impacts on marine mammals.

RECOMMENDATIONS

Establishment of a strandings network

Establishment of a network of individuals and organisations to survey the Iranian coastline for strandings and respond to reported strandings is a relatively low-cost but highly effective way to collect information on marine mammal species occurrence and threats. Training for volunteers will be required and a central location designated to store information, to deposit specimens and arrange sample analysis, etc.

Marine mammal bycatch assessment

It is suspected that bycatch of dolphins and porpoises in fishing gear may be one of the largest threats to marine mammals in Iranian waters. To identify ports, fishing gear and fisheries that result in significant marine mammal bycatch and species that are most susceptible, a study of ports, fish landing sites and fish markets, and interviews with fishermen will need to be conducted. Following this more detailed studies, such as observer programmes, could be initiated.

Conduct baseline distribution and abundance surveys

Initiation of marine mammal distribution and abundance surveys is vital as a precursor to targeted conservation efforts. Areas and species that may be prioritised are: (1) coastal cetaceans in Khuzestan which are likely to be threatened by pollution and military activities; (2) marine mammals around Qeshm Island which records suggest is an important area for finless porpoise and humpback dolphins; (3) humpback whales off the coast of Sistan and Baluchistan; and (4) monitoring of pelagic dolphins in the Gulf of Oman where accidental capture in fishing gear may be significant.

Study of marine mammals in the Hara Protected Area

Three marine mammal species have been recorded in the mangroves of the extensive Hara Protected Area on the north coast of Qeshm Island. Regular sightings of finless porpoise indicate that the Protected Area may be important habitat for this species. The only confirmed records of dugong in Iran also occurred here. As this is a high profile national reserve, it is an ideal location to study marine mammal occurrence, distribution and abundance and to monitor and manage potential threats such as illegal fishing with gillnets that cause porpoise mortality.

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Marine mammal records from Iran

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Correction: The single rough-toothed dolphin (*Steno bredanensis*) record (see Table 1, record no.3 on page 54, and the text and Fig. 4 on page 58) is erroneous and should be recorded as Indo-Pacific bottlenose dolphin (*Tursiops aduncus*). Rough-toothed dolphins have not been recorded in Iran, although they are likely to occur. The number of cetacean species recorded in Iran is thus amended from 14 to 13, the number of Indo-Pacific bottlenose dolphin records from 22 to 23, including two from the Gulf of Oman and 10 skeletal specimens.

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A note on the comparison of humpback whale tail fluke catalogues from the Sultanate of Oman with Madagascar and the East African mainland

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ABSTRACT

The photo-identification catalogue of humpback whale tail flukes from Oman was compared with those from Antongil Bay, Madagascar and study sites in South Africa and Mozambique collectively termed the 'East African Mainland'. No matches were found, supporting other lines of evidence that the humpback whales studied off the coast of Oman form part of a discrete Arabian Sea population, which adheres to a Northern Hemisphere breeding cycle, and has little or no ongoing exchange with the nearest neighbouring populations in the southern Indian Ocean. While the sample size from Oman is small, and low levels of ongoing exchange might not be detected in this type of catalogue comparison, the study nonetheless emphasises the need to pursue research and conservation efforts in the known and suspected range of the Endangered Arabian Sea humpback whale population.

KEYWORDS: HUMPBACK WHALE; SOUTHERN HEMISPHERE; INDIAN OCEAN; ARABIAN SEA; PHOTO-ID

INTRODUCTION

The humpback whale (*Megaptera novaeangliae*) is a cosmopolitan species found in all of the major oceans (Clapham and Mead, 1999). All known populations, with the exception of the population in the Arabian Sea (Minton *et al.*, In press), migrate between breeding grounds in tropical waters and feeding grounds in productive temperate or polar waters.

Soviet whaling data, observations from merchant vessels and recent research (primarily along the coast of Oman) include records of humpback whales from every month and strongly suggest the presence of a resident population in the western Arabian Sea with confirmed historical records indicating a distribution in Yemen, Southern Oman, Iran, Pakistan and India (Brown, 1957; Mikhalev, 2000; Minton *et al.*, 2008; Reeves *et al.*, 1991; Slijper *et al.*, 1964; Wray and Martin, 1983; Yukhov, 1969). These locations are well within the Northern Hemisphere, but offer no feasible migration routes to any of the known Northern Hemisphere humpback whale feeding grounds. Data on reproductive parameters collected during illegal Soviet whaling operations in 1966, as well as observations of calves and recordings of humpback whale song off the coast of Oman, indicate that this population adheres to a Northern Hemisphere breeding cycle, with peak calving taking place between January and May (Mikhalev, 2000; Minton *et al.*, In press).

Recent research has confirmed the continued presence of humpback whales off the Gulf of Oman and Arabian Sea coasts of Oman (e.g. Minton *et al.*, In press). Only limited incidental observations of the species have been recorded for some areas within the remainder of the suspected range. Re-sightings of photographically identified individuals off the coast of Oman in early autumn and late spring provide further evidence of year-round residency (Minton *et al.*, In press). Mark-recapture estimates using three different pairings of tail fluke photographs collected in Oman in two main research areas in the Arabian Sea over a period of four and a half years yielded a population estimate of 82 individuals (95% CI=60-111). However, sample sizes were small and there are various sources of possible negative bias, including insufficient spatial and temporal coverage of the population's suspected range (Minton *et al.*, In press).

Genetic analyses of tissues sampled from live and dead humpback whales in Oman and elsewhere in the Western Indian Ocean provide further evidence for a discrete Arabian Sea sub-population (Pomilla *et al.*, 2006; Rosenbaum *et al.*, 2009). Although this study showed that this sub-population clearly originated from the larger Southern Hemisphere population, analyses of maternally inherited mitochondrial (mt) DNA and nuclear microsatellites confirm genetic differentiation from all other Southern Hemisphere populations including those wintering off Madagascar, the Comoros Islands and Mozambique, and no evidence of current exchanges with these neighbouring areas (Pomilla *et al.*, 2006; Rosenbaum *et al.*, 2009).

The humpback whales in Antongil Bay in Madagascar and the waters of Mozambique and South Africa represent the best studied breeding stocks within feasible migration

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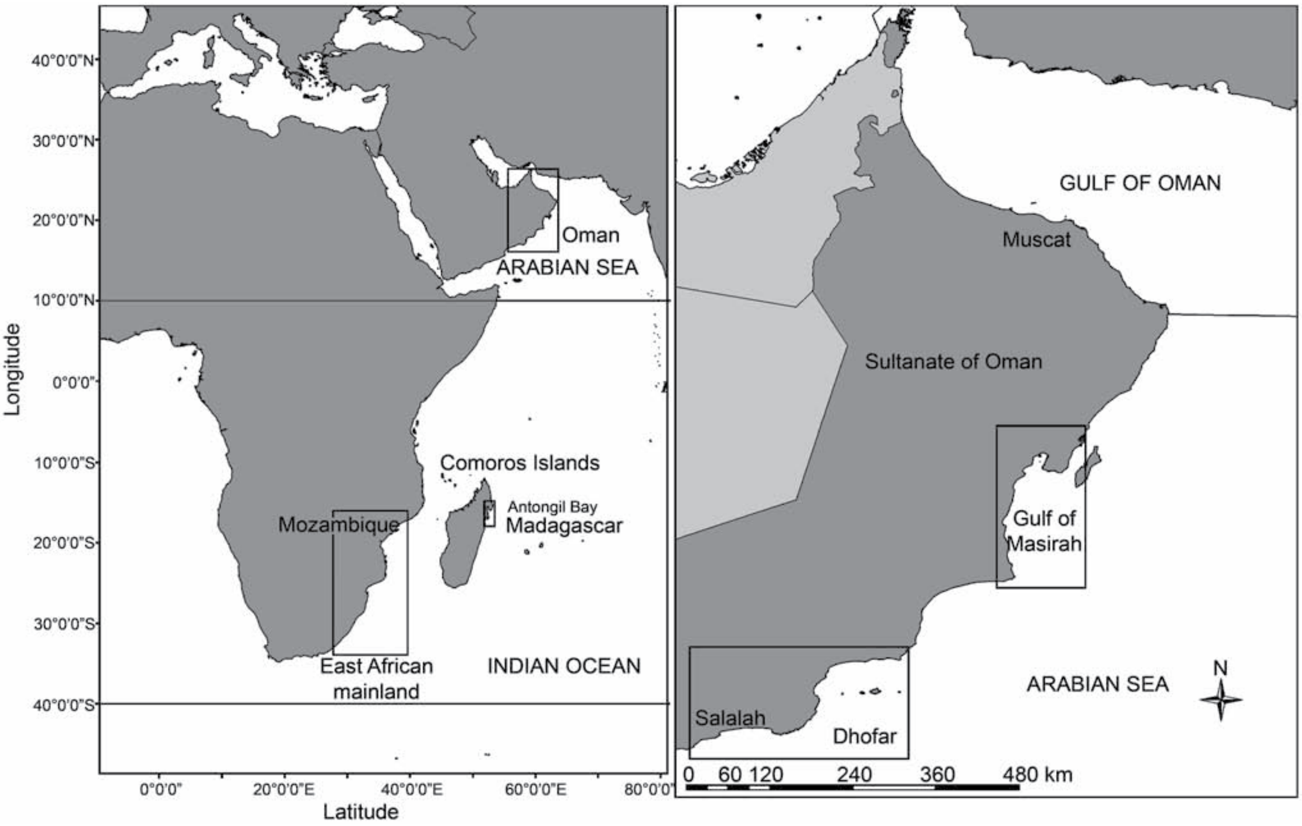

Fig. 1. Left: Three main sampling areas, Oman (breeding and feeding area X), Madagascar (breeding area C3) and the East African Mainland (breeding area C1). Right: Sultanate of Oman, with two main humpback whale survey areas highlighted.

Table 1

(a) Oman (Pop X), (b) Madagascar (BS C3) and (c) East African Mainland (BS C1S) samples with effort by date ranges and number of days on which photographs were collected and samples of individual identifications, ***n***, before and after filtering for quality. Note that in Oman and Madagascar, almost every day between the start and end date was spent observing whales, while in the East African mainland (EAM), the number of survey days are indicated to give a more accurate indication of effort between start and end dates.

Dates of IDs	2000	2001	2002	2003	2004	2005	2006
(a) Oman							
Survey periods	15-24 Jan.	9-22 Feb.	10 Feb.- 2 Mar.	24 Feb.-19 Mar.	4-29 Mar.	No obs	12-28 Feb.
	8-21 Feb.						
	15-17 Oct.	4-27 Oct.	24 Oct.-7 Nov.	15-17 May	4-29 Nov.		
n - all	8	15	23	8	15	0	4
quality filtered	7	14	20	5	13	0	3
(b) Madagascar							
Start date	17 Jul.	10 Jul.	22 Aug.	11 Jul.	10 Jul.	13 Jul.	16 Jul.
End date	17 Sep.	14 Sep.	11 Sep.	9 Sep.	5 Sep.	5 Sep.	4 Sep.
n - all	122	184	24	161	179	170	181
quality filtered	89	159	16	126	151	144	158
(c) East African mainland							
Start date	Jun.	Jun.	4 Jul.	3 Jun.	1 Sep.	25 Jun.	4 Jun.
End date	Jul.	6 Nov.	6 Dec.	28 Oct.	30 Sep.	17 Nov.	12 Nov.
No. of survey days	3	17	29	52	7	58	48
n - all	4	38	69	147	28	157	129
quality filtered	3	24	49	115	21	134	112

range from Oman. As such, the comparison presented here is intended to provide further understanding of the status of the Oman/Arabian Sea population. Comparisons of photo-identification material from Oman and Zanzibar have been carried out previously and no links between these areas were found (Minton *et al.*, In press).

METHODS

Oman (known as feeding/breeding population X by the IWC Scientific Committee - e.g. IWC, 2007)

Photographs were collected using standard procedures during small-boat surveys that were conducted over a period of six years in two main locations: the Gulf of Masirah and

Dhofar (both on the Arabian Sea coast of Oman - see Fig. 1). Surveys were designed to target areas where published (Mikhalev, 2000) and unpublished records (held by the authors) indicated potentially higher abundance of humpback whales. Survey timings are detailed in Table 1. Additional photos were taken during incidental sightings and entanglements in the Muscat region, Gulf of Oman (Minton *et al.*, In press).

Madagascar (known as Breeding Stock C3 - e.g. IWC, 2007)

Madagascar (breeding stock C3) data were collected from Antongil Bay, Madagascar (Fig. 1). Standard procedures were used for identification photography (see Cerchio *et al.*, 2008a). Individual identification photographs used in this analysis were collected from 2000 to 2006 during yearly research field seasons of the Cetacean Conservation and Research Program (CCRP).

East African mainland (known as Breeding Stock C1 - e.g. IWC, 2007)

The photographs collected from the East Coast of South Africa (east of 20ºE) and Mozambique were grouped together in one catalogue as the coasts of both countries are thought to comprise one breeding sub-stock (C1). For convenience, these areas were collectively termed the 'East African Mainland' to differentiate from the Madagascar and Western Indian Ocean island sub-stock. These photos were collected during both whale watch tourism operations and research cruises conducted between 2000 and 2006. Data used in this analysis were collected entirely from sub-region C1S (south of 15°S), with the vast majority (93%) collected off northern KwaZulu Natal and the Eastern Cape, South Africa (Cerchio *et al.*, 2008b).

Photographic comparison procedure

Photographs were compared on a computer screen, and the best representative photograph for each individual whale was chosen for each single survey day. Scanned and digital images were referenced with relevant sighting data in a customised Microsoft *Access* database. Customised forms and queries allowed for comparison of images permitting completion of within-year and between-year matching. Three separate regional catalogues were compiled for Oman and breeding stocks C1 and C3. Additional details of these matching procedures can be found in Cerchio *et al.* (2008b) and Minton *et al.* (In press). The finalised catalogues for each region, consisting of the best quality photograph of each individual identified, were merged into an inter-regional database, facilitating comparison between regions. All matching was completed by researchers with suitable experience in humpback whale photo-identification. All detected matches were confirmed by two other researchers. All photographs used in the comparison were rated for quality on a five-level scale: excellent, good, fair, poor, and not useable, in keeping with 'overall quality' criteria described by Friday *et al.* (2000). Photos of all qualities were compared; however, only photos of a quality of 'fair' or better were considered suitable for mark-recapture procedures and are thus reported (Table 1).

RESULTS

Table 1 shows the total number of photographs collected in Oman, Madagascar and the East African Mainland per year. The finalised catalogues from all three regions through 2006 included a total of 68 tail fluke photos for Oman, 1,041 photos for Madagascar and 559 for the East African Mainland (note that these totals are not the sums of the totals collected each year in Table 1; a number of individuals in each region were photographed more than once between years and are only counted once in the totals above). There were no matches found between Oman and either of the other two regions.

DISCUSSION

The complete lack of recaptures between Oman and either Madagascar or East African mainland suggests little to no exchange between the Arabian Sea population and these southern West Indian Ocean populations. It is important to bear in mind that a comparison of the photo-ID catalogues from breeding stock C1 (458 individuals identified by photos of acceptable quality) and breeding stock C3 (842 individuals of acceptable quality) yielded only one match (two if a poor quality match is included; see Cerchio *et al.*, 2008b). This small recapture rate between C1 and C3 is apparently due to relatively large population sizes combined with a low level of exchange. Given the much smaller sample size from Oman, we recognise that an equivalent exchange as that detected between C1 and C3 would not expect to be detected in this comparison. At the same time, however, mark-recapture estimation for C3 yielded best estimates of abundance in excess of 6,000 individuals (Cerchio *et al.*, 2008a) and line transect estimation for C1 yielded estimates of abundance of 5,965 (CV=0.17) (Findlay *et al.*, In press). As such, the number of individuals represented in the C1 and C3 catalogues represent a smaller percentage of the C1 and C3 populations, while the 68 individuals in the Oman catalogue may represent as much as 90% of the total population off the Coast of Oman. Furthermore, the finding of no recaptures of individuals corroborates the conclusions of genetic comparisons (Pomilla *et al.*, 2006; Rosenbaum *et al.*, 2009) that indicate greater differentiation between Arabian Sea and southern West Indian Ocean populations than between the southern populations. Given the observed genetic differentiation, and lack of recaptures here, we believe there can be no substantial mixing between Oman and other populations, and probably no recent exchange at all.

It is also important to bear in mind that the Oman Photo-ID catalogue does not include any individuals photographed outside of Oman in other parts of the Arabian Sea humpback whale population's suspected range. It is possible that whales in the more southern reaches of the Arabian Sea (e.g. those detected historically in the Gulf of Aden or Sri Lanka) have higher exchange rates with C1 or C3 populations. There has also been speculation that observations of whales in Tanzania, Kenya, and the Seychelles may include whales that move between the Arabian Sea and Southern Indian Ocean, but there is no evidence for this to date, and most observations in those areas appear to be of singing males or females with calves in August-September, which would be more in keeping with a Southern Hemisphere breeding cycle (e.g. Weru, 2001; P. Berggren, pers. comm. and C. Anderson, pers. comm.) rather than the Northern Hemisphere breeding cycle of Oman's whales. A comparison of the Oman catalogue with fluke and dorsal fin photographs taken in Zanzibar between 2000 and 2002 did not yield any matches (Minton *et al.*, In press). Another comparison between these regions with a larger and more recent sample from Zanzibar is planned, but no other catalogues are available to the authors knowledge.

Until further research is conducted in these areas, the results of this comparison, taken together with the results of genetic analysis and the proven year-round residence of whales off the coast of Oman, provide strong evidence for the discrete nature of the population of humpback whales off the coast of Oman. This further justifies the recent International Union for Conservation of Nature (IUCN) Red List designation of the Arabian Sea population of humpback whales as 'endangered' (Minton *et al.*, 2008). It also provides further indication that this population requires continued research and conservation efforts in order to more accurately assess population size and possible threats. There is an urgent need to further investigate the distribution and range of the Arabian Sea population by surveying other areas of the population's historic range, which may extend to Yemen, Iran, Pakistan and India (Minton *et al.*, 2008). Furthermore, as research is conducted in these areas, further photographic comparisons should take place between these new areas and the animals photographed off the coast of Oman.

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A note on long-distance matches of bottlenose dolphins (*Tursiops truncatus*) around the Irish coast using photo-identification

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ABSTRACT

Images of 120 individual bottlenose dolphins from around the Irish coast were obtained from three photo-identification catalogues. Twenty three individuals were subsequently re-sighted, which is a re-sighting rate of 19%. The distance between re-sightings ranged from 130 to 650km and the duration from 26 to 760 days. Images were also compared to a catalogue of resident dolphins from the Shannon Estuary candidate Special Area of Conservation and from Wales but no matches were found. This short study provides strong evidence that bottlenose dolphins in Irish coastal waters are regularly undertaking large movements around the entire Irish coast and must be considered highly mobile and transient. These results have important implications for the conservation and management of this species.

KEYWORDS: NORTHERN HEMISPHERE; BOTTLENOSE DOLPHIN; PHOTO-ID; MONITORING; DISTRIBUTION; CONSERVATION; MANAGEMENT PROCEDURE

INTRODUCTION

Common bottlenose dolphins (*Tursiops truncatus*) are found throughout temperate and tropical waters of the world between 60°N and 50°S of the equator and in the Mediterranean Sea (Reynolds *et al.*, 2000). Bottlenose dolphins are widespread and abundant in Irish waters (Ingram *et al.*, 2001), which contain some of the highest concentrations of this species in Europe (Evans, 1992).

Photo-identification (photo-ID) is a technique commonly used to study the movements and behaviour of whales and dolphins worldwide and was first applied to bottlenose dolphins by Würsig and Würsig (1977). This technique works on the principle of photographing individual animals and identifying natural markings unique to that individual (Thompson and Hammond, 1992; Wilson, 1995; Wilson *et al.*, 1999; Würsig and Würsig, 1977). Photo-identification provides a means to gather information on movement patterns, site fidelity, associations and population dynamics (Hammond *et al.*, 1990; Kerr *et al.*, 2005). Movement patterns are sometimes unpredictable, ranging from year-round residency in a defined area to seasonal or continual migrations (Shane *et al.*, 1986) and the use of natural markings as a means of tracking animals can prove extremely effective.

In Ireland, a number of studies using photo-ID of bottlenose dolphins have been carried out. Most of these were in the Shannon Estuary candidate Special Area of Conservation, cSAC (Berrow *et al.*, 1996; Englund *et al.*, 2007; Ingram and Rogan, 2002; Ingram, 2000). These studies have shown dolphins to be resident with a high level of site fidelity and very limited movements outside the cSAC. The only match outside the boundary of the cSAC was in Tralee Bay, less than 15km away. Additional unpublished studies have also found some degree of site fidelity at a number of other locations in Ireland, including Donegal Bay, Co. Donegal; Broadhaven and Clew Bays, Co. Mayo; Connemara, Co. Galway; Brandon Bay and Kenmare River, Co. Kerry and Cork Harbour (Englund *et al.*, 2007; Ingram *et al.*, 2001; Ingram *et al.*, 2003; O'Brien *et al.*, 2008; O'Cadhla *et al.*, 2003; Wilson and Smiddy, 1988). In this paper, matches of individually recognisable bottlenose dolphins are reported from all around the Irish coast and some implications for management are discussed.

METHODS

Images of bottlenose dolphins from around the Irish coast were obtained from a number of sources (Table 1). The Galway-Mayo Institute of Technology (GMIT) maintain a photo-ID catalogue comprised of 48 identifiable individuals from Galway and Clew Bay (Catalogue 1). Between July and September 2008, systematic surveys were carried out in Donegal Bay by the Irish Whale and Dolphin Group (IWDG), some of which were funded by the National Parks and Wildlife Service (NPWS). A total of eight surveys were carried out and 45 individual dolphins were identified (Catalogue 2). The IWDG have recently established an online photo-ID catalogue for a range of cetacean species recorded in Irish waters. Included in this catalogue are 27 individual bottlenose dolphins with recognisable markings collected from around the Irish coast by IWDG members and the public and it is accessible online at *http://www.iwdg.ie/photo-id* (Catalogue 3). Images from all three catalogues were combined and are referred to as the Irish Coastal Bottlenose Dolphin Catalogue (ICBDC).

Images from these three catalogues totalling 120 individuals were compared to determine whether any matches could be found between them. All images from Donegal Bay, Galway Bay and Clew Bay were taken using high resolution digital cameras, with minimum file sizes of 1.5Mb for each image. Some of the images submitted by the public were of a lower resolution but were still of usable quality. All images were viewed using Adobe *Photoshop* imaging software, in order to identify unique markings.

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Table 1

Summary of individual bottlenose dolphin sightings and re-sightings.

No. animals identified	Details of 1st sighting				Details of 1st re-sighting					Details of 2nd re-sighting				
	Catalogue no.	Date	Lat	Long	Date	Lat	Long	Time (days)	Distance (km)	Date	Lat	Long	Time (days)	Distance (km)
1	BNDIRL1	15/05/2007	51.85	-8.32	10/06/2007	51.74	-9.53	26	175					
2	GB20	26/03/2007	53.14	-9.28	10/05/2008	51.84	-8.27	76	380					
3	GB19	26/03/2007	53.14	-9.28	10/05/2008	51.84	-8.27	76	380					
4	BNDIRL24	17/06/2007	55.07	-6.02	15/08/2008	54.49	-8.37	423	280	30/04/2009	52.1	-10.3	258	390
5	GB01	29/06/2005	53.21	-9.68	30/07/2007	53.86	-9.94	760	130					
6	GB27	26/03/2007	53.14	-9.28	15/08/2008	54.49	-8.37	462	200					
7	GB16	26/03/2007	53.14	-9.28	08/08/2008	54.56	-8.43	506	300					
8	GB18	26/03/2007	53.14	-9.28	23/07/2008	54.56	-8.43	499	300					
9	GB22	26/03/2007	53.14	-9.28	02/07/2008	51.93	-10.28	483	300	23/07/2008	54.56	-8.43	386	375
10	GB23	26/03/2007	53.14	-9.28	23/07/2008	54.56	-8.43	483	300					
11	GB07	26/03/2007	53.14	-9.28	08/08/2008	54.56	-8.43	499	300	19/05/2009	55.1	-6.12	284	240
12	GB25	26/03/2007	53.14	-9.28	08/08/2008	54.56	-8.43	499	300					
13	GB08	26/03/2007	53.14	-9.28	15/08/2008	54.49	-8.37	490	300					
14	CB40	11/06/2007	53.80	-9.90	02/07/2008	51.93	-10.28	385	260					
15	BNDIRL17	02/06/2008	53.35	-6.15	31/08/2008	53.23	-9.56	90	600	19/05/2009	55.1	-6.12	261	460
16	BNDIRL11	10/05/2008	51.84	-8.27	08/08/2008	54.56	-8.43	89	650					
17	BNDIRL22	17/06/2007	55.1	-6.02	30/04/2009	52.1	-10.3	683	575					
18	DB35	15/08/2008	54.5	-8.37	30/04/2009	52.1	-10.3	258	365					
19	DB09	23/07/2008	54.6	-8.43	19/05/2009	55.1	-6.12	277	365					
20	DB18	08/08/2008	54.6	-8.43	19/05/2009	55.1	-6.12	284	260					
21	BNDIRL10	10/05/2008	51.8	-8.27	15/08/2008	54.5	-8.37	97	575	19/05/2009	55.1	-6.12	276	365
22	GB11	26/03/2007	53.1	-9.28	31/08/2009	53.2	-9.57	523	30	19/05/2009	55.1	-6.12	261	460
23	GB47	31/08/2008	53.2	-9.57	19/05/2009	55.1	-6.12	261	460					

Markings used to identify individuals included nicks or notches on the trailing edge of the dorsal fin (ranging from one to several), scratches and a condition described as scoliosis, an abnormal curvature of the spine (Berrow and O'Brien, 2005). Images were graded using a Q-scale (1-3), where grade 1 images were of good quality and were mostly used to initially identify an individual and also to confirm matches. Images of grade 2 were of lesser quality but were sometimes sufficient to verify a match, while grade 3 were determined poor quality and were therefore unusable. The images presented throughout this document are compressed and therefore do not represent their true quality when viewed in their original format. Distances between re-sightings were calculated using Garmin *Mapsource* software as the latitude and longitude was known for all sightings.

In order to further explore the movements of bottlenose dolphins in the ICBDC, comparisons were made with two additional catalogues, one from Ireland and one from the UK. The Shannon Dolphin and Wildlife Foundation (SDWF) manages a catalogue of around 180 individually recognisable bottlenose dolphins from the Shannon Estuary obtained between May 1993 and October 2008. Sea Watch Foundation (SWF) manages a catalogue of bottlenose dolphins from West and North Wales since the 1990s comprising of 219 marked individuals (recognisable from both sides through nicks, big scars or pigmentations), plus 112 individuals identifiable only from one side (with no nicks or big scars/pigmentations).

RESULTS

The ICBDC catalogue included images of 120 individually recognisable dolphins and of these 23 individuals have been re-sighted elsewhere (Table 1). This equates to an overall re-sighting rate of 19%. Most re-sighted individuals (14) were from the Galway Bay (GB) catalogue, 13 from Donegal Bay (DB) and 10 from the IWDG catalogue (Table 2). The latter catalogue included dolphins from Counties Antrim, Cork, Dublin, Kerry, Galway and Mayo (Table 1, Fig. 1). The 23 individual matches are shown below for each re-sighting.

Table 2

Summary of sighting rates from four bottlenose dolphin ID catalogues.

Catalogue	Total identified	Number re-sighted	Re-sighting rate	% of re-sightings
GMIT	48	15	0.3	31
IWDG	25	9	0.4	36
DB	42	14	0.3	33
Total	114	24	0.2	21
SDWF	209*	0	0	0
SWF	204*	0	0	0

*Not identified as part of this study.

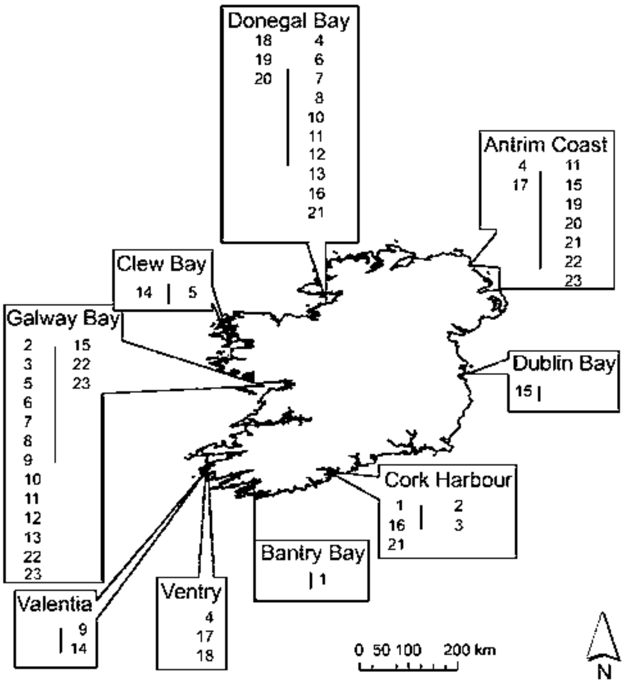

Fig. 1. Distribution map of bottlenose dolphin sightings (under each location column one represents where the animals was first sighted and column two represents where the animal was re-sighted). Numbers are according to Table 1, 'no. of animals identified'.

Of the 23 re-sighted dolphins, 13 animals (57%) were first identified in Galway Bay on 26 March 2007. Only 25 individual dolphins were identified amongst a group of 70-100 dolphins observed in Galway Bay and it is likely that if images of other individuals in this group were obtained, then additional matches would have been made as this group accounted for a high proportion of the long distance matches, e.g. Galway to Dublin (approximately 650km), Antrim (460km), Cork Harbour (380km) and Donegal Bay (300km). This group would appear to be highly migratory and transient as they were recorded across six months and three seasons, between the years 2005 and 2009 and therefore it is unlikely that these movements are seasonally influenced.

The time between sightings ranged from 26 to 760 days with a mean of 379 days (Table 1). The distances apart also ranged greatly from 130 to 650km with a mean of 400km. For three individuals the minimum mean distance travelled per day was recorded as 6.3km (BNDIRL1), 6.6km (BNDIRL17) and 7.3km (DB26).

No matches were found between the ICBDC catalogue and the SDWF or SWF catalogues from the Shannon Estuary and Wales. Intensive photo-ID is being carried at out at both of these sites with high re-sighting rates, therefore re-sightings might be expected if dolphins from the ICBDC catalogue regularly entered these sites.

There was some evidence of associations between individuals; two dolphins (GB18 and GB22) recorded together in Galway Bay on 26 March 2007 were also recorded together in Donegal Bay on 23 July 2008; three dolphins (GB07, GB16, GB25) recorded on 26 March 2007 were together in Donegal Bay on 8 August 2008; two dolphins (GB19, GB20) in Galway Bay on 26 March 2007 were recorded together on 10 May 2008 in Cork harbour and two dolphins (GB07, GB11) recorded together in Galway Bay in March 2007 and a further two (GB11 and BNDIRL17) recorded in August 2008 were recorded together off Antrim in May 2009.

DISCUSSION

Results from the present study provide some of the most comprehensive evidence of wide-scale, long-distance movements of bottlenose dolphins in European waters. Re-sightings were recorded across three seasons between 2005 and 2009. These results demonstrate the potential of photo-ID as a technique for studying long-distance movements in this species. Previous photo-identification studies in Ireland recorded re-sightings of nine individuals, over two years off the south coast, 38km apart between Youghal Bay and Cork Harbour, and one individual first recorded off Connemara was re-sighted off the Cork coast, a distance of 380km (Ingram and Rogan, 2003). The only other comparable study carried out in European waters was by Wood (1998) who reported on the large-scale movements of Cornish dolphins during a three year period over a 650km stretch of coastline between Cornwall and West Wales. On one occasion he recorded a dolphin re-sighting of 1,076km in only 20 days, which was much greater than the maximum (650km) reported in the present study. It is, however, unclear as to whether there were regular movements of these distances or they were unique and may not have been a regular occurrence. More recently, Silva *et al.* (2008) reported long-distance movements of almost 300km by bottlenose dolphins in the Azores which were considered foraging or exploratory trips but they were unable to determine whether these wide-scale movements occurred year-round. Results from studies elsewhere using satellite telemetry studies have recorded bottlenose dolphins travelling over large distances. Tanaka (1987) reported movements of bottlenose dolphins of 604km over an 18 day period, while Wells and Scott (1990) reported movements of 670km over a 74 day period.

The shortest time between sightings during the present study was between Portmagee, Co. Kerry and Donegal Bay (21 days) over a distance of 370km and between Cork Harbour and Glengariff (26 days) over a distance of 175km. This means that these dolphins travelled a minimum of 6.7km and 17.6km per day. The re-sighting of dolphins 1,076km apart within 20 days reported by Wood (1998) requires travelling at an average of 54km per day.

The high re-sighting rate in the present study is remarkable, especially given that the sample size of individual dolphins was small. It is also remarkable that no dolphins from the Shannon Estuary cSAC were recorded outside the cSAC. It is suggested that a relatively small population of dolphins must occur around the Irish coast to produce such a high re-sighting rate. This suggestion is consistent with data from the SCANS II survey (SCANS II, 2008), which reported abundance estimates of bottlenose dolphin of 313 individuals (CV=0.81) for coastal Ireland. The present study suggests dolphins archived in the ICBDC are highly migratory and transient individuals.

Bottlenose dolphins are listed under Annex II of the EU Habitats Directive which requires that they be given strict protection in clearly identifiable areas (SACs). A total of 18 SACs have either been designated or proposed specifically for bottlenose dolphins within EU member states (Anon., 2006). In Ireland, there is currently only one candidate SAC for bottlenose dolphins (Shannon Estuary) on the west coast. It has been suggested from the western north Atlantic, that coastal stocks of bottlenose dolphins are comprised of residents, which are localised to certain areas, and transient animals, which migrate seasonally into and out of areas (Scott *et al.*, 1988). The evidence from Ireland supports this theory, since no matches were found between ICBDC and the Shannon Estuary, home to Ireland's only known resident group of bottlenose dolphins. Thus it can be speculated that the dolphins identified from around the Irish coast are transient and do not mix with the resident animals in the Shannon Estuary. The large-scale movement undertaken by these transient dolphins does create problems when trying to designate sites for their conservation, especially since these movements take them into both Irish and UK waters. Of the 23 re-sighted individuals, nine (39%) have been recorded off the Co. Antrim coast. Therefore the Irish government will need to work with the UK government to ensure successful conservation of the species. Wilson *et al.* (2004) reported on a population range expansion of bottlenose dolphins off northeast Scotland and suggested that site designations may afford less protection than originally envisioned. Our data suggest that some coastal dolphins regularly undertake long movements and site designation may not be suitable for species and habitat conservation. A better approach may involve a network of SACs with migrating corridors or a combination of habitat (site) designation and a more dynamic species conservation approach.

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Date received: January 2009.
Date accepted: July 2009.

(1) BNDIRL1

BNDIRL1 Cork Harbour, 15/05/2007
Photo credit: Conor Ryan

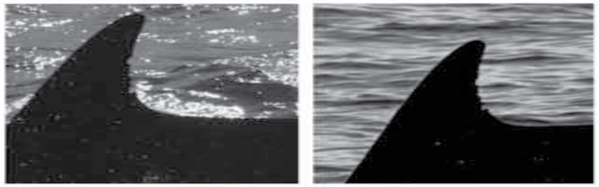
BNDIRL1 Bantry Bay, 10/06/2007
Photo credit: Maurice Fitzgerald

(2) GB20

GB20 Galway Bay, 26/03/2007
Photo credit: Joanne O'Brien

BNDIRL7 Cork Harbour, 10/05/2007
Photo credit: Conor Ryan

(3) GB19



GB19 Galway Bay, 26/03/2007
Photo credit: Joanne O'Brien

BNDIRL8 Cork Harbour, 10/05/2007
Photo credit: Conor Ryan

(4) BNDIRL24

BNDIRL24 Antrim, 17/06/2007
Photo credit: Pauline Majury

DB36 Donegal Bay, 15/08/2008
Photo credit: Simon Berrow

Ventry Harbour, 30/04/2009
Photo credit: Nick Massett

(5) GB01

GB01 Galway Bay, 29/06/2005
Photo credit: Joanne O'Brien

CB01 Clew Bay, 30/07/2007
Photo credit: Joanne O'Brien

(6) GB27

GB27 Galway Bay, 26/03/2007
Photo credit: Joanne O'Brien

DB39 Donegal Bay, 15/08/2008
Photo credit: Simon Berrow

(7) GB16

GB16 Galway Bay, 26/03/2007
Photo credit: Joanne O'Brien

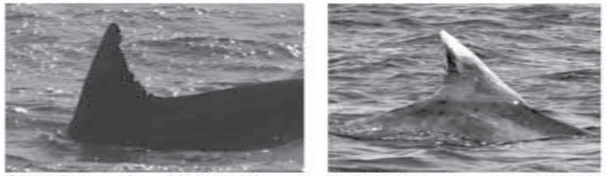
DB02 Donegal Bay, 08/08/2008
Photo credit: Simon Berrow

(8) GB18

GB18 Galway Bay, 23/03/2007
Photo credit: Joanne O'Brien

DB04 Donegal Bay, 23/07/2008
Photo credit: Simon Berrow

(9) GB22



GB22 Galway Bay, 26/03/2007
Photo credit: Joanne O'Brien

BNDIRL21 Portmagee, 02/07/2008
Photo credit: Phyllis Olsen

(10) GB23

GB23 Galway Bay, 23/03/2007
Photo credit: Joanne O'Brien

DB07 Donagal Bay, 15/08/2008
Photo credit: Simon Berrow

(11) GB07

GB07 Galway Bay, 26/03/2007
Photo credit: Joanne O'Brien

DB14 Donegal Bay, 08/08/2008
Photo credit: Simon Berrow

GB07 North Antrim coast, 19/05/2009
Photo credit: Garry Burrows

(12) GB25

GB25 Galway Bay, 26/03/2007
Photo credit: Joanne O'Brien

DB27 Donegal Bay, 08/08/2008
Photo credit: Simon Berrow

(13) GB08

GB08 Galway Bay, 12/04/2007
Photo credit: Joanne O'Brien

DB32 Donegal Bay, 15/08/2008
Photo credit: Simon Berrow

(14) CB40

CB40 Clew Bay, 11/06/2007
Photo credit: Joanne O'Brien

BNDIRL25 Portmagee, 02/07/2008
Photo credit: Phyllis Olsen

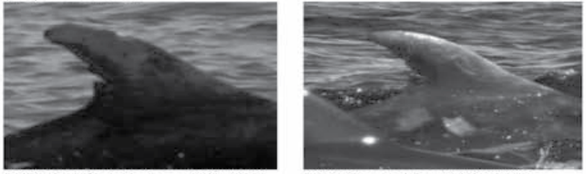
(15) BNDIRL17

BNDIRL17 Dublin Bay, 02/06/2008
Photo credit: Joanne O'Brien

GB46 Galway Bay, 31/08/2008
Photo credit: Joanne O'Brien

North Antrim coast, 19/05/2009
Photo credit: Garry Burrows

(16) BNDIRL11



BNDIRL11 Cork Harbour, 10/05/2008
Photo credit: Conor Ryan

DB26 Donegal Bay, 08/08/2008
Photo credit: Simon Berrow

(17) BNDIRL22

BNDIRL22 Antrim, 17/06/2007
Photo credit: Pauline Murray

BNDIRL22 Ventry Harbour, 30/04/2009
Photo credit: Nick Massett

(18) DB35

DB35 Donegal Bay, 15/08/2008
Photo credit: Simon Berrow

Ventry Harbour, 30/04/2009
Photo credit: Nick Massett

(19) DB09

DB09 Donegal Bay, 15/08/2008
Photo credit: Simon Berrow

North Antrim coast, 19/05/2009
Photo credit: Gary Burrows

(20) DB18

DB18 Donegal Bay, 08/08/2008
Photo credit: Simon Berrow

North Antrim coast, 19/05/2009
Photo credit: Gary Burrows

(21) BNDIRL10

BNDIRL10 Cork Harbour, 10/05/2008
Photo credit: Conor Ryan

DB31 Donegal Bay, 15/08/2008
Photo credit: Conor Ryan

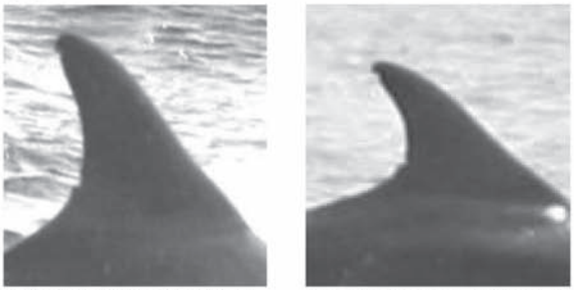
North Antrim coast, 19/05/2009
Photo credit: Gary Burrows

(22) GB11

GB11 Galway Bay, 26/03/2007
Photo credit: Joanne O'Brien

North Antrim coast, 19/05/2009
Photo credit: Gary Burrows

(23) GB47



GB47 Galway Bay, 31/08/2008
Photo credit: Joanne O'Brien

North Antrim coast, 19/05/2009
Photo credit: Gary Burrows