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Editorial

Welcome to this the first issue of the eighth volume of the *Journal of Cetacean Research and Management*. I would like to apologise that certain unforeseen logistical problems have delayed production of this issue. These have now been addressed and the year's remaining issues will be available as scheduled. This volume contains eleven papers covering a wide range of management issues.

One of the potential tools available for informed management is the use of protected areas or sanctuaries. Decisions on the value or otherwise of this approach must not only take in scientific information but also appropriate legal frameworks to address the variety of threats that can potentially or actually affect cetacean populations. The first paper in this volume reviews the International Whaling Commission's Southern Ocean Sanctuary, particularly in the context of recent developments in the field of marine protected areas.

Any conservation and management strategy requires certain basic information and one of the most fundamental parameters is population abundance. There are a number of papers dealing with this topic in this issue. The first, by Cañadas and Hammond uses the rapidly developing technique of model-based abundance estimates and in this case (bottlenose dolphins of southern Spain) has the great advantage of a long-term dataset. The results highlight the importance of long-term monitoring. The paper by Du Fresne et al. looks at the effect of line-transect placement in coastal surveys and in particular the choice of random or systematic designs. Dolar et al. present important new information on the distribution and abundance of cetaceans in the central Philippines, an area where previously there was little or no information. Similarly, Aliaga-Rossel et al. present new information on distribution and encounter rates of the poorly studied river dolphin (Inia geoffrensis) in the central Bolivian Amazon. The note by García-Godos presents the first information on sperm whales off Peru for many years. It is extremely valuable to receive information from these little studied areas to begin the process of assessing potential threats and developing appropriate conservation strategies and the *Journal* is pleased to publish such papers.

One of the most important threats to cetacean populations is their incidental capture in fisheries and the *Journal* has always highlighted the importance of addressing this issue in a rigorous scientific manner. In this issue, the paper by Lesage *et al.* examines bycatches of harbour porpoises in the gillnet fisheries of the St Lawrence River in Canada. The authors conclude these still give cause for concern.

Conservation and management also requires information on stock structure to enable proper interpretation of *inter alia* abundance data and removals. The paper by Robbins *et al.* clarifies the stock structure of the humpback whales taken in the small aboriginal subsistence fishery from the island of Bequia in St Vincent and The Grenadines. The paper by McDonald *et al.* discusses the potential of using song to identify the stock structure of blue whales.

Determining the present status of cetacean populations requires information on past removals and there is a fascinating paper by Reeves *et al.* on the history of Bermuda shore whaling which began in the early 1600s and continued into the 20th century. Determining the levels of these early catches requires a painstaking search of early literature and log books. A number of other pieces of information are necessary for modelling exercises examining the present status of cetacean populations and the paper by Koski *et al.* presents a new approach to minimising bias in the estimation of the length-frequency distribution of bowhead whales from the Bering-Chukchi-Beaufort Seas (animals which are subject to limited aboriginal subsistence whaling).

Finally, 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!

G.P. DONOVAN *Editor*

Review of the Southern Ocean Sanctuary: Marine Protected Areas in the context of the International Whaling Commission Sanctuary Programme

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ABSTRACT

This scientific review of the Southern Ocean Sanctuary (SOS) was commissioned by the IWC Scientific Committee and presented to the IWC Steering Committee on 27-28 June 2004. This review addresses a number of questions related to the effectiveness of the SOS and provides recommendations on how to incorporate Marine Protected Area (MPA) concepts into the SOS and the IWC Sanctuary programme. Overall, the SOS - and IWC Sanctuaries in general - are based on vague goals and objectives that are difficult to measure, lack a rigorous approach to their design and operation and do not have an effective monitoring framework for evaluation. In particular, the SOS represents a 'shotgun' approach to conservation, whereby a large area is protected with little apparent rationale for boundary selection and management prescriptions within the sanctuary. While a vast array of ecosystem-level and precautionary conservation benefits have been invoked for the establishment of the SOS, in reality this sanctuary does little more than provide a false sense of security by assuming that broad protections for whale populations are in place. The SOS was designed to restrict commercial harvests from the low latitude feeding grounds occupied by large whales during the austral summer. However, the SOS does not protect against or mitigate other threats to Southern Ocean whale stocks and the marine ecosystems upon which these populations depend, including pollution, habitat degradation and loss, introduced species and global climate change. We thus contend that sanctuary establishment and evaluation should be guided by a series of measurable and tangible goals, aimed at quantifying the status of both the 'protected' species under consideration and their role in the broader marine ecosystem. In particular, the SOS could be improved substantially to become an important part of IWC management and the larger conservation of Southern Ocean marine ecosystems, if the following steps were implemented: (a) development of formally stated goals (e.g. biodiversity protection, fisheries enhancement); (b) establishment of measurable objectives with which to assess progress towards attaining these goals; (c) creation of a formal management plan, including the establishment of a monitoring framework; and (d) development of more appropriate review criteria, reflecting the ecological objectives of the management plan.

KEYWORDS: SOUTHERN OCEAN; SANCTUARIES; CONSERVATION; MARINE PROTECTED AREA; MARINE RESERVE

INTRODUCTION

Article V of the International Convention on the Regulation of Whaling (the 'Convention' signed in 1946) permits the designation of sanctuaries (IWC, 2006a). In designating a sanctuary under the auspices of the Convention, the only regulatory measures that can be taken involve prohibiting the harvest of all whale species at any time from a specified geographic area, irrespective of their conservation status. A sanctuary in the South Pacific sector of the Southern Ocean was established in 1949. It was deregulated on the advice of the IWC Scientific Committee in 1955 in an attempt to relieve pressure on the other, overexploited areas of the Antarctic (IWC, 1955). Since then, two additional sanctuaries have been adopted: the Indian Ocean Sanctuary (IOS) in 1979 (renewed in 2002) and the Southern Ocean Sanctuary (SOS) in 1994 (Fig. 1). Additional sanctuary proposals in the South Atlantic and the South Pacific Oceans have been tabled at recent IWC annual meetings (IWC, 2004c, pp.372-4; IWC, 2001b, pp.65-7; IWC, 2001a, pp.17-9; IWC, 2000, pp.14-7; IWC, 2002, p.67).

In 2003, the IWC directed the Scientific Committee to undertake a decadal (1994-2004) review of the SOS (IWC, 2004b, pp.47-50). We were appointed by that body to review the effectiveness of the SOS in meeting its objectives and provide general advice on the value of MPA concepts to existing and proposed IWC Sanctuaries, including the establishment of sanctuary monitoring programmes. In particular, we were asked to evaluate the following:

- (1) whether the SOS contributes to the recovery of whale stocks;
- (2) how the SOS can advance the knowledge of whale stocks and their environment;
- (3) whether the SOS boundaries were appropriately established; and
- (4) how MPA concepts might be incorporated into the SOS and other IWC Sanctuaries.

ESTABLISHMENT AND HISTORY OF THE SOS

The original SOS proposal stated that the primary purpose of this sanctuary was to

'contribute to the rehabilitation of the Antarctic marine ecosystem by reinforcing and complementing other measures for the conservation of whales and the regulation of whaling, in particular by the protection of all Southern Hemisphere species and populations of baleen whales and the sperm whales on their feeding grounds' (IWC, 1993).

The SOS, however, was established after the 'moratorium' on global commercial whaling (Paragraph 10e of the Schedule, e.g. IWC, 2006a), which sets commercial whaling catch limits to zero for all species in all areas, irrespective of their conservation status. Thus, the moratorium, adopted in 1982 and implemented in 1985 and a *de facto* global sanctuary was in place before the establishment of the SOS.

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Fig. 1. Map of existing International Whaling Commission (IWC) Sanctuaries in the Indian (A) and Southern (B) Oceans. Proposals for the establishment of the South Pacific (C) and South Atlantic (D) Ocean Sanctuaries failed to gain the required three-quarters majorities at the 56th annual IWC meeting, held in Sorrento (Italy) from 19-22 July 2004.

Critics of the SOS, therefore, have alleged that its establishment reflected a desire to prevent commercial whaling for Antarctic minke whales being allowed if the Revised Management Procedure (RMP), a science-based harvest framework within the broader Revised Management Scheme (RMS) intended to replace the current moratorium. The RMP is a very conservative management approach that takes scientific uncertainty explicitly into account. It would allow limited sustainable whaling on populations meeting certain conditions. No catches would be allowed for any populations below 54% of their estimated unexploited level, with an ultimate general aim of stabilising these populations above the MSY level (e.g. Donovan, 2002; Hammond and Donovan, In press).

In response to a number of criticisms, IWC Resolution 1998-3 outlined a broader set of scientific objectives for the SOS (IWC, 1999):

- the recovery of whale stocks, including the undertaking of appropriate research upon and monitoring of depleted populations;
- (2) the continuation of the Comprehensive Assessment of the effects of setting zero catch limits on whale stocks; and
- (3) the undertaking of research on the effects of environmental change on whale stocks.

The SOS currently prevents commercial whaling being allowed on any nine migratory species/subspecies of large cetaceans in their summer feeding grounds: 'true' blue whale (*Balaenoptera musculus musculus*) and pygmy blue whale (*B.m. brevicauda*); fin whale (*B. physalus*); sei whale (*B. borealis*); Antarctic minke whale (*B. bonaerensis*); dwarf minke whale (*B. acutorostrata*); humpback whale (*Megaptera novaeangliae*); southern right whale (*Eualaena australis*) and sperm whale (*Physeter macrocephalus*). Had the RMP been implemented, catches would only have been allowed on one of these, the Antarctic minke whale. Whaling, however, is currently occurring in the SOS under special permit. Article VIII of the Convention permits any contracting government to authorise its nationals to kill, take, or treat whales for scientific research purposes (IWC, 2006a). Japan harvested up to 440 Antarctic minke whales annually from 1987/88-2004/05 under scientific permits within the SOS; it has since increased this under a new programme to up to 935 Antarctic minke whales and 10 fin whales with the possibility of increasing the number of fin whales to 50 and adding 50 humpback whales after 2006/2007 (IWC, 2006b, pp.48-9). The total abundance of Antarctic minke whales was estimated at 761,000 (95% CI=510,000-1,140,000) during the period 1982/83–1988/89, with more recent estimates under revision (e.g. see IWC, 1991).

REVIEW OF THE SOUTHERN OCEAN SANCTUARY

The SOS (and indeed IOS) lack formally stated goals (e.g. biodiversity protection, fisheries enhancement) and measurable objectives (e.g. recovery targets), without which it is impossible to assess the effectiveness of sanctuary establishment. Consequently, the SOS lacks a formal management plan that specifies objectives in a quantitative manner and provides clear strategies for achieving these goals (e.g. protection of feeding grounds, reducing noise pollution in critical areas, integration with the RMP). It should be noted that given the limitations of the IWC Convention to the regulation of whaling, achieving such goals would require cooperation with other bodies. Similarly, as will be discussed further below, it lacks an appropriate monitoring plan. These fundamental steps in the design and management of marine reserves will be required to incorporate MPA principles into the IWC Sanctuary programme.

The following sections of our review correspond to the questions posed to us by the IWC Scientific Committee.

Contributions of the SOS to the recovery of whale stocks

Given that the moratorium on commercial whaling was instituted prior to the establishment of the SOS, the direct contribution of this sanctuary to the recovery of whale stocks cannot easily be determined given the lack of empirical evidence. In the absence of a formal definition of 'recovery' we have chosen to base it on the concept behind the RMP¹ and consider it as achieving a population approximately 72% of its unexploited level. While it is true that whales are protected from commercial whaling within the SOS, this protection is effectively redundant as long as the moratorium remains in place. If commercial whaling were to resume under the RMP (which only applies to baleen whales and only allows catches from stocks above 54% of their unexploited size), the SOS would prevent commercial catches of stocks for which the RMP would allow catches within its boundaries - at present this would probably only apply to some stocks of Antarctic minke whales - the RMP would probably indicate catch limits of zero for the other stocks of baleen whales for the near-mid future. However, as all baleen whales species and their constituent populations migrate outside of the SOS, it can be said that this sanctuary does not fully protect Southern Ocean large whale species (Davies and Gales, 2004) since catches can be taken outside the SOS boundaries. Only in the Indian Ocean, where the IOS and SOS are adjacent, would the existing IWC sanctuaries protect certain baleen whale stocks during their entire latitudinal seasonal movements. In effect, the value of the SOS and IOS in terms of providing complete protection from whaling (including preventing commercial whaling on stocks for which the RMP would allow catches), will ultimately depend on the discrete nature of Indian Ocean whale stocks. In other words, due to its limited extent, the current configuration of the SOS will probably fail to fully protect large whale populations, in the absence of a well-managed fishery management programme (i.e. RMP). More study is required, however, to evaluate this statement for specific stocks and species, within a broader ecological context of predator-prey dynamics and climatic variability (Hewitt et al., 2002; Mackinson et al., 2003). In particular, the uncertain structure of Southern Ocean whale stocks is a critical consideration for the design of IWC sanctuaries (Davies and Gales, 2004; Hucke-Gaete et al., 2004; Stafford et al., 2004).

Currently, the degree of protection afforded by the SOS to different whale stocks/populations as a refuge from future commercial harvesting is dictated by their natural history (e.g. extent of seasonal migrations, location of summer-time foraging grounds) rather than by their status (e.g. whether they actually require this protection or not). Some additional level of protection in important (e.g. 'critical' or 'vulnerable') areas at key times would benefit whales within the SOS. Examples of this enhanced protection include prohibitions on activities that impact whales (e.g. vessel strikes), their prey (e.g. commercial fisheries), or their habitats (e.g. pollution). In addition, because certain areas currently within the SOS may not contribute to the IWC mandate and objectives (e.g. not used by large cetaceans for any aspect of their life history), they could be removed from the Sanctuary in exchange for more stringent and appropriate prohibitions in more important habitats located within the SOS (e.g. foraging grounds) or elsewhere (e.g. breeding grounds). Most research into habitat-based harvest management and MPAs suggests that integrated management approaches, capable of merging fishery closures with additional regulations and protections, are most effective at meeting Sanctuary goals and conservation objectives, especially for far-ranging species (Boersma and Parrish, 1999; Gilman, 2001).

Contributions of the SOS to the knowledge of whale stocks and their environment

One of the primary anticipated benefits of establishment of the SOS was to create an area where whales would be studied in the absence of commercial harvest. Similarly, many MPAs and sanctuaries are designed to provide baselines to gauge ecological change in areas beyond their boundaries (e.g. Murray *et al.*, 1999; Ainley, 2003). However, because the SOS was established after the moratorium, it could not provide supplemental ecological information for comparing harvested and non-harvested whale populations. Thus, a major potential scientific benefit of sanctuary establishment did not materialise.

The SOS has been credited with fostering a number of ongoing cooperative and integrative research programmes in the Southern Ocean, including multi-national photoidentification studies, international ecosystem research cruises and coordinated surveys of whale distributions and oceanographic conditions. Compared to most other MPAs, however, the number of investigations carried out as a result of the SOS has been limited and is difficult to evaluate. Sanctuary designation has not appeared to result in a significant increase in the number or size of non-lethal research programmes, compared with non-sanctuary areas. Nevertheless, we identified some ongoing research efforts within the SOS, including cooperative studies involving non-governmental organisations and university researchers (e.g. Stevick et al., 2004), collaborative cruises between CCAMLR and Southern Ocean GLOBEC (Hofmann et al., 2002; Thiele et al., 2004), the IWC-SOWER programme in the western Antarctic Peninsula (2001-2004) (Ensor et al., 2004) and studies between the IWC and CCAMLR (1999-2004) (Gillespie, 1997; Leaper and Scheidat, 1998; Leaper and Papastavrou, 1999; Thiele et al., 2004).

Additionally, large-scale monitoring programmes of other upper-trophic consumers (e.g. pinnipeds and seabirds) and their prey (e.g. Antarctic krill, Euphausia superba) are underway, under the auspices of CCAMLR and national research programmes throughout the Southern Ocean (Boyd and Murray, 2001; Croxall et al., 1999; Hewitt et al., 2002; Inchausti et al., 2003; Woehler, 1997). What regional cooperation that does exist appears to be directed at the continuation of the SOS and the establishment of additional sanctuaries. The presumed but unstated rationale behind these efforts appears to be to achieve the precautionary exclusion of whaling from ecologically important areas, in advance of the potential resumption of harvesting under the RMP. While a laudable social goal for some cultures, these are not scientific aims and therefore cannot be regarded as regional cooperation in the context of this review.

In contrast, the IOS does appear to have fostered some cooperative efforts among regional nations and government and non-government organisations (De Boer *et al.*, 2003), although progress towards this has been relatively slow (e.g. see Leatherwood and Donovan, 1991). This may be a function of the number of countries adjacent to the IOS, the encouragement and publicity the establishment of a

¹ Given the variety of scenarios tested under the RMP, there is no formal goal -72% represents the 'tuning' level chosen to compare candidate procedures performance after 100 years for a specific trial (Hammond and Donovan, In press)

sanctuary gave to local researchers, and to some extent opportunity the sanctuary afforded the research community to compare protected whale populations in the Indian Ocean with areas in which whaling continued, at least prior to the establishment of the moratorium. While similar collaborative efforts are underway for the SOS (e.g. Van Waerebeek *et al.*, 2004), it is difficult to evaluate to what extent the creation of this sanctuary motivated and facilitated these synthetic studies.

While designation of IWC Sanctuaries (such as the SOS) is not required to initiate discussions between various jurisdictions and stakeholders, such sanctuaries should provide a focal point for discussions, just as the Particularly Sensitive Sea Area programme has done (Gjerde, 2001). MPA designations in other parts of the world have resulted in significant increases in the amount of research conducted in their waters (e.g. Murray *et al.*, 1999; Halpern, 2003). This may be a temporary benefit; however, as the current interest in MPAs may wane and a lack of future funding may pose additional limitations.

A stated objective of the SOS is to compare stocks within and outside of the boundaries of the protected area. However, because the SOS encompasses the entire Southern Ocean south of 60°S and much of it south of 40°S (see Fig. 1), i.e. much of the feeding grounds of baleen whales, whale stocks within the Sanctuary must be compared to stocks in warm temperate oceans north of 40°S, where threats to whales may be entirely different or of an unequal magnitude. In addition to this logistical difficulty, this approach is fraught with a deeper conceptual limitation. This 'use' of the SOS assumes that comparisons between harvested and non-harvested populations are inherently valid. There are a number of difficulties with this assumption that inhibit comparisons across ocean basins, including:

- (a) potential large-scale differences in the effects and impacts of climatic variability (e.g. magnitude and time lags between local changes in ocean productivity and the Southern Oscillation Index);
- (b) changes to the rest of the food chain via anthropogenic activities (e.g. loss of the prey base due to competition with fisheries and global climate change); and
- (c) additional human impacts, including incidental mortality (e.g. bycatch and ship strikes), habitat degradation and loss (e.g. plastic and acoustic pollution) and introduced species are not uniformly distributed throughout the global ocean.

In particular, the connectivity with the IOS may compromise any comparisons between the Indian Ocean sector of the SOS and other ocean basins where whaling might be permitted. Furthermore, because the SOS encompasses most areas south of 40°S, potential comparisons would likely have to be restricted to those stocks that either do (e.g. harvested outside of SOS) or do not (i.e. protected from harvest throughout life cycle) migrate outside of the Sanctuary waters. Other practical difficulties in making comparisons and detecting changes have been discussed by Butterworth and Punt (1994) and Butterworth and De Oliveira (1994). Additionally, the whaling versus nonwhaling comparison does not consider the potential confounding effects of illegal harvesting, regional disparities in the competition of whale stocks with other upper-trophic predators consuming the same marine resources (e.g. penguins, pinnipeds, petrels) and the inability to detect a recovery in depleted whale populations depressed from past commercial whaling. These two artefacts may yield statistically insignificant comparisons within and between established sanctuaries. While illegal whaling, like other illegal – unreported – unregulated (IUU) fishing activities, is difficult to quantify, there is abundant evidence of the dietary overlap and the fluctuations of many Southern Ocean predator populations (Croxall, 1992; Croxall *et al.*, 1999; Woehler, 1997). Therefore, any geographic comparison across ocean basins should incorporate an understanding of potential spatial/temporal overlap and competition with fisheries and other uppertrophic consumers of whale prey.

Ecological appropriateness of the SOS boundaries

Evaluating the ecological appropriateness of the SOS boundaries is difficult in the absence of a set of formally stated goals and objectives that specifically outline the purpose of the Sanctuary. While there is some broad ecological, biogeographic and oceanographic rationale for the current boundary, the extent of the SOS does not generally conform to the established principles of reserve design (Fig. 2). These include delineating boundaries based on biological, oceanographic and physiographic criteria such as the distributions of water masses, ocean productivity domains, marine communities and 'protected' species (Hooker *et al.*, 1999; Probert, 1999; Hyrenbach *et al.*, 2000; Zacharias and Roff, 2000).

It seems clear that the SOS would benefit by drawing on lessons learned from previous case studies of reserves for wide-ranging species (summarised in Hooker and Gerber, 2004) and from other initiatives directed at identifying important migration routes and foraging grounds of other upper-trophic marine predators (e.g. seabirds, pinnipeds) throughout the Southern Ocean (e.g. Croxall and Wood, 2002; Nel and Taylor, 2003). Gerber *et al.* (2005) modelled changes in population growth rates (λ) as a result of hypothetical changes in the rate of dispersal from sanctuary to non-sanctuary areas. In the future, researchers may wish to contrast the implications of specific sanctuary boundary designs by using an expanded version of this generalised demographic model, capable of incorporating speciesspecific movement data.

The SOS boundary appears to have been delineated primarily through a socio-political compromise (notably with respect to EEZs between 40° S and 60° S), with some consideration given to the multiple species it is designed to protect. Given its stated multi-species objectives, the delineation of the sanctuary boundaries will have to reconcile many compromises.

From an ecological perspective, the following aspects of the SOS boundary are probably appropriately established:

- (a) the boundary meets with that of the IOS to preserve a contiguous marine area, thus ensuring connectivity between the IOS and SOS (Fig. 1);
- (b) the 40°S latitude boundary is roughly consistent with a zone of transition between warm-water and cold-water temperate biogeographic domains associated with the location of the Subtropical Convergence, a broad (~100km) frontal region where subtropical and sub-Antarctic waters converge as a result of the prevalent large-scale wind patterns (Sverdrup *et al.*, 1942; Rio and Hernandez, 2003) however, the frontal boundaries between these distinct water masses vary both spatially and temporally (Belkin and Gordon, 1996; Kostianoy *et al.*, 2004; Fig. 3); and
- (c) it meets a general criteria that a single, large reserve is more beneficial than several small reserves (the SLOSS

– Single Large Or Several Small debate) – although this does not particularly reflect the ecological choice of boundaries, merely that the area it covers is very large.

From an ecological perspective, the following aspects of the SOS boundary are probably not appropriately established:

- (a) although the SOS encompasses a variety of large-scale oceanographic habitats, spanning from the Subtropical Convergence (~35-45°S) south to the permanent ice sheet (~65-75°S), several biogeographic domains and water masses are not represented within this sanctuary (Longhurst, 1998), thus providing a poor degree of representativity;
- (b) the boundary does not contour to any particular oceanographic (e.g. water temperature) or physiographic (e.g. depth) characteristic(s) other than latitude and distance from territorial waters;
- (c) there is no ecological basis for the manner in which the existing boundary excludes waters around landmasses – if the SOS must avoid large landmasses then its boundary could at least be delineated on the basis of biological (e.g. neritic vs. pelagic zooplankton communities), oceanographic (e.g. pycnocline depth), or physiographic (e.g. location of the 200m continental shelf break) which show some relationship to marine community types and ocean productivity patterns;
- (d) good conservation reserve design favours 'smooth' reserve boundaries; square corners such as those around territorial waters should be avoided to minimise the impacts of detrimental edge effects;
- (e) the boundary is static in space and time and does not reflect seasonal changes in the spatial configuration of current systems, ocean productivity patterns and marine communities (Figs 2 and 3); and
- (f) while the SOS is large, several migratory species cross the boundary on their migration routes.

In conclusion, while the SOS boundary appears to have been based primarily on socio-political considerations, certain aspects of the SOS are ecologically justified. Overall, however, boundary adjustments to better reflect ecological processes and structures in the Southern Ocean would prove more effective in achieving the objectives of the Sanctuary. For instance, the now widespread use of GPS navigation equipment facilitates the design (and enforcement) of more complex boundaries, which could follow specific physiographic features and even be dynamic in nature to accommodate spatial and temporal variability in the underlying oceanography (Hyrenbach et al., 2000). This approach would allow reserves to encompass dynamic habitats by shifting location, thus avoiding a major detrimental by-product of MPA designation. Sitting reserves in 'poor' habitats (i.e. sinks) may have the effect of increasing fishing pressure in the 'good' habitats (i.e. sources), resulting in a downward spiral of the whole network as sinks rely on source areas for propagules. In the case of Southern Ocean whales, differences in diet (krillfeeding mysticetes, squid-eating odontocetes), foraging habitats (ice leads, pack ice, open water) and biogeographic affinities (water masses, degree of association with sea ice) will likely influence community structure over time and space and therefore boundary location (Ainley et al., 1986; Stahl et al., 1985; Tynan, 1998). In addition to changing the extent and location of the SOS, the inherent nature of the



Fig. 2. Map of the Southern Ocean, showing the extent of the SOS (dashed line) and a conceptual representation of the major oceanographic fluxes influencing the distributions of water masses and prey community structure along sanctuary boundaries. The arrows show the generalised flow of the major currents in this region: the Antarctic Circumpolar Current (ACC) flowing eastwards around Antarctica; the northward-flowing eastern boundary currents in the Atlantic (Benguela Current, BC), Pacific (Humboldt Current, HC) and Indian (Leeuwin Currents in the Atlantic (Brazil Current, BC), Pacific (East Australia Current, EC) and Indian (Agulhas Current, AG) Oceans.

sanctuary boundaries (static vs. dynamic, core area surrounded by buffers) may change if MPA design concepts are incorporated into the IWC Sanctuary programme.

INCORPORATION OF MPA CONCEPTS INTO IWC SANCTUARIES

Applications of MPAs to marine mammals

Marine reserves are a relatively new approach to marine conservation, with the vast majority of the relevant theory published since 1992 (see Gerber et al., 2003 for a review). MPAs (IWC Sanctuaries are a type of MPA that prohibits commercial exploitation of a particular taxon) can be effective tools for the conservation and management of marine resources (Duggan and Davis, 1993; Gell and Roberts, 2003; Halpern, 2003; Hooker and Gerber, 2004; Roberts and Hawkins, 2000). To date, marine reserve models have largely focused on questions concerning fishery management, with most studies concluding that reserves increase yield when populations would otherwise be overfished. However, few of these existing single-species models have considered all life stages, thereby failing to acknowledge that most marine organisms are wide-ranging and have life history stages that occur in very different habitats.

Currently, marine sanctuaries are being established worldwide on the basis of their marine mammal or bird fauna (for examples see Hooker and Gerber, 2004). However, designation of MPAs for slow growing, long-lived species such as marine mammals and seabirds has largely taken place without ecological input. There is little systematic theory for how to select, design and monitor reserves implemented to protect marine mammals. In



Climatology of temperature fronts

Fig. 3. Seasonal variability in the location of major oceanographic fronts throughout the Southern Ocean, as revealed by the average sea surface temperature (SST) conditions during (A) summer and (B) winter since the SOS was established (1994-2004). These monthly Reynolds Optimally Interpolated Sea Surface Temperature data, with a spatial resolution of 1°×1°, are publicly available at the Jet Propulsion Laboratory's Physical Oceanography Distributed Active Arctive Center (PODAAC) server (*http://podaac.jpl.nasa.gov/*). Four frontal systems, mapped using the location of a specific surface isotherm, are plotted from south to north: the polar front (4°C), the sub-Antarctic front (10°C), the southern subtropical front (17°C). The extent of the Subtropical Convergence (dashed lines), separating sub-Antarctic waters to the south from sub-tropical waters to the north, is generally delineated by the location of the 13°C and 17°C surface isotherms (Belkin and Gordon, 1996; Kostianoy *et al.*, 2004).

protecting a specific population, the optimal protected area would encompass that population's year-round distribution, which is often very large. However, most migratory species have certain critical periods and/or areas in their life cycles in which they congregate for a number of reasons (e.g. staging, foraging, breeding) and are vulnerable to human activities such as capture or pollution (Roberts and Hawkins, 2000). In addition, oceanic and coastal physiography often concentrates migratory species into 'bottlenecks' (e.g. passages, lagoons) where they become more vulnerable to harvest. Since several of the threats faced by marine mammals are either incremental (e.g. pollutant exposure) or instantaneous (e.g. acoustic pollution, fishery bycatch), well-sited MPAs may protect whale populations from specific threats within areas of aggregation during critical times.

Developing a robust MPA design for wide ranging species is challenging. Comparisons of stocks/species with different life-history characteristics (e.g. diets, habitats, migrations) within sanctuary waters may be as ecologically insightful as regional comparisons of the trends and status of the same species in different geographic areas. In addition to these comparisons across whale stocks and species, broad sanctuary management plans may take advantage of ancillary data from other ecosystem constituents, including upper-trophic consumers (e.g. seabirds, pinnipeds) and lower-level prey species (e.g. Antarctic krill, Euphasia superba) (Agnew, 1997; Croxall, 1992). Two types of upper-trophic predator data might be especially valuable to quantify fluctuations in the food-web structure supporting Southern Ocean whale populations: (a) measures of predator dispersion and overall abundance at-sea (e.g. Hunt et al., 1992; Woehler, 1997); and (b) colony-based information on predator diet composition, foraging effort and reproductive success (e.g. Boyd and Murray, 2001; Croxall et al., 1999). In addition to an understanding of the life-history (e.g. recruitment) and the dispersion (e.g. patchiness) of the prey itself, information on other krill consumers will be essential to interpret the geographic comparisons of whale stocks (e.g. Hewitt et al., 2002; Miller and Hampton, 1989). Furthermore, an enhanced understanding of prey availability and consumption will serve as the foundation for the establishment of a precautionary ecosystem-level management plan to protect Southern Ocean upper-trophic predators (whales, seabirds, pinnipeds) from competition with fisheries (Boyd, 2002; Hewitt et al., 2002). Similar considerations have been used to gauge the trophic implications of MPAs and ecosystem-level management plans in other oceanic regions (e.g. Hunt et al., 2000; Hooker et al., 2002).

MPA goals

Fundamentally, MPAs can be considered to have two primary goals; the first is to preserve biodiversity and the second is to produce the highest fishery yields (Hastings and Botsford, 2003). While it may be possible to configure a single MPA to reconcile both of these goals, there has been little work on identifying how specific design concepts can advance these biodiversity and fishery reserves. Generally, MPAs designed to conserve biodiversity favour larger areas that encompass the dispersal distance for recruits. Conversely, protected areas designed to enhance production for sessile species tend to be small, to maximise larval export (Hastings and Botsford, 2003), but may have to be large when dealing with highly mobile pelagic taxa (Parrish, 1999).

A broader suite of goals has been proposed for MPAs, which generally include:

- (a) scientific research;
- (b) wilderness protection;
- (c) preservation of species and genetic diversity;
- (d) maintenance of environmental services;
- (e) protection of specific natural and cultural features;
- (f) tourism and recreation;
- (g) education;
- (h) sustainable use of natural resources;
- (i) restoration or rehabilitation of communities and ecosystems; and
- (j) maintenance of cultural and traditional attributes (after Airame *et al.*, 2003; Kelleher, 1999; Murray *et al.*, 1999).

Many MPA efforts utilise a variety of objectives to further articulate the goals listed above. Objectives in support of the goals outlined above, include the conservation and protection of the following:

- (a) commercial and non-commercial fisheries resources, including marine mammals and their habitats;
- (b) endangered or threatened marine species and their habitats;
- (c) unique habitats and endemic taxa; and
- (d) areas of high biodiversity or biological productivity.

Additionally, MPA objectives focused on biological attributes are often restated in terms of their degree of biogeographic representation. In terms of whale conservation and management these include:

- (a) the protection of larger mobile, entirely marine and generally seasonally migrant species;
- (b) the protection of mobile marine species referenced to the land environment (e.g. nesting sea birds, pinnipeds);
- (c) the conservation of rare/endangered or isolated populations and communities of benthic species, including areas of high local biodiversity for specific taxa;
- (d) the preservation of specific habitats and their associated communities of the wider marine environment (also known as representative habitats);
- (e) the sustainable management of natural marine resources such as fisheries (and fishing/spawning areas) that may not be captured under (a) above; and
- (f) areas of high productivity/predictable upwelling/ retention (after Murray *et al.*, 1999; Palumbi, 2001; Roff *et al.*, 2003).

Selection and boundary delineation of MPAs

At the highest level, MPAs can be selected on the basis of biological, oceanographic, physiographic, socio-cultural, political and economic criteria. The goals of the SOS, as currently stated, appear to balance a number of ecological criteria – management of harvested species and ecosystem-level conservation – as well as other socio-political considerations (IWC, 1993). Reserves designed to either preserve biodiversity or enhance fisheries, however, are generally based on biological criteria (e.g. aggregations of fecund individuals, larval nurseries; Botsford *et al.*, 2003). When biological information are not available, oceanographic and physiographic proxies (frequently termed 'habitat' variables) are often used when the associations between these proxies and a population,

species, or community is known. Species or communities may, for example, be linked to specific habitat structures (e.g. depth + substrate + temperature) or processes (e.g. upwelling + disturbance regimes + seasonal salinity/ temperature variability). Several families of multivariate statistical methods are used for this purpose, though not all have yet been applied to marine environments (Carpenter and Gillison, 1993; Guisan and Zimmermann, 2000; Elith and Burgman, 2003).

Biological, oceanographic and physiographic variables can be used to identify a number of criteria for MPA delineation:

- (a) representation;
- (b) distinctiveness;
- (c) sensitivity;
- (d) vulnerability;
- (e) critical areas and life stages;
- (f) hotspots of diversity (taxonomic or genetic);
- (g) rare and endemic species;
- (h) areas subject to frequent or natural disturbance;
- (i) species of special concern and critical life history stages;
- (j) exploitable species;
- (k) ecosystem functioning and linkages;
- (l) ecosystem services;
- (m) human threats and natural catastrophes; and
- (n) size, shape and connectivity.

In particular, the number, location and design (size and shape) of MPAs are critical considerations (Boersma and Parrish, 1999; Guenette et al., 2000; Halpern, 2003; Kooyman et al., 1992). These considerations will determine the magnitude of potential detrimental effects from MPA implementation, including: (i) the concentration of fishing effort outside of the MPA boundaries (Walters and Bonfil, 1999); (ii) the unpredictability of MPA effectiveness in the face of oceanographic variability across space (advection) and time (climate change); (iii) the inherent time lags required for the effect(s) of MPAs on stocks/populations to become apparent; and (iv) and the impact of overall higher total bycatch of highly migratory species derived from the displacement of fishing effort to less productive areas, where lower catch rates (CPUE) require higher effort to attain constant catches.

There are a number of techniques used to identify and delineate boundaries for conservation purposes. Fundamentally these techniques can be separated into those that seek to protect the maximum (or some target) number of elements of value (as defined by the user) and those that rely on some ecological theory or concept to identify optimal areas. Most of these techniques attempt to identify and maximise values by protecting the smallest possible area.

Well-known examples of the former include Geographic Information System analyses of biogeographic representation, which attempt to identify representative (recurring at a given scale) and distinctive (unique at a given scale) areas (Roff and Taylor, 2000; Zacharias et al., 1998). Given our incomplete understanding of marine communities, many of these analyses are based on identifying representative and distinctive areas defined exclusively by habitat characteristics (oceanographic and physiographic), driven by a limited understanding of the underlying ecological mechanisms. The underlying assumption being that habitat structure can be used to predict species and community composition. A practical application is given in Cañadas et al., (2005).

In addition, considerable effort has been directed at developing stand-alone software that identifies potential conservation areas on the basis of biodiversity targets set by the user (McDonnell *et al.*, 2002). While several iterations of these algorithms exist (e.g. SPEXAN, Sites), the most recent version (MARXAN) has been developed for the Great Barrier Reef Marine Planning Authority (Leslie *et al.*, 2003). MARXAN is used throughout the world for identifying optimal MPA boundaries and is now considered a robust tool for reserve design. However, given the large size of the SOS and the paucity of biological data for the Southern Ocean, MARXAN may not be an appropriate tool to evaluate this and other large-scale whale sanctuaries.

There are a number of examples of reserve design based on ecological theory or concepts. Species-area relationships have been used to encompass the maximum diversity within the smallest possible area, by identifying the asymptote of the species-area curve (Arrhenius, 1921; Neigel, 2003). While the species-area approach has been widely criticised, this technique continues to be widely applied due to the lack of viable conceptual alternatives.

Focal species are a conceptual construct in conservation that may be useful for marine reserve design. Focal species are those which, for ecological or social reasons, are believed to be valuable for the understanding, management and conservation of natural environments. There are four distinct categories of focal species: indicators, keystones, umbrellas and flagships (Simberloff, 1998; Zacharias and Roff, 2001a). Each type of focal species has been operationally defined by Zacharias and Roff (2001a) in terms of their relevance to marine conservation efforts. To summarise, the keystone and umbrella concepts are probably not applicable in most marine environments and the flagship concept is a tool to garner support for conservation efforts but provides little tangible guidance for MPA design. Indicator species, though, may be valuable as they indicate community types that can be related to specific habitat types, which in turn can be mapped and protected. The ability to identify biologically and physically distinct habitat types is a fundamental prerequisite for conservation initiatives based on representation (Roff and Taylor, 2000).

Models initially developed for fisheries management have also been applied to the selection of MPAs. Perhaps the most well-known are ECOPATH and ECOSPACE, which allow the simulation of different types of anthropogenic impacts on spatially-structured populations and can simulate migratory interchange between different patches or habitat types (Christensen and Pauly, 1992; Mackinson *et al.*, 2003; Walters *et al.*, 1997). These whole-ecosystem models, however, require the input of broad, sweeping simplifications and assumptions (e.g. see IWC, 2004a) and thus may not be appropriate given our current level of knowledge of the ecological function of the Southern Ocean.

Zoning within MPAs

Within a no-take zone, additional protection should be based on the vulnerability of the features of interest (e.g. populations, habitats) to various threats. Vulnerability is defined as the probability that a feature will be exposed to a stress to which it is sensitive. In other words, vulnerability is the likelihood of exposure to a relevant external stress factor (sensu Tyler-Walters and Jackson, 1999), combined in some way with the relative exposure (duration, magnitude, rate of change) to that stress. One method that is becoming more widely applied is using the concept of identifying Vulnerable Marine Areas (VMAs) (Zacharias and Gregr, 2005). This methodology, based on the Environmental Sensitivity Index approach used for oil spill response and countermeasures (Gundlach and Hayes, 1978) identifies Valued Ecological Features (VEFs), which are defined as biological or physical features, processes, or structures deemed to have environmental, social, cultural, or economic significance. Once VEFs are identified, they are mapped and their sensitivities and vulnerabilities are determined and finally VMAs are predicted using ecological classifications (Tyler-Walters and Jackson, 1999; Zacharias and Gregr, 2005).

Designing networks or hierarchies of MPAs

This is an area of MPA research that is currently lacking a strong empirical basis. Most studies to date have been able to identify 'sets' of protected areas based on the principles of biogeographic representation, combined with the addition of 'distinctive' or unique oceanic (e.g. persistent fronts) and physiographic (e.g. seamounts) features. Many of the tools discussed previously (e.g. MARXAN) are able to identify sets of MPAs, which simultaneously maximise a number of criteria (e.g. representation, distance from human activities). Many advocate the establishment of 'networks' of MPAs, where discrete protected areas are connected through migration and larval transport. However, the function of networks is not yet clearly understood (Roff *et al.*, 2003).

Other issues that arise in MPA network discussions include the number and size of the sites required within a particular region to accommodate habitat variability over time, particularly in dynamic pelagic environments.

Steps to developing an MPA network include:

- (a) classify the study area into representative and distinctive areas using biogeographic analysis methods based on biological, oceanographic and physiographic information;
- (b) verify species/community relationships within these areas and predict species/community occurrence where biological inventories are unavailable;
- (c) determine patterns of movement and the exchange of individuals between areas;
- (d) develop inventories of conservation and management measures to determine what existing areas already contribute to the network;
- (e) apply algorithms (e.g. MARXAN, S-A curves) to select the smallest areas that maximise the MPA objectives; and
- (f) remove sites deemed non-viable for ecological, political, social, or economic reasons (e.g. proximity to human activities, site already disturbed), from the above analysis.

RECOMMENDATIONS

Marine habitat-based conservation (such as the SOS and other MPAs) has advanced considerably since 1994. However, there is no reason why the SOS cannot be revisited, in light of advances in marine conservation reserve science. Many of the problems highlighted in the previous sections of this review have been addressed in other MPAs and, with some additional research, should be resolvable for the SOS. The following are our recommendations for the establishment and operation of the SOS or other IWC Sanctuaries;

 articulate their purpose through a set of broad overarching goals (e.g. preserve biodiversity, increase fishery yields) – in particular, clearly state the relationship between the RMP and the IWC Sanctuary programme and how sanctuaries are expected to contribute to the management of cetacean stocks and species.

- (2) develop measurable objectives (e.g. increase stock x to size n by time t, decrease the probability of extinction of stock x by y, protect feeding areas for population x) that link the broader goals (discussed above) with field monitoring programmes such as the IWC IDCR/SOWER cruises (e.g. Matsuoka *et al.*, 2003) this clarification will help identify and protect those habitats 'critical' to achieve these management objectives;
- (3) establish systematic inventory and research programmes to build the required information foundation for a sanctuary management plan and subsequent monitoring programmes that *inter alia* support the following efforts:
 - (a) a biogeographic analysis of habitats and communities using the concepts of representativity and distinctiveness at the genetic, stock, species, community and ecosystem levels (Roff and Taylor, 2000; Roff *et al.*, 2003; Zacharias and Roff, 2001b);
 - (b) the identification and mapping of threats to whale populations within and outside of the SOS and the oceanographic/climatic linkages supporting ocean productivity and prey availability across sanctuary boundaries (Fig. 1; Miller and Hampton, 1989; Nel and Taylor, 2003);
 - (c) identification of vulnerable areas and critical habitats at different ecological scales (e.g. individual foragers and population distributions) (Block *et al.*, 2002; Croxall and Wood, 2002; Zacharias and Gregr, 2005), as well as their spatial and temporal variability (Belkin and Gordon, 1996; Hewitt *et al.*, 2002; Kostianoy *et al.*, 2004);
 - (d) investigation of pathways of whale stock structure and connectivity (e.g. gene flow and animal movement) (Dizon *et al.*, 1992; Torres *et al.*, 2003);
 - (e) development of measures of biotic integrity (e.g. standing stocks, productivity) and environmental variability (e.g. oceanography, disturbance regimes), along with appropriate physical and biological indicators of temporal variability at short (inter-annual) and long (climate change) temporal scales (Croxall, 1992; Croxall *et al.*, 1999; Inchausti *et al.*, 2003);
- (4) development of a Sanctuary management plan that clearly outlines the broad strategies and specific actions needed to achieve sanctuary objectives (e.g. how to protect a given feeding area for stock *x*) and the non-IWC mechanisms required to achieve these objectives – key aspects of a sanctuary management plan should include:
 - (a) coordination with the objectives of other conservation and management initiatives (e.g. CCAMLR; Agnew, 1997);
 - (b) integration of fisheries and coastal zone management concepts within sanctuary management objectives (Boyd, 2002; Hewitt *et al.*, 2002);
 - (c) adherence to the tenets of adaptive management and the precautionary principle (Hewitt *et al.*, 2002);

- (5) development and initiation of a monitoring strategy that measures progress towards achieving the sanctuary objectives (an essential component of this monitoring strategy is the development of practical (tested by e.g. power analyses to be achievable) indicators to monitor progress);
- (6) establishment of review criteria that reflect the goals and objectives of the sanctuary, as described above; and
- (7) refinement of the sanctuary management plan at periodic intervals to account for ecological, social and oceanographic changes in an adaptive fashion.

CONCLUSIONS

Even ignoring the fact that the SOS was established during the moratorium, it was based on vague goals and objectives that are difficult to measure, lacks a rigorous approach to its design and operation and does not have an effective monitoring framework to determine whether its objectives are being met. The SOS in particular - and IWC Sanctuaries in general - appear to have been established as a sociopolitical compromise between an area-based fisheries closure and a conservation reserve. Unfortunately, the SOS is neither an effective harvest closure, nor does it meet the generally accepted criteria for conservation reserve design and operation (Botsford et al., 2003). The SOS attempts to fulfil a number of vague objectives (e.g. 'ecosystem rehabilitation', 'critical habitat' protection) without addressing the systematic application of quantitative criteria to attain tangible goals. Any 'scientific' objectives appear to have been added to lend credibility to the SOS after the sanctuary was established. Furthermore, the intent to incorporate MPA concepts into IWC Sanctuaries appears to be in response to the criticisms faced by this programme in the past.

The SOS can be said to represent a 'shotgun' approach to conservation, where a large area is protected with little apparent rationale for boundary selection and management prescriptions. Of even greater concern is the realisation that the Sanctuary was established without a proper understanding, discussion, or prediction of what contributions it is expected to make towards biodiversity protection and fisheries management in the Southern Ocean. Another critical issue is the lack of a general temporal framework for evaluation of the objectives discussed above. Even a broad conservation objective, such as improving the protection of Southern Ocean whale stocks, should include a quantifiable metric to gauge success and a time frame for this objective to be met (e.g. reduce the probability of extinction of species s in the next y years to less than x, determine population numbers with a confidence of n). These criteria are essential to provide the necessary ecological background for the development and testing of population models, to guide the collection of the necessary empirical data to support these modelling efforts and to determine the management approaches and the levels of protection required to meet these conservation goals (Doak and Mills, 1994; Fujiwara and Caswell, 2001; Gerber et al., 2005; Mangel and Tier, 1994). Once these criteria and objectives have been set, they will help define the required temporal and spatial extent of the proposed sanctuary and the baseline information necessary to gauge the current status of the various ecosystem constituents (Dayton et al., 1998; Jackson et al., 2001; Woehler, 1997).

The existence of the moratorium and whaling under special permit has not permitted the SOS to fulfil its role of protecting whales and fostering comparative research of harvested and non-harvested whale stocks. Consequently, we conclude that the SOS has contributed little to the protection and understanding of whales in the Southern Ocean. If the moratorium were lifted and the RMP applied, the SOS may become more relevant to whale conservation and management. However, given that all baleen whales migrate outside of the SOS, it alone would not prevent RMP catches being taken outside its boundaries. Therefore, if the moratorium is lifted, careful integration between the SOS and RMP will be required.

While the SOS could be an important first step towards an ecosystem approach to management in the Southern Ocean, by itself is not an effective management construct. In particular, adequate protection from all potential threats, not simply commercial whaling, for all populations of large whales in the Southern Ocean is an important first step towards promoting the proper function of this large marine ecosystem. If the SOS is to become a cornerstone in ecosystem-based management of the Southern Ocean, the IWC must work with other regional institutions and global initiatives to ensure that threats to large whales other than commercial whaling and environmental variability (e.g. climate change) are considered.

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Model-based abundance estimates for bottlenose dolphins off southern Spain: implications for conservation and management

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ABSTRACT

An EU-funded Life project was initiated off southern Spain in 2002, with the objective of developing a Conservation Plan for bottlenose dolphins in the area. Baseline information and monitoring of abundance and distribution is needed to determine if the conservation objectives are met in the long-term. To estimate abundance, 12,568km of non-systematic line transects conducted from 2000 to 2003, with 72 sightings, were analysed using spatial modelling methods. Transects were divided into 4,575 small segments (average 2.8km) with similar values for sightability conditions and environmental variables. The point estimate of bottlenose dolphin abundance in the area was 584 dolphins (95% CI=278-744). The same method was applied to investigate changes in abundance since 1992 in the eastern section of the research area, where most dolphins were concentrated, stratifying by three groups of years. Point estimates were 111 dolphins for 1992-97, 537 for 1998-2000 and 279 for 2001-03. The higher abundance between 1998 and 2000 corresponded with the observation of an 'immigrant' group of dolphins in these years. These results highlight the importance of long-term studies to understand natural variation in abundance in a specific area subject to conservation activities.

KEYWORDS: ABUNDANCE ESTIMATE; BOTTLENOSE DOLPHIN; ALBORÁN SEA; TRENDS; CONSERVATION; MODELLING; EUROPE; NORTHERN HEMISPHERE; SURVEY-VESSEL

INTRODUCTION

The bottlenose dolphin is widely distributed in the Mediterranean Sea, but is thought to be declining in numbers in this basin (Notarbartolo di Sciara, 2002), with recent genetic studies suggesting fragmented populations (Natoli, 2004). This species is listed in Annex II of the EU Habitats Directive, which considers it a priority species for conservation, and requires the creation of SACs (Special Areas of Conservation) in European waters.

According to the Habitats Directive¹, SACs should be managed through a Management Plan to contribute to the maintenance or restoration of favourable conservation status of the target species and their habitats. There is also a requirement within the Habitats Directive (Article 17) for developing a Monitoring Plan to provide information on the conservation status of the habitats and species which SACs aim to conserve and to assess the effectiveness of the Management Plan in achieving its conservation objectives. The results of the monitoring should inform management and allow for effective revision of any management measures.

In this context, in a previous study for the Spanish Ministry for the Environment between 2000 and 2002, three SACs were proposed in Southern Spain for bottlenose dolphins: one in the Strait of Gibraltar, one around the Island of Alborán and one in southern Almería (Cañadas *et al.*, 2005).

As a follow-up to this study, a project entitled 'Conservation of cetaceans in Murcia and Andalucía' was initiated in 2002, supported by the EU Life Nature programme (LIFE02NAT/E/8610). The main aims are to develop both Management and Monitoring Plans for bottlenose dolphins in the region. Under Spanish legislation, a Conservation Plan for the species that applies not only to

¹ http://europa.eu.int/comm/environment/nature.

the SACs, but to the whole region also needs to be developed. The logic of this is that a Monitoring Plan that only covers the SACs is likely to be inadequate for assessing the conservation status of a mobile species in a highly dynamic environment. In the long term, a Monitoring Plan covering a wider region may pick up shifts in distribution that may lead to revision of SAC boundaries. It may also lead to greater understanding of the causes of any change in abundance within managed sites. The impact on SAC management of a range expansion in bottlenose dolphins off the east coast of Scotland has been discussed by Wilson *et al.* (2004).

Although the Management and Monitoring Plans are still under development within the framework of this project, two main conservation objectives are foreseen as inevitable, arising from the definition of 'favourable conservation status' by the Habitats Directive (Article 1): (1) to avoid a long-term decline in dolphin population (maintaining a stable or increasing population); and (2) to avoid a longterm reduction in the areas used by the population. To determine whether these conservation objectives are being met, monitoring will need to record changes in the population with respect to baseline information.

The main objective of the work presented here was to estimate the current abundance of bottlenose dolphins in the region and to investigate variability in abundance and distribution of this species over recent years. This information will constitute the first step in the development of the Monitoring Plan by serving as a baseline for future work.

Although the project covers the whole area off Southern Spain, including the Gulf of Cádiz, Strait of Gibraltar, Alborán Sea and Gulf of Vera, the work presented here concentrates on the central section; the Alborán Sea. This area is the westernmost part of the Mediterranean Sea, where it connects to the Atlantic Ocean. It is highly dynamic and productive, of great importance for the hydrology of the

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whole Mediterranean basin and hosts a high biodiversity (Rodríguez, 1982; Gascard and Richez, 1985; Parrilla and Kinder, 1987; Tintoré *et al.*, 1988; Rubín *et al.*, 1992; Templado *et al.*, 1993; Cañadas *et al.*, 2002; 2005).

A standard technique for estimating the abundance of biological populations such as cetaceans is line transect sampling (e.g. Hammond, 1986a; Buckland et al., 2001). For this, transects are surveyed in the field and observers record the perpendicular distance (or angle and radial distance) from the line to the detected targets. The most common way of estimating abundance from such data is the 'design-based' method (Buckland et al., 2001), based on a survey design that ensures equal (or at least calculable) coverage probability is achieved across the whole study area, or at least that all portions of the study area have a nonzero coverage probability (Hiby and Hammond, 1989; Buckland et al., 2001). Design-based surveys have been widely used to estimate the abundance of a range of cetacean species (e.g. Gunnlaugsson and Sigurjónsson, 1990; Schweder et al., 1997; Forcada and Hammond, 1998; Hammond et al., 2002).

An alternative technique suitable for estimating abundance from surveys that have not been designed to achieve equal coverage probability, is the model-based approach (Hedley et al., 1999; Marques, 2001), in which line transect sampling is combined with spatial analysis. The perpendicular distance data are used to estimate a detection function, which allows abundance to be modelled as a function of physical and environment data associated with the surveyed transects. Abundance can then be estimated for the entire study area through extrapolation and maps of density created. Model-based abundance estimation does not require a randomised or systematic sampling scheme, and is therefore suitable for data collected from platforms of opportunity or dedicated surveys that did not follow a systematic design. Using features of the environment to predict abundance may increase precision and a further advantage is that abundance can be estimated for any subarea within the study area (Hedley et al., 1999). Although a systematic design is unnecessary, reasonable coverage across the range of values for the explanatory variables used is required, including location. The relatively large number of observations needed to allow modelling means that the method may not work very well in areas of low density without a large amount of effort (Williams, 2004). There is a risk of creating an 'edge-effect'; extrapolation of unrealistically high density at the edges of the study area, where coverage is usually poorer (Clarke et al., 2000; Bravington, 2003). This is a relatively new method that has not yet been widely applied.

This study uses model-based methods to estimate the abundance of bottlenose dolphins in the northern section of the Alborán Sea, following the methods of Borchers and Burt (2002) and Burt *et al.* (2003).

The abundance of naturally marked cetacean species, including bottlenose dolphins can also be estimated using mark-recapture methods applied to data on photo-identified individuals (e.g. Williams *et al.*, 1993; Wilson *et al.*, 1999; Stevick *et al.*, 2003b). Photo-identification can also provide other useful information on movements, birth rates and survival (e.g. Hammond *et al.*, 1990; Barlow and Clapham, 1997; Stevick *et al.*, 2003a; Larsen and Hammond, 2004) and mark-recapture is a possible alternative technique for achieving the aims of this study. Work on estimating the abundance of bottlenose dolphins in the Alborán Sea using these methods is in progress (S. Garcia Tiscar, pers. comm.). The assumptions made by these methods are quite different

to those for line transect and spatial modelling methods. One particularly important assumption concerns avoiding heterogeneity of capture probabilities, which is easy to violate, difficult to account for and can cause substantial bias in estimates of abundance (Hammond, 1986b). In addition, if the study area is not well delimited geographically, it can be difficult to define the population to which the abundance estimate refers. It will be informative to compare estimates of bottlenose dolphin abundance in the Alborán Sea from both methods but line transect/spatial modelling methods are likely to provide more robust estimates for this species in this area, and are more widely applicable for other species in this and other areas.

METHODS

Data collection

Survey area and survey design

Cruise tracks were conducted by the research vessel Toftevaag from 2000-03 in the whole northern section of the Alborán Sea, an area of 11,402km² (Fig. 1). In 1992 and from 1995-99, surveys were only conducted in the eastern part of this area, the waters off Southern Almería, an area of 4,188km² (Fig. 2). During 1993 and 1994, no surveys were conducted in this area. The study area was sampled in January, March, June to September and November from 1999 to 2003. Surveys were also made during March-April, and from June to September from 1992 to 1998. Transects did not follow a systematic design. The relatively small vessel used had a slow cruising speed, was very dependent on weather conditions and had to return to port every night. In addition, time was allocated to other activities during encounters, such as photo-identification. These constraints would reduce considerably the effectiveness of a systematically designed survey. Instead, cruise tracks were designed to cross depth contours and to cover as much of the area as possible (Figs 1 and 2). More detail is given in Cañadas et al. (2005).

Searching effort data

The Toftevaag is a 18m long motor-sailer with two (nonindependent) observation platforms, one on the crow's nest with an eye height of 12m and another on deck with an eye height of 2.5m. Cruising speed was 5 knots (9.3km h^{-1}). Sighting effort was measured as the number of kilometres travelled with adequate sighting conditions (i.e. with sea state Douglas² 0 to 2 and good visibility) and observers on the lookout posts. Sighting effort stopped with sea states of Douglas 3 (Beaufort 3 to 4) or more. Sighting effort was categorised into 'effort types' according to sea state and position of trained observers, because crow's nest observations were cancelled with excessive swell: 1 (sea state 1 in Douglas scale and one observer in the crow's nest), 1S (sea state 1 and no crow's nest watch), 2 (sea state 2 with crow's nest watch) and 2S (sea state 2 and no crow's nest watch). Any change of effort type was recorded in the log book and in the Logger³ software, used for real time data logging.

During searching on effort, data were recorded every 20 minutes ('sampling stations') on: (1) type of effort; (2) sea state; (3) number of ships (discriminating by type) in a radius of 3 n.miles; and (4) other environmental data.

² e.g. see www.eurometeo.com/english/read/doc_douglas and ibid doc_Beaufort.

³ www.ifaw.org/ifaw/general/default.aspx?id=25693.



Fig. 1. Study area and cruise tracks 1992-2003 in Southern Almería.



Fig. 2. Study area and cruise tracks 2000-03 in the Alborán Sea.

In this study it was not possible to implement the accepted methodology using double platforms to estimate the proportion of animals or clusters missed on the transect line (e.g. Borchers *et al.*, 2002; Hammond *et al.*, 2002). As a result, all abundance estimates are potentially negatively biased. Double platform methods would also allow responsive movement to be accounted for (a potential positive bias for bottlenose dolphins); however, no evidence was found for this (see Results).

Sightings data

Once an animal or group of animals was detected, immediate 'primary data' were taken: time, position, name of the observer making the sighting, position of the observer (mast or deck), type of effort, angle from the detected group to the trackline, estimated radial distance from the detected group to the ship, species, cue (blow, jump, splash, fin or back, birds, other), initial behaviour (see below), direction of swimming, wind and sea state. Before 2001, angle boards were not used and all angles were generally rounded to the nearest 10°. Since 2001, angles were measured with an angle board on the crow's nest or on the bridge, avoiding any rounding. Distances were always estimated by naked eye. No distance estimation experiments were carried out before or during the surveys. If distances were consistently under or overestimated, there is a potential for bias in estimates of density. Nevertheless, no changes in methods to collect distance data were made over the course of the study so this should not affect trends in abundance. Distance training and experiments will be carried out in the future.

All detected animals or groups were approached to a distance of 100m or less, at which point new 'contact data' were recorded: time, position and confirmation of species. If the animals allowed a close approach, the encounter could be prolonged up to several hours to carry out other tasks (e.g. photo-identification). On leaving the animals, data were recorded again on time, position, wind, sea state and final behaviour, and searching effort started again.

Behaviour was divided into five categories: (1) feedingforaging (animals observed chasing or eating fish, long synchronised and repeated dives or following trawling fishing boats and repeatedly diving at the level of the trawler net); (2) resting (stationary in one place, almost without movement); (3) socialising (clear and constant interaction between the animals in the group, normally with much aerial activity and stationary in the area); (4) travelling (moving animals, either on steady course or not, differentiated as travelling slowly (0.1-2 knots), travelling moderately (2.1-4 knots) and travelling fast (>4 knots)); and (5) milling (none of the previous categories, usually stationary in the area, with non-synchronised movements and very active).

Group size was assessed several times during the encounter. Animals were counted repeatedly to obtain the best estimate of group size. The number of calves and the estimated number of animals in any subgroups were also recorded. Any changes in group composition (subgroups joining or leaving) were recorded to ensure that the best estimate was of the group initially sighted.

Environmental data

Data were collated throughout the entire study area on physical and environmental features. Depth and slope of the seabed were extracted from nautical charts of the Hydrographic Institute of the Spanish Navy. Sea surface temperature (sst) and chlorophyll concentration (chl) data were obtained from the CREPAD service of INTA (the Spanish Space Agency), which consisted of NOAA AVHRR images with a pixel resolution of 2km² and their associated ascii data. For sst, data were available for the years 1998-2004. For chl, data were available for the years 2000-04. Sst averages were calculated for 1998-2000 and 2001-04, and chl averages were calculated for 2000-04.

Data analysis

Data organisation

The data were organised at two levels: (1) the whole northern section of the Alborán Sea, which was covered from 2000-03; and (2) the waters off southern Almería, using data from 1992-2003. Given the small number of sightings for each year, it was not possible to analyse them separately. The Alborán dataset was therefore pooled over years. In the Almería dataset, samples sizes were also too small to be analysed by year, but did allow grouping over years. Observations in the field recorded the arrival in late 1997 of at least one 'immigrant' group of dolphins (some easily recognisable due to very conspicuous marks) into the study area. These conspicuous animals have not been seen again since 2001. The data were therefore divided into three strata: (1) 1992-97; (2) 1998-2000; and (3) 2001-03 to investigate any changes in abundance resulting from these observations.

The study area was divided into 1,086 grid cells, with a cell resolution of 2 minutes latitude by 2 minutes longitude each. The grid cells were characterised according to several spatial and environmental variables (see below).

All on effort transects were divided into small segments (average 2.8km, maximum 4km) between two consecutive sampling stations, with homogeneous effort along them. It was assumed that there would be little variability in physical and environmental features (like bottom physiography, sst, etc.) within these segments. Each segment was assigned to a grid cell based on the mid point of the segment and values of covariates for each grid cell were associated with the segment.

Encounter rates for each dataset, both of groups and of individuals, were calculated as the average across grid cells. In Almería, only grid cells surveyed during all three periods were considered. To avoid the problems caused by low effort, grid cells with less than 2.8km (1.5 n.miles) of effort were discarded for the calculation of encounter rates.

Spatial modelling of abundance

For model-based abundance estimation, five steps were followed: (1) a detection function was estimated from the distance data and any covariates that could affect detection probability; (2) the number of groups in each segment was estimated through the Horvitz-Thompson estimator (Horvitz and Thompson, 1952; Borchers *et al.*, 1998); (3) the abundance of groups was modelled as a function of spatial and environmental covariates; (4) the groups sizes were modelled as a function of detection probabilities and covariates; and (5) steps (3) and (4) were combined and extrapolated to the whole study area to obtain the final abundance of animals.

The method of fitting separate models for abundance of groups and group sizes (steps (3) and (4) respectively) was based on the two-step method developed by Borchers et al. (1997) for modelling the spatial distribution of fish eggs, fitting separate Generalised Additive Models (GAMs) to presence/absence data and to the non-zero egg count data. A similar approach with two steps was used in Cañadas et al. (2006) for modelling the habitat selection of several species of odontocetes off Southern Spain, using Generalised Linear Models (GLMs). In the latter case, first presence/absence and then group size were modelled, yielding a surface map of relative density. If school size is suspected to vary spatially across the study area, it is preferable to estimate spatial school size surfaces through spatial modelling (Marques, 2001; Borchers and Burt, 2002; Cañadas et al., 2006). To estimate animal abundance, the estimated number of groups can be modelled instead of presence/absence, and the estimated abundance of groups multiplied by the estimated school size (Borchers and Burt, 2002; Burt et al., 2003).

ESTIMATION OF DETECTION FUNCTION

For calculating the detection function, all sightings made on effort since 1992 were used, which totalled 212 observations (including sightings from adjacent study areas, not included here).

Angle data were rounded until 2000, and the distance data were rounded during the whole period because of being estimated by eye. A smearing procedure was adopted following the method described in Buckland *et al.* (2001). Distances were smeared for the whole research period, and angles only for years 1992-2000, keeping the non-rounded angles taken in the field since 2001. The parameters for the smearing procedure were chosen after visual inspection of the data.

The software *DISTANCE* 4.0 release 2 (Thomas *et al.*, 2002) was used to estimate the detection function, using the multiple covariate distance sampling (MCDS) method (Marques, 2001; Thomas *et al.*, 2002). The perpendicular distance data were right truncated prior to the analysis, following the recommendations of Buckland *et al.* (2001). All covariates given in Table 1 and combinations of them, were tried. The selection of the best detection function was made using Akaike's Information Criterion (AIC).

ESTIMATION OF NUMBER OF GROUPS PER SEGMENT

The response variable used to formulate a spatial model of abundance of groups was the estimated number of groups (\hat{N}) in each segment, rather than the actual counts (Hedley *et al.*, 1999). They were estimated through the Horvitz-Thompson estimator (Horvitz and Thompson, 1952), where the probability of detection was obtained from the detection function fitted to the data:

$$\hat{N}_{i} = \sum_{j=1}^{n_{i}} \frac{1}{\hat{p}_{ij}}$$
(1)

Table 1

Covariates incorporated in modelling the detection function, indicating if they were treated as a continuous variable or as a factor, and the levels used in this case.

Covariate	Туре	Levels
Group size	Continuous Continuous (logarithm)	
	Factor	3 levels: 1-10/11-40/41-180
Type of effort	Factor	4 levels: 1/1S/2/2S
••		3 levels: 1/2/1S-2S
		2 levels: 1/1S-2-2S
Observer	Factor	2 levels: M (mast)/D (deck)
Year	Factor	11 levels: 1992 to 2002
		4 levels: 1992-1994/1995-1997/1998-2000/
		2001-2002
Cue	Factor	3 levels: FB (fin-back)/SP (splash)/OT (other)
		2 levels: FB (fin-back)/OT (other)
Sea state	Factor	2 levels: 0-1/2 (Douglas)

where n_i is the number of detected groups in the *i*th segment, and \hat{p}_{ij} is the estimated probability of the *j*th detected group in segment *i*, obtained from the detection function.

MODELLING ABUNDANCE OF GROUPS AND GROUP SIZE

For both models, the potential explanatory variables used were: longitude, slope of the sea floor (metres per km), relative sst in relation to overall average temperature, temporal variability of sst (standard deviation of the weekly average sst in a given grid cell over the year), trawling area (defined as 0 if trawlers were never observed fishing in a given location, and 1 if they were observed at least once), encounter rate of trawlers (number of trawlers observed fishing per sampling station), distance from the 'Seco de los Olivos' sea mount (an underwater mountain located in the north-eastern section of the study area, between 200 and 600m and rising up to 72m depth), and one of the following set of variables: depth, logarithm of depth, distance from the coast, distance from the 200m isobath, distance from the 1,000m isobath and latitude (only one of these was used at a time, because they are all correlated). Interactions between pairs of variables were also investigated.

The abundance of groups was modelled using a GAM with a logarithmic link function. A Poisson error distribution was not considered appropriate for the response variable due to over-dispersion. Therefore, a quasi-poisson family was used, with variance proportional to the mean. The general structure of the model was:

$$\hat{N}_i = \exp\left[\ln(a_i) + \theta_0 + \sum_k f_k(z_{ik})\right]$$
(2)

where the offset a_i is the searched area for the *i*th segment (calculated as the length of the segment multiplied by two times the truncation distance), θ_0 is the intercept, f_k are smoothed functions of the explanatory covariates, and z_{ik} is the value of the *k*th explanatory covariate in the *i*th segment.

Models were fitted using package *mgcv* version 1.0-5 for R (Wood, 2001). Automated model selection by a stepwise procedure was not implemented in the version of R used (1.9.0) (*http://cran.r-project.org*). Therefore, manual selection of the models was undertaken using three indicators: (a) the General Cross Validation score (GCV) which is in practice an approximation to AIC (Wood, 2000) and in which smoothing parameters (in terms of number of knots and degrees of freedom) are chosen by the software to

minimise the GCV score for the model, unless they are directly specified; (b) the percentage of deviance explained; and (c) the probability that each variable is included in the model by chance. The decision to drop a term from the model was adopted following the criteria proposed by Wood (2001). In all models, a visual inspection of the residuals was also made, especially to look for trends.

Group size was also modelled using a GAM with a logarithmic link function. In this case, the response variable was the number of individuals counted in each group (s_j) and, given the large overdispersion due to the wide range of group sizes (1-180), a quasi-poisson error distribution was used, with the variance proportional to the mean. In this case, the detection probability was included as a linear predictor (Borchers and Burt, 2002) in order to avoid the bias introduced by the selective detection of larger groups at larger distances or by other covariates affecting the detection of the groups (Universidad de Barcelona, 2002). The general structure of the model was:

$$E(s_j) = \exp\left[\hat{g}_j(y, v) + \theta_0 + \sum_k f_k(z_{jk})\right]$$
(3)

where $\hat{g}_j(y, v)$ is the conditional detection probability of the j^{th} group given that it was detected at perpendicular distance y and with covariates v, θ_0 is the intercept, f_k are smoothed functions of the explanatory covariates, and z_{jk} is the value of the k^{th} explanatory covariate in the j^{th} group. Manual selection of the models was done following the same criteria described for the models of abundance of groups.

ESTIMATES OF ABUNDANCE

Predictions of abundance of groups and of group size were produced over all the grid cells of the study area, according to the values of the covariates used in the final models. The estimated abundance of animals for each grid cell was calculated as the product of its predicted abundance of groups and its predicted group size. The final point estimate of abundance was obtained by summing the abundance estimate of all grid cells over the study area.

AVAILABILITY ON THE TRACKLINE

Availability was estimated following Forcada *et al.* (2004), to investigate how much the probability of detection on the trackline might be influenced by availability bias. The average dive time (68.7s) and average surface time (231.3s) used were those estimated by Forcada *et al.* (2004) for bottlenose dolphins in the Balearic Islands and northeastern waters of Spain. The amount of time the sea on the trackline was in the observers' view was estimated based on the distances at which bottlenose dolphins may be detected on the trackline (up to 20° on each side) and the speed of the ship.

Estimation of variance

Four hundred non-parametric bootstrap resamples of the whole process were obtained, using day as the resampling unit, to obtain the coefficient of variation and percentile based 95% confidence intervals. For both models in each bootstrap, the degree of smoothing of each model term was chosen by *mgcv*, thus incorporating some model selection uncertainty in the variance. The final CV for each subset was calculated using the delta method (Seber, 1982), combining the CV of the detection function with the CV of the models from the bootstrap. These values were plotted as surface maps of abundance and of variability.

Table 2

Days surveyed, total effort (in km), percentage of segments per effort type, number of groups (number of individuals), mean group size and encounter rates (ER) for groups and for individuals for each subset of data.

		Total	N ^o of groups Mean group							
Year	Days	effort	Effort 1	Effort 2	Effort 1S	Effort 2S	(indiv.)	size (SE)	ER groups (SE)	ER indiv. (SE)
Almería										
1992 - 1997	136	6,251	52.6%	11.8%	13.4%	22.2%	41 (683)	16.8 (2.95)	0.0046 (0.0010)	0.073 (0.020)
1998 - 2000	181	7,715	51.5%	11.3%	17.3%	19.9%	84 (2,851)	33.2 (4.03)	0.0120 (0.0019)	0.406 (0.087)
2001 - 2003	143	5,520	48.2%	12.2%	22.8%	16.8%	34 (833)	26.4 (4.75)	0.0069 (0.0018)	0.164 (0.046)
TOTAL	460	19,485	50.8%	11.7%	17.8%	19.8%	159 (4,367)	27.5 (2.53)	0.0084 (0.0010)	0.238 (0.038)
Alborán										
2000 - 2003	306	12568	55.6%	13%	18.3%	13.8%	72 (2,071)	25.0 (2.84)	0.0043 (0.0008)	0.122 (0.034)
Total										
1992 - 2003	580	24,643	53.9%	11.7%	17.1%	17.3%	177 (3,625)	24.2 (2.19)	0.0052 (0.0009)	0.145 (0.035)

Random and responsive movement

The average searching speed of the ship was 5 knots, which is slow compared to most line transect surveys for cetaceans. Since random movement of animals leads to increasing bias as the ratio of animal speed to ship speed increases (Hiby, 1982), we investigated whether this was a problem in our data. The average speed of the dolphins (at the moment of the encounter) was calculated by assigning an average speed to each behavioural category (from the 'primary sighting data'): 0 knots for socialising, milling, feeding and resting; 1 knots for travelling slowly; 3 knots for travelling at moderate speed and 5 knots for travelling fast. The average speed for all sightings, according to their initial behavioural category was then obtained. For the analysis described here, all sightings of bottlenose dolphins since 1992 were considered.

The occurrence of responsive movement before detection was investigated by calculating the ratio of animals/groups with swimming direction in the third quadrant $(180^{\circ}-270^{\circ})$ to the first quadrant $(0^{\circ}-90^{\circ})$, relative to the transect line following Palka and Hammond (2001). The ratio between these quadrants was evaluated using a chi-square test, to see if there was any evidence of attraction (Q3/Q1>1) or avoidance (Q3/Q1<1).

RESULTS

Effort and sightings

For the sub-area of Almería, surveys were conducted on 460 days between 1992 and 2003, totalling 19,485km on effort (Fig. 1; Table 2). For the area of Alborán, surveys were conducted on 306 days between 2000 and 2003 (including the time spent in Southern Almería since 2000), totalling 12,568km on effort (Fig. 2; Table 2). In total, 24,643km were surveyed on effort in the whole study area since 1992, of which between 48% and 57% (depending on the year) were made under the best conditions (with effort type 1; Table 1). A total of 177 sightings of bottlenose dolphins were made while searching on effort. The effort, number of sightings, average encounter rate and average group size for each of the data subsets is shown in Table 2.

Detection function

Perpendicular distance was truncated at 2,500m after visual inspection of the data. This discarded 5% of the data with the largest distances, leaving 202 sightings for analysis (including those made outside the study area).

Ninety-two models were fitted, starting with single covariates and continuing with combinations of two, three and four covariates. Year had very little effect on the detection function and it is assumed, therefore, that detection probability had not changed over time and data for all years were pooled. The best fitting model was a halfnormal key function with cosine series expansion and two adjustment terms. Four covariates were selected: position of the observer, sea state, group size, and cue. The next best models had $\Delta AIC>4$, so they were not competitive. They all incorporated the position of the observer, the cue and the group size (or its logarithm) as important covariates. Effort type was selected also in all these models, with either 2, 3 or 4 levels, but the best model incorporated sea state instead (the definition of effort type includes sea state). In Table 3, the coefficients for the covariates and the parameters for the detection function are shown. Fig. 3 shows the observed frequencies at given distances, pooled over all covariates, and the fitted half-normal function.





Table 3

Coefficients for the covariates and parameters for the detection function. Covariates modelled together with perpendicular distance for each sighting in these models are: position of the observer (OBS), sea state (SEA), group size (CLSIZE) and cue with 2 levels (CUE).

Parameter	Point estimate	Standard Error
Intercept	773.1	25.92
Level D of factor covariate OBS	-0.5934	0.1241
Level 0-1 of factor covariate SEA	0.5520	0.1631
Covariate CLSIZE	0.0103	0.0041
Level FB of factor covariate CUE	-0.4206	0.1881
Adjustment term of order 2	0.1597	0.1693
Adjustment term of order 3	0.3932	0.1311
f(0)	0.001668	0.000114

Abundance models

The variables retained in the two steps of the model, for each data subset, are shown in Table 4. The shapes of the functional forms for the smoothed covariates used in the models for the four datasets are shown in Figs 4-7. The most important variables, selected in many of the models, were depth (or logdepth), distance from 'Seco de los Olivos' and slope. In the model of abundance of groups for Alborán, the encounter rate of trawlers was selected and in one of the Almería datasets the average chlorophyll concentration contributed significantly to the model, apparently with a preference for areas with high concentration.

The small number of sightings did not allow the use of the best fitting models in the bootstrap simulations in many cases. The best-fitting but more complex models caused the bootstraps to fail frequently, indicating possible overfitting of the data. Therefore, simpler models were used in some cases, both for the point estimate and for the bootstrap simulations, mainly by reducing the degrees of freedom allowed for variables such as depth or slope. This procedure had the disadvantage of using a model that explained a smaller percentage of the deviance. Furthermore, when modelling group size, the 'edge effect' constituted a problem in some models. When this occurred, the covariate causing the 'edge effect' (usually the slope) was either forced to use fewer degrees of freedom or was discarded, with the penalty of yielding a smaller percentage of deviance explained. Visual inspection of the residuals did not show any unacceptable pattern.

Estimated distribution, abundance and trend

Estimates of abundance and variability are given in Table 5. For the Alborán area, the point estimate of abundance for the whole period was 584 dolphins, mainly concentrated in southern Almería, the coastal areas of Granada and south of Punta Calaburras in Málaga (Fig. 8). This abundance estimate yields an estimated average density of 0.049 dolphins per sq km. In Figs 9 and 10, the lower and upper 95% confidence limits are plotted, respectively. The lower and upper 95% CL surface maps still show what seem to be the core areas for bottlenose dolphins.

For Almería, the surface maps of estimated abundance are shown in Fig. 11. The surface maps of variability are not included for the Almería datsets due to space limitations but also showed the core areas. In the second period, after the arrival of the 'immigrant' animals, estimated abundance increased markedly by a factor of four (Table 5). In 2001-03, estimated abundance decreased by a factor of two. The abundance estimate for the second period was significantly different from the first (d_{1-2} =-3.320, *p*<0.001), but abundance estimates in the first and third and second and third periods were not different (d_{1-3} =-1.786; 0.10>*p*>0.05; d_{2-3} =1.844, 0.10>*p*>0.05). Average encounter rates of individuals followed the same pattern and mean group size was also higher in the second period (Table 2).

To test the robustness of the abundance estimates, we ran two additional models: for Alborán 2001-03 to compare to that for Almería 2001-03; and for Almería 2000-03 to compare to that for Alborán 2000-2003. The estimates from the models of Almería were similar to those obtained by summing the estimated abundance of the grid cells corresponding to Almería in the models for Alborán in both periods tested: 2001-03, 228 animals (Alborán model) *vs*. 279 (Almería model); 2000-03, 372 animals (Alborán model) *vs*. 424 (Almería model). This, together with the strong similarities of all surface maps corresponding to different datasets, suggests that the estimates were robust.

Availability on the trackline

Bottlenose dolphins were seen up to a radial distance of more than 3,000m, and regularly up to 2,000m ahead of the ship. Small groups of dolphins (1-5 animals) were regularly detected up to a distance of 1,000m ahead of the ship. Given the average ship speed of 5 knots, the estimated time the 1,000m in front of the ship is in the view of the observer is 6 minutes. Using these data the Forcada *et al.* (2004) method estimates the probability of availability as 1.

Random and responsive movement

There were 271 sightings of bottlenose dolphins on effort (including sightings from adjacent areas) for which data on initial behaviour, and therefore estimated speed, were available. The average estimated speed of the dolphins was 1.3 knots (SE=0.11 knots). The ratio of dolphins speed to ship speed was therefore 0.26, well below the value of 0.5 considered as problematic (Hiby, 1982; Palka and Hammond, 2001).

For the study of possible responsive movement of the animals before detection, data on initial heading relative to the transect line were available for 86 sightings of bottlenose dolphins. Of these, 20 sightings (23.3%) were stationary and not heading in any direction. For the

Table 4

Model results for all the subset data analysed. For each row, the two models are shown (abundance of groups and group size), indicating the variables (':' indicates an interaction between two variables) retained in the best model (estimated degrees of freedom in parentheses: 1 means a linear relationship), and the percentage of deviance explained by the model. The variables are abbreviated as follows: lon = longitude, depth = depth of the sea floor, logdepth = logarithm of depth, slope = slope of the sea floor, distseco = distance from the 'Seco de los Olivos', dist200 = distance to the 200m depth contour, ertr = encounter rate of trawlers, cav0004 = average chlorophyll concentration for 2000-2004, g(y,v) = conditional probability of detection (always as a linear predictor). Variables are ordered from more to less significant according to their p-value in the final model.

Subset	Model	Variables	% Deviance explained
Alborán	Groups	distseco (7.6) + logdepth:lon (13.2) + ertr (2.0)	19.0
2000-2003	Group size	depth:distseco $(11.5) + g(y, v)$	28.0
Almería	Groups	distseco (4.5) + cav0004 (4.3) + depth (3.2)	13.0
1992-1997	Group size	g(y, v) + logdepth (2.4) + slope (5.3)	48.7
Almería	Groups	lat:lon (19.2) + dist200 (4.7)	15.3
1998-2000	Group size	distseco (4.2) + depth:slope (13.3) + $g(y, v)$	37.5
Almería	Groups	distseco (2.3) + logdepth (4.2)	17.8
2001-2003	Group size	slope $(2) + g(y, v)$	20.9

(a) Abundance of groups

(b) Group sizes





Fig. 4. Shapes of the functional forms for the smoothed covariates used in the models for the dataset of Alborán 2000-03. Zero on the vertical axes corresponds to no effect of the covariate on the estimated response (group density on the left and group size on the right). The dashed lines represent twice the standard errors of the estimated curve (95% confidence interval). The locations of the observations are plotted as small tick marks along the horizontal axes. The interactions between two variables are shown as two-dimensional plots. In these cases, the locations of the observations are plotted as small dots. The variables are abbreviated as in Table 4.

rom estimates of abundance, density, and mean abundance, ev and 95% ef anei 400 bootstrap resamples.							
Subset	Area (km ²)	Period	Estimated abundance	Estimated density	Mean abundance after bootstrap	95% CI after bootstrap	CV after bootstrap
		1992-97	111	0.026	113	54 - 234	0.45
Almería	4,232	1998-2000	537	0.127	487	332 - 746	0.24
		2001-03	279	0.066	305	146 - 461	0.28

0.049

584

462

278 - 744

Table 5 Point estimates of abundance, density, and mean abundance, CV and 95% CI after 400 bootstrap resamples.

remaining sightings, the ratio Q3/Q1 was 0.83, which is not significantly different from one ($\chi^2=0.28$, df=1, p>0.05), suggesting no responsive movement of the animals before detection.

11,821

Alborán

2000-03

DISCUSSION

Distribution and abundance

Bottlenose dolphins appear to respond to the different characteristics of their environment by clustering (both in terms of groups and by increased group size) in some parts of the study area, with a preference for waters between 200 and 600m depth and a steep sea bottom (especially around the 'Seco de los Olivos'), areas usually heavily used also by trawlers. This agrees with this species' most common feeding habits reported in the western Mediterranean (mainly demersal fish prey; Gannier, 1995; Blanco *et al.*, 2001; Cañadas *et al.*, 2002). In most models, depth (or logdepth) was the favoured variable over all other related covariates (e.g. distance from coast or from the 200m isobath), indicating that they prefer a certain range of depths, not necessarily linked to distance from features such as the coast. In the models, longitude takes the role of a proxy variable that helps explain the spatial distribution of this species from west to east in the study area. As expected, the results are similar to those from the habitat selection modelling undertaken in the same area (Cañadas *et al.*, 2005).

0.28



Fig. 5. Shapes of the functional forms for the smoothed covariates used in the models for the dataset of Almería 1992-97. Zero on the vertical axes corresponds to no effect of the covariate on the estimated response (group density on the left and group size on the right). The dashed lines represent twice the standard errors of the estimated curve (95% confidence interval). The locations of the observations are plotted as small tick marks along the horizontal axes. The interactions between two variables are shown as two-dimensional plots. In these cases, the locations of the observations are plotted as small dots. The variables are abbreviated as in Table 4.

The distribution and abundance of species with complex ecology, social structure and behaviour living in a highly dynamic and, as yet, mostly unknown three-dimensional environment, are difficult to model. Variables that are expected to influence directly the distribution and abundance of dolphins in the open sea are at best difficult to measure (e.g. distribution and abundance of prey). Furthermore, the very low proportion of positive observations in the datasets (due to the low density of the species and the small size of the segments) might be limiting the variability that could possibly be explained with the available variables. This problem was increased by the need to discard variables yielding a strong 'edge-effect' and to fit simpler models for the bootstraps. Nevertheless, the surface maps, and the fact that they remain very similar across the datasets, suggest that the general distribution pattern of this species in the area has been satisfactorily reflected by the models (Figs 8 to 11). To check if there was overfitting, nominal parameter SEs and bootstrap SEs were compared. If the bootstrap SEs were substantially bigger than the nominal, then the model will tend to be overfitted and undersmoothed. The SEs from both sources in this work were comparable, suggesting that no problem of overfitting existed. Bootstrap at a week level was tried and compared with the daily level in order to explore if some underlying 'spatial week effect' was missed. SEs were similar and therefore the daily level was kept.

In the area of Almería, despite the differences in estimated abundance over time, the core area was the same in the three periods: around the 'Seco de los Olivos' sea mount. This is an important area of upwelling induced by the topography, which has been highlighted for having the highest concentrations of ichthyoplankton of the northern half of the Alborán Sea (Rubín et al., 1992). In the second period with higher abundance, the most heavily used areas are more extensive; they narrow again in the third period following the decrease in estimated abundance. A possible explanation of this might be that when the abundance is relatively low, the dolphins tend to concentrate in the most productive areas, where they may have the highest possibilities of success in finding prey. When abundance is higher, they may also need to explore other areas.

There is potential for the trends in abundance to be confounded with changes in group size because g(0) is assumed to be one but g(0) is expected to be smaller for small groups than for big groups. In the second time period when estimated abundance was higher, group size was also higher than during the other two periods. Although perception bias cannot be estimated here, because there is no availability bias even for small groups of 1 to 5 individuals, we do not believe that the trend in abundance is a consequence of a change in g(0) due to changes in group size.



Fig. 6. Shapes of the functional forms for the smoothed covariates used in the models for the dataset of Almería 1998-2000. Zero on the vertical axes corresponds to no effect of the covariate on the estimated response (group density on the left and group size on the right). The dashed lines represent twice the standard errors of the estimated curve (95% confidence interval). The locations of the observations are plotted as small tick marks along the horizontal axes. The interactions between two variables are shown as two-dimensional plots. In these cases, the locations of the observations are plotted as small dots. The variables are abbreviated as in Table 4.



Fig. 7. Shapes of the functional forms for the smoothed covariates used in the models for the dataset of Almería 2001-03. Zero on the vertical axes corresponds to no effect of the covariate on the estimated response (group density on the left and group size on the right). The dashed lines represent twice the standard errors of the estimated curve (95% confidence interval). The locations of the observations are plotted as small tick marks along the horizontal axes. The interactions between two variables are shown as two-dimensional plots. In these cases, the locations of the observations are plotted as small dots. The variables are abbreviated as in Table 4.



Fig. 8. Surface map of abundance for bottlenose dolphin in the northern section of the Alborán Sea, for 2000-03.



Fig. 9. Surface map of lower 95% confidence limit after 400 bootstrap resamples for the study area of Alborán, for 2000-03.



Fig. 10. Surface map of upper 95% confidence limit after 400 bootstrap resamples for the study area of Alborán, for 2000-03.

As it was not possible to implement a double platform survey method for estimating g(0), the abundance estimates presented here are potentially an underestimation of true abundance. Further data are being collected with a double platform installed on the research vessel, with the aim of estimating g(0) in the near future and therefore correcting the abundance estimates. However, we do not expect this to change the results significantly. Availability bias is unlikely and we believe perception bias is also likely to be small given the sea states in which the survey was carried out, the relatively large group sizes encountered, the slow speed of the ship and the height of the observation platform. Therefore, it is likely that g(0) is close to one.

Implications for conservation and management

It is important to highlight that these estimates represent the average number of bottlenose dolphins in the study areas during the defined periods, not the size of a population using the areas. Neither the area of Alborán nor the sub-area of Almería are closed areas and our results show that they do not contain a closed population, with movement of individuals into and out of the adjacent areas of the Strait of Gibraltar, the Gulf of Vera and the southern portion of the Alborán Sea. This, together with the negative bias produced by assuming g(0)=1, means that the size of the population of bottlenose dolphins that uses the study area is larger (by an unknown extent) than our estimates. In terms of monitoring conservation status within a defined area such as an SAC, we are interested in whether the average number of animals using the area changes over time. If g(0) does not change across years (a reasonable assumption, given that the same research vessel, observers and methodology were used for the whole period and that there was no evidence of any changes in surface behaviour), the estimates obtained are valuable in assessing changes in abundance in the study area.

When dealing with the area of Alborán, four years of survey is too short a period to detect any trend in abundance, and long-term monitoring is required. In the area of Almería, the field observations of the presence of the conspicuous 'immigrant' group between late 1997 and 2001 was echoed by a significant change in estimated abundance. Analysis of the photo-identification data will help to provide more detail of this.

Our results highlight the importance of long-term studies to understand variation in abundance in a given area. For example, if this study had started in 1998, we could be alarmed at detecting an apparent decline in numbers of animals in the Almería area. Instead, the longer time series of data allowed the documentation of an increase and subsequent decrease in abundance that is likely a result of natural fluctuations in abundance. This highlights the need for an adequate long-term monitoring programme. An important question for the Monitoring Plan of the proposed SAC in this area is when should an abundance 'baseline' be established to base future assessments of conservation status. Should this be the lowest abundance estimated over the past 12 years, or perhaps the average over the last 12 years? This will depend in part on the conservation objectives of the Management Plan.

Ideally, the monitoring programme should be developed not only to allow the detection of changes in abundance in the long-term, but also the differentiation between natural fluctuations and real trends in the abundance of the population. The observed fluctuations in abundance in the Almería area stress the need for the monitoring programme to cover not only the proposed SAC but also a wider area outside it to improve our understanding of fluctuations or trends in numbers and shifts in distribution. This wider information may have important implications for the management of the protected areas (Wilson *et al.*, 2004).





There is limited information on abundance of bottlenose dolphins in other areas of the western Mediterranean Sea. Aerial line transect surveys carried out off Valencia (Eastern Spain), from 2000 to 2002 (Gómez de Segura et al., 2006) estimated a density of 0.041 dolphins per sq km, lower than estimated here, except for Almería in 1992-1997. The encounter rates of groups and of individuals were also much lower than in Almería, as was the mean group size (11 in Valencia vs. 24 in Alborán). However, caution must be exercised when comparing these results, as very different survey platforms were used (ship vs. aircrafts) and g(0) was not estimated in either analysis. An abundance estimate for this species has been obtained recently also for the NW Mediterranean (north of Spain and Balearic Islands), from aerial survey data. The estimated density in this area was of 0.085 to 0.088 dolphins per sq km. In this case, the estimate was corrected for availability bias, and underestimation due to perception bias was considered to be small (Forcada et al., 2004; Table 6). The available information suggests that encounter rates, and average group sizes, decrease from west to east in Spanish Mediterranean waters (Table 6). Although there are methodological issues with comparing these results, as described above, they suggest that the Alborán Sea, and especially the area off Southern Almería, are important areas for bottlenose dolphins in the westernmost part of the Mediterranean Sea.

Applicability of the method

The model-based method for estimating abundance is shown to be a good approach for describing cetacean distribution, and estimating abundance based on the data collected in this study. Much of the data on cetacean distribution and density in Europe is being collected through non-systematically designed surveys similar to those presented here. This method constitutes, therefore, a promising way to analyse these large collections of data.

Nevertheless, caution should be exercised when applying very flexible models like GAMs, especially to avoid overfitting the data and the 'edge effect', which could yield unrealistic densities and surface maps. This method is still in a relatively early stage of development, and some questions remain unsolved, such as whether the bootstrap is the most appropriate way of obtaining 95% confidence intervals, or how to deal better with the problem of the 'edge-effect'.

The models described in this paper should be revised when data on more potential explanatory variables become available, and especially when this method becomes better developed and tested (for example through analysis of simulated data).

Encounter rates (ER) of groups and individuals (per km), and mean group sizes of bottlenose dolphins in Spanish Mediterranean waters. Encounter rates and mean group size were calculated as the average over grid cells for this work. Other data represent overall values. '*' means estimated density corrected for availability bias (Forcada *et al.*, 2004); all other densities are underestimations.

Area	Period	Density (animals km ⁻²)	ER of groups	ER of indiv.	Mean group size	e Source
Gibraltar	2001-02		0.0056	0.1157	27.8	De Stephanis et al. (in review)
Alborán	2000-03	0.049	0.0043	0.1220	25.0	This work
Almería	1992-97	0.026	0.0086	0.1356	16.7	This work
Almería	1998-2000	0.127	0.0222	0.7524	33.9	This work
Almería	2001-03	0.066	0.0128	0.3031	24.5	This work
Gulf of Vera	1993-2004		0.0016	0.0161	10.5	Unpublished data of the authors
Valencia	2000-02	0.026	0.0006	0.0066	11	Gómez de Segura et al. (2006)
Catalonia	2001-02		0.0017	0.0117	7	Universidad de Barcelona (2002)
Catalonia and Balearic Sea	2002	0.088*			7	Forcada et al. (2004)
Balearic Islands	2001-02		0.0018	0.0142	6.3	Universidad de Barcelona (2002)
Balearic Islands	2002	0.085*			7	Forcada et al. (2004)

Table 6

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Stock identity of a humpback whale taken in a southeastern Caribbean hunt

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ABSTRACT

North Atlantic humpback whales migrate annually between discrete high latitude feeding areas and shared low latitude breeding areas. St. Vincent and the Grenadines is a low density breeding area in the Lesser Antilles and the site of the only ongoing aboriginal humpback whale hunt in the North Atlantic. The Scientific Committee of the International Whaling Commission recently concluded that catches were likely drawn from a large, pannictic breeding population, but encouraged the collection of additional data. On 6 March 1999, two humpback whales were landed at St. Vincent and the Grenadines and we obtained images from an opportunistic source. Photographic matching identified one individual as 'Haar' (NAHWC #0694), a catalogued whale from the Gulf of Maine. This is the first stock assignment from this fishery and the most southeasterly sighting of a Gulf of Maine whale. Based on its reported length, the second animal was probably a calf and, if so, a member of the same population. This match provides further support for the hypothesis that catches at St. Vincent and the Grenadines involve a variety of high-latitude populations. Furthermore, it reinforces the scientific and management value of collecting and sharing individual identification data when hunts are performed.

KEYWORDS: HUMPBACK WHALE; GULF OF MAINE; WEST INDIES; ATLANTIC OCEAN; MIGRATION; PHOTO-ID; BREEDING GROUNDS; WHALING – ABORIGINAL

INTRODUCTION

North Atlantic humpback whales, *Megaptera novaeangliae*, migrate annually between shared low latitude breeding areas and discrete high latitude feeding areas. The principal North Atlantic breeding range lies along the Atlantic margins of the Antilles, from Cuba to northern Venezuela (Winn *et al.*, 1975; Balcomb and Nichols, 1982; Whitehead and Moore, 1982). Photo-identification research at the northern (Greater) Antilles indicates a large breeding population (Stevick *et al.*, 2003) composed of animals from all primary feeding areas (Mattila *et al.*, 1989; Katona and Beard, 1990; Stevick *et al.*, 1999b). Fidelity to a specific feeding area is strong and maternally directed, such that a calf born in low latitudes is recruited to its mother's stock during an extended period of maternal care (Martin *et al.*, 1984; Clapham and Mayo, 1987; Katona and Beard, 1990).

The eastern and southern (Lesser) Antilles were historically sites of a large humpback whale fishery (Smith and Reeves, 2003) and whale density there remains comparatively low (Swartz *et al.*, 2003). Three free-ranging humpback whales from the Lesser Antilles have been photographically matched to high latitude feeding areas. One was matched to West Greenland (Stevick *et al.*, 1999a), a feeding aggregation estimated at 360 individuals (CV=0.07, 1988-93; Larsen and Hammond, 2004). Two others were matched to Newfoundland and Norway (Stevick *et al.*, 1999a; Bérubé *et al.*, 2004), and exchange with Greater Antilles areas has also been documented (Stevick *et al.*, 1999a).

St. Vincent and the Grenadines, in the Lesser Antilles, is the site of the only ongoing humpback whale hunt in the North Atlantic. Catches have been made at a rate of 0-2 whales per winter over the past two decades (IWC, 2002). In a recent Comprehensive Assessment of the North Atlantic humpback whale population, the Scientific Committee of the International Whaling Commission (IWC) concluded that these animals were probably drawn from the same population studied at the northern end of the breeding range (IWC, 2002). However, it strongly encouraged the collection of additional data with which to assess the high latitude origin of animals taken in this hunt. This paper reports on the stock identity of a humpback whale caught at St. Vincent and the Grenadines based on an opportunistic photograph of the event.

METHODS

Images of two humpback whales landed at Petit Nevis, St. Vincent and the Grenadines were obtained from the website of a tourist who photographed the event on 6 March 1999. One of the images depicted the ventral flukes of the larger of two humpback whales. Individual humpback whales can be identified from the unique pattern of pigmentation on the ventral side of the flukes and the shape of the trailing edge (Katona and Whitehead, 1981). Standard photoidentification techniques were used to match the image against the Gulf of Maine Humpback Whale Catalogue curated by the Provincetown Center for Coastal Studies (PCCS, Massachusetts, USA). The match was subsequently confirmed by the North Atlantic Humpback Whale Catalogue (NAHWC) curated by the College of the Atlantic (Maine, USA). Carcass length data and other hunt details were taken from information provided to the IWC by the government of St. Vincent and the Grenadines (IWC, 2000).

RESULTS AND DISCUSSION

Two humpback whales were caught on 6 March 1999: one 46-foot (14m) female and a second female that was estimated at 20-23 feet (6-7m) in length (IWC, 2000). The ventral flukes of the larger animal were photographically

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matched to a catalogued Gulf of Maine whale known as 'Haar' (NAHWC# 0694). She was first seen in July 1987 and so was at least 13 years old when she died. The PCCS catalogue contained four Gulf of Maine sightings of this animal, none of which were after 1990. The NAHWC reported no other matches to 2,542 individuals catalogued at other feeding areas through 1998.

A fluke image was not available from the second animal. However, at an estimated length of only 6-7m in the late breeding season, it was not likely to have been an independent, catalogued whale. Northern Hemisphere calves are estimated to range from 4.1-6.9m in length during their first winter (Spitz, 1999) and remain dependent until 8-9m in length (Clapham *et al.*, 1999; Doroshenko, 2000). They can be unusually large or small for the season *in utero* (Nishiwaki, 1959; Mikhalev, 1997; Doroshenko, 2000), and one Gulf of Maine yearling died in April at a length of only 7.2m (Barco *et al.*, 2002). However, based on the majority of the available length data, the small whale taken with 'Haar' was probably a calf and, if so, a member of the same stock.

Nearly nine years elapsed between the most recent Gulf of Maine sighting of 'Haar' and her death at St. Vincent and the Grenadines. Although sparse catalogue sighting histories are not unusual, it is also possible that Haar was not a consistent member of the Gulf of Maine population. Low rates of exchange have been documented between the Gulf of Maine and other western North Atlantic feeding areas, including the Canadian Scotian Shelf, the Gulf of St. Lawrence, Labrador, Newfoundland and west Greenland (Katona and Beard, 1990; Clapham et al., 2003). Katona and Beard (1990) hypothesised that animals from other feeding grounds may pass through this area during their northbound migration. At present, however, there is no evidence that Haar used another feeding area. In fact, her presence in the Gulf of Maine at the peak of at least one summer reduces the likelihood that she was simply en route to another feeding area.

The present match represents the most southeasterly sighting of a Gulf of Maine whale. Although this population has the shortest migration to any breeding area in the western North Atlantic, the waters of St. Vincent and the Grenadines are at least 41% (975km) farther than high-density breeding aggregation sites at the Greater Antilles. It is not known if Gulf of Maine whales migrate directly, or routinely, to southeastern Caribbean waters. However, the present match suggests that this species may sometimes travel well beyond its nearest breeding area, even when that area appears to be highly attractive to conspecifics.

This is the fourth high-latitude stock identified at the Lesser Antilles, supporting the hypothesis that catches are drawn from a variety of feeding stocks. It is also the first successful match of a humpback whale from this hunt. Given the low modern abundance of humpback whales in the Lesser Antilles, catches represent an important source of information on the animals that are available to this fishery. The present match was based on photo-identification, but humpback whales can also be individually identified by molecular genetic techniques (Palsbøll et al., 1997). In fact, the stock identity of one free-ranging individual from the Lesser Antilles is known only from a genetic match to a high-latitude sample (Bérubé et al., 2004). The molecular genetic archive for the North Atlantic population (CetaBase, currently housed at the Department of Genetics, Microbiology and Toxicology, Stockholm University, Sweden) now includes over 6,500 skin samples drawn from all known feeding and breeding grounds (P. Palsbøll, pers.

comm.). Even if individuals are not successfully matched, a genetic approach potentially allows for matches to close maternal relatives, and thereby insight into stock identity. This is particularly important for carcasses, as those individuals have no opportunity to be added to the archive at a later date. We therefore encourage efforts to collect and share both types of individual identification data when hunts are performed.

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History of Bermuda shore whaling, mainly for humpback whales

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ABSTRACT

From its first colonisation in the early 1600s, Bermuda was known as a potentially profitable whaling site. Humpback whales (*Megaptera novaeangliae*) were common in coastal waters during the late winter and spring (March-May); sperm whales (*Physeter macrocephalus*), in offshore waters probably throughout much of the year. Initial efforts at shore whaling in 1616-17 were not very successful but whaling continued at least intermittently until 1685 when Bermuda became a Crown Colony and the whaling industry was placed on a firm footing. The shore whaling industry in Bermuda was never particularly large or profitable. Although it continued into the 20th century and was episodically re-invigorated with new financing and equipment, shore whaling never met the high expectations of those who invested in it. In 1780s and for several decades thereafter, a few whaling voyages sailed from Bermuda for distant whaling grounds in the South Atlantic and Indo-Pacific, targeting sperm whales and right whales (*Eubalaena* spp.). There is no evidence to suggest that local catches by Bermudian shore whalers exceeded more than a few tens of whales per year, the vast majority of them humpback whales.

KEYWORDS: DIRECT CAPTURE; EFFORT; WHALING-HISTORICAL; ATLANTIC OCEAN; BERMUDA; HUMPBACK WHALE; SPERM WHALE

'There are also great plenty of Whales, which I conceave are very easie to be killed, for they come to usually, and ordinarily to the shore, that we heard them oftentimes in the night a bed; and have seene many of them neare the shore, in the daytime.'

Silvester Jourdain's 'A Discovery of the Barmudas' (1610)

INTRODUCTION

Whaling for humpback whales (*Megaptera novaeangliae*) in the North Atlantic Ocean has a long and diverse history (Reeves and Smith, 2002). Two previous papers summarised some of the early literature concerning the fishery for this species in Bermuda and confirmed the great antiquity of the whaling enterprise there (Mitchell and Reeves, 1983; Stone et al., 1987). This paper was initiated in response to the IWC Scientific Committee's interest in modelling the North Atlantic humpback whale population (IWC, 2002; 2003). As background for that work, Reeves and Smith (2002) reviewed the fisheries that hunted humpback whales in the North Atlantic and identified the 'Bermuda non-mechanised shore fishery' as the most longstanding (1600s-1941). In a separate exercise, Smith and Reeves (2002) made what they described as 'a series of highly speculative interpolations and extrapolations' to provide input on removals for the Committee's model runs. For modelling purposes, they proposed combining the Bermuda catches with those of the West Indies non-mechanised shore fishery'.

The present paper is the result of a more thorough search of published and archival material and provides the basis for a more precise and accurate catch series than was previously available. It also provides a synthesis of the historical development and decline of the Bermuda shore fishery, with additional information on Bermuda's relatively brief and limited involvement in long-distance offshore whaling.

MATERIALS AND METHODS

The reviews by Mitchell and Reeves (1983) and Stone *et al.* (1987) were greatly expanded and updated. In addition, a search was conducted of customs records and whaling

('fishing') returns deposited in the Bermuda Archives in Hamilton. These records included microfilms of the Bermuda Blue Books submitted to the Colonial Office between 1824-59 (Colonial Secretary, 1824), manuscript quarterly returns of goods exported in British and foreign vessels kept by the Hamilton and St George's customs collectors from 1827-54 (C33/1-C33/5), outbound manifest declarations for the same ports from 1795-97 and 1851-60 (C14, C15, C16) and annual statements of Bermudian exports from 1830-32 (C35).

Bermuda customs records provide sporadic but presumably reliable data for the period 1795-1857. Differences in tariffs between locally produced oil and oil imported into the colonies meant that the products of shore stations were clearly differentiated from those obtained elsewhere. Locally produced oil was frequently marked in quarterly export returns with descriptions such as 'oil drawn here', or 'oil, whale, produce of the fisheries of this colony'. Inbound and outbound manifests - documents required for all inbound and outbound vessels - are available in the Bermuda Archives from the beginning of the 19th century. Customs officials in Hamilton and St George's compiled quarterly cargo returns from these documents in bound blank books specifically printed for the purpose. The books, in turn, helped to ensure that each customs agent had comprehensive lists of all exports when quarterly returns were prepared and submitted to Bermuda's Controller of Customs. Ideally, these data were then used to compile annual export statements, known as Blue Books, which were sent to the Colonial Secretary in London. Rote language submitted between 1832 and 1860 and inconsistencies between Blue Book records and customs records in 1840, however (see later), suggest that this did not always occur.

Bermuda Blue Books in addition to those examined on microfilm in Hamilton, covering 1821-23 and 1860-1935, are available in the Public Record Office (PRO), London (CO 41/18 - 129), but it was not possible to check those due to resource constraints. Given the results from examining the 1824-59 sample and the evident trend in the whale

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fishery from 1860 onwards (see below), however, this was not judged to be a serious omission. A large body of Bermuda 'Correspondence, Original – Board of Trade' extending from 1692-1792 (CO 37/1 – 23) and Bermuda 'Entry Books of Commissions ... Orders in Council, Correspondence ...' extending from 1615-1807 (CO 38/1 – 17) is also available in the PRO. Examination of those materials, although very time-consuming, would have provided a more detailed and exhaustive history of the whale fishery than is presented here.

Defining the various measurement units for whale products in many older whaling records presents an interpretive challenge (cf. Lindquist, 1992). In the case of Bermuda, it is often unclear exactly what was intended by the terms 'gallon' and 'barrel'. Some equivalencies are given in Table 1 but a degree of uncertainty is unavoidable. A small data set from the customs records, 1832-57 (above), implies that barrels (bbl) contained from 20 to 44 gallons (gal), with an average of about 36gal/bbl. Unless there was evidence to the contrary, it was assumed in this paper that quantities of oil expressed in gallons were imperial gallons. Barrels were defined in 1675 as containing 31.5gal (Edwards and Rattray, 1932, pp.274-5), apparently meaning Queen Anne's gallons of 1707, which have since become known as US gallons (Lindquist, 1992). It is thus concluded that barrels in Bermuda could have contained anywhere from 119 litres (assuming 31.5 US gallons) to 164 litres (assuming 36 imperial gallons).

RESULTS AND DISCUSSION

Chronological summary of events and developments

Table 2 provides a chronological summary of Bermuda whaling. Narratives for various periods are provided in the following sections.

Early years (1615-1684)

A successful whaling industry was key to planning and financing Bermuda's early colonisation. The British governor's remuneration was to consist of a land grant together with a twentieth of the net profits on whaling, pearl fishing and farm produce as well as a commission on ambergris (Wilkinson, 1933, p.112), which at the time was obtained primarily if not exclusively by scavenging (e.g. see Jones, 1884, pp.154-6). When the first governor, Daniel Tucker, arrived in 1616 he encouraged the people to hunt whales as well as to fish and farm (Ives, 1984, p.6). However, by all accounts the colonists were not skilled whalers and had little success (Ives, 1984, pp.13, 36). Even after the arrival in about mid-April 1617 of a ship (Neptune) specially fitted out for whaling, many whales were harpooned but none secured (Wilkinson, 1933, p.119; Norwood, 1945, p.lxxvi; Ives, 1984, pp.16, 38). Tucker himself, discouraged, diverted his own energies away from

whaling (Wilkinson, 1933, p.119) and the literature is largely silent on the subject from 1617 until the early 1660s. Indeed, one source claims that 'little experience' with whaling was acquired during the 40-plus years following the initial failed attempts (Wilkinson, 1933, p.323).

Even though no explicit evidence was found for either whaling activities or catches between 1617 and the 1660s, some whaling probably occurred then. Zuill (1972, p.174), for example, noted that tobacco, 'once regarded as the islands' staple, was ... in decline' during the decade of Cromwell's dictatorship (1649-58). As tobacco's importance waned, 'whale-fishing became very important and this business grew rapidly'. In fact, conflict arose between the Bermuda Company's interests and those of local whaling entrepreneurs. The Company having ordered that all whale oil be shipped to London, 'Many of the settlers grumbled at this especially when it became known that there was a good market for whale-oil at Barbados; surely, it was argued, this was a far better plan, for the oil sent to Barbados would be for benefit of the ship and whoever owned the oil' (Zuill, 1972, p.174). As a consequence two prominent colonists, John Somersall and William Reighton, were accused in 1663 of smuggling whale oil from Bermuda to Barbados and they were summoned to London to account for their subterfuge.

Some time in the late 1660s, a Bermuda whaling company was formed under the patronage of the Earls of Manchester and Devonshire. Shares were sold in London at £50 each and islanders were offered shares for 50 shillings. However, the company was under-subscribed and incurred much resentment on the part of local Bermudians who viewed its monopoly on whale products as intrusive on their fishing rights (Wilkinson, 1933, p.323). Whales were certainly killed during the mid to late 1660s, possibly in fairly large numbers, but mismanagement and local hostility ensured that little profit accrued to the company. Stafford (1668), writing to the Royal Society of London, boasted, 'I have my self killed many of them [humpback whales, judging by the context]'. A total of 131 tuns (t) of oil were shipped to London in the four years preceding June 1669 (Verrill, 1907; Wilkinson, 1933, p.324). Of that amount, only 95t was reported to company officials and only 45t was registered as having arrived in London. Of the shortfall, some 29t was accounted for by a ship's having been lost in hostilities with the Dutch. There is no record of what happened to the rest (Wilkinson, 1933, p.324).

Events from 1670 onwards are difficult to reconstruct because of incompleteness and apparent inconsistencies in the literature. A footnote in Wilkinson (1933, p.324) stated that 'additional information on the Whaling Co.' was available at 'St John Baptist College' (presumably presentday St John's College), Oxford, citing an article in *The Times*, 16 October 1931. The company shares in 1670 were said to be worth £16 and the whaling prerogative was leased

Table 1

Measures and equivalencies. Also see Lindquist (1992) and Reeves et al. (1999).

Tun (t) (in some sources spelled 'ton' or tonne') Gallon (gal), US Gallon (gal), imperial (imp.) Barrel (bbl) Hundredweight (cwt) (long)	957.6 litres (L) 3.785 L 4.546 L 119.228 L 50.8 kg	210 imp. gal 0.83267 imp. gal 1.20095 US gal 26 imp. gal 112 lb 100 lb	252 US gal 31.5 US gal	Standardised in 1707 Standardised in 1825 Standardised in 1675
Hogshead (hhd) (British) Pound (lb)	45.56 kg 286.43 L 0.4536 kg	63 imp. gal	76 US gal	

Table 2

Bermuda whaling from the early 1600s to 1942. 'Whales', unspecified to species, are assumed to have been humpbacks. Information from Mitchell and Reeves (1983: table 7) is included (and in some instances, corrected).

Year/period	General information	Oil and baleen exported ('gal' presumably imperial)	Source
1616-17 1621 Dec. 1663	Efforts at whaling unsuccessful; many whales reported to have been struck. Unsuccessful attempt. Stock company organised for whaling; special rules enacted by		Lefroy (1877); Verrill (1907); Ives (1984) Verrill (1907) Verrill (1907)
1664	Bermuda Company. 17 'voyages', 'fastened' to whales 'a dozen' times, secured 2 adult females and 3 juveniles producing 11t oil all told (year unclear; could	44hhd (= 9t) whale-oil and blubber, 4cwt baleen shipped to	Anon. (1665); Verrill (1907)
1665	have been 1665). 16 whales taken.	London in <i>Elias</i> . 50-60t oil from these whales arrived at Limerick, Ireland,	Anon. (1666); Verrill (1907)
1664-65		either late 1665 or early 1666. only 92 tons whale oil were shipped out of Bermuda between	Kennedy (1971): p.269
1666		1004-1005. 117hhd (= 29t) oil shipped to London (on <i>Hercules</i> ?).	Verrill (1907)
1667	"Within these 2 or 3 years, in the spring-time and fair weather, they take sometimes one, or two, or three [probably humpbacks] in a day" (Norwood).	47½ t whale-oil shipped to London (Verrill).	Norwood (1667); Verrill (1907)
1668		13 ¹ / ₂ t oil shipped on <i>Elizabeth</i> and Marie in June.	Verrill (1907)
June 1669		Total of 131t oil exported to London in previous 4yr.	Verrill (1907)
1671 June 1676 1679 1682	Whaling company 'reorganized'. Sperm whale stranded on reef; oil extracted. Taking of whales 'prohibited' but some illegal whaling continued. Whales being killed 'indiscriminately' (i.e. with no royalty paid to		Verrill (1907) Verrill (1907) Verrill (1907) Kennedy (1971): p.249
1685 1691	Bermuda Company). C. 14 whales taken; large whale worth £80 at the time. Four large, 4 small whales taken; 3 (additional?) large ones escaped (after being struck?)		Verrill (1907) Anon. (1946)
1748	Statement that up to 20 whales could be taken in one year by the shore whalers.		Mitchell and Reeves (1983), citing Goode (1884), quoting from Douglas (1755)
Mid-1780s	Five whales taken at St George's parish, apparently in one season, driving local price of oil down from 3s.4d. (as retailed in Somerset) to 2s.8d		Wilkinson (1973)
1792	Right whale taken in Castle Harbour, 'the only known instance of a whale being taken in the enclosed bays of the islands' (Verrill); 12		Verrill (1907); Schortman (1969)
17 April 1817 1819 Spring 1829	F.F. Hinson of Paget Island shot a whale with a 'whale-gun'. Paget's Whale Fishery active on New Ledge. Published results of the season: 3 stations at St George's took 12 whales, 300bbl oil (Mr Hinson's); 3 whales, 80bbl (Mr Higg's); and 1 whale, 14bbl (Mr Athell's); 1 station at Somerset took 1 whale, 40bbl (Mr Burrows')	774gal common oil.	Schortman (1969): p.83 Schortman (1969): p.83 Schortman (1969): p.83
1830		£187 worth of whale oil (sterling).	Schortman (1969): p.83
1832	A sperm whale taken at St David's, by Hayward's whale oil establishment; 12 boats active; 6 whales taken previously that season.	300gal common oil.	Verrill (1907)
1833-34	At least 1 whale taken, 3 more struck.	71gal and 4hhd common, 1833; 490gal common, 1834	Gosling (1952)
1830s/1840s 1839	>12 whales struck in 1 year, nearly as many in another. 40ft sperm whale taken by Devonshire whale boats; 18-20bbl 'sperm' (spermaceti?), 40bbl oil.	450gal sperm	Wilkinson (1973) Schortman (1969): p.83
1839	Sperm whale taken off St David's Island, 84bbl, 'regarded as the largest one ever taken here'; struck by Josiah Smith.		Verrill (1907)
1840	70ft (<i>sic</i>) sperm whale taken by Tucker's Town Whaling Establishment: for some reason much of the oil was lost.	541gal common oil, 1638 ¹ / ₂ gal sperm oil	Schortman (1969): p.83
1840	A 'half-grown' sperm whale taken, 'the first one of the kind that had been captured in nine years (<i>sic</i>)'.		Verrill (1907); also see Table 3
c. 1840 1849	2 right whales taken. 45ft whale towed into Somerset, 21 April after being found dead by the whale boats, either 'killed by the Sword Fish' or stranded on the reefs but 'There is every reason to believe it was killed by an American whaler, sighted off these islands'.	[some sperm oil but no amount indicated]	verrill (1907) Hurdis (1897)

Table 2 cont.

Year/period	General information	Oil and baleen exported ('gal' presumably imperial)	Source
1849	Sperm whale drifted onto shore 1 June, supposedly killed by crew of American whaler that had been cruising nearby		Hurdis (1897)
1851	New whaling company formed, in addition to 'independent whaling crews'; 2 whales taken, c. 30bbl each.		Wilkinson (1973)
July 1851 1852	Sperm whale taken at Hamilton, 'a rare capture'.	464gal sperm oil	Verrill (1907) Wilkinson (1973)
1853	2 adults, 1 'small' whale taken at East End; 1 boat 'smashed'; stations at Port Royal and Somerset also active; total of 12 humpbacks struck, 7 landed total 350bl oil	1,180gal sperm oil	Wilkinson (1973); Mitchell and Reeves (1983), citing <i>Whalemen's Shinning List</i>
1854 1855-58 1859	54ft whale taken. No catch reported. Whale boats deployed at St David's, Tucker's Town and Southampton;	44gal common oil, by 5 April	Wilkinson (1973) Wilkinson (1973) Wilkinson (1973)
May 1863 22 Apr 1866	no catch. Sperm whale taken, 47ft 33ft 'exceedingly fat' whale (female) taken, expected to produce 40bbl: harpooned then shot with bomb lances: 'first whalecaptured		Jones (1884) Jones (1884)
19 June 1869 26 Apr 1871	here for some years'. Sperm whale taken (40ft; 14mi S of David's Head). 22ft calf taken at Port Royal (expected to produce 5½ bbl), mother		Jones (1884) Jones (1884)
c. 1880	struck but lost bleeding 'freely'. Active whale boats included: H.M. Fox's <i>Shamrock</i> (equipped with a 'whale-gun'), T.S. Hayward's <i>Molly</i> , H.W. Lightbourne's <i>Three Sisters</i> and I Minor's <i>Reherca</i>		Schortman (1969): p.84
1892 (late Sept.)	30bbl sperm whale taken.		Wilkinson (1973)
1894 (Dec.) April 1901	56ft whale (presumably humpback) taken. Small sperm whale taken, placed on exhibition, 'regarded as a curiosity'		Wilkinson (1973) Verrill (1907)
1915	Antonio Marshall and Rev. Darrell brought 2 whale boats and £500 worth of whaling equipment from New Bedford		Kan (1933)
c. 1900 1932 1932 1933	Joe Smith and David Burchell whaling with hand harpoons. Young sperm whale taken. Humpback struck but lost. Whale boat and new equipment introduced.		Kan (1933) Wheeler (1933) Kan (1933) Kan (1933)
17 Apr. 1940	1 humpback taken (of 3 sighted 15mi SW of Bermuda); killed with bomb lance; 42ft male; said to have been first whale (presumably meaning humpback) secured in >40yr 'although a number of attempts have been made, especially in recent times'.		Wheeler (1941)
13-18 Nov. 1942	1 humpback taken; struck initially with shark harpoon; killed with 'a shower of machine-gun bullets'; 38ft male.		Wheeler (1943)

to a Mr Crook of London in 1671, for 7yr at £100/yr (Wilkinson, 1933, p.324). Another source (Schortman, 1969, p.78) indicated that a whaling company was formed in 1670 by the governor (Sir John Heyden) and three other prominent colonists. Whether this was the same company as the one to which Wilkinson referred is not clear; Schortman provided no further details. War with Holland continued to plague British shipping until the end of 1673, at which time the whaling industry was 'revived' on the understanding that oil could be exported directly to any part of the British empire rather than solely to London (Wilkinson, 1933, pp.325-6). For obscure reasons, however, it continued to be unprofitable and by 1676, according to Wilkinson (citing Lefroy, 1877, pp.ii, 357-60, 382, 402, 412), 'the vaunted whaling rights had almost lapsed through disuse'. According to Kennedy (1971, p.249) 'whales were being killed indiscriminately' in the early 1680s, meaning that the Bermuda Company's efforts to collect the royalty on whale oil had become ineffectual.

1685-1779

In 1687, the stifling restrictions on whaling (see above) were lifted and this must have encouraged more people to attempt it (Schortman, 1969). Beginning in 1689 Governor Richier petitioned the Lords of Trade and Plantation for more resources to develop the local whale fishery, claiming that the island's only 'staple export' was tobacco (Anon., 1946). By implication, the production of whale oil was modest despite the great demand for it in Britain. At the time, whale oil cost £12/tun in the colony compared with $\pounds 26-\pounds 30$ in London. Richier regarded the whale fishery as 'wholly destroyed' and in great need of restoration. He noted that although the governor's salary was supposed to be supplemented each year by a £100 share from the proceeds of the whale fishery, his predecessor had realised no more than £36 annually. Apparently referring to the period 11 January-20 July 1691, Richier wrote that 4 large and 4 small whales had been taken and that 3 more large ones had 'escaped owing to bad tackle'. He went on to describe the circumstances and prospects of the whale fishery as follows (Anon., 1946):

'... there are but three boats, one at both ends of the Island. I have computed the charge of fitting out six or eight boats, well equipped, with warps, irons, large kettles for boiling and cisterns for preserving the blubber, and all complete. It will amount to £1,100 or £1,200, and such a sum must be disbursed before the trade can become considerable. I am very willing to lay out the money, could I have a grant for a certain term of years; but until such a grant is made not many whales can be killed;

Bermuda became a Crown Colony in 1685 and according to Verrill (1907), the intensity of whaling increased thereafter. The catch that year was 14 whales. At the time a large whale was valued at about £80, presumably in local currency (Verrill, 1907).

for no Governor will risk his money on an uncertainty and the inhabitants will never attempt to build boats and buy utensils when they are only to fish according to pleasure of future Governors.'

The decline in profitability of tobacco farming in Bermuda in the late 1600s apparently made whaling an increasingly attractive alternative as an export industry.

British import records for London and outports, 1697-1731, indicate whale oil returns from Bermuda totalling about 20,000gal(US), equivalent to only about 20 humpback whales at 1000gal(US)/whale (cf. Adams, 1971) over the entire 35yr period (Reeves *et al.*, 1999, table 13). Reference was made in the Calendar of Treasury Books, 1702-03, to the profits accruing to the British Crown from 'Licences for Fishing of Whales' in Bermuda (Shaw, 1936, p.197).

In the 1720s, 1730s and 1740s, the subject of whaling frequently arose in meetings of the Council because a tax on each whale landed was still being used to supplement the governor's salary (Anon., 1950a; b; 1955a; b; 1956; 1959a; b; 1960a; b; c; 1968a; b). The intent was to raise £100 sterling annually from the whale fishery. One proposal discussed in 1732 was that a duty of 40 shillings be imposed 'on every old whale that shall be killed and brought into these Islands' (Anon., 1955b). Alternative proposals were for duties of £10, £12 or £14 per large whale, 'large' being defined as yielding at least 500gal of oil (Anon., 1960b). At the time, local currency was valued such that £140 was equivalent to £100 sterling. One way of interpreting this information is to estimate that the legislators viewed a catch of 12-14 adult whales per year as a reasonable expectation. However, according to Anon. (1960a), whaling 'was destined never to yield £140 currently a year for any governor' (also see Anon., 1950a). In June 1750 the Council received encouragement from the Lord's Commissioners for Trade and Plantations to enlarge the whale fishery (Anon., 1977). Very little information was found on whaling effort or catches from the 1750s through 1770s although one source indicated that there was considerable enthusiasm for whaling in Bermuda during the 1770s (Anon., 1976a).

1780-1850s

In 1782, the licensing fee owed to the governor was dropped and whaling became a 'free' enterprise (Verrill, 1907; also see Anon., 1976b). As Wilkinson (1973, p.31) noted, the prospect of catching even an 'occasional' whale was so poor that the whaling equipment at St George's was put up for sale (see Fig. 1 for locations of places mentioned in text). However, 5 whales were taken one year in the early 1780s and the local glut of oil caused the price in St George's to drop to 2s8d/gal compared with 3s4d/gal retail in Somerset.

The whale fishery in Bermuda was said to have experienced a 'big revival' in 1780 when an American named Pinkham arrived and introduced an improved method of flensing whales, 'thus avoiding waste' (Zuill, 1946, p.259). Loyalist whalers from Nantucket were encouraged to settle in Bermuda after the American War of Independence, which ended in 1783, but there is scant evidence that they did so (Schortman, 1969; Brown, 1976). Although Zuill (1946, p.259) claimed that whaling was 'one of the colony's important industries' for 50 years starting in 1780, the evidence suggests a much briefer surge. Oil production in some years reached 400-500bbl (Zuill, 1946, p.259). In 1786, Bermuda began sending vessels to the South Seas whale fishery (e.g. the ship Queen Charlotte, brig Governor Browne, schooner Governor Hamilton, sloop Mercury and brig Bermuda; Wilkinson, 1973, p.31). In 1788, the Governor Browne returned with 550bbl of oil and 6cwt of bone (baleen) (Anon., 1976b). In 1792, the Bermuda brought home 900bbl of oil and 7000lb of baleen while the *Governor Browne* returned 400bbl and 5000lb (Wilkinson, 1973, p.31). These large quantities of oil and baleen attributed to Bermuda at this time clearly came from whales taken elsewhere. However, Bermuda's fleet experienced a major downturn after the *Bermuda* was wrecked and the *Governor Browne* became 'generally disabled by the sickness of her crew' in 1793 (Schortman, 1969, p.81). Despite the availability of a small government subsidy and the fact that another brig *Bermuda* returned from the South Seas with 800bbl of oil in 1794, the war with France dampened the islanders' enthusiasm and they failed to respond to a call for more long-distance whaling in the early 1800s (*ibid.*).

At least two shore stations were operating in the late 18th century, one on Paget Island owned by the Hon. John Hinson and another on Smith's Island owned by the Forbes family. Relics of the Smith's Island station were still evident in the 1940s (Zuill, 1946, p.259). Schortman (1969, p.31) described the local catch of 12 whales in 1792 as 'unexpectedly good'. The encyclopaedia statement in 1797 that 'all the attempts to establish a regular whale-fishery on the islands have hitherto proved unsuccessful' (Anon., 1972) suggests that the returns from shore whaling remained modest even as Bermuda's offshore fleet prospered in the late 1780s and early 1790s.

Shore whaling persisted into the early 19th century but the annual catch seems not to have exceeded about a dozen whales. In the 1820s, at least one mariner from Bermuda, C.A. White, emigrated to Trinidad, seeking to establish a shore whaling enterprise there (De Verteuil, 1994, p.70; Reeves et al., 2001). Wilkinson (1973, p.656), apparently referring to the 1830s-40s, reported that 'more than a dozen whales were struck' in one year and 'nearly as many during another season'. This led 'several ardent spirits' elsewhere in the colony to start whaling so that in addition to the main 'whale house' on Smith's Island, smaller operations began at Ferry Point and Tucker's Town. Additional 'cottages' were devoted to opportunistic whaling in Devonshire, Warwick and Southampton and at Whale Island in Ely's Harbour (also see Tucker, 1955). This proliferation of whaling sites seems to have impaired rather than improved the overall efficiency of shore whaling, as 'competing boats encumbered each other in chasing the occasional whale which came close to the shore' (Wilkinson, 1973, p.656). Verrill's (1907) perusal of newspaper accounts led him to conclude that humpback whales had become 'comparatively rare' in the coastal waters of Bermuda by about 1840. He attributed this scarcity to a decline in humpback whale numbers caused not only by local whaling around Bermuda, but also by American whalers working in New England and the West Indies, who 'killed as many and perhaps many more, than the Bermudians'.

In 1832, the Hayward establishment at St David's, one of the largest whaling stations in Bermuda, processed at least seven whales, including one sperm whale, *Physeter macrocephalus* (Verrill, 1907). In 1833-34, whalers by the names of Higgs and Howard were whaling at St George's and at least one whale was secured by Howard's crew: it was 'carried up by moonlight and there were five row boats and two whale-boats to tow it' (Gosling, 1952). On another occasion in one of those years a whale was struck and lost (the line had to be cut) but the same crew 'struck' two more as they were returning to shore (Gosling, 1952). At the time 'good money [was] to be made out of whale-oil' (Gosling, 1952). For an unspecified time within the period 1808-43, two whale boats and their crews were 'ready at a moment's



Fig. 1. Place name map of Bermuda prepared by Elizabeth Josephson.

notice' during the whaling season, apparently on the western or south-western part of the main island (Tucker, 1953, p.11).

A new whaling company formed in 1851 was equipped with a darting gun and several new whaleboats, but only one whale was taken that year (plus one more by an 'independent' boat) (Wilkinson, 1973, p.656). The next year a large humpback was taken at St David's as well as a small sperm whale and in 1853 two large whales and one small one were taken at the east end. A 54ft whale was secured in 1854 but for the next five years the company's boats were unsuccessful. Apparently other companies took several additional whales in 1853 (see Table 2).

Customs and export data, 1795-1860

Data from Blue Books reveal little about Bermudian whaling before 1840. In 1824 and 1825, customs agents stated that Bermuda exported 8,390 and 4,002gal of common oil (here interpreted to mean whale oil, i.e. oil from baleen whales), respectively. Thereafter, customs collectors merely reported the total value of the exports by category. Thus, for oil exports the values listed in the Blue Books and reported to London reflected the total value of all kinds of animal fats, oars and ochre, to name but a few of the commodities grouped together under a single heading.

Annual produce of the shore whale fishery was reported almost verbatim year after year for a quarter of a century (1832 to 1858), thus:

There is an inconsiderable Whale fishery carried on in Bermuda that employs about twelve whale boats and their crews, three months in the year: the number of whales taken seldom exceeds 20 in the season; yielding about 1000 barrels of oil. This Fishery, being carried on very near the land, is capable of considerable extension, at small risque, by the employment of additional capital. The reefs that surround the Islands abound in fish of great variety; and the inhabitants being in general exceedingly well supplied with it at all seasons, it constitutes a considerable portion of their food: there is not, however, any Fish cured for exportation (Bermuda Blue Books, 1832-58).

This repetition suggests that the Colonial Secretary paid little attention to the industry and did not bother, except in 1840 (see below), to make a detailed annual inventory of the whaling industry. Rather, the previous year's assessment was simply copied into the Blue Book, year after year, as an expedient. It was not until 1859 that the statement characterising the whaling industry changed (and it was repeated verbatim in 1860), as follows:

The once flourishing whale fishery in Bermuda has declined a long time since; and this business now employs only about 6 boats and their crews, for three months of the year. The number of whales taken seldom exceeds eight in the season, yielding some 200 barrels of oil. This fishery is capable of much extension by the employment of additional capital, and better labour (Bermuda Blue Books, 1859-60).

For two reasons, outbound manifests and quarterly returns are considered to provide a more reliable picture of oil production and export than that provided by the Blue Books, at least during the mid-19th century. Firstly, ship captains and customs collectors had vested interests in ensuring that outbound manifests were both accurate and preserved because these documents served as the basis for levying tariffs. Secondly, quarterly returns submitted by Bermuda's Controller of Customs between 1840-55, when this post was held by John L. Hurdis, are considered reliable because Hurdis was an amateur naturalist and ornithologist with an interest in natural history and thus probably had a personal scientific bent towards accurate reporting.

Throughout Hurdis's tenure as controller, quarterly returns and export data (i.e. outbound manifest declarations) generally matched well. For example, on 1 July 1850 the Bermudian brig Flora, bound from St George's to Antigua, declared a cargo of 3bbl of common oil (108gal if converted at 36gal/bbl - see above) and quarterly returns for the port of St George's during that period indicated a total of 107gal exported to the British West Indies. A number of inconsistencies within the quarterly return data from 1840-55 nevertheless suggest that these sources need to be interpreted cautiously. For example, Hurdis's 1840 census of Bermuda whaling (Table 3) indicated that all 9,449gal of oil was sold domestically, yet outbound manifests for that year indicated 541gal of common oil and 1,6381/2gal of sperm oil exported, all labelled as locally produced. Unfortunate gaps in the available records preclude a systematic comparison between outbound manifests and the quarterly returns submitted to Hurdis. Fig. 2 shows common

oil exports based on outbound manifests; Fig. 3 shows sperm and mixed oil exports, also based on outbound manifests.



Fig. 2. Quarterly exports of 'common' (whale) oil from Bermuda, 1795-7 and 1827-55. Gallons are presumed to be imperial.



Fig. 3. Occasional exports of sperm oil and of mixed cargoes of sperm and common oil from Bermuda, 1839-55. Gallons are presumed to be imperial.

1860s and later

Although whaling 'ceased to be of any importance to the colony' after 1859 (Wilkinson, 1973, p.657) and whale oil may have become insignificant as an export commodity, some effort continued. Jones (1884, pp.148-49) recorded catches in April 1866 (Masters' establishment at Port Royal) and April 1871 (calf secured, mother struck and lost, boats of Port Royal). 'Almost every year some ... whales [were] taken' and at least 20 were taken in one year off the east end. The whaling stations on Paget Island and Smith's Island closed some time in the 19th century but whaling continued 'in a casual way' from St David's (Zuill, 1946, p.260). Henry ('Tommy') Fox was a well-known shore whaler at St David's Island, apparently beginning sometime in the 1870s or early 1880s (Anon., 1973). A sperm whale was processed at the Smith's Island whale house in 1892 and it supposedly had been 23 years since the previous catch there. In December 1894, a 56ft whale, species unspecified, was taken (Wilkinson, 1973, p.657n).

Verrill (1907) claimed that although boats were still 'kept in readiness' through the end of the 19th century, 'very few' whales were taken from the 1860s onwards. Verrill's view that whaling in Bermuda declined to a desultory condition after the American Civil War was echoed by Schortman (1969), who noted that only a few boats 'occasionally' operated out of St George's in the last decades of the 19th century. There were suggestions that the demise of shore whaling in Bermuda was linked to a decline in availability of humpback whales. Some local people believed that the relative scarcity of whales in the late 19th century was due to the fact that the Royal Navy had begun holding 'target practice' on the whaling grounds to the south of the islands (Schortman, 1969, p.85).

Whaling equipment and techniques

The whaling equipment and methods, as described in the 1660s (Norwood, 1667), were essentially the same as those described for 17th century New York and New England

		Note t	that 'Black' in the	No. of whales to	iken' column	refers mostly if n	of entirely to hur	npback whal	es.			
							Whales and	products				
						Black			Spermaceti			
ps.	Date of formation of estab.	No. of whale boats employed	Total no. men employed	No. months employed	No. taken	No. of gal oil sold in island	No. of gal oil exported	No. taken	No. of gal oil sold in island	No. of gal oil exported	Total gal produced	[Race of crew]
Hayward and Co.	1812	2	21	2	5	4,000					4,000	White men
'1 Lightbower and Co.	1838	2	19	2.5	7	2,019					2,019	Ditto
Royal Co.	1839	ŝ	25	2								Coloured men
s, Smith and Co.	1840	2	19	2.5	1	880		1	2,550		3,430	Ditto
	Total	6	84		8	6,899		-	2,550		9,449	

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Table .

shore whaling. The dimensions of the Bermuda whale boat (Schortman, 1969) exactly matched those of a Long Island whale boat (Edwards and Rattray, 1932): 28ft long, 6ft across. Although Schortman (1969, p.84) described a typical Bermuda crew as including five or six oarsmen, a steersman and a harpooner, this may have come from a misunderstanding of roles. A Long Island whale boat carried a crew of six: the harpooner sat in the bow, followed by four oarsmen, with the captain sitting in the stern and steering (Edwards and Rattray, 1932, pp.56-7). The harpooner rowed with his back to the whale until it was time for him to stand up and fasten to the whale. After darting the whale, he switched places with the captain, who was expected to kill the whale with a lance. The whale towed the boat until it became too exhausted and disabled to avoid being approached closely for lancing. In Bermuda, as in other areas where shore whaling was conducted with small open boats, dead whales were towed to shore and flensed in shallow water. A whale-house would often be equipped with a capstan, situated between the high and low water marks, to allow carcases to be hauled into the shallows. In addition, a limestone block would be set in the intertidal zone to receive the tail anchor, allowing the carcase to be securely moored parallel to the beach for flensing (Schortman, 1969, plate I).

Schortman (1969, p.48) considered the Bermudians' use of a relatively short warp (harpoon line) to have been a major handicap. In his view, it helped explain 'the numerous reports of boats that returned with their bow planks sprung from the stem'. The boat and crew must have been under tremendous strain as they attempted to quell a humpback tethered to a line scarcely longer than 100ft (compared with the 100fa lines used by some American whalers; Edwards and Rattray, 1932, p.56). Interesting by its absence in descriptions of Bermuda shore whaling is any kind of 'drug' (drogue), or buoy, as was typical of shore whaling kits in North Carolina (Reeves and Mitchell, 1988). The Carolina whalers seem to have been loath to remain fast to the whales (usually right whales, Eubalaena glacialis, their principal quarry) and instead used the drug to follow the animal's underwater movements and anticipate where it would rise.

Whaling guns were introduced to Bermuda in c.1817 and apparently were prevalent by the 1830s (Schortman, 1969). Details regarding the types of guns are lacking, but one item imported from England in the early 19th century was described as 'a piece of ordnance (half musket, half cannon) ... used to shoot whales with powder and a harpoon made for that purpose; the latter attached to the gun by a coil of rope – a most ingenious affair' (army officer quoted in Schortman, 1969, p.84).

Species hunted

There is no doubt that the humpback whale was the main target of Bermuda's whalers (see Godet, 1860; True, 1904; Verrill, 1907; Mitchell and Reeves, 1983). The whales' appearance near the islands was strongly seasonal. They arrived in January and left towards the end of May (Norwood, 1945, p.lxvi), the main whaling season being from early March to the end of May (Anon., 1665; Zuill, 1946, p.259) and thus bracketing the peak period of the humpback's presence in Bermuda's near-shore waters (Stone *et al.*, 1987). Mothers and calves comprised a large proportion of the catch (Jones, 1884; Verrill, 1907).

Sperm whales were described by some authors as having been taken only occasionally (Jones, 1884, pp.153-54; Zuill, 1946, p.259), yet according to Verrill (1907, p.277) they were taken 'frequently' during the 18th and 19th centuries. He considered them the most frequently caught species in the 1800s and 'almost the only whales taken' during the last three or four decades of that century. Verrill's supposition rested on meagre evidence, however, as he recorded only seven specific catches (in 1832, 1839, 1840, 1851, 1863, 1869 and 1901) and repeatedly discounted comments associated with the records indicating that they were exceptional. For the most part, the term 'whale' in the literature on Bermuda whaling appears to refer to the humpback, whereas references to sperm whales are usually specified as such (e.g. Wilkinson, 1973, p.657).

Right whales would have been welcome targets but there is little evidence of their regular presence around Bermuda. True's (1904, p.29) assessment concerning the literature on Bermuda whaling seems reasonable:

'... whalebone [baleen] is seldom referred to. It is usually mentioned as something which might be expected to form a valuable product of the industry, but never as a product actually in hand. From this it would appear that to the close of the 17th century at least, the Right whale was not taken at the islands, for it is not probable that the valuable whalebone of that species would have been ignored'.

Logbooks of American offshore ('pelagic') whalers during the 19th century give no suggestion that right whales were found regularly around Bermuda (Reeves and Mitchell, 1986; Reeves, 2001). Apparently a few right whales were taken by the shore whalers in Bermuda, one in 1792 and a pair in about 1840 (Verrill, 1907). A sighting of two right whales reported by Payne and McVay (1971) stands as the only recent record in spite of substantial search effort (e.g. Stone *et al.*, 1987). In 1848, 1850, 1852 and 1855 outbound manifests and quarterly returns list whale bone and whale fins (i.e. baleen) as exports (it should be noted, however, that the 1850 and 1852 exports of whale fins did not appear on the corresponding quarterly returns, perhaps suggesting their infrequent occurrence as a valuable export commodity).

Verrill (1907) mentioned that 'fin-back' whales (*Balaenoptera* spp.) were observed around Bermuda occasionally but not hunted, owing to their 'pugnacity'.

Products and yields

References to oil yield must not be taken literally in all cases. The whalers, and those who reported on their activities, typically assigned whales to size categories by a crude assessment of their potential yield. In many instances the realised production fell short of the whaler's initial estimate (cf. Reeves et al., 1999). Scavenging by sharks during towing reduced oil yields in other low-latitude humpback whaling areas (Mitchell and Reeves, 1983; Reeves et al., 2001) and Bermuda was no exception (Schortman, 1969). In fact, the fishermen there used flensed whale carcases as bait for large sharks, which they speared to obtain liver oil to be used in lamps and, later, as lubricant (Verrill, 1907). In Bermuda's warm conditions, some oil was also lost during towing, flensing and mincing in spite of explicit efforts to avoid wastage. At least some of the whalehouses were equipped with cedar cisterns where the blubber was to be placed as quickly as possible to await mincing and boiling (Schortman, 1969). One cistern would rest at a higher elevation than a second one so that any 'naturally' clarified oil would drain into a separate container for sale at a premium price. Otherwise, the blubber was cut into blanket pieces for carrying from the beach, then chopped into smaller pieces, fed into a mincer and cooked in the trypots. The oil in the pots was strained and poured into a cooling pit, either made of copper or plastered with tarras, 'German earth or natural cement' (Schortman, 1969, p.79).

Whale oil was used in the 19th century and earlier as lamp fuel in homes, offices, lighthouses, beacons and lightships and in industry for paints, tanning hides and lubrication (Stackpole, 1972, p.372). It is reasonable therefore to assume that some of the oil obtained from humpback whales in Bermuda was consumed domestically. At a minimum, local people were allowed to scavenge the flensed carcases and recover small amounts of 'low-grade oil for their lamps' (Schortman, 1969, p.79). A certain amount of the better oil also must have been used to meet the needs of islanders. Note, for example, the reference to local prices of whale oil at St George's and Somerset in the 1780s, mentioned earlier. Records of quantities of whale oil exported should be understood as reflecting less than the full amount produced in any given year. At the same time, however, it cannot be assumed that all oil produced in Bermuda, whether for illumination or lubrication, was whale oil. As noted above, sharks were also fished in Bermuda for their oil and there was some agricultural production of plant oils (e.g. castor and olive) (Verrill, 1907). Coconut oil was commonly used for illumination in Trinidad (Reeves et al., 2001) and may have been among the oils produced in Bermuda as well.

The average yield of humpback whales at Bermuda was 30-40bbl, with each barrel containing 33gal according to Schortman (1969, p.80). Maximum yields were 60-70bbl (Jones, 1884, p.149). Hurdis's data (above) suggest that the whales taken in 1840 were somewhat smaller, averaging 26bbl (based on 33gal/bbl *fide* Schortman, 1969).

A 22ft first-year calf taken in late April was expected to yield about $5\frac{1}{2}$ bbl; a juvenile female taken in the same season, 40bbl (Jones, 1884, pp.148-49). If, as Jones claimed, 'cub whales' (first-year calves and juveniles?) were caught more often than adults, the realised per capita yield in the fishery would have been lower than from a non-selective or primarily adult catch composition. As Schortman (1969, p.83) observed, 'The size of the whales caught must ... have been small or the methods of extracting the oil inefficient'.

No specific reference was found to the Bermuda whalers saving baleen from humpback whales although according to Verrill (1907), 'small quantities were shipped to London'. The export of 4cwt of 'fins' in 1664 (see earlier) is a clear reference to baleen, but this amount could represent the yield from a single right whale.

Like their counterparts in parts of the Lesser Antilles (see Mitchell and Reeves, 1983), the local people in Bermuda relished whale meat (especially that of young animals) and it was less expensive than livestock meat or poultry (Jones, 1884, p.151; also see Godet, 1860). A newspaper report in 1827 described the scene when a whale was towed near shore and local people gathered to claim 'the fleshy parts – called "sea beef"...' (Schortman, 1969, p.82). Although British residents were said to have 'a strong prejudice against this food,' the Bermudians had 'a method of cleansing it, which leaves no fishy flavour and it is tender as veal' (*ibid.*). In times of economic depression, the local importance of 'sea beef' as an inducement for whaling may have rivalled that of oil (*ibid.*).

Sites of whale-houses

During the early years of whaling, humpback whales came very near shore and could be attacked in shallow water. The difficulty and danger of striking them in deep water meant that they were usually struck in 'shoal-water' (Norwood, 1667). At some sites lookouts were stationed on shore to watch for whales and a conch horn was blown to signal a sighting (Schortman, 1969). During the second half of the 18th century most of the whale-houses were at the east end of the archipelago. Schortman (1969) listed six sites, noting that they were not necessarily all active simultaneously: 'Old Whale-House' at Richardson's Bay, Ferry Reach; Green Bay, Castle Harbour; Smith's Island; East Whale Bay, Southampton; Tucker's Town, Devonshire; and Whale Island, Sandy's Parish (at the west end of the island).

In the early 19th century there seems to have been a need to extend operations farther from the coast or at least to more remote areas within the range of the shore whalers. For example, in 1819 the owners of Paget's Whale Fishery advertised that they were stationing a brig on New Ledge 'for the accommodation and security of the Men and Boats' (Schortman, 1969, p.83). They invited anyone with whaling experience to use this platform and hunt whales 'on shares' with the understanding that if no whales were taken, 'no charge will be made'. A chart published in 1814 shows whaling grounds off St David's Head and off Southampton Elbow (western end) (Fig. 4).

CONCLUSIONS

Published sources refer to only 43 successful captures of individual whales and ten additional strikes of what were presumably humpback whales in Bermuda between 1664-91 (Table 2). However, if the 11t of oil obtained from five whales in 1664 were used as a standard (i.e. 2.2t/whale), then the reported amounts of oil exported during that period (Table 2) would indicate about twice that many whales taken. The published record may be only minimally illustrative of the scale of removals in the 1600s.

Little information is available on catch levels at the end of the 1600s and into the early 1700s but they appear to have been fairly low, perhaps only a few whales/yr until the 1730s (see above). Douglas's (1755, in Goode in Mitchell and Reeves, 1983) reference to single-season catches of up to 20, apparently referring to the late 1740s, is difficult to interpret, as is Tucker's (1959) statement that in some years less than ten whales were taken, apparently referring to the 1700s. All indications are that catch levels declined from the mid- to late 1700s, such that by the early 1780s a singleseason catch of 5 whales was regarded as exceptional (Wilkinson, 1973) and 12 (in 1792) as 'unexpectedly good' (Schortman, 1969, p.81). As mentioned earlier, Bermuda exported a total of only 5,478gal of common oil from 1795-97, implying a total catch of 5 or 6 whales by the shore stations in 2 or 3 years.

The available information on catches during the 1800s suggests that rarely more than 10, and never as many as 20, whales were taken by the Bermuda shore whalers in a single year (Table 2). One problem in interpreting the published information is that, with the proliferation of newspapers and growing literacy, the probability that a whaling event would have been recorded in a printed source and thus become available for the edification of 21st century scholars steadily increased with time. Therefore, any impression of increased whaling effort or take could be at least partly a reporting artefact. Another (lesser) problem is determining the species taken. In the early years (e.g. before about 1750), it is possible that right whales were taken more often than seems to have been the case in the last two centuries of Bermuda shore whaling. Also, it is difficult to gauge the relative importance of sperm whales. Their capture appears, judging by the 19th century reports in Table 2, to have been especially noteworthy. Thus, it seems likely that whilst catches of a few humpback whales in a given year may not have been mentioned in newspapers and therefore in derivative compilations such as those by Verrill (1907) and



Fig. 4. Heathers Improved Chart of the Bermudas (Norie, 1814). Image courtesy of Bermuda Maritime Museum, Hamilton.

Wilkinson (1973), any catch of a sperm whale (with its relatively valuable spermaceti and sperm oil) was considered worthy of notice.

The conclusion of Mitchell and Reeves (1983, citing Wilkinson, 1973) that by about 1860 whaling in Bermuda had declined to a desultory level still seems valid. With no oil exported and several thousand barrels imported, it appears that Bermudians had opted for more reliable import sources to meet their needs. In fact, despite repeated calls for increased whaling effort, Bermudian shore whaling from the early 1800s onwards is probably best characterised as an intermittent industry of opportunity. From 1860 until 1942 only about a dozen whale catches were explicitly mentioned in the literature and nearly half of those were of sperm whales (Table 2).

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An approach to minimise bias in estimation of the lengthfrequency distribution of bowhead whales (*Balaena mysticetus*) from aerial photogrammetric data

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ABSTRACT

Past attempts to estimate the length structure of the Bering-Chukchi-Beaufort (B-C-B) stock of bowhead whales have yielded quite different results from one study to the next because of size segregation on the summering areas or because of size segregation during the spring migration combined with inconsistent sampling during the migration period. A new approach is presented to document the length-frequency distribution of the B-C-B stock using length measurements from 3,107 whale images collected during the spring migrations of 1985, 1986, 1989-1992 and 1994. This method provides estimates of the proportion of calves (length <6m), subadults (length 6-<13m) and adults (length ≥13m). The data from all years are combined by weekly period and a bootstrap sampling procedure is used to construct the lengthfrequency by week. The distributions for each week are then combined to obtain the overall distribution, with each week's contribution being in proportion to the fraction of the migration estimated from ice-based census studies to pass during that week. Corrections for differential detectability of mother/calf pairs and for calves born after they pass Point Barrow, Alaska, are allowed for in the analysis. This new approach eliminates some of the biases that affected past attempts to estimate the length-frequency distribution for the B-C-B population of bowhead whales. It is robust to inclusion or exclusion of data for any given year and the time interval chosen to define repeat images. The new approach estimates a slightly higher proportion of subadults and lower proportion of adults in the population than most previous studies. The proportion of calves is also lower, but that is suspected to result from our inability to accurately estimate the proportion of the migration late in the season when many of the mother-calf pairs pass Point Barrow. These late season migrants have not been accounted for during past photogrammetry studies or the ice-based census. Although the results do not differ substantially from those of most previous studies, sensitivity analyses indicate that several biases existed in the previous methods, but largely cancelled each other out.

KEYWORDS: BOWHEAD WHALE; ARCTIC; PHOTOGRAMMETRY; PHOTO-IDENTIFICATION; POPULATION PARAMETERS; LENGTH DISTRIBUTION; BERING SEA; CHUKCHI SEA; BEAUFORT SEA

INTRODUCTION

Several past studies have attempted to establish the length structure of the Bering-Chukchi-Beaufort (B-C-B) stock of the bowhead whale (Balaena mysticetus) using aerial photogrammetry. The earliest studies were conducted in 1982 and 1983 by Davis et al. (1983) and Cubbage and Calambokidis (1987), respectively, who photographed bowhead whales on their summer feeding grounds in the eastern Beaufort Sea and Amundsen Gulf. These and later studies conducted during the summer were successful at obtaining large numbers of photographs of bowhead whales, but it was difficult to assess whether the photographs were representative of the overall population because of segregation of bowhead whales of different sizes during the summer (Cubbage and Calambokidis, 1987; Koski et al., 1988). During some years, such as 1985, it was clear that the sample was not representative of the overall population because few large whales were photographed even though whales were abundant in the survey area and 1,601 photographs were obtained (Davis et al., 1986).

From 1985-1994, studies attempting to document the length structure of B-C-B bowhead whales were conducted near Point Barrow, Alaska (Withrow and Angliss, 1992; 1994; Angliss *et al.*, 1995), primarily by the National Marine Mammal Laboratory (NMML). Most B-C-B bowhead whales are thought to pass relatively close to Point Barrow during their spring migration from early April to

mid-June toward summer feeding areas in the Beaufort Sea (Braham et al., 1980; Braham et al., 1984; Moore and Reeves, 1993). It was thought that photographic surveys at that time of year would provide unbiased estimates of the length structure of the population. However, the length structures obtained during different years differed substantially (Withrow and Angliss, 1992; 1994). The biases associated with the photographic surveys near Point Barrow are discussed by Angliss et al. (1995). The two main biases are associated with (1) the differences in behaviour and hence detectability, of the different size classes of bowhead whales; and (2) the fact that the migration is size segregated and sampling has not been constant throughout the period of the migration. The behavioural biases affect collection of photographs throughout the season. Interruptions in surveys due to poor weather, not starting surveys until the migration is well underway, or terminating surveys before the end of the migration result in unequal sampling of different size classes of whales. By analysing data from several years simultaneously, Angliss et al. (1995) were able to derive a better estimate of the length structure of the population by averaging biases associated with (2) over several seasons. However, they were not able to directly address bias (1) and that had unknown effects on the population structure that they presented. Additional biases identified by Koski et al. (2004) include: (3) mothers and calves linger near Barrow, sometimes for several days, whereas other whales rarely linger, making mothers and calves more likely to be

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photographed; and (4) the surface and dive times of bowhead whales vary with their size and so large whales are less likely to be seen and photographed than small whales or calves.

The purpose of this paper is to present a new method of estimating the length structure of the B-C-B bowhead population that minimises most of the biases that exist in previous methods. It uses the combined data from photographic surveys conducted near Point Barrow during the springs of 1985, 1986, 1989-1992 and 1994. In order to calculate an unbiased length-frequency distribution, data on average rates of passage by weekly interval from the ice-based censuses from 1985 to 2001 (see Zeh *et al.*, 1986a; b; 1991; 1993; George *et al.*, 2003; 2004) are incorporated. Factors to account for biases attributable to differences in the behaviour of mothers and calves relative to other whales (Koski *et al.*, 2004) are also incorporated.

METHODS

Field effort

The surveys that contributed to the current analysis were conducted primarily by the NMML and were designed and conducted to cover most of the bowhead migration past Point Barrow. The surveys were conducted from about mid-April to early June in 1985, 1986 and 1989-1992. Less extensive spring surveys by LGL Limited (LGL) were used to supplement the NMML surveys during 1989 and 1991. LGL surveys were the only source of data in 1994.

Photographic surveys were carried out in twin-engine (for safety), high-wing (for visibility) aircraft (Twin Otters), with large bubble windows on the sides and a photographic port in the floor, either open or covered with optical quality glass. Flight altitudes for photography were generally 122-152m (400-500ft) above sea level as measured by a radar altimeter and airspeed was usually about 185km hr^{-1} (100kt). During the whales' spring migration past Point Barrow (April to early June), the search efforts were conducted over sea ice and leads but were focused along open water areas, especially near the land-fast ice edge. After finding bowhead whales, a series of aerial passes was made to obtain vertical photographs through the port in the floor of the aircraft. Medium format cameras (70mm) were used for photogrammetry in all years. Fixed focal length lenses were used and all lenses were calibrated to determine their true focal length. Cameras were either hand-held or rigidly mounted. Each year, calibration targets were set up and photographed to permit scaling of radar altimeter altitudes recorded during photography to actual altitudes. For more information on field methods, see Rugh (1990), Koski et al. (1992), Withrow and Angliss (1992; 1994) and Angliss et al. (1995).

Photo review

After processing and cataloguing, useable whale images were custom-cropped and printed to nearly fill 12.7cm \times 17.8cm (5in \times 7in) colour prints (Rugh *et al.*, 1992). The images were assigned quality and identifiability scores for each of four dorsal areas on each photograph of each whale: rostrum; mid-back; lower back; and fluke (Rugh *et al.*, 1998). All images within five days of each other were compared to each other to identify both repeat and duplicate photographs, so that a number of images for that individual could be used to calculate a best estimate of length (see below). Repeat photographs were those taken <60s apart and were treated as a single record during analyses. Duplicate photographs were those taken ≥ 60 s apart during the same study and were included as separate records during analyses. Although past studies have created lengthfrequency distributions after eliminating repeat and duplicate images from the database, this study uses lengths from all measured images in the analysis in order to minimise biases associated with the ability to reidentify whales of different sizes. Five days was the maximum interval examined for duplicates because that was the maximum resighting interval detected by Rugh (1990). He examined 488 identifiable bowhead whales photographed near Barrow in the springs of 1984-87 for resightings at a later date. Fourteen whales were resighted on a subsequent date; eight, four, one and one were resighted after one, two, three and five days, respectively.

Measurements of whales

Whales were measured directly from the film using a stereomicroscope (LGL), a dissecting microscope and digitising pad (NMML) or computer image analysis software (NMML). At least three measurements by one person (LGL) or two measurements each by a different person (NMML) were made of each whale image and the measurements were averaged. If individual measurements differed by more than 1% (LGL) or 3% (NMML) the image was remeasured. If the measurements did not converge, the measurements were discarded or downgraded so that they were not used for photogrammetric purposes. The quality of each measurement was evaluated based on the clarity of the end points and the straightness of the whale. The criteria used by each organisation were similar, but with slightly different cut points and are described in Appendix 1. Equivalent grades of measurements (GRL) and the criteria for inclusion in the category are given in Table 1. More details of the measurement techniques and evaluations can be found in Koski et al. (1992) for LGL data and Angliss et al. (1995) for NMML data.

Table I

Equivalent quality ratings for length measurements of bowhead whales as documented in various studies. Measurement qualities for each organisation are defined in Appendix 1. (Cascadia data were not used in this study.)

Measurement quality	LGL	NMML and Cascadia 1985 to present	Cascadia 1983
Good	1, 2, and 3	1 and 2	1 to 6
Fair	4, 5, and 6	3 and 4	7
Approximate	8 and 9	none	None
Negatively biased (oblique)	7	5	8

Criteria for analyses of lengths

Previous studies have shown that the major source of between-image variation in the calculation of whale lengths is error in radar altimeter output, with lesser contributions from the posture of the whale or the quality of the photograph (Koski *et al.*, 1992; Angliss *et al.*, 1995). The mean CV of a single length measurement of good or fair quality is ~2.1% (unpublished data). Table 2 shows the mean CV and mean SE of the 'best estimate' of length (BESTLEN in Appendix 1) of whales in this study according to a subjective rating (GRLEN). The better the quality of GRLEN, the more precise the length measurement. Therefore BESTLEN is used for each whale image regardless of the actual measurement made from that image. All good and fair length measurements for each whale in a given year, categorised as shown in Table 1, were averaged to calculate best length. The quality rating for the best length (GRLEN) takes account of the number of measurements and the quality of the original measurements that make up the best length as described in Appendix 1. Although the best length may be available for a particular image, it was not included in the length-frequency analysis if the image itself did not have a measurement rated as good or fair (GRL) as described in Table 1 and Appendix 1.

Table 2 Mean BESTLENs, mean CVs of each BESTLEN and mean SEs of each BESTLEN of whales photographed near Point Barrow, Alaska, during spring 1985-86, 1989-92 and 1994.

		Mean		
BESTLEN quality (GRLEN)	BESTLEN	CVs (%) of each BESTLEN	SEs of each BESTLEN	n
1	10.48	1.25	0.1206	23
2	12.77	1.62	0.1852	97
3	12.23	1.81	0.2027	164
4	11.87	1.89	0.2037	77
5	11.76	NA*	NA*	641
6	11.29	NA*	NA*	816

*Not available – only one measurement is available for each whale.

Creation of the length-frequency distribution

Data from nine surveys conducted from 1985 to 1994 (six by NMML and three by LGL) were used to construct lengthfrequency distributions of the BCB bowhead whale population. The six NMML surveys were selected because each of them includes a sampling of most or all of the spring migration in the Point Barrow area. Results from two overlapping surveys (one each by NMML and LGL) are available for each of 1989 and 1991, while results from a single survey are available for each of 1994 (LGL), 1985, 1986, 1990 and 1992 (NMML). Earlier studies have shown that the techniques used by the two organisations provide results that are comparable (Koski *et al.*, 1992).

Initially, whale length was plotted against the date on which the photograph was taken for each year and for all years combined. These plots showed that although there were gaps in coverage of 1-7 days during individual years, the combined dataset provided length data for each day during the main part of the migration (Fig. 1b). They also confirmed that migration timing in 1985 was unusual (Fig. 1a). The 1985 migration appears to have been 5-11 days late based on ice-based census data and on photogrammetry data that provide passage dates of whales of a given size in other years (Fig. 1b). A marker for this shift is the end of the migration of small whales, excluding yearlings and youngof-the-year calves (see Koski et al., 2004). Many small whales were present near Point Barrow on day 146 (26 May) in 1985 (Fig. 1a); whereas, in other years, all but a few small whales had passed by day 135 (Fig. 1b). Because 1985 provided the largest number of measured whales, we did not want to exclude it from the analysis. Shifts of 5-11 days were examined to see which best matched the other years' photogrammetry distributions in terms of quartiles of length distributions by week; number of measured whales by week; and % calves, subadults and adults by week. By all criteria, a 9-day shift in the 1985 timing resulted in the best match with other years' data. Thus length data from 1985 were combined with data from other years that were collected nine days earlier as indicated in Table 3.



Fig. 1. Lengths of bowhead whales photographed in spring of (a) 1985 and (b) 1986, 1989-92 and 1994. The solid squares in panel (a) are whale sizes that were not seen during that same time period (i.e. were seen earlier) during 1986, 1989-92 and 1994.

The procedure used to construct length-frequencies involved first developing a database of 'useable' images (and their associated lengths and quality codes) based on the following criteria.

- (1) Any photographs from 71-72°N and from 153-157°30'W were included. This area was chosen because it was surveyed regularly during the selected studies. It would be traversed by a typical whale in about 1-2 days of migration.
- (2) Images that did not have a good or fair measurement quality as defined in Table 1 were deleted. The 'best length' for each animal was used rather than the measurement obtained from an individual photograph when more than one photograph of that whale was available. The 'best length' was determined using the approach outlined in Appendix 1 and was taken to be the same for all photographs of each animal in the same year.
- (3) Any repeat photographs (i.e. photographs of the same whale taken at the same time) were deleted. 'Same time' was defined as <60s apart. Sensitivity was explored by, alternatively, defining repeats as photographs taken 0 seconds apart (i.e. at the same time) and <5min apart.</p>
- (4) During the length sampling, lone calves were discarded and mother/calf pairs were treated as a unit because lone calves often cannot be matched with themselves or with their mothers. When a record indicated that a whale was a mother, but the calf was not measured, the length of the calf was selected at random from the lengths of lone calves.

The length-frequency was computed using a bootstrap process with 10,000 samples being drawn during each bootstrap. This bootstrap process replicated the distribution

Table 3	
ates used to combine length data into 'weekly periods' for years except 1985 (1986, 1989-1992 and 1994) and 19	985
Weeks 1 and 7 are longer than 7 days.	

				Weekly period	1		
Year	1	2	3	4	5	6	7
Except 1985 1985	<23 Apr <2 May	23-29 Apr 2-8 May	30 Apr-6 May 9-15 May	7-13 May 16-22 May	14-20 May 23-29 May	21-27 May 30 May-5 Jun	>27 May >5 Jun

of photographs across the season, accounted for disproportionate sampling at certain times during the season (the number of photographs taken during a week was not necessarily proportional to the number of animals that are estimated to pass Point Barrow during that period) and accounted for over-sampling of mother-calf pairs. This oversampling occurs because mother/calf pairs are much more likely to be photographed than other whales during their spring migration past Point Barrow (Koski *et al.*, 2004). The surfacing and dive behaviour and swimming speeds of mothers and calves are noticeably different from those of other whales. These biases are described in detail in the section on 'Bias corrections'.

Each bootstrap replicate involved the following steps for each 'week', *w*, of the season.

- (1) Determine the number of 'useable' photographs, N_w , for 'week' w and the proportion of the migration, R_w , that passes Point Barrow during this 'week' as determined from the ice-based census data (see 'Proportion of migration by week').
- (2) Sample photographs (with replacement) from the 'useable' photographs for the week, discarding photographs of mother-calf pairs with a probability that accounts for 'over-sampling' of mother-calf pairs (a probability of inclusion of 0.406 for the baseline calculations see 'Bias corrections' below), until the total number of sampled (but not discarded) photographs for the week is N_w .
- (3) After the length-frequency for 'week' w is created, divide the number of calves in that week by 0.89 to account for calves that are born after they pass Point Barrow (see 'Bias corrections' below for the rationale for the choice of 0.89 for this correction factor).
- (4) Add the length-frequency for week w to the total length-frequency weighting it by R_w .

Bias corrections

A systematic bias was found in the 1986 NMML length data, based on comparisons of individual whales photographed in two or more years (Koski *et al.*, 1992, p.494). The source of the error could not be identified but it probably was either related to an error in the calibration of the radar altimeter output or an adjustment to the radar altimeter after calibration. Of 19 whales measured both during 1986 and in other years, all were larger (mean 1.066 ±SE 0.012 times) than expected in 1986 after adjusting for expected growth between years (*t*-test, P<0.001). Therefore, it appears that a consistent upward bias of 6.6% was present in the original length calculations for 1986. This bias was not allowed for in previous publications based on the photogrammetry database but has been accounted for here by dividing the original 'best lengths' from the 1986 spring study by 1.066. Analyses by Koski *et al.* (2004) indicate that mother/calf pairs (in spring, calves are <5.5m long) are photographed more often than other whales. Thus adjustments were needed to allow for the greater number of photographs of mother/calf pairs compared to other whales. Three biases have been described that contribute to the additional photographs of mothers and calves.

- (1) The surfacing, respiration and dive cycles of calves are such that they are at or near the surface and therefore available to be photographed 1.69 times more frequently than other whales (Koski *et al.*, 2004).
- (2) Both LGL and NMML made extra passes over mothers and calves to increase the probability of obtaining high quality images of the mother because of interest in documenting calving intervals. Two biases resulted: (a) a higher proportion of mothers than other whales that were encountered had at least one useable length measurement; and (b) more photographs were obtained of individual mothers and calves than of other whales. As a results of these two effects, there are 1.71 measured images (GRL≥1 and GRL≤6) of each mother and only 1.17 measured images of other whales.
- (3) The average swimming speed of mother/calf pairs is much slower than that of other whales during their migration past Point Barrow in spring. As a result, mother/calf pairs sometimes remain in the survey area for more than one day and, unlike other whales, could be first photographed on their second or subsequent days in the area. This bias has not been quantified, but results in the proportion of mother/calf pairs in the length-frequency distribution being over-estimated (Koski *et al.*, 2004). Note that step 2 adjusts for mother/calf pairs that are photographed on more than one day but not for those that would not have been photographed if they travelled as fast as other whales.

The first two biases increase the probability that a given mother/calf pair will be sampled by a factor of about 2.46 ($1.69 \times 1.71/1.17$). Accordingly, during the bootstrapping process, images of mother/calf pairs were ignored with probability 0.594 (1-1/2.46) when constructing the length-frequencies. As has been the case for previous analyses of the length-frequency distribution of the B-C-B bowhead whale, it was not possible to account for the third bias.

Estimates of the annual calving rate based on data from the Point Barrow area during spring migration also need to include a factor for pregnant whales that deliver a calf after passing through the study area. An estimate can be made from the number of images with mother/calf pairs by assuming that 11% of calves are born east of Point Barrow, i.e. by dividing the observed number of calves by 0.89 (see Koski *et al.*, 1993). It is assumed that the mothers of these late-born calves are included in the sample of adults for the respective season.

Proportion of migration by week

The proportion of the migration that passed Point Barrow during each weekly period was estimated from data from the census years 1985, 1986, 1988, 1993 and 2001. Zeh and Punt (2005) summarise the data and methods used to determine abundance. Data for 1985 were shifted 9 days earlier because of the unusual migration timing, discussed above and 1987 was excluded because the ice-based census started late and ended early that year. Daily estimates of whales passing within visual range were obtained as described by George et al. (2004) and were summed for each week. The first and last weeks' estimates were scaled up to account for days before the census started and after the census ended when whales were known to have passed Point Barrow based on ice-based and aerial survey observations (Clark and Ellison, 1988; George et al., 1987; 1990; 1995; 2003). This procedure may underestimate the numbers passing early and especially late in the season because the actual start and end dates of the migration in each year are unknown. Each weekly visual estimate was corrected by dividing by the proportion of whales estimated from acoustic and aerial transect survey data to have passed within visual range during the week. This provided an estimate of the total number of whales that passed each week. The weekly total estimates were divided by their sum for each year to estimate the proportion of the migration for that year represented by each week. Finally, the proportions for each week were averaged over the five census years.

The migration was divided into one week (7 day) bins starting with 23 April and ending on 27 May (Table 3). The proportions of the migration before 23 April and after 27 May each included >7 days because photographic effort during these periods was low and the early and late stages of the migration extended well beyond 7 days earlier and later than these dates.

RESULTS

A total of 4,828 whale images were obtained within the study area during 1985, 1986, 1989-1992 and 1994. Fig. 2 shows the locations where these images were obtained during April, early-to-mid May and late May to early June. Numbers of whale images with reliable lengths during each year by weekly period are shown in Table 4. Reliable length measurements (GRLEN=1-6 in Appendix 1) are available

for 3,107 images or 64% of the available images. Of these measurements, 41% (1,288) are based on more than one measurement (GRLEN=1-4 in Appendix 1C) and 59% (1,819) are based on a single measurement that is precise enough to be used to determine life-history information (GRLEN=5 or 6). Some other whales (109) were measured but were not included in the analysis because they were negatively biased or imprecise because (1) the radar altimeter was unstable, (2) they were estimated from a measurement of a part of the whale or (3) the photograph was not vertical to the water surface.

Revised length-frequency distribution

The approach to estimating the length-frequency distribution of the population given here assumes that migration timing is similar from year to year, unless, as in 1985, the migration was delayed for a prolonged length of time. Over- and under-sampling during parts of the migration is accounted for by weighting the size distribution for each week based on the proportion of the migration that passes during that week in an average year. The impact of excluding the 1985 data, which were adjusted for the unusual migration timing, is examined in one of the tests of sensitivity described below.

The total number of whale images within the study area and the number of useable lengths after each exclusion are given in Table 5. The numbers of images in the right-most column of Table 5 are those that were used to create the length-frequency distributions. The proportion of the migration that passed Point Barrow during each of the seven periods and the proportion of useable images are shown in Table 6. The periods through 6 May tended to have fewer length measurements and the later periods more than should have been obtained if sampling were proportional to the migration. Fig. 3 shows the length-frequency distributions generated from the weekly samplings. Primarily subadult animals were photographed before 29 April and the sizes of whales gradually increased throughout the migration period with few small whales and primarily large whales during the 14-20 May period. The small whales on the left side of the 14-20 May plot represent calves and yearlings (see Koski et al., 2004). After 27 May, only mothers with calves and large whales were seen. The overall length-frequency distribution generated using these data is shown in Fig. 4.

Table 4

Numbers of reliable (GRLEN=1-6) whale measurements obtained in the study area by week during each study. For the 1985 NMML study, raw numbers for the weeks shown in the column headings and adjusted numbers for the 1985 weeks in Table 3 are presented.

	Weekly period								
Study	<23 Apr	23-29 Apr	30 Apr-6 May	7-13 May	14-20 May	21-27 May	>27 May	Total	
1985 - raw	0	8	9	28	299	117	274	735	
1985 - adjusted	8	12	25	336	117	229	8	735	
1986 - NMML	0	0	93	121	57	139	65	475	
1989 - NMML	53	66	70	14	59	26	27	315	
1989 - LGL	0	0	2	0	17	36	32	87	
1990 - NMML	4	54	1	178	66	24	42	369	
1991 - NMML	2	37	54	120	41	55	12	321	
1991 - LGL	0	1	24	12	68	65	0	170	
1992 - NMML	20	151	36	84	80	45	49	465	
1994 - LGL	0	0	20	94	53	3	0	170	
Total*	87	321	325	959	558	622	235	3,107	

*Totals are based on adjusted numbers for 1985.

The examination of the sensitivity of the results to the various corrections and selection criteria is based on how the proportions of calves, subadults and adults changes (Table 7). The greatest sensitivity is associated with excluding lengths with GRLEN=6; the proportion of subadults declined from 0.569 to 0.483 and the proportion of adults increased from 0.398 to 0.448. None of the other sensitivity cases had a major influence on the proportions of subadults and adults. The proportion of calves was, however, sensitive to the mother/calf corrections; this proportion increased from 0.034 to 0.049 when the correction for diving behaviour was ignored and to 0.063 when all corrections were ignored. Excluding the 1985 data increased the overall proportion of calves slightly.

Table 5

The number of 'useable' whale measurements for the base-case analysis by week after each of the exclusions.

		Numł	Number of images remaining after exclusion of					
Week	Number of images	GRLEN <1 or >6	Lengths assigned to images without good lengths	Repeat images	Calves			
All	4,828	3,107	2,433	2,235	2,069			
1	210	87	73	71	71			
2	543	321	289	266	266			
3	690	325	258	246	246			
4	1,588	959	832	778	774			
5	773	558	400	357	322			
6	721	622	439	393	311			
7	303	235	142	124	79			



Fig. 2. Locations of measured bowhead whales photographed near Point Barrow, Alaska during photographic studies, 1985, 1986, 1989-1992 and 1994. The top, middle and lower panels show images obtained 15-30 April, 1-21 May and 22 May-6 June, respectively.



Fig. 3. The weekly length-frequency distributions generated from length measurements obtained during each weekly period 1985, 1986, 1989-1992 and 1994. The solid line is the median from the bootstrap procedure and the dotted lines are bootstrap 95% confidence intervals.

Table 6

The numbers and proportions of 'useable' images obtained in the study area by week after all exclusions and the relative proportions of the bowhead migrations passing Barrow, Alaska, by weekly period. The proportion of images is based on shifting the 1985 images 9 days earlier (1985 – adjusted) in Table 4. The proportion of the migration by week is estimated from ice-based census data from 1985, 1986, 1988, 1993 and 2001.

	<23 Apr.	23-29 Apr.	30 Apr 6 May	7-13 May	14-20 May	21-27 May	>27 May
'Useable' images	71	266	246	774	322	311	79
Proportion of images	0.034	0.129	0.119	0.374	0.156	0.150	0.038
Proportion of migration	0.0613	0.1168	0.2087	0.3235	0.1508	0.0787	0.0602

Table 7

Proportions of calves ($\leq 6m$), subadults (6-<13m) and adults ($\geq 13m$) for each of the 13 cases. The base case includes: length data from all study years, both m/c corrections, measurements with GRLEN=1-6 and photographs of the same whale taken <60 seconds apart are considered repeats and are only included once.

		No.	Calves		Subadults		Adults	
Case	Description	Images	Estimate	SD	Estimate	SD	Estimate	SD
1	Base-case	2,069	0.0339	0.0040	0.5686	0.0105	0.3975	0.0100
2	No m/c corrections	2,069	0.0627	0.0045	0.5440	0.0103	0.3933	0.0095
3	No 1.69 correction	2,069	0.0493	0.0044	0.5556	0.0103	0.3951	0.0097
4	GRLEN ≤5	1,290	0.0691	0.0051	0.4825	0.0138	0.4484	0.0132
5	Repeats $= 0 \sec$	2,247	0.0337	0.0037	0.5622	0.0101	0.4041	0.0096
6	Repeats <5 mins	1,898	0.0341	0.0044	0.5711	0.0108	0.3948	0.0103
7	Without 1985 data	1,544	0.0436	0.0052	0.5623	0.0128	0.3941	0.0120
8	Without 1986 data	1,819	0.0326	0.0052	0.5937	0.0183	0.3737	0.0174
9	Without 1989 data	1,839	0.0281	0.0046	0.5727	0.0141	0.3992	0.0135
10	Without 1990 data	1,805	0.0297	0.0045	0.5708	0.0119	0.3995	0.0115
11	Without 1991 data	1,750	0.0302	0.0043	0.5774	0.0125	0.3925	0.0121
12	Without 1992 data	1,751	0.0369	0.0046	0.5683	0.0125	0.3947	0.0120
13	Without 1994 data	1,906	0.0363	0.0042	0.5513	0.0113	0.4124	0.0108



Fig. 4. Length-frequency distribution of the Bering-Chukchi-Beaufort stock of bowhead whales based on measurements from photogrammetric studies conducted in spring 1985, 1986, 1989-1992 and 1994.

DISCUSSION

The length-frequency distribution of the BCB bowhead whales presented here accounts for most of the potential biases associated with the collection of the length data. However, three biases could not be addressed: (1) mother/calf pairs move more slowly past Point Barrow than do other whales (Koski et al., 2004) and the effect of this slower travel on the probability of photographing a mother/calf pair has not been quantified; (2) mortality among new-born calves has not been quantified and may be significant; and (3) some of the migration passes Point Barrow before the census starts and after the census ends. Although the fraction of the migration after the census ends is small, it may have significant impacts on the estimate of the proportion of calves in the population because mothers and calves make up about half of the whales during the last sampling period (Fig. 3).

The robustness of the method is confirmed by the minor changes in the proportions of each age class during the sensitivity runs. No noticeable change in the proportion of each age class was found when any of the years was excluded from the analysis, although those proportions are highly variable among years (Table 8). Similarly, the results were insensitive to whether 0s, <60s or <5min between photos was selected to designate when images are repeats (i.e. those images treated as a single photograph for sampling purposes).

Corrections to the proportions of mother/calf pairs during the bootstrapping procedure had the greatest effect on the proportions of calves in the population, but exclusion of the mother/calf corrections had little effect on the proportions of adults and subadults other than the obvious effect of slightly decreasing the proportions of subadults and adults as the proportion of calves increased. Studies by Withrow and Angliss (1992; 1994) and Angliss et al. (1995) attempted to account for increased effort to photograph mothers and calves by including only one photograph of each whale when constructing their distribution (i.e. they removed known repeat and duplicate measurements). However, their method causes overestimation of small, unmarked whales in the length-frequency distribution because duplicates of small whales are less likely to be recognised and eliminated as duplicates. Our method samples all measured whales, whether or not they are duplicates (except for repeats which are multiple simultaneous or nearly simultaneous images of the same whale which are treated as a single image) and so does not rely on accurate re-identification of whales to

 Table 8

 Percentages of calves, subadults and adults estimated during different analyses.

2		
Calves	Subadults	Adults
1.0	56.9	42.1
6.6	48.7	44.7
8.1	53.4	38.6
4.0	64.1	31.8
0.7	65.5	33.7
3.3	57.5	39.2
5.2	53.7	41.1
3.4	56.9	39.7
	Calves 1.0 6.6 8.1 4.0 0.7 3.3 5.2 3.4	Calves Subadults 1.0 56.9 6.6 48.7 8.1 53.4 4.0 64.1 0.7 65.5 3.3 57.5 5.2 53.7 3.4 56.9

obtain an unbiased sample. The procedure of Withrow and Angliss (1992; 1994) and Angliss *et al.* (1995) also assumes that mother/calf pairs are no more likely to be detected and photographed than other whales. Analyses conducted by Koski *et al.* (2004) show that mother/calf pairs are about 1.69 times more likely to be detected than other whales because dives of small calves are much shorter than those of other whales.

Previous analyses have found that small whales are more difficult to measure and that the quality of measurements of small whales tends to be poorer than that of large whales (see Davis *et al.*, 1983, table 8). For that reason, all measurements with quality considered suitable for lifehistory studies were used (GRLEN = 1-6, Appendix 1). Sensitivity analysis that restricted the calculation of the length-frequency to higher quality measurements (Table 7 – case 4) resulted in a 103% increase in the proportion of calves (from 0.034 to 0.069), a 13% increase in adults and a 15% decrease in subadults. These results are consistent with the finding of the previous study by Davis *et al.* (1983) and was the only sensitivity analysis that had a noticeable impact on the proportions of subadults and adults.

Although earlier attempts to construct length-frequency distributions yielded relatively similar results to those of this study (Table 8), it was coincidental that negative and positive biases in the earlier methods for determining the length-frequency of the population largely cancelled each other out. Even after combining data from seven spring seasons, photographs from some weekly periods were not proportional to the migration passing during that period (Table 6). There is a tendency to under-sample whales passing early in the season because heavy ice cover makes detection and photography of whales difficult and a tendency to over sample near the end of the migration when open water makes detection and photography relatively easy. However, the adequacy of sampling at the end of the season, when the majority of mothers and calves pass Point Barrow (Fig. 1b), has been variable. In all of the seasons reported here, photography stopped before the migration ended and the end dates were variable among years.

The remaining weakness in the analysis presented here is the inability to accurately estimate the proportion of whales passing after the census ended. This is true for all years, but is more problematic during years when aerial surveys were not conducted after the ice-based census ended. For example, 1993 was a year with large numbers of calves but no census observations or aerial surveys after 4 June. Based on data from other years, the migration may have continued for another week, therefore resulting in a possible underestimate of the proportion passing after 27 May. Based on the available 1993 data, an estimated 3.5% of the migration passed after 27 May, but in 2001, which was a high calf year when survey data were available later in the season, an estimate of 8.6% of the migration passing after 27 May was obtained. This bias causes an underestimate of the proportion of calves in the population.

Krogman (1980) estimated that <4% of the bowhead migration passes Point Barrow after the end of the ice-based census. Here data from ice-based observations, acoustic arrays and aerial surveys were used to estimate the proportion of the population passing Point Barrow before and after the census. While some animals may have passed before the nominal start date or after the nominal end date for the respective years, these numbers were probably small and would not alter the overall length-frequency distribution. However, as noted above, failure to account for small numbers passing at the end of the migration probably led to an underestimate of the proportion of calves in the population.

Data obtained from photography/photogrammetry studies of bowhead whales have made major contributions to our knowledge of the biology and life history of this species. Continuation of these studies will allow us to refine estimates made from past studies and estimate parameters that have not yet been examined. Unlike some other forms of observation, photographs provide permanent records of whales at a point in time.

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Appendix 1

(a) Length grades (GRL) as documented by NMML

Definitions of quality ratings assigned to bowhead whale morphometric measurements as documented for NMML (from Table 1 in Angliss et al., 1995).

Quali	ty Description			
Total length, fluke width and rostral length				
1	Good view of measurement points; clear, unambiguous end points.			
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- Fair view of measurement points; edges fuzzy, but discernible endpoints 3
- Poor view of endpoints; edges hazy; questionable as to where endpoints are; judgement required.
- 4 Points estimated or interpolated; one end obscured; tail or snout not visible.
- 5 Endpoints not visible.

Flatness

- Whale is flat relative to the sea surface.
- 2 Whale is slightly flexed upward or downward at snout or flukes; slight bow in the back; one end is higher than the other; twist in one plane.
- 3 Whale is clearly flexed; foreshortening undisputed.

(b) Length grades (GRL) as documented by LGL

Grade

Total length, fluke width and rostral length

- The whale was flat, horizontal and straight. The extremities are distinct. 1
- 2 The whale is approximately flat but may be slightly twisted. The extremities are distinct.
- The whale is slightly inclined, arched or flexed or severely twisted and horizontal or the extremities are indistinct, but visible. 3
- 4 The whale is arched, flexed or severely twisted and the extremities could be indistinct. If the whale is straight and horizontal the end points may not be visible but nearby areas are visible, such as the trailing edge of the fluke.

Description

- Whale is severely arched or flexed. Measured lengths are multiplied by 1.0185 to account for the average underestimate of lengths of this grade of 5 measurement.
- The tail is down or the end points are not visible but some feature is available which will permit an estimation of the end points. Also used when the radar altimeter is fluctuating 8-12 feet within a few seconds of the photo.
- Measurement is negatively biased because the photograph was oblique or the whale was too severely arched or inclined to measure accurately.

8 & 9 Adequate calibration data were not available; measurement is approximate.

(c) Best length grades and calculations

Best length (BESTLEN)

For purposes of most analyses, each whale photographed must be assigned a single length value - the best length. This value is assigned to each duplicate and repeat image of that whale. (That is, within each year, the same length is given to all images of the same whale).

For whales measured once, it is of course the same as the length measurement (LEN). However, in cases where duplicate and repeat images have been obtained, the evaluation of the best estimate of length is somewhat more complicated.

For LGL images with measurement grades 1-6, the average value is the best estimate; for NMML images, the best length is the average of all measurements of grades 1-4. Poorer measurements are not used unless they are the only option.

In addition, lengths derived from regressions based on snout-to-blowhole or fluke width measurements are used if a better measurement is not available.

Quality of best length (GRLEN)

- BESTLEN was obtained from 5 or more measurements of grades 1-6 for LGL or grades 1-4 for NMML. 1
- 2 BESTLEN was obtained from 2 to 4 measurements of grades 1-3 for LGL or grades 1-2 for NMML.
- BESTLEN was obtained from 2 to 4 measurements of grades 1-6 for LGL or grades 1-4 for NMML. 3
- BESTLEN was obtained from 2 to 4 measurements of grades 4-6 for LGL or grades 3-4 for NMML. 4 5
- BESTLEN was obtained from 1 measurement of grades 1-3 for LGL or grades 1-2 for NMML. 6
- BESTLEN was obtained from 1 measurement of grades 4-6 for LGL or grades 3-4 for NMML. 7
- BESTLEN was obtained from lengths derived without rigorous correction factors (i.e. grades 8 and 9 lengths). 8 BESTLEN was obtained from a snout-to-blowhole or fluke width measurement and regression equation.
- 0 BESTLEN was derived from an oblique photograph.

Biogeographic characterisation of blue whale song worldwide: using song to identify populations

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ABSTRACT

Blue whale songs provide a measure for characterising worldwide blue whale population structure. These songs are divided into nine regional types, which maintain a stable character. Five of the nine song types have been recorded over time spans greater than 30 years showing no significant change in character. The nine song types can be divided into those containing only simple tonal components (high latitude North Pacific, North Atlantic and Southern Ocean song types), those comprised of complex pulsed units in addition to the tonal components (Pacific Ocean margin song types from California, Chile and New Zealand), and those which have the greatest complexity of all and the longest cycling times (Indian Ocean song types from Sri Lanka, Fremantle and Diego Garcia). We suggest that temporally stable differences in song provide another characteristic for comparison with genetic and morphological data when defining blue whale populations. Furthermore, as Mellinger and Barlow (2003) recommend, when there is a lack of other data or lack of clarity in other data sets, evidence of distinct differences in songs between areas should be used as a provisional hypothesis about population structure when making management decisions. Worldwide study is needed to better understand the various populations.

KEYWORDS: BLUE WHALE; ACOUSTICS; VOCALISATION; COMMUNICATION; DISTRIBUTION; TAXONOMY; EVOLUTION; GENETICS

INTRODUCTION

Traditional studies based on external morphology, osteology and results of ongoing genetic analyses, have not produced an accurate picture of blue whale (Balaenoptera musculus) population structure or phylogeography (e.g. Reeves et al., 1998). Collecting samples is not only logistically and geographically challenging, it is also difficult to obtain enough samples to have sufficient power to detect structure. In addition, over the ecological time scales relevant for management, traditional markers may fail to detect population structure because they may evolve too slowly and may not reflect present day movement and association patterns. Biochemical analyses of pollutants or the fatty acid signatures in blubber may better reflect the recent past. Here, we examine another line of evidence, acoustic characters, and blue whale song in particular, which provide a potentially rich source of data which can help delimit the population structure of blue whales worldwide (Cummings and Thompson, 1977; Thompson et al., 1979; Edds, 1982; Stafford et al., 1999a; Mellinger and Clark, 2003). Song types may be a useful indicator of population identity because they are likely to reflect present day movement and association patterns. Regional differences in song provide hypotheses of structure to be compared with genetic and morphological data when defining blue whale populations (e.g. Gilpatrick et al., 1997; Le Duc et al., 2003; Conway, 2005). Moreover, acoustic recording of songs offers a relatively cost-effective means of obtaining samples of sufficient size for population structure analyses.

The production of high intensity, low frequency, long duration acoustic calls is a trait common to blue whales worldwide (e.g. Cummings and Thompson, 1971). These calls often form repetitive multi-part songs, which have been documented to be constant in character over decadal time scales (c.f. Thompson, 1965; McDonald *et al.*, 2001). Although the function of song is unknown (see below), it is safe to assume that these are social signals used by the animals themselves to mediate social interactions and maintain associations between interacting animals. This paper reports on the characteristics, geographic range and seasonality of blue whale songs worldwide. We describe nine distinctive regional types of songs, which are produced with stereotyped character in distinct geographic regions with distinct oceanographic characteristics.

BACKGROUND

Blue whale subspecies and populations

Commercial whaling harvested more than 360,000 blue whales, primarily in the Southern Ocean, but with significant numbers from almost every part of the world's oceans (Clapham and Baker, 2001). Changes in population boundaries or other adjustments in population structure may be responding to recovery from these depletions and other environmental and anthropogenic changes, over the postwhaling era. However, despite considerable effort by the Scientific Committee of the IWC, the systematics of blue whales remains problematic. This uncertainty, in turn, hinders efforts to effectively monitor and manage blue whale populations at global and regional scales. Currently, blue whales are divided into four subspecies based on morphologic and geographic distinctions (Rice, 1998) and these have been further subdivided into populations for cetacean management and endangered species recovery plans (Gambell, 1979; Donovan, 1991; Reeves et al., 1998). However, the subspecies and population divisions are poorly understood and the distinctions among them are vague beyond their presumed geographical separation (Reeves et al., 2004). B.m. musculus includes all blue whales in the

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Northern Hemisphere. In the North Atlantic, eastern and western subdivisions were recognised, while in the North Pacific as many as five population subdivisions were thought to exist. B.m. intermedia is the high latitude Southern Ocean and Antarctic waters blue whale. Whaling data suggest discrete feeding stocks, and consistent with these, the International Whaling Commission has assigned six stock areas in the Southern Ocean (Donovan, 1991). B.m. brevicauda, the pygmy blue whale, is distributed in sub-Antarctic waters of the Indo-Pacific Ocean and southeastern Atlantic Ocean (Zemsky and Sazhinov, 1994; Kato et al., 2002; IWC, 2003, pp.264-5). B.m. indica is from the northern Indian Ocean. Unfortunately, the utility and validity of these subspecies descriptions is uncertain because osteological studies have been based on only a few specimens (Omura et al., 1970) and external measurement comparisons often yield equivocal or even contradictory results (Gilpatrick et al., 1997). Additional lines of evidence can improve taxonomy and population designations (Reeves et al., 2004).

Blue whale song

Blue whale calls are among the most powerful $(188dB_{RMS})$ re: 1µPa @ 1m) and lowest frequency (16-100Hz) sounds made by any animal (Cummings and Thompson, 1971; McDonald et al., 2001). Singing is the behaviour during which a limited number of stereotypic sound types are produced in regular succession and form a recognisable pattern in time. Calling is the behaviour in which individual, transient sounds are produced at irregular intervals or as call and counter-call between two or more individuals. Blue whale calls are often downswept tones (80-30Hz) of moderate duration (2-5s), with seasonally variable occurrence (Thompson et al., 1996; McDonald et al., 2001). It is not our intent to completely describe the acoustic repertoire of blue whales worldwide, but only to describe the sounds which are known to be used in blue whale song. The acoustic repertoire includes calls which are never seen in song and song units which are sometimes used alone, apparently as calls.

The songs are divided into units, which are continuous segments of sound, and phrases, which are repeated combinations of units (Payne and McVay, 1971; Mellinger and Clark, 2003). Blue whale call units are classified as primarily pulsed or tonal. A unit boundary is defined here as any abrupt change in call character (frequency, sweep rate or modulation rate) regardless of whether there is a pause between units. This usage differs slightly from that of Payne and McVay (1971) in that their definition classifies a new sound as a subunit if there is no pause to separate it. Their definition is problematic because, in blue whale song, certain sounds are sometimes separated by a pause, yet sounds are used with the same syntax, regardless of the presence of a pause. Overall, blue whale song is much less complex than humpback whale (Megaptera novaeangliae) song, requiring less nomenclature and making it possible to represent all the basic song units in spectrograms, rather than only representative phrases as is normally done for humpback whale song. One to five call units are combined to produce a phrase and a song is composed of many repeated phrases, each made up of only these units. Breaks in the song typically coincide with respiration, but the songs themselves may continue for many hours or even days (Cummings and Thompson, 1971; McDonald et al., 2001; Clark and Ellison, 2004). The units are sometimes combined in different sequences, these apparently having rules or syntax, by which only certain combinations are allowed. When units are combined in more than a single sequence we refer to this as mixed mode phrasing. When only one sequence has been observed we refer to this as single mode phrasing.

The function of blue whale song

The function of blue whale song, as with other mysticete songs, is not well understood. Social functions proposed for mysticete calls (calls in this case refers to all types of mysticete vocalisations, including song) include foraging, mating and parental behaviour, long range contact, assembly, sexual advertisement (male-male or malefemale), greeting, spacing, threat, individual identification and sensing of the environment (Tyack, 1999; Tyack, 2000; Clark and Ellison, 2004). However, only rarely has a specific call been associated with a given behavioural event. Regarding mysticete song specifically, in species such as humpback and fin whales, the evidence to date indicates that only males sing (Watkins, 1981; Darling and Berube, 2001; Croll et al., 2002). Much of the prevailing speculation on the function of song in these species has revolved around if, and how, singing functions as a mating display (Payne and McVay, 1971; Tyack, 2000; Darling and Berube, 2001; Croll et al., 2002; Darling, 2002) but recent data indicate that males also sing during migration and on feeding grounds, suggesting that there is much yet to learn about the function of song (Norris et al., 1999; Clark and Clapham, 2004).

In blue whales, it is known that males sing (McDonald *et al.*, 2001), but it remains unknown if females also sing. Animals vocalise throughout the year with peaks from midsummer into winter (Burtenshaw *et al.*, 2004; Širović *et al.*, 2004). Field observations suggest that singers are solitary animals (Calambokidis, pers. comm.). Diel chorusing at dusk and dawn increases the number of singers during these periods (Thompson, 1965) and tracking, either visually or acoustically has shown that blue whales swim at 2-10km hr⁻¹ while producing songs (Kibblewhite *et al.*, 1967; Northrop *et al.*, 1971; McDonald *et al.*, 1995; Thode *et al.*, 2000; McDonald *et al.*, 2001). Blue whale songs can be detected for hundreds, and under optimal conditions, thousands of kilometres (Stafford *et al.*, 1998).

Individual, temporal and spatial variation in blue whale song

From personal observation based on the data presented below, the songs of individual blue whales are known to be variable, but individual variability within a song type is much less than that which distinguishes among song types. Variability within a song type has been shown to be useful to distinguish between individual whales off California over the long time periods during which whales were observed (McDonald et al., 2001). Individual signature information in blue whale song has been reported for many days for North Atlantic blue whales (Clark, 1995). More work is needed to determine if and how individuals vary their calls spatially, seasonally or functionally and whether individual whales ever change song type (Stafford and Moore, 2005). The utility of relatively subtle individual variation to further subdivide blue whale populations acoustically remains a topic for further research.

Regional and spatial variation in blue whale song is among the better documented of the baleen whale songs, although the data have yet to be compiled on a global scale. Previous studies have used the characteristics of vocalisations to determine the seasonal presence and movement of blue whales through a region (e.g. Clark, 1995; Stafford *et al.*, 1999a; Moore *et al.*, 2002), including the possibility of populations mixing within a region (Stafford *et al.*, 2001) and have used differences in blue whale song to identify populations and to distinguish populations from neighbouring ones (e.g. northeastern vs northwestern Pacific (Stafford *et al.*, 2001; Moore *et al.*, 2002) and Antarctic versus others (Stafford *et al.*, 2004)). For the global comparison described below we build upon the excellent work in these previous studies.

The case of using vocalisations as a proxy for population identity

In many species, vocalisations are the predominant means by which individuals communicate; species-level and regional variation is well known and song can be a powerful isolating mechanism among taxa (Marler, 1957; West-Eberhard, 1983; Slabberkoorn and Smith, 2002). Due to recent advances in bioacoustics, vocal differentiation has become increasingly important in the taxonomy of many terrestrial species and the structure of vocalisations is becoming common in the descriptions of populations and closely related species of birds (Baptista, 1975; Catchpole and Slater, 1995; Martens, 1996; Wright, 1996; Irwin et al., 2001b), mammals (Maeda and Matasaka, 1987; Gautier, 1988; Bearder, 1999; Kingston and Rossiter, 2004; Siemers and Schnitzler, 2004), amphibians (Ryan, 1990) and insects (Wells and Henry, 1998; Gray and Cade, 2000). Acoustic characteristics may be the key distinguishing feature used in the identification of otherwise 'cryptic' taxa (e.g. nocturnal primates, Anderson et al., 2000; green warblers, Irwin et al., 2001a), resulting in significant increases in diversity (Price, 1996; Bearder, 1999).

While regional diversity in vocalisations is well-known, some researchers regard vocal displays as too ephemeral and too influenced by ecological (e.g. habitat matching) and social (including learning, imitation and mating with individuals singing other songs) factors to be useful in elucidating genetic relationships (Harvey and Pagel, 1991; but see Wimberger and de Queiroz, 1996). In birds, the relationship between song dialects and population structure show conflicting results (reviewed in Catchpole and Slater (1995) and Slabberkoorn and Smith (2002)). Some studies find little evidence of genetic differentiation (Fleischer and Rothstein, 1988; Wright and Wilkinson, 2001) while others show a strong correlation between dialects and genetic variation (MacDougall-Shackleton and MacDougall-Shackleton, 2001) sometimes indicating higher level divergence (Irwin et al., 2001a). Several factors contribute to these differences, including the social function and the timing of vocal learning relative to dispersal (Wright and Wilkinson, 2001). In addition, genetic subdivisions may exist but go undetected (Bossart and Pashley Powell, 1998; Taylor and Dizon, 1996; 1999), or differences in song features across different populations may have occurred too recently to be detected genetically (Hatch and Clark, 2004).

Cetacean biologists have long noted the potential utility of whale songs as an indicator of biologically meaningful stocks for blue whales (Cummings and Thompson, 1971; Edds, 1982), humpback whales (Payne and Guinee, 1983; Cerchio *et al.*, 2001), fin whales (Thompson *et al.*, 1992; Hatch and Clark, 2004) and Bryde's whales (Oleson *et al.*, 2003). Geographic variation of non-song calls is also known in killer whales (Ford, 1991) and sperm whales (Weilgart and Whitehead, 1997). Mellinger and Barlow (2003) recently reviewed intraspecific acoustic structure in cetaceans with notations on temporal stability and its utility for stock assessment. Hatch and Clark (2004) examined the concordance between fin whale song and genetic divergence among eleven geographic regions in the North Atlantic and North Pacific Oceans. They found that acoustic differences were not correlated with estimates of genetic divergence among regions, and suggested that the patterns of acoustic dissimilarity may reflect demographic discontinuities in behaviour and/or movement that are too recent to be reflected genetically, but that exist on the shorter time scales relevant to management (i.e. decadal time) scales. As a more complete understanding of the acoustic repertoire of each whale species is acquired, we may be able to distinguish regionally distinctive sounds from those common throughout the species' range in these and other species and to test these acoustic patterns for concordance with patterns of morphological and genetic variation.

Biogeographic characterisation of blue whale song worldwide

The objective of this paper is to describe blue whale song on a worldwide scale. The approach used intentionally simplifies since the focus is to look for big picture patterns and gross differences among regions, while for many biologists, the focus is on the subtleties of natural variation, as these may provide clues to the underlying behavioural, demographic and evolutionary processes. Much additional research is needed to more fully describe the individual, temporal, seasonal and microgeographic variability of the acoustic repertoire of blue whales. The intriguing exceptions to the rules may indicate there is more to the story than that provided here, but the objective here is to highlight the value of acoustic information as a tool in marine mammal conservation and management.

METHODS

Recordings and spectrograms of blue whale songs from publicly available literature, from recordings offered by colleagues and from our own research have been reviewed. From these data, spectrograms have been studied from as few as 10 songs for some of the least well known Indian Ocean song types to as many as 100,000 songs for the northeast Pacific where millions of song recordings are now available. A typical acoustic encounter with a singing blue whale resulted in recording about twenty songs before either the whale stops singing or the signal to noise ratio becomes undesirably low, thus the number of whale encounters examined scales more or less by a factor of twenty fewer. It was possible to compare songs between regions as the differences were apparent visually in the spectrograms. A typical song phrase or in some cases several phrases for each song type are presented, representing nearly all the well known song units. Undoubtedly, detailed study will reveal additional, less common units, for some song types. To investigate temporal variation within a region, as many as 15 different years of recordings from the Northeastern Pacific song were looked at and as few as two different years of recordings for the Indian Ocean song types. For this study, 'acoustic-types' were established for each of the geographic regions described with the acoustic measures above, much as morphologists identify 'morpho-types' when a new species is described.

RESULTS

Blue whale song can be categorised into nine types, each of which was associated predominantly with a geographic region (see Table 1 for a listing of source data). The best known songs were from the Pacific Ocean, which had four

song types. The Indian Ocean, although poorly studied, had at least three song types, whereas the Atlantic Ocean and Southern Ocean each had a single song type. Additional song types may remain undiscovered, for instance, no recordings are available for the South Atlantic. Locations for all known blue whale recordings are shown in Fig. 1, the locations being numbered corresponding to the song type listed in Table 1. Stability of the song character is illustrated in Fig. 2. Changes in song character through time are small relative to differences between song types, the common change being a slow and regular drift in the frequency of the tonal components. Spectrogram displays of each song type are grouped into three figures, the first two (Figs 2 and 3) are grouped based on similarity of character, while Fig. 4 illustrates the Northern Indian Ocean types which do not readily group with the others in call character.

Northeast Pacific

Blue whale songs have been recorded off the coast of California since 1963 (Thompson, 1965), the northeast Pacific song being the best documented for any worldwide. The character of this song has remained stable over the past four decades. This song has two call units (Fig. 3A). The first unit (A) is pulsed with multiple, time-offset nonharmonic components. The second unit (B) is tonal, with a series of harmonically related higher frequencies. Single mode (ABABAB or ABBBABBB) phrasing is common, with the A unit always initiating the song sequence.

The geographic range for the northeast Pacific blue whale song (type 1 in Fig. 1) is primarily along the west coast of North and Central America. The type 1 locality is off the coast of California, where these calls have been well described (Thompson, 1965; Rivers, 1997; Stafford et al., 2001; McDonald et al., 2001). In the northern part of this region, off the coast of Washington, Oregon and British Columbia, they are heard seasonally, beginning in the summer and continuing into the autumn and early winter (Stafford et al., 2001; Stafford, 2003; Burtenshaw et al., 2004). In the south of their range, at the Costa Rica Dome region and in the Gulf of California, calls from these whales are present year-round, but with a peak occurrence in the winter and spring (Thompson et al., 1996; Stafford et al., 1999a). This pattern suggests a seasonal movement with a spring peak presence in the Costa Rica Dome region, and fall peak presence off the California coast and points further north, substantiated by photo-identification studies (Calambokidis et al., 1999) and satellite tagging (Mate et al., 1999). These calls also have been heard further offshore, where they mix with the North Pacific song type (Stafford et al., 2001; Stafford, 2003).



Fig. 1. Distribution of blue whale song, classified into nine regional types (numbers). See Table 1 for regional designations.

Southeast Pacific

Southeast Pacific blue whale song has been described off the west coast of South America (Cummings and Thompson, 1971; Stafford et al., 1999b), maintaining the same character for 27 years. This song contains three pulsed call units, closely spaced in time, with a total duration of 37 seconds (Fig. 3B). The call units are repeated about every 100 seconds, with single mode phrasing (ABCABC).

The southeast Pacific blue whale song (type 2 in Fig. 1) is observed along the west coast of South America and adjacent offshore waters, with the type locality in the Isla Guafo region of southern Chile (Cummings and Thompson, 1971). In the northern part of the range, off the coast of Peru, the songs are recorded year-round, but in greater numbers during the austral fall and winter (March-August) (Stafford et al., 1999b). In the south of their range, the song has been heard in the summer (Cummings and Thompson, 1971). These data suggest a seasonal movement with a winter peak presence in tropical waters, and summer peak presence further south. Sightings and whaling data confirm blue whale presence in southern Chile year-round (Tonnessen and Johnsen, 1982; Aguayo-Lobo et al., 1998; Findlay et al., 1998). A variant of this song has been detected on the Eastern Tropical Pacific hydrophones south of the equator (Stafford et al., 1999b). This song (Fig. 3C) consists of four pulsive units, making it more similar to the Isla Guafo song type than the New Zealand song type, although it is somewhat intermediate in character. As more data becomes available, it may be appropriate to categorise this variant as a separate song type.

Southwest Pacific

Southwest Pacific blue whale song has been recorded off North Island, New Zealand (Kibblewhite et al., 1967), with no apparent change in character over the 33 year time span between recordings (Fig. 2, Fig. 3D). This song consists of three pulsed call units (A, B, C) followed by a tonal call unit

Blue whale song type by region.	The type locality and type reference refer to the best/first/most complet
published reference for each song	type. Song character is stable over the known time spans, listed as the year
of the first and the most recent rec	ordings available. See the text for the time span references.

Table 1

Туре	Time span	Region (abbreviation)	Type locality	Type reference
1	1963-2003	Northeast Pacific (NEP)	California	McDonald et al. (2001)
2	1970-1997	Southeast Pacific (SEP)	Isla Guafo, Chile	Cummings and Thompson (1971)
3	1964-1997	Southwest Pacific (SWP)	New Zealand	Kibblewhite et al, (1967)
4	1967-1997	North Pacific (NP)	Aleutian Islands	Stafford et al. (2001)
5	1959-2001	North Atlantic (NA)	Eastern north Atlantic	Clark and Charif (1998)
6	1997-2003	Southern Ocean (SO)	W. Antarctic Peninsula	Širović <i>et al.</i> (2004)
7	1984-2002	North Indian (NI)	Sri Lanka	Alling et al. (1991)
8	1993-2000	Southeast Indian (SEI)	Fremantle	McCauley et al. (2000)
9	2002	Southwest Indian (SWI)	Diego Garcia	This paper



Fig. 2. Recordings from New Zealand (A), the Central North Pacific (B), Australia (C), the Northeast Pacific (D) and North Indian Ocean (E) illustrate the stable character of the blue whale song over long time periods. All song types for which long time spans of recording are available show some frequency drift through time, but only minor change in character. These examples were chosen because recordings over a significant time span were available to the authors in raw form, and not because these song types are more stable than the others. The stability of song character in the other types and for longer time spans in these types is available to various degrees in copyrighted spectrograms and/or written descriptions. The missing first units in the 1964 New Zealand example and 2002 Sri Lanka example are probably due to lower signal to noise ratio, rather than a change in the song.

(D), with a total duration of about 55 seconds (Fig. 3C). The first pulsed unit (A) has lesser amplitude than the following units (B and C). The call units are repeated approximately every 108 seconds, with single mode phrasing (ABCDABCD). This song has been recorded in waters off North Island, New Zealand; twice near Three Kings Island (Kibblewhite *et al.*, 1967) and on four occasions near Great Barrier Island, scattered throughout the year (author's unpublished data).

North Pacific

North Pacific blue whale song, first reported from Midway Island recordings made in 1967 (Northrop *et al.*, 1971), consists of 2-4 tonal units with frequencies near 20Hz (Fig. 4A and 4B). Six different call units have been reported, with varying usage over the North Pacific (e.g. Stafford *et al.*, 2001), suggesting that it may be possible to break this song region into finer subdivisions. The call units typically last for 5-20 seconds. Fig. 4A shows representative calls



Fig. 3. Blue whale songs for: (A) Northeast Pacific – California, recorded June 2001 near San Clemente Island, California, (B) Southeast Pacific – Chile, recorded May 1970 near Isla Guafo, Chile, (Cummings and Thompson, 1971). Spectrogram produced from archival tape in Hubbs SeaWorld Sound Library, (C) 8°S 95°W – recorded 1996 (Stafford *et al.*, 1999b) and (D) Southwest Pacific – New Zealand, recorded December 1997 near Great Barrier Island, New Zealand. Recording from the Centre for Monitoring Research collected as part of the Comprehensive Test Ban Treaty. The numbers in brackets refer to song types.

recorded near Midway Island (Northrop *et al.*, 1971). The call units are repeated about every 85-95 seconds, with single mode phrasing (ABABAB). Fig. 4B shows song recorded near Wake Island (author's unpublished data) with three tonal units (A, B, C). The phrasing of the Wake Island call is single mode, with a repeated second unit (ABBCABBC). Other variants for the North Pacific blue whale song type have been reported by Stafford *et al.* (2001).

The range for the North Pacific blue whale song type (Type 4 in Table 1) is primarily from the Aleutian Islands, stretching to about 40°N (Moore *et al.*, 2002). Lesser numbers of calls are heard as far south as Hawaii and Wake Island (Watkins *et al.*, 2000; Stafford *et al.*, 2001). In the Aleutians region, these songs are abundant in the summer and fall, and are detected nearly every hour on fixed hydrophones. Aleutian calling is diminished during the winter and is nearly absent in the spring. This pattern suggests a strong seasonal movement with summer and fall spent at high latitude and spring spent at lower latitudes.

North Atlantic

North Atlantic blue whale song was first described in detail for the St. Lawrence River Estuary (Edds, 1982), consisting of a single tonal unit near 19Hz (Fig. 4C), although descriptions date back to 1959 (Weston and Black, 1965).



Fig. 4. Blue whale songs for (A) North Pacific – Midway Island, recorded on December 1967 near Midway Island (Northrop *et al.*, 1971). Spectrogram produced from archival tape in Hubbs SeaWorld Sound Library, (B) North Pacific – Wake Island, recorded January 1997 from the Wake Island MILS hydrophone array. Data provided by the Centre for Monitoring Research, (C) North Atlantic, recorded in 1993 in the northeast Atlantic between Iceland and Spain. Data from the Integrated Undersea Surveillance System (Clark, 1996), and (D) Southern Ocean – West Antarctic Peninsula, recorded February 2002 at 66°S, 71°W off Adelaide Island (Širović *et al.*, 2004). The numbers in brackets refer to song types.

The most thorough description of this song type is found in Mellinger and Clark (2003). Each phrase consists of two units, although there is sometimes no gap between the two units as is the case in Fig. 4C. The first unit is of nearly constant frequency, with a duration of about 8 seconds, while the second unit sweeps down having a duration of about 11 seconds (Mellinger and Clark, 2003).

The range for the North Atlantic blue whale song (Type 5 in Table 1) stretches from the Arctic Ocean south to at least 35°N. Off the coast of Great Britain it is reported year-round (Clark and Charif, 1998). Using military hydrophone arrays, a singing blue whale was shown to move along a northeast-southwest track in the western north Atlantic during February-March 1993 (Clark, 1995). The probable pattern for North Atlantic blue whale song is year-round residence at high latitude, with some seasonal movement to lower latitudes during spring.

Southern Ocean

Southern Ocean blue whale song recently has been reported from offshore Antarctica (Ljungblad *et al.*, 1998; Matsuoka *et al.*, 2000; Širović *et al.*, 2004). The song consists of three tonal units with frequencies near 20Hz (Fig. 4D). The phrase is repeated about every 65 seconds, typically with single mode phrasing (ABCABC), although mixed mode phrasing also has been observed.

The reported locations for Southern Ocean blue whale song recording suggest a circumpolar distribution around the Antarctic Continent (Type 6 in Table 1). A year-round presence is documented from fixed hydrophones deployed near the West Antarctic Peninsula (Širović *et al.*, 2004). The Southern Ocean blue whale song has also been recorded at tropical latitudes during the southern winter (Stafford *et al.*, 2004).

North Indian

North Indian Ocean blue whale song is best known offshore from Sri Lanka (Alling and Payne, 1987; Alling *et al.*, 1991). The song consists of four units, three pulsive and one tonal (Fig. 5A). The call units are repeated about every 210 seconds, with single mode phrasing (ABCDABCD).

The North Indian Ocean blue whale song (Type 7 in Table 1) is reported from the near-shore waters of Sri Lanka, (Alling and Payne, 1987; Alling *et al.*, 1991), where it was recorded on two consecutive seasons, both in the spring, and the whales are reported to be present between January and May. It is also known of from deep ocean hydrophones near Diego Garcia (Tolstoy and Bohnenstiehl, 2002; Maya Tolstoy, pers. comm.).

Southeast Indian

The southeast Indian Ocean blue whale song (Type 8 in Table 1) has been observed in waters off northern and southwestern Australia, in the Timor Sea (Lindsay Hall, pers. comm.) and near Fremantle (McCauley *et al.*, 2000; 2001). These songs were heard in the southern summer and autumn (January-March), although data are not available for other seasons. This song contains four pulsed call units and one tonal call unit, with a total duration of about 120 seconds (Fig. 5B). The call units are repeated about every 180 seconds, with single mode phrasing (ABCDEABCDE).

Southwest Indian

The southwest Indian Ocean blue whale song has been recorded south of Madagascar (Ljungblad *et al.*, 1998) and on a fixed hydrophone array south of Diego Garcia Island. The Madagascan songs consist of four call units with a total duration of about 60 seconds (Fig. 5C). The call units are repeated about every 90-100 seconds, with single mode phrasing (ABCDABCD). The Diego Garcia variant of this song consists of five units, two pulsive and three tonal (Fig. 5D). The call units are repeated every 200 seconds, with single mode phrasing (ABCDEABCD).

The southwest Indian Ocean blue whale song (Type 9 in Table 1) has been observed south of Madagascar, at 32° S (Ljungblad *et al.*, 1998). The songs were heard in the southern summer (December) on two successive years. No data are available for other seasons. A seasonality analysis of the Diego Garcia song is in progress (Maya Tolstoy, pers. comm.).

DISCUSSION

Acoustic identification of regional differences

Blue whale song types can be helpful in defining population boundaries. There are distinct differences, outlined above, between songs recorded in different regions. We have identified nine acoustic types, many of which are known to have remained stable for decades. These results suggest that there are at least nine distinct populations of blue whales worldwide, with the possibility of more as acoustic data are collected in unstudied areas. These distinct differences between areas provide another data set for comparison with genetic and morphological data when defining blue whale populations (e.g. Gilpatrick *et al.*, 1997; LeDuc *et al.*, 2003; Conway, 2005). As Mellinger and Barlow (2003)



Fig. 5. Blue whale songs for: (A) North Indian Ocean – Sri Lanka, recorded April, 1984 within 5 miles of the entrance to Trincomalee Harbour (Alling and Payne, 1987). Spectrogram produced from archival tape at the British Library, Natural Sound Archive, London, (B) Southeast Indian Ocean – Fremantle, recorded west of Perth, Australia (courtesy of R. McCauley), (C) Southwest Indian Ocean – Madagascar, recorded December 1996, south of the Madagascar Plateau (after Ljungblad *et al.*, 1998), and (D) Southwest Indian Ocean – Diego Garcia, recorded October 2000, south of Diego Garcia, by the Comprehensive Test Ban Treaty Organisation. The numbers in brackets refer to song types.

recommend, in regions where data are lacking, or resolution of traditional markers is insufficient, distinct differences in songs between areas may be used as evidence for provisional population structure in management decisions. For these reasons, we provisionally recommend nine acoustic populations of blue whales worldwide.

Blue whale song may be grouped into three categories based on their similar characteristics. Song types bordering the Pacific Ocean, which may be grouped together due to common characteristics, are: California; Chile; and New Zealand (Type 1, 2, and 3; Fig. 3A, B, C). These songs have the following characteristics: (1) pulsed call units; (2) when present, tonal call units contain higher harmonics; and (3) song cycle times of intermediate length (102-118s). High latitude North Pacific, North Atlantic, and Southern Ocean songs (Type 4, 5 and 6; Fig. 4A, C, D) have a simple character, with only tonal call units lacking harmonics, and a short cycle time (35-90s). Indian Ocean songs (Type 7, 8 and 9; Fig. 5A, B, C, D) have the highest level of complexity. There are similarities in the structure of the Fremantle song (Type 8) and Sri Lanka song (Type 7). They have a comparable number, type and ordering of call units, with long song cycle times (198 and 210s).

Acoustic characteristics are increasingly being investigated as cost-effective means of obtaining data with which to determine population identity and structure (Mellinger and Barlow, 2003). The recording of sound at sea also offers a relatively fast and efficient means of gathering information on marine mammal populations remotely and in difficult visual or sea conditions and locations (e.g. Širović *et al.*, 2004). Furthermore, because vocalisations may evolve more rapidly than traditional markers, such as genetic or morphological characteristics, acoustic recordings may be particularly useful in detecting cryptic, insipient and sibling cetacean populations and/or species.

These data and those from other recent studies provide a growing body of evidence that geographic differences in whale songs can provide useful information for discovering and determining population boundaries (Fig. 6). As noted above, a recent study of the acoustics of fin whales (Hatch and Clark, 2004) showed that fin whale song varied significantly among regions in two ocean basins, although the differences were not reflected in genetic differentiation, suggesting that the patterns of acoustic dissimilarity may represent recent discontinuities in movement/behaviour that exist on the shorter time scales relevant to management. Recent studies of the acoustics of minke whales suggest a simple downswept call is used across geographic regions (Edds-Walton, 2000; Schevill and Watkins, 1972), but a complex song-like vocalisation often referred to as the 'starwars', 'thump-train' or 'boing' sound is regionally distinctive (Gedamke et al., 2001; Mellinger et al., 2000; Jay Barlow, pers. comm.; Wenz, 1964; Thompson and Friedl, 1982; author's unpublished data). For minke whales, the limited data available are consistent with the hypothesis that the complex sound appears to be produced only during the breeding season, while the simple sounds are produced throughout the year.

Understanding the regional variation, function and significance of differences among blue whale songs requires a variety of approaches. Future work is likely to include a quantitative analysis of the differences within and between call types to better quantify the categories suggested here and help distinguish the variants in a more quantifiable way. Such analysis would likely parameterise the start frequency, end frequency, duration and gap for each unit of a song and apply statistical methods such as used by Anderson et al. (2000). For the better studied songs such as the northeast Pacific, there are millions of calls recorded to which such a system could be applied, while other regions such as the Indian Ocean need more data to meaningfully measure the variation within the song types for comparison to other types. Future work is also needed to tease apart the various historical, ecological, morphological and behavioural factors that influence these geographic patterns while investigation into the relative complexity of blue whale calls may provide insights into the differences in the intensity of selection and density of individuals among regions as predicted by studies of birds (Catchpole, 1980; Price, 1998; Kroodsma, 1983). Ultimately, the goal is to understand the potential significance of acoustic differences in the evolution of blue whale populations; if it is a part of their systematics, it should be a part of ours.



Fig. 6. Blue whale residence and population divisions suggested from their song types. Arrows indicate the direction of seasonal movements.

CONCLUSIONS

Blue whale songs provide a new means for characterising blue whale population structure worldwide. Song types may be a useful indicator of population identity because they are social signals, which are likely to reflect present day movement and association patterns. Recent advances in technology make the collection and analysis of long-term acoustic records practical, even for remote regions of the world's oceans and at moderate costs. The availability of these data will enhance the potential for blue whale song to play a key role in describing population structure worldwide. We provisionally recommend nine acoustic populations for management.

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Bycatch of harbour porpoises (*Phocoena phocoena*) in gillnet fisheries of the Estuary and Gulf of St. Lawrence, Canada, 2000-02

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ABSTRACT

The incidental catch of harbour porpoises (Phocoena phocoena) in the gillnet fishery of the Estuary and Gulf of St. Lawrence, Canada, was examined using: (1) questionnaires mailed to fishermen inquiring about bycatches in 2000 and 2001 (n=2,277 or 44% of the fishermen with valid licenses); and (2) using data from an at-sea observer programme and sentinel fishery programme in 2001 and 2002. The questionnaire survey had a low response rate (22%) and provided bycatch estimates of 2,215 (95% CI 1,151-3,662) and 2,394 (95% CI 1,440-3,348) porpoises in 2000 and 2001, respectively. The low number of hauls monitored by at-sea observers prevented the estimation of bycatch levels for several zones and the study area as a whole, and provided only imprecise estimates for all other zones. The results from questionnaires indicated a 24-63% reduction in harbour porpoise bycatches since the late 1980s, whereas the at-sea observer programme provided bycatch levels for 2001 and 2002 that were unreliable and underestimated, approaching one quarter of those documented in the late 1980s. Although both indices indicated a decrease in bycatches since the late 1980s, the magnitude of this change remains uncertain given the weaknesses associated with the two approaches. Considering the maximum population rate of increase (R_{max}) for harbour porpoises as 4% and the lower and upper 95% confidence limits (1,440-3,348) of our most reliable estimate of bycatches (i.e. the 2001 questionnaire survey results), the harbour porpoise population in the Gulf of St. Lawrence would need to be at least 36,000-83,700 individuals for current incidental catches to be sustainable. If the rate of increase is less than maximal, e.g. 0.5R_{max} or 2%, then 72,000-167,400 harbour porpoises would be needed to attain sustainability. Kingsley and Reeves (1998) estimated that an average 36,000 to 125,000 porpoises occupied the Gulf of St. Lawrence during the summers of 1995 and 1996. Although the trajectory of the population since it was last surveyed in 1996 is uncertain, these findings suggest that bycatch levels might remain a cause for concern for the harbour porpoise population in the Gulf of St. Lawrence. The results from the comparison between the sentinel fishery and the commercial fishery subjected and not subjected to at-sea observations suggest that fine-scale temporal and spatial changes in fishing activities may greatly affect harbour porpoise bycatch levels.

KEYWORDS: GILLNETS; INCIDENTAL CATCHES; HARBOUR PORPOISE; ATLANTIC OCEAN; NORTH AMERICA; CONSERVATION; SUSTAINABILITY; FISHERIE

INTRODUCTION

The management of natural resources and fisheries has traditionally focussed on the effects of directed harvests on the survival and conservation of species or populations. However, the mortality of non-target species through bycatch may represent a significant source of mortality for some species. This is the case for harbour porpoises (Phocoena phocoena), a species particularly vulnerable to incidental catches in fishing gear (Perrin et al., 1994). A number of reviews have shown interactions between this species and fisheries throughout most of its range (Gaskin, 1984; Jefferson and Curry, 1994; Bjørge et al., 1994; Stenson, 2003). Although several types of gear such as fish weirs and traps may be involved in these interactions, mortalities are most often associated with fisheries using pelagic or bottom-set gillnets (Smith et al., 1983; Gaskin, 1984; Fontaine et al., 1994a; Jefferson and Curry, 1994; Lien et al., 1994; Stenson, 2003).

Harbour porpoises are widely distributed in the temperate coastal waters of the Northern Hemisphere (Gaskin, 1984). The species occurs at least seasonally in the Estuary and Gulf of St. Lawrence (e.g. Sergeant *et al.*, 1970; Laurin, 1976; Kingsley and Reeves, 1998) and genetics and contaminant profiles suggest that individuals from this region may constitute a distinct population (Gaskin, 1984; Wang *et al.*, 1996; Rosel *et al.*, 1999; Westgate and Tolley, 1999; Tolley *et al.*, 2001; Anderson, 2003). Aerial surveys, which sampled a large portion of the Gulf of St. Lawrence in 1995 and its northern shelf in 1996, provided estimates

(uncorrected for visibility biases, such as g(0)), of 12,100 (CV=26%) and 21,720 (CV=38%) harbour porpoises in 1995 and 1996, respectively (Kingsley and Reeves, 1998).

Laurin (1976) was the first to suggest that bycatch might represent a non-negligible source of mortality for harbour porpoises in the Estuary and Gulf of St. Lawrence. Two studies conducted during the late 1980s and early 1990s confirmed the existence of substantial harbour porpoise bycatches in the groundfish gillnet fisheries of the Estuary and Gulf of St. Lawrence (Fontaine et al., 1994a; Larrivée, 1996). These mortalities were thought to approach or exceed sustainability levels. Similar concerns were raised for harbour porpoises off Newfoundland and Labrador and for other populations in the northwest Atlantic, including West Greenland and the Bay of Fundy/Gulf of Maine (Gaskin, 1984; 1992; Lien, 1987; Read and Gaskin, 1988; Bravington and Bisack, 1996; Trippel et al., 1996; Bisack, 1997a; Caswell et al., 1998; Teilmann and Dietz, 1998; Department of Fisheries and Oceans, 2001).

During the early 1990s, the collapse of several groundfish stocks in the northwest Atlantic resulted in substantial reductions, and even moratoria, of several fisheries. In the Gulf of St. Lawrence, the Atlantic cod (*Gadus morhua*) fishery, which accounted for most of the harbour porpoise incidental catches in this area in the late 1980s (Fontaine *et al.*, 1994a), was closed in 1993 (southern Gulf) and 1994 (northern Gulf). The fishery in the northern Gulf was reopened at a low level in 1997, but restricted to longlines for 1997 and 1998, and was closed again in 2003. In the southern Gulf of St. Lawrence, the gillnet fishery reopened
in 1997 at reduced levels, but was closed again in 2003. The reduction in groundfish fishery activities should have had beneficial impacts on harbour porpoise populations by reducing incidental catches in fishing gear (Department of Fisheries and Oceans, 2001). These suspected trends were confirmed in the Gulf of Maine where a decrease in bycatch levels was observed following the reduction in fishing effort and implementation of the Take Reduction Plans in 1999 (Waring *et al.*, 2001). A reduction in harbour porpoise bycatch was also observed in the Bay of Fundy component of this population during 1998-2001 (Trippel and Shepherd, 2004). However, bycatches in the nearshore Atlantic cod fishery of Newfoundland were not negligible during 2002, although confidence intervals around the estimates are large (Lawson *et al.*, 2004).

The objectives of this study were to describe the distribution and level of gillnet fishing activity in the Estuary and Gulf of St. Lawrence in 2000-02 and to estimate incidental catches of harbour porpoises in this fishery. An approach similar to the one used in the late 1980s and early 1990s, i.e. questionnaires mailed to gillnet fishermen, was employed to allow comparisons between the two periods (Fontaine et al., 1994a; Larrivée, 1996). Bycatch estimates obtained through questionnaires suffer from numerous problems, as they are based usually on a small number of respondents whose capacity of recollection of bycatch numbers varies depending on the number of incidents, motivation, time elapsed since the end of the fishing season and their trust in the interviewer (Lien et al., 1994). Therefore, harbour porpoise incidental catches were also examined using a more reliable (when properly implemented) technique: independent observers onboard fishing vessels (IWC, 1994; 1997; Donovan and Bjørge, 1995).

MATERIALS AND METHODS

The study area encompassed the Lower St. Lawrence Estuary and the entire Gulf of St. Lawrence, i.e. Northwest Atlantic Fisheries Organisation (NAFO) Divisions 4R, 4S and 4T. These divisions were partitioned into five zones based on the spatial distribution and intensity of gillnet fishing activities: northwestern Gulf; Miscou; southern Gulf; North Shore; and 4R (Lesage *et al.*, 2004; Fig. 1).

Data on incidental catches of harbour porpoises were obtained using two approaches: (1) questionnaires mailed to fishermen after their fishing season; and (2) collection of bycatch numbers directly from fishing vessels, either by the fishermen themselves or by independent observers.

Mail survey

During October-November 2001, questionnaires were mailed to a random sample of 2,277 (or 44%) of the 5,137 owners of gillnet fishery licenses valid in 2000 for groundfish, Atlantic herring (*Clupea harengus harengus*) or mackerel (*Scomber scombrus*) of the Estuary or Gulf of St. Lawrence. Fishermen were asked similar questions to those formulated by Fontaine *et al.* (1994a), i.e. the number of harbour porpoises caught during 2000 and 2001, month and location of capture and type of fishing gear. Fishermen were also asked to report observations of harbour porpoises, incidental catches of other marine mammals, damage to fishing gear and their impressions on the trends of populations of harbour porpoises and pinnipeds. Only the information related to harbour porpoise bycatches is presented here.



Fig. 1. Distribution of Atlantic cod (squares) and Greenland halibut (crosses) commercial fishing activities using bottom-set gillnets in the Estuary and Gulf of St. Lawrence in 2001 and 2002. Information on fishing location was unavailable for 90-94% of the fishing activities in zone 4R. The thick solid lines delimit the five zones referred to in the document, whereas the dotted line prolongs the limit between NAFO zones 4S and 4T.

Data obtained directly from fishing vessels

An at-sea fisheries observer programme had existed in the Gulf of St. Lawrence since the early 1980s. This programme consists of having an independent observer onboard commercial fishing vessels to collect information on fishing activities, including fishing location, gear type, catches and discards. Observers are not specifically dedicated to the collection of data on marine mammal bycatches. However, in area 4R, datasheet coding for harbour porpoise bycatches have existed since 1989 and marine mammal bycatches have been documented routinely and consistently over the years (D. Kulka, DFO, St. John's, NL, pers. comm.). In areas other than 4R, no such coding existed on the datasheets prior to 2001 and observers may not have collected this information systematically during this period. In 2001 and 2002, coding for each marine mammal species was added to datasheets, and the importance of noting marine mammal bycatches was emphasised during the annual training sessions of observers. When not specified in the remarks section, the number of captured porpoises was estimated from the reported mass, assuming a mean mass per individual of 50-60kg (Read and Tolley, 1997).

The intensity of observation of the fishery by the at-sea observer programme is dictated by harvesting plans and varies with the type of fishery. During 2001 and 2002, coverage for the fixed gear Atlantic cod fishery should have been at least 5% for vessels less than 45 feet in length and at least 10% for larger vessels during both years. Coverage should also have been at least 5% for the fixed gear Greenland halibut (*Reinhardtius hippoglossoides*), winter flounder (*Pleuronectes americanus*), American plaice (*Hippoglosoides platessoides*) and witch flounder (*Glyptocephalus cynoglossus*) fisheries.

A second monitoring programme of the fisheries of the Gulf of St. Lawrence, the sentinel fishery programme, was initiated in 1994. The intent of this programme was not to monitor commercial fishing activities, but to obtain information on population trends of commercially valuable but non-abundant species using predefined scientific fishing protocols and gear types. In this context, fishermen can be asked to deploy their fishing gear in non-traditional fishing

areas during periods of low abundance or low density of the targeted fish species. Data collected through the sentinel fishery programme are very similar to those obtained through the at-sea observer programme and include incidental catches of marine mammals and measurements or sampling of targeted species. In area 4T, every fixed gear sentinel fishing vessel has an observer who handles the data collection and fish sampling when catches are hauled on board. In areas 4R and 4S, information on catches and discards associated with the fixed gear fishery are noted by fishermen themselves since there are no observers dedicated to these vessels. During 2001 and 2002, Atlantic cod was the only species targeted by the fixed gear sentinel fishery programme in the study area.

Total fishing effort and bycatch estimates

An index of the level of activity by the commercial fishing fleet was obtained from data on total landings of all fish species in terms of 'live' kilograms of fish through purchase slips, logbooks and dockside monitoring. This database provided information on target species and type of fishing gear, but was incomplete with respect to fishing location, gear length, soak time, etc. because logbooks are not mandatory for all types of fisheries and, in the case of some of the NAFO Divisions, for smaller vessels. The information presented here on the distribution of the fishery was available from only one of the three possible sources of information in the commercial fishery database (i.e. logbooks) and thus, must be viewed as incomplete.

In the questionnaire survey, harbour porpoise bycatch estimates were calculated using an active fisherman as the unit of effort, i.e. bycatch estimates were expressed as a number of bycaught porpoises per respondent (Fontaine et al., 1994a; Larrivée, 1996). A fisherman was considered active if he had landed fish at least once during the fishing season. Data were partitioned by year. However, the relatively low response rate from the mail survey (see Results) precluded any spatial or seasonal stratification of the data for the calculation of bycatch rates. An estimate of the total number of bycatches for the study area during a given year was obtained by extrapolating the average bycatch rate of respondents to the total number of gillnet fishermen active during that year. Active fishermen in the different NAFO areas were assumed to have had an equal chance of receiving or completing the questionnaire, i.e. the number of answers that were received was considered proportional to the number of active fishermen in each NAFO area. One way of verifying this assumption would have been to resample both respondents and nonrespondents shortly after questionnaires were returned. However, this verification could not be done in a timely fashion following the receipt of questionnaires.

Total landings per haul was chosen as the unit of effort for the calculation of bycatch estimates from the at-sea observer programme and sentinel fishery data. A haul was defined as the retrieval of a string of nets. Because there was no direct measure of the number of hauls in the commercial fishing database, this measure of effort (total landings per haul) by the fisheries under the at-sea observer programme was used to back-calculate total hauls (i.e. the effort) by the commercial fishery from fish landings and to estimate bycatch rates by the entire fishing fleet. Given the low coverage by at-sea observers in several zones, mean landings per haul was calculated globally and not per zone for each target species and year. Bycatch estimates were calculated separately for the Greenland halibut and Atlantic cod fisheries, since the Greenland halibut fishery typically occurred in deep waters of the channels in contrast with the Atlantic cod fishery, which mostly operated in shallower waters (Fig. 1). The low levels of activity by at-sea observers precluded any seasonal stratification of the data.

The spatial distribution of bycatches was examined in relation to fish landings in the different NAFO areas using a single classification goodness-of-fit g test (Sokal and Rohlf, 1969). In cases where respondents to the mail survey fished in more than one NAFO area, bycatch numbers were associated with the NAFO area central to the distribution of their fishery.

Standard bootstrap re-sampling techniques were used to calculate the 95% confidence limits of the bycatch estimates.

RESULTS

The bycatch information from at-sea observers and sentinel fisheries indicated that harbour porpoise bycatches were associated exclusively with gillnets and the Atlantic cod and Greenland halibut fisheries; no bycatches were associated with the other fisheries covered by these programmes, i.e. American plaice and winter flounder fisheries. Consequently, other types of gear (e.g. longlines) and other groundfish fisheries are not further dealt with in this paper. The spatial and seasonal distribution of the American plaice and winter flounder fisheries and winter flounder fisheries and bycatch rates are presented in detail in Lesage *et al.* (2004).

Fishing activities in 2001 and 2002

The Atlantic cod fishery occurred mainly in the 4R and Miscou zones, whereas the Greenland halibut fishery was almost exclusively in the northern Gulf of St. Lawrence (i.e. northwestern Gulf and North Shore zones) and along the northwestern coast of Newfoundland (zone 4R) (Table 1; Figs 2-3). Commercial fishing activities for Atlantic cod were at least twice as intense in zone 4R as they were in Miscou during both 2001 and 2002. However, the number of hauls monitored by at-sea observers in 4R was three to four times less than in Miscou, resulting in a stable coverage of about 9% in Miscou compared to less than 1% in 4R. While the intensity of cod fishing was comparable in the North Shore and southern Gulf zones, coverage by at-sea observers was nearly null in the former and 6-35% in the latter. Similarly, coverage of the Greenland halibut fishery by at-sea observers was relatively high (7-17%) in the northwestern Gulf but nearly null in the North Shore and 4R zones, where intense halibut fishing occurred during both years.

The at-sea observer activities followed relatively closely the seasonal distribution of the commercial fishery for both Atlantic cod and Greenland halibut. Most of the commercial fishery and at-sea observer efforts for Atlantic cod occurred early and late in the season (late July and late September) in the southern Gulf, and mainly in July and early August in the more northerly areas of the Gulf (Fig. 2). For the Greenland halibut fishery in the northwestern Gulf, 4R and North Shore zones, at-sea observer and commercial fishery efforts peaked between early July and late September (Fig. 3).

In contrast, the spatial and temporal distributions of the sentinel fishery for Atlantic cod appeared to be independent of the commercial fishery activities. Sentinel fisheries were the most intense in zone North Shore, with a steady 100



Fig. 2. Seasonal distribution and level of commercial fishing (bars), at-sea observer (solid lines) and sentinel fishery (dotted lines) activities for Atlantic cod in five zones of the Estuary and Gulf of St. Lawrence in 2001 and 2002.



Fig. 3. Seasonal distribution and level of commercial fishing (bars) and at-sea observer (solid lines) activities for Greenland halibut in the four zones of the Estuary and Gulf of St. Lawrence where some fishing occurred during 2001 and 2002.

hauls per year, even though commercial fishing activity was low in this zone compared to Miscou and 4R. Similarly, substantial levels of sentinel fisheries occurred in the southern Gulf in 2002 in spite of little commercial fishing in this zone. Sentinel and commercial fishing activities for cod were low during both years only in the northwestern Gulf. In addition, sentinel fisheries remained highly active over extended periods and included areas and periods with little or no commercial fishing activities (Fig. 2).

Incidental catches of harbour porpoises in 2000-2002 *Mail survey*

A total of 57% of the 2,277 questionnaires were mailed to fishermen who owned either a groundfish gillnet fishery licence (n=230) or both a groundfish gillnet licence and a herring or mackerel gillnet license (n=1,064). The remaining 983 questionnaires (43%) were mailed to fishermen with only a herring or mackerel gillnet fishery licence. Response rates from groundfish fishermen (57%) and those who

					Ob	server			N l	narbour po	rpoises (N	hauls)
	N commerc	ial hauls	N obser	ved hauls	cover	age (%)	N sent	inel hauls	Obse	ervers	Ser	ntinels
Zone	2001	2002	2001	2002	2001	2002	2001	2002	2001	2002	2001	2002
Atlantic cod												
NW Gulf	9	60	1	1	10.9	1.0	22	12	0	0	0	0
North Shore	1,428	2,529	1	17	0.1	1.0	539	457	0	1(1)	26 (14)	14(7)
4R	8,814	9,404	70	80	0.8	0.9	512	403	1(1)	0	11 (6)	13 (7)
Miscou	3,887	2,522	362	232	9.3	9.2	195	329	0	2 (2)	46 (27)	50 (21)
Southern Gulf	1,116	139	67	48	6.0	34.5	135	233	3 (3)	0	3 (2)	0
Greenland halibut												
NW Gulf	2,686	2,835	190	468	7.1	16.5	0	0	0	3 (3)	-	-
North Shore	475	328 ^a	4	0	0.8	0	0	0	0	-	-	-
4R	4,716	4,047	16	19	0.3	0.5	0	0	0	0	-	-
Miscou	61 ^a	31 ^a	0	0	0	0	0	0	-	-	-	-
Southern Gulf	0	0	-	-	-	-	-	-	-	-	-	-

Table 1 Distribution of at-sea observer and sentinel fishery efforts (n of hauls) relative to the different types of commercial gillnet fisheries in 2001 and 2002.

^aEstimation based on species' annual mean landing per haul.

possessed only a herring or mackerel gillnet licence (43%) were proportional to the number of questionnaires assigned to each group. Of the 5,137 owners of valid licences, 1,744 (34%) were active in 2000 (Table 2). Assuming that the 2,277 questionnaires were sent randomly to active and inactive fishermen, an expected 774 questionnaires (i.e. 34%) were sent to active fishermen. Based on this assumption, response rates from active fishermen (n=258) and active fishermen who provided useful information on bycatch levels (n=173) were 33% and 22%, respectively (i.e. 258 and 173 of 774 active fishermen).

In total, 188 and 296 harbour porpoise bycatches were reported by 37 (24%) and 47 (27%) fishermen in 2000 and 2001, respectively (Table 2). Bycatches were the highest in the northeastern Gulf (i.e. NAFO areas 4Sv, 4Sw, 4Ra and 4Rb), in the southern Gulf near Prince Edward Island and western Cape Breton (i.e. NAFO areas 4Tg, 4Th and 4Tj), at the entrance of Baie des Chaleurs (i.e. NAFO area 4Tn) and in the northwest extreme of the Gulf of St. Lawrence (i.e. NAFO area 4Sz) (Fig. 4). The overall distribution of bycatches among the 19 NAFO areas where bycatch data were available from questionnaires differed significantly (g=278.3 and 337.7 in 2000 and 2001, respectively; df=18; p < 0.0001) from the distribution expected if proportional to fish landings. Bycatches were generally higher than expected from landings in 2000 and 2001 in NAFO areas 4Sv and 4Sw (31 and 6% of total bycatches vs 5 and 9% of total landings), 4Tg, 4Th and 4Tj (9 and 22% of bycatches vs 7 and 5% of landings), 4Tn (31 and 28% for bycatches vs 19 and 12% of landings) and 4Sz (4-8% of bycatches vs 0.1 and 0.1% of landings). However, this was not the case in NAFO areas 4Ra and 4Rb, where bycatch numbers were either proportional or lower than expected from landings (19 and 32% of bycatches vs 22 and 49% of landings in 2000 and 2001, respectively). The seasonal distribution of bycatches also did not follow the seasonal distribution of fishing effort (g=121.8 and 33.6 in 2000 and 2001,respectively; df=6; p < 0.0001). Bycatches were the highest in July and August during both years, and were higher than expected from fish landings during these months in 2000 (38 and 38% of bycatches vs 20 and 24% of landings) but not in 2001 (35 and 26% of bycatches vs 36 and 28% of landings). However, bycatches remained high during September in 2001 when fishing activity declined and thus, were

Table 2

Estimates of harbour porpoise bycatches during 2000 and 2001 calculated from a mail survey of fishermen with valid groundfish, Atlantic herring, or mackerel gillnet fishery licenses for the Estuary or Gulf of St. Lawrence in 2000. Confidence intervals (CI) were estimated using standard bootstrap techniques.

	Estuary and Gulf of St. Lawrence		Area similar to Fontaine <i>et al.</i> (1994a)		
	N (in %)	2000	2001	2000	2001
Fishermen with valid licences in 2000	5,137				
Questionnaires sent to fishermen with valid licenses in 2000	2,277 (44%)				
Questionnaires returned	294 (13%)				
Questionnaires returned by inactive fishermen	36				
Questionnaires returned by active fishermen unwilling to participate	35				
Active fishermen willing to participate	223 (10%)				
Questionnaires with information on harbour porpoise bycatches		152	173	78	89
Fishermen who caught harbour porpoises (in %)		37 (24.3%)	47 (27.2%)	19 (24.3%)	21 (23.6%)
Total number of harbour porpoise bycatches ^a		188	296	133	132
Mean number of bycaught harbour porpoises per fisherman (CV); (95% CI) ^b		1.24 (352%) ^b	1.71 (267%) ^b	1.72 (348%)	1.49 (276%)
		[0.66 - 2.10]	[1.02-2.38]	[0.39-3.05]	[0.63-2.35]
Active gillnet fishermen in the fishing fleet		1,744	1,408	781	472
Extrapolation of the number of bycatches to the fishing fleet $(95\% \text{ CI})^{\text{b}}$		2,215	2,394	1,343	703
		(1,151-3,662)	(1,440-3,348)	(307-2,379)	(300-1,107)

^a Assuming a bycatch of one harbour porpoise for fishermen who indicated 'some bycatches'; ^b between-year differences were not significant (*t*-tests, p>0.05).

significantly higher than expected from fish landings during this month (19% of bycatches vs 12% of landings; Fig. 5). Atlantic cod, herring and mackerel were the species most often associated with porpoise bycatches during both years (Table 3).



Fig. 4. Distribution of harbour porpoises bycaught in the gillnet fishery in (a) 2000 (n=188 porpoises) and (b) 2001 (n=296), as indicated by a mail survey of gillnet fishermen active during the 2000 fishing season. Ten and 15 porpoises were caught in undetermined locations in 2000 and 2001, respectively. The solid thick lines delimit the five zones referred to in the document (see Fig. 1).

These mortalities resulted in mean bycatch rates of 1.24 (SD=4.4) and 1.71 (SD=4.6) porpoises per reporting fisherman in 2000 and 2001, respectively. Mean catch rates did not differ significantly between years (t=-0.70, p>0.05). Extrapolation of these rates to the entire active fishing fleet using bottom-set gillnets resulted in an estimated total bycatch of 2,215 (95% CI 1,151-3,662) and 2,394 (95% CI 1,440-3,348) porpoises for the Estuary and Gulf of St. Lawrence in 2000 and 2001, respectively. The use of a survey area similar to Fontaine *et al.* (1994a), i.e. the Miscou, North Shore and northwestern Gulf zones, including the area of the Îles-de-la-Madeleine, provided bycatch estimates of 1,343 (95% CI 307-2,379) and 703 (95% CI 300-1,107) porpoises in 2000 and 2001, respectively.



Fig. 5. Monthly distribution of activities (lines) by (a) at-sea observers and (b) sentinel fisheries and incidental mortalities of porpoises reported by these two groups (bars) in 2000 and 2001.

Table 3

Species associated with incidental catches of harbour porpoises during 2000 and 2001 as indicated by a questionnaire survey of fishermen with valid groundfish, herring, or mackerel gillnet licenses for the Estuary or Gulf of St. Lawrence in 2000.

	2000		2001	
Species associated with harbour porpoise bycatches	N of respondents	%	N of respondents	%
Atlantic cod	14	41	18	40
Atlantic herring	12	35	18	40
Atlantic mackerel	15	44	17	38
Capelin	5	15	9	20
Flounder	3	9	3	7
Greenland halibut	1	3	1	2
Hake	1	3	1	2
Lumpfish	3	9	3	7
Undetermined	7	21	8	13

At-sea observer and sentinel fishery programmes

Ten harbour porpoise bycatches were reported by at-sea observers in 2001 (n=4) and 2002 (n=6) (Table 1). The Atlantic cod and Greenland halibut bottom-set gillnet fisheries were responsible for seven and three of these catches, respectively. At least six of the seven porpoises caught as part of the Atlantic cod fishery were taken in late July, when most of the at-sea observer activities took place; the date of bycatch was unavailable for an animal caught in zone 4R. The three porpoise bycatches associated with the Greenland halibut fishery occurred in 2002 in the northwestern Gulf and were spread out in time between late July and early September (Fig. 5a). Porpoise bycatches associated with the Atlantic cod fishery occurred in waters shallower than 60m, whereas at least two of the three captures associated with the Greenland halibut fishery occurred at deeper depths. The low number of hauls monitored by at-sea observers prevented the calculation of bycatch estimates for several zones and the study area as a whole, and provided only imprecise estimates (i.e. large CVs) for all other zones (Table 4). Using the upper confidence limits of mortality estimates, and assuming that bycatches were proportional to fishing effort, total bycatch of harbour porpoises, as estimated from the available at-sea observer data, was probably of the order of 1,000 individuals or fewer in 2001 and 2002.

The sentinel fishery activities resulted in 86 and 77 harbour porpoise bycatches in 2001 and 2002, respectively (Tables 1 and 4). Bycatches in this fishery peaked in late August in 2001 and in early September in 2002, even though commercial fishing activities (g=195.0 and 461.5 in 2001 and 2002, respectively; df=11; p<0.0001) and sentinel fishery activities (g=55.6 and 90.2 in 2001 and 2002, respectively; df=12 and 11; p<0.0001) peaked earlier in the season, i.e. in late July to late August (Fig. 5b). Between 53 and 65% of these harbour porpoise bycatches occurred in the Miscou zone; most of the other mortalities occurred in the 4R and North Shore zones (Table 4).

It is noteworthy that the highest bycatch rates were associated with the sentinel fishery, whose activity occurred over extended periods compared to commercial or at-sea observer fisheries and included areas where target species might have been less abundant. The larger number of bycatches observed in the sentinel fishery (n=31 for 14 hauls in 2001, n=48 for 19 hauls in 2002) compared to the at-sea observer programme (n=0 in 313 and 212 hauls in 2001 and 2002, respectively) at the Miscou Bank (NAFO area 4Tn) was puzzling. The vast majority (26 of 31 and 46 of 48) of

the mortalities inflicted by the sentinel fishery occurred in late August and September, when commercial cod fishery activities had decreased (Figs 2 and 5b). Commercial fishing was nearly null and coverage by at-sea observers was nonexistent during this period in 2002, which might partly explain why no harbour porpoises were reported that year. During the same period in 2001, 37 hauls were subjected to at-sea observations, but still, none of these hauls were associated with bycatches. A comparison of different parameters related to operations, including fishing depth, number of gear, soak time and fishing location, for periods when the different types of activity occurred at the same period (August and early September) revealed significant differences in fishing characteristics between commercial fisheries, commercial fisheries with at-sea observers on board and sentinel fisheries. Specifically, sentinel fisheries soaked nets of similar length (455m) but with smaller mesh, at deeper depths, for longer periods and for a lower quantity of landed fish than did the commercial fisheries with an observer on board (Table 5). Plotting cod fishing locations in the Miscou zone (NAFO 4Tn) indicated that, at least for August and early September 2001, there was little overlap in fishing location between the two fisheries. There was also little overlap between commercial fisheries with observers on board and commercial fisheries not subjected to at-sea observations (Fig. 6a). Commercial and sentinel fisheries generally followed the 60m isobath, whereas fishing activities with at-sea observers on board occurred in shallower waters, inside the Miscou Bank. In 2002, periods of activity by at-sea observer and sentinel fisheries in area 4Tn did not overlap in time but did overlap spatially (Fig. 6b).

DISCUSSION

The at-sea observer programme and the questionnaire survey provided somewhat inconsistent indices of harbour porpoise bycatch levels in the gillnet fisheries of the Estuary

Table 4

Estimates of incidental catches of harbour porpoises in the bottom-set gillnet fishery in the Estuary and Gulf of St Lawrence using information obtained from the at-sea observers and sentinel fishery programs. The 95% confidence intervals (CI) were estimated using standard bootstrap re-sampling techniques.

				At-sea observ	/ers		Sentinel f	ishery
Targeted species	Zones	N of commercial hauls	N of bycatches per haul (n hauls)	Estimated mortalities	CV (%)	95% CI	N of bycatch per haul (N of hauls)	Total <i>n</i> of bycatches
2001								
Atlantic cod	NW Gulf	9	_a	_ ^a	_ ^a	_ ^a	0(22)	0
	North Shore	1,428	_a	_ ^a	_ ^a	_ ^a	0.048 (539)	26
	4R	8,814	0.0143 (70)	126	99	0-378	0.021 (512)	11
	Miscou	3,887	0 (362)	0			0.236 (195)	46
	Southern Gulf	1,116	0.04478 (67)	50	53	0-100	0.222 (135)	3
Greenland halibut	NW Gulf	2,686	0 (190)	0	-	-	· /	
	North Shore	475	_a	_ ^a	_ ^a	_ ^a		
	4R	4,716	0 (16)	0	-	-		
	Miscou	61	_a	_ ^a	_ ^a	_ ^a		
2002								
Atlantic cod	NW Gulf	60	_a	_ ^a	_ ^a	_ ^a	0(12)	0
	North Shore	2,529	0.05882 (17)	149	98	0-446	0.031 (457)	14
	4R	9,404	0 (80)	0	-	-	0.032 (403)	13
	Miscou	2,522	0.0086 (232)	22	74	0-54	0.152 (329)	50
	Southern Gulf	139	0 (48)	0	-	-	0 (233)	0
Greenland halibut	NW Gulf	2,835	0.0064 (468)	18	57	0-42		
	North Shore	328	_a	_ ^a	_ ^a	_ ^a		
	4R	4,047	0(19)	0	-	-		
	Miscou	31	_a	_ ^a	_ ^a	_ ^a		

^aThe at-sea observer coverage was too low to estimate harbour porpoise bycatch rates.

Comparisons of median values and the 10th and 90th percentiles (P10–P90) of different parameters of Atlantic cod fishing operations between sentinel fisheries (sentinels) and commercial fisheries conducted under the at-sea observer program (observers) in area 4Tn during August and early September 2001.

	Sentinels $(N = 51)$	Observers $(N = 188)$		
Parameter	Median (P10-P90)	Median (P10-P90)	$F_{ m ANOVA \ on \ ranks}$	P > F
Depth (m) Soak time (h) Mesh (mm) Landings (kg)	44 (35–96) 19.7 (17.8–24) 145 (140–146) 11 (0–377)	40 (34–56) 7.3 (2.5–18) 145 (140–152) 134 (30–409)	14.6 178.7 10.5 4.3	0.0002 0.0001 0.001 0.040



Fig. 6. Spatial distribution of commercial cod fishery activities with and without at-sea observers on board, and of sentinel fisheries that did or did not report harbour porpoise bycatches in NAFO Area 4Tn. Fishing activities in 2001 all took place in August and early September. In 2002, at-sea observer activities occurred between late July and early August and did not overlap temporally with activities by sentinel fisheries, which occurred in late August and September.

and Gulf of St. Lawrence. Estimates obtained using at-sea observer data suggested that 1,000 harbour porpoises or fewer were caught by this fishery during 2001 or 2002, whereas the mail survey estimated a total bycatch of twice as many (2,215 and 2,394) harbour porpoises for 2000 and 2001, respectively. There are some weaknesses associated with the two approaches used in this study to estimate bycatch levels. In contrast to the study by Fontaine et al. (1994a), which surveyed all (100%) active fishermen, our study questioned 44% of the fishermen with licences and an estimated 34% of active fishermen. Return rates of questionnaires in the study by Fontaine et al. (1994a) were 33% and 18% for 1989 and 1990, respectively. In this study, the return rate from fishermen who provided useful information on bycatch was 22%. Response rates of this magnitude were considered low and their reliability in providing accurate bycatch estimates has been questioned (e.g. Palka, 1994). The quality of the information obtained from questionnaire surveys also depends on diverse biases associated with the willingness of fishermen to transmit information that might impede their future fishing activities (e.g. bias of non-respondents, accuracy of the information provided; Usher and Wenzel, 1987). Mail surveys or interviews also suffer from the capacity of fishermen to recall events that took place weeks or months earlier (Lien et al., 1994). Questionnaires in this study were distributed shortly after the end of the fishing season, which helped reduce the latter bias. While fishermen were asked to provide information on harbour porpoises caught incidentally over the past two seasons, bycatch estimates from the fishing season just preceding the distribution of questionnaires (2001) were considered the most reliable.

There are some indications that bycatch rates obtained through the at-sea observer programme might represent underestimates. The zones identified as being associated with high bycatch levels differed between the mail survey and the fishery-monitoring programme. Fontaine et al. (1994a) and Larrivée (1996) had both identified the Gaspé Peninsula (NAFO areas 4Tn and 4To) and the Lower North Shore (areas 4Sv and 4Sw) as being important areas of harbour porpoise bycatch. The sentinel fishery programme and the questionnaires, but not the at-sea observer data, confirmed the importance of these areas for incidental catches of harbour porpoises (Fig 4; Table 1). The absence or low coverage of the Atlantic cod fishery by at-sea observers in the North Shore zone, and to a lesser extent in area 4To, may in part explain the absence of reported bycatches in these sectors.

The use of an independent observer, ideally dedicated to marine mammal research (so-called 'on-watch'), is recognised as being the most desirable approach for obtaining information on marine mammal bycatches (Perrin *et al.*, 1994; Trippel *et al.*, 1996; Bisack, 1997a; Department of Fisheries and Oceans, 2001). However, the amount and distribution of observer coverage must be adjusted so to ensure the detection of a reasonably high number of events and thereby achieve an acceptable coefficient of variation (Bisack, 1997b). As stated by Wade (1999), '... a five percent observer coverage may be sufficient for a very large fishery, but may be grossly inadequate for a smaller fishery'. In this study, the number of hauls monitored by observers was low throughout the Estuary and Gulf of St. Lawrence and for all groundfish fisheries with the exception of the Greenland halibut fishery in the northwestern Gulf and the Atlantic cod fishery in the Miscou zone (Table 1). In addition, the observers on sentinel fishery or at-sea observer vessels were not entirely dedicated to marine mammal watch, thereby causing an underestimation of incidental mortalities of harbour porpoises in these fisheries. Studies that have compared incidental catches reported by at-sea observers while they were 'on-watch' and 'off-watch' for marine mammals, i.e. while they were or were not actively watching for harbour porpoises in nets being hauled, indicated that a non-negligible (about 18-37%) proportion of bycaught harbour porpoises fall out of the net before being brought on deck (Palka, 1994; Bravington and Bisack, 1996).

The Miscou zone (NAFO area 4Tn) was identified as one of the most problematic areas for harbour porpoise bycatches in the Gulf of St. Lawrence by both Fontaine et al. (1994a) and Larrivée (1996). This one sector contributed 13% and 18% of all the bycatches reported by fishermen through questionnaires in 2000 and 2001, respectively, and 62-65% of those reported by sentinel fisheries in 2001 and 2002. However, no bycatches were detected by at-sea observers in this area in 2001 and 2002 in spite of the high number of hauls that were monitored (Table 1). Inconsistencies in data collection between observers are unlikely to be the reason for this discrepancy since the same individuals served as observers onboard sentinel and at-sea observer fishery vessels (M. Jean, Biorex Inc., Caraquet, N.B., pers. comm.). An experimental study conducted by Larrivée (1996) between May and August 1992 in this area (4Tn) indicated a mean bycatch estimate of 3.85 harbour porpoises per landed metric ton of fish. Applying this estimate to the landings reported in this area in 2001 (705t) and 2002 (496t) would have yielded bycatch estimates of 2,714 and 1,910 harbour porpoises, respectively, for area 4Tn alone. The bycatch rate obtained by Larrivée (1996) is probably unrealistic for the 2001 and 2002 situation in this area given the profound changes observed in fishing practices, fishing season and number of operating vessels. However, the results from this simple calculation suggest that a meticulous examination of the data available for this area is warranted.

The comparison of fishing location and timing between sentinel fisheries and commercial fisheries subjected and not subjected to at-sea observation indicated that fine-scale differences in the temporal and spatial distribution of fisheries may greatly influence rates of harbour porpoise bycatch. Fisheries that occurred later in the season (late August and September) and closer to the 60m isobath appeared more prone to causing incidental mortality of harbour porpoises (Figs 5 and 6). Larrivée (1996) obtained similar results in a controlled fishing experiment between the 36m and 55m isobath of the Miscou Bank (area 4Tn) during the period 19 August to 29 September 1994. She observed a decline in cod landings with date and soaking depth, and a parallel increase in harbour porpoise bycatches. Consequently, a larger effort by at-sea observers, closer to the 60m isobath where most of the commercial fisheries activity occurred, might have revealed higher bycatch estimates in area 4Tn. The difference that was observed in 2001 in the spatial distribution between commercial fisheries subjected and not subjected to observer monitoring suggests that fishermen might distribute their fishing effort differently in the presence and absence of at-sea observers. This pattern was not observed in 2002. The absence of information on soak time, depth and other descriptors of the commercial fishery not subjected to at-sea observations precluded further analyses of these patterns that were observed among the different fisheries.

Significant differences in the characteristics of hauls were also observed between the sentinel and at-sea observer fisheries (Table 5). One striking difference was the short soak time (median=7.3h; range 2.5-18h) of the commercial fishery subjected to at-sea observation compared to sentinel fisheries (median=19.7h; range 17.8-24h). These results suggest a deployment and retrieval of nets in the same day by the fisheries subjected to at-sea observations, compared to an overnight deployment by the sentinel fisheries. The effect of soak time on bycatch levels is unclear, with some studies indicating an increase in the number of captures per haul with the amount of time nets are left in the water (Vinther, 1999) and other studies showing a reversed trend or unclear patterns (Palka, 1994; Larrivée, 1996; Department of Fisheries and Oceans, 2001; Hood, 2001). A positive correlation between soak time and harbour porpoise bycatch, if it was to occur, might represent a plausible explanation for the higher bycatch rates associated with the sentinel fisheries.

The increase in harbour porpoise bycatches during late summer could be linked to an influx of harbour porpoises inshore in response to an increase in the abundance of Atlantic herring in coastal waters of the Baie des Chaleurs (LeBlanc et al., 2002a; b). This species, which spawns in the spring and autumn, represented an important prey of harbour porpoises in the Miscou zone both in the late 1980s and in 2001-02 (Fontaine et al., 1994b; Guimont, 2003). This species is also regularly associated with harbour porpoise bycatches in eastern Canada (Fontaine et al., 1994a; Trippel et al., 1999; Hood, 2001; this study). The distribution of Atlantic herring closely follows the 60m isobath in the Miscou Bank area and likely overlaps to some extent the distribution of Atlantic cod (LeBlanc et al., 2002a; b). Harbour porpoises might have sought this abundant and rich food resource during late summer in the vicinity of the Miscou Bank, making them vulnerable to incidental mortalities in Atlantic cod fisheries. Two studies conducted in the Bay of Fundy and Newfoundland indicated a close relationship between harbour porpoise and Atlantic herring catch rates and support this hypothesis (Trippel et al., 1999; Hood, 2001).

Bycatch estimates obtained through the mail survey and the at-sea observer programme both suggest a decrease in harbour porpoise bycatches since the late 1980s, although the magnitude of this change remains uncertain. The use of a survey area similar to Fontaine et al. (1994a) resulted in estimates from questionnaires 24-63% lower in 2000-2001 compared to the late 1980s (bycatch estimates = 1,907 [95% CI 1,235-2,579] and 1,762 [95% CI 563-3,251] harbour porpoises in 1989 and 1990, respectively; Fontaine et al., 1994a). Using at-sea observer data and an area similar to Fontaine et al. (1994a), 500 individuals or fewer were probably caught in 2001 and 2002, representing a reduction in bycatch levels of at least 72-75% compared to the late 1980s. Although results from questionnaires suffer from a number of weaknesses associated with the method, the consistency in the areas identified as the most problematic for harbour porpoise bycatches between this study and two similar mail surveys conducted in the late 1980s and early 1990s lends confidence to the general trend observed since the late 1980s. The 24-63% reduction in bycatch levels

obtained through the questionnaire survey is probably more realistic than the 72-75% reduction suggested by the at-sea observer programme, given the incomplete and generally low coverage of the fishery by the latter programme. No comparisons were possible between bycatch estimates from our study and those obtained from a similar survey mailed in 1992 and 1993 (Larrivée, 1996) since the latter study was conducted over an undefined portion of the Estuary and Gulf of St. Lawrence. In addition, bycatch estimates in the latter study (i.e. mean estimates of 3,650 in both years, with 95% CI of 1,493-5,806 and 1,657-5,642 harbour porpoises in 1992 and 1993, respectively) were overestimates, since they were produced while assuming that all fishermen with valid licenses had been actively fishing in each of these years, which was most probably not the case (M. Larrivée, Centre spécialisé des pêches, C.P. 220, Grande-Rivière, Qc, pers. comm.).

Bycatch estimates obtained through questionnaires and the at-sea observer programme, although imprecise, indicate that the incidental mortality of harbour porpoises in the gillnet fishery of the Estuary and Gulf of St. Lawrence remained substantial in 2000-02 (i.e. mean estimates of 1,000-2,400 individuals per year), in spite of a decrease in the groundfish fishing activities and total bycatches compared to the late 1980s and early 1990s. Whether current removals are sustainable for the harbour porpoise population depends on a variety of factors, including population size and rate of increase (reviewed in Donovan and Bjørge, 1995; Hall and Donovan, 2002). The abundance of harbour porpoises in the Gulf of St. Lawrence was last assessed in 1995 and 1996 using systematic line-transect aerial surveys (Kingsley and Reeves, 1998). Sampling of a large portion of the Gulf of St. Lawrence in 1995 and its northern portion in 1996 yielded estimates of 12,100 (CV=26%) and 21,720 (CV=38%) harbour porpoises, respectively. Once corrections were applied to the estimates to account for visibility biases associated with observer experience, availability and detectability of porpoises, Kingsley and Reeves (1998) estimated that an average 36,000 to 125,000 porpoises occupied the Gulf of St. Lawrence during the summers of 1995 and 1996. In the absence of empirical measurements of population rate of increase for harbour porpoises, several studies attempted to estimate maximum rate of increase (R_{max}) for this species using mortality schedule of humans or other mammals. These exercises provided R_{max} varying between 4% and 10%, although some authors debated the validity of the higher values (reviewed in Stenson, 2003). Considering the lower and upper 95% confidence limits of our most reliable estimate of bycatch (i.e. the 2001 questionnaire survey results; Table 2), and assuming an R_{max} of 4%, the harbour porpoise population in the Gulf of St. Lawrence would need to be at least 36,000-83,700 individuals for current incidental catches to be sustainable. If the rate of increase is less than maximal, e.g. $0.5R_{max}$ or 2%, then 72,000-167,400 harbour porpoises would be needed to attain sustainability. Although the trajectory of the population since it was last surveyed in 1996 is uncertain, these findings suggest that bycatch levels might remain a cause for concern for the harbour porpoise population in the Gulf of St. Lawrence. An update of population estimates may assist in putting bycatch estimates into perspective. The differences observed in by catch rates between the sentinel fisheries and commercial fisheries subjected to at-sea observations in NAFO area 4Tn indicate that slight changes in the spatial and temporal distribution of fishing activities might result in substantial changes in harbour porpoise incidental catches. Our results also emphasise the sensitivity of bycatch estimates to the spatial and temporal distribution of the effort by at-sea observers. Clearly, a better understanding of the seasonal and fine-scale spatial distribution of harbour porpoise bycatches would help mitigate the impacts of the commercial fisheries for groundfish on this harbour porpoise population. This goal might be achieved by the intensification of the at-sea observer monitoring programme in areas of the Gulf of St. Lawrence where harbour porpoises are known to be abundant, such as the Lower North Shore and zone 4R, and where much of the Atlantic cod gillnet fishery takes place.

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The effect of line-transect placement in a coastal distance sampling survey

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ABSTRACT

Distance sampling surveys are commonly used to estimate animal abundance (*N*). The choice of survey design has only recently received attention in the line-transect research literature, which has tended to focus more on the violation of assumptions. In this study, simulation methods were used to assess the effect of line placement on the accuracy and precision of a line-transect survey for estimating dolphin abundance. In 1998, a vessel-based line-transect survey of Hector's dolphin (*Cephalorhynchus hectori*) was carried out around Banks Peninsula (New Zealand). These data were used to generate a spatially realistic dolphin distribution onto which different survey designs were overlaid. Eight types of design were considered, consisting of four types of stratification and two methods for allocating lines: random or systematic. None of the designs showed any evidence of significant bias in the estimate of $N(\hat{N})$. Systematic placement of \hat{N} , $[CV(\hat{N})]$. These results correspond well with those expected from classical sampling theory for the case of estimating a population mean. However, these designs also overestimated $CV(\hat{N})$ by 10-28% (mean=22%). Systematic line-placement has several practical advantages over random placement, including more uniform spatial coverage. For coastal cetacean populations with spatial dynamics similar to the one considered here, we recommend the use of systematic line-placement, with the proviso that the estimate of $CV(\hat{N})$ is likely to be overestimated by 10-28%.

KEYWORDS: ABUNDANCE ESTIMATE, DISTRIBUTION, SURVEY-VESSEL, SURVEY DESIGN, MODELLING

INTRODUCTION

For ecologists, the question of 'how many are there?' is one of the most fundamental and for managers who need information on impacts, or an assessment of efficacy of intervention, it is one of the most crucial. It has always been a difficult question to answer with precision. In cetacean research, abundance information is generally gained via mark-recapture analyses of data from resightings of tags or natural markings, or from sighting surveys, of which linetransect methods are the most important. Line-transect sampling belongs to a more general class of methods called distance sampling (Buckland *et al.*, 2001). In the work presented here, the focus is on the design of a line-transect survey, particularly the effect of line placement.

Line-transect surveys for cetaceans rely on the following critical assumptions (Buckland *et al.*, 2001):

- (1) the probability of detection on the trackline equals one (i.e. g(0) = 1), or at least known;
- (2) animals are detected prior to responsive movement;
- (3) measurements are recorded accurately, with no observer bias;
- (4) line-transects are located randomly with respect to the distribution of the animals;
- (5) detections are independent events.

Violations of these assumptions will result in biased estimates of density and abundance (Hiby and Hammond, 1989; Buckland *et al.*, 2001). As a result, many line-transect studies have focussed on the development of methods to allow for such violations (e.g. Barlow, 1999; Schweder, 1999). Until recently there has been less guidance available for designing robust, cost-effective surveys. Hiby and Hammond (1989) recommend using a saw-tooth (zig-zag) survey design to achieve uniform coverage probability and for efficiency, and this design has subsequently been used in several surveys (e.g. Miyashita, 1993; Forcada *et al.*, 1994; 1995; Forcada and Hammond, 1998).

In fact, zig-zag sampling does not provide uniform coverage probability in many circumstances (Strindberg and Buckland, 2004). A simple zig-zag pattern around a convex coastline, for example, results in a proportionately greater amount of effort inshore, which may bias abundance estimates, particularly if there is an inshore-offshore density gradient. Strindberg and Buckland (2004) provided guidance for both design and analysis of zig-zag surveys to account for uneven coverage probability, however such sampling may still have associated practical problems such as swell and glare, particularly for small-boat surveys (e.g. Dawson *et al.*, 2004).

Buckland *et al.* (2001) made some comments on survey design, noting that there is no compelling reason to use completely random lines, and that systematic designs should often result in greater precision. They also offer advice on how to set out lines, pointing out that parallel lines will provide uniform coverage probability. Buckland *et al.* (2004) provides more detailed discussion of survey design. They introduce many new or recently developed ideas such as integrating geographic information systems (GIS) for automated survey design (Strindberg and Buckland, 2004) and adaptive survey designs (Pollard and Buckland, 2004). However several practical design issues, particularly for small boats, remain unresolved.

In January and February of 1998, a line-transect survey was carried out to estimate Hector's dolphin (*Cephalorhynchus hectori*) abundance between Motunau and Timaru on the east coast of the South Island of New Zealand (Dawson *et al.*, 2000; 2004; and see Fig. 1). Data from this survey were used to investigate the accuracy and precision of different survey designs, focussing on two

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aspects: (1) the effect of stratification, involving both the choice of strata and the effort allocated to each one; and (2) the choice of a systematic or random selection of lines within each stratum.

These two aspects of survey design have been considered at length in classical sampling theory (Cochran, 1977). It is known that the sample mean is unbiased for both random and systematic sampling, and that systematic sampling will often lead to a more precise estimate than random sampling. These results involve 'design-based' inference and do not automatically apply to a line-transect survey, as distance sampling involves a combination of model-based and design-based inference, the former arising as a consequence of estimating the detection function, and the latter being used to estimate density given a detection function (Fewster and Buckland, 2004).

The survey data were used to develop a spatial model of dolphin distribution, which was repeatedly sampled using different survey designs. The spatial model was not intended to characterise the true distribution of Hector's dolphin, and the aim was not to provide an exhaustive assessment of survey design for populations displaying different characteristics. Rather, our objective was to compare the accuracy and precision of the different designs for a realistic 'population'.

METHODS

The idea behind generating a spatial model for the dolphin distribution was to allow any sample of transect lines to be chosen. Each line would have an expected number of sightings, E(n), predicted by the spatial model. The observed number of sightings on each line could then be generated from a Poisson distribution with mean equal to E(n). In this way, the original survey data can generate appropriate perpendicular distances and group sizes for each 'sighting'.

Data simulation and analysis

Data from the 1998 survey formed the basis of the spatial model of dolphin distribution described here.

Buckland et al. (2001) recommended sampling across known density gradients. For the 1998 survey, it was known that there were both alongshore and offshore density gradients of Hector's dolphins, therefore lines were plotted at 45° to the shore. Sampling in this manner helps to minimise encounter rate variance, and has practical advantages since it means alternative transects can be plotted, depending on daily swell and glare conditions (Dawson *et al.*, 2004). Designing the simulations in this manner ensures consistency with the survey on which this analysis is based. This design is in contrast to the simulation work of Fewster and Buckland (2004), who generated a hypothetical population with two density gradients, but sampled in a unidirectional manner. In other word, lines were plotted horizontally or vertically and sampled across one gradient only.

To ensure uniform coverage around Banks Peninsula the coast was divided into short sections, plotting lines at 45° to the baseline of each. Transect lines extended to 4 n.miles offshore (Fig. 7). In the 1998 survey, transects were spaced 2 n.miles (New Brighton to Rakaia River) or 4 n.miles apart (New Brighton to Motunau; Rakaia River to Timaru; Dawson *et al.*, 2000).

The first step in simulating the data was to create plots showing the coastline that had been surveyed in 1998, together with contour lines of density based on observed encounter rates (number of groups seen per kilometre of survey trackline, nL^{-1}). This process created continuous density zones, extrapolated from our data, using Surfer Surface Mapping System (Smith et al., 1995). The Minimum Curvature method was chosen, which attempts to generate the smoothest surface while honouring the original data as closely as possible. A digitiser was used to generate base maps onto which contours were overlaid (e.g. Fig. 1). A further overlay was created that contained a theoretical set of possible transect lines (e.g. Fig. 2). Note that the contouring in these figures is different for illustrative purposes only, for the actual analysis all plots used the same contour intervals as in Fig. 2. These lines were separated by a distance equal to our estimated effective strip width from the 1998 survey; hence the complete set of lines provided full sampling coverage of the survey area.



Fig. 1. Survey area with encounter rate (sightings/km trackline) contours. Highest encounter rates are off the eastern side and to the south of the peninsula. Contouring interval is 0.2 (groups seen per kilometre of trackline).

A total of 672 lines were overlayed onto the density contours. For each line, the proportion that fell within each density zone was calculated. This provided a mean encounter rate for the line and was multiplied by the length of the line to obtain an expected number of encounters, E(n). For example, if the mean encounter rate for a transect was $nL^{-1} = 0.5$ groups km⁻¹, and the length of the transect was 7.5km, then $E(n) = 0.5 \times 7.5 = 3.75$. The rationale was that each line had a unique encounter rate based on where it fell, that could then be converted to E(n). The 'observed' number of encounters was selected at random from a Poisson distribution with mean equal to the value of E(n) for that line (Buckland *et al.*, 2001).

For each encounter, group size, *s*, was determined by randomly selecting a value from the distribution of group sizes observed in the original survey. Perpendicular distances, *x*, were generated by replicating the uniform key function model with two cosine adjustments, as this was the model that best fitted data from the 1998 survey. Using one metre increments from 0-594m (our truncation distance from the 1998 survey), this model was used to generate values for g(x), and these were used to randomly select sighting distances.



Fig. 2. The sub-region of Birdlings Flat-Rakaia River, encounter rate contours and full set of transect lines for this section. Contouring interval is 0.5 (groups seen per kilometre of trackline).

Data generation therefore resulted in a single spreadsheet containing the following information:

- (1) a total of 672 possible lines, each with a sample of 200 possible values for *n*;
- (2) 1,000 possible sighting distances and group sizes.

These numbers for n and sighting distances were chosen because when plotted on frequency histograms they closely approximated the appropriate distributions.

The simulations were run within Microsoft *Excel*, and followed the steps described in the flow chart in Fig. 3. Data analysis was carried out using the program *Distance 3.5* (Thomas *et al.*, 1998). It is worth noting the two main steps in the simulation process.

Step 1. A 'snapshot' of the population was created by generating a fixed number of sightings on each of the 672 possible lines (together with a group size and distance from the transect line).

Step 2. A survey for each of the eight designs being considered was conducted, by selecting a subset of the lines in Step 1.

There was some choice as to how often Steps 1 and 2 were carried out and in order to cover a wide range of plausible spatial distributions Step 1 was performed 199 times and Step 2 just once. Carrying out Step 1 once and Step 2 many times, would assess the performance of the designs for only one spatial distribution.



Fig. 3. Flow diagram illustrating the simulation procedure run within *Excel* using the programming language Visual Basic for Applications.

For each iteration, the 'true' abundance (N_T) , was calculated from all the lines, and compared with the estimated abundances $(\hat{N}_1, \hat{N}_2, \dots, \hat{N}_8)$ obtained from the subsets of lines selected by the eight survey designs.

Survey designs

For each survey design, the overall effort was chosen to be roughly the same as in the inshore zone (0-4 n.miles) of the original survey (440km), in order to represent what could realistically be achieved in one field season. The offshore zone and harbours and bays strata of the 1998 survey were both excluded.

Eight survey designs were compared (Figs 4-11), consisting of four types of stratification and two methods for allocating lines (random or systematic). The four types of stratification are summarised below.

Type 1 —single stratum.

Type 2 —stratification and effort as per 1998 survey. Areas to the north and south of the sanctuary were treated as one stratum. Effort was split roughly 40:60 for nonsanctuary:sanctuary. Effort intensity was greater in the sanctuary, with lines spaced at 2 n.miles compared to 4 n.miles outside the sanctuary for systematic line selection.

Type 3 -two strata (split at Goughs Bay, Banks Peninsula), effort was split roughly 38:62 for north:south. Intensity of effort (i.e. line-spacing) was the same for both strata.

Type 4 - stratification as per 1998 survey, with equal effort in the two strata. Effort was split 53:47 for non-sanctuary:sanctuary.

Design type 2 represents a 'good' stratification scheme, type 3 a 'poor' stratification scheme (given the hypothetical density illustrated in Fig. 1), and type 4 a 'good' scheme with 'poor' effort allocation. For systematic selection, the first line in each coastline block was selected randomly, with subsequent lines at regularly spaced intervals. Examples of each survey are given in Figs 4-11.

Measures of accuracy and precision

For each design, the relative bias, B_1 , on the *i*th iteration was calculated as:



Fig. 4. Single stratum with random line selection.

where

 \hat{N} = estimated abundance from the 'survey',

 N_{Ti} = the 'true' abundance of the *i*th iteration (i.e. estimated using all lines).

For each design, an average bias, \overline{B} , was calculated as:

$$\overline{B} = \frac{\sum_{i=1}^{199} B_i}{199}$$

The precision associated with each design was summarised by:

$$CV(\hat{N}) = \frac{SD(\hat{N})}{\hat{\overline{N}}}$$

where \overline{N} is the mean and $SD(\overline{N})$ is the standard deviation of the 199 estimates of N for that design. This is denoted the true $CV(\hat{N})$ to distinguish it from the mean of the estimates of $CV(\hat{N})$ provided by the program *Distance*.



Fig. 5. Single stratum with systematic line selection.



Fig. 6. Sanctuary treated as separate stratum, line selection is random, with greater effort inside the sanctuary. Effort is split roughly 40:60 for non-sanctuary:sanctuary, and intensity is double within the sanctuary.



Fig. 7. Sanctuary treated as separate stratum, line selection is systematic. Lines spaced at 2 n.miles within sanctuary and at 4 n.miles to the north and south.



Fig. 8. Poor stratification scheme, effort is equal in both strata, and is weighted by area, line selection is random.

In order to assess the precision of our estimate of the true $CV(\hat{N})$ from 199 iterations, its standard error was also calculated using the formula:

$$SE[CV(\hat{N})] = \frac{CV(\hat{N})}{\sqrt{2n_s}}$$

where n_s (=199) is the number of iterations for each design (Kotz and Johnson, 1982, p.29).

A further measure of interest is the confidence interval error rate, i.e. how often the interval does not contain the 'true' N. The upper rate (how often the true value of N is higher than the upper limit of the interval) will not necessarily be equal to the lower rate (how often the true value of N is less than the lower limit of the confidence interval) because the intervals are log-based and therefore asymmetrical.

The nature of the simulations means that survey design affects the encounter rate, but not the mean group size nor



Fig. 9. Poor stratification scheme, effort is equal in both strata, and is weighted by area, line selection is systematic.



Fig. 10. Sanctuary is treated as a separate stratum, effort is equal in both strata.

the effective strip width. Therefore, summary statistics for the encounter rate were calculated in addition to those for the estimate of abundance.

RESULTS

The results indicate that for the type of situation presented here, a systematic survey design generally provides a more precise estimate of abundance than a random design (Table 1a), with an average gain in true $CV(\hat{N})$ of 14% (the relative difference between true $CV(\hat{N})$ for systematic and random designs). However, for systematic designs this CV is overestimated by an average of 22%. For all designs, the estimated amount of bias is small (mean = 2.7%) and the standard errors indicate that there is no evidence of real bias for all but one of the designs. The average 'true' abundance was 777 (CV=7%), and the estimates ranged from 648-905.

Encounter rates were similar for all designs, while the CVs were on average 8% lower for systematic designs (Table 1b). For the stratified designs, some differences in

			Mean N , mea	an bias B (%) and rele	evant statistics.		
Survey Results							
Туре	Random or systematic	\hat{N}	True $CV(\hat{N})$	SE[True $CV(\hat{N})$]	Mean estimated $CV(\hat{N})$	\overline{B} (%)	$SE(\overline{B})(\%)$
1	Random	775	0.340	0.017	0.388	0.1	2.4
1	Systematic	784	0.301	0.015	0.385	0.9	2.0
2	Random	809	0.365	0.018	0.400	4.1	2.7
2	Systematic	800	0.319	0.016	0.395	3.1	2.3
2	Random	796	0.354	0.018	0.394	2.2	2.5
3	Systematic	819	0.303	0.015	0.388	5.3	2.2
	Random	801	0.340	0.017	0.390	3.6	2.5
4	Systematic	796	0.281	0.014	0.309	2.6	2.0

Table 1a Mean \hat{N} , mean bias \overline{B} (%) and relevant statistics



Fig. 11. Sanctuary is treated as a separate stratum, effort is equal in both strata.

encounter rate between strata were apparent for systematic designs, but not for random designs (Table 1b). In general, stratification did not offer any clear benefits, with no significant gains in precision (Table 1a).

All the overall error rates were less than 5%, indicating that the intervals were a little too wide (Table 2). This was particularly true for the systematic designs. For all designs, the lower limit was too low, while for systematic designs the upper limit was too high.

Note that the standard errors for the true $CV(\hat{N})$ are all small, indicating that there would be little gain from increasing the number of iterations in the simulation.

DISCUSSION

The pattern of lower true $CV(\hat{N})$ for systematic surveys is consistent with results from classical sampling theory (Cochran, 1977). The mean estimated precision was broadly the same for random and systematic designs. This would be expected, as the calculation of $CV(\hat{N})$ within *Distance* assumes a random line placement.

It is worth noting that the systematic designs used in these simulations have an element of randomisation, resulting in uniform coverage probability throughout the area. However, because only the first line in each block is selected randomly, the lines are not selected independently. Hiby and Hammond (1989) argue that this can result in a biased variance estimator. Our results confirm this, and suggest that there is also some bias associated with random designs,

Table 1b Results for encounter rate n/I

	Survey	Ov	erall	Strat	um 1	Stra	tum 2
Туре	Random or systematic	Mean	CV	Mean	CV	Mean	CV
	Random	0.111	0.262				
1	Systematic	0.110	0.180				
	Random	0.113	0.279	0.112	0.427	0.114	0.356
2	Systematic	0.113	0.211	0.104	0.372	0.123	0.182
	Random	0.114	0.277	0.116	0.456	0.111	0.329
3	Systematic	0.103	0.181	0.068	0.312	0.138	0.218
	Random	0.113	0.267	0.110	0.396	0.117	0.383
4	Systematic	0.112	0.182	0.104	0.277	0.120	0.239

Table 2 Confidence interval error rates.

S	Survey	Confidence interval error rates (%)				
Туре	Random or systematic	Lower	Upper	Overall		
1	Random	0.0	3.5	3.5		
1	Systematic	0.0	0.5	0.5		
2	Random	0.5	2.5	2.0		
2	Systematic	0.0	1.0	1.0		
2	Random	0.0	3.0	3.0		
3	Systematic	0.5	0.5	1.0		
	Random	1.5	2.5	4.0		
4	Systematic	0.0	0.5	0.5		

albeit to a lesser extent. This is in contrast with classical sampling theory, where random sampling leads to an unbiased estimate of variance for the sample mean. For a systematic design, \hat{N} would be biased if dolphin density varies according to a repeating pattern that matches the distance between transects, because we may consistently sample all high or all low density areas. Also, true $CV(\hat{N})$ would be underestimated, as there would be little variation in encounter rate between transects. In practice, this situation seems highly unlikely to occur.

When sampling clumped distributions, randomly placed transects may fall predominantly in areas of especially high or low density. This is far less likely in a systematic design such as that shown in Fig. 7, and explains why the CV for encounter rate, and therefore \hat{N} , is greater for random designs.

Our results are in agreement with Strindberg and Buckland (2004) who showed that systematic grids of parallel lines have better spatial distribution than random lines. Other simulation work has also confirmed that when there is a trend in density, systematic surveys will show less variation in \hat{N} (Fewster and Buckland, 2004; Strindberg and Buckland, 2004). Additionally, if density is variable, precision of estimates of *N* are often poor; a situation which is somewhat improved by using a systematic design (Strindberg and Buckland, 2004).

A practical consideration for cetacean surveys is that the presence of the survey vessel is likely to influence animal distribution, either as a result of vessel avoidance or vessel attraction (Turnock *et al.*, 1995; Dawson *et al.*, 2004). It would make little sense to re-sample an area, a situation possible with a random design, unless sufficient time had passed that the assumption of uninfluenced distribution was again satisfied. Providing line spacing is adequate, this problem is minimised by using a systematic design.

These results do not show any clear benefit of the stratification schemes considered, there being little gain in terms of precision. Stratification will generally lead to a more precise estimate if the variation between stratum means is high. It is unlikely to offer any gains if the spatial scale of the patchiness of the population is smaller than the scale of the stratification. An important consideration is that stratification will be beneficial when substantial distribution data are available during the design phase. When this is not the case there are alternatives such as a two-phase design and post-stratification (although this comes at a cost, since it can lead to biased abundance estimates; Buckland et al., 2001). However, there are often practical reasons for stratification, such as when there are areas of specific interest to management, as in the case of the original Banks Peninsula survey. Stratification may also offer more benefits (in terms of precision) in areas where animals are more highly clustered than in the population considered here.

In summary, these results suggest that systematic designs should be given preference over random designs, even though variance is overestimated. Systematic designs have important practical advantages (see Dawson *et al.*, 2004) and provide better information on spatial distribution than random designs. Where there are no existing data with which to decide upon an appropriate stratification scheme, or if there are no areas of intrinsic interest, a non-stratified, systematic survey would be the best choice and provide data necessary for potential stratification of future surveys.

The approach taken in this study, creating a spatial model of density and overlaying different survey designs in order to explore their performance, is useful beyond what has been considered here. An obvious next step could be to vary the degree of clustering to see under what circumstances stratification makes appreciable differences to precision.

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Distribution and encounter rates of the river dolphin (*Inia geoffrensis boliviensis*) in the central Bolivian Amazon

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ABSTRACT

The ecology and conservation status of river dolphins (*Inia* sp.) distributed in the lowland rivers of Bolivia are poorly understood and only recently have basic studies been conducted to investigate their population size, taxonomic status, distribution, behaviour, environmental threats and ecology in this region. This paper examines the distribution and encounter rates of the bufeo (*Inia* sp.) in the middle reach of the Bolivian Amazon and was conducted in the Mamoré River and four of its tributaries during the low water season. Methods were employed which can be replicated during future surveys of Bolivian river dolphins and the results can be compared with those from surveys of *Inia* throughout its range. Sixty-two hours were spent surveying for dolphins, with 68% of the effort in Mamoré River and 32% in its tributaries. The *Inia* encounter rates reported here (1.6-5.8 dolphins km⁻¹) are the highest recorded anywhere in its broad geographic range; (3.3±2.96) and smallest in the Yacuma River (1.8±0.75) and the maximum group size was 14. The high bufeo encounter rates in the central Bolivian Amazon can be taken as a reflection of the general environmental status of the region; however, a growing human population, associated with an increase in boat traffic and fishing activity, poses a future threat to bufeos and their aquatic habitats.

KEYWORDS: BOLIVIA; RIVER DOLPHIN; DISTRIBUTION; ABUNDANCE ESTIMATE; MAMORÉ RIVER; HABITAT; SURVEY-VESSEL

INTRODUCTION

River dolphins of the genus *Inia* are widely distributed in the low-lying areas of the Orinoco and Amazon basins and are the only exclusively freshwater cetaceans in South America. Our knowledge of the basic ecology of *Inia* comes from research conducted in Brazil (Magnusson *et al.*, 1980; Best and da Silva, 1984; 1989; Best and da Silva, 1989; Best and da Silva, 1993; da Silva, 1994; da Silva and Martin, 2000), Colombia (Layne, 1958; Trujillo, 1992; Hurtado Clavijo, 1996; Vidal *et al.*, 1997), Ecuador (Utreras, 1995; Herman *et al.*, 1996), Peru (Leatherwood, J.S., 1996; Henningsen, 1998; Reeves *et al.*, 1999; Zúñiga, 1999; Leatherwood, S. *et al.*, 2000; McGuire, 2002) and Venezuela (Trebbau and Van Bree, 1974; Trebbau, 1978; Pilleri *et al.*, 1982; Meade and Koehnken, 1991; Schnapp and Howroyd, 1992; McGuire, 1995; McGuire and Wienemiller, 1998).

While *Inia* is considered vulnerable by the IUCN¹, the populations appear to be in good condition relative to the other obligate freshwater dolphin taxa, such as the endangered South Asian river dolphins (*Platanista gangetica*) and the critically endangered baiji (*Lipotes vexillifer*). With multiple, potentially adverse development pressures occurring in the major river basins of South America, such as mining, logging and oil and gas exploration, a more detailed understanding of the ecology of *Inia* throughout its range is important to ensure populations remain in good condition.

Little is known about the status of the *Inia* population inhabiting the lowland rivers of Bolivia. The first studies were conducted by Pilleri (1969) and Pilleri and Gihr (1977) and consisted of informal surveys of various waterways, descriptions of behaviour and preliminary population estimates. They speculated that there had been a dramatic reduction in the population size due to anthropogenic influences. More recently, Yañez (1999) described the general behaviour and ecology of the *Inia* in the Iténez and Paragua rivers of the Noel Kempff Mercado National Park. The work presented here forms part of a longer-term project by Aliaga-Rossel (2000; Aliaga-Rossel, 2002), who studied the ecology and conservation status of bufeos in the Tijamuchi River throughout four hydroclimatic seasons (i.e. high, low, falling and rising water).

The taxonomic status of Inia in Bolivia is unresolved. The Bolivian river dolphin is geographically isolated from main stem Amazon Inia populations by a series of rapids between Guayaramerin, Bolivia and Porto Velho, Brazil. While some studies suggest the Bolivian Inia is sufficiently morphologically disparate to warrant separate species status (Pilleri and Gihr, 1977; da Silva, 1994), others interpret the morphological variation more conservatively (Casinos and Ocaña, 1979; Best and da Silva, 1989). Currently the Bolivian form of Inia is recognised as the subspecies Inia geoffrensis boliviensis (Rice, 1998). Recently, comparative mitochondrial DNA sequence analysis has been used to investigate taxonomic relationships within Inia (Hamilton et al., 2001; Banguera-Hinestroza et al., 2002) and these studies find substantial sequence divergence between Bolivian Inia and Inia geoffrensis in the Amazon and Orinoco rivers. Banguera et al. (2002) further suggest that the Inia population in Bolivia warrants status as a separate species (Inia boliviensis) or evolutionary significant unit² (Inia geoffrensis boliviensis). The morphologic and molecular data clearly indicate the uniqueness of Bolivian Inia, highlighting the importance of obtaining further knowledge of its distribution, abundance, ecology and

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¹ www.iucnredlist.org/info/categories_criteria2001.html

² As defined by Mortiz (1994).

conservation status. In order to reflect the distinctness of *Inia* in Bolivia, we hereafter refer to it by the local name of bufeo; the present IWC-designated common name of 'boto' is of Brazilian origin and is not used by Bolivians. *Inia* is the only cetacean in this land-locked country.

This paper examines the distribution and encounter rates of the bufeo in the middle reach of the Bolivian Amazon and was conducted in the Mamoré River and four of its tributaries during the low water season. The study employed standardised methods which can be replicated in future surveys of Bolivian river dolphins. This work contributes to our knowledge of the cetaceans in Bolivia and provides baseline data that may aid in the creation of management plans and more active protection of the bufeo in Bolivia.

METHODS

Description of the study area

The study area is located in the Department of Beni, in the region known as the 'Llanos de Mojos' (Fig. 1). The region is characterised by two types of water: white waters of Andean origin which are non-acidic, turbid and of medium conductivity; and black waters, which are of local origin, acidic, poor in suspended sediments and have low conductivity (Loubens et al., 1992). The vegetation along the riverbanks is characteristic of a tropical gallery forest. Much of the region is flooded during the high-water season. The principal economic activities for human settlements along the riverbanks are cattle ranching, fishing and smallscale agriculture. The average air temperature for the region is 26.5°C, although between May and September sporadic southern cold fronts known as 'surazos' may cause temperatures to fall to 15°C. The relative humidity ranges between 64% in August and 77% in January and February.



Fig. 1. Map of the study area, Central Mamoré Basin. Beni, Bolivia.

Between August and September of 1998 (the low water season), the bufeo survey was conducted along the middle reaches of the white-water Mamoré River, the most important navigable river in the region, from 14°35'60"S, 65°00'26"W downriver to the town of Santa Ana del Yacuma, 13°43'54"S, 65°25'08"W. Four mixed black and white water tributaries of the Mamoré River were also surveyed: the Tijamuchi, the Apere, the Yacuma and its tributary, the Rapulo (Fig. 1). This field work was conducted as a pilot study of bufeo ecology in the Mamoré Basin, with the goal of selecting one tributary to be the site of a yearlong study (Aliaga-Rossel, 2000; Aliaga-Rossel, 2002). Logistical constraints necessitated a rapid assessment of the area and survey areas were selected based on their accessibility from the main survey route along the Mamoré River.

From August to September 1998, 222km of the central Mamoré River and approximately 65km of tributaries were surveyed (Fig. 1). Surveys consisted of two transects of the same river reach and the elapsed time between surveys was two weeks on the Mamoré River and one week each on the Tijamuchi and Apare rivers (bad weather prevented repeat transects of the Yacuma and Rapulo Rivers).

Surveys were conducted between 08:00 and 17:15, with a one-hour break around midday. Surveys of the Mamoré River were divided into upriver and down river transects. Each transect was further divided into six legs of 37km each. Legs were determined by the length of river that could be surveyed during a morning or afternoon work period and actual leg length varied as observations were suspended when weather conditions were unfavourable for detecting dolphins, such as high winds (>13km h^{-1}), waves, or heavy rain. Survey were conducted using a 100% strip width transect, from a vessel with a 70 horsepower (hp) engine, with an average speed of 11.3km h⁻¹ and observer eye height of 3.5m above water level. The boat travelled along the centre of the river, except when prevented from doing so by obstacles. Because of the reduction in river width during the low water season, it was possible to detect dolphins from edge-to-edge of the river. One observer was stationed at either side of the bow of the boat, each with an angle of detection of 60° (120° total of coverage with two observers). Occasionally a third person observed dolphins behind the boat in order to confirm group size. For each sighting, observers used a GPS to determine the coordinates of the vessel, vessel speed and time of day and laser rangefinder to measure the width of the river. River width was measured on the downstream transect, but not on the returning upstream transect. When a dolphin or group of dolphins was sighted, the observers noted the numbers of dolphins per group. The term group was used to refer to the number of animals observed in association or apparent aggregation and could refer to a solitary animal, or to multiple animals.

Surveys of the four tributaries (the Tijamuchi, Apere, Yacuma and Rapulo rivers) were conducted with 100% strip-width transects from a skiff with 25hp outboard motor, with two observers watching for dolphins in front of and along side of the boat. The standing observer eye height was approximately 2m above water level and the mean survey speed was 10km h^{-1} , although this varied somewhat according to the sinuosity of the river, water depth and obstacles present.

The aquatic habitat of the tributaries was characterised every km by measuring the pH, water transparency (with Secchi disk), surface temperature and at 2m depth and water depth (with sounding line). The Apere River was the deepest and widest of the four tributaries, while the Rapulo River

River	Mean velocity of survey vessel (km hr ⁻¹)	Area surveyed (km)	Mean channel width (m) and CV	Number of bufeos (SD)	Encounter rates (bufeos km ⁻¹) and CV		
Main river							
Mamoré*	11.3	222.2	329.0 (0.39)	361 (±32.23)	1.6 (0.06)		
Mamoré upstream	9.3	222.2	329.0 (0.39)	384 (NA)	1.7 (0.40)		
(6 legs combined)							
Mamoré downstream	13.4	222.2	NA	337 (NA)	1.5 (0.51)		
(6 legs combined)							
Tributaries							
All tributaries combined	10.2	64.0	81.8 (0.23)	229 (±42.1)	3.41 (0.46)		
Tijamuchi*	10.8	19.8	80.6 (0.17)	115 (±17.67)	5.8 (0.19)		
Apere*	11.2	18.5	96.0 (0.21)	52 (±11.31)	2.9 (0.24)		
Yacuma	10.4	20.4	75.0 (0.17)	48 (NA)	2.4 (NA)		
Rapulo	8.3	5.3	63.7 (0.22)	14 (NA)	2.6 (NA)		

 Table 1

 Encounter rates (bufeo km⁻¹), survey effort, and channel width for different rivers.

was the narrowest and shallowest. The Mamoré River was approximately four times as wide and deep as the tributaries. All of the tributaries were mildly acidic and pH varied little between locations.

RESULTS

Encounter rates

In the Mamoré River, mean encounter rates and mean river widths were calculated for each of the six legs of the two transects. The mean encounter rate, mean river width and the associated coefficients of variance were then determined for each transect and then for both transects combined. Results were further stratified according to hydrologic habitat (i.e. main river or tributary). Sixty-two hours were spent conducting systematic surveys for dolphins, with 68% of the effort in the Mamoré River and 32% in its tributaries. This does not include time spent exploring the study area, photographing dolphins, or maintaining survey vessels.

Dolphin encounter rates were higher in the tributaries than in the main river; encounter rates were highest in the Tijamuchi River, lowest in the Mamoré River and intermediate in the Apere, Yacuma and Rapulo rivers (Table 1).

Group size

The mean group size was greatest in the Tijamuchi River and smallest in the Yacuma River (Table 2). Median group size differed significantly according to river (Kruskal-Wallis H=21.18, p=0.0003) and median group size was significantly higher in the Tijamuchi River than in the others (Bonferroni multiple range test). The largest group comprised 14 dolphins and occurred in the Tijamuchi River. The majority of observations were of pairs, triplets or solitary individuals.

DISCUSSION

Encounter rates

The *Inia* encounter rates reported here of 1.6-5.8 dolphins km⁻¹ are the highest reported anywhere in its broad geographic range. In comparison, other studies have reported river dolphin encounter rates of 0.13-1.50 dolphins km⁻¹ in Peru (Leatherwood, J.S., 1996; Henningsen, 1998; McGuire, 2002), 0.28-0.40 dolphins km⁻¹ in the Colombian Amazon (Trujillo, 1992; Vidal *et al.*, 1997), 0.02-1.16 dolphins km⁻¹ in Venezuela (Pilleri *et al.*, 1982; Schnapp and Howroyd, 1992; McGuire and Wienemiller, 1998),

Table 2

141	wear and maximum bureo group size on different rivers.					
River	Mean group size (SD)	Maximum group size	No. of groups			
Mamoré	2.1 (±1.34)	11	340			
Tijamuchi	3.3 (±2.96)	14	71			
Apere	2.3 (±0.98)	5	47			
Yacuma	1.8 (±0.75)	3	27			
Rapulo	2.0 (±0.81)	3	7			

0.08-0.40 dolphins km⁻¹ in Brazil (Best and da Silva, 1989; da Silva and Martin, 2000) and 0.23-0.40 dolphins km⁻¹ in Ecuador (Utreras, 1995; Deniker, 1998), although, as is later discussed, different methods employed by different researchers undoubtedly account for some of the differences in encounter rates.

In the Bolivian Amazon, these high densities may be due in part to the region's relatively low human population. Motorised boat traffic in the area is light and there seem to be few other human activities that would negatively impact the population status of bufeos. The region has little commercial fishing activity beyond locally important subsistence fishing (pers. obs.). Humans are therefore unlikely to be competing with bufeos for fish and consequently prey abundance may be high. In addition, bufeo encounter rates may be influenced by hydroclimatic seasons. During the low water season, the average river width and volume decrease, which may facilitate bufeo sightings. During his 17-month study in the same region and using the same methods described in this paper, Aliaga-Rossel (2000; 2002) found that bufeo encounter rates were highest during the low water season and lowest during the high water season, although these differences were not statistically significant. However, even after combining all observations across all seasons (with equal sampling effort within seasons) Aliaga-Rossel (2000; 2002) still calculated a mean encounter rate of 1.12 bufeos km⁻¹ in the Tijamuchi River, which remains high in comparison to other study areas both within and outside Bolivia.

The high dolphin encounter rates for the Tijamuchi River in comparison with the other rivers may in part be because the Tijamuchi River is a mixed black and white water river, with multiple connections in the middle area to the white water Mamoré River. Similar rivers with exceptionally high dolphin encounter rates were reported by McGuire (2002) in the Peruvian Amazon. She speculated that the mix of white and black waters may result in higher than average productivity, as well as greater diversity and abundance of fishes from the physical connection between two different aquatic habitat types along the ecotone. Boat traffic may be another factor influencing encounter rates: the Tijamuchi had the least amount of boat traffic and the highest dolphin encounter rates; while the Yacuma had the highest boat traffic and lowest dolphin encounter rate. Boat traffic was described qualitatively in this study, however, future studies should quantify rate and type of boat traffic in order to investigate their possible effects on bufeo distribution and abundance.

In this study, downriver transects were slightly faster than upriver transects of the same river; 0.6km h⁻¹ in the Tijamuchi River; and 2.0km hr⁻¹ in the Apere River. Although the survey speeds in the Mamoré River differed by 4.1km hr⁻¹, dolphin encounter rates from upriver and downriver transects were very similar (1.7 and 1.5 respectively), which suggests that these differences in survey speed had very little effect on our ability to detect dolphins.

Encounter rates are presented rather than density estimates, as standard line transect techniques were not employed due to logistical constraints in sampling. The addition of correction factors (to account for dolphins missed along the trackline) used in standard line transect density estimates (Leatherwood, J.S., 1996; Vidal et al., 1997; McGuire, 2002), as well as the addition of rear-facing observers used in some river dolphin surveys (Henningsen, 1998; da Silva and Martin, 2000) undoubtedly would have led to increases in encounter rates; therefore the encounter rates presented here should be considered 'minimum counts' (da Silva and Martin, 2000). We believe the use of strip-surveys was warranted, given the narrowness of the rivers surveyed: in the main stem Mamoré River our mean effective strip width was 164m and was comparable to strip widths used in similar studies of Inia elsewhere in its range (e.g. 150m in the Amazon and Japurá rivers (Martin and da Silva, 2004) and 245m on the Amazon River (Vidal et al., 1997). In the tributaries, the effective strip width ranged 32-48m; in comparison, others have used widths of 75m (McGuire, 2002) and 35m (Martin et al., 2004). It is difficult to compare Inia encounter rates among different studies because differences in survey methods, such as number and experience of observers, vessel height and speed, season, habitat, width of survey angle, track line (mid-line or zigzag) and effective strip width all influence encounter rates (see McGuire, 2002 for further discussion).

These results are preliminary and limited in that they represent one season with few replicates within the same river. However, we believe their presentation is justified as they are among the first of their kind for this species in this region and may be viewed in the context of a resulting longer-term study of one of the tributaries surveyed (the Tijamuchi River; Aliaga-Rossel, 2000; 2002).

Group size and structure

Mean group size in the study area was found to be within the range of 1.2-6.1 *Inia* per group as has previously been reported for their entire geographic distribution (Magnusson *et al.*, 1980; Trujillo and Diazgranados, 2000). For a review of *Inia* group size from different regions and of the variation due to different operational definition of groups by different researchers, see McGuire (2002). During this pilot study and in the earlier longer-term study (Aliaga-Rossel, 2000; 2002), bufeos were generally encountered as solitary animals, pairs, or triplets. More dolphins were seen in pairs during

the low and falling water seasons, which were found to coincide with the peaks in the calving and mating seasons (Aliaga-Rossel, 2000; 2002).

As with bufeo encounter rates, the Tijamuchi River is markedly different from the other rivers surveyed because of its larger group sizes (mean and maximum). The mean group size was greatest in the Tijamuchi River and smallest in the Yacuma (Table 2), which is notable as these rivers are of comparable width. The Yacuma River has much more boat traffic than the Tijamuchi River, as one of the largest human settlements in the region is found along its banks and perhaps this disrupts bufeo social structure. In addition, we hypothesise that the Tijamuchi River, with its influx of white water from the Mamoré, is richer in nutrients and prey than the primarily black water Yacuma River and thus better able to support large groups. However, care must be taken in interpreting the results of this pilot study, as sampling effort in the Yacuma and Rapulo rivers was relatively small and reported differences in group size may actually be artefacts of uneven sampling between rivers.

Bufeos of all age classes (i.e. neonates, calves, juveniles, adults; inferred by body length and behaviour) were observed in the Mamoré River and in the tributaries. This study occurred during low water, which was later found to be the peak of a year-round bufeo calving season (Aliaga-Rossel, 2000; 2002). It was often difficult to distinguish age class, as relative differences in body size were difficult to discern from glimpses from a moving vessel of these low-surfacing animals and because little is known about their size relative to their age/maturity. We recommend that future studies of bufeos include investigations of animals from strandings, fisheries by catch and capture during marking/tagging operations, in order to correlate age with length.

Aquatic habitat

Little variation in water temperature existed within a single river, although temperatures varied between rivers (24-32°C). These differences were most likely temporal due to a cold-weather system that moved into the area mid-study, rather than spatially-related to hydrologic differences. Water transparency and pH likewise varied minimally between rivers and seem unlikely to directly affect bufeo distribution and abundance. Indeed other studies have not detected significant associations between *Inia* abundance and water transparency, pH, or temperature (da Silva, 1994; Hurtado Clavijo, 1996; Zúñiga, 1999; Aliaga-Rossel, 2000; McGuire, 2002). Although not directly examined in this study, biotic factors such as prey biomass and availability probably have more of a direct influence on *Inia* abundance and distribution (McGuire and Wienemiller, 1998).

This study provides baseline data regarding river dolphins in Bolivia and highlights the importance of continuing and expanding a long-term study of the distribution, abundance and basic ecology of this unique Bolivian dolphin. Due to its exceptionally high bufeo encounter rates and large group sizes compared with studies from elsewhere in *Inia's* range, the Tijamuchi River is an area that merits further investigation. The high bufeo encounter rates in the central Bolivian Amazon can be taken as a reflection of the general environmental status of the region; however, a growing human population, with its associated increases in boat traffic and fishing activity, may pose a future threat to bufeos and their aquatic habitat. We believe that attention to environmental management and biodiversity conservation in the Bolivian Amazon is merited at the present time.

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Abundance and distributional ecology of cetaceans in the central Philippines

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ABSTRACT

In general, little is known about cetacean abundance and distribution in Southeast Asia. This paper investigates the species composition, interactions/associations, abundance and distribution of cetaceans in an archipelagic tropical habitat characterised by deep, oceanic waters approaching the shore, high water temperatures and deep, stable thermoclines. Abundance is estimated using line transect methods. In addition, the cetacean fauna of the Sulu Sea is compared with those of other tropical marine ecosystems: the eastern tropical Pacific, the western Indian Ocean and the Gulf of Mexico. The most abundant species in the two study sites (eastern Sulu Sea and the Tañon Strait) was the spinner dolphin, *Stenella longirostris*; with a population estimate of 31,512 (CV=26.63%) in the eastern Sulu Sea and 3,489 (CV=26.47%) in the Tañon Strait. Other abundant species were the pantropical spotted dolphin (*S. attenuata*), Fraser's dolphin (*Lagenodelphis hosei*) and the short-finned pilot whale (*Globicephala macrorhynchus*). Density and species-abundance rank varied between the two study sites, with generally higher densities in the Sulu Sea than in the Tañon Strait. An exception was the dwarf sperm whale, *Kogia sima*, whose density was 15 times higher in the Tañon Strait. Fraser's dolphin ranked third in abundance in the Sulu Sea but was absent from the Tañon Strait. Environmental factors such as depth, site and temperature were observed to have a significant influence on the distributions of various species.

KEYWORDS: SPINNER DOLPHIN; PANTROPICAL SPOTTED DOLPHIN; FRASER'S DOLPHIN; PILOT WHALE; DWARF SPERM WHALE; MELON-HEADED WHALE; RISSO'S DOLPHIN; BOTTLENOSE DOLPHIN; BRYDE'S WHALE; ROUGH-TOOTHED DOLPHIN; PYGMY KILLER WHALE; SPERM WHALE; ECOLOGY; HABITAT; SULU SEA; TAÑON STRAIT; ASIA; SURVEY-VESSEL; g(0); ABUNDANCE ESTIMATE; DISTRIBUTION; SCHOOL SIZE

INTRODUCTION

With few exceptions, there is a general lack of information on cetacean habitat, abundance and distribution in Southeast Asian waters. Habitat degradation and cetacean bycatch in numerous fishing operations are widespread and are possibly threatening many dolphin populations in the region (Perrin et al., 2005). One of the reasons for this lack of information is the high cost of abundance surveys. Line transect surveys mounted by developed countries use large ships suitable for high-seas travel, with high sighting platforms and long cruising ranges (e.g. Wade and Gerrodette, 1993; Barlow, 1995; Forney et al., 1991; Jefferson, 1995). These surveys are often prohibitively expensive for developing countries. The survey methods used here follow the same distance-based approach (e.g. Buckland et al., 1993) as the studies mentioned above but modified to utilise a small boat with a relatively low sighting platform and shorter cruising range in order to reduce costs. Estimates of abundance are critical to assessing the impacts of fisheries known to incidentally kill cetaceans (Dolar, 1994).

Sites included in this study were habitats that are more or less representative of the Philippines (Fig. 1): deep, oceanic waters close to shore (as seen in the Sulu Sea); narrow, semienclosed areas with terraced slopes (the Tañon Strait); and shallow, flat areas contiguous to deep waters (northeastern part of the Sulu Sea). The Sulu Sea and the Tañon Strait are connected via the Mindanao Sea and are only approximately 85km apart. It is assumed that large, highly mobile animals such as cetaceans can move freely between them, but whether the species assemblages, relative densities and species associations of cetaceans in these two areas are similar has not been known. These questions are addressed by comparing and contrasting the cetacean fauna in the two marine habitats, including species composition, abundance or relative density and associations among species and relating these patterns to physical parameters such as water depth and water temperature. The cetacean fauna of the Sulu Sea was also compared to faunas in other tropical oceans/seas to broaden the understanding of tropical cetacean habitats.

The study sites

The study sites were the eastern part of the Sulu Sea with an area of 23,014km², or approximately 9% of the total Sulu Sea's area of approximately 250,000km², and all of the Tañon Strait with an area of 4,544km² (Fig. 1). The Sulu Sea is a semi-isolated deep marine basin completely surrounded by a shelf, most of which is shallower than 100m (Linsley *et al.*, 1985). Shallow straits connect it to the South China Sea, the Pacific Ocean and the Celebes Sea. In general, surface water of the basin exhibits high temperature (27-28°C), low salinity (34.2-34.4 ppt) and a deep, stable thermocline, located at about 250m (Linsley *et al.*, 1985), that gets uplifted during tropical cyclones (Frische and Quadfasel, 1990). Deep waters approach very close to shore.

The Tañon Strait in contrast is much smaller and shallower. It is only 15-27km wide and 220km long. The deepest portion (~555m) is central (Hayasaka *et al.*, 1987) and extends south. Although the near-surface circulation is also subjected to the seasonal reversal of the monsoon

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Fig. 1A. The study sites and planned tracklines, B. completed tracklines. Boundaries (thick lines) of study sites are shown. Mapping with SURFER 7.0.

winds, the strait is partially protected by the islands of Negros and Cebu. Sea surface temperature (SST) is about 30°C, gradually decreasing to about 25°C at 100m (Hayasaka *et al.*, 1983). The temperature from 200m to the bottom is relatively stable at about 17°C. The salinity is 32-34 ppt and the thermocline is 100-150m deep. Transverse and longitudinal profiles of the strait show very steep slopes with submarine terraces (Hayasaka *et al.*, 1983).

Both sites belong to the ecoregion with the highest marine biological diversity in the world. The interesting bottom topography in the Sulu Sea provides a rich and dynamic ecosystem of coral reefs, seamounts, seagrasses, lagoons, steep slopes and deep sea communities that supports a myriad of marine organisms. It shares with its contiguous Sulawesi Sea more than a thousand species of fish, 500 species of corals, about 400 species of algae, possibly up to 30 species of marine mammals and 5 species of marine turtles. It also has one of the two most important turtle breeding and nesting sites in Southeast Asia. The Tañon Strait, though much smaller, is home to more than 70 species of fish and over 20 species of crustaceans (Dolar, 1991; Fishbase website http://www.fishbase.org/search.php). Its narrow shelf is fringed with intermittent strands of coral reefs, mangroves and seagrasses. It has a thriving squid fishery and an abundant nautilus population.

MATERIALS AND METHODS

Survey

Cetacean distribution and abundance were determined using line transect methods developed to estimate abundance of small cetaceans in the eastern tropical Pacific (Holt, 1987; Wade and Gerrodette, 1993). These methods were modified to suit the local conditions and the resources available. Since the boat used was relatively small and the area surveyed was not safe from dangers of piracy and possibility of being run over by large ships, drifting at sea at night was not an option. To maximise the distance covered from shore seaward, yet still being able to dock on shore at night, our transect lines were systematically designed in a continuous zigzag or sawtooth design based on waypoints along the boundaries of the study sites. This type of design is recommended for efficiency when time and/or cost of a survey platform are an issue (Buckland et al., 2001). The systematic spacing of the zigzag lines did not coincide with a regular topographic or spatial feature. Twenty four 60-70km long transect lines were traversed in the Sulu Sea extending from the coast seaward set at 20km apart at their base, with 22 lines approximately 20km long and 30km apart at their base in the Tañon Strait (Fig. 1A).

To assure good sighting conditions, surveys were carried out during the break between the two alternating monsoon seasons, i.e. 9-27 May 1994 (Sulu Sea) and 3 May-5 June 1995 (Sulu Sea and the Tañon Strait), using a 20m boat with a sighting platform 2.5m above the water at a cruising speed of 17-20km hr⁻¹. Some segments of the trackline were cancelled due to three days of bad weather. Five observers rotated through four primary positions (positions 1-4) on an hourly basis and took a break on the fifth hour, and two additional observers alternated on position 5 on an hourly basis (Fig. 2). The five positions and their coverage were as follows:

position 1: In front using 20x spotting binoculars mounted on the deck of the boat; covered 180° ;

positions 2 and 3: Using 10x handheld binoculars; covered 90° from directly in front to the right and the left sides of the boat;

position 4: In the bow of the boat (without binoculars) guarding the trackline;

position 5: A professional dolphin spotter (ex dolphin hunter) who scanned the waters 180° forward to the horizon without using binoculars.

Searching covered the entire region from directly in front of the vessel to 90° left and right and out to the horizon. Two other members were assigned permanently to record data and navigate. Four of the seven observers were present in both years of survey.



Fig. 2. Observer positions during the survey.

When an observer saw a positive cue (e.g. splash, blow or the animals), all observers were alerted to the animal's location and searching effort was suspended. Vessel position was noted using the global positioning system (GPS) and the angle of the sighting to the trackline was measured using binoculars with a compass (*Fujinon* 7×50 FMTRC). The best estimator as determined by previous training and exercises estimated the distance to the sighting. Distances were also measured using the GPS whenever animals were seen to be just logging on the surface. Deviations between estimated and measured distances were then determined. The binocular reticle scale was not used to estimate distance because the sighting platform was so low that pitching of the boat greatly affected the reading and islands also often obscured the horizon. Sightings were approached and the species (collectively decided by the team), group size and exact location of the animals were recorded. Photographs and behavioural notes were also taken. The trackline was then resumed by following a convergent course towards the end of the trackline leg, rather than returning to the exact point where the sighting was made. Sighting effort was maintained between 06:00 and 18:00 hours whenever weather conditions allowed (Beaufort sea state 0-4).

Auxiliary data were recorded: time, geographical location, boat speed and bearing, viewing conditions (sea state, wind direction, sun position, visibility and presence of rain or fog) and observer's identification and position. This information was updated hourly or whenever conditions changed. The tenth member of the team recorded SST and salinity hourly and at locations of sightings, using a bucket thermometer and a refractometer.

Analysis

The program *REPORT*, developed by the Protected Resources Division of the Southwest Fisheries Science Center, was used to summarise information on the total number of sightings, the species sighted, average school size for each species, species association, total distance of effort covered, sighting rates at different Beaufort sea states and perpendicular distances needed for density and abundance estimations. The total areas of the study sites were estimated using *ArcView GIS* (3.0).

Calibration of distance estimates

The regression between the distance estimated by eye and the GPS-measured distance was significant (R^2 = 0.996 and P<0.001) with a slope of 0.851 that differed significantly from zero (one tailed *t*-test [α = 0.05] P<0.005; Fig. 3). The distances estimated by eye were corrected using the inverse prediction method (Zar, 1996) in order to be able to gauge the general magnitude of how systematically biased observer distance estimates may affect abundance estimates.



Fig. 3. Regression of the on distance estimated by eye on measured distance. N=32.

Density and abundance estimates

Density and abundance of species with sufficient sample sizes were estimated using the program DISTANCE 4.1, Release 2 (Buckland et al., 2001; Laake et al., 1993; Thomas et al., 2003). Generally, a sample size of at least 60-80 sightings for the determination of the probability density function is desired, but occasionally 40 may be considered adequate (Buckland et al., 1993; 2001). Sightings from the two study sites for two years of survey, and in some cases for two species, were pooled to obtain an adequate sample size. Encounter rate, school size, density and abundance were estimated by stratum, i.e. for each species, site and year of survey. Before pooling, the distribution of perpendicular distances was tested to determine if it differed between the two study sites, between years or between species (Kolmogorov-Smirnov test). The hypothesis that school size differed between species (Wilcoxon rank test) was also tested. For only four species (spinner dolphin, Stenella longirostris; pantropical spotted dolphin, S. attenuata; Fraser's dolphin, Lagenodelphis hosei; and shortfinned pilot whale, Globicephala macrorhynchus) were there adequate numbers of sightings for the two study sites and two survey years (148, 61, 39 and 42 sightings, respectively) to allow reasonably precise estimation of abundance. Sightings data for Fraser's dolphin and the short-finned pilot whale were pooled because they were often found associated with each other, e.g. 62% of Fraser's dolphins sighted in 1994 and 49% in 1995 were with shortfinned pilot whales. On these occasions, the very large dorsal fins of the pilot whales contributed to the sightability of the associated Fraser's dolphins (Kolmogorov-Smirnov test on the distributional pattern of perpendicular distances between the two species, P=0.183). Rather than providing no estimates for the more rare species (bottlenose dolphin, Tursiops truncatus; melon-headed whale, Peponocephala electra; dwarf sperm whale Kogia sima and Risso's dolphin, Grampus griseus), provisional estimates were calculated with caveats. Sightings of the bottlenose dolphin and melonheaded whale (total=31) were pooled because of the similarity in their general body size, behaviour, school size (Wilcoxon rank test, P=0.225) and distribution of perpendicular distances (Kolmogorov-Smirnov test, P=0.156).

For the estimation of abundance (using the multivariate mode of DISTANCE 4.1), the strata site and year were used as factor covariates and Beaufort sea state as a non-factor covariate. School size, however, was not used as a covariate because its use prevented analysis by stratum (a limitation of the program). Thus, in order to avoid an upward bias in abundance brought about by large schools having greater probabilities of detection at greater distance than small schools, a size-bias regression was performed on the logarithm of school size and the detection probability. Statistical power was estimated whenever the mean school size was used in the calculation of abundance (Zar, 1996). Knowledge of statistical power helps with interpretation of the results and evaluation of the strength of conclusions (Taylor and Gerrodette, 1993). Low power to reject the null hypothesis of no difference (and hence the use of the mean school size) could result in overestimation of abundance.

For cetaceans, the assumption that all groups on the trackline were detected (i.e. g(0)=1) may be violated because some cetaceans (e.g. dwarf sperm whales and beaked whales) may be beneath the surface during the entire passage of the boat and therefore missed. This negatively biases abundance estimates. Barlow (1999) developed a simulation model to estimate the probability of detecting

species that dive for long periods, such as the dwarf sperm whale and beaked whales, during line-transect effort. He found that the detection probability, g(0), was 0.35 for dwarf and pygmy sperm whales (*Kogia* spp.). This value was used to estimate dwarf sperm whale abundance in this study. For dolphins and whales occurring in medium-to-large schools, the assumption that g(0)=1 is probably true.

Models of the detection probability function, f(0), were fitted to the data and the best fitting model chosen using the Akaike Information Criterion, AIC (Akaike, 1973; Buckland et al., 2001). In addition, results of the Qq plot, Kolmorov-Smirnof Test and Cramer von-Misses Family Tests were also considered when choosing the best-fit model. The CV and the 95% confidence intervals (CI) were calculated for density and abundance estimates using bootstrap methods (Efron and Tibshirani, 1993; Buckland et al., 1993) built into the program DISTANCE, with 200 resamples with replacement. Density and abundance of other species such as the rough-toothed dolphin (Steno bredanensis), pygmy killer whale (Feresa attenuata), Bryde's whale (Balaenoptera edeni or B. omurai), sperm whale (Physeter macrocephalus) and killer whale (Orcinus orca) were not estimated owing to insufficient sightings.

The abundance estimates and encounter rates obtained were compared with those from other tropical seas such as the eastern tropical Pacific (ETP), the western tropical Indian Ocean (WTIO) and the Gulf of Mexico (GM) by comparing the abundance ranks and standardising the encounter rates obtained in this study using the method described by Ballance and Pitman (1998). These standardised encounter rates are referred to as corrected encounter rates.

Distribution

The same data collected for the abundance estimations were used for the determination of the distributional patterns of selected species (only species with more than 20 sightings were included).

Bathymetric data were obtained from the General Bathymetric Chart of the Oceans (GEBCO) Digital Atlas¹ and depths were interpolated from the data points on a gridded field having a cell resolution of 0.01° latitude by 0.01° longitude using the software *ArcView GIS* (v.3.0). Similarly, SSTs and sea state contours were interpolated from the temperature and sea state data points collected during the survey, on a gridded field having a cell resolution similar to that of the water depth and using the same software. Survey effort and number of sightings under the same environmental parameters were summarised using *ArcView GIS*. A constant 0.001 was added to each value to avoid a value of zero in transects where there were no sightings.

A Generalised Additive Model (GAM) was used to investigate possible patterns in the distribution of the selected species (Forney, 1999; Barlow *et al.*, 2006). Encounter rate and school sizes were used as response variables, and water depth, SST and site (Sulu Sea *versus* the Tañon Strait) were included as predictor variables. The predictor variables help define the habitat and can potentially affect the distributional patterns of cetaceans. Beaufort sea state was also included in the model to account for potential bias that it can cause in the sightability (and therefore of the encounter rate) of animals and the estimation of school sizes. Effort covered under Beaufort 0 and 1 were combined, owing to the low survey effort in

¹ http://www.ngdc.noaa.gov/mgg/gebco/gebco.html

Beaufort sea state 0, and effort under 3 and 4 were also pooled due to the low survey effort in Beaufort sea state 4. A step-wise model selection was used with each variable added sequentially, using the GAM function of the statistical package *S-PLUS* (v.3.3). The GAM extends the generalised linear model (GLM) by fitting non-parametric functions (which were estimated from the data using smoothing operations) of predictor variables to estimate the relationships between the response variable and the predictors. The general form of GAM is (Hastie and Tibshirani, 1990):

$$g(E(Y|x)) = g(\mu) = \alpha + \sum_{i=1}^{p} f_i(x_i) = \eta(x)$$

where g is the link function, α is a constant intercept term, f_i corresponds to the non-parametric function describing the relationship between the mean response and the *i*th predictor and $\eta(x)$ is the additive predictor (analogous to the linear predictor for a GLM). The level of smoothing was explored from 1 to 4 degrees of freedom for water depth. The *s* function which fits cubic B-splines was used to estimate the smooth relationship between the response and the predictors. Exploratory plots indicated linear relationships between the response variables (encounter rate and school size) and Beaufort sea state as well as sea surface temperature, so they were added into the model as linear terms. An Analysis of Deviance was used to compare the various models (Forney, 1999). Deviance is defined as (McCullagh and Nelder, 1997):

$$D = \sum i \left(r_i^D \right)^2$$

with signed residual deviance, $r_i^D = sign(y_i - \hat{\mu})\sqrt{d_i}$, where y_i is each observation and d_i is the contribution of the *i*th observation to the deviance.

RESULTS

A total of 2,313km of on-effort trackline were covered over an area of 23,014km² during the two survey years in the Sulu Sea and 434km over an area of 4,544km² in one year of survey in the Tañon Strait (Fig. 1B). The ratios of the oneffort trackline to area were nearly equal: 10.0km/km² for Sulu Sea and 10.5km/km² for the Tañon Strait. These surveys yielded a total of 578 cetacean sightings, 510 of which were on-effort and 451 (or 78%) identified to the species level. Table 1 summarises the percentage of effort spent in each sea state.

 Table 1

 Percentage of effort spent at different Beaufort sea states.

	Percentage of effort						
Beaufort	Sulu Area = 23	Sea ,014km ²	Tañon Strait Area = $4,544$ km ²				
Sea state	1994 (1,161km)	1995 (1,152km)	1995 (434 km)				
0	2.6	6.0	8.2				
1	19.4	30.4	25.8				
2	51.6	29.4	24.4				
3	22.4	25.3	29.1				
4	4.0	8.9	12.5				

Species composition and school sizes

Fourteen cetacean species were identified in the Sulu Sea; only six of these were seen in the Tañon Strait (Table 2). In addition, two unidentified beaked whales (*Mesoplodon* sp.

and an unidentified large ziphiid whale with a pronounced bulbous head and long beak, possibly Longman's beaked whale (Indopacetus pacificus) were seen in the Sulu Sea during the 1994 survey. Only two large whale species were sighted, Bryde's and sperm whales, both in 1994. No large whales were sighted in the Tañon Strait. 'Unidentified cetaceans' were cetaceans seen from afar which disappeared when approached; most were singletons but a few were in groups of two to fifteen. There were four species with notably high encounter rates in the Sulu Sea (spinner dolphin, spotted dolphin, short-finned pilot whale and Fraser's dolphin) and two in the Tañon Strait (spinner dolphin and dwarf sperm whale) (Table 2). The spinner dolphin had the highest number of sightings and highest encounter rates in both areas. Although Fraser's dolphins ranked fourth in the Sulu Sea, they were absent in the Tañon Strait.

Mean school size varied greatly from one for dwarf sperm whales to 143 for melon-headed whales (Table 2). Large schools of up to more than a thousand animals were observed when several species occurred together. Mean school sizes for spinner and spotted dolphins were significantly smaller in the Tañon Strait than in the Sulu Sea (Wilcoxon-rank sum test, P=0.009 for spinner and P=0.018 for spotted dolphins).

Species associations

Sulu Sea

In the Sulu Sea (Table 3), spinner dolphins were found in pure schools 59% of the time, with the remainder of the time in mixed schools with eight other species: spotted dolphins, short-finned pilot whales, Fraser's dolphins, Risso's dolphins, bottlenose dolphins, rough-toothed dolphins, pygmy killer whales and Bryde's whales. Association was highest between Fraser's dolphins and short-finned pilot whales, which were found together more than half of the time. A similar close association was also observed between spinner and spotted dolphins. Excluding species with fewer than five sightings, Fraser's dolphins had the highest percentage of mixed-species sightings (84.2%) and Risso's dolphins the lowest (26.8%) (Table 4).

Tañon Strait

Spinner dolphins in the Tañon Strait (Table 3) were found more commonly in pure than mixed schools (86% compared to Sulu Sea's 58%). Although dwarf sperm whales were seen associated with other species, only approximately 15% of the total sightings were of mixed species associations (Table 3). Overall, there was a predominance of pure schools over mixed-species sightings in the Tañon Strait, and mixed species sightings did not involve more than three species at a time (Table 4).

Density and abundance estimates

Overall, sea state affected sighting rates in both the Sulu Sea and the Tañon Strait. As one would expect, encounter rates (per 1,000km) were highest at Beaufort zero (355 in Sulu Sea and 428 in the Tañon Strait) and lowest at Beaufort 4 (31 in Sulu Sea and 74 in the Tañon Strait).

The best-fit model for all but one species was the halfnormal model (Table 5). The model that best fitted the data for the dwarf sperm whale was the hazard rate model, with the probability plot showing a rather peaked nature. The AIC increased by 31% when the half-normal model was tested for this species. In addition, the results of the Qq plot showed a poor fit for the half-normal model, as did the Kolmogorov Smirnoff and the Cramer von-Misses family

Table 2	Ta	bl	e	2
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Summary of cetacean sightings for the two years of survey in the Sulu Sea and one year of survey in Tañon Strait. N_r =total number of sightings, n_e =number of on-effort sightings, S=mean school size, E=encounter rate (number of schools 1,000km⁻¹).

		Sulu	Sea	Tañon Strait					
Species	$N_t(n_e)$	S	S range	E	$N_t(n_e)$	S	S range	Ε	
1. Spinner dolphin	111 (97)	90	1-644	42.0	52 (51)	39	1-900	117.5	
2. Spotted dolphin	63 (57)	84	1-540	24.6	4 (4)	8	1-25	9.2	
3. Short-finned pilot whale	48 (42)	52	1-350	18.2	1 (0)	50	50	2.3	
4. Fraser's dolphin	44 (39)	92	3-475	16.9					
5. Risso's dolphin	26 (22)	8	1-40	9.5					
6. Bottlenose dolphin	24 (21)	26	1-93	9.1	3 (2)	6	1-12	4.6	
7. Dwarf sperm whale	12 (9)	1.6	1-4	3.9	27 (21)	2.4	1-10	48.0	
8. Melon-headed whale	7 (6)	34	7-52	2.6	2 (2)	143	40-210	4.6	
9. Rough-toothed dolphin	3 (3)	2	1-4	1.3					
10. Bryde's whale	3 (3)	1.8	1-3	1.3					
11. Pygmy killer whale	1(1)	3	3	0.4					
12. Sperm whale	1 (0)	4	4	-					
13. Killer whale	1(1)	3	3	0.4					
14. Blainville's beaked whale	1(1)	4	4	0.4					
15. Ziphiid whale	1(1)	1.3	1-2	0.4					
16. Mesoplodon sp.	16 (8)	2	1-4	3.5					
Summary	362 (311)			134	89 (80)			184	
Unidentified cetaceans	112 (104)	3.6	1-15	45.0	15 (15)	1	1-5	34.0	

Table 3

Species associations. Numbers are percentages of on+off effort sightings (can total more than 100 since several species can co-occur). Numbers in bold diagonal represent the percentage of the time the species seen in pure schools. There is no symmetry in the matrix because the number of sightings varies by species.

	Spinner dolphin	Spotted dolphin	Short-finned pilot whale	Fraser's dolphin	Risso's dolphin	Bottlenose dolphin	Melon-headed whale	Rough-toothed dolphin	Pygmy killer whale	Bryde's whale	Dwarf sperm whale
A. Sulu Sea											
Spinner dolphin (111)	59	30	6	11	3	4		0.9	0.9	2	
Spotted dolphin (63)	52	46	6	10		5			2		
Short-finned pilot whale (48)	12	8	38	50	6	12		4	2		
Fraser's dolphin (44)	30	14	54	16	7	6	8		2		
Risso's dolphin (26)	12	8	12	12	73	4					
Bottlenose dolphin (24)	17	12	25	25	4	50	4		4		
Melon-headed whale (7)				43		14	57				
Rough-toothed dolphin (3)	3		66							33	
Pygmy killer whale (1)	100	100	100	100		100					
Bryde's whale (3)	66							33		33	
B. Tañon Strait											
Spinner dolphin (52)	87	6	6			2	2				6
Spotted dolphin (4)	75	25									
Dwarf Sperm whale (27)	11						4				85
Melon-headed whale (2)	50		50				50				
Bottlenose dolphin (3)	33					67	33				

tests (uniform weighting and cosine weighting; p=0.03, 0.02, 0.01 respectively). Fig. 4 shows histograms of the perpendicular sighting distance data and the fitted models for the seven cetacean species. Abundance and density estimates with their corresponding confidence intervals for the seven cetacean species are given in Table 6. In all cases, the estimates using the corrected distance did not vary statistically from the uncorrected estimates. Based on data pooled over the two years of survey, the most abundant species in both sites was the spinner dolphin, although the density in the Tañon Strait was only about half that of the

Sulu Sea. This lower density was owing to smaller school sizes rather than lower encounter rates; in fact encounter rate in the Tañon Strait was almost three times higher than in the Sulu Sea (Table 2). Other relatively abundant species in the Sulu Sea were the spotted dolphin, Fraser's dolphin and the short-finned pilot whale (Table 6). One significant observation was the much higher density $(15\times)$ of dwarf sperm whales in the Tañon Strait than in the Sulu Sea. The abundance estimate was double, despite the fact that the Tañon Strait is only approximately one-fifth of the size of the eastern Sulu Sea study site.

Table 4
Percentage of on+off effort sightings associated with 1, 2, 3, 4 and 5 other species at one time.
Percentage of mixed and pure schools also shown.

Species (no. of on-effort sightings)	Perce	entage of other s	sightings	0/	0/		
plus	1 <i>sp</i>	2spp	3spp	4 <i>spp</i>	5spp	mixed school	pure school
A. Sulu Sea							
Spinner dolphin (111)	32.1	4.6	2.8	0.9	0.9	41.3	58.7
Spotted dolphin (63)	44.4	3.2	3.2	1.6	1.6	54.0	46.0
Short-finned pilot whale (48)	43.8	8.3	6.2	2.1	2.1	62.5	37.5
Fraser's dolphin (44)	61.4	11.4	6.8	2.3	2.3	84.2	15.8
Risso's dolphin (26)	19.2	3.8		3.8		26.8	73.2
Bottlenose dolphin (24)	29.1	12.5	4.2		4.2	50.0	50.0
Melon-headed whale (7)	28.6	14.3				42.9	57.1
Rough-toothed dolphin (3)	66.7	33.3				100	
Bryde's whale (3)	33.3	33.3				66.6	33.4
Pygmy killer whale (1)					100	100	
B. Tañon Strait							
Spinner dolphin (52)	11.5	1.9				13.4	86.6
Dwarf sperm whale (27)	14.8					14.8	85.2
Spotted dolphin (4)	75.0					75.0	25.0
Bottlenose dolphin (3)		33.3				33.3	66.7
Melon-headed whale (2)	50.0	50.0				100	0.0



Fig. 4. Probability detection plot and model fit for A=spinner dolphin, B=Pantropical spotted dolphin, C=Fraser's dolphin and short-finned pilot whale, D=bottlenose dolphin, E=dwarf sperm whale and F=Risso's dolphin.

Table 5

Truncation distance (w), number of sightings used after truncation (n), estimated value of probability density function [f(0)], effective strip width (ESW), Akaike Information Criterion value (AIC) and the model used for different species and species groups.

Species/species group	w (km)	n	$f(0) (\rm{km}^{-1})$	ESW(km)	AIC	Model
Spinner dolphin	4.0	142	0.75	1.3	265.0	Half-normal
Spotted dolphin	4.0	62	0.81	1.2	112.4	Half-normal
Fraser's dolphin and short-finned pilot whale	3.0	76	0.75	1.3	119.6	Half-normal
Bottlenose dolphin and melon-headed whale	3.0	31	1.01	1.0	37.5	Half-normal
Risso's dolphin	2.0	21	0.85	1.2	29.3	Half-normal
Dwarf sperm whale	2.8	30	1.34	0.7	41.1	Hazard-rate

Table 6

Parameters for density estimation, estimates of density $(D)(km^{-2})$, species abundance (N), the 95% upper and lower estimations of abundance and the coefficient of variation (CV) for seven species of cetaceans. The CVs were computed by the program DISTANCE using the bootstrap method, with samples=200 with replacement. *n*=number of sightings after truncation; E(s)=school size (either mean or regressed school size). The last column shows the abundance estimates using uncorrected observer distance estimation.

Species	п	E(s)	Р	D	N	L95%	U95%	%CV	Uncorrected N (%CV)
Spinner dolphin									
Sulu Sea 1994	46	88.4	0.99	1.24	28,586	16,121	52,601	35.37	24,886 (37.90)
Sulu Sea 1995	45	97.9		1.33	30,707	14.901	63,278	37.32	33,845 (33,50)
Sulu Sea 1994 and 1995	91	92.4	0.79	1.37	31,512	18,760	52,931	26.63	33,272 (23.60)
Tañon Strait	51	17.4		0.77	3,489	2,074	5,876	26.47	3,433 (21.00)
Spotted dolphin									
Sulu Sea 1994	23	92.5	0.69	0.75	17,325	7,466	40,203	43.04	17,041 (47.75)
Sulu Sea 1995	35	82.4	0.68	0.94	21,715	9,755	48,336	41.61	18,402 (55.56)
Sulu Sea 1994 and 1995	58	66.4		0.65	14,930	6,841	32,583	40.88	16,413 (44.08)
Tañon Strait	4	7.9	0.73	0.14	640	284	1,443	26.64	624 (42.72)
Fraser's dolphin									
Sulu Sea 1994	21	107.6	0.84	0.73	16,931	9,032	31,738	31.16	13,199 (28.61)
Sulu Sea 1995	16	83.5	0.79	0.43	10,080	4,315	22,547	43.06	7,178 (61.12)
Sulu Sea 1994 and 1995	37	97.2	0.64	0.58	13,518	7,958	22,962	26.93	10,914 (28.00)
Tañon Strait									
Short-finned pilot whale									
Sulu Sea 1994	19	41.0	0.95	0.25	5,827	2,348	14,460	45.86	5,138 (42.90)
Sulu Sea 1995	19	63.0	0.95	0.40	9,170	4,044	20,793	41.71	9,462 (37.00)
Sulu Sea 1994 and 1995	38	52.4	0.92	0.32	7,492	4,189	13,400	29.67	7,292 (27.15)
Tañon Strait	1	50.0		0.04	179	23	1,407	95.64	159 (88.76)
Bottlenose dolphin									
Sulu Sea 1994 and 95	22	23.7	0.96	0.11	2,628	1,211	5,703	40.23	2,469 (43.03)
Tañon Strait	1	5.7		0.01	30	3	269	104.87	88 (64.86)
Melon-headed whale									
Sulu Sea 1994 and 1995	6	30.5	0.97	0.04	921	211	4,019	82.62	875 (80.16)
Tañon Strait	2	143.5		0.30	1,383	167	4,268	81.57	1,299 (128.25)
Risso's dolphin									
Sulu Sea 1994 and 1995	21	8.4	0.90	0.03	1,514	611	3,754	47.16	1,682 (54.60)
Tañon Strait									
Dwarf sperm whale									
Sulu Sea 1994 and 1995	10	1.7	0.96	0.01	326	129	827	58.41*	381 (36.11)
Tañon Strait	20	1.7		0.15	670	179	2,512	62.33*	866 (64.01)

Comparison of the Sulu Sea with other tropical seas

Abundance rank, school size and corrected encounter rate were compared with those for cetaceans found in the WTIO, ETP and the GM, as reported in Ballance and Pitman (1998) using the same standardising procedure used by them (Table 7). All the species found in the Sulu Sea were also seen in all three of the other tropical regions. The most abundant species in the Sulu Sea, the spinner dolphin, was also the most abundant in the WTIO, second in rank in the GM, but only fourth in the ETP. The second most abundant, the pantropical spotted dolphin, ranked first in the GM and second in the ETP but only sixth in the WTIO. The additional differences observed were: (a) the two other more abundant species in the Sulu Sea, Fraser's dolphin and the short-finned pilot whale, ranked lower in the other three tropical regions; (b) the striped dolphin, *Stenella coeruleoalba* and a species of common dolphin, *Delphinus* sp., were absent from the Sulu Sea but highly abundant in the WTIO and the ETP; (c) the clymene dolphin, *S. clymene*, which ranked fourth in the GM, was not found in the Sulu Sea (it is endemic to the Atlantic); (d) school sizes of spinner, spotted and Fraser's dolphins and melon-headed whales in the Sulu Sea were smaller than those of the WTIO and the ETP; and (e) corrected encounter rates of spinner, spotted and Fraser's dolphins and pilot whales were notably higher in the Sulu Sea than in the WTIO, ETP and the GM.

Table 7

Comparison of abundance ranks, mean school sizes and corrected encounter rates of cetaceans found in the Sulu Sea (SS), western tropical Indian Ocean (WTIO), the eastern tropical Pacific (ETP) and the Gulf of Mexico (GM). Table obtained from Ballance and Pitman (1998) with the results of the present study added (ne=no estimate; nd=no data).

		Abundanc	e rank		Mean school size (CV)					Corrected encounter rate (schools 1,000km ⁻¹)				
Species	SS	WTIOO	ETP	GM	SS	WTIO	ETP	GM	SS	WTIO	ETP	GM		
Stenella longirostris	1	1	4	2	91.8 (0.14)	169.8 (1.37)	120.5	70.8 (24.62)	39.14	7.39	5.19	14.28		
Stenella attenuata	2	6	2	1	83.5 (0.27)	147.2 (1.52)	127.9	57.7 (7.67)	21.35	1.13	5.97	9.68		
Lagenodelphis hosei	3	10	5	16	87.6 (0.18)	183.3 (0.57)	394.9 (0.20)	34.0 ()	16.86	0.25	0.25	8.48		
Globicephala sp.	4	8	8	13	56.7 (0.26)	30.7 (0.66)	18.3 (0.08)	16.6 (21.16)	18.16	2.17	3.66	3.87		
Tursiops sp. (truncatus)	5	4	6	3	23.9 (0.21)	53.1 (2.39)	22.7 (0.22)	14.0 (11.81)	7.87	4.92	4.72	10.16		
Peponocephala electra	6	7	10	6	56.8 (0.38)	283. (0.97)	199.1 (0.20)	119.6 (22.50)	2.24	0.38	0.10	8.36		
Grampus griseus	7	5	7	8	8.4 (0.18)	48.3 (2.29)	11.8 (0.08)	10.7 (9.44)	6.34	4.85	6.27	3.49		
Kogia sima	8	15	17	14	1.3 (0.14)	1.6 (0.55)	1.7 (0.07)	2.2 (13.77)	1.29	3.19	3.20	1.93		
Mesoplodon sp.	ne	14	13	17	2 ()	2.0 (0.53)	3.0 (0.11)	1.9 (13.56)	ne	3.03	3.10	4.82		
Ziphiid whale (Z. cavirostris)	ne	19	15	20	1.3 ()	3.0 ()	2.2 (0.06)	1.2 (16.67)	ne	0.16	3.25	4.73		
Steno bredanensis	ne	9	9	9	2.0 ()	21.4 (0.70)	14.7 (0.18)	14.4 (12.18)	ne	2.58	4.63	19.09		
Balaenoptera edeni	ne	18	16	19	1.8 ()	1.2 (0.37)	1.7 (0.07)	2.7 (45.07)	ne	0.91	2.46	4.69		
Feresa attenuata	ne	13	12	11	3.0	15.8 (0.44)	27.9 (0.12)	29.2 (62.44)	ne	1.17	0.63	5.73		
Orcinus orca	ne	17	18	15	3.0	8.0 ()	5.4 (0.09)	10.0 (15.28)	ne	0.33	0.66	4.09		
Physeter macrocephalus	ne	12	14	10	1	2.8 (0.96)	7.9 (0.17)	2.6 (7.87)	ne	9.78	1.24	3.67		
Stenella coeruleoalba		2	3	5		42.6 (0.99)	60.9 (0.05)	36.1 (11.63)	0	8.44	14.34	1.79		
Delphinus spp.		3	1			221.2 (1.32)	380.1		0	1.63	3.02			
Pseudorca crassidens		11	11	12		41.3 (0.88)	11.4 (0.12)	20.4 (42.07)	0	0.84	1.21	4.98		
Balaenoptera musculus		16	19			1.6 (0.39)	1.5 (0.13)			1.93	0.36			
Kogia breviceps		20	nd	18		1.0 ()	nd	2.2 (11.75)		0.32	nd	3.32		
Stenella clymene				4				63.7 (26.67)				14.13		
Stenella frontalis				7				21.2 (15.89)				5.46		
					SS	SS WTIO ETP		'P	GM					
Total number of species:					15	20		19	20					
Area (km ²):					23,014		19,148	3,000						
On-effort transect line (km):					2,313	9,784	135	5,300						
Encounter rate for all cetacean	s (ani	mals 1,000	(km^{-1})		134	60.2		32.2						

Distribution

Fig. 5 is the plot of sighting locations in relation to water depth and Fig. 6 shows the results of the smoothed functions of the predictor variables incorporated into the encounter rate GAM for the various species. Table 8 summarises the results of the GAM analysis. The results of the GAM analysis for school size and encounter rate as response variables are similar for all species except the spinner and bottlenose dolphins. For the spinner dolphin, the encounter rate does not appear to be affected by Beaufort sea state (cues were leaping and splashing), whereas estimation of school size was affected. For the bottlenose dolphin, water depth appears to be an important factor in its distribution (as shown by a much higher encounter rate in shallow waters), whereas school size was more or less the same at various depths (Table 8, Fig. 6). Beaufort sea state affected encounter rates for the spotted, Fraser's and Risso's dolphins and dwarf sperm whale (Fig. 6). After adjusting for sea state, water depth appeared to be an important determinant in the distribution of Fraser's, bottlenose and Risso's dolphins and the short-finned pilot whale. SST also appeared to be important in the distribution of all species except Fraser's and Risso's dolphins. Site was an important factor for spotted, Fraser's and Risso's dolphins and dwarf sperm whale.

DISCUSSION

The 14 species observed in the Sulu Sea and the Tañon Strait in this survey constitute 54% of the total number of cetaceans known from Philippine waters and 47% of the total number of cetacean species recorded in Southeast Asia. Species not seen in this survey but which are found in Philippine waters include the striped dolphin, Irrawaddy dolphin (Orcaella brevirostris), Indopacific humpback dolphin (Sousa chinensis), Indopacific bottlenose dolphin (T. aduncus), pygmy sperm whale (K. breviceps), false killer whale (Pseudorca crassidens), Blainville's beaked whale (M. densirostris), Cuvier's beaked whale (Ziphius cavirostris), fin whale (B. physalus), humpback whale (Megaptera novaeangliae), blue whale (B. musculus) and Longman's beaked whale (Leatherwood et al., 1992; Perrin et al., 1995; Dolar, 1999b; Yaptinchay, 1999; Bautista, 2002; Dolar et al., 2002; Perrin et al., 2005; Acebes et al., 2005; Trono and Wang, pers. comm.; Yaptinchay and Alava, pers. comm.; Digdigan, pers. comm.).

Interspecific interactions

Almost half of the sightings of spinner dolphins in the Sulu Sea were with eight other species, and the relative frequency that they were seen with them appeared to be positively correlated with the abundance of the species. For example, 30% of the sightings were with spotted dolphins (abundance rank=2), 11% with Fraser's dolphins (rank=3), 6% with short-finned pilot whales (rank=4), etc. In the Tañon Strait, the great majority (87%) of sightings were of pure schools and the most frequent associations were with dwarf sperm whales and spotted dolphins. This association with dwarf sperm whales was not observed in the Sulu Sea, where density of dwarf sperm whales was 15 times less than in the Tañon Strait. A close association between spinner and spotted dolphins was also observed in the ETP, where 73% of spinner dolphin sightings were with spotted dolphins (Reilly, 1990) and in the WTIO (Ballance and Pitman, 1998). In the GM, however, these two species did not form mixed schools (Jefferson and Schiro, 1997).



Fig. 5. Sightings of cetaceans in the Sulu Sea and the Tañon Strait (●) Other species: (□) Bryde's whale; (★) Roughtoothed dolphin; (+) Sperm whale; (▲) Pygmy killer whale; (𝔅) Killer whale.



[Figure 5 continued overleaf]


Fig. 5 (continued). Sightings of cetaceans in the Sulu Sea and the Tañon Strait (●) Other species: (□) Bryde's whale; (★) Rough-toothed dolphin; (+) Sperm whale; (▲) Pygmy killer whale; (𝔅) Killer whale.

Fraser's dolphins interacted with other species more than any of the other species seen in this study; 84.2% of all the sightings were of mixed schools. They were observed associated mostly with short-finned pilot whales and spinner dolphins when in deep waters and with melon-headed whales and bottlenose dolphins when in relatively shallow waters or when close to shore. The close association between Fraser's dolphins and short-finned pilot whales has not been observed elsewhere, even in the ETP where the species overlap in their habitats (Au and Perryman, 1985; Wade and Gerrodette, 1993)². There and in the GM, Fraser's dolphins have been found to be associated with melonheaded whales (Au and Perryman, 1985; Perryman et al., 1994). In the WTIO however, Fraser's dolphins have not been seen associated with other species (Ballance and Pitman, 1998).

The degree of association of pilot whales with other species in our study (63%) is among the highest observed for this species. In the ETP, only 15% of pilot whale sightings involved other cetaceans (Bernard and Reilly, 1999). When in the deep waters of the Sulu Sea it associated mostly with Fraser's dolphins and when in shallow waters mostly with bottlenose dolphins. Association with bottlenose dolphins in coastal waters has been reported to be common in the ETP (Bernard and Reilly, 1999), the Canary Islands (Heimlich-Boran and Heimlich-Boran, 1990) and in the WTIO (Ballance and Pitman, 1998).

There are no previous reports of dwarf sperm whales being associated with other species. In the Tañon Strait however, about 11% of the sightings of dwarf sperm whales were with spinner dolphins and 4% were with melon-headed whales.

Distribution and abundance

Although tropical waters seem more homogenous in terms of the habitat they provide than temperate or Arctic waters and thus may be expected to harbour similar patterns of cetacean habitat use, we found surprising differences between the two nearly contiguous bodies of tropical waters that we studied. The Sulu Sea has a more diverse cetacean fauna than the Tañon Strait, with more than twice as many species. It can be characterised as an area dominated by spinner, spotted and Fraser's dolphins and the pilot whale, whereas the Tañon Strait can be characterised mainly as a spinner dolphin and dwarf sperm whale area. The high cetacean diversity in the Sulu Sea can be explained in part by its much larger size, a greater variety of habitat types and a wider range of prey species. In contrast, the smaller Tañon Strait, with its narrower range of habitats, greatly favours certain species but cannot support many others. As in most ecosystems, the assemblage of species in each site is a result of the diversity of habitats as well as of competition among the various cetacean species. Below, the fairly abundant species have been grouped into two categories; those with (a) restricted and (b) general or flexible habitat preferences.

Species with restricted distributions

Fraser's dolphin

Fraser's dolphin distribution, as noted during this study, is influenced by water depth, with highest sighting rates and largest school sizes found in waters beginning at about 700-800m deep and extending to waters deeper than 3.5km. This species has been characterised as a tropical and oceanic species (Wade and Gerrodette, 1993; Perrin et al., 1994). In the ETP, it was observed to occur at least 15km from the coast and mostly on the high seas approximately 45-110km offshore in waters 1.5-2km deep (Wade and Gerrodette, 1993; Perrin et al., 1994). It has not been observed in shallow waters close to shore except when deep water approached the coast, as the case may be in the Lesser Antilles and Indonesia (Jefferson et al., 1992). The occurrence of Fraser's dolphins in the shallow waters south of Negros Island, but not in the Tañon Strait gives support to this suggestion. A compilation of cetacean sightings over seven years also showed that although the Tañon Strait was the most surveyed area for cetacean occurrence, Fraser's dolphins were never seen within it (Dolar and Perrin, 1996). Hammond and Leatherwood (1984) observed high numbers only in the lower third of the Bohol Strait and at the centre of the Camotes Sea, where waters are deeper than 500m. Thus, as in the ETP, Fraser's dolphins in the Sulu Sea appear to prefer very deep waters. However, if deep waters approach the coast, as is the case in the Sulu Sea, then they can become coastal animals as well. The apparent dependence of Fraser's dolphins on deep waters could be associated with their preference for mesopelagic prey. In the Sulu Sea, they may dive to as deep as 600m to capture nonmigrating deep-water fish, squids and shrimps (Dolar et al., 1999; Dolar et al., 2003).

Risso's dolphin

As noted previously, the Sulu Sea appear to be a better habitat for Risso's dolphin than the Tañon Strait (Dolar and Perrin, 1996). Its distribution clearly shows a preference for

² The information in Dolar (2002) and Olson and Reilly (2002) regarding association between pilot whales and Fraser's dolphins was obtained from this study.





Fig. 6. Smoothed functions of the predictor variables included in the encounter rate and school size GAMs for selected cetacean species. When the trend of the smoothed functions of predictor variables is similar in both encounter rate and school size GAM, only the former is shown.

Table 8

Summary of the GAMs for seven cetacean species for encounter rate and school size. Change in deviance was calculated as: [(null deviance - residual deviance)/null deviance] x 100 (Barlow *et al.*, 2006).

Response variables	No. of sightings used	Change in deviance (%)	Predictor variables (associated degrees of freedom)
Spinner dolphin			
Encounter rate	146	7.172	SST(1)
School size		15.062	Beauf(1) + SST(1)
Spotted dolphin			
Encounter rate	62	37.433	Beauf(1) + SST(1) + Site(1)
School size		36.369	Beauf(1) + SST(1) + Site(1)
Fraser's dolphin			
Encounter rate	39	36.920	Beauf(1) + Depth(3) + Site(1)
School size		34.912	Beauf(1) + Depth(3) + Site(1)
Short-finned pilot v	whale		
Encounter rate	42	15.428	Depth(2) + SST(1)
School size		17.014	Depth(3) + SST(1)
Bottlenose dolphin			
Encounter rate	23	15.888	Depth(1) + SST(1)
School size		9.690	SST(1)
Dwarf sperm whale	e		
Encounter rate	30	28.622	Beauf(1) + SST(1) + Site(1)
School size		29.088	Beauf(1) + SST(1) + Site(1)
Risso's dolphin			
Encounter rate	22	8.854	Beauf(1) + Depth(1) + Site(1)
School size		19.199	Beauf(1) + Depth(1) + Site(1)

a depth range of 200 to 400m overlying a steep slope in the Sulu Sea (Figs 5 and 6). This depth is less than the 400 to 1,000m preferred depth observed in other tropical and subtropical areas (Leatherwood et al., 1980; Kruse, 1989; Davis et al., 1998; Baird, 2002). In the GM, it was found to have a very narrow core habitat, bounded by the 350 and 900m isobaths and depth gradients greater than 23 or 24m per 1.1km (Baumgartner, 1997). Steep slopes at the shelf break can enhance physical processes such as tidal stirring, dissipation of internal waves and or eddy-slope interaction that can cause increased vertical mixing. This in turn, can increase productivity of phytoplankton, fish and cetaceans (Huthnance, 1981; Baumgartner, 1997; Kruse et al., 1999). As with other physical parameters, bottom topography can therefore influence cetacean distribution indirectly by concentrating prey species (Hui, 1979; Hui, 1985; Selzer and Payne, 1988).

Dwarf sperm whale

Although the raw data showed distinctly high encounter rates at depths of 200-400m, the GAM analysis and the Analysis of Deviance showed that the best-fit model did not include depth as an important predictor variable. It appears that site is the most important predictor (p=0.002). The unusually high abundance of dwarf sperm whales in the Tañon Strait suggests that it is a preferred habitat. The mean depth of all sightings here (255m) is much lower compared

with those in the Sulu Sea (1,824m) (Table 9) and the GM (928m; Davis et al., 1998). In general, dwarf sperm whales inhabit waters over the edge of continental shelves close to shore and feed mainly on cephalopods and occasionally on benthic fishes and crustaceans (Gaskin, 1982; Ross, 1979; McAlpine, 2002). The Tañon Strait, especially the southern half, has a complex bottom topography of very narrow shelves on either side and submarine terraces that go down to 555m. This and the warm bottom temperatures of about 17°C make the conditions there suitable for benthic cephalopods such as squids and nautilus and for benthic fish and crustaceans (Hayasaka et al., 1987; Tucker and Mapes, 1978). In addition, there are fewer deep-diving competitors in the Strait such as the short-finned pilot whales and Risso's dolphins. Fraser's dolphins are absent from the strait.

Common bottlenose dolphin

Although found in both the Sulu Sea and the Tañon Strait it is clear that the bottlenose dolphin is restricted to shallow and intermediate depths on the inside of the shelf break. This coastal distribution is consistent with what is known about the distribution of the species in many areas (Würsig and Würsig, 1979; Shane, 1990; Jefferson and Lynn, 1994; Wells and Scott, 1999). The bottlenose dolphins observed in the Panay Gulf (or northeastern Sulu Sea) were seen on several occasions following shrimp trawlers. This ability to take advantage of human activities has also been observed in several other places (Leatherwood, 1975; Corkeron et al., 1990).

Species with more general or flexible habitat preferences

Spinner dolphin

The spinner dolphin ranked first in abundance in both sites and was found inhabiting both coastal and oceanic and both shallow and deep waters. Neither depth nor site appears to be important in its distribution, though its density was slightly higher in the Tañon Strait than in the Sulu Sea. Its predominance in the two sites supports the hypotheses of Au and Perryman (1985), Reilly (1990) and Reilly and Fiedler (1994) regarding the characteristics of the habitat of this species, i.e. warm with low variation in surface conditions throughout the year. Surface temperatures recorded during the surveys were 25-32°C in both sites. The difference in the depth of the thermocline between the Sulu Sea and the Tañon Strait suggests that the thermocline may not be an important factor in the distribution of this species here. In the ETP, the depth of the thermocline was found to be an important oceanographic factor separating the distribution of the eastern from the whitebelly forms of spinner dolphins (Reilly and Fiedler, 1994). Overall, the thermocline in the ETP where spinner dolphins were found was shallower (mean = 67.72m; Reilly, 1990) compared to both the Tañon Strait and the Sulu Sea. Spinner dolphins in the Sulu Sea feed primarily on mesopelagic prey that migrate in the upper 200m at night and occasionally may dive to greater depths of perhaps to 400m (Dolar et al., 2003). They appear to coexist with Fraser's dolphins, which are even deeper divers, by resource partitioning. The spinner dolphin has extended its foraging range horizontally to include shallow water; Fraser's dolphin on the other hand appears to have extended its foraging range vertically by diving deeper (Dolar et al., 2003).

Spotted dolphin

The distribution of spotted dolphins is similar to that of spinner dolphins and is not affected by depth. A similarity in the distributions of these two species was also observed in the ETP (Au and Perryman, 1985; Reilly, 1990). Although it also occurs in the Tañon Strait, the Sulu Sea is its preferred habitat as shown by the best-fit model (GAM) and by the density, which is seven times higher in the Sulu Sea than in the Strait.

Short-finned pilot whale

To some extent, the distribution of the short-finned pilot whale in the Sulu Sea is similar to that of Fraser's dolphin (Figs 5 and 6). Globally, short-finned pilot whales are found in steep-slope waters, over continental breaks and in areas with high topographic relief (Olson and Reilly, 2002); these features are abundant in the Sulu Sea. Here, they were found in deep waters of 200-5,000m. Like Fraser's dolphins, they

Table	9
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Depth and SST	profiles for	cetacean enecie	s that had 20	or more sightings
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		Depth (m)				SST (°C)			
Species and area	N	Range	Mean	SD	% <i>CV</i>	Range	Mean	SD	% CV
Spinner dolphin									
Sulu Sea	97	2-4,339	1,080	1,161	107.5	26.2-31.0	29.20	0.93	3.2
Tañon Strait	51	10-484	171	127	74.3	28.4-30.7	29.38	0.49	1.7
Spotted dolphin									
Sulu Sea	57	39-4,142	1,201	1,185	98.7	28.0-31.0	29.32	0.85	2.9
Tañon Strait	4	72-388	183	125	68.3	28.0-30.0	29.25	0.29	0.1
Fraser's dolphin									
Sulu Sea	39	158-3,793	1,341	1,141	85.0	27.0-31.0	29.33	1.08	3.7
Short-finned pilot wi	hale								
Sulu Sea	42	222-3,406	1,334	923	69.2	26.0-31.0	29.64	0.83	2.8
Tañon Strait	1	160	160	0	0.0	29	29.00	0.00	0.0
Dwarf sperm whale									
Sulu Sea	9	117-3,744	1,824	797	43.7	29.0-31.0	30.40	0.66	2.2
Tañon Strait	21	94-443	255	96	37.6	28.0-30.0	29.30	0.37	1.3
Bottlenose dolphin									
Sulu Sea	21	19-2,381	498	560	112.4	27.0-31.0	29.56	0.85	2.9
Tañon Strait	2	24-328	141	133	94.3	29	29.00	0.00	0.0
Risso's dolphin									
Sulu Sea	22	150-1,872	420	377	89.8	28.2-30.4	29.16	0.63	2.2

are deep diving and feed mostly on squid (Bernard and Reilly, 1999), but unlike them they seem to move more freely in and out of the Tañon Strait. A separate study showed that short-finned pilot whales move between the southern part of the Tañon Strait and the Sulu Sea (unpublished data) and their occurrence in the Strait appears to be seasonal; timed with the influx of frigate mackerels (*Auxis thazard*), (pers. obs. by MLLD). Although shortfinned pilot whales feed primarily on squid, they are also known to feed on fish such as cod, herring and mackerel and seasonally move onshore/offshore in pursuit of their prey (Bernard and Reilly, 1999; Olson and Reilly, 2002).

The relationship seen between water temperature and the distribution of the seven species tested is most likely an indirect one, a reflection of the distribution of the cetaceans' prey species. Following the migration of prey (e.g. mullet and snook), which in turn follow warmer waters, has been documented for bottlenose dolphins at Sanibel Island, Florida (Shane, 1990).

Other species

Except for the killer whale, all the species seen in this survey have been previously recorded in Philippine waters. The sighting of three killer whales (male, female and a calf) is the first record for the Philippines.

Bryde's whales have been hunted in the region for almost 100 years (Dolar *et al.*, 1994; Perrin and Dolar, 1998) and the very low sighting rate observed in this study is an indication that the population has decreased significantly in recent years. One of the two sightings off the northern coast of Mindanao was of a mother and a calf.

Survey method, assumptions, biases and limitations

The histograms of perpendicular distances (Fig. 4) are suitable for obtaining abundance estimates (Buckland et al., 1993; 2001). The peaked nature of the histogram for dwarf sperm whale suggests that the ability to spot these whales drops drastically at about 0.5km from the trackline and could be attributed to the cryptic behaviour of this species. The modified technique used in this survey differed from those used in large-scale surveys using large ships in the following respects: (a) the range of the small boat was limited and it could not have been used to survey the high seas or areas farther than 70km offshore (therefore the species composition and abundances found within this distance from shore may be different from those at the centre of the Sulu Sea); (b) the survey could only be carried out in the period between the monsoon seasons when the seas were calm and therefore the results should only be interpreted to apply to this period in time; and (c) the low sighting platform, presence of islands which obscured the horizon and the pitching movement of the boat prevented the use of a reticle to measure distances accurately. Thus distance estimation could only be done by eye and therefore replicability may be compromised because of reliance on the skill of one observer to estimate distance.

Care was taken to ensure that the following three key assumptions necessary for a reliable estimation of density and abundance using the line transect method were met to a good approximation (Burnham *et al.*, 1980; Buckland *et al.*, 2001).

(a) Animals on the trackline are always detected. For delphinids, this may not be a serious problem (Marsh and Sinclair, 1989) but could present a problem for cetacean species which dive for long periods of time such as the dwarf sperm whale and beaked whales (Barlow, 1999). In order to limit this possible source of bias, three

precautionary measures were taken. (1) Large $(20 \times)$ binoculars were used at the trackline to enable the observer to examine the trackline for a relatively longer period of time. This however, may have also limited the observer's field of view and caused them to miss animals which surfaced near the boat. Therefore, (2) an observer without binoculars was assigned to the bow to ensure that the animals missed by the observer using the large binoculars were seen. (3) An experienced dolphin spotter without binoculars was assigned to scan the waters 180° forward to the horizon, including the trackline scanned by the observer assigned to the large binoculars. Even though these precautions were taken, it is possible that long-diving animals were missed. Therefore, for dwarf sperm whale 0.35 was used (Barlow, 1999) as an approximation to g(0). Although vessel speed was similar to that of the vessel used in the simulation experiments, the platform height was much lower and only one $20 \times$ instead of two $25 \times$ mounted binoculars could be used. Therefore there is a chance that g(0) could actually be lower than 0.35 for that species, which would cause underestimation of abundance. For other species, g(0) was assumed to be equal to one.

(b) Animals are detected at their initial location (i.e. before they move in response to the observer). Although it was observed that some species like spinner and spotted dolphins were attracted to the boat and others such as Fraser's dolphins and dwarf sperm whales avoided it, the onset of these behaviours started after the animals had been detected, suggesting that most detections occurred beyond the likely range of the effect of the boat. The detection ranges of the binoculars used were from approximately 5km (for the $10\times$) to about 7km (for the $20\times$), and evasive or attractive behaviour was most often observed when the cetaceans were a kilometre or less away. Double counting was avoided by: (1) rejoining the trackline by following a convergent course towards the end of its leg being followed rather than returning to the exact point where the sighting was made; and (2) disregarding the animals sighted right after the vessel turned back to shore upon finishing the first of the day's two legs (see Fig. 1) unless they were of different species than seen just before the turn. Moreover, the probability that groups were counted again within the same line transect is small, since the cruising speed of the boat (17-20km hr-1) was faster than the sustained swimming speed of most cetaceans.

(c) Distances and angles are measured correctly. The binoculars with the compass allowed measurement of angles to the nearest degree. Estimates of distance were made by the best estimator among the observers as determined by calibration exercises. The estimates were then further calibrated using the measurements made with the GPS, using animals that were not moving away or towards the boat. The use of a reticle would have introduced more errors, considering the low sighting platform, the small size of the boat and the presence of islands obscuring the horizon.

CONCLUSIONS AND RECOMMENDATIONS

The low-cost abundance surveys conducted resulted in population estimates that can serve as baseline information for the two study sites. This information is important in the assessment of fishery impacts in the area and in developing sound management advice for cetacean conservation. In the Sulu Sea dolphins are incidentally caught during various fishing operations and there are some indications that these takes may not be sustainable (Dolar, 1994; Dolar, 1999a). This type of survey can be replicated in many areas in the Philippines and other developing countries where cetacean bycatch is prevalent but its impacts on cetacean populations are unknown. Equally important is the collection of good data on the anthropogenic induced cetacean mortality to determine sustainability of takes.

The archipelagic nature of the Philippines offers an interesting contrast with other tropical areas such as the ETP and the Indian Ocean where coastal and oceanic habitats are clearly defined. In the Philippines, islands are often surrounded by deep oceanic waters and some cetacean species, which are thought to be typically oceanic, can be found near shore. The relatively shallow Tañon Strait abutting the deeper oceanic basin of the Sulu Sea demonstrates the effect of depth on the distributions and interactions of certain species. It also shows that generalisations cannot be made regarding the habitat preferences of some species, as exemplified by the dwarf sperm whale whose preferred habitat in Tañon is 200-400m whereas in the Sulu Sea it is >1,000m. The relationships between the physical variables (such as water depth, slope and temperature) and cetacean distribution and abundance are often indirect, through links in the food web. Thus for species like the dwarf sperm whale, where there may be a shift in food preference depending on what is locally available, a global generalisation of habitat type may not apply.

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A note on the occurrence of sperm whales (*Physeter* macrocephalus) off Peru, 1995-2002

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ABSTRACT

Thirty-eight sightings of sperm whales (*Physeter macrocephalus*) were recorded off Peru (3-18°S) during 21 surveys conducted aboard platforms of opportunity, 1995-2002, with a search effort of 33,407 nautical miles of observation. Two main areas of concentration were detected: northern Peru (19 sightings) and southern Peru (16 sightings). Almost 58% of sightings occurred during the same or consecutive days. Group size ranged 1-18 individuals, with a mean of 3.5 (SD=3.9). The modal group size was one, accounting for 36.8% of sightings. Groups of three or more individuals accounted for 39.5%. An important increase in sightings occurred between 2001 and 2002, accounting for 68% of the records and suggesting migration into Peruvian waters from other regions. Positive correlations between indices of relative abundance and the anomaly of sea surface temperature were found, although warm events such as El Niño increased the uncertainty in sighting rates, reducing correlation values. The positive relationship between indices of relative abundance and commercial catch per unit effort for the squid *Dosidicus gigas* suggests some degree of interaction, although the extent of the role of this squid in the diet of sperm whales in the area requires further study.

KEYWORDS: SPERM WHALE; PACIFIC OCEAN; SOUTH AMERICA; DISTRIBUTION; CONSERVATION; SURVEY–VESSEL; MOVEMENTS; SQUID; WHALING-HISTORICAL; FISHERIES; FEEDING

INTRODUCTION

The sperm whale (Physeter macrocephalus) was the most heavily exploited large cetacean in Peruvian waters during the last century (e.g. Saetersdal et al., 1963; Clarke, 1980); between 1951 and 1981 Peruvian whalers killed a total of 49,858 sperm whales off Peru (Ramírez, 1989a; b). Information about this species in Peru was mainly gained from whaling areas and is based on whalers' data. The probable overexploitation of the population was recognised as early as 1961 by Saetersdal et al. (1963), on the basis of the whaling data from Pisco, Peru. Ramírez (1989a; b) reported indications of stock depletion in northern Peru where there was a decrease in the length of adult males and a decline in catch per unit effort (CPUE) between 1976 and 1981. Despite the cessation of whaling in Peru in 1982, the effects of the overexploitation are still apparent (Whitehead et al., 1997), although information about this species in Peruvian waters has become scarce. However, a few cetacean-oriented surveys have been performed. Dufault and Whitehead (1995) recorded sperm whales off Peru during their survey in the south Pacific in 1993, and Kinzey et al. (1999; 2000; 2001) recorded this species along tracklines off northern Peru between 1998 and 2000 during regional surveys in the Eastern Tropical Pacific (ETP). However, population estimates (e.g. Wade and Gerrodette, 1993; Whitehead, 2002) do not consider the waters off southern Peru and Chile.

Since 1995, the Instituto del Mar del Perú (IMARPE) has conducted research on the distribution of cetaceans in Peru, using pelagic and oceanographic surveys as platforms of opportunity. The objective of the present work was to describe the general distribution of sperm whales off Peru and to begin to address other information gaps in this formerly important whaling ground.

METHODS

Sighting data were collected during three kinds of surveys conducted by IMARPE 1995-2002: (1) pelagic surveys designed for evaluation of the population of Peruvian anchovy (*Engraulis ringens*) and other pelagic resources, covering the entire Peruvian Sea, from the coastline to 200 n.miles offshore; (2) demersal surveys, designed to evaluate the hake (*Merluccius gayi*) population off northern Peru; and (3) oceanographic surveys, designed to monitor oceanic conditions, covering either the northern, the southern or the entire Peruvian seas out to 300 n.miles offshore. Table 1 summarises the 21 surveys conducted by IMARPE, which had cetacean observers onboard.

During these surveys at least one and a maximum of three cetacean observers were placed onboard two research vessels: the R.V. Humboldt (with the observation deck at 15m above the water line) and the R.V. Olaya (with the observation deck at 10m above the water line). The number of observers depended on the availability of funds. Data collection consisted of visual scanning 90° either side of the trackline out to the horizon during daylight hours (06:00-18:00) using 10×50 binoculars. Group size was determined visually. A group was defined as the number of individuals counted during a sighting, since no association between individuals could be determined. As surveys were conducted from platforms of opportunity, the ships did not approach or follow a cetacean sighting but continued on their planned course. Observers spent all daylight hours at work, only resting during fishing operations, oceanographic stations or meals. The locations of sightings were recorded using a Global Positioning System (GPS). Fig. 1 shows the linetransects followed by the ships. Unfortunately complete data sets of effort are not available for all surveys and thus no complete analysis of effort was possible.

Indices of relative abundance were calculated as: (1) the number of sightings per 100 miles surveyed or 'sighting rate'; and (2) the actual number of sperm whales observed per 100 n.miles surveyed (Clarke, 1962; Clarke *et al.*, 1978). These rates were applied to every survey and year. Chi-square tests were used to examine seasonal and regional differences in sightings. The low quantity of data, as well as the lack of normality, required the use of the non-parametric Spearman's correlations (Siegel, 1956). Sea surface temperature (SST) during surveys and the mean of anomaly

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Surveys conducted by IMARPE research vessels with cetacean observers on board. Indices of relative abundance per survey are indicated.

No.	Effort (n.miles)	Date	Survey type	Research vessel	No. sightings	No. individuals	Sighting rate (100 n.miles ⁻¹)	Whales (100 n.miles ⁻¹)
1	004.0	Mary Jun 1005	Occarcomentic	Humboldt	0 0		· · · · ·	· · · · ·
1	904.9	May-Juli 1995	Oceanographic		1	2	0.049	0.000
2	2,094.0	Nov-Dec 1995	Oceanographic	Humboldt	1	2	0.048	0.096
3	876.5	Mar 1996	Oceanographic	Humboldt				
4	1,347.0	May-Jun 1996	Oceanographic	Humboldt				
5	1,739.0	Aug-Oct 1996	Demersal	Humboldt	1	4	0.058	0.230
6	1,420.7	Nov-Dec 1996	Oceanographic	Humboldt	1	1	0.070	0.070
7	842.6	May-Jun 1997	Demersal	Humboldt				
8	1,467.4	Jun-Jul 1997	Oceanographic	Humboldt	1	2	0.068	0.136
9	1,512.5	Sep-Oct 1997	Pelagic	Humboldt				
10	2,019.0	Mar-May 1998	Pelagic	Humboldt	5	17	0.248	0.842
11	1,577.3	Aug-Sept 1998	Pelagic	Humboldt				
12	984.0	May 1999	Oceanographic	Olaya	1	3	0.102	0.305
13	744.8	Jul 1999	Pelagic	Humboldt	1	1	0.134	0.134
14	645.0	May 2000	Oceanographic	Humboldt				
15	417.9	Sep 2000	Other	Humboldt	1	2	0.239	0.479
16	1,299.0	Oct-Nov 2000	Pelagic	Olaya				
17	2,126.0	Mar-Apr 2001	Pelagic	Olaya				
18	2,063.0	Jul-Aug 2001	Pelagic	Olaya	6	34	0.291	1.648
19	4,378.0	Oct-Nov 2001	Pelagic	Humboldt - Olaya	4	9	0.091	0.206
20	1.341.0	Feb-Mar 2002	Pelagic	Olava	5	23	0.373	1.715
21	3,607.0	Oct-Nov 2002	Pelagic	Humboldt - Olava	11	35	0.305	0.970
Total	33,406.6		@		38	133	0.114	0.398



Fig. 1. Simplified tracklines of 21 surveys conducted by IMARPE off Peru, 1995-2002, aboard *R.V. Humboldt* and *R.V. Olaya*. The complete tracklines for only four surveys are shown.

of SST (ASST) were used to perform correlations with the indices of relative abundance described above. ASST data used were those of the large time series collected in the different IMARPE coastal stations along the Peruvian coast (IMARPE, unpublished data). The mean ASST corresponding to each year (n=8) or survey with sperm whales recorded (n=12) was used as an environmental variability measure.

CPUE data for an industrial fishery of the large squid, *Dosidicus gigas*, expressed as total mass (MT) over total hours fishing (IMARPE, unpublished data), were used to perform correlations with the indices of relative abundance described above. CPUE data were grouped for the respective years and months when sperm whales occurred; CPUE data for geographic zones were not available.

RESULTS

A total of 38 sightings of sperm whales were recorded during 21 surveys conducted by IMARPE between 1995 and 2002, with a daylight search effort of 33,406.6 n.miles of observation. Table 2 indicates the date and geographic position of each sighting and Fig. 2 shows their locations. The NMFS/SWFSC also sighted sperm whales during their surveys conducted in 1998, 1999 and 2000 (Kinzey *et al.*, 1999; 2000; 2001); these records are included in both Table 2 and Fig. 2. An important proportion of sightings (22 or 57.9%) occurred during the same or consecutive days (Table 2). Group size observed was variable, ranging from 1 to 18 individuals, with a mean of 3.50 (SD=3.9). The modal group size for all sightings was one, accounting for 36.8% (14) of sightings. Pairs accounted for 23.7% (9 sightings), while groups of three or more individuals accounted for 39.5%.

The mean SST observed during sightings was 20.23 °C \pm 3.31°C, ranging 16.02-29.1°C. Of the 15 sightings consisting of groups of three or more individuals, 14 occurred in waters of SST 16-21°C. Except for two sightings, which occurred on 3 and 9 November 2002, all sightings were recorded in offshore waters, beyond the continental shelf (Fig. 2). Sightings were concentrated in two main areas: northern Peru from 7°S northward to the border with Ecuador, accounting for 44.74% of the sightings, and southern Peru from 16°S southward to the border with Chile, accounting for 42.11% of sightings. Some 70% of the sightings that occurred during summer and autumn were in northern Peru, while during winter and spring more sightings occurred in southern Peru (68%), although no statistical difference was found by season nor between both regions (Chi-square, p>0.05).

Indices of relative abundance are shown in Table 1. The maximum sighting rate calculated was that for 2002 (0.324 sightings 100 n.miles⁻¹) and the survey with highest sighting rate was that performed in summer 2002 (0.373 sightings 100 n.miles⁻¹). The number of sightings increased from one in 1995 to 16 (42% of the total) sightings in 2002, with an indication of increased relative abundance between those years (Fig. 3). Another increase in sightings also occurred in 1998 coinciding with an El Niño. There was a

Records of sperm whales sighted off Peru between 1995 and 2002, including those from SWFSC.

No.	Date	Position		Number of individuals	SST (°C)	Source	
1	19 Dec 1995	16° 47'S	75° 23' W	2	21.5	This work, R.V. Humboldt	
2	24 Sep 1996	5° 12'S	81° 47' W	4	16.8	This work, R.V. Humboldt	
3	25 Nov 1996	12° 59'S	78° 17' W	1	19.4	This work, R.V. Humboldt	
4	20 Jun 1997	17° 16'S	74° 37' W	2	21.4	This work, R.V. Humboldt	
5	31 Mar 1998	6° 00'S	81° 26' W	1	29.1	This work, R.V. Humboldt	
6	31 Mar 1998	6° 04'S	81° 18' W	2	28.8	This work, R.V. Humboldt	
7	26 Apr 1998	16° 19'S	74° 27' W	9	21.0	This work, R.V. Humboldt	
8	27 Apr 1998	16° 40'S	74° 06' W	4	19.6	This work, R.V. Humboldt	
9	30 Apr 1998	17° 45'S	71° 27' W	1	19.5	This work, R.V. Humboldt	
10	22 Nov 1998	10° 39'S	79° 39' W	15		Kinzey et al. (1999)	
11	22 Nov 1998	10° 36'S	79° 41' W	2		Kinzey et al. (1999)	
12	22 Nov 1998	10° 39'S	79° 41' W	2		Kinzey et al. (1999)	
13	22 Nov 1998	10° 35'S	79° 43' W	5		Kinzey et al. (1999)	
14	22 Nov 1998	10° 38'S	79° 42' W	8		Kinzey et al. (1999)	
15	28 Nov 1998	05° 47'S	81° 22' W	1		Kinzey et al. (1999)	
16	23 May 1999	17° 55'S	74° 52' W	3	20.8	This work, R.V. Olava	
17	11 Jul 1999	3° 44'S	82° 59' W	1	20.1	This work, R.V. Humboldt	
18	27 Oct 1999	13° 51'S	78° 07' W	1		Kinzey et al. (2000)	
19	27 Oct 1999	13° 40'S	77° 42' W	9		Kinzey et al. (2000)	
20	6 Nov 1999	5° 27'S	84° 24' W	67		Kinzey et al. (2000)	
21	26 Sep 2000	5° 00'S	84° 04' W	2	18.9	This work, R.V. Humboldt	
22	24 Oct 2000	12° 41'S	78° 28' W	11		Kinzey et al. (2001)	
23	3 Nov 2000	6° 19'S	81° 14' W	27		Kinzey et al. (2001)	
24	8 Jul 2001	5° 08'S	81° 59' W	7	17.2	This work, R.V. Olaya	
25	9 Jul 2001	5° 50'S	82° 45' W	1	19.7	This work, R.V. Olava	
26	9 Jul 2001	5° 60'S	82° 56' W	2	20.6	This work, R.V. Olaya	
27	15 Jul 2001	8° 42'S	80° 17' W	15	17.7	This work, R.V. Olava	
28	19 Jul 2001	9° 47'S	79° 35' W	8	18.2	This work, R.V. Olaya	
29	3 Aug 2001	17° 44'S	74° 15' W	1	16.0	This work, R.V. Olaya	
30	8 Oct 2001	17° 31'S	72° 02' W	6	16.8	This work, R.V. Humboldt	
31	4 Nov 2001	5° 60'S	83° 24' W	1	19.7	This work, R.V. Olaya	
32	4 Nov 2001	5° 60'S	83° 25' W	1	19.7	This work, R.V. Olaya	
33	5 Nov 2001	5° 46'S	82° 32' W	1	17.1	This work, R.V. Olaya	
34	22 Feb 2002	3° 45'S	81° 27' W	2	25.4	This work, R.V. Olava	
35	22 Feb 2002	6° 01'S	81° 31' W	1	24.2	This work, R.V. Olaya	
36	1 Mar 2002	7° 00'S	81° 21' W	1	26.1	This work, R.V. Olaya	
37	1 Mar 2002	6° 59'S	81° 20' W	1	26.0	This work, R.V. Olaya	
38	1 Mar 2002	6° 54'S	81° 11' W	18	25.3	This work, R.V. Olava	
39	2 Oct 2002	17° 41'S	72° 12' W	1	18.8	This work, R.V. Humboldt	
40	2 Oct 2002	17° 42'S	72° 13' W	10	18.8	This work, R.V. Humboldt	
41	2 Oct 2002	17° 44'S	72° 17' W	3	18.9	This work, R.V. Humboldt	
42	2 Oct 2002	17° 47'S	72° 18' W	3	19.0	This work, R.V. Humboldt	
43	3 Oct 2002	17° 11'S	72° 42' W	4	18.2	This work, R.V. Humboldt	
44	3 Oct 2002	17° 14'S	72° 44' W	4	18.4	This work, R.V. Humboldt	
45	3 Oct 2002	18° 03'S	73° 13' W	2	18.0	This work, R.V. Humboldt	
46	10 Oct 2002	16° 02'S	76° 12' W	3	17.6	This work, R.V. Humboldt	
47	21 Oct 2002	12° 52'S	77° 41' W	2	17.9	This work, R.V. Olava	
48	3 Nov 2002	8° 34'S	79° 23' W	1	18.2	This work, R.V. Olaya	
49	9 Nov 2002	6° 21'S	80° 59' W	2	18.4	This work, R.V. Olaya	

significant correlation between the total annual search effort and the number of sightings ($R_{\text{Spearman}} = 0.702$, p < 0.05, n=8). No correlation was found between the mean sighting rate and SST ($R_{\text{Spearman}} = 0.304$, p > 0.05, n=8). However, a positive correlation (although not significant at the 5% level) was found between the mean ASST with both the sighting rate ($R_{\text{Spearman}} = 0.529$, p=0.053, n=12) and the number of sperm whales per 100 n.miles ($R_{\text{Spearman}} = 0.571$, p=0.077, n=12; Fig. 4). In addition, if the extreme ASST values obtained from surveys conducted during El Niño 1997-98 are excluded, significant correlation values are obtained for both the sighting rate ($R_{\text{Spearman}} = 0.845$, p<0.01, n=10) and the number of sperm whales per 100 n.miles ($R_{\text{Spearman}} = 0.705$, p<0.05, n=10).

The *D. gigas* fishery's pooled CPUE for the period sampled (Fig. 5) was significantly correlated with both the sighting rate ($R_{\text{Spearman}} = 0.855$, *p*<0.01, *n*=10) and the number of sperm whales per 100 n.miles ($R_{\text{Spearman}} = 0.782$,

p<0.01, n=10). ASST was significantly related to CPUE (R_{Spearman} = 0.838, p<0.01, n=8) when the highest ASST values were excluded. No *D. gigas* catch occurred during the 1998 El Niño (PRODUCE, 2003).

DISCUSSION

Although sperm whales were seen all along the coast of Peru, they tended to concentrate in the northern and southern portions of the study area (Fig. 2). Northern Peru had a higher concentration of sightings than might be expected on the basis of former work (Saetersdal *et al.*, 1963); animals seen there are probably from the Ecuador/northern Peru stock (Dufault and Whitehead, 1995). Animals seen off southern Peru are probably related to animals seen off northern Chile, as tracking of sperm whales off northern Chile suggests (Rendell *et al.*, 2004). In the former whaling zone off central Peru (Pisco, 13°S),



Fig. 2. Sperm whale sighting locations off Peru based on shipboard surveys. Crosses indicate new records during 21 surveys conducted by IMARPE between 1995 and 2002. Triangles indicate SWFSC records between 1999 and 2000 (Kinzey *et al.*, 1999; 2000; 2001).



Fig. 3. Annual sightings and number of individuals sighted per 100 n.miles of observation off Peru during 21 surveys conducted 1995-2002.

where one might expect high concentrations (Ramírez and Urquizo, 1985; Ramírez, 1990), only two sightings of a solitary sperm whale and a pair of sperm whales occurred during the present study, although eight sightings were recorded there during October and November by SWFSC 1998-2001 (Kinzey *et al.*, 1999; 2000; 2001; see Table 2).

Present information was consistent with the seasonal trend reported by Saetersdal *et al.* (1963), who suggested seasonal migrations between the whaling grounds off Paita (5°S) in summer and off Pisco (13°S) in winter. However, although more sightings occurred off northern Peru during summer and autumn, seasonality could not be confirmed because of the few records off central Peru. Conversely, more sightings occurred during winter and spring in southern Peru.

The tendency of sightings to occur during the same or consecutive days in several years, as well as the relatively large fraction of groups (almost 40%) with three or more animals, suggests that sperm whales most commonly occur in aggregations off Peru. However, as shown in Table 2, the mean group size observed during IMARPE's surveys was



Fig. 4. Relationship between ASST and two indices of relative abundance: (a) Sightings per 100 n.miles surveyed; and (b) Whales per 100 n.miles surveyed. Labels indicate the dates of surveys when warm oceanographic events occurred.



Fig. 5. Relationship between CPUE of a *D. gigas* fishery and two indices of relative abundance: (a) Sightings per 100 n.miles surveyed; and (b) Whales per 100 n.miles surveyed.

low (3.5 individuals) compared with that observed during SWFSC's surveys off Peru (13.5 individuals) and other areas of the South Pacific (Whitehead, 2003). This difference is probably due to different surveying methods. Our surveys could neither approach cetaceans sighted nor use acoustic monitoring or follow cetaceans for hours. The small number of cetacean observers and the different purposes for which the surveys were designed would suggest that the frequency and group size of sightings recorded during the IMARPE's surveys underestimated true numbers. In fact the mean group size found in the present study is consistent with the cluster (as opposed to school) size found in other studies (Whitehead, 2003).

It must be stressed that the oceanographic conditions off Peru during the present work were strongly influenced by an El Niño - Southern Oscillation (ENSO). Years 1995, 1996 and early 1997 were characterised by cold SST (Pizarro and Tello, 1996; Ganoza et al., 1997; Pizarro et al., 1997), a state know as La Niña, and sperm whales were infrequently sighted in these cold waters. During 1997 and 1998, the SST increased, leading to an El Niño (Gutiérrez et al., 1998; Vasquez and Tello, 1998), however sightings during the February/March 1998 survey, revealed an increase in the number of sperm whales in the area (Fig. 3). Kinzey et al. (1999) also recorded sperm whales more frequently during this period than in other SWFSC surveys (e.g. Kinzey et al., 2000; 2001). In 1999, the SST was warm in summer (Vasquez and Tello, 1999) with normal conditions for the rest of the year, but with a nucleus of positive anomalies off central Peru in May (IMARPE, 1999), where sperm whales were sighted. The year 2000 was characterised by average conditions (IMARPE, 2000) and fewer sightings. During early 2001 positive ASSTs were detected in northern and southern Peru, where sperm whales were frequently sighted (Table 2), while central Peru had negative ASSTs (IMARPE, 2001), with no sperm whales sighted. During the following months, a large area of oceanic-neritic mixed waters predominated off northern Peru, where sperm whales were sighted. During 2002, there were positive ASSTs off central and northern Peru, with similar temperatures in nearshore and oceanic waters off the entire Peruvian coast and the movement of equatorial waters southward (Estudio Nacional del Fenómeno El Niño, 2002a; b) coinciding with a higher frequency of sightings (Table 2). Therefore, despite the relatively small sample sizes, there appears to be a positive correlation between the relative abundance of sperm whales and ASST.

However, the warming produced during El Niño seems to affect this relationship, reducing correlation values with respect to indices of relative abundance by increasing environmental uncertainty. If the plots in Fig. 4 are separated at 0°C, there appear to be two possible scenarios for the distribution of sperm whales. The first occurs when ASST is below or close to 0°C; this correlates positively with the number of sightings. The second scenario occurs when a high positive ASST reaches a threshold value $(\geq +2^{\circ}C, \text{ when El Niño occurs})$, when negative tendencies appear to occur and uncertainty in indices of relative abundance would increase. While this latter scenario is not evident in Fig. 4, due to the high variation of values and the low number of data points, it is supported by the findings of Ramirez and Urquizo (1985) for northern Peru and by the fact that from five surveys conducted in 1997-1998, sperm whales were recorded only in two surveys (see Table 1). More survey effort during El Niño events is needed to confirm or deny this hypothesis. The present work is in agreement with the suggestion of Jaquet and Whitehead (1996), who consider it important to investigate the influence of SST by region for this species.

Other authors have described the effects of El Niño on sperm whales in the Eastern Pacific. During El Niño, sperm whales reduce their feeding (Smith and Whitehead, 1993; Whitehead, 1996; Jaquet and Whitehead, 1999; Jaquet *et al.*, 2003), as well as their residency time around Galapagoos (Whitehead, 1996) and in the California Gulf (Jaquet *et al.*, 2003). In the California Gulf, during the 1998 El Niño, sperm whales changed their foraging effort, resulting in an increased energy expenditure and a decrease in socialising (Jaquet *et al.*, 2003). In Peru, whalers detected sperm whale aggregations 600km further to the south of their usual whaling grounds during the 1982-83 El Niño (Ramírez and Urquizo, 1985). Nevertheless, during the strong 1997-98 El Niño, sperm whales were seen by the author off northern and southern Peru in March/April 1998 and Kinzey *et al.* (1999) also recorded them off central and northern Peru (Table 2).

The increase in the sightings rate during the final years of this study (Fig. 3) is greater than one would expect from natural population increase and suggests population movements produced by eastward movements from the offshore Southeast Pacific, from the Galapagos grounds (Whitehead et al., 1997) or from more distant areas. Some evidence of large population movements already exists for this species in the Eastern Pacific Ocean. Sperm whales tagged with Discovery marks in the central Eastern Tropical Pacific were recovered by Peruvian whalers off Paita in 1975 and 1976 (Ramírez, 1989a) and Whitehead (2001) recorded movements of photo-identified sperm whales from Galapagos to mainland Ecuador and Peru. Jaquet et al. (2003) recorded female sperm whales in the Gulf of California that had been previously photo-identified in Galapagos. Whitehead et al. (1998) found non-geographical population structure in South Pacific sperm whales. It is highly likely that sperm whales from different grounds of the Eastern Pacific Ocean converge in Peruvian waters during the same or different seasons as a response to changes in oceanographic conditions or food availability in their 'original' grounds.

The available abundance estimates for the Eastern Pacific (Wade and Gerrodette, 1993; Whitehead, 1995; 2002; Whitehead et al., 1997) do not cover waters off southern Peru and northern Chile (Whitehead, 2002) and few sperm whale surveys have been conducted in the area to obtain indices of relative abundance. Clarke et al. (1978) reported a sighting rate of 0.46 sightings per 100 n.miles during a survey off Chile, October/November 1964. During a cruise carried out in the same months of 1959 between Ecuador and Galapagos, Clarke (1962) reported seven sightings of sperm whales and an average of 0.305 sightings (any group size) per 100 n.miles (6.1 sperm whales per 100 n.miles). Later, Clarke et al. (2002) failed to sight sperm whales during surveys in this former whaling area off Ecuador and northern Peru in 2001, assuming that this species had 'disappeared' from the area. However, this conclusion does not agree with our findings and probably reflects their low survey effort (252 n.miles in Peru). During surveys by IMARPE in July/August conducted and October/November 2001, a total of 34 sperm whales were recorded, with sighting rates of 0.291 and 0.091 respectively. Moreover, the highest values of sighting rate during the present work occurred during 2002 (0.305 and 0.373, Table 1). It should be remembered, however, that comparison of sightings rates between vessels, crews, effort and survey design are inherently problematic.

Clarke *et al.* (2002) suggested that the exploitation of *D. gigas*, which supports a large fishery by an international fleet in Peruvian waters, had led to the disappearance of sperm whales from Ecuadorian and northern Peruvian waters. Clarke *et al.* (1993) expressed early concern over its impact on the sperm whale population of the Southeast Pacific, arguing that in this area sperm whales feed exclusively on this squid, based on the analysis of flesh remains from stomach contents (Clarke *et al.*, 1987). However, there is also evidence indicating that *D. gigas* is not the primary food source of sperm whales. Both Clarke *et al.* (1976) and Smith and Whitehead (2000a) found squids of the genera *Histioteuthis* as the main prey of sperm whales

off South America. Clarke et al. (1976) estimated D. gigas to constitute 32% of the diet of sperm whales caught off Peru and Chile, based on squid beaks collected from stomach contents, while Smith and Whitehead (2000a) did not record beaks of D. gigas in faeces collected around the Galapagos Islands. Due to this, doubts have been raised over the conclusion of Clarke et al. (1987), suggesting that they over-estimated the importance of D. gigas in the diet of sperm whales (IWC, 1988; Smith and Whitehead, 2000a; b), despite the later argument of Clarke and Paliza (2001). However, a predator-prey relationship between sperm whales and D. gigas has been suggested by analysis of stable isotopes in the Gulf of California (Ruiz-Cooley et al., 2004) and the use of this technique would clarify the situation with respect to the trophic relationships of sperm whales in the Southeast Pacific.

The high correlation between the indices of relative abundance for sperm whales and the CPUE of D. gigas by the industrial fishery suggest some degree of trophic interaction and raises again the question of the importance of D. gigas in the diet of sperm whales off Peru; the correlation suggests that the argument that D. gigas is an important species for sperm whales is still valid. However, the available CPUE information is not in sufficient detail to define geographic zones where overlap could occur, confounding the interpretation of the results. In addition, there are also periods when no relationship can be found between sperm whale occurrence and squid availability. For example, the observed increase in sightings in 1998 (Fig. 3) could be related to more than just prey availability (e.g. population movements), since the D. gigas fishery collapsed that year due to the El Niño (PRODUCE, 2003; IMARPE, unpublished data).

While the indirect interaction of the D. gigas fishery with the sperm whale population off Ecuador and northern Peru has not been confirmed, former over-whaling has been argued as a more consistent cause for their population decline around the Galapagos Islands. Whitehead et al. (1997) found an annual decline of 20% in the population off Galapagos between 1985-95 and a recruitment rate of 0.05 calves/female/year, suggesting that the decline could be due to this low recruitment rate, as well as eastward migration into waters off Central and Southern America. The authors associated both findings with the long-term negative effect of intensive whaling in Peruvian waters, which dramatically reduced the number of mature males in the area (Ramírez, 1989a). Other factors such the global warming, prey availability (Whitehead, 1997; 2003) and population movement (Jaquet et al., 2003) should also be considered.

Direct fishery interactions with sperm whales have not been reported for Peruvian waters and so information about sperm whales cannot be obtained from this source. However, fishery-related mortality has been acknowledged in Ecuador and Chile (Haase *et al.*, 1994; González and Aguayo, 2002), suggesting this interaction does indeed occur in the Southeast Pacific. Although some strandings have occurred in Peru (García-Godos, pers. obs.), they were not properly investigated and thus provide no information on this subject. Only a single stranding related to a collision with a vessel is known to have occurred in central Peru (during 2003; García-Godos and Santillán, 2004).

The information presented in this work underlines the urgent need for dedicated cetacean surveys in the Southeast Pacific which would provide abundance estimates for sperm whales and other cetaceans. Non-lethal research into feeding habits is a priority, as well as research into the direct and indirect impacts of commercial fisheries on sperm whales.

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