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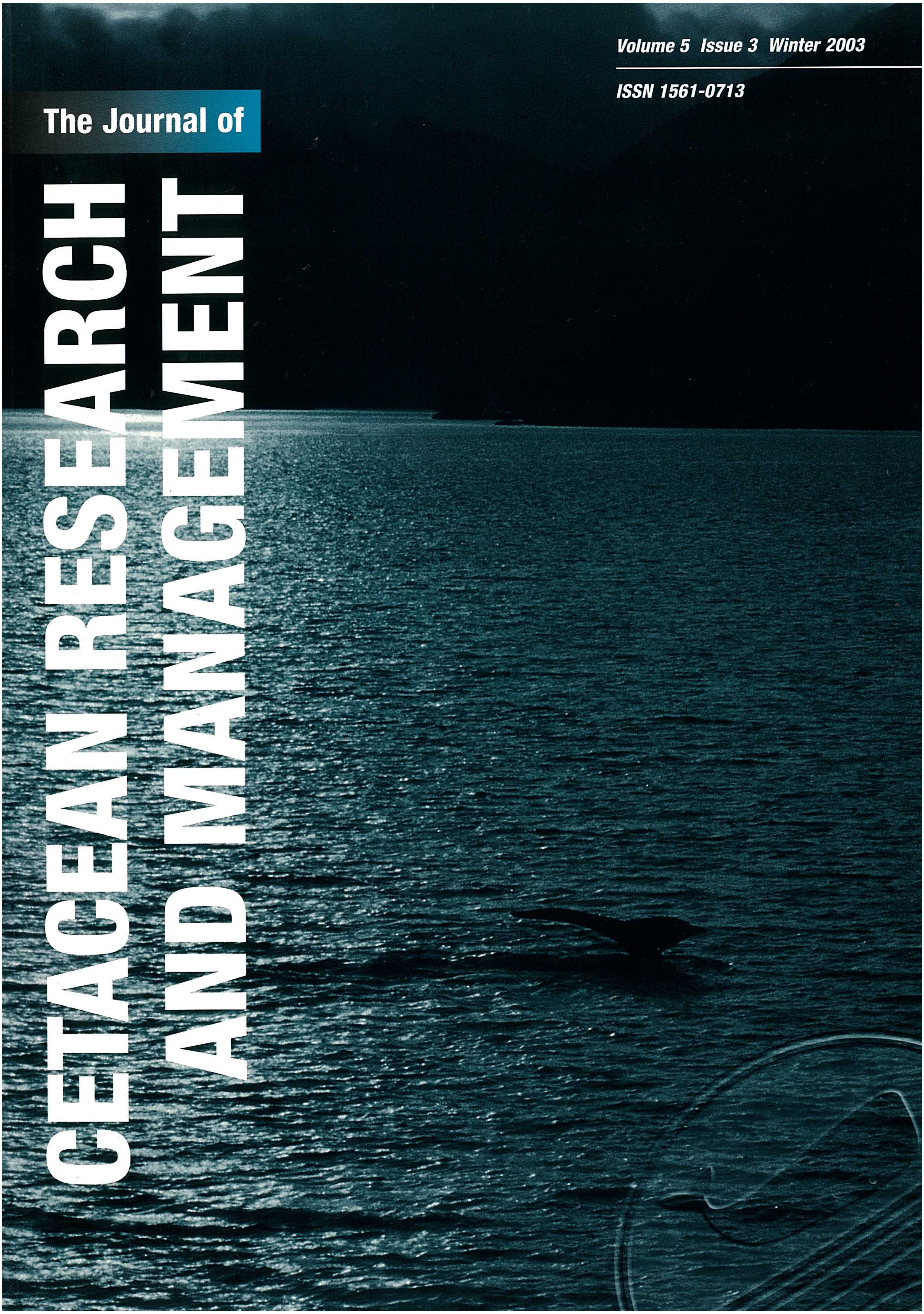

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Editorial

Welcome to the final issue of the fifth volume of the *Journal of Cetacean Research and Management.* This has been another good year for the Journal. A total of 32 papers have been published involving some 120 authors from 24 countries (including from Europe, Africa, Asia, Australasia, North America and South America). I am particularly pleased at the wide geographic spread and range of disciplines included. The published papers once again serve to illustrate that the *Journal* is fulfilling its aim of improving conservation science in general and in particular the conservation and management of cetaceans throughout the world. An author and keyword index to Volume 5 appears at the end of this issue.

The present issue again covers a broad range of subjects, areas and species; I am particularly pleased that we have received another contribution to our occasional series on early descriptions of whales.

Any effective conservation and management strategy requires knowledge of the stock structure, distribution and movements of the animals concerned. Despite (and indeed perhaps because of) advances in genetic techniques, this remains one of the most complex and difficult issues facing cetacean biologists. There are several interesting papers on this subject in the present issue, ranging from the general issue of the use of hypothesis testing (Martien and Taylor), case studies of single species/areas (the bowhead whale, Rugh *et al.*; the sperm whale in the Faroe Shetland Channel, Hastie, Swift *et al.*), to the use of satellite telemetry to study movements (Heide-Jørgensen *et al.*). The paper by Hastie, Barton *et al.* links the study of distribution and stock structure to the problems of managing and determining special areas of conservation. Two of the papers in this issue advance our knowledge of previously little studied areas; Frantzis *et al.* review what is known about the cetaceans of the Greek Seas and Best *et al.* provide the first abundance estimate for blue whales on the Madagascar Plateau. The eastern gray whale represents one of the success stories of cetacean conservation, with its population estimated to be at or near its pre-exploitation levels despite heavy over-harvesting in the 19th century. Under such circumstances it is particularly interesting to study reproductive behaviour and the paper by Urbán *et al.* looks at this aspect of gray whales in Mexican waters. Continuing the reproductive theme, the paper by Kjeld *et al.* shows that measurements of the sex hormone levels in the blood of sei whales provides a powerful tool for examining both pregnancy and the seasonal changes in the male reproductive cycle.

The quality of any Journal is a reflection of the quality and dedication of its reviewers. I would like to thank publicly here all those scientists who dedicate a considerable period of time to offering constructive and valuable criticism and advice on submitted manuscripts. This not only ensures the high quality of published papers but also serves to improve the quality of cetacean management science throughout the world. An updated list of referees can be found on the journal website (http://www.iwcoffice.org/Publications/reviewers.htm).

G.P Donovan
Editor

Early descriptions of whales

Many of the early descriptions of whales and their behaviour and ecology were published in languages other than English. These were often sections in books or articles that were more broad in scope, for example general works on zoology or geography. If translations into English exist at all, they are often not precise with respect to the cetacean component. The Journal invites submissions of such descriptions. Submissions should include: full bibliographic information; a brief introduction to the author and the work in which the description is included; the full text in the original language; and a careful translation.

D'ORBIGNY, A. 1834. NOTE ON A NEW CETACEAN GENUS, FROM THE RIVERS OF THE CENTRAL PART OF SOUTH AMERICA. [*NOTICE SUR UN NOUVEAU GENRE DE CÉTACÉ, DES RIVIÈRES DU CENTRE DE L'AMÈRIQUE MÉRIDIONALE. NOUVELLES ANNALES DU MUSÉUM D'HISTOIRE NATURELLE, 3:28–36*].

Introduction

Alcide Dessalines d'Orbigny (1802-1857) spent his youth in La Rochelle, collecting and studying marine animals during his free time. He was the son of Charles Marie Dessalines d'Orbigny, a surgeon of the French Navy, and a distinguished naturalist. Appointed as a correspondent of the *Muséum d'Histoire Naturelle*, Paris in 1821, d'Orbigny became a naturalist traveller for this institution during the following years. In 1826 he was nominated by the *Académie des Sciences* for a mission in South America, where he explored between 1826 and 1833 (Taquet, 2002). D'Orbigny began his journey up the Parana River, and systematically visited its banks and those of its tributaries over the next 14 months. Upon returning to Buenos Aires, he explored the pampas surrounding the capital on the request of the Government of Argentina. His first scientific exploration of the northern part of Patagonia followed for the next eight months. At the end of his travels, he sailed from Montevideo to Chile, and then on to Bolivia, where he stayed from early 1831 until June 1833 (Pilleri and Gihr, 1977). D'Orbigny finally returned to France in February 1834. He had collected more than 400 insect species, 150 crustacean species, 150 fish species, more than 100 reptile species, more than 600 species of molluscs (Gaudry, 1859) and several mammalian species. His travels are described in the first two tomes of a series entitled *Voyage dans l'Amérique méridionale* (Travel Through South America), including 7 tomes and 11 volumes (illustrated by some 500 plates), that he published alone or in cooperation between 1835 and 1847. Tome IV (1), entitled *L'homme américain* (The American Man), is considered a pioneering contribution to anthropology in France. In 1853, d'Orbigny became Professor and the first Curator of Palaeontology at the *Muséum d'Histoire Naturelle*, Paris. He subsequently concentrated most of his activity on fossil invertebrates (Taquet, 2002).

The new cetacean species described by d'Orbigny in 1834 (*Inia boliviensis*) was later reviewed and confirmed by d'Orbigny and Gervais (1847), who recorded that '*Inia boliviensis* might have been known to naturalists earlier than supposed'. Indeed, they compared it with *Delphinus geoffrensis* (de Blainville, 1817), which was represented by one stuffed specimen in the *Museu da Ajuda* of Lisbon, and was thought to originate from Brazil[1]. However, it was not until 1870, when the skull of this specimen was prepared separately, that the generic identity of these two species could be settled (Robineau, 1989). The two were considered synonyms by all authors until van Bree and Robineau (1973), while conducting a study on skulls, observed that the specimens from Bolivia had more teeth than non-Bolivian specimens. Moreover, these authors pointed out that the rapids and water falls of Rio Madeira, between Porto Velho and Guajara Mirim, constitute a barrier likely to isolate Bolivian dolphins. Therefore, they proposed a sub-specific status for this population: *Inia geoffrensis boliviensis*. The study by Pilleri and Gihr (1977) revealed additional morphological differences, and the specific status of *Inia boliviensis* was finally restored, a conclusion supported by Da Silva (1999) (original article not seen but cited in da Silva and Martin, 2000). However, Rice (1998) acknowledged only one species for the genus *Inia*, with three sub-species. Indeed a third sub-species was recognised as *I. g. humboldtiana* (Pilleri and Gihr, 1978), from the Orinoco River system. It is noteworthy that d'Orbigny also contributed to the description of another South American cetacean species, the Franciscana *Pontoporia blainvillei* (Gervais and d'Orbigny, 1844) (Robineau, 1989).

In addition to the description of *Inia boliviensis* (not quoted integrally hereafter), which was illustrated by two good figures, d'Orbigny's text is interesting for several reasons. The initial range assigned to this species appears to be much larger than it is today (Pilleri and Gihr, 1977, fig. 5; da Silva and Martin, 2000), and according to d'Orbigny, the species was usually observed in groups of three to four individuals. Pilleri and Gihr (1977) considered that such groups were rare. D'Orbigny's remarks on the species colouration and behaviour are also interesting; moreover the anthropologic dimension of his work is clearly revealed by, e.g. considerations of language diversity derived from the variety of the names given by local people to *Inia boliviensis*. D'Orbigny chose as a generic name the word used by the Guarayos, a small nation then completely unknown to scientists that he highly appreciated.

We have tried to reproduce as closely as possible d'Orbigny's style (clarifying information is given in square brackets). The punctuation reproduces that of d'Orbigny as far as possible.

English translation

When we entered into High Peru (or Bolivia), the inhabitants of the city of Santa Cruz de la Sierra described to us a large fish that we identified as a cetacean; this animal was

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[1] The type of *Inia geoffrensis geoffrensis* was collected by Alexandre Rodriguez Ferreira in about 1790, and first deposited in the *Museu da Ajuda*. In 1810 the specimen was transferred to the *Muséum d'Histoire Naturelle*, Paris by E. Geoffroy St Hilaire.

supposed to be present in all rivers of Moxos territories, up to the river ports of Santa Cruz and Chiquitos; this relation appeared all the more strange to us as the rivers quoted were the first tributaries of the Rio Mamoré, that flows into the Amazon, at a distance of more than seven hundred leagues from the sea. We first saw these animals near the places inhabited by the Guarayos, hence we could easily be convinced that they were true cetaceans; we subsequently encountered them in all the rivers of Moxos Province; but all attempts we made to obtain some of them were fruitless since at no instance were the Indians of this country able to use a harpoon; and we had lost the hope of ever obtaining them when we were informed that the Brazilian soldiers of Principe de Beira Fort were accustomed to catch them to obtain oil for lighting. Although it was a long and perilous travel, we hesitated no longer to undertake it in order to collect this animal.

On our arrival in these wild regions, separated from civilised places by a huge distance, the captain of this *presidio* or galley gave, on our request, the necessary orders to prepare harpooning operations ... The fourth day we were informed that one of these cetaceans had just been harpooned, and indeed it was quickly brought to us still alive. It was placed on a large table, where it remained alive for five to six hours, which gave us time enough to study it; we immediately recognised its similarity of shape with the dolphins, but with fairly different features than those displayed by the entire order of piscivorous cetaceans, such as the presence of hairs on its snout, and teeth that nearly become molars posteriorly. We made drawings from life of this animal that was immediately described with great care.

When learning, on our arrival in France, that a dolphin from the Ganges was known, we thought to find in this animal similar characteristics as those of our species; but comparative observations revealed the huge difference that exists between them: this difference is so great that it can be considered as generic … All these characteristics, together with a poorly visible dorsal fin, incite us to propose the creation of a new genus … We assign to it the following characteristics [p.31–32: description of the genus *Inia* and the species *Inia Boliviensis*] …The specimen described was female, it was pregnant and its foetus was ready to be delivered; its vulva was much swollen, the mammary glands, which are lateral to the vulva, were full of milk that we expelled by pressing them. On a table where we had placed it, this female cetacean gave birth to a fully grown foetus the snout of which was also displaying hairs. The colours most characteristic for this species are the following: the upper part of the body is pale bluish, turning to pinkish underneath; the tail and arms are bluish, but these colours are quite variable; we observed some specimens that were reddish nearly all over, others entirely covered with a blackish colouration, and at last spotted or striped individuals. Those inhabiting large rivers generally display a paler colour; but those entering the numerous lakes connected to rivers during the rainy season, and that stay entrapped in these lakes during the dry season, become nearly black and lose this colour but a long time after returning to the rivers.

We found this species in all the rivers running in the huge plains of Moxos Province (Republic of Bolivia), and those that form the Rios Mamoré and Guaporé, which themselves constitute the Madeira River, one of the main arms of the Amazon; this cetacean is present up to the foot of the last mountains along the East side of the eastern Cordillera, more than seven hundred leagues from the sea; we are sure that it never goes to the ocean, and that it permanently remains in the rivers quoted above; it would actually be difficult for this slow swimming animal to proceed up the nineteen cascades of the Rio Madeira that are situated between 9° and 10° South. Brazilian traders who did several times the trip from Matogrosso to Para, assured us that these dolphins are present only above the level of the cascades, in the numerous rivers situated between 10° and 17° South, and between 64° and 70° West of Paris [meridian].

These dolphins are caught only by Brazilian people from the Beira Fort on Guaporé River … the peaceful inhabitants of Moxos Province just admire them and never try to catch them. According to Brazilian people, this dolphin never bears more than one calf at once, and truly has an extraordinary attachment for it; indeed, it often occurs that a female, reluctant to abandon her calf that has just been harpooned, follows the pirogues until she shares the same fate. Conversely, calves seem to have a great affection for their mothers and follow her for a long time; we have seen very large calves still accompanying their mothers.

When the cetaceans are not disturbed, they will come slowly and much more frequently than marine species to breathe at the water surface; but if they are scared by something, they double their swimming speed that is never as fast as that of marine dolphins. They are almost never seen isolated; most often, three or four individuals are gathered, and their groups are seldom larger. Their hearing seems to be much more developed than that of other dolphins; we have often seen them stopping at the noise of pirogue paddles, and approaching to blow several times as if to express some curiosity behaviour. They chase the numerous fishes that abundantly stock all the rivers, and from time to time they come to the surface to chew their prey, which is never done by marine species…

Brazilian people from Principe de Beira Fort call these dolphins *Bote*, and the Spanish *Bufeo*. The natives of the countries inhabited by this animal also have their own words for naming it in their languages: the Guarayos name it *Inia*, the Chapacuras *Sisi*, the Baure *Ihui*, the Jtonamas *Puchca*, the Cayuvava *Potohi*, the Jten *Sata*, the Pacaguaras *Cachoïcana*, the Movimas *Pathi*, the Canichacas *Nituya*, and lastly the Moxos *Aico*. These names are all very different, and are given to the same animal by small tribes all neighbouring each other, which may give some idea of the language diversity encountered in South America, especially in its warm parts.

Original text

En pénétrant dans l’intérieur du Haut-Pérou (ou Bolivia), les habitants de la ville de *Santa Cruz de la Sierra* nous parlèrent d’un grand poisson que, par leur description, nous reconnûmes comme un cétacé; cet animal habitoit soi-disant dans toutes les rivières de *Moxos*, et remontoit jusqu’aux ports de *Santa-Cruz* et de Chiquitos; cette relation nous parut d’autant plus étrange, que les rivières qu’on me citoit étoient les premiers affluents du rio Mamoré, qui va se jeter dans l’Amazone, c’est à dire à plus de sept cents lieues de la mer.

Nous vîmes les premiers de ces animaux près des lieux habités par les Guarayos, et dès lors il fut facile de nous convaincre que c’étoient de véritables cétacés; nous les rencontrâmes ensuite dans toutes les rivières de la province de Moxos; mais tous les moyens que nous employâmes pour les obtenir furent inutiles, les indiens de ce pays n’ayant jamais su se servir d’un harpon; et nous désespérions de parvenir à les posséder, lorsque nous apprîmes que les soldats brésiliens du fort du *Principe de Beira* en faisoient la pêche pour se procurer de l'huile nécessaire à leur éclairage. Quoique ce voyage fut périlleux et long, nous n'hésitâmes plus à l'entreprendre afin d'obtenir cet animal.

A notre arrivée dans ces contrées sauvages, séparées des lieux civilisés par un espace immense, le commandant de ce *presidio* ou galère, donna, sur notre prière, les ordres nécessaires pour faire harponner… le quatrième jour on vint nous prévenir qu'un de ces cétacés venoit d'être harponné, et en effet on ne tarda pas à nous l'apporter tout vivant.

Nous le fîmes placer sur une grande table, où il vécut pendant cinq à six heures, ce qui nous donna suffisamment de temps pour l'étudier; nous reconnûmes dès ce moment son analogie de forme avec les dauphins, mais avec des caractères bien différents de ceux de l'ordre entier des cétacés piscivores, tels par exemple que la présence de poils sur le museau, et des dents qui deviennent presque molaires postérieurement. Nous avons dessiné sur le vivant cet animal que nous avons immédiatement décrit avec beaucoup de soins.

Lorsque nous apprîmes à notre arrivée de France que l'on connaissoit un dauphin du Gange, nous pensions y retrouver des caractères analogues à ceux de notre espèce; mais des observations comparatives des deux espèces nous ont fait connoître l'énorme différence qui existe entre les deux: cette différence est telle qu'elle peut-être considérée comme générique…Tous ces caractères, réunis à une dorsale peu apparente, nous font proposer la formation d'un nouveau genre… Nous lui assignons les caractères suivants [p.31-32: description du genre *Inia* et de l'espèce *Inia Boliviensis*]. L'individu qui a servi de type à cette description était une femelle, elle était pleine et prête à mettre bas; sa vulve étoit fortement gonflée; les mamelles qui sont latérales à la vulve, étoient remplies de lait que nous fîmes sortir par la pression. Ce cétacé femelle accoucha sur une table où nous l'avions placé, et mit au monde un fœtus à terme, dont le museau étoit également muni de poils. Les couleurs les plus propres à cette espèce sont les suivantes: le dessus du corps est bleuâtre pâle, passant au rosé en dessous; la queue et les bras sont bleuâtres, mais ces teintes sont très variables; nous avons observé des individus presque entièrement rougeâtres, d'autres entièrement recouverts d'une teinte noirâtre, et enfin d'autres individus tachetés ou rayés. Ceux qui habitent les grandes rivières sont généralement d'une couleur plus pâle; mais ceux qui s'introduisent dans les nombreux lacs qui communiquent avec les rivières à la saison des pluies, et qui y restent retenus au temps des sécheresses, deviennent presque noirs, et ne perdent cette couleur que long-temps après être rentrés dans les fleuves.

Nous trouvâmes cette espèce dans toutes les rivières qui traversent les immenses plaines de la province de Moxos (république de Bolivia), et qui vont former les rios *Mamoré* et *Guaporé* qui constituent plus loin la rivière de Madeiras, un des premiers bras des Amazones; ce cétacé remonte jusqu'au pied des dernières montagnes du versant E. de la Cordillière orientale, à plus de sept cents lieues de distance de la mer; il nous paroit certain qu'il ne descend jamais jusqu'à l'Océan, et qu'il se tient constamment dans les rivières que nous venons de citer; d'ailleurs il seroit difficile à cet animal, qui nage peu rapidement, de pouvoir remonter les dix-neuf cascades du *rio Madeiras*, qui se trouvent entre les 9° et 10° de latitude sud. Des négociant brésiliens, qui ont fait plusieurs fois le voyage de *Matogrosso* au *Para*, nous ont assuré que ces dauphins habitent seulement au-dessus des cascades, c'est à dire dans les nombreuses rivières comprises entre les 10° et 17° de latitude sud, et entre les 64° et 70° de longitude ouest de Paris.

C'est seulement au fort de *Beira* sur la rivière du Guaporé, que les Brésiliens en font la pêche… les paisibles habitants de toute la province de Moxos, se contentent de les admirer, sans jamais chercher à les prendre. D'après la narration des Brésiliens, ce dauphin ne fait jamais plus d'un petit à la fois, pour lequel il paroît avoir un attachement vraiment extraordinaire; en effet, il arrive souvent qu'une femelle, pour ne pas abandonner son petit qu'on vient de harponner, suit les pirogues jusqu'à ce qu'enfin elle partage le même sort. De leur côté les jeunes dauphins paroissent avoir également beaucoup d'affection pour leur mère, qu'ils suivent pendant long-temps; nous en avons vu de très grands qui l'accompagnoient encore.

Lorsque rien n'inquiète les cétacés, ils viennent lentement et beaucoup plus fréquemment que les espèces marines, respirer à la surface de l'eau; mais si quelque chose les effraie, ils doublent la vitesse de leur marche qui n'est jamais aussi rapide que celle des dauphins marins. On ne les voit presque jamais isolés; le plus souvent trois ou quatre individus sont réunis, et il est rare que leur troupe soit plus nombreuse. Le sens de l'ouie paroit être bien plus prononcé que dans les autres dauphins; nous les avons vus souvent s'arrêter au bruit des pagaies des pirogues, et venir souffler à plusieurs reprises de manière à annoncer un certain mouvement de curiosité. Ils poursuivent les nombreux poissons qui abondent dans toutes les rivières, et ils viennent de temps en temps à la surface mâcher leur proie, ce que ne font jamais les espèces marines …

Les Brésiliens du fort du *Principe de Beira* nomment ces dauphins *Bote*, et les Espagnols *Bufeo*. Les nations indigènes des contrées qu'habite cet animal ont aussi leur nom propre pour le désigner dans leur langage: les Guarayos le nomment *Inia*, les Chapacuras *Sisi*, les Baures *Ihui*, les Jtonamas *Puchca*, les Cayuvava *Potohi*, les Jten *Sata*, les Pacaguaras *Cachoïcana*, les Movimas *Pathi*, les Canichanas *Nituya*, et enfin les Moxos *Aico*. Tous ces noms si disparates entre eux, donnés au même animal par de petites tribus voisines les unes des autres, peuvent donner une idée de la diversité des langages qu'on rencontre dans l'Amérique méridionale, et particulièrement dans les parties chaudes.

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Limitations of hypothesis-testing in defining management units for continuously distributed species

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ABSTRACT

Estimating the risk to wildlife populations resulting from human-induced mortality relies on adequately defining population structure. For marine populations, including cetaceans, identifying population boundaries is difficult because most species have large continuous distributions with no obvious barriers to dispersal. For many species, the extreme ends of the range differ in morphology, indicating that population structure exists. However, the lack of distributional hiatuses often makes this structure difficult to detect. A common method of defining structure in such situations is to use genetic differentiation as a proxy for limited movement between areas. Genetic analyses of population structure usually take the form of hypothesis testing, which requires the *a priori* definition of hypothesised units and testing for significant genetic differentiation between them. Simulations are used to examine the performance of hypothesis testing to correctly define population structure. Results show that hypothesis testing is likely to lead the researcher to define fewer management units than are necessary to adequately protect local populations from over-exploitation. The need for the development of new methods of defining management units and for rigorous performance testing of all methods applied in a management context is highlighted.

KEYWORDS: GENETICS; CONSERVATION; MANAGEMENT

INTRODUCTION

Many cetaceans are subject to human-induced mortality, either through direct commercial harvest, subsistence harvest by native communities, or incidental mortality due to entanglement in fishing gear. Regulation of human-induced mortality is usually accomplished through the definition of management units, also known as stocks. However, stock definition has proven notoriously difficult (Donovan, 1991), in large part because distributions are large for cetacean species and barriers to dispersal are not obvious. Nevertheless, successful management requires that human-induced mortality limits be based on units that reflect the actual spatial population structure of the species. To illustrate this problem, consider the management of harbour porpoise (*Phocoena phocoena*) within the state of California. Pollutant analyses (Calambokidis and Barlow, 1991) suggest there are two harbour porpoise populations off the California coast, between which dispersal is limited. Most of the human-induced mortality (due to entanglement in commercial fishing nets) is concentrated in the central California population, which is only about half the size ($n = 5{,}732$) of the northern population ($n = 11{,}066$) (Forney, 1999). Were these two populations managed as a single unit, the number of animals that could be killed would be calculated based on their combined abundance of 16,798. However, since most of those animals would be taken out of the smaller central California population, that population would quickly become depleted and face possible extirpation if dispersal from the northern population is not sufficient to compensate for the excess mortality. To some degree, errors in stock definition can be compensated for by making precautionary adjustments to the data rather than using 'best estimates' (Taylor *et al.*, 2000b). Such precautionary measures are incorporated into the management scheme used to manage harbour porpoises off California. However, even precautionary management schemes are unlikely to succeed in the face of a 200% overestimate of the abundance of the impacted population, as would occur if the northern and central California populations of harbour porpoises were managed as a single unit.

Over the past decade, genetic studies have become a valuable tool in defining units of conservation. The most common method of investigating population structure is to calculate some measure of genetic differentiation between two hypothesised populations and then test to see if the observed differentiation is statistically significant. Many researchers have pointed out several problems with this approach, calling into question its utility in applied studies (e.g. Bossart and Pashley Powell, 1998; Johnson, 1999; Paetkau, 1999; Taylor and Dizon, 1999; Anderson *et al.*, 2000). Nonetheless, hypothesis-testing remains the most common method of using genetic data to investigate population structure. Consequently, it is important to quantify the frequency and magnitude of errors that are likely when hypothesis-testing is used to define management stocks. It is hoped that this quantification will help scientists to better interpret the results of hypothesis tests of population structure and will enable decision makers to better understand the magnitude of bias likely present in such analyses. This paper outlines two of the major difficulties with using hypothesis tests to determine the population structure of marine species. A simulation approach is then used to estimate the probability of defining fewer stocks than there are populations in an area when using a common hypothesis testing method, Analysis of Molecular Variance or AMOVA (Excoffier *et al.*, 1992).

Hypothesis tests of population structure

Defining hypothesised units

Hypothesis tests of population structure require the researcher to construct an *a priori* hypothesis regarding the number and location of population boundaries. If rates of gene flow between populations are low enough to allow the development of a strong phylogeographic signal (i.e. samples from the same geographic area clustering together on a genetic tree), researchers can use gene trees to guide

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boundary placement (e.g. Brown Gladden *et al.*, 1997). However, even demographically trivial levels of gene flow will prevent such a phylogeographic signal from developing (Taylor, 1997; Bérubé *et al.*, 1998). For instance, a minimum spanning network for the harbour porpoise discussed above shows no apparent geographical clustering of samples despite the fact that gene flow between the northern and southern populations is low enough to require separate management of the two populations (Chivers *et al.*, 2002).

In most published studies of population structure, the authors give no justification for the hypothesised units chosen, nor do they specify whether or not alternative hypothesised structures were examined. Thus, a rigorous analysis of the frequency of different strategies for stratifying data is not possible. Nevertheless, based on both examination of the literature and conversations with researchers regarding their methods of defining hypothesised units, it is possible to discern three commonly employed approaches in genetic studies. First, data are often divided on the basis of political boundaries (Graves *et al.*, 1992; Moritz *et al.*, 1997). Second, samples are divided so as to ensure equal sample size among all units. Typically these units are rather large because researchers realise that increasing the number of samples per unit will increase statistical power and therefore make it more likely that they will obtain statistically significant results. A final, and perhaps most common, method of defining hypothesised units is to simply place hypothesised boundaries in areas where there are gaps in the distribution of samples. Since sampling is often difficult, few investigations of population structure have a deliberate sampling design; rather, samples are gathered opportunistically, with the highest sampling effort concentrated in easily accessible areas. This method of dividing samples into units can be particularly misleading when researchers only publish a map of the distribution of samples (which may be patchy and discontinuous) and no map or description of the actual distribution of the species (which may be continuous).

Statistical power of hypothesis tests

The usefulness of hypothesis tests in defining management units is limited by their reliance on finding statistically significant genetic differentiation. The ability to detect genetic differentiation is often hampered by low statistical power, which is the probability of rejecting the null hypothesis of panmixia when it really is false. Statistical power depends in part on the effect size (F_{st}), which in tests of population structure is given by Wright's (1932) formula (modified for mitochondrial DNA [Takahata and Palumbi, 1985] and finite number of populations [Latter, 1973]).

$$F_{st} = \frac{1}{2NdT + 1}$$

where:

N = the effective number of females in the population;
d = the annual dispersal rate; and
T = generation time.

Therefore, statistical power is inversely related to both the abundance of populations and the rate of dispersal between them. Many marine populations, especially those of commercial value, have large abundances, resulting in small effect sizes and limited power to distinguish them through a hypothesis test. In addition, when defining management units we may want to be able to distinguish between populations with dispersal rates as high as a few tenths of a percent per year. While such movement rates are low enough to have relatively little impact on the demographics of a population, they are high enough to prevent much genetic differentiation from developing, again resulting in low statistical power.

The problem of low statistical power has long been recognised and some authors argue that hypothesis-testing approaches in general are not appropriate for applied studies (Johnson, 1999; Anderson *et al.*, 2000). One of the major difficulties in using hypothesis tests to elucidate population structure is the interpretation of non-significant results. While most researchers are well aware that failure to reject the null hypothesis does not mean that the null hypothesis is true, many continue to make the mistake of interpreting a non-significant result from a hypothesis test of population structure as evidence that the region in question ‘lacks’ structure and should therefore be managed as a single unit. Even when they are correctly interpreted, non-significant results leave the researcher attempting to define management units in an awkward position. Defining units in the face of non-significant results will appear arbitrary, but failing to define management units will result in the entire region being managed as a single unit and is likely to result in under-protection.

METHODS

To emulate the problem of defining management units for marine mammals, a simulation model was used to generate data for which the actual population structure is known. The study focuses on a stepping-stone model where the level of genetic differentiation is controlled by the dispersal rate between adjacent populations. This stepping-stone model results in isolation-by-distance, one of the most common forms of spatial structure in natural populations and should adequately represent the population structure of most coastal marine mammals. Many pelagic species, particularly large, migratory whales, may exhibit more complicated forms of population structure. Thus, estimates of the performance of hypothesis testing may be conservative since population structure may be even more difficult to detect for species with these more complicated structures.

The model used here was developed by Taylor *et al.* (2000a) and is available from the authors upon request. The evolution of mitochondrial haplotypes was tracked in five populations arranged in a linear stepping-stone. The choice to simulate mitochondrial sequence data was made because it is commonly used in studies of population structure and is particularly useful in identifying demographically independent units (Moritz, 1994; Avise, 1995; 2000). However, as discussed below, the results of this analysis should generalise to the use of nuclear markers, such as microsatellites. The populations were allowed to evolve for 200,000 years and the complete haplotype profile (the sequence of each haplotype and its frequency in all five populations) was recorded from the simulation every 500 years for the last 50,000 years, resulting in 100 haplotype profiles for each combination of effective population size (N_e) and dispersal rate (d).

Annual dispersal rates ranging from 0.002 to 0.01 were examined, along with effective population sizes of $N_e = 100$, $N_e = 300$ and $N_e = 1{,}000$ effective adult females. Annual rates of dispersal were focused on rather than the more familiar per-generation gene flow ($N_e m$) because dispersal rate is the critical parameter in determining whether two populations can be safely managed as a single unit. Taylor (1997) showed for marine mammals that if two populations are managed together but only one is being harvested (as in the case of the harbour porpoise discussed above), dispersal rates in excess of 1 to 3% per year are probably necessary if the harvested population is to escape extirpation. The generation time for the model was four years, so the per generation dispersal rate was four times the annual dispersal rate. Most cases examined for this paper involved dispersal rates greater than one disperser per generation, but were still sufficiently low that if the management objective is to conserve the species' range then the populations should be managed separately. Thus, we chose a difficult test representative of the performance expected when using hypothesis testing to define management units.

For each haplotype profile, 18 samples were chosen at random from each of the five populations, for a total of 90 samples. This represents a typical sample size for studies of population structure. In order to examine the sensitivity of the results to sample size, some of the analyses were repeated with 36 samples from each population, for a total of 180. The samples were divided into two, three or five equally sized units. These represented three different hypothesised structures that a researcher could use when investigating population structure. In one of the structures (five units), the hypothesised boundaries corresponded to actual population boundaries, while in the other two structures (two or three units), the hypothesised boundaries cut through the middle of actual populations. The average pair wise genetic differentiation between adjacent units was calculated for the three hypothesised structures using the statistic Φ_{st}, the analogue of Wright's F_{st} used in Analysis of Molecular Variance (AMOVA; Excoffier *et al.*, 1992). A permutation test (500 permutations) was used to assign a *p*-value to each measure of differentiation and the results used to determine how many management units should be defined. To mimic the decision process researchers are likely to use in defining management units, the greatest number of units for which all adjacent units were significantly differentiated at the 0.05 level were defined. If none of the three hypothesised structures yielded significant results, the entire region was designated a single unit. We feel that this process roughly approximates the approach that most researchers take to the definition of management units for species with cryptic structure. For each trial, the number of units that would be defined under this criterion was determined. This procedure was repeated five times for each of the 100 haplotype profiles for a given combination of dispersal rate and effective population size. The proportion of the 500 trials that resulted in the correct definition of five units was then determined.

In addition to determining the probability of defining the correct number of management units, three other quantities derived from the statistical analyses were also recorded: average *p*-value between adjacent units; average differentiation (Φ_{st}) between adjacent units; and average statistical power to detect differentiation assuming $\alpha = 0.05$. These averages were taken across all 500 trials and across all pair-wise comparisons between adjacent units. For instance, when the samples were divided into five units, there were four pair-wise comparisons between adjacent units. Power was calculated for each of these four comparisons, and the resulting estimates were averaged to obtain an estimate of the average statistical power when the samples were divided into five units. Since the estimates of average *p*-value, average Φ_{st} and power were based on 500 different samples taken from 100 different points in time, they take into account both sampling error and temporal variation in the degree of genetic differentiation (Whitlock, 1992; Taylor *et al.*, 2000a).

RESULTS

The probability that a hypothesis test will result in the definition of the correct number of units for a species with cryptic population structure is quite low (Table 1). For all parameter combinations examined, the correct definition of five units was the least likely outcome (Fig. 1a). When $N_e = 300$ and $d = 0.002$, the lowest dispersal rate examined, power to detect differentiation between a pair of adjacent units was 0.54 when the samples were divided correctly into five units (Fig. 2a). However, in order to define five units, all four pair-wise comparisons had to be statistically significant, which only occurred with a probability of 0.06 (Table 1). As dispersal rate increased, the probability of defining either five or three units declined, while the probability of defining a single unit increased, resulting in a decrease in the average number of units defined (Fig. 1). Results were similar for effective population sizes of 100 and 1,000 (Table 1). Increasing the sample size improved performance, as expected. However, even for the larger sample size examined, the correct definition of five units was the least likely outcome for all but the lowest dispersal rate (Fig. 1b).

Table 1

Probability of correctly defining five management units as a function of the effective abundances (N_e) of the model populations, the annual rate of dispersal between them (*d*) and the sample size (*n*).

Annual dispersal rate (*d*)	N_e				
	100	300		1,000	
	$n = 18$	$n = 18$	$n = 36$	$n = 18$	$n = 36$
0.002	0.27	0.06	0.31	0	0.022
0.004	0.12	0.02	0.066	0	0
0.006	0.07	0.004	0.042	0	0
0.008	0.03	0	0.006	0	0.002
0.01	0.02	0	0	0	0

Statistical power, average *p*-value and average differentiation were also correlated with the number of units into which the samples were divided. The average degree of genetic differentiation between adjacent units, as measured by Φ_{st} (Fig. 3) and power to detect that differentiation (Fig. 2a) were highest when the samples were divided into just two units rather than being correctly divided into five units. Both Φ_{st} and power declined with increasing dispersal, as expected. The average *p*-value showed the opposite pattern: average *p*-value increased with increasing dispersal rate and was consistently lowest when samples were divided into only two hypothetical populations (Fig. 2b).

The relationships between hypothesised structure and genetic differentiation, power and average *p*-value were consistent across all three effective population sizes examined. Both power and the degree of genetic differentiation were highest, and average *p*-values were lowest, when effective population size was low, as expected.

DISCUSSION

Hypothesis testing is likely to result in the definition of fewer management units than there are distinct populations within a region. Only three of the 25 parameter combinations

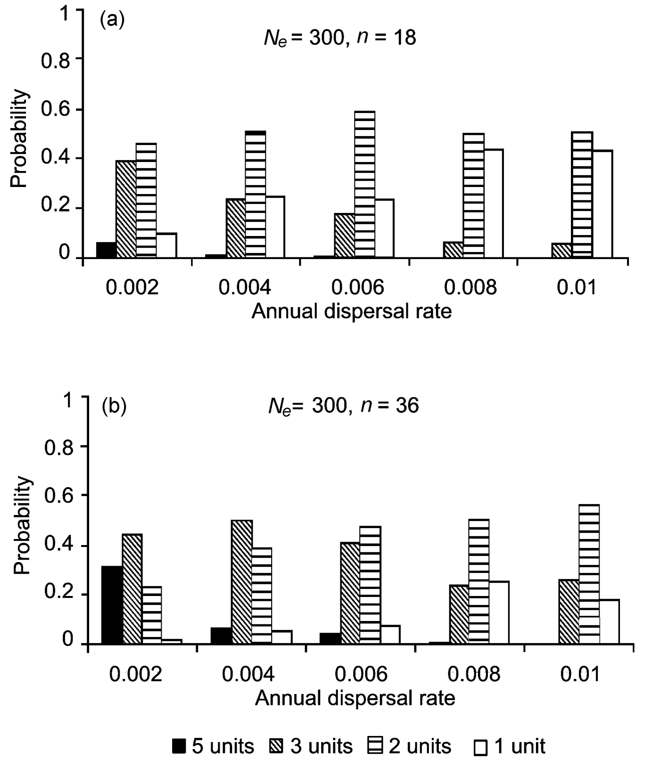

Fig. 1. Probability of defining one, two, three or five units as a function of dispersal rate. The number of units defined was determined by choosing the finest division of the samples that still resulted in significant differentiation between all pairs of adjacent units. Results are for populations with 300 effective adult females with (a) 18 and (b) 36 samples drawn from each population. Results were similar for other effective population sizes (not shown).

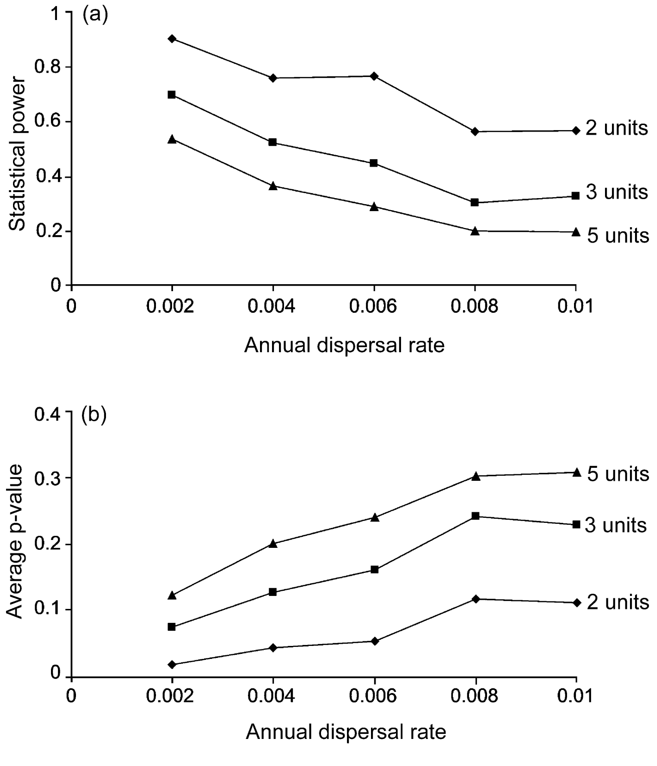

Fig. 2. (a) Power to detect differentiation between adjacent units; and (b) average p-value between adjacent units as a function of dispersal rate between adjacent populations when samples are broken into two (◆), three (■) or five (▲) units. Eighteen samples were drawn from each of five model populations arranged in a stepping-stone manner, each with an effective population size of 300 effective adult females.

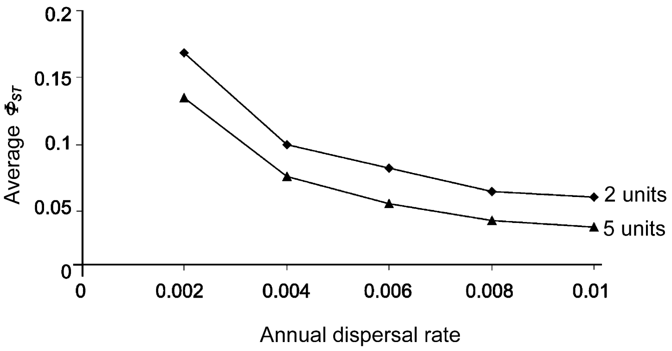

Fig. 3. Average degree of genetic differentiation, as measured by Φ_{st}, observed between units as a function of the dispersal rate between adjacent populations. The model populations had effective abundances of 300 effective adult females. Eighteen samples were drawn from each population and were broken into two (◆) or five (▲) units.

examined resulted in greater than a 10% probability of correctly defining five units (Table 1). Furthermore, the errors made when using hypothesis testing were large, in that for most parameter combinations the researcher would define only one or two units in a region that should be divided into five (Fig. 1). Consequently, hypothesis testing alone is unlikely to result in the definition of management units that adequately protect marine species with cryptic population structure.

The decision criterion used here in deciding how many units to define is probably more conservative than those used by most researchers, in that all four pair-wise comparisons of adjacent units were required to be significant before five units were defined. In reality, many researchers might choose to combine adjacent putative populations that did not show significant differentiation. This approach would not lead to the definition of five units any more often than predicted here, but it would be more likely to lead to the definition of three or four units, reducing the magnitude of the under-protection errors. Nonetheless, based on the results it is hard to imagine any decision criterion that would result in a high probability of defining the correct number of units.

There are two explanations for the inverse relationship between the number of units defined and statistical power. The first, and most obvious, is that by dividing a constant number of samples into more units, you reduce the number of samples per unit. This reduction in sample size reduces the power of the pair-wise comparisons between units (Fig. 2a). However, even when sample sizes are equalised, power is still highest when a region is divided exactly in half, though the disparity is less. Thus, the second explanation is that when a region is divided into only two units, samples from the two extremes of the range are placed in adjacent units. For instance, when the five populations from the computer simulation are divided exactly in half, a comparison is made between a unit containing individuals from population 1 to a unit containing individuals from population 5. Populations 1 and 5 are at opposite ends of the range in question, and thus are maximally differentiated. Comparing units containing these two distant populations inflates the overall degree of genetic differentiation (Fig. 3), resulting in higher power when samples are divided into only two units.

Any series of populations characterised by isolation-by-distance will show this property of increased effect size with decreased number of units. Thus, the results generalise to any model that captures isolation-by-distance, including diffusion models. Indeed, theoretical studies have shown that stepping-stone and diffusion models produce remarkably similar results (reviewed in Felsenstein, 1976). Similarly, although statistical power was estimated using Φ_{st}, the basic findings that changes in both effect size and per-unit sample size will result in higher power and lower *p*-values when the researcher defines fewer units are robust to the statistic used to measure genetic differentiation.

In species that do not exhibit isolation-by-distance, the inverse relationship observed between the number of units defined and statistical power might not be as strong, because dividing samples coarsely would not necessarily place samples from very distant populations in adjacent units. However, dividing samples coarsely would still increase the number of samples per unit, resulting in increased power. Furthermore, the estimates of statistical power when the samples are divided correctly into five putative populations depend only on the effective abundance of the populations and the rate of dispersal between them, not on the assumption of isolation-by-distance. Consequently, there is no reason to expect better performance when population structure is more complicated than isolation-by-distance. Indeed, the probability of correctly describing population structure through hypothesis testing would probably be even lower than has been estimated here for populations with more complex structure due to the problems associated with correctly stratifying samples *a priori*.

The hypothetical populations simulated for these analyses were all of equal abundance. The problems associated with using hypothesis testing to describe population structure would likely be exacerbated if neighbouring populations differed substantially in size. The populations that need the greatest attention in a management context are those with smaller abundances, since they are the most vulnerable to over-exploitation. While small populations diverge more quickly due to genetic drift, if they are situated next to populations that are substantially larger then the effects of drift can easily be swamped by gene flow from the neighbouring populations, leaving the small, vulnerable populations extremely difficult to detect genetically.

These analyses examined the ability of hypothesis tests to detect differentiation between populations that were in mutation/migration/drift equilibrium. In reality, most natural populations are not in such equilibrium. Rather, populations change through time in concert with their ever-changing environment, resulting in fluctuations in population size, changes in distribution and changes in the rates of exchange with other populations. The impact of non-equilibrium dynamics on our ability to distinguish populations through hypothesis-testing will vary widely. For example, if the abundance of a population has fluctuated through time, the genetic makeup of that population will be much more heavily influenced by its lowest than its highest historic abundance, with the result that it will be much more differentiated from neighbouring populations, and therefore easier to detect using hypothesis-testing, than our analysis would predict. On the other hand, two populations that experience very little gene flow currently but diverged from an ancestral population in the recent evolutionary past will be far less differentiated and far more difficult to distinguish via hypothesis-testing than our results indicate.

While this analysis focused on the use of mitochondrial DNA (mtDNA) data, the conclusions also generalise to the use of microsatellite loci, which are becoming increasingly popular in studies of population structure. Because of higher mutation rates at microsatellite loci and because they are not limited to the use of a single locus, investigations that utilise microsatellite data sometimes have higher statistical power for detecting differentiation than those using mtDNA data. However, in species where dispersal is primarily male-mediated, as is the case for many mammals (Greenwood, 1980), power to detect differentiation will actually be higher for mtDNA due to its strictly maternal inheritance. The effective population size for mtDNA is also four-fold smaller than for nuclear loci, resulting in a larger effect size and higher power to detect differentiation using mtDNA (Avise, 1995). Consequently, in many cases hypothesis testing will be even more likely to result in the definition of too few units when the analysis is based on microsatellite loci rather than mtDNA. Furthermore, the patterns discussed above regarding the number of samples per unit and the average degree of differentiation as a function of the number of units will also apply to microsatellite data. Thus, even when the use of microsatellites does result in an overall increase in statistical power, power and the average degree of differentiation will still be highest when the samples are divided coarsely, into only two units.

Many authors interpret a significant result from a hypothesis test as evidence that the hypothesised structure accurately reflects the underlying spatial structure. The results in this paper show that such an interpretation is not justified. This study has shown that statistical power is highest when a region is divided coarsely, into only two units, even when the boundary defining those units goes through the middle of an actual population. Thus, a finding of significant differentiation across a particular hypothesised boundary does not mean that the hypothesised boundary corresponds to an actual restriction in dispersal. Rather, such a result only indicates that genetic structure is present without lending support for any particular boundary location.

The results of this study highlight two critical needs: the need to both develop better methods to investigate population structure and to subject all methods used in management applications to rigorous performance testing similar to that done here. New methods should move away from the traditional hypothesis-testing paradigm and approach the problem of defining management units from the point of view of parameter estimation and model selection. Given that dispersal rate is the parameter of interest in defining management units, a parameter estimation approach aimed at estimating dispersal rates is likely to be the most fruitful method of defining management units. Critics of hypothesis testing have advocated parameter estimation as a more informative alternative in other applied settings (Johnson, 1999; Anderson *et al.*, 2000). Though it would still require an *a priori* definition of units, such an approach would avoid many of the problems associated with a lack of statistical power that are inherent in hypothesis testing. Pursuing analyses within a parameter estimation framework would provide greater flexibility to managers by allowing them to evaluate the resulting estimates in light of their specific management objectives rather than simply giving them a yes-or-no answer as to whether or not a region is genetically structured, as is the case with hypothesis testing. An estimate of dispersal rate with some measure of uncertainty could also be incorporated quite easily into a formal decision analysis framework. Though analytical approaches are unlikely to result in reliable estimates of dispersal rate (Whitlock and McCauley, 1999), simulation techniques that are free from many of the unrealistic assumptions inherent in analytical methods, such as those of Beerli and Felsenstein (1999; 2001), are likely to be very useful.

Traditional hypothesis-testing approaches to investigating population structure, such as AMOVA, only allow each population structure model to be compared to the null model of panmixia. A model selection approach to defining management units would have the advantage of allowing for direct comparisons between competing models. Some progress has been made in this area. Several new Bayesian and likelihood-based approaches have been published in recent years (Pritchard *et al.*, 2000; Dawson and Belhkir, 2001; Cui *et al.*, 2002). However, these methods have undergone little or no performance testing and none have been tested in a context relevant to management. The results from this study emphasise the need for caution in applying any of these techniques until such performance tests have been completed and have shown that these techniques have a high probability of resulting in the definition of management units that will adequately protect exploited populations. An international programme to develop such a testing framework has recently begun (IWC, 2004).

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Current knowledge of the cetacean fauna of the Greek Seas

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ABSTRACT

From 1991-2002 data on the presence and distribution of cetaceans in the Greek Seas have been systematically collated in a database (821 sightings and 715 strandings). Data originated from dedicated surveys, stranding reports, opportunistic sightings and published or unpublished photographic and video documents. Twelve cetacean species have been recorded. Seven of them are permanently present and commonly observed in one or more of the Greek Seas: striped dolphin, common bottlenose dolphin, short-beaked common dolphin, Cuvier's beaked whale, sperm whale, Risso's dolphin and fin whale. In addition, the harbour porpoise is present locally in the Thracian and northern Aegean Seas. The humpback whale, false killer whale and common minke whale are occasional Mediterranean species that were sighted or stranded infrequently; the Sowerby's beaked whale is an accidental species that was found floating dead only once. Five other species (white whale, Blainville's beaked whale, long-finned pilot whale, killer whale, blue whale) have been erroneously included in the Greek cetacean fauna in the past due to wrong assumptions, false identifications or lack of supporting evidence. The occasional occurrence of pilot and killer whales in the Greek Seas should still be regarded as unconfirmed. The distributional range, stranding numbers and sighting frequencies of sperm whales, Cuvier's beaked whales and short-beaked common dolphins in the Greek Seas indicate that their local 'sub-populations' are among the most important in the entire Mediterranean Sea. Harbour porpoises in the Thracian and northern Aegean Seas are important from a conservation perspective since this species does not inhabit any other part of the Mediterranean Sea.

KEYWORDS: MEDITERRANEAN; EUROPE; DISTRIBUTION; SURVEY-COMBINED; INCIDENTAL SIGHTINGS; STRIPED DOLPHIN; COMMON BOTTLENOSE DOLPHIN; SHORT-BEAKED COMMON DOLPHIN; CUVIER'S BEAKED WHALE; SPERM WHALE; RISSO'S DOLPHIN; FIN WHALE; HARBOUR PORPOISE; FALSE KILLER WHALE; HUMPBACK WHALE; COMMON MINKE WHALE; SOWERBY'S BEAKED WHALE

INTRODUCTION

The Greek Seas include the eastern Ionian, Aegean, Cretan and northwest Levantine Seas as well as the northern Cretan Passage between Crete Island and North Africa (Fig. 1). These seas occupy the northern part of the eastern Mediterranean (roughly between 35°-41°N and 19°-30°E) and are characterised by: (1) pronounced oligotrophy in most of their range; (2) highly irregular and very long coastlines (>15,000km) that account for one third of the total Mediterranean coastline; (3) almost 10,000 islands and islets; (4) some extended plateaux; and (5) steep underwater relief of depressions and trenches reaching a maximum depth of 5,121m (Stergiou *et al.*, 1997). This rich geomorphology creates a variety of marine ecosystems and potential habitats for various cetacean species. Nevertheless, until recently the Greek Seas have been seen only as part of the oligotrophic eastern Mediterranean basin − considered poor in terms of its cetacean fauna (Marchessaux, 1980; Viale *et al.*, 1988; Notarbartolo di Sciara and Demma, 1997). This general view was not based on data, since no dedicated surveys were made in this part of the Mediterranean (Notarbartolo di Sciara and Gordon, 1997) before those described in this study.

Although Aristotle (345 BC [1994a; b]) was the first to study and classify cetaceans (he did so in the Aegean Sea), little further interest in his research was expressed until the early 1980s. Due to the absence of any commercial exploitation and the lack of significant scientific interest from naturalists, extremely few skeletal materials exist in museum collections and no records of origin are available in most cases. The first 'modern' studies with references to cetaceans of the Greek Seas were based on the few historical or anecdotal stranding records, the rare museum material and a few opportunistic sightings that were often second hand and difficult to confirm (Marchessaux, 1980; Pilleri and Pilleri, 1982; 1987; Kinzelbach, 1985; 1986a; b; 1991). Occasional efforts to record cetacean strandings along the Greek coasts started in the late 1980s, however, the establishment of a national stranding network did not occur until the end of 1991 (Frantzis, 1997). The first systematic efforts to explore the cetacean fauna of the Greek Seas *in situ* started in 1991 and 1993, by two independent teams that surveyed parts of the Ionian (Politi *et al.*, 1994) and Aegean Seas (Carpentieri *et al.*, 1999). Some additional studies were stimulated by the die-off that affected Mediterranean striped dolphins when the epizootic reached the Greek Seas in summer 1991 (Aguilar and Raga, 1993; Cebrian, 1995). Although those studies gave a useful first picture of cetacean presence in the Greek Seas (Cebrian and Papaconstantinou, 1992; Androukaki and Tounta, 1994), they were mostly based on reports made by unskilled observers and have since been shown to contain erroneous species identifications (Frantzis, 1997).

There are several references to cetacean presence and distribution in the western and central parts of the Mediterranean Sea, however, the literature covering the eastern basin is scarce (Notarbartolo di Sciara and Gordon, 1997). Recent studies have shown that important population units of cetacean species that are the subject of conservation priorities for the entire Mediterranean Sea (ACCOBAMS, 2002) are found within the Greek Seas (Politi *et al.*, 1999; Frantzis *et al.*, 1999; 2001). The Agreement on the Conservation of the Cetaceans of the Black Sea,

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Mediterranean Sea and contiguous Atlantic Area (ACCOBAMS) recommended that urgent measures are undertaken to address the status of those species and identify key areas containing critical habitats for them (ACCOBAMS, 2002). The aim of this paper is therefore to review current knowledge of the presence and distribution of cetacean species in the Greek Seas, and discuss preliminary information regarding their status and relative abundance.

DATA AND METHODS

Data collection

Over the last decade, all available data concerning the cetaceans of the Greek Seas have been systematically collated in a database. The sources for these data included dedicated surveys conducted by the authors, opportunistic sightings, stranding reports from stranding networks, occasional stranding records previously published in the scientific literature, a few samples of skeletal material and published or unpublished photographic and video documents. Sightings from a previously published work on the cetaceans of the Aegean Sea (Carpentieri *et al.*, 1999) and all confirmed, first hand sightings found in the literature have also been included in the database, which totalled 1,536 records.

Surveys and sighting data

Eighteen dedicated surveys were organised during the summer and autumn months between 1991 and 2002. Survey length ranged from ten days up to three months and covered the eastern Ionian Sea, the sea area off southwest Crete, the Gulf of Corinth and to a lesser degree the Myrtoon Sea and the sea area between the Northern Sporades Islands and the Chalkidiki Peninsula (Figs 1, 2a). Ferries with standard routes were used as platforms of opportunity by Carpentieri *et al.* (1999) for their surveys in the Aegean and Cretan Seas. Conventional visual methods for detecting cetaceans were used in most survey areas. At least one experienced observer continuously scanned the sea surface, 180° in front of the vessel. Observers used binoculars intermittently and observations were interrupted when sea surface conditions reached sea state 3 (appearance of the first white caps). Sightings made at sea state ≥3 (when it is known that sighting efficiency for at least smaller cetaceans is poor) were not taken into consideration in the sighting frequencies calculated in this study. Geographic coordinates of the sightings were recorded with the aid of a Global Positioning System (GPS). Only the initial position of each sighting was considered, disregarding sighting duration or group-size changes, resulting in plots of one spot per sighting. Minimum distances from the closest coast and approximate bottom depths for all sightings were calculated *a posteriori*

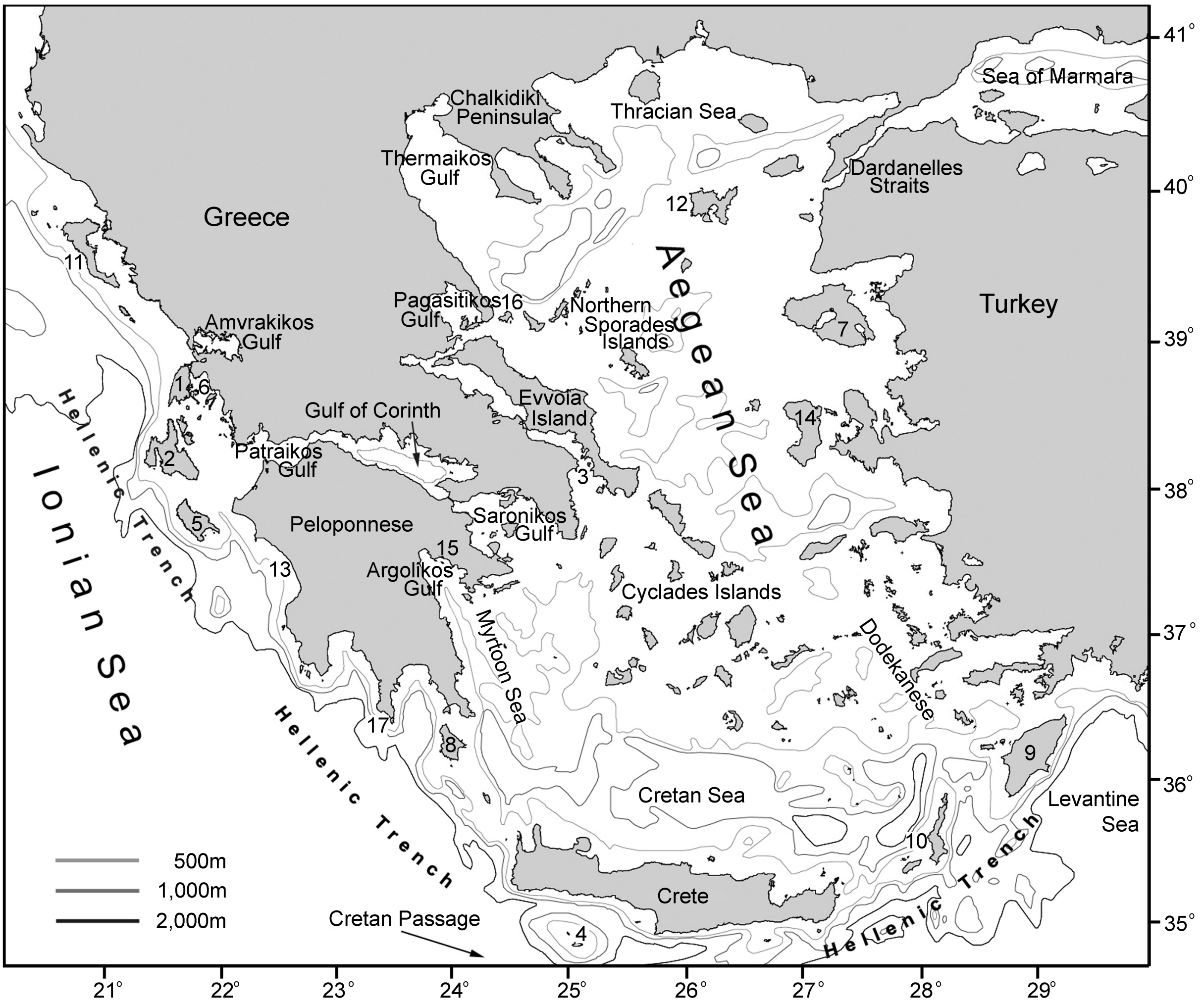

Fig. 1. Map of the Greek Seas showing their bathymetry and the locations cited in the text: (1) Lefkada Island; (2) Kefallonia Island; (3) South Evvoikos Gulf; (4) Gavdos Island; (5) Zakynthos Island; (6) Kalamos Island; (7) Mytilini Island; (8) Kythira Island; (9) Rodos Island; (10) Karpathos Island; (11) Corfu Island; (12) Limnos Island; (13) Kyparissiakos Gulf; (14) Chios Island; (15) Bay of Tolo; (16) Skiathos Island; (17) Gerolimenas.

by plotting the geographical coordinates of the sightings on bathymetric maps from the Hellenic Hydrographic Service. In surveys off southwest Crete, in the southeast Ionian Sea, in the northern Sporades-Chalkidiki area and Myrtoon Sea, joint acoustic and visual methods were used. A stereo towed hydrophone array was used to allow passive acoustic localisation of sperm whales. Opportunistic sightings recorded up to the end of 2002 in the Greek Seas have also been included in the database, when supported by photos or videos. Sightings from the core research area of a long-term study on short-beaked common dolphins and common bottlenose dolphins in the inner east Ionian Sea (Politi, 1998; Politi *et al.*, 1999) were not used, since the high numbers would have created a very significant geographical unbalance in the dataset.

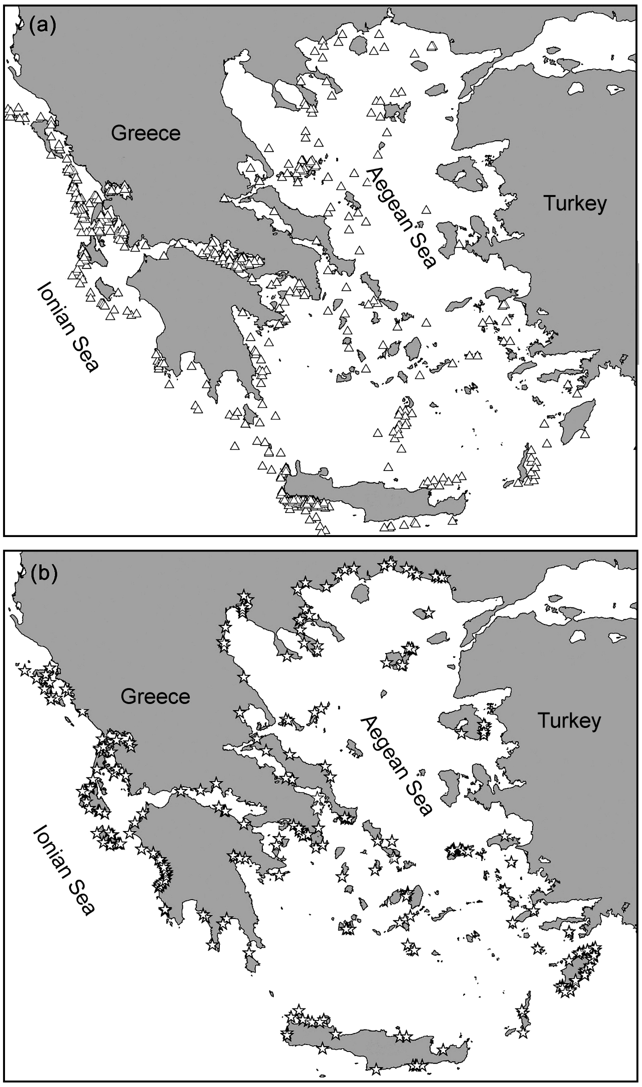

Fig. 2. Distribution of all identified cetacean sightings (a) and strandings (b) recorded in the Greek Seas. The higher density of sightings in some areas (a) is due to the larger effort during short or long-term dedicated surveys or while using ferries as platforms of opportunity.

Caution is due in the interpretation of the number of sightings recorded per species (Table 1) since data include both opportunistic sightings and results of dedicated surveys which used different methods (e.g. visual versus joint visual-acoustic surveys). In addition, some areas have been surveyed more intensively than others (Fig. 2a) for the known or expected, frequent presence of the targeted study species. As a result the number of sightings recorded per species is not directly indicative of the relative sighting frequencies per species in this study.

Strandings data

Strandings data (including floating carcasses and incidentally caught animals) were obtained mainly through a national network organised and coordinated by the National Centre for Marine Research and the Pelagos Cetacean Research Institute. The network's data cover the period September 1991-December 2001, and were derived from standardised forms completed by local port-police authorities. This network cannot be considered complete since the number of unreported strandings (from sources other than the network) is not negligible; this was particularly true during the first years of its existence. Therefore, stranding numbers have to be interpreted with some caution, since they may be biased in favour of the larger whales (mainly fin, sperm and to a lesser degree Cuvier's beaked whales), which are conspicuous and constitute 'exceptional' events of high interest when they strand. In addition, port-police and local veterinarians did not have the required knowledge to identify cetaceans to species as witnessed by the conflicts between the recorded species and the associated photos. The use of such erroneous data resulted in inaccurate results in older studies, therefore, all information coming from the network was initially considered with caution, except for the fact that a stranding did occur. After meticulous checking, stranding reports were classified as 'unidentified' if no visual documents (photos or videos) allowed reliable species identification – this applied to 63.3% of the total stranding network records. Unidentified animals were not homogeneously distributed among all species, and appeared to be exclusively the smaller delphinids (bottlenose dolphins, striped dolphins and short-beaked common dolphins). This is problematic given that they were actually the most abundant among strandings (Table 1).

In order to overcome this problem and reach a better approximation of the true situation, the category of unidentified small delphinids was split into common bottlenose dolphins, striped dolphins and short-beaked common dolphins according to the ratio 59:37:16 found among 112 identified stranded dolphins from 1996 to 2001 (Table 1). This seven-year period was selected for two reasons: (1) before 1996 and depending on the year, either the bottlenose dolphins or the short-beaked common dolphins or both species were not among identified strandings; and (2) the ratio among these species' strandings stabilised only after 1995. Previously it had been strongly altered in favour of striped dolphins due to the Mediterranean morbillivirus epizootic, which peaked in 1992 in Greece (Aguilar and Raga, 1993; Cebrian, 1995; Aguilar, 2000). Except for calculating new percentages for the occurrence of the small delphinid species among strandings from 1996 to 2001 (Table 1), the results of the above extrapolation were not used for any other analysis of strandings data (i.e. seasonal presence, monthly average, mass strandings and distribution maps). A total of 34 records from the period 1840 –August 1991 were also included in the database since they were accompanied by photos or were cited in credible scientific literature. The sex of stranded animals was determined only after examination *in situ* or when good photos of the genital area were available. Data on total lengths were retained only if taken by specialists *in situ*, or by local authorities guided by our instructions. Strandings data refer to number of animals stranded and not to stranding

Table 1

Number of sightings and stranded animals per cetacean species. The 428 unidentified strandings concern the small delphinids: bottlenose dolphin, striped dolphin and short-beaked common dolphin (the latter to a lesser degree). The three unidentified cetaceans were probably Risso's dolphins according to the reports, but no photos were provided. Results marked with an asterisk have been extrapolated according to methods described in the text.

				Stranded animals					
	Species	Sightings	Total stranded animals	1840- Aug. 1991	Sept. 1991-2001		1996-2001	Extrapolated 1996-2001	
1	Striped dolphin	258	63	1	62	9.1%	37	115*	27.4%*
2	Bottlenose dolphin	224	65	1	64	9.4%	59	183*	43.6%*
3	Short-beaked common dolphin	68	17	-	17	2.5%	16	50*	11.9%*
4	Cuvier's beaked whale	53	86	13	73	10.7%	46	46	11.0%
5	Sperm whale	166	17	7	10	1.5%	8	8	1.9%
6	Risso's dolphin	21	22	6	16	2.3%	10	10	2.4%
7	Fin whale	27	8	5	3	0.4%	3	3	0.7%
8	Harbour porpoise	1	3	-	3	0.4%	3	3	0.7%
9	False killer whale	1	1	-	1	0.1%	-	-	-
10	Humpback whale	2	-	-	-	-	-	-	-
11	Minke whale	-	1	-	1	0.1%	1	1	0.2%
12	Sowerby's beaked whale	-	1	1	-	-	-	-	-
Total identified		821	287	34	250	36.7%	183	419*	99.8%*
Unidentified small delphinids			428	-	428	62.9%	236	0*	0.0%*
Unidentified cetaceans			3	-	3	0.4%	1	1	0.2%
Total		**821**	**715**	**34**	**681**	**100.0%**	**420**	**420**	**100.0%**

events (unless otherwise stated). A single factor ANOVA (Zar, 1984) was applied to test for the effect of the month on the recorded number of strandings. Statistical significance was set at $p = 0.05$.

RESULTS

Recorded species

Twelve cetacean species have been identified from a total of 821 sightings and 715 stranded animals (involved in 669 stranding events) recorded in the Greek Seas (Table 1). Seven of these species are permanently present and commonly observed in one or more of the Greek Seas: striped dolphin (*Stenella coeruleoalba*), common bottlenose dolphin (*Tursiops truncatus*), short-beaked common dolphin (*Delphinus delphis*), Cuvier's beaked whale (*Ziphius cavirostris*), sperm whale (*Physeter macrocephalus*), Risso's dolphin (*Grampus griseus*) and fin whale (*Balaenoptera physalus*). Among the remaining five species, the harbour porpoise (*Phocoena phocoena*) is restricted to a relatively small area; the humpback whale (*Megaptera novaeangliae*), the false killer whale (*Pseudorca crassidens*) and the common minke whale (*Balaenoptera acutorostrata*) are occasional Mediterranean species that have been sighted or stranded infrequently; and finally the Sowerby's beaked whale (*Mesoplodon bidens*) is an accidental species that has been recorded only once in the Greek Seas.

After checking the original data of some older studies, five more species were found to have been erroneously included in the Greek cetacean fauna in the past. Original photos showed that a stranded 'pilot whale' (Androukaki and Tounta, 1994) was actually a misidentified false killer whale. The same happened with a floating carcass of a supposed Blainville's beaked whale (*Mesoplodon densirostris*; Cebrian and Papaconstantinou, 1992), which was in fact a Sowerby's beaked whale according to the existing documents. Due to a wrong assumption, the white whale (*Monodon monoceros*) was referred to as accidental in the Greek Seas (Cebrian and Papaconstantinou, 1992). The authors thought that a specimen found along the coast of the Black Sea had previously crossed the Aegean Sea, however, later it became known that the whale had escaped from an Ukrainian dolphinarium in the Black Sea. The blue whale (*Balaenoptera musculus*) incorrectly appeared in editions, leaflets and posters of some public services, based on a single fisherman's report referring to a '30m long whale'. McBrearty *et al.* (1986) reported a sighting of a lone killer whale (*Orcinus orca*) in the Aegean Sea and a sighting of long-finned pilot whales (*Globicephala melas*) in southern Greece. One more killer whale sighting from the Aegean Sea exists in the literature as personal communication from McBrearty (Hammond and Lockyer, 1988). However, McBrearty's original data were destroyed some decades ago after he wrote his paper (Evans, pers. comm.). These data originated from individual observers who were not specialists (i.e. fishermen, yachtsmen, captains, etc.), and species identifications were often retained even without supporting photographic documents (McBrearty *et al.*, 1986; Evans, pers. comm.). Long-finned pilot whale and killer whale sightings were also reported during this study, but whenever photos or videos were available they turned out to be misidentifications (mainly of Risso's dolphins). In conclusion, no records of pilot or killer whales accompanied by supporting evidence were found, although the accidental or occasional occurrence of pilot and killer whales in the Greek Seas cannot be ruled out.

Stranding data

The national stranding network was set up in the summer of 1991; records started to become available in September of the same year, shortly after the appearance of striped dolphins infected by morbillivirus (Cebrian, 1995; Aguilar, 2000). The maximum number of stranded cetaceans was recorded in 1992 (97 animals); in 1993 strandings dropped to less than half that of the previous year (Fig. 3). Since 1994, the year of the minimum number recorded (40 animals), the number of stranded cetaceans per year increased steadily and within six years reached the levels of 1992, with 94 and 89 stranded animals in 2000 and 2001, respectively. This rapid increase may be due mostly or partly to the parallel increase in public awareness and the port-police authorities, which resulted in a higher ratio of reported to non-reported strandings.

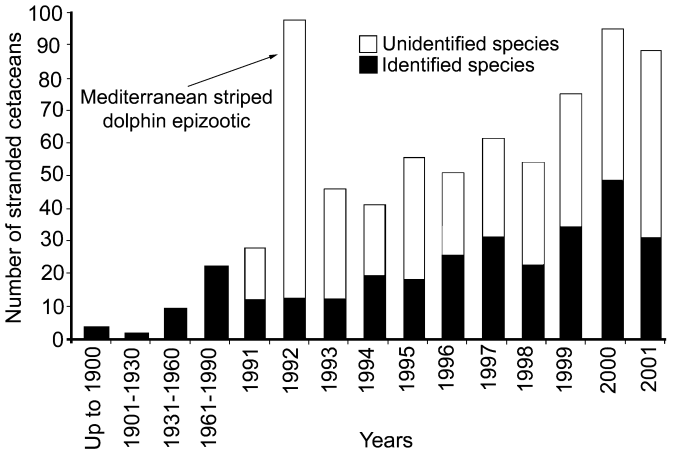

Fig. 3. Number of stranded cetaceans recorded per year. The national stranding network started to provide data in September 1991.

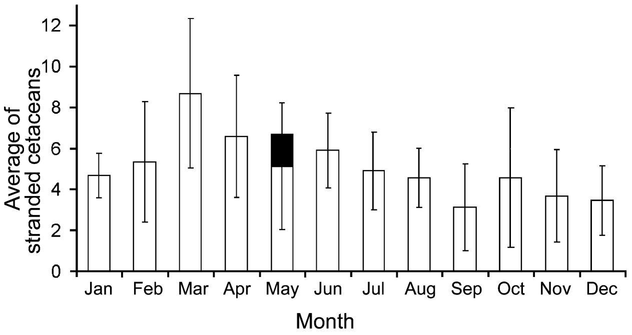

Fig. 4. Average number of stranded cetaceans per month and 95% confidence intervals from years 1993-2001. Strandings from the years of the epizootic (1991-1992) have been excluded, so that they do not affect any yearly pattern related to seasons. Similarly, the mass stranding of 14 Cuvier's beaked whales is presented separately (additional black column in May), because of its anthropogenic cause, which was independent of any seasonal factor.

Eleven species (all but the humpback whale) have been identified among strandings (Table 1). As noted earlier, the percentage of identified animals among 681 strandings from 1991 to 2001 was low (36.7%). As the unidentified animals belonged almost exclusively to three small delphinid species, extrapolated numbers (see methods) are considered here. The common bottlenose dolphin is the most common species among strandings (43.6%) followed by the striped dolphin (27.4%). Averages of *ca* 31 and 19 stranded animals per year were recorded respectively for these two dolphin species. The short-beaked common dolphin and the Cuvier's beaked whale were commonly found among strandings, with about 8 stranded animals per year (11.9 and 11.0%, respectively). The Risso's dolphin (2.4%) and the sperm whale (1.9%) accounted for about 1.5 strandings per year. Finally, the fin whale, the harbour porpoise and the common minke whale represented rare stranding events (less than 1% of the total strandings each).

All seven of the common cetacean species in the Greek Seas were present among the strandings in all seasons of the year, with the exception of fin whales for which the few stranded animals were recorded in November, December and January. The average number of stranded cetaceans per month is presented in Fig. 4. The differences observed between months are significant (ANOVA, $F = 1.95$, $F0.05(1),11,96 = 1.89$, $p < 0.05$). The maximum (8.7 strandings) occurred in March and is followed by a gradual decrease in number until it reaches its minimum in September (3.1 strandings). Numbers remain low in November and December, then increase gradually until March. Further analysis showed that: (1) this pattern is due to unidentified small delphinids and to common bottlenose dolphins which dominate the strandings; and (2) the maximum is not due to strandings of young specimens (total length < 1.5m), which present a clear peak in July and August.

Mass strandings were relatively rare. Twenty-one strandings involving more than one animal (couples, mass strandings *sensu* Geraci and Lounsbury, 1993, or atypical mass strandings as described in Frantzis, 1998) have been recorded during the period September 1991 – December 2001. They represent 3.3% of the total stranding events (641) for the same period of time. Two older mass strandings of four Cuvier's beaked whales in each case were recorded in 1987 and 1988. If all the data including the strandings before September 1991 are considered, 715 cetaceans have stranded in 669 stranding events (Table 2). In 23 stranding events involving more than one individual, 12 cases (52%) concerned Cuvier's beaked whales, 3 cases (13%) concerned striped dolphins, and 8 cases (35%) concerned unidentified small delphinids. The mass stranding of 14 Cuvier's beaked whales in 1996 was linked with military exercises (Frantzis, 1998). In at least two cases, striped dolphins and unidentified small delphinids bore obvious anthropogenic wounds. In another case three unidentified delphinids were found dead in neighbouring sites of the same coast during the same day. Their sizes (2.65, 2.80 and 2.90m) suggest that these were probably common bottlenose dolphins since short-beaked common dolphins and striped dolphins do not reach such lengths, especially in the Mediterranean Sea (Notarbartolo di Sciara and Demma, 1997; Aguilar, 2000; Bompar, 2000). In two other cases, striped dolphins stranded alive showed symptoms similar to those of striped dolphins infected by the Mediterranean morbillivirus. No data are available for the rest of the strandings which involved more than one individual.

Table 2

Number of animals and cetacean species per stranding event. Key: Cb = Cuvier's beaked whale; Sd = Striped dolphin; Unid.S.del = unidentified small delphinid.

Individuals stranded per stranding event	Stranding events	Stranding events with more than one individual per species		
1	646	Cb	Sd	Unid.S.del.
2	14	6	1	7
3	5	3	1	1
4	3	2	1	-
14	1	1	-	-
Total	669	12	3	8

Sightings data

Ten free-ranging cetacean species have been recorded in the Greek Seas (Table 1). These include seven common species, two occasional or rare species (the humpback whale and the false killer whale) and one species present only locally (the harbour porpoise). Two dolphin species, the striped dolphin (31.4%) and the common bottlenose dolphin (27.8%) accounted for more than half of the total number of sightings recorded (31.4 and 27.8%, respectively). Due to the occurrence of dedicated sperm whale surveys (joint acoustic and visual methods), the sightings of this species represented a large part of the total (20.2%). Sightings of short-beaked common dolphins and Cuvier's beaked whales were less frequent (8.3 and 6.5%, respectively); sightings of fin whales and Risso's dolphins were relatively rare (3.3 and 2.6%, respectively). Finally, sightings of humpback whales, false killer whales and harbour porpoises were very rare (less than 0.3% for each of these species. If only the surveys made in pelagic waters and those near or over the edge of the continental shelf are considered, the striped dolphin was the most abundant species, followed by the Cuvier's beaked whale, the sperm whale, the Risso's dolphin and the fin whale (Frantzis *et al.*, In prep.). If the coastal areas of the Greek Seas are considered as a whole, the common bottlenose dolphin was the most abundant species followed by the short-beaked common dolphin.

Distribution, biological data and status of species

The distributions of all known records of cetacean species found in the Greek Seas are presented in Figs 5 and 6. Although some geographical areas have yet to be surveyed sufficiently and gaps in some species' distribution may reflect the absence of effort in these particular areas (Figs 2a and 2b), the available data provide a reasonably good approximation of the real figures. It appears that cetacean species can be divided into three major categories according to their distribution: (1) the striped dolphin, the common bottlenose dolphin, the sperm whale and the Cuvier's beaked whale are present in the entire range of the habitat that is considered typical for them; (2) the short-beaked common dolphin, the fin whale and the harbour porpoise present heterogeneous distributions within their potential habitats; (3) the Risso's dolphin cannot be predictably found in any area or habitat, although its presence has been recorded in most geographical areas of the Greek Seas. The available data per species are summarised below. Although no abundance estimates are available, the species are listed in decreasing order based on absolute number of individuals in the Greek Seas.

Greek common names

The Greek common names of cetacean species given in this paper are those proposed by a monograph of the Greek National Marine Research Centre (Frantzis and Alexiadou, In press) and adopted by ACCOBAMS (2002). Greek names are followed by their transcription in Latin characters in parenthesis (according to ELOT, 1982), and by their pronunciation in Greek. The symbols of the International Phonetic Alphabet (IPA) and tonic accents have been used to describe this pronunciation. For the reader who is not habituated to these symbols a few examples through English words follow: i = see, ð = this, j = yours, ŋ = ring, x =

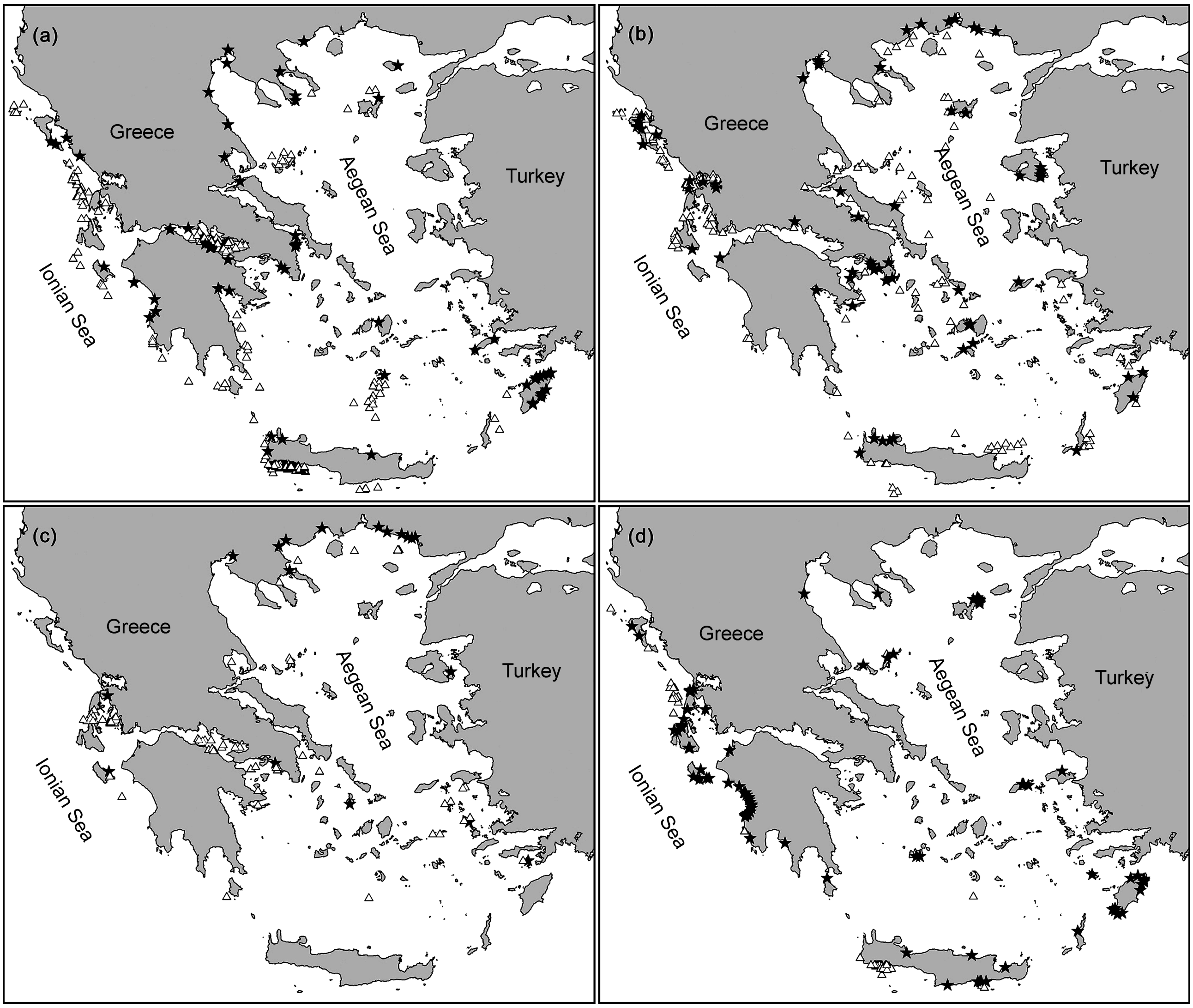

Fig. 5. Distribution of all known sightings (triangles) and strandings (asterisks) of: striped dolphins (a); common bottlenose dolphins (b); short-beaked common dolphins (c); and Cuvier's beaked whales (d) in the Greek Seas. Some hundreds of sightings of short-beaked common dolphins and common bottlenose dolphins available for the sea area around the Kalamos Island in the Ionian Sea are not shown in the relevant figures (see Methods).

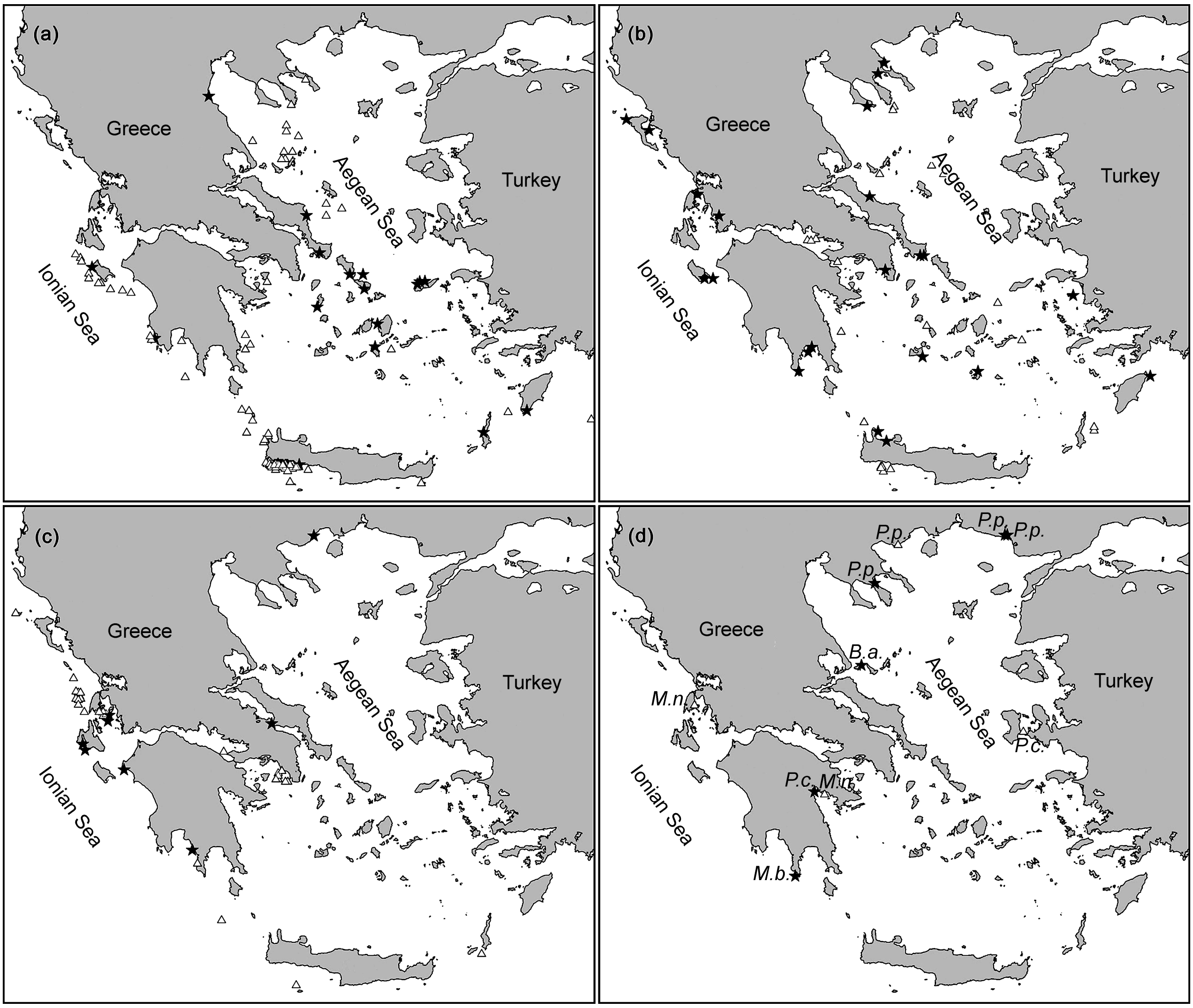

Fig. 6. Distribution of all known sightings (triangles) and strandings (asterisks) of sperm whales (a); Risso's dolphins (b); fin whales (c); and occasional or rare cetacean species (d) in the Greek Seas. Key to (d): *P.p.* = harbour porpoise; *P.c.* = false killer whale; *M.n.* = humpback whale; *B.a.* = common minke whale; *M.b.* = Sowerby's beaked whale.

Scottish loch. No English equivalents exist for the symbols 'c' and 'γ'. However the closest sounds for the use of 'c' are 'kye' in fócena (= harbour porpoise) and 'kyee' in cinó ðelfíni (= common dolphin). The sound of 'γ' in meγápteri fálena (= humpback whale) is between 'g' in the word 'mega' and 'y' in the word 'yes'.

Striped dolphin – Stenella coeruleoalba (Meyen, 1833)
Greek name: Ζωνοδέλφινο (Zonodélfino), pronunciation: zonoðélfino

In all surveys conducted for this study in pelagic or deep waters, the striped dolphin was the most frequently sighted species and presented the highest number of encountered individuals. It was also the second most frequent species found among strandings (extrapolated data 1996-2001), following the common bottlenose dolphin. Although some authors considered the striped dolphin 'less common' or locally rare in the Eastern Mediterranean (Kinzelbach, 1997; Aguilar, 2000), this is the most abundant species in the Greek Seas. There are no geographical areas where it could be considered absent, with the probable exception of the shallow northern Thracian Sea. Its regular presence in this sea is doubtful, since no sightings and only two strandings have been recorded. There is a lack of data for striped dolphins in the central Aegean Sea and the Cyclades Islands (Figs 1 and 5a), where their presence remains to be confirmed because no surveys have been made in this area. Very few sightings occurred above the shallow waters of the continental shelf, where striped dolphins are probably rare. For example, there are only two sightings in the area between Lefkada Island, Kefallonia Island and the mainland (inshore east Ionian Sea), which has been surveyed intensively during the last ten years. Nevertheless, more than ten strandings (including individuals that stranded alive) occurred several tens of miles away from pelagic waters, in shallow (less than 100m) and often enclosed gulfs (South Evvoikos Gulf, Thermaikos Gulf, Saronikos Gulf, Pagasitikos Gulf and North Evvoia), indicating that striped dolphins may visit those areas occasionally. Due to some steep depressions and trenches, striped dolphins are often found close to the coast in Greece (less than 2km south of Crete and in the Gulf of Corinth). In the long, deep, but almost enclosed Gulf of Corinth, striped dolphins are encountered much more frequently (0.043 sightings/km) than in the neighbouring pelagic waters of the Ionian Sea, and they often form mixed groups with short-beaked common dolphins and Risso's dolphins (Frantzis and Herzing, 2002; Frantzis and Paximadis, unpublished data). It is possible that their population unit is isolated from offshore striped dolphins in the Ionian Sea (there are no records for the shallow western part of the gulf and the neighbouring Patraikos Gulf and inshore east Ionian Sea). Genetic evidence is needed to test this hypothesis, since it may represent a rare or even unique case of an enclosed population unit of this species, offering a great opportunity to use study methods that are not applicable in the open sea. Among 47 stranded striped dolphins that were measured, the maximum total length was 2.15m for each of the sexes. The minimum length recorded was 0.81m (in the Gulf of Corinth). As far as it is known, this is the smallest individual with erupted teeth ever recorded in the Mediterranean Sea (Aguilar, 2000; Bompar, 2000), where striped dolphins are the smallest length in the world (Aguilar, 2000). Among the five youngest stranded striped dolphins that measured less than 1m, three (0.81, 0.88, 0.89m) were found on 13, 16 and 22 August respectively, the fourth (0.93m) on 10 September and the fifth (0.97m) on 24 July. These dates suggest a peak in births by the end of July and beginning of August, although births may also occur in late spring or early summer.

Common bottlenose dolphin – Tursiops truncatus (Montagu, 1821)

Greek name: Ρινοδέλφινο (Rinodélfino), pronunciation: rinoðélfino

The common bottlenose dolphin is the most common species in coastal waters and probably the second most abundant species after the striped dolphins. In some areas it shares the same habitat with short-beaked common dolphins, but in a few areas (e.g. the inner east Ionian Sea; see Politi *et al.*, 1999) it is or may be the minority cetacean species. The common bottlenose dolphin is present in all coastal areas, straits and gulfs, but also between islands in the Ionian Sea and in the Aegean Sea from the northern Thracian Sea to the southern Gavdos Island (Figs 1, 5b). It is the only cetacean species present in the shallow and enclosed Amvrakikos Gulf, with an important and possibly isolated population unit. The common bottlenose dolphin is also present along steep coasts with no continental shelf (such as those in southern Crete), although less common compared to shallow areas and plateaux. It is by far the most common species among strandings (Table 1). The largest stranded individuals measured 3.30 and 2.95m for males and females, respectively. Both of these dolphins had extremely worn teeth, indicative of old age. Two individuals with total lengths of 2.16 and 2.54m were one and twelve years old respectively (ages estimated through GLG counting in their teeth according to Pierce and Kajimura, 1980). The two smallest individuals found measured 1.20m each and stranded in early June and late April.

Short-beaked common dolphin – Delphinus delphis (Linnaeus, 1758)

Greek name: Κοινό δελφίνι (Koinó delfíni), pronunciation: cinó ðelfíni

Most observations of short-beaked common dolphins recorded in the Greek Seas come from shallow and coastal areas (Fig. 5c). Until recently, a resident, coastal community was the dominant species in the waters of the inner east Ionian Sea, between the islands of Lefkada and Kefallonia and the mainland (Politi, 1998; Politi *et al.*, 1999). However, ongoing rarefaction has been recently observed, resulting in a significant and continuous decrease in sighting frequency and number of encountered individuals (Politi and Bearzi, In press; Bearzi *et al.*, 2003). The range of this population unit extends south to southeast Zakynthos Island, but its core area is located north, around the island of Kalamos. No more than 100-150 individuals (Bearzi *et al.*, 2003) live in that area, above depths that usually do not exceed 150m. Another, smaller population unit lives in the pelagic (although enclosed) environment of the neighbouring Gulf of Corinth, over depths of 340-910m (Frantzis and Herzing, 2002). These short-beaked common dolphins live permanently in mixed-species groups with the dominant striped dolphins, and occasionally also with Risso’s dolphins. No short-beaked common dolphins have been observed in the western Gulf of Corinth, and in the inner and outer Patraikos Gulf. Although their presence there cannot be ruled out, it seems that there is no significant exchange (if any) between the population units of the inner east Ionian Sea and the Gulf of Corinth. The short-beaked common dolphin is present, common or even abundant in at least five coastal, shallow areas of the Aegean Sea. These are the Dodecanese, the Saronic Gulf, the South Evvoikos Gulf, the Northern Sporades Islands and the Thracian Sea. Sightings and strandings have also been recorded in Thermaikos Gulf, Mytilini Island, Pagasitikos Gulf, Cyclades Islands and Kythira Island. It is probable that short-beaked common dolphins are not rare around most islands of the Aegean Sea, however, dedicated surveys are needed to evaluate their abundance. It is worth noting that half of the recorded strandings of short-beaked common dolphins and three opportunistic sightings originate from the Thracian Sea (Figs 1, 5c), although no surveys were conducted in this area. Short-beaked common dolphins are absent or very rare south of the line that links south Kythira and the Rodos Islands. Despite intensive searching effort in northeast Crete, southwest Crete and around Karpathos Island, they have never been observed there.

Cuvier’s beaked whale – Ziphius cavirostris (G. Cuvier, 1823)

Greek name: Ζιφιός (Zifiós), pronunciation: zifjós

The Cuvier’s beaked whale was observed in all surveys made near or above the waters of the continental shelf edge. Surprisingly for this elusive species (Heyning, 1989), there were more individuals observed in the open sea (112) than recorded as stranded (73) for the period 1991-2001. Sighting frequencies reached 13 sightings 100h^{-1} under favourable conditions in some areas (Pelagos Cetacean Research Institute, unpublished data). Both sightings and strandings indicate that the Cuvier’s beaked whale is regularly present along the Hellenic Trench, from eastern Rodos Island to northwest Corfu Island (Fig. 5d). In addition, Cuvier’s beaked whale seems to be present over all steep depressions of the Aegean plateau, such as the sea area between the Northern Sporades and the Chalkidiki peninsula, the trench north of Limnos Island (Figs 1, 5d). Sightings occurred above depths of 500-1,500m (except one in 250m), at distances ranging from 2-36km from the closest coasts, depending on the underwater topography. It is not actually known if Cuvier’s beaked whales are also present further offshore, over the abyssal plains. Very few strandings were recorded away from steep depressions and deep trenches and no sightings were made in the shallow waters of the continental shelf and the enclosed gulfs, where the Cuvier’s beaked whales are apparently absent. The Cuvier’s beaked whale is common among strandings, often coming ashore in groups of 2-4 individuals (Table 2). It is the only species that has mass-stranded on the Greek coasts (at least 14 individuals), during military exercises in Kyparissiakos Gulf in 1996 (Frantzis, 1998). At least nine more individuals stranded along the coasts of the Ionian Islands the following year, in a short period of two weeks. Although military exercises were also taking place in that case (documents of the Hellenic Hydrographic Service, 1997), no detailed data are available to allow a clear spatio-temporal link.

Sperm whale – Physeter macrocephalus (Linnaeus, 1758)

Greek name: Φυσητήρας (Fysitíras), pronunciation: fysitíras

The existence of a deep trench around Greece (Hellenic Trench) and smaller steep depressions and trenches in the Aegean Sea (Fig. 1) make the Greek Seas an important habitat for sperm whales (Fig. 6a; see also Gannier *et al.*, 2002). Almost all sightings were recorded along the Hellenic Trench from west of the Ionian Islands and the Peloponnese to south Crete and southeast Rodos Island, in the Myrtoon Sea, in steep depressions of the Aegean Sea and particularly in the area between the northern Sporades and Chalkidiki peninsula. Strandings and one sighting in the shallow Cyclades Islands area (not yet surveyed) indicate that sperm whales may cross it while moving from one area of steep underwater relief to another. Most observations (80%) were recorded in depths of 500-1,500m, and at distances ranging between 2.5-8km from the closest coast (range 200-2,100m and 1-36km). It is not known if sperm whales are also present further offshore, over the abyssal plains. Resightings of photo-identified individuals on a yearly basis from 1998 to 2002 indicate that sperm whales are at least seasonally resident in the Greek Seas, and may spend many years of their life here (Frantzis *et al.*, 1999; Pelagos Cetacean Research Institute, unpublished data). Solitary mature males, as well as social groups of females with calves of four to 12 individuals are observed year round. The sighting frequency of young calves among social groups is high (Frantzis *et al.*, 1999; Pelagos Cetacean Research Institute, unpublished data). According to indirect measurements of free-ranging animals and stranded specimens, sperm whales inhabiting the Greek Seas appear smaller than Atlantic individuals. The lengths of the largest solitary males (obtained through both photographic (Gordon, 1990) and acoustic (Gordon, 1991) methods) range between 12.5 and 13.8m. The length of the lower jaw of a sperm whale stranded on Rodos Island indicates a total length of about 15m for that individual. One female and one male of 10.0 and 12.8m, respectively, were surprisingly old with respect to their total length. Their ages have been estimated at about 25 and 44 years, respectively, based on GLG counting of teeth (Frantzis and Lockyer, unpublished data).

Risso's dolphin – Grampus griseus (G. Cuvier, 1812)

Greek name: Σταχτοδέλφινο (Stachtodélfino), pronunciation: staxtoðélfino

The distribution of the recorded sightings and strandings of Risso's dolphins in the Greek Seas is relatively homogeneous (Fig. 6b) and indicates that the species may be present in all geographical areas of deep water or steep underwater relief. However, sighting frequencies were low in almost all surveys conducted for this study, and there were no areas where Risso's dolphins can be considered common, regular, or of predictable abundance. It is worth noting that in the waters off southwest Crete that have been surveyed more intensively, Risso's dolphins were encountered several times in 1998 and 1999, but were not observed in the years 2000-2001. The presence of two photo-identified individuals observed from 1997 to at least 2001 in mixed-species dolphin groups in the enclosed Gulf of Corinth (Frantzis and Herzing, 2002; Frantzis and Paximadis, unpublished data) is rather surprising considering that no other Risso's dolphins have been observed so far. The recorded sightings of Risso's dolphins occurred in depths of 200-1,700m (except for one in 80m). Sightings distance from the closest coast ranged from 0.5-32km. The two younger individuals found among strandings measured 1.73 and *ca* 1.70m, found in late November and late June, respectively.

Fin whale – Balaenoptera physalus (Linnaeus, 1758)

Greek name: Πτεροφάλαινα (Pterofálaina), pronunciation: pterofálena

The fin whale seems to be predictably present only off the northern Ionian Islands (Figs 1, 6c). Four sightings and four strandings were recorded along the rest of the Hellenic Trench. Fin whales seem to be rare in the Aegean Sea and probably occur only exceptionally. In 1998, single individuals and small groups of fin whales were observed repeatedly in the Saronic Gulf from February to May. Similar, exceptional near-coast observations were made in the western Mediterranean Sea during summer and autumn 1997, and were related to particular oceanographic conditions (Beaubrun *et al.*, 1999; Notarbartolo di Sciara *et al.*, 2003). Except for the sightings in the Saronic Gulf, all other sightings occurred in the warm season from June to September. Three strandings have been recorded in November and December; however, a regular presence during the winter months remains to be confirmed. All fin whale observations in the Ionian Sea were made in pelagic waters 9-36 n.miles from the closest coasts, in depths of 1,000-2,000m. However, fin whales have occasionally been observed in shallow coastal waters or enclosed sea areas such as the inner eastern Ionian Sea or even the Gulf of Corinth (Fig. 6c). Fin whale strandings are relatively rare in Greece (Table 1).

Harbour porpoise – Phocoena phocoena (Linnaeus, 1758)

Greek name: Φώκαινα (Fókaina), pronunciation: fócena

The presence of harbour porpoise in the Thracian and northern Aegean Seas (Figs 1, 6d) has recently been confirmed (Frantzis *et al.*, 2001) by one sighting and five strandings, the last two strandings were recorded on 17 January 2003 (Nea Peramos Bay, Thracian Sea) and 25 March 2003 (Strymonikos Gulf, Thracian Sea) (Koutrakis and Kallianotis, pers. comm.). The small size for their age and the genetic signature of two of the stranded animals suggest that they originate from the Black Sea population (subspecies *Phocoena phocoena relicta)* rather than from the Atlantic. It has been suggested that movement of porpoises out of the Black Sea and into the Mediterranean Sea occurs through the Bosporus Straits, the Marmara Sea and the Dardanelles Straits (Rosel *et al.*, 2003). The stranded harbour porpoises had total lengths of 1.57m (female), 1.46m (female), 1.26m (male), 1.25m (unknown sex) and 1.13m (male). The two male specimens were 13.5 and one year old, respectively (Rosel *et al.*, 2003).

False killer whale −Pseudorca crassidens (Owen, 1846)

Greek name: Ψευδόρκα (Psevdórka), pronunciation: psevðórka

Only one observation of false killer whales in the open sea exists. At least seven individuals were photographed in 1992 in the straits between Chios Island and the Turkish coast (Chesme), in the Aegean Sea. This is one of the very few sightings of a false killer whale pod in the Mediterranean Sea, represented by vagrant individuals from the Atlantic Ocean and perhaps from the Red Sea (Notarbartolo di Sciara and Birkun, 2002). One stranding record exists of a single individual found in 1993 in the Argolikos Gulf, Aegean Sea (Fig. 6d). One other stranding was recorded in 1995 along the Turkish coast of the Aegean Sea (Öztürk and Öztürk, 1998).

Humpback whale – Megaptera novaeangliae (Borowski, 1781)

Greek name: Μεγάπτερη φάλαινα (Megápteri fálaina), pronunciation: meγápteri fálena

Two humpback whales were observed (Frantzis *et al.*, 2004) in coastal areas of both the Aegean (spring 2001) and Ionian (summer 2002) Seas (Fig. 6d). The first of these whales spent one month feeding in the vicinity of the Bay of Tolo. These two sightings together with a probable resighting of the second whale in the Adriatic Sea (Affronte, pers. comm.; Frantzis *et al.*, 2004) are the only records existing for the entire East Mediterranean Sea (Frantzis *et al.*, 2004).

Common minke whale – Balaenoptera acutorostrata (Lacépède, 1804)

Greek name: Ρυγχοφάλαινα (Rynchofálaina), pronunciation: riηxofálena

The only record of this species in the Greek Seas concerns a floating carcass of a young common minke whale found off Skiathos Island (Fig. 6d) in May 2000 (Verriopoulou *et al.*, 2001). A few days earlier, a mature female and a calf were found dead on the Mediterranean Israel coast (Goffman, pers. comm.). These are the only available records in the east Mediterranean Sea, although two historical strandings in 1880 and 1926 in the Black Sea (Tomilin, 1957) suggest a passage through the Aegean Sea. A common minke whale skeleton exists in the Zoological Museum of the University of Athens; however, research in the museum archives showed that the skeleton was not recovered in Greece, but bought in England in 1881.

Sowerby's beaked whale – Mesoplodon bidens (Sowerby, 1804)

Greek name: Δίδοντος μεσοπλόδοντας (Dídontos mesoplódontas), pronunciation: ðíðondos mesoplóðondas

A floating carcass of a ziphiid was found and photographed in March 1989 3.5km off Gerolimenas, in south Peloponnese (Fig. 6d). The photo and observers report were published in a small bulletin of the Hellenic Society for the Protection of Nature (Poulopoulos, 1989). According to the observer's description, a 5cm long tooth —which is not clearly visible in the photo —was apparent in the middle of the lower jaw. Mead and Heyning (pers. comm.) inspected the photo and agreed that this was a *Mesoplodon sp*., which could only be a Sowerby's beaked whale if the observer's description was correct. Cebrian and Papaconstantinou (1992) incorrectly reported this specimen as a Blainville's beaked whale. There is only one other record in the Mediterranean Sea (a live stranding in southwest France in 1996) that could be attributed to a Sowerby's beaked whale (Bompar, 2000).

Long-finned pilot whale – Globicephala melas (Traill, 1809)

Greek name: Μαυροδέλφινο (Mavrodélfino), pronunciation: mavroðélfino

The long-finned pilot whale is the only regular Mediterranean cetacean species (Notarbartolo di Sciara, 2002) that has not been recorded in the Greek Seas. Only one record exists (a floating carcass in the Gulf of Taranto, Ionian Sea, Italy; Centro Studi Cetacei, 1996) in the entire East Mediterranean Sea. The long-finned pilot whale has been reported a few times during this study by unskilled observers, but whenever photos or videos were available, it appeared that other species (mainly the Risso's dolphin or the false killer whale) had been falsely identified. Although the accidental or occasional occurrence of long-finned pilot whales in the Greek Seas cannot be refuted, it should be regarded as unconfirmed due to lack of supporting evidence.

Killer whale – Orcinus orca (Linnaeus, 1758)

Greek name: Όρκα (Órka), pronunciation: órka

There are no records of killer whale strandings or sightings directly made by specialists, or supported by irrefutable evidence (photos or videos) in the Greek Seas. Unconfirmed reports of killer whales have been collected during this and older studies (McBrearty *et al.*, 1986; Hammond and Lockyer, 1988). Some reports accompanied by photos or videos appeared to correspond with Risso's dolphins. Although killer whales may occasionally occur in the Greek Seas, their presence should be regarded as unconfirmed.

White whale – Delphinapterus leucas (Pallas, 1776)

Greek name: Μπελούγκα (Beloúga), pronunciation: belúga

This species has never been recorded in the Greek Seas. Due to a wrong assumption, a white whale — escaped from an Ukranian delphinarium and observed in the Black Sea — was assumed to be a free-ranging individual which had crossed the Aegean Sea, and was therefore reported as an accidental species in the Greek Seas (Cebrian and Papaconstantinou, 1992).

Blue whale – Balaenoptera musculus (Linnaeus, 1758)

Greek name: Γαλάζια φάλαινα (Galázia fálaina), pronunciation: γalázja fálena

The blue whale has never been recorded in the Mediterranean Sea (Bompar, 2000; Notarbartolo di Sciara, 2002). However, it has been incorrectly included in editions, leaflets and posters of the Greek Ministry of Agriculture as a species belonging to the Greek cetacean fauna. The only evidence provided was a fisherman's oral report referring to an observation of a '30m long whale' in the Ionian Sea some decades ago.

DISCUSSION

There are no published studies of comparative cetacean surveys conducted along the longitudinal axis (east-west) of the Mediterranean Sea (Notarbartolo di Sciara and Gordon, 1997). Nevertheless, the number and abundance of cetacean species have always been considered lower in the eastern than in the western basin (Marchessaux, 1980; Viale *et al.*, 1988; Notarbartolo di Sciara and Demma, 1997; Notarbartolo di Sciara and Gordon, 1997). This hypothesis was based on the absence of direct contact with the Atlantic Ocean which would limit the possibility of cetacean migrations from the Atlantic Ocean, and the pronounced oligotrophy which would reduce its carrying capacity (Marchessaux, 1980; Notarbartolo di Sciara and Demma, 1997).

The Greek Seas are part of the eastern Mediterranean basin and although they occupy less than one quarter of its surface, they present a high diversity of cetacean fauna, which contradicts in part what was believed until recently. All cetacean species represented by resident populations in the Mediterranean Sea inhabit the Greek Seas, except for the long-finned pilot whale. In addition, the harbour porpoise which is absent from all other parts of the Mediterranean Sea and was once considered extinct (Frantzis *et al.*, 2001) is locally present in the Greek Seas. It has been suggested that movement of porpoises out of the Black Sea and into the Mediterranean Sea occurs through the Bosphorus Straits, the Marmara Sea and the Dardanelles Straits (Rosel *et al.*, 2003). Nevertheless, it remains to be clarified if the harbour porpoises of the Thracian and northern Aegean Seas are occasional visitors from the Marmara Sea, or resident animals that belong to a small separate sub-population, which is more or less isolated from the Black Sea (Frantzis *et al.*, 2001; Rosel *et al.*, 2003). Three of the five cetacean species that occur occasionally in the Mediterranean Sea (false killer whale, humpback whale and common minke whale) have been documented in the Greek Seas. The current number of occasional species and relevant records are likely to increase in the Greek Seas, since current knowledge results from a relatively modest research effort (no systematic surveys, unexplored sea areas, incomplete stranding network) compared with the northwestern Mediterranean.

Abundance estimates for Mediterranean cetaceans are available for just a few species and only a portion of the west Mediterranean Sea (Forcada *et al.*, 1994; 1995; 1996; Forcada and Hammond, 1998). The surveys conducted for this current study and the relative searching effort were not distributed homogeneously in the Greek Seas. Some areas have been surveyed more intensively than others because of the known, or expected, frequent presence of the targeted study species (e.g. sperm whales off southwest Crete). As a result the total sighting numbers recorded are biased in favour of some species, and cannot be used as an index of relative abundance. Consequently, abundance comparisons between basins or particular seas of the Mediterranean are not possible at this stage. However, there is some evidence (distribution range, strandings and encounter frequencies) that the abundance of three species in the Greek Seas (sperm whale, Cuvier's beaked whale and short-beaked common dolphin) could be higher than in most other Mediterranean areas that have been surveyed so far.

Until recently, sperm whales were considered rare or infrequent in the eastern Mediterranean Sea; few historical strandings or opportunistic sightings were known (Marchessaux, 1980; Notarbartolo di Sciara and Demma, 1997). Since 1998, when the regular presence of sperm whales off southwest Crete was discovered (Frantzis *et al.*, 1999), wide areas of the Greek Seas have been shown to host this species. The year-round presence of both mature males and social groups of females with young calves indicate that the Greek Seas are a breeding and nursing ground. This is particularly important if we consider that the encounter frequency of social groups with calves recorded during surveys in the west and central Mediterranean Sea is low (Notarbartolo di Sciara *et al.*, 1993; Pavan *et al.*, 1997; 2000; Gannier *et al.*, 2002). Ten social groups of 4-13 members totalling at least 74 individuals were photo-identified and repeatedly resighted in the Greek Seas in a 172-day effort from 1998 to 2002 (Pelagos Cetacean Research Institute, unpublished data). This evidence suggests that the Greek Seas are an important habitat for the Mediterranean population of this species and supports the hypothesis that sperm whales may complete their life cycle in the Mediterranean Sea or just in its eastern basin.

The sighting frequency of Cuvier's beaked whales in the Greek Seas can reach locally 13 sightings $100h^{-1}$ under favourable sea conditions (Pelagos Cetacean Research Institute, unpublished data). This value is several orders of magnitude higher than that recorded during all surveys in the west and central Mediterranean Sea, from the Alboran Sea to Maltese waters. In all of those surveys, Cuvier's beaked whales were either not recorded at all or were very rare (see Marini *et al.*, 1992; Notarbartolo di Sciara *et al.*, 1993; Forcada *et al.*, 1994; Viale and Frontier, 1994; Gannier and Gannier, 1997; Sagarminaga and Cañadas, 1997). The average number of Cuvier's beaked whale strandings along the coasts of the Greek Seas is 5.6 individuals per year (CI 95% = 2.78) for the decade 1990-1999 (excluding 14 individuals mass stranded in 1996). This number is significantly higher than the respective average for each of the three northern countries of the west and central Mediterranean (Spain 1.9, France 0.2, Italy 2.6) for the same time interval (Bortolotto and Podestà, 1997; Duguy, 1990; Centro Studi Cetacei, 1997; 1998; 2000; 2001; Duguy, 1992; Van Canneyt *et al.*, 1998; 1999a; b; 2000; Van Canneyt, 2001; 2002; Universidad Autónoma de Madrid and Alnitak, 2002; Universidad de Barcelona, 2002; Universidad de Valencia, 2002). Both sightings and strandings indicate that Cuvier's beaked whales occur in higher numbers in the Greek Seas than any other equivalent area of the Mediterranean Sea for which data are available. The apparent abundance of Cuvier's beaked whales and sperm whales suggests that the underwater topography of the Greek Seas makes them an appropriate habitat for deep diving, teuthophagous species.

After a recent, drastic decline in their numbers since the 1970s, Mediterranean short-beaked common dolphins are now uncommon or absent in many parts of the west and central Mediterranean. (Bearzi *et al.*, 2003). Although not fully assessed, their regular presence and distribution in many areas of the Greek Seas show a completely different situation. The results in this paper suggest that short-beaked common dolphins could be particularly abundant in the Thracian Sea in comparison with all other areas. The Greek Seas seem to host an important pool of the Mediterranean short-beaked common dolphin population, in addition to the north Alboran Sea (Cañadas *et al.*, 2002; Bearzi *et al.*, 2003).

The rarity or absence of long-finned pilot whales from the Greek Seas, and probably from the entire east Mediterranean Sea, is a notable biogeographical pattern. Risso's dolphins (Kruse *et al.*, 1999), Cuvier's beaked whales (Heyning, 1989) and sperm whales (Rice, 1989), which all have habitats and feeding preferences similar to long-finned pilot whales (Bernard and Reilly, 2000; Cañadas and Sagarminaga, 2000), are widely distributed in the Mediterranean Sea (Notarbartolo di Sciara, 2002; this work). The reasons contributing to the rarity or absence of long-finned pilot whales in the Greek Seas could be due to either: (1) an important geographical barrier, such as the shallow waters of the Sicilian Channel, which may prevent them from reaching potentially convenient and exploitable habitats; or (2) the absence of specific hydrobiological conditions and phenomena (such as upwellings) that may be vital for the trophic requirements of the pods of this large delphinid. It is noteworthy that in the western basin long-finned pilot whales are abundant only in regions where a permanent frontal system increases productivity, namely the Alboran Sea (Cañadas and Sagarminaga, 2000) and the Liguro-Provençal region (Gannier, 1999).

The results in this paper show that the lack of direct contact with the Atlantic Ocean and the pronounced oligotrophy of the Greek Seas (Stergiou *et al.*, 1997) do not limit the presence of all but one resident Mediterranean cetacean species. In addition, the pronounced oligotrophy does not seem to prevent two deep diving, teuthophagous species such as the sperm whale and the Cuvier's beaked whale, from being abundant in comparison with most other Mediterranean areas that have been surveyed. Nevertheless, the available data cannot contradict the hypothesis of reduced sighting frequency of Atlantic species due to the distance of the Greek Seas from the Gibraltar Strait. Underwater topography, degree of oligotrophy, distance from the Atlantic Ocean, particular oceanographic features (such as gyres, upwellings and fronts), climate change and anthropogenic pressure on the marine environment have variable specific weights in the complex 'equation' that determines the distribution and the abundance of each cetacean species in the Greek Seas. Although basic knowledge on the cetaceans of the Greek Seas has substantially improved in recent years, we are still far from understanding the complexity of their ecology, and remain unable to predict their status in the near future.

CONCLUSION

The lack of basic knowledge on cetacean populations that inhabit the eastern Mediterranean basin presents a serious obstacle in the elaboration of effective conservation measures (Notarbartolo di Sciara and Birkun, 2002). Although still incomplete, the current knowledge on the Greek cetacean fauna, in terms of species presence and distribution, provide a reasonably good approximation of the real figures. The variety of cetacean habitats that surround the Greek coasts is reflected by a species diversity that had been underestimated in the past. In addition, the local population units of four species (sperm whale, Cuvier's beaked whale, short-beaked common dolphin and harbour porpoise) represent an important part of their total Mediterranean population. Nevertheless, there are no quantitative data regarding the absolute abundance or population status of any cetacean species in the Greek Seas. Without such data, it is difficult to adopt proper conservation policies and to monitor the effectiveness of any conservation measure. Therefore, future effort has to focus on: (1) abundance estimates; (2) the assessment of population status, trends, and degree of isolation for cetacean species that constitute conservation priorities at the local or regional level; (3) the definition of critical areas for these species; and (4) the establishment of a properly organised national stranding network that will not hamper the collection of valid stranding data in the future.

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Sex hormone concentrations in the blood of sei whales (*Balaenoptera borealis*) off Iceland

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ABSTRACT

Blood samples were collected postmortem at sea, from 195 sei whales (127 females and 68 males) caught southwest of Iceland between 1983 and 1988. The reproductive status of the whales was determined by anatomical/histological methods. The blood samples were measured by radioimmunoassays for progesterone (P), testosterone (T) and oestradiol concentrations, which were then related to the reproductive status, the length of the whales and the days of the hunting season. Serum P concentrations in females were found to be clustered mainly into two groups, one with values at or below the detection limit (0.1nmol/L) of the assay (Group I) and the other with values about two orders of magnitude higher (Group III) with intermediate values (Group II) in between. Anatomical results showed that Group I ($n = 73$) was largely a mixture of immature and anoestrous mature females. Group III ($n = 39$), with a significantly ($p < 0.01$) greater mean body length than Group I, had a distinct frequency distribution of serum P values with a mean (SD) concentration of 10.3nmol/L (4.1) and consisted predominantly of pregnant females. Many foetuses were lost at sea due to a slit in the abdomen for cooling purposes, but all 13 foetuses (1.5-3.7m in length) recovered belonged to females of Group III. Group II ($n = 15$) consisted mainly of anoestrous mature animals. When pregnancy was estimated by serum P values and sexual maturity by the anatomical findings, the apparent pregnancy rate of mature females was 0.37, agreeing reasonably with earlier reports. Male sei whales were classified into immature, pubertal and mature groups by anatomical/histological methods and had mean T concentrations (nmol/L, ranges) of 0.85, 0.1-4.5; 3.3, 0.1-14.7 and 4.8, 0.1-14.8, respectively. Serum T concentrations did not correlate significantly with body length in the groups but pubertal and mature males had significantly higher geometric mean T values than immature males. Mean serum T concentrations in males, classified as sexually mature by anatomical/histological methods, rose approximately 3.2-fold every 30 days during July-September indicating a seasonal breeding cycle. It is concluded that measurements of sex hormone concentrations in sei whales make a powerful addition to the earlier anatomical/histological methods for determination of reproductive status, not only corroborating them but apparently surpassing them in sensitivity of detecting pregnancy and cyclical changes in serum T values during the male reproductive cycle.

KEYWORDS: SEI WHALE; SEX HORMONES; REPRODUCTION; BREEDING SEASON; OVULATION; PREGNANCY; HORMONES; SEASONALITY

INTRODUCTION

Sei whales (*Balaenoptera borealis*) migrate seasonally every year, feed on their main prey (euphausiids and copepods) at higher latitudes, and breed about every second year at lower latitudes (Boyd *et al.*, 1999). Their presence in Icelandic waters in summer and autumn months is irregular and their abundance varies (Martin, 1983; Cattanach *et al.*, 1993), but in the North Atlantic this species has been found to be genetically uniform (Árnason, 1995).

The gestation period of female sei whales is not known exactly but is reported to be more than 10.75 months, with lactation lasting about 6 months (Lockyer, 1984). The reproductive state of sei whales has been assessed by postmortem studies of various anatomical parameters of their sex organs, both macro- and microscopically (Gambell, 1968; Mitchell and Kozicki, 1974; Masaki, 1976; Lockyer, 1984). Pregnancy of females has been assessed by the presence of a foetus in the uterus, a large corpus luteum in the ovaries, the width of the uterine cornua and by histological study of the uterine mucosa (Lockyer and Smellie, 1985). The presence of a corpus luteum or corpus albicans in either ovary has been used as an indication of sexual maturity in females. Using these methods, an apparent pregnancy rate (lactating females with calves not included) of 0.40-0.44 and an ovulation rate of 0.59 has been calculated for Icelandic mature female sei whales (Lockyer and Martin, 1983).

The testicular weight, the diameter of the seminiferous tubules and the presence of spermatozoa in the tubules have been used to assess the sexual condition of males (Gambell, 1968; Mitchell and Kozicki, 1974; Masaki, 1976; Lockyer, 1984). While Gambell (1968) found no evidence of a sexual cycle for the Southern Hemisphere male sei whale, Mitchell and Kozicki (1974) reported an increase in testes weight from May/June until September/October for the North Atlantic male sei whale and increasing sperm counts during late summer.

Life span related cyclic reproductive events are programmed to begin after sexual maturity in most mammals. Considerable effort has, therefore, been put into age estimation of the whales. The age estimates, however, have been variably successful in different species as briefly reviewed by Lockyer (1984) and Horwood (1987). Sex hormones are obviously involved in the process of sexual maturation and their concentrations might relate more strongly to growth than age. Age versus length curves have been reported for the sei whale (Mitchell and Kozicki, 1974; Lockyer and Martin, 1983).

After the radioimmunoassay (RIA) revolution in the early 1970s, blood sex hormone measurements have been used in domestic animals to confirm pregnancy by monitoring interrupted progesterone cycling and male fertility by measuring serum Testosterone (T) values, replacing less sensitive urine measurements before that (Edquist and Stabenfeldt, 1989). Studies on progesterone (P)

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concentrations in blood from small toothed whales in captivity, where serial measurements can be made on the same animal, have shown that serum P is a good indicator of ovulation and pregnancy (Sawyer-Steffan *et al.*, 1983; Ozharovskaya, 1990). Serum P together with its metabolites and bioactive follicle-stimulating hormone in urine has been measured in captive killer whales (*Orcinus orca*) to study their ovarian cycles and gestation period, which is 17 months (Walker *et al.*, 1988). Serum T concentrations in the captive male bottlenose dolphin (*Tursiops truncatus)*, a seasonal breeder, were reported to reflect sexual maturation and sexual activity (Schroeder and Keller, 1989). There are few reports on serum sex hormone concentrations in both sexes of the large baleen whales and only on two species, i.e. the North Atlantic fin whale, *Balaenoptera physalus* (Kjeld and Árnason, 1990; Kjeld *et al.*, 1992) and the Antarctic minke whale, *Balaenoptera acutorostrata* (Yoshioka *et al.*, 1990; Yoshioka and Fujise, 1992; Iga *et al.*, 1996).

This paper presents the first data on reproductive hormone concentrations in sei whales. Both sexes of sei whale were classified by anatomical methods into reproductive groups, in which the hormonal levels were then studied and compared. The study also involved the distributional pattern of the hormones, their relationship to the body length of the whales and date of capture during the hunting season.

MATERIALS AND METHODS

Blood samples were obtained from a total of 195 sei whales (127 females and 68 males) which were caught southwest of Iceland from late June to late September-October during the summers of 1983-1988 (Fig. 1). The collection and use of postmortem blood samples collected in the same way and the excellent short-term stability of steroid hormones in serum has been described (Kjeld *et al.*, 1981; Kjeld, 2001). Briefly, within about 15 minutes following the death of the animal, the skin of the fluke was dried with a cloth followed by cutting its lateral third off and blood from the wound was collected into plastic test tubes. The samples were centrifuged at 2,000 rpm at sea and the supernatant serum kept frozen at −20°C; 3-6 months later, the samples were stored again at −80°C for half a year up to eight years until analysed. Serum concentrations of T and P measured in 18 serum samples after three months storage at −20°C and then again after about eight years storage at −80°C, showed no significant difference for either sex hormone. This stability of the steroids in frozen serum samples is borne out by their stability in the human serum controls used in the assays, where they showed no significant change in concentration over 18 months. Foetuses were collected from the uteri of the whales by biologists at the whaling station who recorded their sex and length. However, until 1986, a number of foetuses were lost at sea, when the belly of the adult was cut open to cool the meat. Sometimes one or both ovaries were lost as well, making the diagnosis of pregnancy by anatomical indicators uncertain.

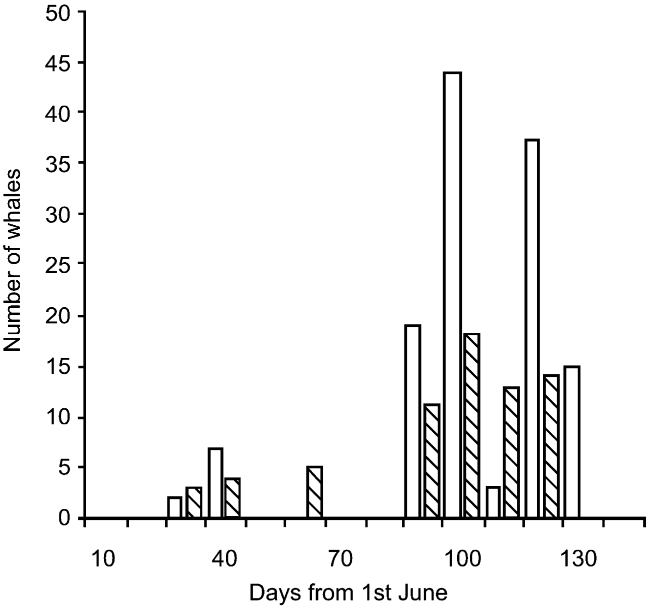

Fig. 1. Frequency distribution of sei whales caught every 10 days during the summer hunting season. Open columns: females; hatched columns: males.

Radioimmunoassays (RIAs)

RIAs with extraction and internal standards were chosen to measure the hormones. Precision of RIAs is generally less than that of enzyme immunoassays and Elisa assays, but RIAs are robust and the extraction step avoids possible matrix effects from the little known serum of whales. The assays for the total (protein bound and free) sex hormone concentrations in serum have been described in some detail by Kjeld *et al.* (1992) with regard to their sensitivity and specificity.

The testosterone antiserum was raised in rabbits against testosterone–3-carboxymethyl-oxime-bovine serum albumin. It had a 66% cross-reaction with 5a–dihydrotestosterone, but 3% and 2% with 5α-androstane–3β, 17β–diol and 5α-androstane–3α, 17β–diol, and less than 0.7% for a number of other structurally related steroids. The cross-reaction of 5α–dihydrotestosterone was not considered a problem as it is an androgen of which testosterone is the main precursor and, in human serum, known to be of ten times lower concentration. After addition of tritium labelled internal T standard, serum samples (0.5ml) were extracted with six volumes of diethyl ether, and then evaporation at 40°C under a gentle airstream followed by dissolution in 0.5ml of assay buffer. The assay had a mean inter-assay imprecision of 14% for a sample with T concentration of 3.6nmol/L and intra-assay imprecision of 8% for a sample with T concentration of 4.9nmol/L. The lower detection limit for this assay was 0.1nmol/L. Mean recovery of T from the internal standard was 82%.

Progesterone was measured by a modified radioimmunoassay method, using a more sensitive and specific antiserum. The antiserum was a rabbit anti-progesterone-11; (Fitzgerald, USA; cat no.: 20-PR20) with a crossreactivity of < 1% for 17-hydroxyprogesterone, pregnenolone, cortisol and 11-deoxycorticosterone and none for androstenedione. Serum samples (0.5ml), after addition of internal tritiated P standard, were extracted in eight volumes of petroleum ether (boiling range 40-80°C; Merck, Darmstadt, Germany). Mean inter- and intra-assay imprecision was 12% and 7% respectively for a serum sample with a P concentration of 4.8nmol/L. The detection limit was 0.1nmol/L. An internal tritiated standard used to assess procedural losses had a mean recovery of 76%.

A highly specific and sensitive antiserum raised against oestradiol-6-carboxymethyloxime-bovine serum albumin was used for the oestradiol assay. Structurally related steroids such as oestriol, oestrone and ethynyl-oestradiol had a cross-reaction of 0.4, 0.2 and 0.16%. Serum samples of 0.4ml were extracted in 4.0ml of diethyl ether, which was evaporated at 40°C under a gentle airstream. The assay had a mean inter- and intra-assay imprecision of 16 and 9% respectively for a serum pool of 141pmol/L. The detection limit for this assay was 15pmol/L.

Conversion factors for the hormones are: testosterone, nmol/L × 0.288 = ng/ml; progesterone, nmol/L × 0.315 = ng/ml; estradiol, pmol/L × 0.272 = pg/ml.

Anatomical/histological measurements

The anatomical measurements used to decide the reproductive status of the female sei whales were conducted according to earlier reports on the species (Gambell, 1968; Mitchell and Kozicki, 1974; Masaki, 1976). All ovaries were inspected and the presence of corpora lutea (CL) and albicantia recorded. To confirm pregnancy in females with CL, but a slit uterus without a foetus, the width of the uterine cornua were measured in order to decide further if the whale had been pregnant (Lockyer and Smellie, 1985).

For males, the methods of the above cited references dealing with sei whales were also used. The testes were weighed and the width of the seminiferous tubules and their preponderance in the testes studied. Spermatogenesis and the presence of spermatozoa in the tubuli were recorded. From these studies the males were divided into three groups: immature, pubertal (intermediate) and mature (Masaki, 1976). These histological techniques are further described in more recent publications on studies of odontoceti (Collet and Saint Girons, 1984; Sørensen and Kinze, 1994).

Total body length was measured from snout tip to tail fluke notch in a straight line on the whaling platform. Measurements were originally made in feet (ft), but they have been converted into meters (m). The mean (SD, ranges) length (m) of females and males averaged 13.7m (0.98, 10.4-15.8) and 12.9m (0.7, 10.97-14.63), respectively. The mean lengths at sexual maturity for males and females have been reported to be 12.9m (42.5ft) and 13.3m (43.5ft), respectively (Mitchell and Kozicki, 1974; Lockyer and Martin, 1983; Boyd *et al.*, 1999).

Statistical analysis

The student's t-test was used to compare groups by their means. A linear regression model was adapted to the $\log_{10}$ of the T values related to the days (daycount) of the hunting season counted from the 1st of June. Association between variables was assessed by the Pearson correlation coefficient. The significance level was set at 0.05.

RESULTS

Females

The serum P values in female sei whales clustered mainly into two groups, one with values at or below the detection limit (0.1nmol/L) of the assay (Group I) and another one with values about two orders of magnitude higher (Group III). In between these two groups was a smaller number with intermediate values (Group II). There is no distribution for Group I but the frequency distribution of the serum P concentrations ($\log_{10}$) for Group II and Group III is presented in Fig. 2. Group III ($n = 39$) displays a distinct frequency distribution. The hatched upper parts of the columns show the females in which foetuses were present. The lower limit of the serum progesterone for Group III is apparently between $\log_{10}P = 0.4\text{-}0.6$ or 2.5-4.0nmol/L. The concentration of 3.5 nmol/L ($\log_{10}3.5 = 0.54$) was chosen as a working limit and using that limit the mean (SD) for Group III was 10.3 (4.1) nmol/L. Group II is more scattered but with values sufficiently above 0.1nmol/L ($\log_{10}0.1 = -1$) to make it a separate group. The classification by serum P values is further analysed in Table 1. The number of individuals, mean P concentration with range, mean length with range and the number of foetuses found are recorded for each group in Table 1. The mean body length of Group III (which has been divided into those with and without foetuses) was significantly longer than that of Group II ($p = 0.039$) and Group I ($p < 0.0001$), but there was no significant difference between the latter groups. No foetuses were found in females from Group I or Group II. By contrast, 13 foetuses were found in females of Group III. Table 1 also shows that of the 73 females in Group I, 33 were classified anatomically as immature and of the 39 in Group III, 27 were classified as pregnant.

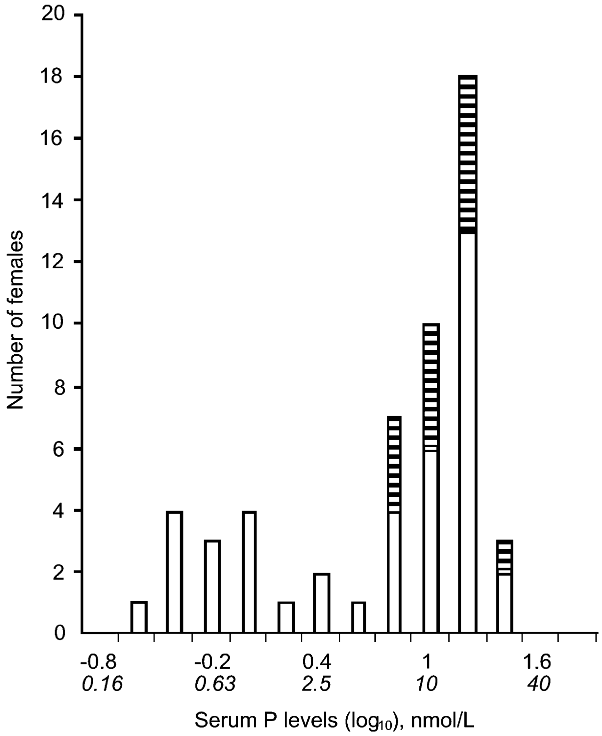

Fig. 2. Frequency distribution of serum $\log_{10}P$ values above 0.1nmol/L (detection limit of assay). Striped parts of columns indicate females with foetus present. A near normal distribution curve for serum values above $\log_{10}2.5$ to 4.0nmol/L (0.4 to 0.6) is observed. On the x-axis, below the $\log_{10}P$ values, the actual concentrations in nmol/L have been inserted.

In Table 2 the anatomical classification of reproductive status of the females is further compared with the serum progesterone levels. Besides the classes of immature, anoestrous, pregnant and lactating females, there are six females that could not be definitely classified and five that were not classified at all, probably because the ovaries were missing as well as the uterus. Table 2 shows that 95% of Group I was made up of immature and anoestrous females. Of the 39 females in Group III ($P \geq 3.5$nmol/L), 27 were classified as pregnant and six and three were indecisive and not classified, respectively. The shortest whale of the anatomically defined pregnant group was 12.8m. The apparent pregnancy rate of that group (ratio of mature females pregnant, females with calves excluded) is 0.38 by the anatomical data, but 0.37 if pregnancy is judged by serum P values and sexual maturity, which P values do not indicate, by anatomical data. If, however, the six indecisive cases (Table 2), which all have serum P values above 3.5nmol/L, are added to both groups (mature and mature pregnant females) the rate becomes 0.41.

Table 1

Female sei whales classified by serum progesterone (P) values (nmol/L). Group III has been divided into those with and without foetuses detected in the uterus. Mean values of serum P (range) and length are given together with foetuses detected and the number of immature and pregnant whales, decided by anatomical methods, counted in each group.

Groups (G I, G II, G III) with P limits, nmol/L	*n*	Mean P values (range)	Mean body length (range), m	Foetuses detected	Anat. immat.	Anat. pregn.
G I, $P \leq 0.1$	73	≤ 0.1	13.4 (10.4-15.9)	0	33	1
G II, $0.1 < P < 3.5$	15	0.81 (0.2-2.5)	13.7 (11.6-15.2)	0	3	2
G III, $P \geq 3.5$ (no foetus)	26	10.4 (3.9-19.5)	[a]14.2 (13.1-15.2)	0	1	14
G III, $P \geq 3.5$ (foetus)	13	10.0 (4.9-19.7)	[a]14.2 (12.8-14.9)	13	0	13

[a]Significantly different (p<0.01) from Group I.

Table 2

Female sei whales classified into reproductive groups by anatomical findings. Mean values of serum P (range) and length are given together with foetuses detected and the number of low (≤ 0.1 nmol/L) and high (≥ 3.5 nmol/L) serum P values in each group.

Reproductive groups by anatomical methods	*n*	Mean P values (range), nmol/L	Mean body length (range), m	Foetuses detected	$P \leq 0.1$, number in group	$P \geq 3.5$, number in group
Immature	37	0.40 (0.1-10.2)	12.6 (10.4-14.3)	0	33	1
Anoestrous	45	0.49 (0.1-7.3)	*14.2 (12.8-15.9)	0	36	2
Pregnant	30	*9.43 (0.1-19.7)	14.0 (12.8-14.9)	13	1	27
Lactating	4	*0.40 (0.1-0.8)	13.9 (13.1-14.9)	0	2	0
Indecisive	6	*9.73 (5.9-12.1)	14.3 (13.7-14.6)	0	0	6
Not classified	5	8.08 (0.1-19.5)	14.5 (14.0-15.2)	0	1	3

*Significantly different (p < 0.01) from the value above.

Serum P concentrations did not change significantly with daycount in any of the reproductive groups during the summer. Serum P concentrations (10 ± 4.48, range 4.9–19.7nmol/L) of the 13 females with foetuses in their uteri were not significantly different from the pregnant ones without foetuses, and did not have any relationship with the size of the foetuses, the length of which however, increased significantly ($p < 0.01$) during the summer (Fig. 3). The equation for the regression line in Fig. 3 agrees well with the equation given by Lockyer and Martin (1983) for the sei whales off Iceland and their 'best fit' birth date of 29 November with a foetus length of 4.5m.

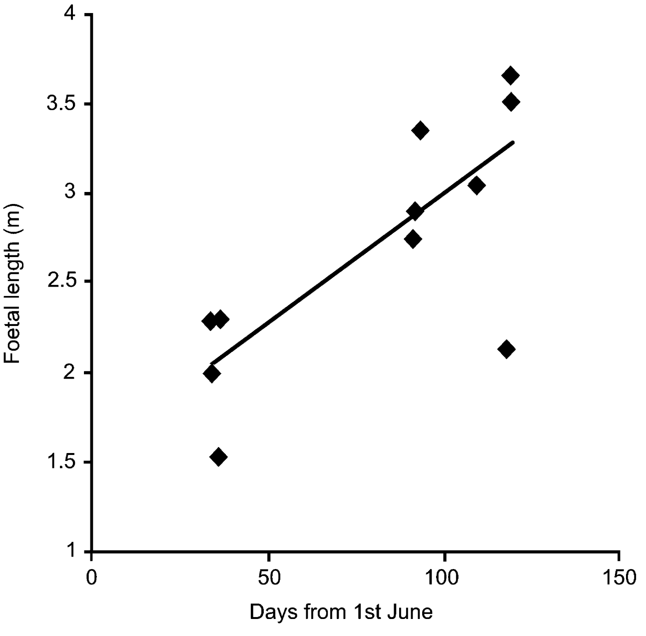

Fig. 3. The length of the 13 recorded foetuses plotted against day of catch. The equation for the regression line was $y = 0.0144x + 1.5544$ ($R^2 = 0.592$, $p = 0.002$).

Serum 17ß-oestradiol (E2), T and P concentrations were measured randomly in a different group of 26 females, 6 immature, 13 non-pregnant mature and 7 pregnant individuals. E2 concentrations varied widely and did not correlate with changes in serum concentrations of P or T. However, in this limited number of individuals the mean E2 concentrations were found to be significantly ($p < 0.01$) higher in pregnant females (171 ± 50pmol/L) than in the non-pregnant mature females (49 ±10pmol/L), which in turn were not significantly different from the immature females (41 ± 6pmol/L). Mean serum T concentrations in the above female groups, with an overall mean of 1.5 ±0.3nmol/L, did not differ significantly between each other.

Males

Using the anatomical/histological methods the 68 male sei whales were classified into three reproductive groups in Table 3: immature, pubertal and mature. Three individuals were unclassified. Mean values with ranges are given for serum T and body length for each class of whales. The number of whales with T values equal or below 0.1nmol/L and equal or above 1.0nmol/L for each group is also given. The number between the two limits is obtained by subtraction (14 immature whales), with 19 (86%) below 1.0nmol/L. In contrast, about 80% of the pubertal and mature males have serum values above 1.0nmol/L. Serum T values do therefore agree reasonably with the anatomical and histological classification of reproductive status in male sei whales.

While pubertal males had significantly higher mean serum T values than the immature males, there was no difference between the pubertal and mature whales (Table 3). The mean

Table 3

Male sei whales by anatomical classification in three reproductive classes: immature, pubertal and mature. Mean levels (SD) and ranges (nmol/L) for serum testosterone (T) and length are given as well as the number of T ≤ 0.1 and T ≥ 1.0 in each group.

Classification	*n*	T	Range	Length	Range	T ≤ 0.1	T ≥ 1.0
Immature	22	0.85 (1.32)	0.1-4.5	12.12 (0.50)	11.0-13.1	5	3
Pubertal	11	*3.27 (3.94)	0.1-14.7	*12.89 (0.36)	12.2-13.4	1	9
Mature	32	4.82 (4.12)	0.1-14.8	*13.43 (0.48)	12.8-14.6	2	25
Not classified	3	0.57	0.1-1.5	13.31	13.1-13.7	2	1

*Significantly different (p<0.01) from the value above.

length, on the other hand, increased significantly for each group with increased maturity.

Serum T concentrations in sexually mature male sei whales did not have a significant correlation with the body length of the whales. There was no significant change in the mean length of males caught during the summer hunting season. The mean (geometric) measurable serum T concentrations of the 30 sexually mature (anatomical/histological) males, on the other hand, increased significantly ($p < 0.001$) with daycount during the hunting season. This is shown in Fig. 4 where the $\log_{10}$ values of the T concentrations of the sexually mature males are plotted against the days (daycount) of the summer season. The equation for the regression line was: $\log_{10}T = -1.10 + 0.017\text{daycount}$; $R^2 = 40$, $n = 30$. This signifies an approximate 3.2-fold increase in the geometric mean of the T concentration for each interval of 30 days during the observation period. The two mature males with T values of 0.1nmol/L or less (detection limit of assay) are shown as open diamond marks in Fig. 4. The pubertal and immature males (Table 3) also showed a tendency of increase in serum T values with daycount, but not significantly so.

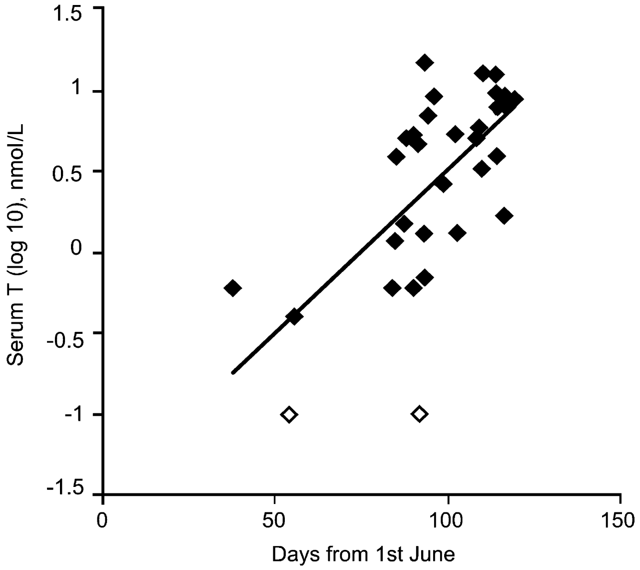

Fig. 4. Scatter plot of $\log_{10}$ serum T concentrations in mature male sei whales (decided by anatomical/histological methods) versus days (daycount) of the hunting season. A regression line has been adapted to the data, $\log_{10} T = -1.10 + 0.017\text{daycount}$ (R^2, adjusted = 40%; $n = 30$; $p < 0.001$). Serum T values of 0.1nmol/L (assay detection limit) from two mature whales are shown by open diamonds but have not been included in the regression analysis.

Mean (SD) serum oestradiol of 39.9 (27.7) pmol/L and P of 2.3 (3.2) nmol/L concentrations in 11 randomly selected mature males were not significantly different from the respective mean concentrations in 13 non-pregnant mature females.

DISCUSSION

Sample limitations

The material used is a selected sample since the whalers work under strict regulations with regard to the smallest size and the maximum number they may catch. Moreover, a punishment is incurred if they accidentally catch a nursing cow with a calf. The sample material is therefore selected with regard to size and sexual status in general. Furthermore, the short hunting season from June to September and fluctuations in the abundance of sei whales off western Iceland (Martin, 1983) allow us to study only a limited part of the yearly cycle of hormonal changes in the whales. This paper represents the first data on sex hormones in the sei whale.

A number of mammalian hormones show diurnal variation in their serum concentrations. This applies to several pituitary hormones and hormones of their target organs such as ACTH and cortisol, which show one of the largest variations, besides responding to stress with elevation. Growth hormone and prolactin, both with diurnal variation, also respond to stress. Sex hormone levels with episodical changes have smaller diurnal variation, but are also known to be influenced by stress (Schroeder and Keller, 1989). In this study the sex hormone concentrations were compared with the time of day at which the whales were caught. No pattern was detected. In a recent study on fin whales, cortisol levels were studied in relation to time of day and the length of time they were chased by the whaling boats (mostly 0 to 90mins). Serum cortisol did not correlate with either time of day or chase time (Kjeld, 2001). Hence, sex hormone concentrations in this study are not likely to be influenced by either diurnal variation or stress due to the capture process.

Females

The females with the lowest P concentrations in Group I (Table 1) were the most numerous. Since these concentrations were at the detection limit of the assay, their distribution remains unknown but the values of the group were well separated from the rest. Table 2 shows that about one half of this group consisted of resting (non-oestrous, non-lactating) sexually mature females. A more sensitive assay might show whether these groups had a different distribution of serum P values. The number of resting females may have been relatively high during the observation period as the mating season was approaching. With a gestation period of about 11 months and a suckling period of 6-8 months there should be at least four to five months rest in the reproductive cycle for mature sei females.

The serum P concentrations of the 39 females in Group III clearly show a distinct group with respect to their distribution, and this is born out by data from the anatomical studies in Table 2. Of the 30 females judged pregnant by the anatomical study, 27 belonged to Group III; nine other females from Group III could not be definitely judged by the anatomical method because of an abdominal slit at sea, injuring or removing the internal sex organs. Thirteen foetuses were, however, recovered from uteri, mainly after 1985 when the whalers dropped the practice of slitting the belly at sea for cooling purposes. The serum P concentrations of these mothers of the 13 foetuses recovered were not significantly different from the other females in Group III (Table 1). This is further illustrated in Fig. 2, where the values from these females have been hatched and added to the other Group III females.

The lowest P concentration in a female with a foetus present was 4.9nmol/L. However, the mean (SD) P concentration of Group III was 10.3 (4.1) nmol/L, and 2.1nmol/L would therefore be the cut off point for the 2.5% fractile of pregnancy or the lower tail of the 95% confidence intervals. If so, two additional females with serum P values of 2.5 (judged pregnant by anatomical methods) and 2.1nmol/L (mature anoestrous) would have been added to Group III.

Using anatomical methods, three females of Group III were judged not to be pregnant, one immature and two anoestrous (Table 2). These (13.4m or longer) had serum P values of 10.2, 5.1 and 7.3nmol/L, respectively, all well above the lower limits of Group III discussed above. While the immature case might best be explained by some mishandling of a specimen, the other two raise the question of non-pregnant ovulators in Group III. Serum P elevations in these ovulations last for about 12 to 28 days in odontocetes (Schroeder, 1990; Robeck *et al.*, 1993). In man and some other mammal species (Niswender and Nett, 1994), including captive killer whales (Robeck *et al.*, 1993) and bottlenose dolphins (Kirby, 1990), P concentrations are considerably higher in pregnancy than during ovulation. Lockyer and Martin (1983) stated that summer ovulations in sei whales were undoubtedly rare and, for the closely related fin whale, Lockyer and Sigurjonsson (1991) reported that for the months of June and July almost all the corpora lutea present indicated pregnancy. However, further studies are needed to see if some of the mature non-pregnant sei females might be ovulating in July-September.

Individuals from Group II consisted mainly of anoestrous mature females as shown in Table 1. Of 15 in the group, 3 were considered immature (serum P values, 0.3, 0.4, 0.7; length 12.5m or less) and 2 pregnant (serum P values, 0.3, 2.5; length 13.7m, 12.8m) but the 10 remaining were judged to be anoestrous, mature females. One can only speculate as to why these animals have higher levels than the majority (Table 2), which has values of 0.1 or less. Some might have aborted recently with decreasing P concentrations, although most abortions happen in the very early months of pregnancy (Niswender and Nett, 1994). Little is known about abortion rates in baleen whales, particularly in early pregnancy (Lockyer, 1984). Foetus death *in utero* in Antarctic fin whales was estimated to be a minimum of 0.14% (Ichihara, 1962). The serum P values might also have been rising slightly in preparation for the upcoming mating period. Such preliminary ovarian follicular development in ruminants occurs in wave-like patterns where P levels have a definite modulating role (Adams, 1999). Increasing serum P values have been observed in minke whale females during a similar period of the year (Kjeld *et al.* 2004).

Serum P concentrations after ovulation without pregnancy are not known in rorquals, nor is the relative role of the placenta in P production. Since the corpus luteum remains functional until the end of pregnancy although not increasing in size during its last seven months (Gambell, 1968), it seems likely that the placenta produces a cetacean chorionic gonadotropin, the measurement of which in blood or urine, like in other mammals, should be the most reliable pregnancy index.

The apparent pregnancy rate of mature females was 0.37 to 0.38, but 0.41 if indecisive results from the anatomical assessments are included. The shortest female decisively pregnant by both anatomical and hormonal methods was 12.8m (42ft). The pregnancy rate and the length at sexual maturity estimated by the P concentrations agreed closely with earlier reports based on biological and anatomical data for the Icelandic sei whale mentioned in Materials and Methods (Lockyer and Martin, 1983).

In a small number of sei whales from a separate group, serum oestradiol values did not change with length, daycount, sex or serum P or T values. Oestradiol values were, however, significantly higher in pregnant than in non-pregnant females, which does not agree with fin whale results (Kjeld *et al.*, 1992). Serum oestradiol values in sei whales need further study.

Males

Mean serum T concentrations in all male sei whales (3.10nmol/L) were a little higher than in male fin whales (2.0nmol/L; Kjeld *et al.*, 1992) but five times higher than in male minke whales (0.6nmol/l) off Norway during a similar time of year (Kjeld *et al.*, 2004).

When the serum T levels within reproductive groups classified by anatomical/histological methods were compared (Table 3), reasonable agreement was evident. Most of the immature males shorter than 12.9m had serum values below 1.0nmol/L and the pubertal and mature males had values generally above 1.0nmol/L.

Serum T concentrations in the mature males increased exponentially and significantly with daycount during the summer, with a 3.2-fold rise for every 30 days (Fig. 4). Since the mean length of caught whales remained more or less unchanged, the T increase with daycount must have been caused by other factors. The rise of serum luteinizing hormone (LH) and follicular stimulating hormone (FSH), with increased mass of the testicular parenchyma, could bring about such an effect. Mitchell and Kozicki (1974) found only a modest monthly increase in testicular weight during four months (see below), so the serum T value is obviously a more sensitive index of the male reproductive cycle than testis weight. The additional effect of the increasing number of grown bulls reacting to reproductive cues may probably also influence this exponential serum T elevation. As can be seen in Fig. 4, two of the mature males (length 12.8m and 13.1m) had serum T values of 0.1nmol/L or less. If these two were included in the regression calculation the increase would be faster still, or fourfold every 30 days.

It is not known when this rise in serum T concentrations stops. At the finish of the hunting season towards the end of September, serum T values are about 8.0nmol/L and at the end of October they will be 25nmol/L according to the equation, if they do not level off before that. At the end of September when the catch stops, the results did not indicate a halt in the serum T increase. Shortly after the serum T levels stop increasing, the mating season usually begins (Bronson and Heideman, 1994). For the captive bottlenose dolphin (Schroeder and Keller, 1989) and terrestrial herbivores with seasonal breeding (Lincoln and Short, 1980;

Bronson and Heideman, 1994), the serum T concentrations generally reach a peak or an elevated plateau before the rutting period starts and then begin to fall during the rut.

While Gambell (1968) did not find any evidence of a male sexual cycle in Southern Hemisphere sei whales based on testis examination, Mitchell and Kozicki (1974) reported strong evidence for such a cycle in sei whales of the northwest Atlantic Ocean. The main evidence was supported by two observations: (1) a 60% increase in the weight of the testes of mature males from June and July until September and October; and (2) the increasing presence of sperm in the seminiferous tubuli from June to October. In this study, the serum T rise with daycount during the summer supports the results of Mitchell and Kozicki and indicates a yearly seasonal breeding cycle in the North Atlantic male sei whale as reported for the North Atlantic fin whale (Kjeld *et al.*, 1992). Recent articles (Yoshioka and Fujise, 1992; Mogoe *et al.*, 2000) on Antarctic male minke whales report no increase in serum T concentrations or testicular weight from December to March. This does not agree with results of studies on the Northern Hemisphere minke whale (Kjeld *et al.*, 2004). Gambell's (1968) data on southern sei whales together with the above reports on minke whales in the Southern Hemisphere suggest lower serum T levels or some physiological differences between the whale counterparts of the Southern and Northern Hemispheres, or that they might somehow be out of phase.

The serum T rise with daycount observed in this study in the mature male sei bulls is estimated to be faster than that for fin and minke whales during the same period of the year (Kjeld *et al.*, 1992; Kjeld *et al.*, 2004). The most likely explanation is an earlier mating period for sei whales, but could also indicate a shorter endocrine preparation time corresponding to a shorter breeding period for sei whales than for the other two species. Lockyer (1999) reviewed the peak time of conception for baleen whales, as has Horwood (1987) for the sei whale. The North Atlantic sei whale was estimated to have a peak conception rate from November to February, whereas fin and minke whales had their peaks in December and February, respectively. The results from this study would seem to support the months of November/December as the peak conception months, or even December/January as suggested by Lockyer and Martin (1983) for sei whales caught off Iceland.

It is concluded that measurement of serum concentrations of progesterone and testosterone are a potent addition to biological anatomical methods for investigating reproduction in sei whales, apparently surpassing them in sensitivity of detecting pregnancy by serum P values and cyclical changes by serum testosterone values during the male seasonal reproductive cycle. The present results do corroborate earlier results by the anatomical/histological methods and suggest new possibilities in the study of baleen whale reproduction, besides constituting a reference for much needed hormonal measurements on the species in different locations at different times of the year.

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Inshore-offshore movements of two fin whales (*Balaenoptera physalus*) tracked by satellite off West Greenland

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ABSTRACT

Two fin whales (*Balaenoptera physalus*) were tagged with satellite linked radio transmitters in a costal area near Aasiaat in West Greenland and tracked for 76 and 32 days in 2000 and 2001 respectively. In 2000, one whale was tagged on 30 September; it stayed in the tagging area until at least 13 October. On 16 and 17 October it was found further south off the coast of West Greenland. On 20 October it had moved approximately 250km southeast to another inshore area. It moved another 100km south along the coast and up to 50km off the coast until 2 November, then appeared back in the area it was located on 20 October until contact was lost on 20 December. In 2001, one whale was tagged on 24 August, it stayed in the coastal area until mid September, where it travelled south along the coast to an area approximately 100km off the coast. From here it continued south to the same inshore area occupied by the whale in 2000. It remained in this area until the last position was received on 25 September. The tracking data suggest a connection between inshore and offshore (> 22km) fin whales and indicates the potential range of fin whales in West Greenland.

KEYWORDS: FIN WHALE; SATELLITE TRACKING; TELEMETRY; MOVEMENTS

INTRODUCTION

A main factor of uncertainty in recent assessments of fin whales (*Balaenoptera physalus*) in the North Atlantic (e.g. IWC, 1991; 1992; 1999; NAMMCO, 1998; 2000) is the question of stock identity. In relation to the aboriginal harvest that is conducted in the coastal areas (< 22km) of West Greenland, it is important to gain insight into the stock discreteness of fin whales found in coastal and offshore areas.

Berubé *et al.* (1998) found that genetic studies suggest more than one breeding stock of fin whales in the North Atlantic, but they were unable to distinguish between fin whales from West Greenland and adjacent areas. Although a considerable amount of data on the occurrence of fin whales off West Greenland have been collected during both the commercial and the aboriginal whaling operations (Kapel, 1984; Witting, 2000) as well as dedicated sighting surveys (e.g. Larsen *et al.*, 1989; Larsen, 1995), no data exist on the relationship between the inshore (< 22km) and offshore (> 22km) occurrences of fin whales in West Greenland. This study used satellite telemetry on tagged fin whales in West Greenland in the autumn, to examine the local movements within the West Greenland area.

In contrast to traditional tagging methods, satellite tracking of whales offers direct insight into the movements, travel speed and habitat utilisation of the whales. Satellite tracking also allows collection of information from areas and seasons where it is logistically difficult to locate whales. Finally, satellite tracking does not depend on recaptures of whales thus it can be conducted without a simultaneous harvest operation. Genetic studies provide additional information but depend again on sampling programmes restricted by logistics. The main problem with satellite tracking of baleen whales is that the longevity of the tags is either restricted by the ability to maintain them on the whales or by battery drainage. Recent results suggest however that it is possible under optimal conditions to maintain the tags on the whales for the entire period of the battery life and perhaps long after (Heide-Jørgensen *et al.*, 2003). Tags need to be small to be successful and battery power is restricted to what can be housed in small transmitter packages.

MATERIALS AND METHODS

The satellite transmitter used was a ST-15 (Telonics Inc.) transmitter unit equipped with two lithium thianyl batteries (M1) that was pre-programmed to be on for 24 hours and off for 72 hours. It had a salt water switch that only allowed transmission if the transmitter was out of the water for more than approximately 250ms. The repetition period of the transmissions was 45s. The transmitter was cast in epoxy in the shape of a cylinder 110mm in length and 28-35mm in diameter. The antenna extended from one end of the transmitter while the other end was glued to a stainless steel cup. In 2000, this cup was mounted on an 8mm diameter stainless steel dart 27cm in length equipped with two barbs (Fig. 1). In 2001, the cups were mounted on an 8mm diameter titanium dart 33cm in length equipped with three barbs (Fig. 1). The barbs act to anchor the dart in the blubber and muscle layers below the skin. The stainless steel cup acts as a flange that stops the transmitters from penetrating through the skin.

The transmitters were launched with the Air Rocket Transmitter System (see Heide-Jørgensen *et al.*, 2001a), a modified gun-shaped line-thrower powered by compressed air from a scuba tank. The 'rocket' consisted of the transmitter in combination with a finned tailpiece. The tailpiece provides stabilisation during flight as well as flotation, ensuring retrieval of the transmitter in case of a missed hit. The tailpiece is loosely attached to the transmitter so that it falls off after attachment to the whale. The pressure

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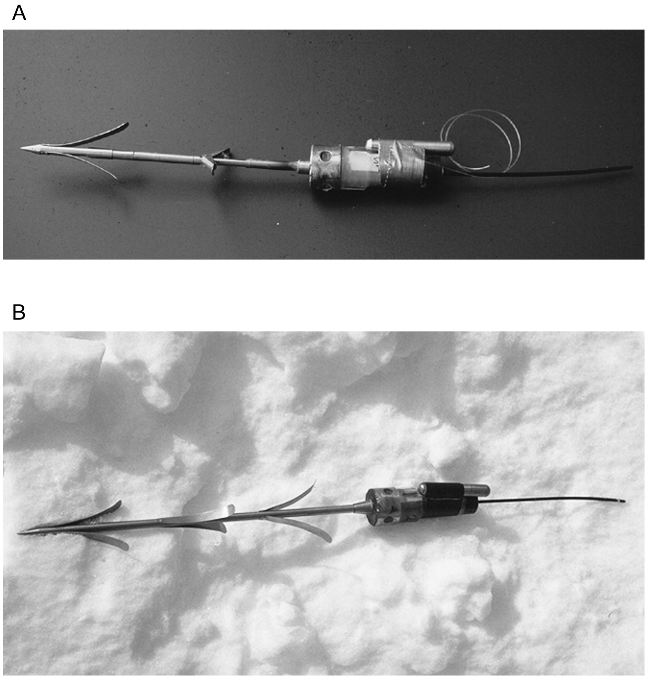

Fig. 1. Transmitter used for the fin whale tags in 2000 (above) and 2001 (below). The magnet attached with tape is removed before launching and the nylon line secures the tag in case of misses. The 2000 model had an adjustable stainless steel spear of 27cm with stainless steel barbs and the 2001 model had a fixed titanium spear of 33cm with stainless steel barbs.

(chosen in advance) and distance to the fin whale when the rocket was launched was 12 bars and 12m in 2000, and 14 bars and 15m in 2001.

The tagging operation in West Greenland was conducted from a 5.1m rigid hull inflatable (*Yonah*) with a 40hp outboard motor, a steering panel, and a maximum speed of 24 knots in 2000, and a 5m aluminium boat (*Arfivik*, model Buster L) with a 50hp outboard motor and a maximum speed of 34 knots in 2000 and 2001.

Positioning was facilitated through Service Argos Data Collection and Location Service. Location data were obtained from five classes of precision: 2, 1, 0, A and B. Positions of class 1-2 have an estimated precision (standard error) of <1km with class 2 being the best (Service Argos, *in litt.*). Experimental studies however indicate that for tracking of marine animals, slightly lower precision can be expected for all three location classes (Hays *et al.*, 2001; Vincent *et al.*, 2002). For tracking of marine mammals, it is important to note that the precision of class 0, A and B locations has not been specified by Service Argos. Precision of location class 0, A and B has been tested experimentally in two studies and apparently class A has a higher precision than both class 0 and class B and the precision of class A position may approach the precision of class 1 positions (Hays *et al.*, 2001; Vincent *et al.*, 2002). Hays *et al.* (2001) found that the distance of class 0 and B positions to the actual position was 10 and 7km on average, however, the longitudinal error is usually larger than the latitudinal (Vincent *et al.*, 2002). In any case all three classes of low precision positions contribute important information to the tracks of the whales and the errors seem insignificant relative to the scale of the movements.

In order to reduce the importance of the errors in the low-precision location data, an average position was calculated on the basis of all positions for each day (24hr periods) with data. These means deviated from the occasional positions of good precision (quality 1 and 2) by an average of 5km ($SD = 0.8$, $n = 6$) in 2000 and 7km ($SD = 1.8$, $n = 7$) in 2001.

The distribution of inshore catches (1988-1999) and offshore sightings of fin whales in Greenland (1980 and 1983) was plotted to show the known areas of concentrations of fin whales in West Greenland.

RESULTS

An approximately 18m long fin whale was tagged with a satellite transmitter (20685) on 30 September 2000 in the archipelago at Aasiaat (69°42’N, 52°50’W N, Fig. 2). A total of 200 positions covering 77 days were obtained from the whale (Table 1). Occasional signals were received until 20 December indicating that the instrument stayed on the whale for at least 81 days.

The fin whale appeared to stay in the coastal area where it was tagged until at least 13 October. On 16 and 17 October it was found about 225km south and about 130km off the coast of West Greenland based on an average of 1 quality 1 (67°N, 57°W), 2 quality 0, 7 quality A and 6 quality B positions. On 20 October it appeared approximately 250km southeast in another inshore area. It moved another 100km south along the coast and up to 50km off the coast until 2 November, then appeared back in the area where it was located on 20 October. It apparently stayed in that area until 16 December when the last position was obtained. Contact with the transmitter was lost on 20 December. During the period from 30 September through 16 December it travelled a minimum of 989km.

The average daily travel rates ($n = 19$) between the average daily positions for the fin whale was 13km day^{-1} with a range from 1-66km day^{-1}. The fastest travel rates were observed when the whale was moving to and from its offshore position at approximately 56°30’W.

Another fin whale (20158) estimated to be 18m long was tagged on 24 August 2001 in the archipelago at Aasiaat (68°32’N, 53°16’W). A total of 71 positions covering 32 days were obtained from the whale (Table 1). The whale stayed in the coastal areas of Disko Bay where it visited the southeastern part of the bay on 9 September. On 13 September it was located further to the southwest in an area approximately 30km off the coast based on an average of 5 quality B and 1 quality A (67°52’N, 55°08’W) positions. From here it continued south to the same coastal area north of Nuuk that was used by the whale tracked in 2000 between 20 October and 16 December (Fig. 2). Here it stayed until the last positions were received on 25 September. During the period from 24 August through 25 September it travelled a minimum of 625km.

The average daily travel rates ($n = 9$) between the average daily positions for the fin whale was 20km day^{-1} with a range from 1-70km day^{-1}. The fastest travel rate was observed when the whale was moving south from Disko Bay to the coastal area at 65°N between 13 and 17 September.

Fin whale catches in West Greenland were concentrated in two coastal areas during 1988-1999: the northern area is located in the archipelago of Aasiaat and the southern area is located between Nuuk and Maniitsoq (at 64°-65°N, Fig. 3). The fin whales tracked were initially sighted and tagged in the northern area and later moved into the southern area. Fin whales are frequently found in the central part of northern Davis Strait west of 57°W between 67°-68°N and approximately 400km off the Greenlandic coast (Fig. 3). The whale tracked in 2000 left the northern coastal area after 13 October and travelled to the offshore area and stayed there

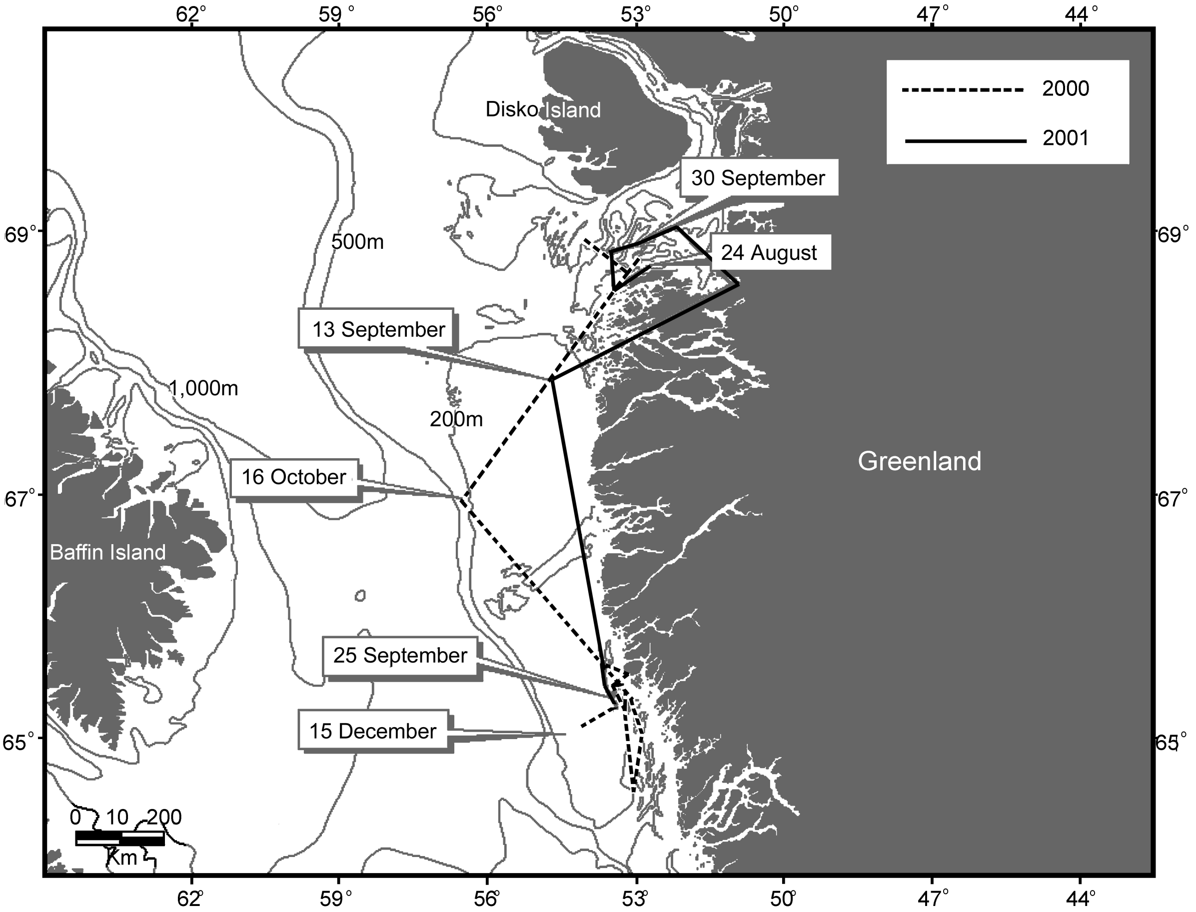

Fig. 2. Tracking of fin whales in West Greenland. Only the mean position for every 4 days is given. The track in 2000 (whale 20685) lasted from 30 September 2000 through 16 December. The track in 2001 (whale 20158) lasted from 24 August through 25 September.

Table 1

Details of instrumentations of two fin whales tagged with satellite transmitters in West Greenland in 2000 and 2001. Standard deviation given in parenthesis. For the locations precision classes 2 indicate positions with a nominal precision of 350m, 1 a precision of <1,000m and class 0, A and B has no assigned precision.

ID No.	Tracking period	No. of days	Position of tag	Total distance travelled	Daily horizontal speed	Number of positions	Distribution of positions on precision classes of locations (LC)				
							2	1	0	A	B
20685	30/09-16/12 2000	77	Midway between head and dorsal fin about 0.5-1 m to the right of the dorsal line.	989km	13km/day (17)	200		6	9	54	131
20158	24/08-25/09 2001	32	3m in front of dorsal fin, about 40cm to the left of the dorsal line.	625km	20km/day (24)	71	2	5	1	17	46

until 20 October, when it appeared at the southern coastal area where it remained until mid-December (compare Figs 2 and 3).

DISCUSSION

The ST15 transmitters equipped with two M1 batteries have a nominal longevity of 20-25 days with continuous transmissions. They were programmed only to transmit every four days and only when at the surface, thus the longevity should be at least four times the nominal capacity, i.e. around 80 to 100 days. The fin whale from West Greenland tagged in 2000 seems to have approached the expected transmitter longevity and it is thus likely that the ultimate failure of the tracking of this whale was due to exhaustion of batteries. For the other tag it seems plausible that the tags migrated out through the skin of the whale and eventually fell off.

In a study of bowhead whales (*Balaena mysticetus*), it was shown from voltage readings transmitted to the satellite that the batteries were drained when the transmitters ultimately failed after two months of operations (Heide-Jørgensen *et al.*, 2003). It thus seems possible that the present technique could be used for long-term tracking if sufficient battery capacity is supplied with the transmitter.

The large number of positions of low precision contributes some uncertainty about the exact location and routes of the whales; however, the uncertainty is reduced by the use of a daily average position. The overall movement pattern as estimated by the means of low precision positions is confirmed by the occasional positions of high precision.

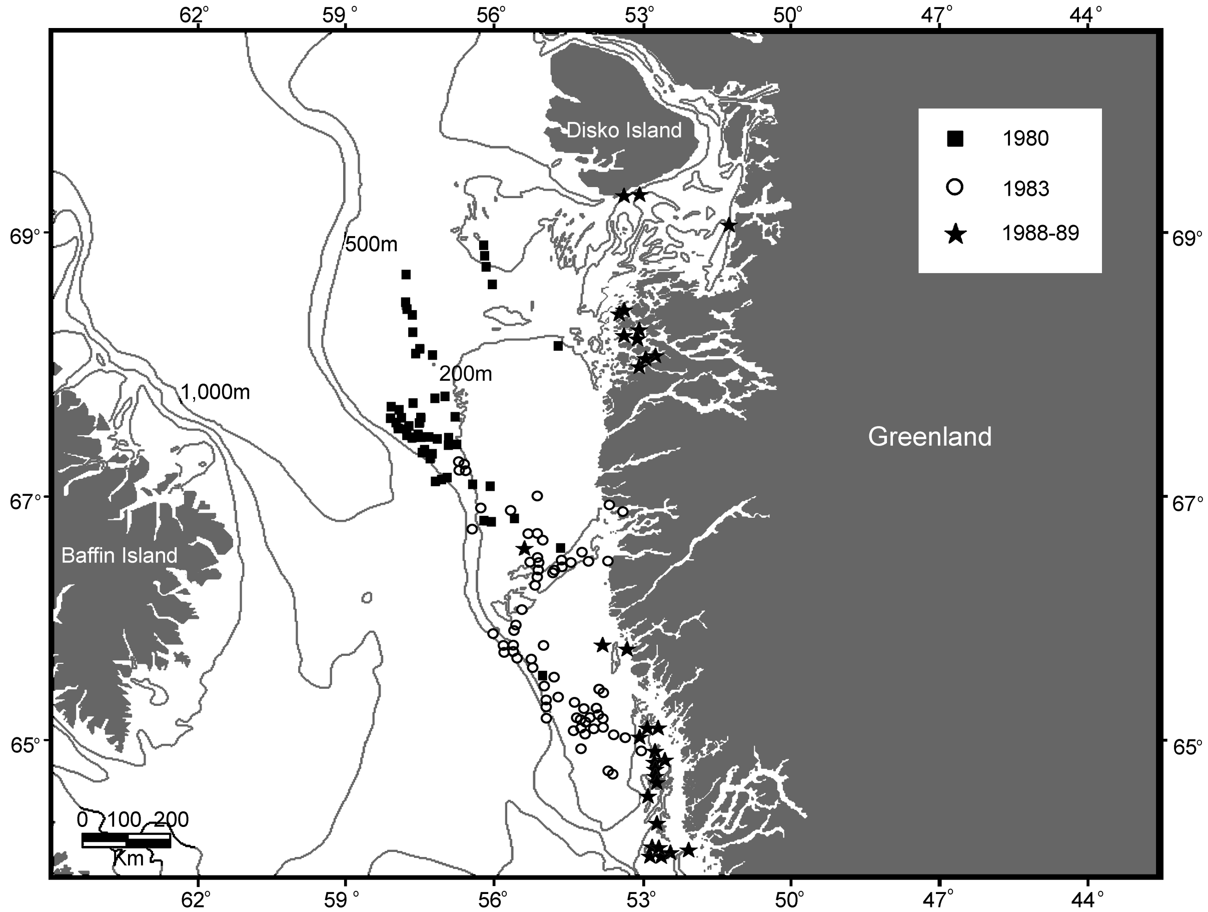

Fig. 3. Positions of offshore observations from *Kato* (squares and circles 1980 and 83) and inshore catches (stars 1988-99; Witting, 2000) of fin whales in West Greenland. The 200m depth contour is indicated.

Satellite tracking of a fin whale tagged in Iceland in 1994 provided location data for 43 days and, although not reported in detail, the frequency of good quality positions was generally better than that obtained in this study (Watkins *et al.*, 1984b). No details on signal strength or repetition rate for the tag are provided but it differed from this study by having a longer delay (550ms) before transmissions, which together with an implant closer to the dorsal ridge may have provided a better chance for precise positions.

The duration of the tags, the number of positions and their quality was better for the fin whales in this study compared to those obtained during satellite tracking of minke whales in 1994 and 1999 (Heide-Jørgensen *et al.*, 2001b). Some of the improved performance is due to the larger size of the fin whale which provides a better platform for transmissions because more of the body is exposed for a longer time during surfacing.

The tracking of a minke whale in 1994 used a transmitter attached to an anchoring dart with a wire and thus the transmitter was hanging more loosely on the skin of the whale. For the tracking in 1999, part of the transmitter was buried into the blubber (Heide-Jørgensen *et al.*, 2001b). A blue whale (*Balaenoptera musculus*) tracked in 1999 was also tagged with a transmitter intended to be partly buried into the blubber (Heide-Jørgensen *et al.*, 2001a); contact was lost after 22 days but the proportion of good quality positions (NQ > 0) obtained resembled that achieved in this study (Table 1). The transmitter design with an anchoring dart inside the whale and the transmitter unit with antenna and salt-water switch outside the skin pointing away from the whale may also have improved the tag performance.

Radio tracking (HF and UHF-satellite) experiments off Iceland have shown that fin whales are capable of moving rapidly between different areas. A whale tracked for 9.5 days in 1980 moved more than 1,700km at an average speed of 7.4km h^{-1} for the entire period (Watkins *et al.*, 1984a). Apparently the whale made a directional movement towards an area where it joined other fin whales. Another whale tracked for 43 days in August-September 1994 moved 1,546km at an average speed of 1.5km h^{-1} (Watkins *et al.*, 1984b). This whale apparently explored the waters along the 2,000m depth contour and it seemed more stationary during the tracking period. Both whales preferred areas with water depth in excess of 1,500m. The fin whales tracked in this study also indicate that fin whales can move at considerable speeds and cover considerable distances. Travel speeds of 13 and 20km on average per day and minimum distances of 989 and 625km covered during 76 and 32 days is below Watkins *et al.*'s (1984a) observations during 9.5 days but it resembles the values obtained from a 22-day track of a North Atlantic blue whale in 1999 (Heide-Jørgensen *et al.*, 2001a). However, the travel distances were measured in a relatively crude way in the present study and it is likely that larger distances would have been measured with more frequent locations of the whales.

The two fin whales tagged in Greenland mostly remained in coastal areas, but they also spent some time in offshore waters in the central Davis Strait. Observations from a commercial minke whaler documented offshore concentrations of fin whales from 1979 to 1983 as late as mid September (Larsen, 1981; Kapel and Larsen, 1982; 1983; Kapel, 1984). According to the whalers, the offshore areas are used during the northward migration of the fin whales (Larsen, 1981). The appearance of one of the tracked fin whales at the offshore area in October indicates that fin whales are still present in that area during autumn – at least for one day. Kapel (1984) also shows from observational data that rapid changes in the abundance of fin whales in the offshore area do occur.

The information presented here, although based on only two animals, suggests that the offshore and inshore aggregations of fin whales belong to the same stock. Any enumeration of fin whale abundance in West Greenland used for assessing the sustainability of the coastal harvest will thus gain from the inclusion of the offshore areas. Offshore fin whale distribution extends at least as far west as 58°W (Fig. 2) and possibly even further west. Little or no effort occurred to the west of 57°W in previous aerial surveys off West Greenland (Larsen *et al.*, 1989; Larsen, 1995).

The present study illustrates the potential for elucidating the movement patterns of baleen whales through satellite tracking. Future tagging should aim at longer duration of the trackings and better quality of the positions obtained. Tagging later in the season may also reveal more information on the whereabouts of the whales during winter (e.g. IWC, 2003).

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Sperm whale distribution and seasonal density in the Faroe Shetland Channel

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ABSTRACT

Results from previous surveys suggest that an area of the northeast Atlantic, the Faroe Shetland Channel, is important for cetaceans. This study utilised passive acoustic survey techniques to evaluate the density of sperm whales in the Channel. Two-week surveys were carried out during oceanographic cruises in May and October 2001, and May 2002. A two hydrophone array was towed behind the vessel throughout the majority of the survey routes and was monitored by a two-person team and by software designed to automatically detect and measure bearings to whales. Distances of individual sperm whales from the trackline were determined using target motion analysis. Standard line transect techniques were applied to calculate the density of whales during surveys. The effects of sea conditions and survey vessel on the ability to detect whales were tested; the encounter rate and effective stripwidth (*esw*) were estimated independently for each sea state and for each of the vessels. A total of 79 individual whales were detected, and their distances from the trackline were calculated. As a probable result of insufficient sample size and a small effects size, neither the *esw* nor the encounter rates varied significantly with sea state or between the two survey vessels. The density of sperm whales during each of the surveys was estimated to be 2.05, 0.52 and 1.75 whales per 1,000km^2 for the May 2001, October 2001 and May 2002 surveys respectively. Sperm whales were distributed across the majority of the Faroe Shetland Channel. This study has provided the basis for meaningful hypothesis generation in future studies and to gain a better understanding of the factors underlying the spatial and temporal distribution patterns of sperm whales in this area; data on oceanographic, biological and anthropogenic determinants should now be examined.

KEYWORDS: ATLANTIC OCEAN; INDEX OF ABUNDANCE; SURVEY–ACOUSTIC; SURVEY–VESSEL; ACOUSTICS; VOCALISATION; DISTRIBUTION

INTRODUCTION

There has been little dedicated research on sperm whales (*Physeter macrocephalus*) in the northeastern Atlantic but a number of data sources (Thompson, 1928; Brown, 1976; Gunnlaugsson and Sigurjónsson, 1990; Weir *et al.*, 2001) indicate that this may be an important area for this species.

Historical whaling records show that sperm whales were hunted in large numbers throughout the northeastern Atlantic (Brown, 1976; Jonsgård, 1977). More recently, dedicated sightings surveys have shown that sperm whales are distributed widely throughout oceanic waters in the northeastern Atlantic (Martin *et al.*, 1984; Sigurjónsson, 1985; Sigurjónsson *et al.*, 1989; Øien, 1990; Lens, 1991; Ciano and Huele, 2001). From boat based sighting surveys, Øien (1990) estimated a population size of 2,500 sperm whales in the Norwegian Sea and surrounding waters with densities ranging from 0.82 to 10.16 whales 1,000km^{-2}. Gunnlaugsson and Sigurjónsson (1990) estimated a population of 1,234 sperm whales to the east of Greenland and around Iceland. A population size of 308 sperm whales was estimated for waters around the UK and the Faroe Islands during the same study. However, the authors of these studies (Gunnlaugsson and Sigurjónsson, 1990; Øien, 1990) highlight that the numbers may be significant underestimates as no corrections were made for animals that may not have been seen because they were submerged.

Sperm whales are also frequently sighted to the northwest of the UK from opportunistic survey platforms (Evans, 1997; Weir *et al.*, 2001). Sightings typically peak during the summer and are rare between December and April. However, this may be a result of unfavourable sighting conditions due to poor weather in these waters during winter (Evans, 1997). This possibility is supported by recent acoustic surveys in these areas which indicate that sperm whales may be present in significant numbers during winter months (Lewis *et al.*, 1998) and by the fact that strandings of sperm whales have been recorded from the coasts around the UK and Ireland throughout the year (Evans, 1997).

Recent opportunistic surveys to the northwest of the UK found significant numbers of sperm whales within the Faroe Shetland Channel (Lewis *et al.*, 1998; Weir *et al.*, 2001). This area provides one of the few deep water links between the northeastern Atlantic and polar waters, and is potentially an important corridor for migrating whales. However, to assess the biological and anthropogenic factors influencing the ecology of cetaceans in this region, more detailed survey work on their distribution, habitat use and behaviour is required.

The Faroe Shetland Channel encompasses part of the Scottish continental shelf and Faroese plateau, and is intersected by a deep channel approximately 1,400m deep that runs northeast through the area. At its northern entrance, the channel is connected to the Norwegian Sea and at its southern end, to the Atlantic Ocean (Turrell *et al.*, 1999). The hydrographic regime of the Faroe Shetland Channel is complex and it has long been recognised as one of the major conduits connecting the warm waters of the Atlantic with the cold waters of the Nordic seas (Sherwin *et al.*, 1999).

Over the last 100 years, the FRS Marine Laboratory in Aberdeen has conducted oceanographic research in the Faroe Shetland Channel (Heath and Jónasdóttir, 1999;

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Turrell *et al.*, 1999). Throughout the year, systematic surveys are carried out to assess both the hydrographic and biological characteristics of this area. These surveys provide an ideal platform to study the density of sperm whales within this unique area.

Conventionally, cetacean surveys have used visual techniques to search for animals at the water surface. However, sighting efficiency can be severely affected by weather conditions; it rapidly decreases in rough seas, and is curtailed by factors such as fog. Sperm whales can be particularly difficult subjects because they make long deep dives which may last for over an hour. However, sperm whales are highly vocal animals, producing loud clicks (Backus and Schevill, 1966), for most of the time spent underwater. They can be detected at ranges of several miles using simple hydrophone systems, and acoustic monitoring (whether used alone or in conjunction with visual methods) has proven to be a highly effective survey method for this species (Leaper *et al.*, 1992; Gillespie and Leaper, 1996; Barlow and Taylor, 1998).

The primary aim of this study was to estimate the density and distribution of sperm whales in the Faroe Shetland Channel using passive acoustic survey techniques from oceanographic survey vessels.

METHODS

Passive acoustic surveys for sperm whales were carried out in the Faroe Shetland Channel (Fig. 1) during oceanographic cruises from 7-21 May 2001 and 4-18 October 2001 from the *FRV Scotia*, a 68m oceanographic research vessel, and from 15-28 May 2002 from the *FRV Cirolana*, a 73m oceanographic research vessel.

Equipment

The acoustic equipment consisted of a towed stereo hydrophone streamer, an amplification and filtering unit and a computer for making recordings. The hydrophone was specially designed and built for this project but was based on systems developed in previous studies (Leaper *et al.*, 1992). The streamer consisted of two AQ4 elements (*Benthos*, Falmouth, USA) with individual preamplifiers (*Magrec*, Devon, UK) mounted 3m apart in a 10m, oil-filled, 1” diameter polyurethane tube. The preamplifiers had a low-cut filter designed to provide –3dB gain at 100Hz to limit low frequency tow and water noise. The system was otherwise flat to 15kHz and had good sensitivity to well above the 22kHz upper limit of the computer sound card. The streamer was towed behind the vessel on a 400m strengthened cable. At speeds of 10 knots, this design of array with a 400m cable has been found to tow at around 5-6m below the surface (Gillespie, 1997). For retrieval and storage, the cable and streamer were coiled onto the main net drum winch situated centrally above the aft deck of the vessels. A 60m extension cable was connected to the tow cable once it was deployed linking the array to recording equipment located within the vessel’s laboratories.

Signals from the hydrophones were filtered using high pass filters set at 400Hz or 1,600Hz depending on background noise conditions, and amplified by 20dB or 30dB using a custom built differential amplifier/filter unit (*Magrec*, Devon, UK). The data logging software package

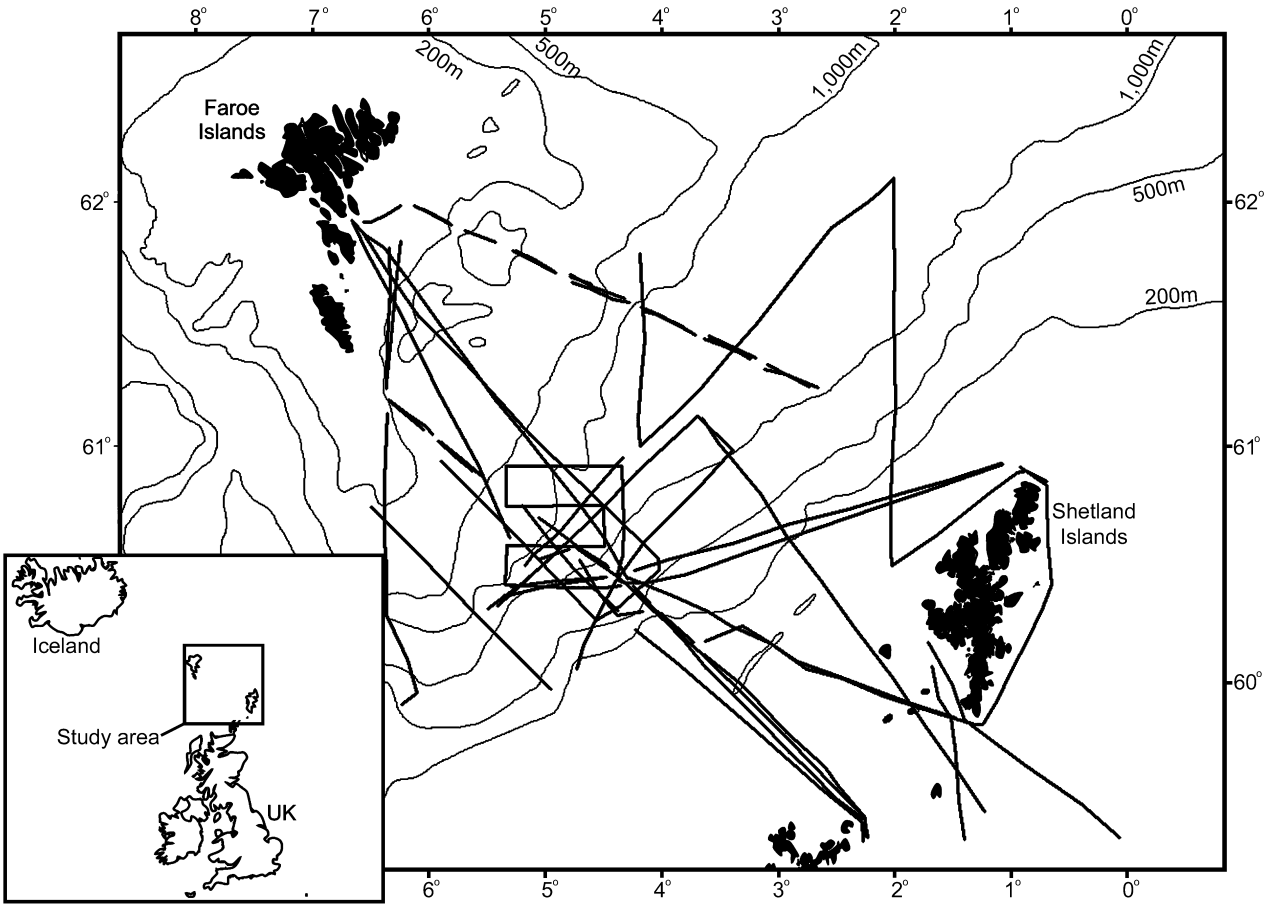

Fig. 1 The location of the study area in the Faroe Shetland Channel (inset), showing the track of the acoustic surveys for sperm whales during May and October 2001 and October 2002. The 200m, 500m and 1,000m contour lines are shown.

Logger2000 (Gillespie, 1997) ran in real time throughout the surveys and maintained a database of monitoring effort, recordings and acoustic detections.

Field protocol

A two-person team worked in shifts to monitor the signals from the hydrophone 24 hours a day. Hydrophones were monitored carefully for one minute every 15 minutes and a qualitative assessment of the strength, from 0 (absent) to 5 (high), of the following acoustic information was recorded to a database using the *Logger2000* software: vessel noise; sea noise; remote ship noise; number of sperm whales; and strength of sperm whale clicks. In addition, an automated recording module within *Logger2000* made 32 recordings direct to the computer's hard disk every 2 minutes.

Throughout the surveys, an automatic click detection and classification program, *Rainbow Click* (Gillespie, 1997) ran continuously. *Rainbow Click* identifies putative sperm whale clicks, calculates their bearings and attempts to distinguish sperm whale clicks from other transients based on their duration and spectral content. To optimise detection of sperm whale clicks, the program's software filters were set to a band pass between 2 and 6kHz to reduce false triggers from low frequency vessel noise and from the survey vessel's 18kHz echo sounder. In addition, the 'forward veto' facility in the software was used to reject any detections within a 20° cone ahead of the array, further eliminating false triggers due to vessel noise.

Rainbow Click calculates bearings to each click from the relative time of arrival of the click at the two hydrophones in the array. Distances of sperm whales from the trackline were determined using target motion analysis as described by Gillespie (1997) and Leaper *et al.* (2000). As the survey vessel travels past individual whales, bearings change, tending to move astern. A series of bearing lines to a vocalising whale plotted from different points on the trackline will cross at the whale's estimated location, and distance from the trackline can be measured from plots. The accuracy of the bearing estimations were assessed by Leaper *et al.* (2000) during a study which utilised similar equipment. Errors were small but increased with wind speed, due to increased movement of the array, from ±1.3° in 14 knots of wind to ±2.3° in 28 knots of wind.

Sperm whale density

Standard line transect techniques were applied to calculate the density of whales during surveys. Effective strip widths (*esw*) were estimated from acoustically derived perpendicular distances from the trackline using the software *DISTANCE* Version 4.0 Beta 6 (Thomas *et al.*, 2001). Two models (hazard rate and half-normal) were fitted to the data and the most parsimonious model was selected based on minimising Akaike's Information Criterion (Buckland *et al.*, 1993). Distance data were truncated to exclude the largest 5% of distances.

For the purposes of this study, it was assumed that $g(0) = 1$; i.e. that all whales on the survey track would be detected. Diving sperm whales typically do not vocalise when they are at the surface but surfacing intervals are generally less than 15 minutes (Gordon and Steiner, 1992). Furthermore, during previous studies of sperm whales using similar equipment, whales were never sighted before being detected acoustically (Leaper *et al.*, 1992; Gillespie, 1997).

To assess the potential effects of sea conditions and survey vessel on the ability to detect whales, the encounter rate (number of whales 100km^{-1}) and *esw* were estimated independently for each Beaufort sea state and for each of the vessels. Standard errors were calculated for each estimate and *z*-tests were used to assess whether there were significant differences in encounter rate and *esw* during different sea states and for each vessel. The density of whales was estimated for each of the cruises independently. A combined estimate was then evaluated as a mean of the estimates for each cruise, weighted by the total effort during each cruise. Density ($\hat{D}$) was estimated by:

$$\hat{D} = n/L{\cdot}(2{\cdot}esw)$$

where:

n = the number of whales detected within the *esw*;
L = distance surveyed;
esw = the effective strip width.

RESULTS

The array was deployed successfully across the majority of the survey routes on each cruise (Fig. 1). A total of 1,676km were surveyed in May 2001, 1,536km in October 2001 and 1,365km in May 2002. A total of 356, 339 and 366 one-minute monitoring periods were made during May 2001, October 2001 and May 2002 respectively. It proved practical to deploy the array and collect useful data during an oceanographic cruise without any significant negative impacts on the survey's primary work. The hydrophone towed steadily behind the vessels and noise levels were reasonable at the vessels' cruising speed of 12 knots. However, at speeds of 14 knots, only occasionally achieved on *FRV Scotia* when travelling down large waves, the hydrophone came to the surface and could not be monitored.

Sperm whale density

Sperm whales were heard in a total of 185 (17.4%) of the monitoring periods. The majority of these sperm whales were also detected by the *Rainbow Click* detection program. From visual inspections of the bearing lines to clicks, it was determined that a total of 79 individual whales were detected. These ranged in distance from 378m to 14.1km from the survey track. Single whales were detected aurally but were not detected by the software on four occasions. These were usually faint clicks that were presumed to be from distant whales.

The *esw* was largest in sea states 1 and 4, was at a minimum during sea state 3 and was higher for the survey vessel *FRV Scotia* than for the *FRV Cirolana*. The encounter rates decreased with increasing sea state and were higher for the *FRV Cirolana* than for the *FRV Scotia* (Tables 1 and 2). However, as a probable result of insufficient sample size and a small effects size, neither the *esw* nor the encounter rates varied significantly with sea state or between the two survey vessels. The data were therefore pooled for all subsequent analyses of whale density.

The perpendicular distance data from both the May 2001 and May 2002 were best fitted by a half-normal model with cosine adjustment terms. Data from October 2001 were best fitted to a Hazard rate model with cosine adjustments (Fig. 2). These resulted in *esw* of 5.53km, 7.6km and 5.41km for the data from the May 2001, October 2001 and May 2002 cruises (Table 3).

Sperm whales were heard in 105 (29.5%), 29 (8.6%) and 50 (13.7%) of the monitoring periods during May 2001, October 2001 and May 2002 respectively. The estimated density of sperm whales during each of the surveys is shown

Table 1

Number of whales (after truncation), *esw* and encounter rate stratified by sea state. Standard errors in parentheses.

Beaufort sea state	Number of whales (*n*)	*esw* (km)	Encounter rate (*n*/100km)
1	14	7.29 (1.99)	2.43 (0.33)
2	24	5.59 (0.76)	2.25 (0.23)
3	25	5.46 (1.27)	2.27 (0.59)
≥4	13	7.92 (2.71)	0.69 (1.04)

Table 2

Number of sightings (after truncation), *esw* and encounter rate stratified by survey vessel. Standard errors in parentheses.

Vessel	Number of whales (*n*)	*esw* (km)	Encounter rate (*n*/100km)
FRV Cirolana	26	5.41 (0.95)	1.89 (0.37)
FRV Scotia	50	5.97 (0.76)	1.54 (0.75)

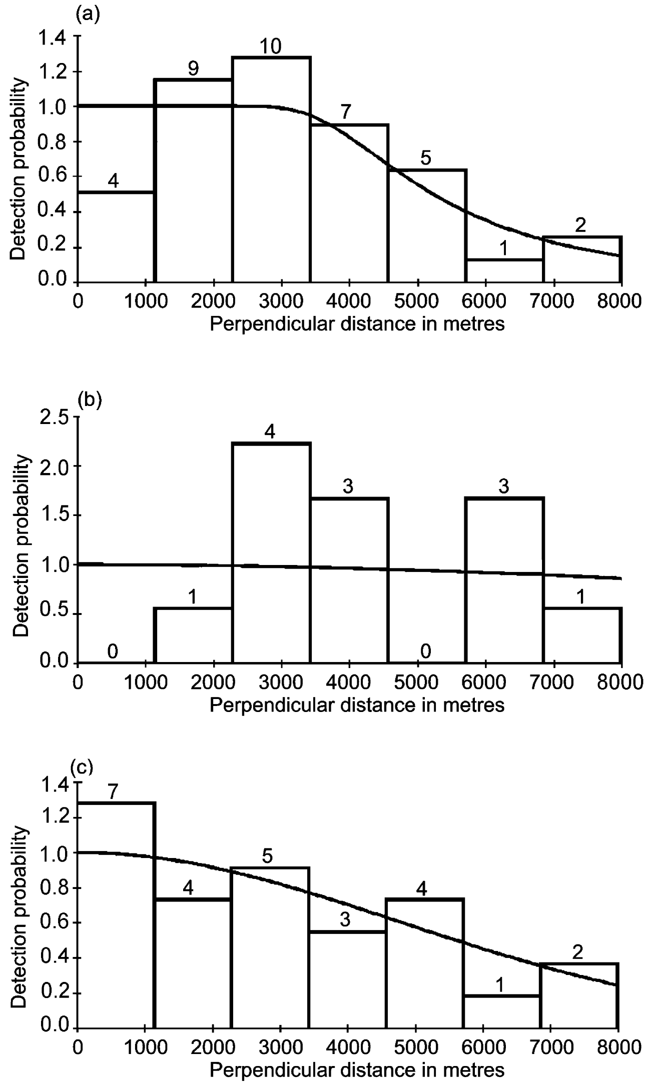

Fig. 2(a-c). Detection functions for sperm whales. Data is from the (a) May 2001; (b) October 2001; and (c) May 2002 surveys. The numbers above the bars represent the number of whales detected.

Table 3

Estimates of sperm whale density for each survey, where *esw* is the effective strip width, *n* is the number of whales used in the estimate (after truncation) and $\hat{D}$ is the estimate of the density of whales. Standard errors in parentheses. The combined estimate of density is expressed as a mean density, weighted by survey effort during each survey.

Date	Effort (km)	*esw* (km)	*n*	$\hat{D}$ (whales/1,000km^2)
May 2001	1676	5.53 (0.77)	38	**2.05** (0.44)
Oct. 2001	1536	7.6 (2.93)	12	**0.51** (0.24)
May 2002	1364	5.41 (0.947)	26	**1.75** (0.46)
Combined	–	–	–	**1.44** (0.83)

in Table 3. The highest estimated density was during the May 2001 and the lowest was during the October 2001 cruise.

Sperm whales were distributed across the majority of the Faroe Shetland Channel. Although the majority of whales were detected within the deeper water of the mid-channel, 13 whales were detected in waters shallower than 500m on the Faroese side of the channel. In contrast, no whales were detected over the shallow water on the Shetland side of the channel (Fig. 3).

DISCUSSION

This study presents current data on density of sperm whales within the Faroe Shetland Channel which complements the results of earlier surveys in the North Atlantic (e.g. Gunnlaugsson and Sigurjónsson, 1990; Øien, 1990).

This study has demonstrated that by using passive acoustic monitoring equipment, small field teams can collect high quality data on the density and distribution of sperm whales (and possibly other cetaceans) utilising oceanographic research vessels as platforms of opportunity. The primary research activities of the survey vessels were not affected and the simple acoustic monitoring and detection system used here, tended by a team of two, proved perfectly adequate for this purpose.

No significant effects on *esw* or encounter rates due to sea state or survey vessel were detected. This highlights advantages of using passive acoustics to survey for sperm whales in regions such as the northeast Atlantic, where sighting conditions are often poor due to rough seas. However, it should be noted that other factors that could affect the detection rate of whales were not examined in this study; these are likely to include underwater propagation conditions and background noise levels.

Esw were estimated to be between 5km and 7km in this study. This is lower than the *esw* calculated in a previous study using similar equipment (Leaper *et al.*, 2000); a factor which could result from differences in the acoustic properties of the water or from variations in noise levels. The cruising speed of the vessel used by Leaper *et al.* (2000) was around 2 knots slower than the vessels used in this study. Therefore, increased vessel noise could potentially be a factor that reduced the detection range of the array in this study. In addition, the hydrophones are likely to tow closer to the water surface at higher speeds, potentially also reducing the range of the array due to noise interference from breaking waves.

As in previous acoustic studies (Barlow and Taylor, 1998; Leaper *et al.*, 2000), it was assumed in this study that *g*(0) was equal to one, that is to say that all whales on the survey track were detected. Sperm whales are not generally vocal

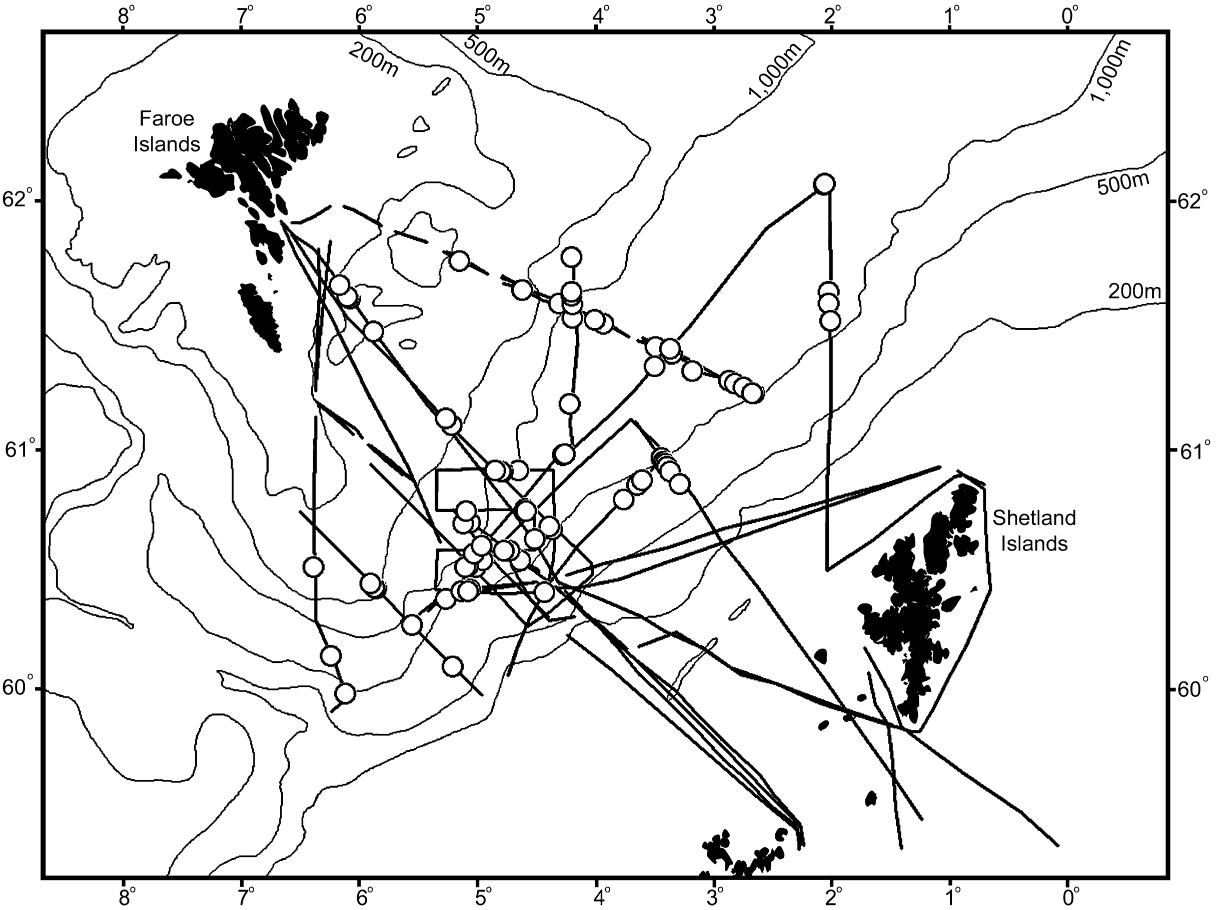

Fig. 3. Acoustic survey track (grey lines) and the locations of individual sperm whales (open circles) in the Faroe Shetland Channel during surveys in May and October 2001 and May 2002. The 200m, 500m and 1,000m contour lines are shown.

when at the water surface and therefore, there was the potential to miss whales on such occasions. Male sperm whales off the coast of Canada typically spend around 8 minutes near the water surface between dives, during which time they are generally silent (Whitehead *et al.*, 1992). At the survey speed of 12 knots in this study and with an effective detection range of 6km, a whale on the trackline would have to be silent for around 32 minutes to remain undetected. It is therefore unlikely that a significant proportion of diving whales were missed during this study, and the assumption that $g(0) = 1$ appears to be valid. However, female sperm whales and their young, living in temperate waters, have been observed to spend several hours a day in a resting or socialising mode during which they rarely produce the sort of regular clicks detected during acoustic surveys. This makes such animals undetectable during acoustic surveys for periods of several hours (Hiby and Lovell, 1989). Although it is not known whether the mature males found in the current study area also have significant non-vocal resting periods, males off Nova Scotia and New Zealand rarely stayed near the surface for prolonged periods (Gordon *et al.*, 1992; Whitehead *et al.*, 1992). To better assess the need for a correction factor to account for silent animals, it would be useful to collect data on patterns of vocal output in this study area and/or to directly measure detection probability using dual-mode independent platform survey techniques.

The estimates of whale density in this study ranged from 0.51 to 2.05 with a combined mean of 1.44 whales per 1,000km^2. The mean estimate in this study is almost exactly the same as a recent mean density estimate for the 25% of the worlds oceans that have been visually surveyed (Whitehead and Planck, 2002). The estimates are within the lower range of previous estimates of density in the northeast Atlantic which varied from 0.82 to 10.16 whales per 1,000km^2 (Øien, 1990). They are also similar to estimates made within the eastern tropical Pacific, where densities of between 0.26 and 1.16 per whales 1,000km^2 have been recorded (Hammond and Laake, 1981; Laake and Hammond, 1984). However, it is important to note that because the survey tracks in this current study are not a representative sample of the entire region, it is not possible to compute abundance estimates and comparisons with other areas are difficult. Furthermore, it is unlikely that the results are directly comparable to previous estimates from sightings data where it was not possible to correct the estimates for submerged animals. Perhaps more comparable are the results from a similar passive acoustic survey in the Southern Ocean (Leaper *et al.*, 2000) where estimates were lower (between 0 to 0.13 whales per 1,000km^2) than those made during this current study.

There appeared to be differences in the density of whales between May and October with fewer whales detected during October than May. This contrasts with results from previous opportunistic surveys that suggested that sightings of sperm whales in the northeast Atlantic peak during the second half of the year (Evans, 1997). However, sample sizes were small and sighting conditions were likely to have played a significant role in the results from this previous study (Evans, 1997). Alternatively, as different routes were surveyed during each of the cruises in this present study, the variation in density may represent relatively fine-scale spatial patterns of whale distribution.

The distribution of whales in the Faroe Shetland Channel is consistent with previous studies showing that sperm whales primarily occur adjacent to, or over the continental shelf break (e.g. Griffin, 1997; Gordon *et al.*, 1999; Waring *et al.*, 2001; Weir *et al.*, 2001); the majority of whales were detected within the deeper water around the middle of the channel with a smaller number detected over the Faroes Plateau. As with most predators, this pattern is likely to reflect spatial variations in the distribution of prey (Hairston *et al.*, 1960). However, a lack of reliable information about the distribution of prey species in the channel makes it extremely difficult to explore links between the predator and prey distributions.

More survey effort is now required to quantify changes in seasonal and spatial patterns of distribution. With increased effort, it will be possible to collect better information on the effects of background noise and propagation conditions on detection range. In addition, it will be useful to explore how oceanographic, topographical, biological and anthropogenic factors affect seasonal distributions and abundance.

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The abundance of blue whales on the Madagascar Plateau, December 1996

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ABSTRACT

As part of the International Whaling Commission's SOWER blue whale research programme, two sighting vessels, the *Shonan Maru* and the *Shonan Maru No.2,* surveyed the Madagascar Plateau between 25° and 35°S, 40° and 45°E, in December 1996. A total of 95 sightings of 110 blue whales (assigned in the field as pygmy blue whales – see discussion), 14 sightings of 21 blue whales (subspecies undetermined) and 12 sightings of 13 'like blue' whales was made in 23 days. In the first half of the survey, the whole research area was covered in a mainly pre-determined zigzag search pattern, and the associated sightings and effort have been used to derive density estimates for blue whales for the area. Sightings in the second half of the survey, where effort was directed at blue whale concentrations, have only been used to provide supplementary data for calculation of the effective search half-width and mean school size. The resulting population estimate is 424 (CV = 0.42), or 472 (CV = 0.48) whales when 'like blue' sightings are included. Dive times and surfacing behaviour recorded in just over 21h of monitoring suggest that the assumption that all groups on the trackline were seen ($g(0) = 1$) is reasonable. As the geographical extent of the survey area was substantially less than that of past catches of blue whales in the region in December, this estimate must refer to only a portion (possibly about one third) of the total population. Some evidence of feeding on euphausiids in the region was detected, possibly as a consequence of a localised upwelling cell at the southern tip of Madagascar.

KEYWORDS: ABUNDANCE ESTIMATE; BLUE WHALE; INDIAN OCEAN; LINE TRANSECT; RESPIRATION; FEEDING

INTRODUCTION

In the Southern Hemisphere there are two generally recognised 'forms' of blue whales (*Balaenoptera musculus*), which have been taxonomically referred to the sub-species Antarctic blue whale *B. m. intermedia* and pygmy blue whale *B. m. brevicauda* (Rice, 1998). Pygmy blue whales were originally described as occurring mainly in the sub-Antarctic Zone of the Indian Ocean, between 0° and 80°E, especially in the waters round the Prince Edward Islands, Crozet and Kerguelen Islands (Ichihara, 1966). Subsequently Zemsky and Sazhinov (1982) described three independent sub-populations of pygmy blue whales in the Indian and South Atlantic Oceans:

(a) the Northwest Region, including the tropical and equatorial waters of the Arabian Sea, waters round the Laccadive Islands and the Maldives, and westward to Sri Lanka;
(b) the sub-Antarctic Region, including the tropical and subtropical waters of the east coast of South Africa and Madagascar, as well as the sub-Antarctic waters round the Crozet and Prince Edward Islands; and
(c) the Australian Region, including the tropical, subtropical and sub-Antarctic waters of the southeastern Indian Ocean and Tasman Sea.

The population of blue whales that inhabits the Peru Current, off the coasts of Peru and Chile, may also include pygmy blue whales (Aguayo L, 1974; Donovan, 1984).

Zemsky and Sazhinov (1982) believed that whales in the Northwest Region were largely non-migratory, owing to the high zooplankton productivity of the northwestern portion of the Arabian Sea. However, based on seasonal distributions they believed whales from the other two regions to be migratory. Whales from the sub-Antarctic Region were postulated to move south from the Seychelles and Amirante Islands through the Mozambique Channel past Madagascar and the Walters Shoal to the Crozet and Prince Edward Islands during spring/summer, and back again in the autumn. Whales from the Australian Region moved south from the Banda Sea along the western coast of Australia in spring/summer, then split into a group that went west to Amsterdam and St Paul, and a group that went east towards the Tasman Sea, returning again in autumn.

Mikhalev (2000) also concluded that the blue whales of the Northwest Indian Ocean were isolated from other populations in the Indian Ocean, but that they ranged as far south as 5°S, thereby including those found around the Seychelles. Foetal size composition data, however, suggested that whales from the Seychelles aggregation (unlike others from the Arabian Sea) experienced a Southern Hemisphere breeding season. This paper follows the distribution and migration links postulated by Zemsky and Sazhinov (1982; see Fig. 1).

In December/January 1996/97, the second cruise in the International Whaling Commission's Southern Ocean Whale and Ecosystem Research (SOWER) programme on Southern Hemisphere blue whales took place in the waters

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immediately south of Madagascar, and so presumably on the migration route of whales from the sub-Antarctic Region. Its objectives followed those of the SOWER programme, namely, to establish criteria for distinguishing between the two sub-species at sea and to develop techniques for assessing the current status of blue whales. Some of the results of the cruise are presented in this paper, and include an assessment of the number of blue whales and some description of their behaviour in the area. This is the first published research on the status of this population since the cessation of commercial whaling.

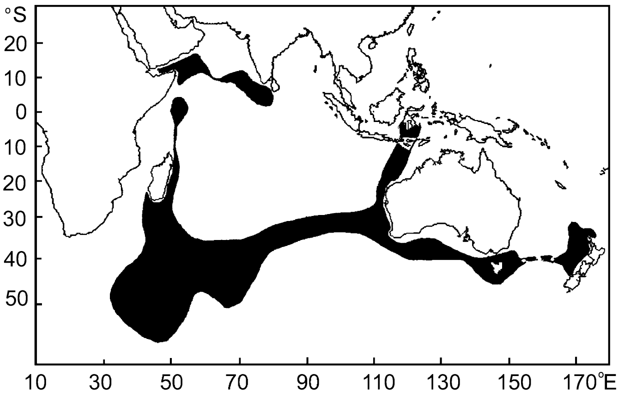

Fig. 1. Distribution of pygmy blue whales in the Indian Ocean, based largely on Soviet whaling operations (after Zemsky and Sazhinov, 1982; Mikhalev, 2000).

MATERIAL AND METHODS

Cruise overview

The Japanese Government made two survey vessels, *Shonan Maru* (SM) and *Shonan Maru No. 2* (SM2), available for the survey. They were converted whale catchers, each 916 gross tons, 64.8m long, with a masthead lookout 20m above sea level and a further lookout position on the upper bridge 11m above sea level.

The research area, chosen largely on the basis of past sightings of blue whales from Japanese scouting vessels and catches by Soviet expeditions, was defined as between latitudes 25° and 35°S, and longitudes 40° and 45°E, or straddling the Madagascar Plateau (Fig. 2). This area was divided into northern (25°-30°S) and southern (30°-35°S) sectors. Both sectors were searched in the initial phase of the survey.

As the cruise track on this half of the cruise (7-18 December) was designed to cover the whole research area evenly, without reference to suspected blue whale concentrations, the search effort has been considered as essentially unbiased, and used in density estimation.

Based mainly on prevailing weather conditions and the distribution of past blue whale catches by the USSR, effort in the second half of the cruise was redirected to the southern half of the research area, but extended one degree of longitude to the east. In this sector of the cruise (21 to 29 December), blue whale concentrations were specifically sought out; consequently the associated effort cannot be used for density estimation. On the other hand, the methods of looking for whales were identical to those used in the first half of the cruise, so that the angle and distance data can be used in determining effective search half-widths, and group size information for determining mean school size, for each vessel.

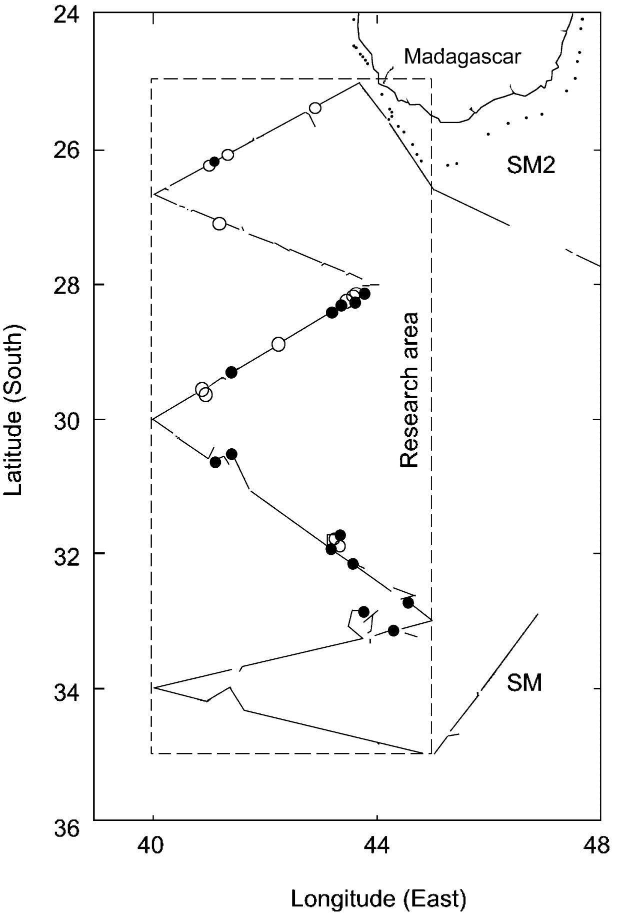

Fig. 2. Research area, cruise track and blue whale sightings (solid dot: primary, open dot: secondary) south of Madagascar, 7-18 December 1996.

Sighting protocol

The normal searching speed for each vessel was 11.5 knots. Two crewmembers kept a lookout from the masthead with three to five crewmembers or scientists from the upper bridge. Searching was carried out by naked eye or using 7×50 binoculars. When a sighting was made, the person making the sighting estimated its angle from the ship's track and its radial distance from the ship. This information was relayed to a recorder on the front bridge. If the description of the sighting suggested that it was a target species (e.g. a blue whale), or potentially could be a target species, the ship would turn immediately towards the sighting and approach close enough to make a positive identification and estimate of group size. Once the vessel had finished working with a sighting, it did not return directly to the trackline, but steered a course that converged at 45° with the track-line.

For each blue whale sighting, the observers on the masthead were to be interrogated regarding the criteria they used to make their identification as pygmy or Antarctic blue whale. The questions asked were:

(1) Relatively large head? Yes/No/Unknown.
(2) Relatively short tail (posterior end of dorsal fin to fluke notch)? Yes/No/Unknown.
(3) Dorsal fin/keel submerge almost simultaneously before long dive? Yes/No/Unknown.
(4) Relatively dark body colour? Yes/No/Unknown.

Surfacing rates of blue whales were investigated through visual observations. When a sighting of a large whale that might be a blue whale was made, it was approached only close enough to make a positive identification (usually within 0.5 to 1.0 n.mile). If a blue whale was identified, and while the ship drifted on acoustic watch (with engines off but other machinery running), continuous observations were made of the surfacing and blowing behaviour of the group. The times at which these observations began (and ended) were supposed to be independent of the surfacing behaviour of the group. Observers in the masthead or on the upper bridge assisted in calling out each surfacing, and the production and disappearance of each blow (as seen through polarised glasses) were also noted. The data were either recorded manually in real time using a digital stopwatch (SM), or spoken into a cassette-recorder and analysed later (SM2).

The following definitions were used in analysis.

(1) Blow intervals: the time between successive blows of the same group.
(2) Blow duration: the time that a blow, once produced, was visible to an observer wearing polarised glasses. The time of disappearance was, as far as possible, taken as that at which an observer scanning the sea (as opposed to the researcher who was aware of the blow's presence) would have failed to detect it.
(3) Surfacing time: the time between the production of the first and last blows of a sequence, when such a sequence was obvious. The last blow of a sequence was frequently indicated by an animal subsequently rounding out or even fluking.
(4) Dive time: the time between the production of the last blow of a surfacing sequence and the production of the first blow of the next sequence.
(5) Blows per surfacing: the number of visible blows produced in one surfacing sequence.
(6) Blow production rate: the number of blows produced per individual per unit time.

For all parameters apart from blow duration, only observation periods lasting 20mins or more were used in analysis. This was to reduce bias caused by the exclusion of longer dive times in very short periods of observation. For measurements of blow intervals and blow production rate, only observations involving single animals were used to avoid confusion. For measurements of surfacing times and dive times, only completed sequences were used. For estimation of blow production rate, however, the total monitoring period (including incomplete dive or surfacing sequences) was used, but experiments in which a number of cues were believed to have been missed were excluded. Blow durations were calculated from all available data.

Abundance estimation

Abundance estimation was carried out using the DISTANCE package (Buckland *et al.*, 1993). The basic formula for the abundance in a stratum is:

$$P = \frac{A \cdot \overline{s} \cdot n_s}{2 \cdot w_s \cdot L} \qquad (1)$$

where:

P = uncorrected abundance (assumes all schools on the trackline are sighted);
A = open ocean area of stratum;
$\overline{s}$ = mean school size;
n_s = number of schools sighted during primary search mode;
w_s = effective search half-width for schools;
L = search effort (distance steamed in primary search mode).

All units of distance are in nautical miles. The components of this formula were evaluated as set out below.

Stratum areas (A)

For the analysis, the two strata within the overall area surveyed were divided at 29°30'S, corresponding to the sectors surveyed by each vessel. *A* refers to the open ocean area of each of these strata.

Search effort and sightings (L and n_s)

Search effort was classified according to the following codes:

BB = Full search effort on trackline, in closing mode for large whales only;
CO = Confirming sighting information;
BR = Full search effort, returning to trackline in closing mode at an angle of 45° (for large whales only);
TD = Steaming, on the constructed trackline, without full search effort;
TF = Steaming, off the constructed trackline, without full search effort;
BX = Begin experiment;
DR = Drifting.

Sightings were either primary (made while the vessel was on full searching effort, i.e. BB or BR codes) or secondary (made while the vessel was not on full searching effort, i.e. in all other codes). Only primary sightings (and the associated search effort in BB and BR modes) have been used for abundance estimation; n_s is the number of such primary sightings made of blue whale schools.

Sighting rates (n_s/L) and their CVs were estimated separately for the northern and the southern sectors. The variance estimate was obtained by treating days as the sampling units.

Distance and angle estimation bias

No experiment to identify and calibrate any biases in individual observer's estimation of angle and distance was carried out on the cruise, but the same vessels and crew participated in such experiments as part of the subsequent 1996/97 IWC-SOWER circumpolar Antarctic cruise. Consequently the latter correction factors were adopted for the distances and angles estimated by the same personnel on the blue whale cruise. These factors are listed in the files associated with the validated data for the SOWER surveys stored in DESS (Strindberg and Burt, 2000), specifically file C:/iwcdb/idcr/getdata/unbias.db.

Effective search half-width (w_s)

The estimated perpendicular distance distributions of schools in each sector were smeared using smearing parameter values of 3.24° (angle) and 0.29 (relative distance), these were the smearing values used for blue whales in Branch and Butterworth (2001a). Effective search half-width was then estimated by fitting the hazard-rate model to the data grouped into perpendicular distance intervals of 0.1 n.mile and truncated at 2 n.miles (i.e. discarding about 5% of the data, as recommended by Buckland *et al.*, 1993). Since the same methods of searching for whales were used in both halves of the cruise, the angle and distance data collected during both halves were used in determining effective search half-widths for each vessel.

M*ean school size* ($\overline{s}$)

A regression of *ln* (school size) against the detection function $g(y)$ was used to obtain a mean school size when the regression was significant at the 15% level; when the regression was not significant, average school size was used: this is the standard approach adopted by the IWC Scientific Committee for minke whale abundance estimation from the IDCR/SOWER surveys (Branch and Butterworth, 2001b). The data from both phases of the cruise were used to estimate mean school size in each sector and the sizes of all schools were assumed to have been confirmed.

General

Unless otherwise indicated, all values following a ± sign indicate one standard error of the mean.

RESULTS

Whales seen

The two vessels combined made a total of 95 sightings of 110 animals assigned in the field to pygmy blue whales, 14 sightings of 21 'unidentified' blue whales and 12 sightings of 13 'like' blue whales. There were no sightings classified as Antarctic blue whales.

The results of the crew questionnaire on SM were positive for the questions regarding large head, short tail and dorsal fin/keel exposure on 35 occasions, and negative or doubtful on none. For the question regarding a relatively dark colour, the reply was positive on 23 occasions and doubtful on 5 occasions; on another 7 occasions the reply was left blank but there were no negative responses. On SM2 there were positive responses on 4 occasions to all four questions (completion of the questionnaire was abandoned on 10 December). No attempts were made on either vessel to sketch the blowhole shape. Qualifying remarks were made on 6 occasions. These were:

9 December —'Spotting different from Antarctic blue —under dorsal fin spots are larger' (Boatswain, SM2); 'Darker than Antarctic blue' (Captain, SM2).
11 December —'95% confidence as 'pygmy' by Boatswain and Captain' (SM).
12 December —'Animals do not show body much. Show the head very briefly. Show the fin and keel only before longer dive. One animal [fluked] one time when *Shonan* approached to whales' (SM).
15 December —'Very large tadpole-like head' (SM).
23 December —'Fluke-up two times' (SM).
29 December —'85% pygmy blue' (SM).

Blue whale density estimates inside research area

Abundance estimates in each sector, and the values of the parameters used to compute these estimates, are presented in Table 1, with their associated CVs. Plots showing the fit of the hazard rate function to the perpendicular distance distributions for the sightings data are given in Fig. 3. The total population of pygmy blue whales in the research area is estimated to be 424 (CV = 0.419).

Only one 'like blue' sighting occurred in primary search mode during the first half of the cruise; when this sighting is included in the analysis, the abundance estimate increases to 472 (CV = 0.477), i.e. an increase of about 11%.

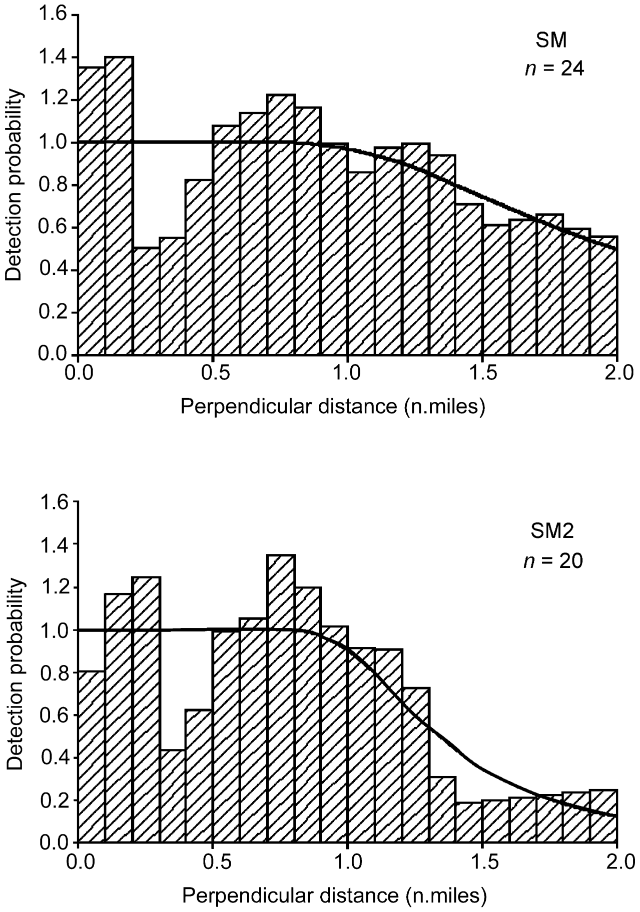

Fig. 3. Hazard rate model fits to smeared perpendicular distance distributions from blue whale sightings south of Madagascar, December 1996.

Blue whales outside the research area

When the boundaries of the research area were chosen, it was realised that they did not cover the entire range of the population at that time of year. The distribution of Soviet catches in the southwest Indian Ocean in December, for instance, showed that blue whales were taken between 10° and 44°S, and from 37° to 55°E , with only 373 (or 37%) of the catches occurring within the research area (Table 2).

This might suggest that the total population is of the order of three times the abundance estimates obtained here. However such an extrapolation factor could be biased if

Table 1

Abundance estimates and associated parameters for blue whales south of Madagascar; the figures in parenthesis are CVs. The criteria used to select the method of mean school size estimation opted for the average school size for the SM's, and for the regression method for the SM2's observations. Symbols are defined in the text (see equation 1), except that $D_s = P/A$ is the density of schools per unit area.

Year	Vessel	Sector	A (n.mile^2)	n_s^*	L (n.mile)	n_s/L	w_s (n.mile)	$\bar{s}$	D_s (n.mile^{-2})	P	Total P
96/97	SM	S	83,820	6	1,006.1	0.0067 (0.455)	1.74 (0.190)	1.24 (0.084)	0.0019 (0.493)	199 (0.500)	424 (0.419)
	SM2	N	71,410	4	538.1	0.0088 (0.632)	1.40 (0.164)	1.00 (0.030)	0.0032 (0.653)	226 (0.654)	

*After truncation at 2 n.miles.

Soviet catches were not spread uniformly over the distribution area of the population, and have high variance if there is large inter-annual variability in the whales' distribution pattern.

Estimated body lengths

Just before leaving each sighting, one of the crew in the masthead lookout would provide an estimate of the body length of all whales present. Such estimates are available for 95 blue whales, 38 from the SM and 57 from the SM2 (Fig. 4).

The estimated lengths ranged from 40 to 72ft, but those provided by the SM were smaller than those from the SM2 (medians = 62.5ft and 66ft respectively, Mann-Whitney T = 1235, $p < 0.0001$). This difference extended to the calves, which were estimated at 40-43ft long ($n = 3$) on the SM and 46-59ft ($n = 5$) on the SM2.

Incidence of calves

Of the 95 blue whales approached close enough to obtain estimates of size, 8 (8.4%) were classified as calves. Such a classification was based on both size and behaviour (associative with a larger individual).

Evidence of feeding

No direct observations of feeding behaviour were made, but faeces were seen produced on four occasions between 21 and 29 December, in the southern half of the research area. One of these instances occurred on 25 December at 32°49.1'S 43°02.6'E, and a second at 32°52.6'E 43°34.6'E on 28 December. A faecal sample was collected on 28 December and proved to contain digested euphausiid remains. Variation in the morphology of the mandibles and spermatophores present suggested three and two different species of euphausiid respectively, but none could be specifically identified (M. Gibbons, pers. comm.).

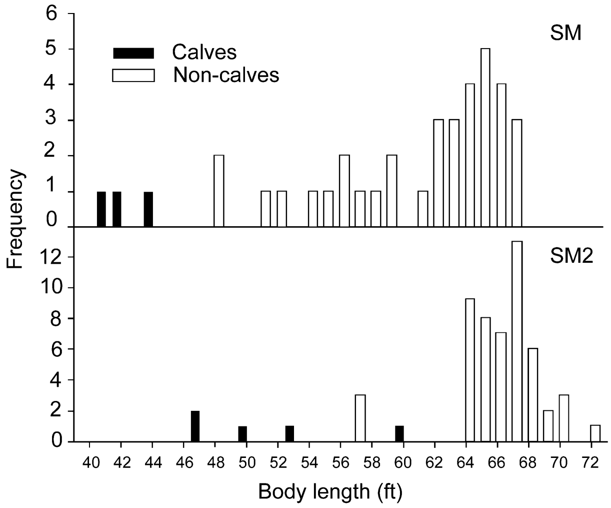

Fig. 4. Frequency distribution of estimated sizes of blue whales seen south of Madagascar, December 1996.

Surfacing behaviour

In total, 21h 14min of observations were available, from a total of 40 groups containing 47 whales (Table 3). Overall blow rates ranged from 0.5 to 1.4 per min, with an average of 0.95 ± 0.05 ($n = 20$) blows/min per individual. The distribution of surfacing intervals, however, was markedly bimodal (Fig. 5). Although short blow intervals (less than 40s apart) predominated, other intervals were markedly longer, ranging from about 180 to 660s with a mode at around 300-360s. This reflected a somewhat stereotyped respiratory cycle, in which surfacing sequences of several blows close together were separated by longer dives.

Average surfacing times for 27 single animals ranged from 47 to 222s, with a mean of 109 ± 8s, while for 7 pairs average surfacing times ranged from 59 to 115s, with a mean

Table 2

Soviet catches of pygmy blue whales in the southwestern Indian Ocean in December (box represents research area with a total catch of 377).

Latitude (°S)	Longitude (°E)																
	39	40	41	42	43	44	45	46	47	48	49	50	51	52	53	54	Total
10													21				21
11										3		3					6
12												25					25
14														1	22		23
15																8	8
18													4				4
24			4	70							4						78
25			28	13							1						42
26		9		22	25	4	3										63
27		7	5	14	6						1						33
28				8	8	2	2	2									22
29				3		15	3	2	7								30
30						37	2		2		3						44
31				15	11	33	47	1				2	5				114
32						23	4	25		2							54
33	1			2	5	66	71		2								147
34					1	15	32		6		7	6	2				69
35								1		6	5	38	17		4		71
36						18						15	10	6	21	20	90
37												35	17	1			53
38																	
39							2										2
40																	
41											4						4
43								7									7
Total	1	16	37	147	56	213	166	38	17	11	25	124	76	8	47	28	1,010

of 94 ± 7s. During these periods the average number of blows produced ranged from 4 to 13 (mean 8.0 ± 0.5) for single animals and 3.7 to 9.2 (mean 7.4 ± 0.7) for pairs.

The durations of 908 blows were recorded, being highly variable and ranging from 0.9 to 18.8s. Such variability is to be expected, given that the estimated duration is dependent not only on the strength of the initial expiration (which may be related to body size or behavioural state) but also on the prevailing meteorological conditions (with wind strength and back-lighting being perhaps the most important). The duration of blows produced in the first half of a surfacing sequence was more often longer than for those produced in the second half (38 vs 21, Chi-square = 4.898, $p < 0.05$). Mean blow durations calculated for the SM (4.7 ± 0.5s) and for the SM2 (6.2 ± 0.3s) were significantly different ($t = -2.29$, two-tailed $p = 0.03$), possibly indicating differences in observer criteria rather than animal behaviour.

Average dive times (or intervals between surfacing sequences) for 32 single whales ranged from 145 to 896s, with a mean of 428 ± 28s, while for 7 pairs, average dive times ranged from 340 to 606s, with a mean of 501 ± 36s.

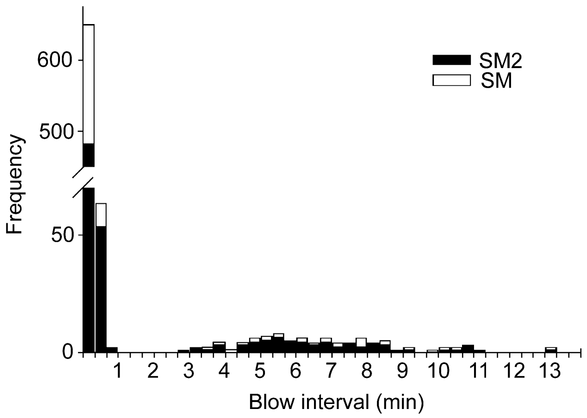

Fig. 5. Frequency distribution of blow intervals for blue whales south of Madagascar, December 1996.

DISCUSSION

The questionnaires completed regarding what characteristics of the whales were used in sub-species determination were fairly consistent in giving definite responses, suggesting that the observers were confident of their identifications. However, this confidence might have been somewhat misleading, as the sighting on 29 December that was classified as positive by SM for all four questions, was annotated that it was ‘85% pygmy blue’, indicating that the crew were not totally confident of their identification. Some of this uncertainty may have arisen from the fact that the whales fluked up occasionally, a behaviour that the crew did not expect to see in pygmy blue whales (KS, pers. comm.). On the SM2 at least, there was the feeling that the way the questions were phrased was producing ‘standard’ answers, and that (combined with the lack of adequate interpretation) led to their discontinuation.

The estimated sizes of the blue whales from both ships were much smaller than those reported earlier for pygmy blue whales, where over 90% of the catch in 1959/60 exceeded 70ft in length (Ichihara, 1961). Although 70ft was the minimum legal length in operation at the time these catches were made, the size difference seems too great to be just the result of selection. Given the significant inter-vessel difference in length estimates (which might have been influenced by the fact that one bosun had much more experience in whaling for pygmy blue whales than the other −KS, pers. comm.), and the known difficulty in making such estimates at sea (Best, 1984), it seems likely that both vessels consistently underestimated the sizes of the blue whales they saw. The incidence of calves confirms that adult animals were present.

Ichihara (1966) reported monthly pregnancy rates for pygmy blue whales in the Antarctic of 35.6% for February, 23.1% for March and 6.9% for April, a trend that he attributed to the progressive emigration of pregnant females to the north. Consequently he felt the value for February (35.6%) should be regarded as the mean pregnancy rate for pygmy blue whales, which he considered extremely low compared to the figure of 49.4% for the Antarctic blue whale in February/March. Figures given by Mikhalev (2000) indicate an observed pregnancy rate of 41.3% for blue whales from the Northwest Region, but this is in a sample that only contained 1.3% lactating animals. Assuming that the proportion of lactating females should be roughly equivalent to the number of pregnant females, a ‘corrected’ pregnancy rate from these data would be 41.3/(100 + (41.3 - 1.3)) = 29.5%. Mikhalev also commented on the low reproductive capacity of these blue whales. Assuming an equal adult sex ratio, and that mature animals comprised about 56% of the population (Ichihara and Doi, 1964), then the pregnancy rate observed for the sub-Antarctic population would translate into an expected calving rate of $(35.6/2) \times 0.56 = 10\%$ of the total population. Given that this pregnancy rate value probably does not take selection against lactating females fully into account, the estimated calving rate compares well with an observed calf percentage of 8.4% during the IWC SOWER cruise.

Given (a) the small estimated sizes of the animals seen; (b) an incidence of calves suggesting that mature animals were fully represented; (c) the results of the questionnaires; and (d) the composition of historical catches in the region, there seems little doubt that most if not all the animals seen were pygmy rather than Antarctic blue whales.

Based upon catch age-composition and CPUE data, Ichihara and Doi (1964) estimated the initial (1960) population size (all ages) of pygmy blue whales in the region north of 54°S and from 0° to 80°E (equivalent to the sub-Antarctic Region) as 7,600 or 11,000. These alternatives depended on whether ages and mortality rates were calculated on the basis of one or two laminations being deposited annually in the ear plug. More recent work has supported an annual rather than biannual deposition rate in at least fin whales (Lockyer, 1984), so the initial population size is more likely to have been 7,600 animals. Ichihara and Doi estimated that this would have been reduced to 6,000 animals by the start of the 1963/64 season.

Zemsky and Sazhinov (1982) extended this assessment forward in time, using the initial population estimate of 7,600, a catch series that included previously unreported Soviet takes and assuming a net recruitment rate of 5%. They estimated that by the close of the 1971/72 season, this population had been further reduced to some 4,000 animals. The next season international observers were introduced to Antarctic fleets, at which time all hunting of pygmy blue whales ceased. In total, some 6,875 blue whales were removed from the sub-Antarctic population between 1960/61 and 1971/72 (Zemsky and Sazhinov, 1982).

The population estimate, albeit partial, of 424-472 blue whales obtained here is the first for the sub-Antarctic population since the close of commercial whaling.

Table 3

Details of monitoring blue whale surfacing behaviour, Madagascar, December 1996 (means are given ± one standard error, sample size in parentheses).

Date	Sighting no.	Group size	Surfacing times (*s*)	No. blows/ surfacing	Blow intervals* (*s*)	Dive times (*s*)	Blow duration (*s*)	Duration of observation	Blow rate/ min**
Shonan Maru									
11 Dec.	22	2	99 ± 39 (4)	8.3 ± 2.4 (4)	17.3 ± 2.6 (34)	606 ± 139 (5)	2.8 ± 1.4 (4)	59min 49s	
12 Dec.	15	2	115 (1)	8.0 (1)	16.9 ± 1.5 (16)	526 (1)	4.8 ± 0.9 (8)	31min 46s	
13 Dec.	6	1	-	-	13.3 ± 2.9 (11)	-	3.6 ± 1.6 (5)	2min 26s	
14 Dec.	3	2	92 ± 11 (3)	6.3 ± 0.3 (3)	16.5 ± 1.4 (19)	441 ± 44 (4)	6.7 ± 0.7 (18)	34min 44s	
15 Dec.	1	2	106 ± 3 (3)	7.7 ± 1.7 (3)	14.8 ± 1.3 (34)	579 ± 20 (4)	10.6 ± 1.0 (36)	45min 23s	
	2	1	148 (1)	10 (1)	17.2 ± 1.2 (21)	620 (1)	3.1 ± 0.6 (10)	40min 01s	
17 Dec.	1	1	78 ± 1 (2)	6.5 ± 1.5 (2)	13.9 ± 1.3 (15)	510 ± 25 (3)	5.6 ± 1.2 (10)	28min 58s	0.6
	4	1	86 ± 36 (3)	7.0 ± 2.3 (3)	14.9 ± 0.9 (24)	413 ± 55 (3)	4.7 ± 0.5 (10)	39min 37s	1.4
18 Dec.	7	1	47 ± 8 (5)	4.8 ± 1.0 (5)	12.1 ± 1.2 (20)	320 ± 34 (6)	5.3 ± 1.1 (10)	36min 5s	0.7
21 Dec.	1	1	112 ± 14 (5)	7.4 ± 0.7 (5)	13.4 ± 1.0 (34)	340 ± 26 (5)	3.2 ± 0.3 (29)	38min 9s	1.2
	9	1	49 ± 19 (2)	7.0 ± 3.0 (2)	8.1 ± 1.3 (12)	335 ± 25 (2)	-	12min 36s	
23 Dec.	3	1	74 ± 7 (6)	6.7 ± 0.9 (6)	12.9 ± 0.6 (41)	375 ± 41 (6)	1.6 ± 0.2 (9)	46min 18s	1.0
24 Dec.	1	1	-	-	13.8 ± 0.8 (13)	354 (1)	5.2 ± 0.5 (13)	8min 57s	
	7	1	94 (1)	5.0 (1)	23.5 ± 5.5 (4)	349 ± 8 (2)	-	13min 12s	
26 Dec.	2	1	88 ± 15 (2)	8.0 ± 1.0 (2)	12.5 ± 0.6 (14)	528 ± 59 (2)	4.0 ± 0.8 (8)	20min 40s	0.8
	3	1	-	-	-	688 (1)	-	13min 4s	
27 Dec.	4	1	-	-	36.7 ± 17.4 (6)	423 (1)	-	11min 43s	
28 Dec.	9	1	-	5.0 (1)	11.4 ± 1.3 (7)	288 ± 75 (2)	-	10min 56s	
	11	1	146 (1)	13.0 (1)	12.2 ± 0.8 (12)	258 ± 54 (2)	3.6 ± 0.4 (9)	11min 6s	
29 Dec.	1	1	91 (1)	5.0 (1)	18.3 ± 3.3 (9)	145 ± 47 (2)	5.4 ± 1.0 (5)	7min 36s	
	3	1	-	-	-	896 (1)	-	14min 56s	
Shonan Maru No. 2									
10 Dec.	3	1	121 ± 8 (5)	9.2 ± 0.7 (5)	15.0 ± 0.4 (41)	496 ± 21 (4)	6.4 ± 0.4 (45)	53min 17s	0.9
	2	2	59 ± 4 (3)	3.7 ± 0.3 (3)	22.2 ± 3.2 (8)	601 ± 90 (2)	5.8 ± 0.4 (11)	32min 17s	
12 Dec.	4	1	133 ± 4 (4)	11.0 ± 0.4 (4)	14.1 ± 0.4 (49)	689 ± 34 (4)	6.9 ± 0.2 (53)	64min 44s	0.8
16 Dec.	4	2	92 ± 8 (5)	9.2 ± 0.7 (5)	10.7 ± 0.8 (39)	340 ± 19 (4)	5.2 ± 0.4 (38)	43min 6s	
	7	1	134 ± 6 (4)	9.0 ± 0.7 (4)	16.6 ± 0.9 (40)	468 ± 22 (4)	4.9 ± 0.3 (43)	46min 32s	1.0
	11	1	222 ± 22 (3)	12.0 ± 0.6 (3)	20.0 ± 0.9 (41)	391 ± 22 (4)	7.2 ± 0.3 (45)	44min 5s	1.1
17 Dec.	2	1	190 ± 4 (3)	13.0 ± 0 (2)	16.0 ± 0.8 (25)	617 ± 7 (3)	7.9 ± 0.5 (35)	46min 26s	
19 Dec.	2	1	56 ± 8 (5)	6.2 ± 1.0 (5)	10.8 ± 0.7 (26)	393 ± 36 (4)	4.6 ± 0.2 (30)	38min 51s	0.8
22 Dec.	2 + 3	2	95 ± 9 (6)	8.3 ± 1.1 (6)	13.0 ± 1.1 (44)	460 ± 35 (5)	3.9 ± 0.4 (45)	58min 16s	
	6	1	91 ± 14 (4)	7.0 ± 0.7 (4)	14.7 ± 1.1 (22)	515 ± 6 (3)	7.1 ± 0.4 (26)	41min	0.7
23 Dec.	1	1	62 ± 7 (6)	6.2 ± 0.5 (6)	12.1 ± 0.6 (32)	256 ± 17 (6)	7.6 ± 0.6 (39)	38min 16s	1.0
24 Dec.	2	1	64 ± 6 (4)	4.0 ± 0 (4)	21.4 ± 3.6 (12)	329 ± 24 (3)	3.8 ± 0.3 (14)	30min 13s	0.5
	3	1	110 ± 35 (3)	8.0 ± 2.1 (3)	15.8 ± 0.5 (30)	513 ± 79 (3)	5.5 ± 0.5 (33)	36min 4s	1.0
25 Dec.	2	1	151 ± 22 (5)	9.8 ± 0.7 (5)	17.1 ± 0.9 (49)	358 ± 15 (5)	7.1 ± 0.4 (58)	52min 18s	1.1
	5	1	89 ± 7 (7)	8.1 ± 0.6 (7)	12.6 ± 0.4 (49)	259 ± 23 (7)	8.6 ± 0.3 (60)	46min 8s	1.3
	6	1	187 (1)	12 (1)	17.2 ± 0.9 (19)	334 ± 16 (2)	4.2 ± 0.3 (24)	16min 52s	
26 Dec.	1	1	133 ± 11 (3)	8.3 ± 0.7 (3)	18.2 ± 1.7 (22)	355 ± 16 (3)	7.1 ± 0.7 (30)	28min 53s	1.1
27 Dec.	38	1	101 ± 33 (4)	7.0 ± 1.7 (4)	16.9 ± 1.1 (24)	385 ± 64 (4)	6.6 ± 0.4 (28)	35min 33s	0.8
28 Dec.	6	1	93 ± 20 (6)	8.0 ± 1.3 (6)	12.8 ± 0.3 (56)	335 ± 19 (7)	6.0 ± 0.4 (64)	51min 18s	1.2

*Only for surfacing sequences. **Includes blows for which no duration estimated.

The data on dive times and surfacing behaviour can be used to examine whether it is reasonable to assume (as was done in calculating the above estimate) that all the schools on the trackline were seen. The distribution of dive times, for instance, can be compared with the radial distances at which primary sightings were made. At a searching speed of 11.5 knots, the vessels would have travelled 419/3,600(11.5) = 1.3 n.miles during the average dive of a single whale, or 896/3,600(11.5) = 2.9 n.miles during the longest recorded dive. Estimated radial distances at which primary sightings of blue whales were made during the cruise ranged from 0.6-5 n.miles with a mode at 2.5-2.9 n.miles ($n = 51$). This suggests that few if any dive intervals would have been long enough for the vessel to have passed the location of the whale (if it was on the trackline) before it underwent at least one surfacing period. Furthermore, during surfacing periods, which averaged 109 secs for single whales, an average of 8 blows would be produced, each lasting about 5 secs. This means that a sighting cue would be visible for about 40/109 or 37% of the time during a surfacing period. Overall, therefore, the assumption in the population estimate that all schools on the trackline were seen seems reasonable.

It should be mentioned, however, that dive times considerably longer than those recorded on the survey have been reported for blue whales (27 min —Donovan, 1984; 35 min —Tomilin, 1957; 50 min —Yablokov *et al.*, 1974). Most of the observation periods in this paper were too short to detect such dives. Nevertheless, results from the satellite-tagging of blue whales in the North Pacific (Lagerquist *et al.*, 2000) strongly suggest that the data obtained here are representative. Blow rates of the tagged whales averaged 1.0 per min, compared to 0.95 ± 0.23 per min south of Madagascar, while the longest of 2,007 dives recorded from the tagged whales was 18 mins, compared to 14.9 mins south of Madagascar.

The evidence of feeding in the region is consistent with the report of Gambell *et al.* (1975), who described defecations in two blue whales out of a total of 15 seen south and west of Madagascar in summer 1973/74. The two incidences occurred on 30 November 1973 at 27°52’S 48°24’E, and 13 January 1974 at 31°10’S 35°69’E (PBB field notes). Although very little is known of the oceanography in this region, a localised upwelling cell has recently been described inshore of the East Madagascar

Current where it diverges from the coast at the southern tip of Madagascar. This cell seems to be a very persistent phenomenon, being current- rather than wind-driven, and may be the source of filaments of biologically enriched water that are carried further south as part of the retroflection of the East Madagascar Current (Lutjeharms and Machu, 2000). Such conditions might create a predictable feeding ground for migrating blue whales of the sub-Antarctic Region, similar to those reported off southern Australia (Gill, 2002), and off the Channel Islands, California (Fiedler *et al.*, 1998).

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Distribution of small cetaceans within a candidate Special Area of Conservation; implications for management

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ABSTRACT

Information on cetacean distribution plays an important role in the identification of suitable boundaries for marine protected areas, but is also crucial for developing management and monitoring programmes. In response to the European 'Habitats Directive', a candidate Special Area of Conservation (cSAC) has been established in the Moray Firth, northeast Scotland to protect a small and isolated population of common bottlenose dolphins (*Tursiops truncatus*). Limited data on the distribution of bottlenose dolphins and on temporal changes in distribution have recently constrained attempts to mitigate against the impacts of new developments upon this population. In response to the need for current information on the distribution of dolphins throughout the cSAC, this study aims to provide data on the distribution of dolphins and other small cetaceans throughout the Moray Firth. Changes in the distribution patterns of dolphins in the inner Moray Firth were examined using data collected between 1990 and 2000. In addition, combined passive acoustic and visual survey techniques were used to determine the distribution of dolphins and harbour porpoises (*Phocoena phocoena*) on a broader scale across the whole Moray Firth. Dolphin schools were distributed throughout the inner Moray Firth, but there were concentrations of sightings around three deep, narrow channels that were consistent over the ten year study period. Results from surveys across the whole of the Moray Firth showed that all sightings and acoustic detections of dolphins were made within the area of the cSAC. In contrast, porpoise sightings were widely distributed throughout the Moray Firth. The median encounter rate of porpoises across the whole Moray Firth was 1.69 per 100km. Encounter rates of porpoises were similar in the outer Moray Firth and the cSAC. This combination of distribution studies at differing spatial scales provides a valuable tool for monitoring the distribution of animals and identifying important habitats, and the results of this study have directly supported efforts to manage the cSAC.

KEYWORDS: AREA-SCOTLAND; INDEX OF ABUNDANCE; SURVEY-ACOUSTIC; MANAGEMENT PROCEDURE; CONSERVATION; SANCTUARIES; DISTRIBUTION

INTRODUCTION

In recent years, many studies of distribution have aimed to identify critical habitats for cetaceans (Gregr and Trites, 2001; Harwood, 2001) and, in several cases, such data have been used to support the establishment of marine protected areas (Dawson and Slooten, 1993; Hooker *et al.*, 1999). In European waters, the European Union's (EU) Habitats Directive requires member states to identify Special Areas of Conservation (SAC) for certain species such as common bottlenose dolphins (*Tursiops truncatus*). In several countries, information from previous (Evans, 1992; Berrow *et al.*, 1996; Wilson *et al.*, 1997) or ongoing (Ingram and Rogan, 2002) studies of dolphin distribution have allowed the identification of boundaries for candidate SAC (cSAC), and management plans for these new marine protected areas are currently being implemented (Baxter, 2001).

Whilst most attention has previously focused on identifying suitable boundaries for marine protected areas, it is clear that information on cetacean distribution may subsequently be required to support management actions. This could simply form part of ongoing site monitoring to confirm that distribution patterns remain similar through time. Alternatively, additional data may be required to assess the potential impact of proposals for new human activities within the area, and to advise on mitigation against the impact of such developments. Although the details will vary depending upon the species and area in question, it is likely that data to support these designation and management phases will need to be collected at different temporal and spatial scales. This paper illustrates these issues by outlining recent studies of the distribution of bottlenose dolphins carried out in response to concern over the potential impact of industrial developments within the Moray Firth cSAC in northeast Scotland.

The inner Moray Firth was one of the first areas in Europe to be identified as a marine cSAC for bottlenose dolphins (Thompson *et al.*, 2000). In recent decades, the area has been used predictably and intensively by the only known 'resident' population of bottlenose dolphins remaining in the North Sea (Wilson *et al.*, 1999). No dedicated surveys have been carried out to permit the identification of critical habitats for this species in UK waters but regional data from seabird sighting cruises (Mudge *et al.*, 1984), a network of volunteer observers (Evans, 1992) and ongoing photo-identification surveys (Wilson *et al.*, 1997) were used to identify boundaries of the Moray Firth cSAC. Proposals to include this Moray Firth cSAC in a suite of UK marine sites were submitted to the European Union in 1994, and responsibility for managing the site was taken on by the Moray Firth Partnership (MFP) —a voluntary organisation representing a wide range of statutory and non-statutory organisations. A management scheme was subsequently developed, involving widespread public consultation, and the management plan was launched in January 2002 (MFP, 2001).

In 2001, prior to the launch of the management scheme, plans were put forward to replace a sub-sea oil pipeline that was routed through the Moray Firth cSAC from the Beatrice oilfield to an onshore terminal in the inner Moray Firth (Fig 1). Although the EU had not yet ratified this (or any other) cSAC, it was assumed that the Habitats Directive should

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immediately be applied to all cSACs (Baxter, 2001). Consequently, the developers were required to conduct an environmental assessment to determine whether the pipeline replacement could have a significant impact on the bottlenose dolphin population, and to develop mitigation measures to minimise any potential impacts (Talisman Energy (UK) Ltd, 2001b). Furthermore, it was decided that, whilst the cSAC was primarily to protect bottlenose dolphins, mitigation procedures should minimise potential impacts on all cetaceans using the area, particularly harbour porpoises (*Phocoena phocoena*) known to occur regularly in the Moray Firth (Mudge *et al.*, 1984; Sheldrick *et al.*, 1994). This case represented the first occasion on which statutory organisations were required to consider impacts upon a cetacean population within a cSAC. Despite this population being the most intensively studied coastal cetacean population in Europe, this process immediately identified uncertainties about cetacean distribution that constrained management decisions. In particular, information on the distribution of bottlenose dolphins in the offshore and northern parts of the cSAC was limited to data collected in 1982 and 1983 (Mudge *et al.*, 1984), and data from inshore areas was collected prior to 1993 (Wilson *et al.*, 1997). Although these sources suggested that there were almost no bottlenose dolphin sightings in the part of the cSAC affected by the pipeline, there was emerging evidence that the population has extended its geographical range during the last ten years (Stone, 2001; Wilson *et al.*, In review). Consequently, the distribution patterns previously underpinning the designation of this cSAC may have changed, making it difficult to assess the probability that bottlenose dolphins would interact with the pipe-laying activities.

This study was designed to provide current information on the distribution of bottlenose dolphins and harbour porpoises throughout the Moray Firth, with emphasis on the waters within the Moray Firth cSAC. In particular, the study aimed to determine whether there have been temporal changes in the relative distribution of dolphins within the Moray Firth cSAC during a period in which they are known to have extended the southern boundary of their geographical range (Wilson *et al.*, In review). To achieve this, the distribution of bottlenose dolphins within the Moray Firth is described at two spatial scales. First, data from regular photo-identification surveys were used to extend analyses carried out by Wilson *et al.* (1997) and examine whether there have been changes in distribution patterns within the inner Moray Firth. Secondly, the broader-scale distribution of dolphins was examined using ship-based surveys across the outer Moray Firth, focusing particularly on the areas affected by the recent pipeline replacement.

METHODS

Inner Moray Firth

Regular boat-based surveys were made within the inner Moray Firth between 1990 and 2000 along a standard survey route (Fig. 1). Two surveys were made each month between May and September using an established field protocol and data collection described in detail by Wilson *et al.* (1997). A total of 103 surveys were carried out between 1990 and 2000. Data on the distribution of dolphin schools for each year between 1990 and 2000 were compared.

To map the distribution of dolphins within the inner Moray Firth, locations of all schools of dolphins were plotted using a GIS software package (Arcview version 3.2, ESRI Inc.). The inner Moray Firth was divided into eight sub-regions as used in analyses by Wilson *et al* (1997), and the number of schools sighted in each sub-region was calculated. Each year, the sub-regions were ranked from lowest to highest based on the number of schools sighted in each of them divided by the area of each sub-region. A Friedman test was then used to test for consistency in the pattern of distribution in each year between 1990 and 2000.

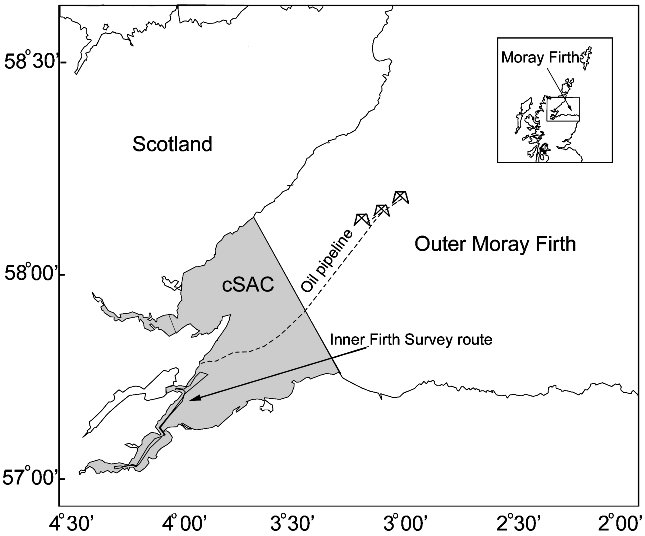

Fig. 1 Map of Scotland (inset) showing the Moray Firth, the area of the cSAC (shaded area) in the west of the Moray Firth and the outer Moray Firth. The dashed line and symbols represent the Beatrice oil pipeline and platforms and the solid line shows the inner Moray Firth survey route.

cSAC and outer Moray Firth

Combined boat-based passive acoustic and visual surveys were conducted in the cSAC and outer Moray Firth between January 2001 and October 2001. Ten surveys were made, collecting a total of 2,128km of acoustic data and 785km of visual data. The majority of surveys were made from *Seaspring*, a 56m pollution control vessel. In addition, three surveys were made in the outer Moray Firth from *Scotia* a 60m oceanographic research vessel. Survey speeds of *Seaspring* and *Scotia* were 9 knots and 12 knots respectively.

Although surveys covered most of the cSAC and the Moray Firth, effort was not distributed evenly across the region. Due to concerns about the impact of the sub-sea oil pipeline replacement on cetaceans (Talisman Energy (UK) Ltd, 2001b), much of the survey effort focused on the route of this pipeline, in the northern Moray Firth (Fig. 1).

A three-person team worked in shifts 24 hours a day to search for cetaceans from *Seaspring*. During daylight hours, two people searched visually and one person continually monitored signals from a towed hydrophone array. Each hour, observers alternated between visual searching and acoustic monitoring to ensure that concentration was maintained. At night, the three-person team worked in shifts to monitor the hydrophone array. Visual searches were made by eye and using 7 × 50 binoculars from either side of the bridge of the ship, approximately 11m above sea level. When a school was sighted, information on the geographic location, species and number of individuals, estimated distance, bearing from the bow and school heading were noted and recorded in a database using the *Logger2000* software (Gillespie, 1997). In addition, environmental details including an estimate of sea state, cloud cover, wind direction, precipitation and visibility distance were recorded each hour. No visual searches were made from *Scotia*; a two-person team worked in shifts to continually monitor the hydrophone array. Weather conditions encountered during the visual observation periods were good; no precipitation occurred and sea states were generally less than force 3. Furthermore, the proportion of survey hours in each sea state within the cSAC and outer Moray Firth were not significantly different (Chi-squared test, $\chi^2 = 0.225$, $p = 0.894$)

The acoustic equipment consisted of a towed stereo hydrophone streamer, an amplification and filtering unit and a computer for making recordings (Gillespie, 1997; Leaper *et al.*, 2000). The system was flat to frequencies to 15kHz and had good sensitivity up to 22kHz. The streamer was towed on a 400m strengthened cable behind the vessel. At speeds of 10 knots, this design of array generally tows at around 5-6m below the surface (Gillespie, 1997). The array was towed from the stern of the vessel and attached by means of a rope and rubber bungee, designed to minimise the shock loads during towing.

Signals from the hydrophones were filtered using high pass filters set at 400Hz or 1600Hz depending on background noise conditions, and amplified by 20dB or 30dB using a custom-built differential amplifier/filter unit. This recording system is capable of detecting bottlenose dolphin vocalisations but not those from harbour porpoises. Signals from the hydrophones were monitored continuously and the occurrence of dolphin vocalisations was noted using *Logger2000* (Gillespie, 1997). In addition, the software made recordings to hard disk for 30 seconds every 2 minutes. This program also maintained a database of monitoring effort and aural detections.

Sample sizes for both porpoise and dolphin sightings were insufficient to make reliable estimates of density or abundance. Therefore, the median encounter rates of each species, expressed as the number of schools encountered per 100km of survey effort, were calculated for waters within the cSAC and in the outer Moray Firth. Independent encounters were defined as those sightings or acoustic detections of schools greater than 2km apart. On occasions when acoustic detections of dolphins were made together with a visual sighting, a single encounter was recorded. Survey tracks and the positions of sightings and acoustic detections were plotted in a GIS software package (Arcview version 3.2, ESRI Inc.).

RESULTS

Inner Moray Firth

A total of 243 schools of dolphins were sighted during photo-id surveys within the inner Moray Firth between 1990 and 2000. These ranged in size from 1 to 35 dolphins, with a mean of 5.1. Although dolphin schools were distributed along the whole of the inner Moray Firth survey route, the distribution of schools showed a distinctive pattern that was consistent in each of the years between 1990 and 2000 (Friedman test, $\chi^2 = 53.37$, $p < 0.001$); being concentrated in and around three narrow channels at the entrances to the Cromarty, Inverness and Beauly Firths (Table 1). Sightings of schools of porpoises along the survey route were infrequent; only twelve schools were sighted on ten of the surveys. The majority of the sightings were along the north-eastern sections of the survey route.

cSAC and outer Moray Firth

A total of 30 sightings were made during the combined acoustic and visual surveys; 23 schools of porpoises were sighted and 7 schools of bottlenose dolphins. The mean school size of porpoises and bottlenose dolphins was 1.83 and 6.7 respectively.

The hydrophone array was deployed successfully across the majority of the survey route. It proved practical to deploy the array and collect useful data from both survey vessels. Noise levels were reasonable at both vessel's regular cruising speeds. The combination of visual and acoustic detection methods produced ten encounters with dolphins (three schools of dolphins were detected acoustically but were not sighted). All sightings and acoustic detections of dolphins were made within the area of the cSAC (Fig. 2 and Table 2). Encounter rates of dolphins in the cSAC and outer Moray Firth were significantly different (Kruskall Wallis test, $\chi^2 = 6.88$, $p = 0.009$).

Porpoise sightings were distributed throughout the Moray Firth (Fig. 3). The median encounter rate of porpoises across the whole Moray Firth was 1.69 schools per 100km (Table 3). Encounter rates of porpoises in the cSAC and outer Moray Firth were not significantly different (Kruskall Wallis test, $\chi^2 = 0.054$, $p = 0.816$).

DISCUSSION

This study has provided a current evaluation of the distribution of small cetaceans throughout the Moray Firth cSAC and outer Moray Firth. Although based on a few

Table 1

The number of dolphin schools sighted during boat-based surveys in sub-areas of the inner Moray Firth between 1990 and 2000 (the region names used by Wilson *et al.* (1997) are shown in parentheses if different from the current study). Each year, the sub-regions were ranked from lowest to highest based on the number of dolphin schools sighted per km^2 and a test for consistency in the pattern of distribution was carried out. Mean rank of each area is shown in the right hand column. There was no significant variation in the pattern of distribution over the years (Friedman test, χ^2=53.37, p<0.001).

	Number of dolphin schools sighted per km^2											
Region	1990	1991	1992	1993	1994	1995	1996	1997	1998	1999	2000	Mean rank
Cromarty Firth entrance (Sutors)	1.89	1.14	0.97	0.16	0.38	0.65	0.92	0.54	0.65	0.86	1.08	7.27
Cromarty Firth	0.00	0.13	0.13	0.13	0.00	0.00	0.00	0.50	0.13	0.00	0.00	3.14
Three Kings	0.00	0.00	0.26	0.00	0.05	0.11	0.05	0.05	0.11	0.16	0.05	3.23
Eathie	0.10	0.17	0.17	0.02	0.14	0.12	0.22	0.12	0.14	0.12	0.14	4.73
Inverness Firth entrance (Chanonry)	0.40	0.56	0.81	0.08	0.65	0.40	0.56	0.56	0.40	0.48	0.56	6.55
Inverness Firth	0.00	0.09	0.09	0.04	0.00	0.04	0.13	0.09	0.06	0.00	0.02	2.95
Beauly Firth entrance (Kessock)	1.25	2.50	1.00	0.00	0.50	1.25	1.50	1.25	0.25	0.25	0.00	6.32
Beauly Firth	0.00	0.01	0.01	0.01	0.00	0.00	0.00	0.05	0.01	0.00	0.00	1.82

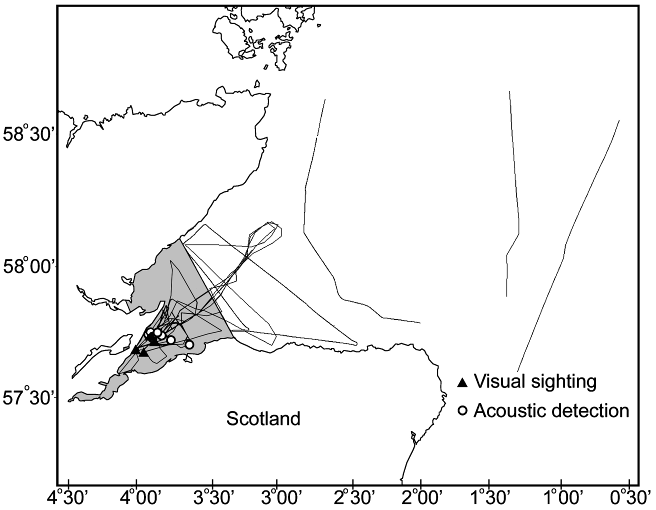

Fig. 2 The distribution of dolphins across the Moray Firth from ten combined visual and acoustic surveys carried out during 2001. The black line represents the survey track; visual sightings of dolphins are shown by the triangles and acoustic detections by the circles.

Table 2

Encounter rates of bottlenose dolphins in the Moray Firth. Results from the combined visual and passive acoustic surveys are expressed as the number of dolphin schools sighted per 100km of survey track, for the Moray Firth, within the candidate Special Area of Conservation (cSAC) and in the outer Moray Firth. Standard deviation is shown in parentheses. Encounter rates of dolphins in the cSAC and outer Moray Firth were significantly different (Kruskall Wallis, $\chi^2 = 6.88, p = 0.009$).

	Effort (km)	*n*	Median encounter rate (schools per 100 km)
Moray Firth	2,204	10	0 (1.24)
cSAC	1,293	10	0.45 (1.25)
Outer MF	911	0	0 (0)

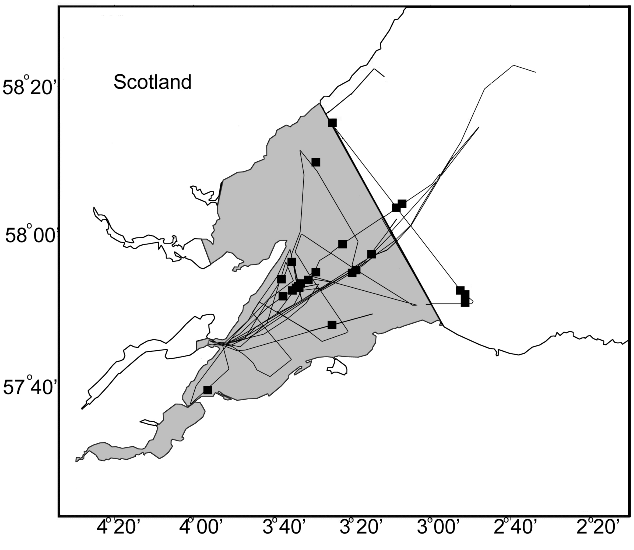

Fig. 3 The distribution of porpoises across the Moray Firth from visual surveys carried out during 2001. The black line represents the survey track and visual sightings of porpoises are shown by the squares.

Table 3

Encounter rates of harbour porpoises in the Moray Firth. Results from the visual surveys are expressed as the number of porpoise schools sighted per 100km of survey track, for the Moray Firth, within the candidate Special Area of Conservation (cSAC) and in the outer Moray Firth. Standard deviation is shown in parentheses. Encounter rates of porpoises in the cSAC and outer Moray Firth were not significantly different (Kruskall Wallis, $\chi^2 = 0.054, p = 0.816$).

	Effort (km)	*n*	Mean school size	Median encounter rate (schools per 100km)
Moray Firth	685	22	1.83	1.69 (3.96)
cSAC	610	17	2	0.78 (5.42)
Outer MF	175	5	1.33	0 (2.22)

wide-scale surveys, these results provide a basic framework for monitoring the distribution of dolphins within the Moray Firth cSAC and hence provide a valuable tool in the management of this population. More specifically, the results of the study provide a focus for the establishment of monitoring strategies and can be used to target regions of the cSAC for the implementation of specific levels of monitoring effort or particular survey methods (e.g. Talisman Energy (UK) Ltd, 2001a).

Although dolphins were sighted along the whole of the inner Moray Firth survey route, there was a distinctive distribution pattern of sightings that was consistent throughout the study period. This pattern is the same as that identified by Wilson *et al.* (1997) from data collected between 1990 and 1993, with sightings being centred around three main areas, the deep narrow entrances to the Cromarty, Inverness and Beauly Firths. Although there were distinctive inter-annual changes in the relative number of schools sighted within the inner Moray Firth (Table 1), the stability of the distribution pattern over the decade highlights the importance of these small deep areas for dolphins during the summer months and emphasises the importance of detailed management plans for key areas such as these (MFP, 2001).

The broader-scale distribution of dolphins throughout the cSAC and outer Moray Firth also showed a distinctive pattern, with all sightings and acoustic detections of dolphins made within the cSAC, around the coastal margins of the inner Moray Firth. This is similar to the results from earlier surveys previously undertaken over the whole Moray Firth. During these surveys, Mudge *et al.* (1984) noted that all sightings of bottlenose dolphins were made within narrow firth entrances in the inner Moray Firth and this led, in part, to the setting of the current geographical boundaries of the cSAC. The median encounter rate of dolphin schools in this study was estimated to be 0.45 schools per 100km within the cSAC. This is similar to sighting rates of bottlenose dolphins in several other areas: 0.98 in the northern Gulf of Mexico (Baumgartner *et al.*, 2001); 0.07-0.29 in the north-central Gulf of Mexico (Mullin *et al.*, 1994); 0.81 off South Africa (Ross *et al.*, 1987). However, it appears markedly lower than in others: 7.6 in the Gulf of California (Silber *et al.*, 1994) and 7.36 off Texas (Barham *et al.*, 1980).

Recent evidence suggests that, over the last decade, the distribution of dolphins has extended southwards down the Scottish coast leading to concerns about the management of the population (Wilson *et al.*, In review). Nevertheless, the data presented in this current study suggest that the importance of different areas within the Moray Firth has remained relatively stable. However, there remain few data from the winter months, when dolphin abundance in the inner firth is lower (Wilson *et al.*, 1997). Further work in offshore areas is required to determine which areas are used at these times of year, and combined visual and acoustic surveys provide a promising method for collecting such data in poor sea conditions.

The lack of porpoise sightings around the inner Moray Firth suggests that this region, although important for dolphins (Wilson *et al.*, 1997), does not represent a particularly suitable habitat for porpoises. As the two species appear to occupy different niches (Santos *et al.*, 1994), it is likely that they are exploiting different habitat types. However, recent discoveries that bottlenose dolphins attack and kill harbour porpoises in this area (Ross and Wilson, 1996) cannot exclude the possibility that porpoises actively avoid areas with higher dolphin density.

The median encounter rate of porpoise schools in this study was estimated to be 1.69 schools per 100km within the Moray Firth. Although estimates in other studies are highly variable, this current result is generally in the lower margins of porpoise encounter rates: 0.85-2.4 schools per 100km in the Bering Sea (Moore *et al.*, 2002); 3.4-7.8 in the Gulf of California (Carretta *et al.*, 2000); 43.5 off the San Juan Islands (Raum-Suryan and Harvey, 1998) and 9-70 around the coast of the UK (Northridge *et al.*, 1995). However, no attempt was made to stratify the data for variables likely to affect sighting rates (such as environmental conditions or observer configuration) therefore direct comparisons of the encounter rates of dolphins and porpoises between this study and other studies are difficult. Furthermore, it is unclear whether data collected from combined passive acoustic and sighting surveys are directly comparable to data collected during visual surveys.

Despite these caveats, the distribution of porpoises throughout the Moray Firth was clearly different to the distribution of dolphins, with porpoises sighted throughout the survey route within the cSAC and the outer Moray Firth. This concurs with sightings made from previous seabird surveys, showing that porpoises were present all year round throughout most of the Moray Firth (Mudge *et al.*, 1984). In addition, this result also emphasises the fact that the visually more obvious dolphins were not present on the offshore legs of the surveys.

Combined acoustic and visual methods proved to be practical and cost effective for monitoring the distribution of dolphins throughout the Moray Firth. Acoustic monitoring worked well aboard the survey vessels and data collection was achieved around the clock using a small, two to three-person team. Indeed, no dolphin schools were sighted without being detected first using the hydrophone. This study assumed that all whistles were produced by bottlenose dolphins. This assumption is reasonable within the inner Moray Firth, where sightings of other dolphin species are rare (University of Aberdeen, unpublished data). However, this may not be the case in waters further offshore where species such as white-beaked dolphins (*Lagenorhynchus albirostris*) and white-sided dolphins (*Lagenorhynchus acutus*) may be more common (Mudge *et al.*, 1984; Hammond *et al.*, 2002). Although no dolphins were heard in these offshore waters in this study, future work may need to differentiate between species using analyses to discriminate between the acoustic characteristics of the vocalisations (e.g. Rendell *et al.*, 1999). Furthermore, although the current system allows the detection of bottlenose dolphin whistles, this could be extended to include an automated detection system to record porpoises (Chappell *et al.*, 1996; Gordon *et al.*, 1998). When used alongside visual methods, these acoustic monitoring techniques can provide markedly enhanced estimates of density and distribution (Fristrup and Clark, 1997). This is especially important where year-round coverage is required in areas such as the outer Moray Firth, where rough seas are common and winter days are short.

Implications for management

This combination of distribution studies at differing spatial scales is an extremely valuable tool in monitoring the distribution of animals and identifying important habitats (Pribil and Picman, 1997). Data from this study have provided a basis for the management of this coastal population of dolphins; data have already supported the development of management plans for the cSAC and been used in environmental assessments for industrial developments (e.g. Talisman Energy (UK) Ltd, 2001a).

The results support evidence from studies in the inner Moray Firth which show that the narrow entrances to coastal inlets provide the most intensively used areas by bottlenose dolphins within the cSAC. This emphasises the importance of these coastal channels and when building management plans for the cSAC, particular care is needed to mitigate against potential impacts from activities in these core regions. Although fewer dolphins were sighted in outer firth areas, there are known to be distinctive seasonal variations in the use of more coastal areas and therefore, it would be pertinent to conduct dedicated surveys when major new activities are planned in the less intensively used regions of the cSAC.

Further work should aim to achieve year-round, representative coverage of the cSAC and surrounding areas, integrating broader scale survey data, such as those used in this study, with more detailed work in areas of particular interest or concern (e.g. Hastie *et al.*, 2003). This multi-scale approach should ultimately lead to the identification of oceanographic, biological and anthropogenic determinants that underlie the distinctive patterns of distribution seen in this population of bottlenose dolphins.

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A review of bowhead whale (*Balaena mysticetus*) stock identity

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ABSTRACT

For management purposes, the Scientific Committee of the International Whaling Commission has considered bowhead whales as having five stocks (geographically distinct segments of the population): Spitsbergen, Davis Strait, Hudson Bay, Okhotsk Sea and Bering-Chukchi-Beaufort Seas (B-C-B). These divisions are defined primarily by known distribution and seasonal movements. Historically, bowhead whales had a circumarctic distribution, with several periods of range expansion and contraction depending upon access through Arctic straits. Heavy exploitation by pre-20th century commercial whalers reduced bowhead whale abundance, further segregating stocks. A portion of the B-C-B stock escaped whalers by migrating into the pack ice each spring and summering in the Beaufort Sea. Few bowhead whales are now found in the summer in the Chukchi or Bering Seas. The distribution of this species should be considered labile, affected by sea ice and availability of prey, a factor that improves the likelihood of genetic mixing between stocks. Genetic variability has remained relatively high in spite of the severe depletion of the population, and there is no evidence of any recent genetic bottleneck. Besides geographic distribution and genetics, stock identity may be studied via morphological differences, reidentification of individuals between different stock areas, acoustic signatures, pollutant burdens, parasites and predators, feeding ecology and conception dates. Harpoon heads, research tags and lens racemisation indicate that bowhead whales are long-lived, can travel over large areas and may mix among stocks. Because conception occurs during or near the time of the spring migration, there are opportunities for genetic mixing among whales that might use different summering areas.

KEYWORDS: BOWHEAD WHALE; STOCK IDENTITY; DISTRIBUTION; GENETICS; ARCTIC; MOVEMENTS; WHALING-HISTORICAL

INTRODUCTION

As part of an ongoing process to develop a systematic approach to defining stocks within the management regime of the International Whaling Commission (IWC), this review was developed originally at the request of the Scientific Committee (IWC, 2000, p. 292).

Since 1984, the IWC Scientific Committee has considered the issue of bowhead stock structure many times (e.g. IWC, 1984; 1985; 1986; 1988; 1989; 1991; 1992b; 1995b; 1997). IWC (1984) concluded that the number of whales that fail to migrate past Pt Barrow in any one year is very small, and autumn sightings in the Chukchi Sea along the northeast Siberian coast were early returns from the Beaufort Sea, not a separate stock in the western Chukchi Sea. This view was reiterated in IWC (1985) supported by the recovery of a USSR discovery tag found in a bowhead taken off Wainwright, Alaska, in May 1983 (along the typical migratory route from the Bering Sea to the Beaufort Sea); the whale had been marked in October 1981 off Chukotka (Dronenburg *et al.*, 1984).

A major review took place in 1991 (IWC, 1992a). Although Fraker (1984) proposed that there had originally been two stocks, one of which was exterminated by commercial whalers, the Committee concluded that the present apparent absence of large numbers of bowhead whales in the summer in the Chukchi Sea relative to large takes in the summer during commercial whaling efforts is not evidence for two stocks. Subsequent discussions have not altered the Committee's conclusions (e.g. IWC, 2001a; b).

This review begins with definitions of stocks as presented by the IWC. This is followed by a description of each bowhead stock in terms of abundance (original and current), distribution and seasonal movements to give a context for the detailed analysis of stock identity. Following this background information, a summary of IWC Scientific Committee assessments of the western Arctic stock is presented. Available methods applicable to discriminating whale stocks are presented. To conclude, a summary is given of historical findings regarding stock identity for bowhead whales, and a list of additional research that would be useful is provided.

BACKGROUND

IWC approach to stock identity

Hoelzel and Dover (1989) considered three types of stocks: (1) dynamic stock ('the fundamental unit described by a population model or assessment procedure'); (2) management unit ('a group of whales occurring within a specific geographical boundary which is actively or potentially exploited'); and (3) genetic stock ('a genetically differentiated population within a species'). Regarding existing IWC stock boundaries, Donovan (1991) noted that:

> 'Much of the data historically used to examine stock identity (examination of catch and sightings distributions, differences in biological parameters and length distributions, mark-recapture data) are not capable of being used to define biological stocks and provide equivocal information on 'management' units'.

In simple terms, he distinguished between management stocks ('population units that can be 'successfully' managed') and biological stocks ('based on genetic separation'). He noted that, for the IWC, management stocks are more important but that it may not be possible to define an appropriate management stock without some knowledge of the relevant biological stock(s).

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In practice, the IWC's operational definition of a stock (or population) has been the same as a management unit. That is, a management unit is defined such that specific management goals (e.g. harvesting does not reduce populations below a certain level or result in local extirpation, etc.) are met (Donovan, 1991). Prior to the development of molecular techniques, management units were sometimes coarsely defined on the basis of one or more of a number of factors including: discontinuities in the distribution of animals on their feeding and breeding grounds based on catch and sightings data; morphology; differences in life history parameters; and compatibility with models (Donovan, 1991). The rate of gene flow between putative stocks was unknown, nor was there any information on the degree to which an area could be 'recolonised'.

Throughout the 1980s and 1990s, however, putative stocks were defined based on inferences that gene flow was unlikely. More recently, Taylor and Dizon (1996) showed that the rate of interchange needed to maintain genetic diversity between populations is several orders of magnitude less than that needed to maintain demographic viability. Subsequently, others have incorporated these ideas; for example, Clapham and Hatch (2000) and Clapham and Palsbøll (1999) have suggested a definition of a large whale management unit (or stock) as a grouping of individuals that, if extirpated, would probably not be recolonised via immigration from other areas on a time scale relevant in management terms.

In 2001, the IWC Scientific Committee developed the following stock definitions (IWC, 2002):

(1) Biological stock – all of the individuals in an area that are a part of the same reproductive process. They form a self-contained unit, with emigration/immigration rates far lower than the intrinsic rate of population growth.
(2) Management stock/management unit – a human construct defined in the context of management, that may or may not be equivalent to a single biological stock. It refers to animals that happen to be present in a defined region and defined season where management is taking place or is contemplated.
(3) Simulation stock/simulation sub-stock – a computational approximation denoting a homogenous group of animals, used to obtain inferences for management (as used in *Implementation Simulation Trials*, e.g. IWC, 1994).
(4) Sub-stock – this deliberately vague term describes a group of animals with some degree of biological cohesion. There are circumstances (e.g. on a feeding ground where animals from two breeding stocks are mixed) where other terms might be more appropriate.
(5) Closed sub-stock – this refers to a sub-stock which has negligible interchange with animals outside the sub-stock (i.e. at rates far lower than the intrinsic rate of population growth).

Review of bowhead stocks worldwide

Bowhead whales probably arose during the Pliocene in the Northern Hemisphere (McLeod *et al.*, 1993) and are endemic to Arctic and sub-Arctic waters (Moore and Reeves, 1993). These whales have an extremely thick epidermis of up to 25mm and a layer of blubber of up to 28cm (Haldiman and Tarpley, 1993), indicating their adaptation to the near-freezing temperatures of their environment. Historically, bowhead whales had a circumarctic distribution (Dyke *et al.*, 1996). More than pelagic species, littoral species (like bowhead whales) tend to have a continuous, although dispersed, distribution (McLeod *et al.*, 1993). Dyke *et al.* (1996) and Savelle *et al.* (2000) used remains of bowhead whales found in the Canadian Arctic to demonstrate that over the past 10,500 years there were several periods of expansion and contraction of the east-west distribution of these whales. In particular, bowhead whales were able to cross from the Beaufort Sea to Baffin Bay 10,500-8,500 years ago and again 5,000-3,000 years ago. At times, the climate was warmer than at present, possibly allowing bowhead whales to travel north of even the northernmost Canadian Arctic islands (Bednarski, 1990). This would have been an avenue to genetic mixing among the stocks.

Bowhead whales are known to migrate long distances (Moore and Reeves, 1993), moving southward in the autumn with the advance of the pack ice and returning northward with break-up the following spring. They commonly travel along shallow inner-shelf waters when ice conditions are moderate and light, but they use deeper slope habitat in heavy ice (Moore, 2000). Bowhead whales can average 5km/hr over thousands of km, even through areas covered with >90% ice, and they are capable of diving for over an hour (Krutzikowsky and Mate, 2000). This complex behavioural relationship of bowhead whales to sea ice (a dynamic and changing feature) can lead to fragmentation or integration of populations (Reeves *et al.*, 1983). Although extreme ice fields can form a barrier to even large bowhead whales (Moore and Reeves, 1993) and ice entrapment is a cause of mortality (Savelle *et al.*, 2000), this species shows an attraction to ice fields possibly to avoid killer whales, *Orcinus orca* (George *et al.*, 1994; Finley, 2001) or to take advantage of prey concentrations near and under sea ice (Finley, 2001), such as *Calanus* (Lowry, 1993). When bowhead abundance was high, their range may have included most Arctic areas with seasonal sea ice. However, strong fidelity to essential habitats (Finley, 2001) may have limited mixing, and commercial whaling further segregated bowhead whales into what are currently described as five stocks (geographically distinct segments of the population): Spitsbergen, Davis Strait, Hudson Bay, Okhotsk and western Arctic (IWC, 1992a, p.27). The western Arctic stock is now usually referred to as the Bering-Chukchi-Beaufort Seas (B-C-B) stock (e.g. Zeh *et al.*, 1995a) although occasionally it is simply the Bering Sea stock (e.g. Burns, 1993). In this review the term B-C-B stock is used.

Spitsbergen stock

Bowhead whales in the eastern North Atlantic have been observed as far east as the Laptev Sea, Severnaya Zemlya, Novaya Zemlya, Zemlya Frantsa-losifa (Franz Josef Land), Svalbard, north of Norway and north of Iceland along the coast of Greenland (Fig. 1), but only 40 sightings have been made since 1940 (Belikov and Boltunov, In press; Born, in litt.; Moore and Reeves, 1993). Possibly now numbering only 'in the tens' (Christensen *et al.*, 1990), the Spitsbergen stock is thought to have originally been the largest of the bowhead whale stocks (Braham, 1984; Woodby and Botkin, 1993). From 1660-1912, commercial whalers took over 90,000 bowhead whales. There may have been roughly 25,000 bowhead whales in this stock prior to commercial whaling (Mitchell, 1977; Woodby and Botkin, 1993). Hacquebord (1999) reconstructed records of whaling activities in the 17th and 18th centuries and examined how a changing climate may have affected whaling productivity; this led to his proposal that it was not only human hunting activities but changes in climate that may have caused the elimination of the Spitzbergen stock, or limited its ability to recover.

Jonsgård (1981; 1982) suggested that the historic Spitsbergen stock is extinct and that recent sightings may actually be immigrants circumventing Greenland (Davis Strait stock) or arriving via the East Siberian Sea (B-C-B stock). This was based on the lack of bowhead sightings in ice-covered waters of the northeast Atlantic in spite of many surveys. However, others (Reeves and Leatherwood, 1985; McQuaid, 1986; Moore and Reeves, 1993) believe that the present population between Greenland and Russia is probably a remnant of the severely depleted Spitsbergen stock. When bowhead whales were more plentiful, some overlap in ranges would have been more likely.

Movement patterns of bowhead whales within the Spitsbergen stock are not well known. Variations in the routes taken during the southbound migration have been attributed to the existence of separate 'tribes' (sub-species or species) of bowhead whales (Scoresby, 1820) or segregation of the population into age- or sex-specific groups (Southwell, 1898; de Jong, 1983).

Davis Strait stock

Bowhead whales west of Greenland and in northeastern Canada are recognised as two stocks (Moore and Reeves, 1993): the Davis Strait stock (centred in Davis Strait, Baffin Bay and waters of the Canadian Arctic Archipelago) and the Hudson Bay stock (found in Hudson Strait, Hudson Bay and Foxe Basin). The initial basis for defining these two stocks was the geographic separation of their summer feeding distributions (Reeves *et al.*, 1983; Reeves and Mitchell, 1990). A recent genetic study (Maiers *et al.*, 2001) not only provides supporting evidence for genetic separation of these two stocks, but it indicates that the Hudson Bay stock is more closely related to the B-C-B stock than to the Davis Strait stock. This suggests that bowhead whales in Hudson Bay originally immigrated from (or mixed with) the B-C-B stock, and those in Davis Strait may have come from the Spitsbergen stock. The Spitsbergen stock became established >13,000 years ago (Dyke *et al.*, 1996). Regular intermingling of the B-C-B and Hudson Bay stocks could have occurred 10,000-8,500 years ago and 5,000-3,000 years ago (Dyke *et al.*, 1996; Savelle *et al.*, 2000). There is no direct evidence that the Davis Strait stock existed prior to 10,000 years ago, at a time when much of Baffin Bay was impenetrable, but by 9,500 years ago this stock had become established and could have intermixed with the B-C-B stock (Dyke *et al.*, 1996).

The reidentification of a whale photographed northeast of Baffin Island in September 1986 and again near Disko Bay, West Greenland, in April 1990 (Heide-Jorgensen and Finley, 1991) and the tracks of two bowhead whales with satellite transmitters showing travel from Disko Bay to northeastern Baffin Island (Heide-Jorgensen *et al.*, 2001) support the hypothesis that there is only one stock in Baffin Bay. Whalers did not attribute variations in body size and migration patterns to the existence of multiple stocks in Davis Strait, unlike the variations recognised in the Spitsbergen stock (Reeves *et al.*, 1983).

Almost 29,000 bowhead whales were harvested in Davis Strait between 1719 and the end of commercial whaling in 1915 (Ross, 1993) from an estimated original stock of over

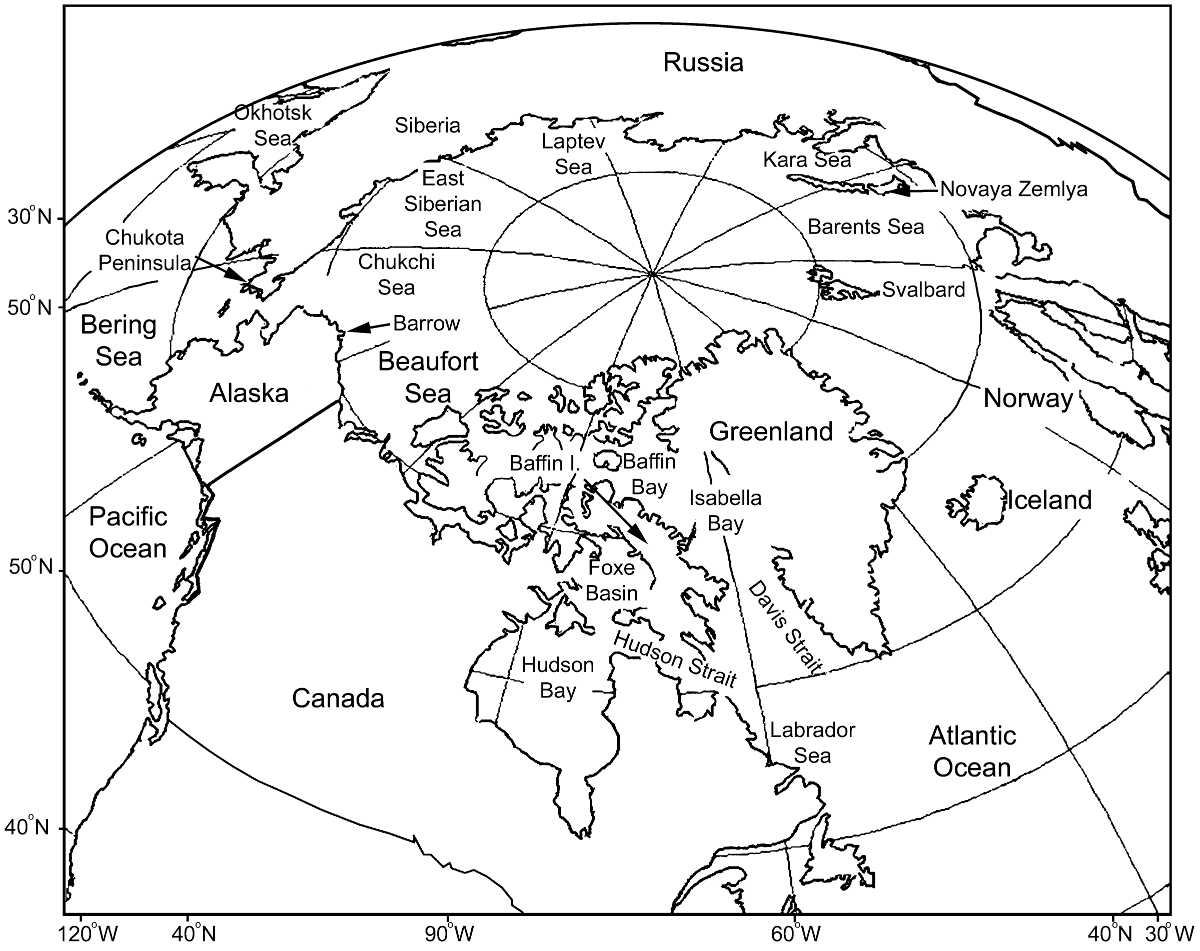

Fig. 1. Map of circumpolar area, including North Atlantic.

11,700 (Woodby and Botkin, 1993), although some whales were still being taken as recently as the 1970s (Reeves and Heide-Jorgensen, 1996). Current estimates of abundance are near 350 (Koski and Davis, 1980; Finley, 1990; Zeh *et al.*, 1993), and the viability of this stock is in doubt (Finley, 1990).

Hudson Bay stock

As mentioned in the preceding section, the Hudson Bay stock is not only genetically discrete from the Davis Strait stock but more closely related to B-C-B bowhead whales (Maiers *et al.*, 2001). Combining estimates from 1994 (Cosens *et al.*, 1997) and 1995 (Cosens and Innes, 2000) resulted in a minimum abundance of 345 (DFO, 1999), not including animals missed during the surveys. The original stock may have consisted of approximately 580 whales (Mitchell, 1977) as modified by Woodby and Botkin (1993).

Okhotsk Sea stock

There has been difficulty in assessing the historical distribution and abundance of bowhead whales in the Okhotsk Sea. North Pacific right whales (*Eubalaena japonica*) and gray whales (*Eschrichtius robustus*) were sometimes misidentified as bowhead whales, and whaling records collected during the short period of time (1848-57) this stock was hunted were incomplete (Bockstoce and Botkin, 1983; Bockstoce, 1986). In 1967-68, during a period of Soviet whaling, some of the misidentifications may have been deliberate to avoid laws protecting bowhead whales (Doroshenko, 2000). Pre-exploitation abundance was approximately 3,000 (Ross, 1993) or 6,500 (Mitchell, 1977).

Although Scammon (1874) stated that bowhead whales were hunted 'throughout the whole extent' of the Okhotsk Sea, certain areas were occupied by concentrations of animals during the summer months. In the northeastern Okhotsk Sea, whales were found in Penzhinskaya Gulf and Gizhiginskaya Gulf. The next area of concentration was to the southwest in Tauyskaya Bay. Farther south, the best whaling grounds were within the gulfs and bays south of the Shantarskiye Islands and west of Sakhalin Island (Moore and Reeves, 1993 provide additional details). Almost all of the areas where summer concentrations of bowhead whales occurred in the past are still occupied today, albeit in very low numbers.

In August 1995, during joint USA-Russian surveys, a few dozen bowhead whales were observed in a feeding aggregation south of the Shantarskiye Islands (Brownell *et al.*, 1997). Berzin *et al.* (1990) estimated the population in this area to be at least 250-300 animals. An estimate of abundance of 300-400 was made for the entire Okhotsk Sea based on data collected since 1979 (Vladimirov, 1994). However, 'no quantitative data are available to confirm' these estimates (Berzin *et al.*, 1995; Brownell *et al.*, 1997). There is some speculation as to whether animals found during the summer in the northeastern Okhotsk Sea form a distinct population separate from those in the Shantar region (Vladimirov, 2000). Doroshenko (2000) describes two routes used during the spring migration: some whales travelling to the Gulf of Shelikov, and others to the Shantar Islands. By July, these two groups appear to have joined in the Shantar Islands. The winter distribution is unknown because whalers left the Okhotsk Sea before the onset of winter storms in early November and did not return until June. Although some authors (e.g. Townsend, 1935; Tomilin, 1957) suggest that originally there was a common stock between the Okhotsk and Bering Seas, others (e.g. Lindholm, 1863; Bockstoce and Botkin, 1983) have argued that the Okhotsk Sea stock has always been discrete from the B-C-B stock; recent genetic studies indicate a small but significant difference between these stocks (LeDuc *et al.*, 1998).

Bering-Chukchi-Beaufort Seas stock

The B-C-B stock is the only bowhead population showing appreciable recovery since the impact of commercial whaling over a century ago. An abundance estimate of 8,200 was derived from sightings and acoustic records made in 1993 at Barrow, Alaska (Zeh *et al.*, 1995b), indicating an annual increase of 3.2% since 1978 (IWC, 1995a; Zeh *et al.*, 1995b). George *et al*. (2003) presented the results of the 2001 survey, giving an abundance estimate of 10,020 (95% CI of 7,800 to 12,900) and an updated annual rate of increase of 3.4% (95% CI 2.1% to 4.8%). Despite this current increase, bowhead whales have not yet recovered large parts of their historic range; pre-exploitation feeding areas were much larger than at present (Bockstoce and Botkin, 1980). During the first decade of exploitation, 1848-58, bowhead whales were taken from April through October from the coast of Asia to 173°W and north to 69°N in the southern Chukchi Sea (Bockstoce and Botkin, 1980). The logbook data extracted by Bockstoce and Botkin (1980) indicate that during this decade, 105 whales were taken south of 60°N, and only 27 whales were taken here in the following decade (1859-68). In 1867, during an exceptionally light ice summer, several whaling ships went as far to the northwest as Wrangel Island, at the western edge of the Chukchi Sea, but no bowhead whales were encountered (Bockstoce and Burns, 1993). During the third decade, 1869-78, whales were only occasionally taken south of 60°N, and after 1878, whales were essentially eliminated from the area between 60°-63°N (Bockstoce and Botkin, 1980). As hunting continued and the population was reduced, the whalers travelled farther and farther north and east. The southern limit of the hunt retreated northward at a rate of about 3° latitude every 10 years (Bockstoce and Burns, 1993). Bockstoce and Burns (1993) noted the possibility that these whales responded to this intense hunting by leaving the accessible hunting areas, an observation made originally by both commercial and subsistence whalers. In 1889, steamships reached the summer feeding grounds off the Mackenzie River Delta in the Beaufort Sea, which remained the major focus of the industry until 1914, about the time that commercial whaling collapsed (Bockstoce and Botkin, 1980).

Stoker and Krupnik (1993) commented that early records from Siberia mention whaling as a summer activity (July-August), whereas commercial whaling in the late 1800s and early 1900s was carried out primarily during the spring and autumn migrations (April-early June and October-November). They contended that this difference in the timing of the hunt may support the hypothesis (e.g. Bogoslovskaya *et al.*, 1982; Bockstoce, 1986) of a separate bowhead stock which summered in the northern Bering Sea and Bering Strait before it was decimated by commercial whalers. Bockstoce and Botkin (1980) speculated (as did Fraker, 1984) that the bowhead population originally consisted of several discrete sub-populations, each with its own feeding area; however, these authors also recognised the possibility (as did Bockstoce and Burns, 1993) that there was originally only a single population that responded to exploitation by moving farther north and east to safer areas near the ice or to areas that had not been previously exploited.

Burns (1993) supports the idea of a single stock. He has suggested that the records of relatively high numbers of bowhead whales summering in the Bering Sea prior to intense commercial whaling may reflect that: (1) some proportion of the commercially harvested whales in the Bering Sea may have actually been right whales, not bowhead whales; (2) commercial whaling in the North Pacific began after the ‘Little Ice Age’, and during colder periods, bowhead whales may have had a more southerly distribution than now; or (3) there have not been adequate surveys in the northwestern portion of the Bering Sea in summer. That is, the change in summer distribution may not be as dramatic as currently portrayed. Additionally, Burns (1993) points out that the documented increase in abundance of the B-C-B stock may lead to an expansion of its summer range. Indeed, the increase in sightings made in the Chukchi and Bering Seas in recent years (see below) may be an indication of a growing population expanding its range to refill former habitat (unless the increase in sightings is only the result of increased survey effort). Burns (1993) argued that the distribution of this species should be considered labile, affected easily by sea ice and availability of prey. In summary, then, the strongest evidence is for a continuous stock from the Bering to Beaufort Seas rather than multiple stocks summering in different areas.

Currently, the B-C-B stock is widely distributed in the central and western Bering Sea in winter (November-April), generally associated with the marginal ice front and found near the polynyas of St Matthew and St Lawrence Islands and the Gulf of Anadyr (Bogoslovskaya *et al.*, 1982; Brueggeman, 1982; Braham *et al.*, 1984; Ljungblad *et al.*, 1986; Brueggeman *et al.*, 1987; Bessonov *et al.*, 1990; Moore and Reeves, 1993; Mel'nikov *et al.*, 1998). From April to June, most of these whales migrate north and east, following leads in the sea ice in the eastern Chukchi Sea until they pass Pt Barrow where they travel east toward the southeastern Beaufort Sea (Braham *et al.*, 1980; 1984; Marko and Fraker, 1981). Most of the summer (June to September) bowhead whales range through the Beaufort Sea (Hazard and Cubbage, 1982; McLaren and Richardson, 1985; Richardson *et al.*, 1986; 1987a; b; Richardson, 1987; Moore and Clarke, 1991), predominately over outer continental shelf and slope habitats but independent of ice cover (Moore *et al.*, 2000). Distribution varies annually (Davis *et al.*, 1983; Thomson *et al.*, 1986; Richardson *et al.*, 1987a), affected in part by prey availability which is affected by surface temperature or turbidity fronts and anomalies (Borstad, 1985; Thomson *et al.*, 1986) and drilling rigs (Schick and Urban, 2000). During autumn (early September to mid-October), bowhead whales migrate across inner shelf waters (Moore *et al.*, 2000), moving west out of the Beaufort Sea, as evidenced during aerial surveys (Ljungblad *et al.*, 1987; Richardson, 1987; Moore *et al.*, 1989a; Moore and Clarke, 1992), radio-tracking (Wartzok *et al.*, 1990) and satellite-tracking (Mate *et al.*, 2000). From mid-September to mid-October bowhead whales are seen in the northeast Chukchi Sea, some as far north as 72°50’N (Moore and Clarke, 1993; Moore *et al.*, 2000). Whales migrate from Pt Barrow into the Chukchi Sea, with some whales turning southwest (247°True) along the axis of Barrow Canyon headed toward the Chukotka Peninsula (Moore and Reeves, 1993), while others head toward Wrangel Island (Mate *et al.*, 2000; Moore *et al.*, 2000), one group reaching the northern coast of the Chukotka Peninsula about the same time that others arrive off the peninsula’s eastern coast in the Bering Strait (Mel'nikov *et al.*, 1998). After reaching the coast, the whales follow it southeast to the Bering Strait (Bogoslovskaya *et al.*, 1982; Zelensky *et al.*, 1995). Autumn migrants begin arriving on the northern coast of the Chukotka in mid-September (Mel'nikov *et al.*, 1998), October (Mel'nikov *et al.*, 1997), November (Mel'nikov and Bobkov, 1994) or even December (Mel'nikov *et al.*, 1998) with large inter-year differences in the timing of the autumn migration through the Chukchi Sea (Melnikov *et al.*, 1998). By late October and November, many whales arrive in the Bering Sea (Kibal'chich *et al.*, 1986; Bessonov *et al.*, 1990), where they spend the winter.

Very few bowhead whales were found in the Bering or Chukchi seas in summer in the late 1970s and early 1980s (Dahlheim *et al.*, 1980; Miller *et al.*, 1986); however, there have been enough sightings to indicate that not all bowhead whales migrate to the Beaufort Sea. Mel’nikov *et al.* (1998) suggested that most bowhead whales make the Pt Barrow area the goal of their spring migration, and from there some continue east to the Beaufort Sea, some stay and others return to the west. Bowhead whales were consistently seen in the northeastern Chukchi Sea (near Pt Barrow) in summer from the mid-1980s to at least the early 1990s (Moore, 1992), and since then, summer sightings have included eight whales on 25 July 1999 near Pt Barrow (Moore, pers. obsv.) and 50 bowhead whales feeding off Cape Simpson on 19 August 2000 (C. George, pers. comm., North Slope Borough, Barrow, Alaska). In addition, small groups have been observed travelling northwest along the Chukotka Peninsula in May (Bogoslovskaya *et al.*, 1982; Bessonov *et al.*, 1990; Ainana *et al.*, 1995; Zelensky *et al.*, 1995), June (Mel'nikov and Bobkov, 1993) and July (Mel'nikov *et al.*, 1998). One group of seven whales was observed off Cape Netten, Chukotka Peninsula, on 26 July 1991 travelling north, and a group of seven was seen there on 27 September travelling east (Mel'nikov and Bobkov, 1994). Farther northwest, near Cape Schmidt, single animals were observed on 5 August and 1 September by the crew of the Russian ice-breaker *Krasin*. Bowhead whales were present throughout the summer of 1994 along the southeastern Chukotka Peninsula (127 sightings in June, 59 in July, 5 in August, and 6 in September; Ainana *et al.*, 1995) and the easternmost portion of the peninsula (21 sightings in June and 39 in August; Zelensky *et al.*, 1995). On 10 and 11 August 1995, four groups of bowhead whales, with 5-10 per group, were seen off the southern tip of the Chukotka Peninsula, moving west into the Gulf of Anadyr (Mel'nikov *et al.*, 1998). Moore *et al.* (1995) suggested that bowhead whales seen in the Chukchi Sea in early October could have migrated from the Beaufort Sea three weeks earlier, as whales seen in the Alaskan Beaufort Sea in August and early September were often swimming west (Moore *et al.*, 1989b). There appears to be an increase in summer sightings in the Bering and Chukchi Seas, perhaps as a function of increased survey effort but possibly also representative of increased range expansion as the population abundance increases.

EVIDENCE FROM VARIOUS METHODS USED TO INVESTIGATE STOCK IDENTITY

Geographic distribution and abundance

Commonly, information on where animals have been sighted or harvested has been important in discussions of stocks differentiation. The five stocks of bowhead whales were originally delimited essentially from information on their distribution, and the stocks were named according to the principal areas in which they were found. Much of the original data on distribution come from records of whaling effort (e.g. Scammon, 1874; Bockstoce and Botkin, 1983) whereas current distribution is recorded from aerial observations (e.g. Moore and Clarke, 1991; Rugh *et al.*, 1994), vessels (e.g. Miller *et al.*, 1986), acoustics (e.g. Moore *et al.*, 1989a), shore (e.g. Rugh and Cubbage, 1980), ice-based sites (e.g. George *et al.*, 1995), satellite tags (e.g. Mate *et al.*, 2000) or reidentifying individuals (see section below). Apparent gaps in distribution between areas of relatively high sighting rates have been attributed to stock separation (Perrin, 2001). The reasons for these gaps sometimes appear obvious (e.g. when there are barriers such as land masses), but there are less obvious features (such as ocean fronts) that may also be effective (Perrin, 2001).

Stocks may be differentiated if abundance changes in one stock relative to another. The reverse of this is also true in that abundances rising proportionally in two areas might indicate a common stock. This argument has been used to show that the B-C-B stock of bowhead whales should not be separated into a Bering/Chukchi population and a Beaufort Sea population (see section on B-C-B stock).

Genetics

Genetics has recently become an important tool for the discrimination of whale stocks. Punt *et al.* (2000) used North Pacific minke whale (*Balaenoptera acutorostrata*) allele frequency data to evaluate the relative probabilities of alternative stock structures. Baker *et al.* (1998) examined Southern Hemisphere humpback whale (*Megaptera novaeangliae*) stocks through mitochondrial DNA variation and maternal gene flow. Richard *et al.* (1996) used multiple molecular genetic analyses to study patterns of kinship in groups of sperm whales (*Physeter macrocephalus*). The practicality of assessing gray whale (*Eschrichtius robustus*) management units was explored using mitochondrial DNA and was found to have good potential for providing unambiguous answers (Ramakrishnan and Taylor, 2001).

There have been only a few genetic studies that examined the relationships among bowhead whale stocks or putative sub-stocks. Previous genetic studies conducted by Rooney *et al.* (1999; 2001) focused primarily on investigating the extent of potential bottleneck effects on genetic variability in the B-C-B stock. Some preliminary work has been done on the degree of genetic differentiation between the B-C-B stock and the Okhotsk Sea stock (LeDuc *et al.*, 1998) as well as between the B-C-B and the Hudson Bay and Davis Strait stocks (Maiers *et al.*, 2001). Rosenbaum *et al.* (2001), proposed further research to evaluate bowhead whale genetic diversity and population structure through historical and extant samples such as the DNA extractions done from bowhead skulls at an archaeological site on the Chukotka Peninsula (Kellar and Brownell, 2001). The findings of some of these studies are summarised below, and potential avenues for investigating stock structure within the western Arctic are also discussed.

Analyses of mitochondrial DNA polymorphism

Rooney (1998) analysed the first 455 nucleotides of the mitochondrial DNA (mtDNA) control region from 99 bowhead whales taken from the B-C-B stock, and Rooney *et al.* (2001) analysed patterns of genetic variability among these whales. The samples were taken from the northern coast of Alaska, with the exception of six that were from whales landed on St Lawrence Island in the Bering Sea. The primary conclusion of this research was that there was no genetic bottleneck in the B-C-B stock and that the level of genetic variability has remained relatively high (nucleotide diversity = 1.63%) in spite of the depletion of the population before the 1900s. The population reached its lowest abundance around 1914, when commercial whaling ceased; at that time there were probably 1,000-3,000 bowhead whales (Woodby and Botkin, 1993). However, the mtDNA data indicate that the effective population size had remained large despite the extensive reduction in total population numbers (Rooney *et al.*, 2001). These researchers were further interested in determining the time to the most recent common ancestor of mtDNA haplotypes in the B-C-B stock. By using phylogenetic and coalescent approaches, further analyses revealed that this population had undergone a size expansion initiated approximately 267,000 years before the present (Rooney *et al.*, 2001). These results suggest that the formation of the M'Clintock Channel sea-ice plug roughly 8,500 years ago did not influence the signature of historical population size change in the mtDNA sequence data (Rooney *et al.*, 2001). Analyses of mtDNA control region sequence data indicate that the Hudson Bay stock is more closely related to the B-C-B stock than to the Davis Strait stock (Maiers *et al.*, 2001). This confirms the suggestion of Rooney (1998) and Rooney *et al.* (1999) that the Hudson Bay and B-C-B stocks were a part of a larger stock until relatively recent times, which is consistent with the idea that only recently the M'Clintock Channel sea-ice plug served as a barrier to gene flow between these two stocks (Dyke *et al.*, 1996; Rooney *et al.*, 1999).

To investigate the possibility that the B-C-B stock might be further sub-divided, the pattern of polymorphism in the mtDNA control region sequences was compared between the six samples from St Lawrence Island (in the Bering Sea) and 93 samples from sites in northern Alaska where the whales presumably were migrating to the Beaufort Sea (Rooney, 1998; Rooney *et al.*, 2001). No differences were found. The average number of nucleotide substitutions per site between these groups (D_{xy}; Nei, 1987, equations 10.20 and 10.24) was 0.01744±0.00214, while the net number of nucleotide substitutions per site between groups (D_a; Nei, 1987, equations 10.21 and 10.23) was −0.00017±0.00237; there were no fixed differences between these groups. The sample size from St Lawrence Island was small, and more samples are needed to increase the power of this test. However, it is not known whether whales taken at St Lawrence Island were part of the northward migration through the Bering Strait and into the Beaufort Sea or whether they represent whales that remain year round in the Bering Sea. It would be more definitive if samples were collected from whales in the Bering Sea in July or August, but this effort has been limited by poor access and the scarcity of these whales. A similar comparison was made between whales in the B-C-B and Okhotsk Seas using mtDNA data, revealing small but significant differences (LeDuc *et al.*, 1998).

Analyses of microsatellite marker polymorphism

Rooney *et al.* (1999) investigated the patterns of microsatellite DNA polymorphism in the B-C-B stock from 108 bowhead whales, six of which came from St Lawrence Island. As with the analysis of mitochondrial DNA polymorphism, these researchers found no evidence of any recent genetic bottlenecks. In this study, five out of 15 polymorphic loci showed evidence of heterozygote deficiency. However, Hardy-Weinberg equilibrium could not be rejected at a table-wide level based on analyses using Fisher's exact test. The observed heterozygote deficiencies at four of the five loci are apparently the result of high frequencies (0.089, 0.206, 0.348 and 0.539) of null alleles. Similar to the mtDNA studies of Rooney *et al.* (2001), further analyses of the microsatellite marker polymorphism data indicated bowhead whales had a period of historical population growth. As mentioned earlier, Maiers *et al.* (2001) found that the B-C-B and Hudson Bay stocks are more closely related to each other than either is to the Davis Strait stock based on studies of microsatellite polymorphism patterns. This may have resulted from two genetically distinct stocks, one from the west and one from the east, immigrating into the eastern Arctic after the last glaciation and subsequently mixing (Maiers *et al.*, 2001).

When data from Rooney *et al.* (1999) were used to compare the St Lawrence Island whales to the remaining B-C-B whales, no evidence of genetic differentiation could be found ($0.05 < p < 0.1$). This result was obtained by using an exact test (probability test) of population differentiation (Raymond and Rousset, 1995; Goudet *et al.*, 1996), specifically the genic test of population differentiation. Exact tests of population differentiation are reported to be accurate and unbiased in the case of small sample size or low-frequency alleles (Raymond and Rousset, 1995; Goudet *et al.*, 1996). However, such results should be used with caution because a larger sample size might reveal different patterns of genetic polymorphism, which could in turn influence tests of genetic differentiation.

While no evidence of stock substructuring was found in the comparison between bowhead whales landed at St Lawrence Island and whales landed along the north coast of Alaska, the summer feeding destination of the whales collected from St Lawrence in the spring is unknown. As with the analysis of mitochondrial DNA polymorphism, this compromises the interpretation of these results. And as mentioned in the previous section, a more appropriate comparison would be between whales that remain associated with the Chukotka Peninsula in the summer and those that migrate along the north coast of Alaska, past Pt Barrow, into the Beaufort Sea. A sufficient sample is already available for the latter (108 animals examined by Rooney *et al.*, 1999); however, it is very difficult to collect samples from whales that undoubtedly stay in the Bering or Chukchi Seas in the summer. Sampling of these whales will need to be made through biopsies from live whales rather than relying on a subsistence harvest or opportunistic strandings.

Ongoing studies of genetic diversity and population structure in the bowhead whale can be evaluated through an expanded database that includes samples from all regions where bowhead whales are currently found as well as from museums where baleen or bone samples may be archived. For example, Rosenbaum *et al.* (2001) reported that DNA has been extracted from tissue over 1,000 years old (a bone from the Viking era in Norway and baleen from excavations of a Thule Inuit whaling village on Somerset Island); such data may be useful for examining historical patterns of population structure. Currently studies are underway to learn more about genetic identity of the Okhotsk Sea stock (e.g. LeDuc *et al.*, 1998) and the eastern Arctic stocks (e.g. Maiers *et al.*, 2001). Previously, LeDuc *et al.* (1998) compared patterns of microsatellite polymorphism in the Okhotsk Sea and B-C-B stocks and found small differences, similar to their study on mtDNA polymorphism patterns.

Morphology and morphometrics

Morphological differences between putative stocks may provide evidence of low genetic dispersal, but these differences might be effected by environmental factors, so differences in habitat or geographic distribution should be examined before making conclusions about stock separation (Perrin, 2001). Morphological comparisons among various whale stocks have used various body proportions (including length), baleen, throat grooves, skeleton, internal organs and pigmentation (Perrin, 2001). No comparative studies of morphology and morphometrics have been conducted yet among the five bowhead whale stocks. Within-stock variability has been mentioned for nearly all of the stocks though insufficient data have been gathered to confirm these differences. For the Spitsbergen stock, whalers described how a group of whales would arrive out of the east during heavy ice years to summer along the southern coast of Spitsbergen, then return east as the ice retreated (Zorgdrager, 1720; summarised in Eschricht and Reinhardt, 1866). These whales were said to look and behave differently from the other Spitsbergen whales. Establishing any genetic or morphological variations between these groups is now virtually impossible given how rare sightings are. Similar references to ‘small whales’ or different ‘races’ were made by whalers operating in the Okhotsk Sea (e.g. poggy: Scammon, 1874) and in Davis Strait (e.g. middle-icers, rock-nosers, Pond’s Bay fish: Brown, 1868). A possible morphological variant of the B-C-B stock (the *ingutuk*) has been described as smaller, paler and possessing denser bones than other bowhead whales (Braham *et al.*, 1980; Fetter and Everitt, 1981); however, Jarrell (1981) showed that ingutuks are yearling bowhead whales and are not genetically distinct from other bowhead whales, a finding confirmed by phylogenetic analyses based on morphometric data and mtDNA polymorphism (A. Rooney, R. Tarpley and J.C. George, unpubl. data).

Individual identification

There are several relatively simple approaches to stock identity using reidentification of individual whales. When a whale is found with an identifiable harpoon head or other marker used on whales in a different stock, then it is clear that the whale travelled between stock boundaries. Aerial photography allows for reidentification of individual whales which could, in the same way as harpoon markers, show movements of whales between stock areas.

Tags and other marks

Identifiable markers, such as parts of harpoons or discovery tags, provide insights on longevity or movements of individual whales. Ivory or stone harpoon heads, not used by Eskimos for over a century, were found in five recently harvested whales. If these represent some of the last primitive harpoons ever used, and if they struck very young whales, then this evidence indicates that bowhead whales may live >50yrs (Philo *et al.*, 1993), >75yrs (George *et al.*, 1995) or >100yrs (George *et al.*, 1999). Such longevity has also been indicated via eye lens aspartic acid racemisation (George *et al.*, 1999). Commercial whalers reported incidents in which ‘unsuccessfully harpooned’ whales from one stock (Davis Strait or Spitsbergen) were later killed or found dead in the waters inhabited by the other stock (Eschricht and Reinhardt, 1866; Reeves *et al.*, 1983). Also, some exchange between the North Atlantic and the B-C-B stock has been documented. Bockstoce and Burns (1993) described two incidents in which whaling irons used in the western North Atlantic fishery were later found in whales taken in the Chukchi Sea, and Tomilin (1957) reviewed at least four reports, some as far back as 1643, of European-made harpoons found in bowhead whales in the Bering or Chukchi Seas.

A USSR discovery tag found in a bowhead whale that had been marked in October 1981 off Chukotka was recovered when the whale was taken off Wainwright, Alaska, in May 1983 (Dronenburg *et al.*, 1984).

In 1992, 12 whales were tagged off the Mackenzie Delta in the Canadian Beaufort Sea with Argos satellite-monitored radio tags (Krutzikowsky and Mate, 2000; Mate *et al.*, 2000). Although only one whale was successfully tracked out of the Beaufort Sea, it documented the autumn migration across the Chukchi Sea to Wrangel Island and south through the Chukchi Sea, a migration that had been inferred through sighting data (Moore and Reeves, 1993).

In 2001, five bowhead whales were instrumented with satellite transmitters in northwestern Disko Bay, West Greenland (Heide-Jorgensen *et al.*, 2001). Two of the whales travelled west on different routes across Baffin Bay toward Lancaster Sound, northern Canada, in 9-10 days. This confirms that bowhead whales on both sides of Baffin Bay are from the same stock.

Photo-identification

Aerial photography has proved to be a viable technique for identifying individual bowhead whales (Rugh *et al.*, 1992). Most images have been collected during the whales' spring migration past Pt Barrow (Rugh, 1990) and in the summer in the Beaufort Sea (Miller *et al.*, 1992); a few have been taken in the Bering Sea in winter (NMFS, unpubl. data) and in the Canadian Arctic (Finley, 1990). As more images become available from other areas, comparisons may be made that could establish movements of whales between stocks, if these movements do occur. It would be especially interesting to collect photographs of bowhead whales in the summer in the Chukchi and Bering Seas for the possibility that the same whales may have been seen in the Beaufort Sea during other summers.

Acoustics

If whale stocks have been isolated for a long time, their call types may change. For example, blue whale (*Balaenoptera musculus*) calls recorded in the Northeast Pacific are quite distinct from calls recorded in the western Pacific, and both show characteristic differences from southern blue whale calls (e.g. Stafford *et al.*, 1999).

To date, comparison of the limited recordings available has not resulted in positive attributions of call differences among bowhead stocks. Call types have been compared between bowhead whales migrating past Pt Barrow in the spring and whales in the Beaufort Sea during summer and autumn, and comparisons have been made between bowhead whales in the Davis Strait and the B-C-B (Würsig and Clark, 1993). Calls recorded from whales migrating past Pt Barrow were 85% simple-calls and 15% complex-calls, while those recorded near whales socialising in the Beaufort Sea during late summer and autumn were 52% simple-calls and 48% complex-calls. These differences are likely due to differences in sampling methods (ice-based continuous recordings vs 1-2 hour recordings from expendable sonobuoys) and primary behaviours (i.e. migrating vs socialising) in each locale. Differences in call characteristics as well as call proportions were found between recordings of western Arctic and Davis Strait bowhead whales (Würsig and Clark, 1993). In general, calls recorded near socialising whales in Isabella Bay were most often the complex-type, and these pulsed-tonal calls were often two to four times longer in duration than similar calls recorded from the B-C-B stock. Again, differences in recording circumstances probably contribute to the variability in call proportions. To make call-type comparisons reliable, environmental, temporal, behavioural parameters and sampling methods must be considered and standardised to the extent possible.

Passive acoustics has proven itself a reliable tool to monitor the timing, and sometimes the spatial distribution, of migrating bowhead whales. Acoustic detection methods have augmented the spring visual census of bowhead whales off Pt Barrow since 1984 (Clark *et al.*, 1996; Clark and Ellison, 2000). Passive acoustic location based on arrival-time differences on a sparse array of three to five hydrophones deployed from 1.5-4.5km along the ice edge has provided detailed information on the variability of bowhead distribution offshore the counting stations, both within and among years. This information is fundamental to improving estimates of stock abundance (Zeh *et al.*, 1993). In autumn 1986 and 1987, acoustic monitoring augmented sightings from aerial surveys to determine migration timing past Barter Island and Barrow, respectively (Moore *et al.*, 1989a). Three periods of peak calling activity were recognised over the course of each season, with the temporal pattern described by calling rates generally agreeing with those from aerial survey sighting rates.

Pollutant burden

Pollutant levels in tissue samples represent a potential source of information for investigating stock structure (e.g. Fujise *et al.*, 1997), assuming that individuals from distinct stocks display different levels of contaminants. This technique has the advantage over some of the other stock identification methods in that samples can be collected by biopsy from live animals (Perrin, 2001). Unfortunately, data only exist for animals that pass Pt Barrow during the spring migration. However, stock identification studies using information on pollutant levels presume that such levels will change imperceptibly through time for the respective areas. If such changes are substantial or if pollutant levels fluctuate moderately over the short term, then the reliability of studies based on pollutant levels would be called into question.

Parasites and predators

The possibility that distinct stocks of whales will harbour different parasites or different levels of infestation of the same parasites has been suggested as a useful tool for stock discrimination (e.g. Balbuena *et al.*, 1995). Such information has been used in studies of other cetaceans, such as the southern minke whale, *Balaenoptera bonaerensis* (Bushuev, 1990), sperm whales, *Physeter macrocephalus* (Dailey and Vogelbein, 1991) and pilot whales, *Globicephala melas* (Balbuena *et al.*, 1995). Virtually all information concerning bowhead whale parasite burden comes from studies of the B-C-B area, as this is the only regularly exploited stock with access to samples demonstrating parasite profiles. As yet, there are no data from animals from other stocks or geographic locales, so comparative analyses are not yet possible.

Whales in different areas may be differentially impacted by predators, as indicated by scarring (Perrin, 2001). For example, Bryde's whales (*Balaenoptera edeni* and *B. brydei*) off South Africa have differences in scarring depending on whether the whales inhabit primarily offshore or coastal areas (Best, 1977), and sperm whale populations have been differentiated based on environmental marks, including scars caused by killer whales (Dufault and Whitehead, 1993). Bowhead whales can reach great ages (George *et al.*, 1999) and accumulate many scars (Rugh *et* *al.*, 1992). Bowhead whales that tend to explore deep into the ice pack are more vulnerable to having ice-caused scarring than bowhead whales that spend most of their time near the ice front or in open water. The reverse may be true for scarring caused by killer whales, in that bowhead whales are more vulnerable to killer whale attacks when they are away from sea ice. Bowhead whales in the western Arctic do not appear to have as many scars from killer whale bites as do those from the eastern Arctic (George *et al.*, 1994; Finley, 2001), but this is clearly insufficient information upon which to base stock differentiation.

Feeding ecology

Differences in feeding ecology may also provide a basis for differentiating between stocks. For instance, two morphologically distinct forms of Bryde's whale off South Africa have consistent dietary differences (Best, 1977). However, gut contents are a very transient index and may be easily affected by ecological factors, whereas isotope ratios in hard tissues, parasites and tooth ultrastructure reflect characteristics over much of the lifetime of an individual (Perrin, 2001). In bowhead whales, $\partial^{13}C$ techniques have been used to establish tracer 'signatures' in zooplankton from various seas to indicate the respective feeding areas of bowhead whales across a chronological record of as much as 20 years stored in their baleen (Schell and Saupe, 1993). However, if whales that migrate to the Beaufort Sea for the summer do a preponderance of their feeding in the Bering and Chukchi Seas in autumn and winter (as presented by Schell and Saupe, 1993), it will be difficult to discriminate them from whales that reside year-round in the Bering and Chukchi Seas.

Fatty acid analysis, tracing signals from the prey to lipid deposits in a whale, may become a powerful tool in describing the feeding ecology of bowhead whales through a better understanding of their physiology, biochemistry and anatomy (Castellini, 2000).

Biological features

Differences in biological parameters or factors such as conception dates can provide valuable information on stock identity; for example, minke whales off Japan have two foetal cohorts per year, indicating a separation in breeding seasons of two stocks (Kato, 1992). However, the mating period for bowhead whales is not well defined. Apparent sexual activity has been observed in most months of the year (as reviewed in Koski *et al.*, 1993). Although the calving period may extend across half of the year, it seems that most calving occurs from April to early June. Therefore, most conceptions must occur approximately one gestation period (i.e. 13-14 months) earlier (Nerini *et al.*, 1984; Koski *et al.*, 1993), from March to May. Foetus sizes indicate that most conceptions occur during late winter or spring, and there is no evidence of delayed implantations (Koski *et al.*, 1993). This would mean conceptions occur during the spring migration, which provides a distinct possibility that bowhead whales who share a wintering area have opportunities to mate with animals that feed (spend the summer) in various geographic regions.

Other means that may potentially be used for discriminating stocks, such as differences in reproductive rates or age and sex structures (Perrin, 2001), will probably not help discriminate bowhead stocks. There is a very low probability that sufficient sample sizes will be collected for any stock other than the B-C-B stock.

CONCLUSIONS

The most effective way to examine questions of stock identity is to consider results from a suite of genetic and non-genetic techniques (e.g. Donovan, 1991; Perrin, 2001). The discovery of genetic differences between the Hudson Bay and Davis Straits stocks with no land barrier between them, provides a reason to investigate whether a similar separation occurs within the B-C-B management stock. To examine this question, one or more of the following approaches should be attempted: (1) genetic analysis of bowhead whales in the Bering Sea or Chukchi Sea in summer should be compared with samples collected from animals migrating past Pt Barrow; (2) multi-year aerial or vessel surveys, augmented by acoustic detection of calling whales, should be carried out along the Russian coast of the Chukchi Sea and north of Pt Barrow during the spring migration and during the summer feeding season to detect the consistency of whale occurrence; (3) satellite tagging of animals should be carried out in late spring in the Bering Sea to determine if whales seen there still migrate to the Beaufort Sea; (4) aerial photography should be attempted to capture images of bowhead whales summering in the Bering and Chukchi Seas for comparison to images collected from Pt Barrow during the spring migration and images from the summer in the Beaufort Sea; (5) acoustic recordings should be made to determine if there are differences in call characteristics, or proportions, that can be attributed to stocks in different areas; and (6) tissue analysis should be conducted to differentiate pollutant, parasitic or isotope levels.

At this time, the recognition of a single B-C-B stock is the most appropriate interpretation of the available data. In the many reviews of this issue undertaken by the IWC Scientific Committee, it has always concluded that a single-stock designation was appropriate based on evidence from a number of techniques as listed below.

(1) Very few bowhead whales are seen in the Bering or Chukchi Seas in the summer or early autumn, at a time when bowhead whales are common in the Beaufort Sea; however, bowhead occurrence seasonally increases in each of these areas at a time best explained as a migration of one stock from the Bering to the Beaufort Seas and back.

(2) There may have been an increase in summer sightings in the Chukchi and Bering Seas over the past several decades. This increase is probably due to the increase in abundance of the B-C-B stock. Such an increase would not be discerned if there were separate, small stocks.

(3) The highly labile nature of the bowhead migration (affected by sea ice, food availability and potentially by anthropogenic perturbations) allows for whale occurrence in areas other than the expected migratory routes. Some whales might migrate east in the spring and return west well before the typical autumn migration; some whales might not migrate east of the Chukchi Sea in some years; and some whales might not migrate out of the Bering Sea.

(4) Virtually all of the whales harvested by subsistence hunters on St Lawrence Island are taken in the winter or spring, a time when whales are probably migrating to or from the Beaufort Sea.

In conclusion, the available evidence (mostly through geographic distribution) indicates that there are currently five stocks of bowhead whales: the Spitzbergen, Davis Strait, Hudson Bay, Okhotsk and B-C-B stocks. Although there appears to be some degree of geographical and genetic differentiation between these stocks, there are also many indications that these whales can and have intermingled across the Arctic.

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A review of gray whales (*Eschrichtius robustus*) on their wintering grounds in Mexican waters

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ABSTRACT

The Eastern North Pacific gray whale (*Eschrichtius robustus*) is one population of large cetacean that has recovered from depletion resulting from commercial harvest in the mid- to late-1800s. It is believed that this population may be approaching, or possibly exceeding its carrying capacity as suggested by recent increases in mortality of all age and sex classes. Research on the breeding biology and phenology of gray whales that spend the winter in the coastal waters and lagoons of Baja California, Mexico has been conducted for many years. These studies contribute valuable information on the reproductive biology of this species, and the importance of their coastal lagoon habitats to their reproductive success. This paper reviews and summarises historical exploitation, conservation measures, the findings of research conducted on gray whales in their winter breeding range, potential natural and anthropogenic threats to this population, and makes recommendations for future research and monitoring. This review concentrates on the findings of research conducted since the mid-1970s.

KEYWORDS: EXPLOITATION; CONSERVATION; GRAY WHALE; BAJA CALIFORNIA; MORTALITY; BIRTH RATE; GENETICS; HABITAT; DISTURBANCE; NORTH PACIFIC

INTRODUCTION

The Eastern North Pacific gray whale population (*Eschrichtius robustus*) has been the focus of ongoing research and population monitoring. It is an example of a population of large whales that has successfully recovered from over-exploitation (Jones, M.L. and Swartz, 2002). This population may be approaching, or possibly already exceeding its carrying capacity level (Moore *et al.*, 2001). Recent range-wide increases in mortality of all age and sex classes suggest the population may have become food limited (Le Boeuf *et al.*, 2000). Research on the breeding biology and phenology of gray whales has contributed and continues to contribute valuable information on the importance of their coastal lagoon habitats to their reproductive success. This paper reviews and summarises whaling history, conservation measures and the findings of research conducted on gray whales in their winter breeding range. The latter concentrates on work conducted since the mid-1970s. Natural and anthropogenic threats to gray whales are discussed and suggestions are made for additional research and monitoring.

STUDY SITE

The main winter breeding range of the eastern gray whale population extends from about Point Conception in southern California to Cabo San Lucas, Baja California (Jones, M.L. and Swartz, 2002). Gray whales concentrate in specific areas, particularly near and within coastal lagoons and bays including: Laguna Guerrero Negro; Laguna Ojo de Liebre (Scammon's lagoon); Laguna San Ignacio; Santo Domingo Channel; Bahia Magdalena and Bahia Almejas (Fig. 1). Some gray whales journey around the cape of the Baja California peninsula, into the Gulf of California and along the coasts of Sonora, Sinaloa and Nayarit in mainland Mexico (Berdegué, 1956; Gilmore, 1960a; b; Henderson, 1972; Tershy and Breese, 1991). The ecological characteristics of the wintering grounds presumably offer reproductive advantages to gray whales (Fleischer *et al.*, 1984; Jones, M.L. and Swartz, 1984; Fleischer and Beddington, 1985).

History of exploitation in Baja California

While there are no accounts of gray whale hunts in Mexican waters before the nineteenth century, it is clear that aboriginal Mexicans and Spaniards recognised this species long before the 1800s. It is believed that some indigenous native groups from Baja California occasionally may have eaten meat of gray whales that had died and washed ashore (Russell, 2001). Information on gray whale hunting in Baja California is summarised in the following paragraphs. Information from mainland Mexico is presented elsewhere in detail (Rice and Wolman, 1971; Henderson, 1972; 1984; Reeves, 1977; 1984; Reeves and Mitchell, 1988; Dedina, 2000; Donahue and Brownell, 2001; Russell, 2001).

Nineteenth Century

Bahia Magdalena

The first documented catches of gray whales in Baja California are from the winter of 1845-46 in Bahia Magdalena with the arrival of the ships *United States* and *Hibernia* under Captains Joshua Stevens and James Smith, respectively. During this first season, approximately 32

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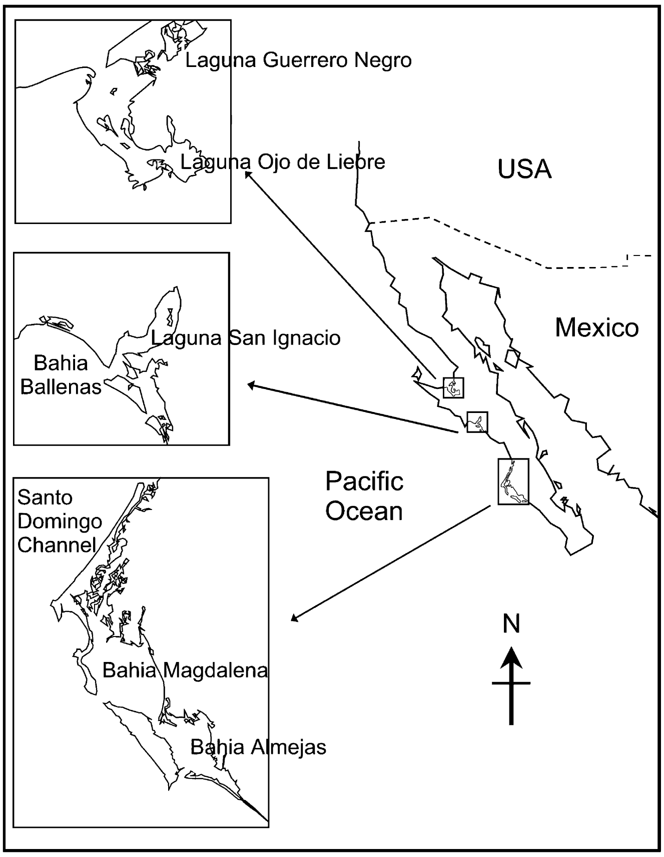

Fig. 1. Study site.

whales were taken[1] (Henderson, 1972; 1984). The peak years of whaling in Bahia Magdalena were from 1845-1847 and from 1851-1865, when 125 whaling vessels captured between 1,950-2,000 whales. During the later period, 34,425 barrels of oil brought US$516,375. The number of whales killed in Bahia Magdalena from 1845-46 to 1873-1874 was estimated at 2,145-2,200; roughly 9% of these whales were lost (Henderson, 1972; 1984).

Laguna Ojo de Liebre and Laguna San Ignacio

In 1855, whaling started in the two lagoons north of Bahia Magdalena: Ojo de Liebre (Scammon's Lagoon) and San Ignacio. In the former, 36 cruises from 1854-1855 to 1864-1865 secured 553 whales but probably killed 608 (Henderson, 1972; 1984). From then until the 1873-1874 seasons, approximately 650 whales were killed and from those about 590 were secured. Laguna Guerrero Negro and Manuela, north of Ojo de Liebre, were not important whaling grounds.

Whaling also took place in the lagoon of San Ignacio and adjacent waters. From 1854-1855 to 1864-65 approximately 350 whales were secured and probably 385 killed. By the 1873-1874 seasons a total of 400 had been secured from 440 killed (Henderson, 1972; 1984).

Western coast of Baja California and Gulf of California

Additional gray whales were killed and taken along the Pacific coast and Islands of Baja California, particularly San Martin, San Benitos, Cedros, Natividad and Asuncion Islands. Henderson (1972; 1984) pinpoints the new whaling grounds including San Diego Bay, San Quintin Bay and Turtle Bay (San Bartholomeu Bay) and indicates that 990 gray whales were killed and 900 were secured from 1854-1865. However this figure seems to include whales taken along the coast of California as well. Within the Gulf of California during this same period 150 whales were taken from 165 killed. By 1874, a total of 220 whales were killed (200 taken) in these waters (Henderson, 1984).

Whaling summary

During the Nineteenth Century, more than 3,200 whales were killed in the bays and lagoons of Baja California (Dedina, 2000). Henderson (1984) reports a similar amount 3,235-3,290 killed with 2,941-2,991 taken. If those from the Gulf of California are added, at least 3,465-3,510 gray whales were killed in Mexican waters in a period of 29 years ranging from 1845-1874, or an average of about 120 per year.

The lagoon complex of Bahia Magdalena sustained more whaling for a longer period of time than Ojo de Liebre and Laguna San Ignacio. The total kill in Magdalena Bay was probably around 2,200 whales during a period of 25-30 years. Even though Magdalena remained the most important whaling ground, it is interesting to note that based on recent surveys, Laguna Ojo de Liebre is currently used by more whales than Bahia Magdalena and Laguna San Ignacio (Urbán *et al.*, 2001).

Twentieth Century

Bahia Magdalena again became the main focus for commercial whaling in Mexico in the 20th century. Thirty years after the American whalers had withdrawn, Norwegian whalers started whaling with the factory ship *Capella I*. Between 28 November, 1913 and 14 May 1914 they took a total of 19 gray whales. In the next decade the exploitation of gray whales increased with the presence of the Norwegian factory ships *Kommanddoren I, Mexico, Ragnhild Bryde I* and the *Esperanza*. The former two took at least 129 whales between mid-November 1924 and February 1926 in Bahia Magdalena. From 1913 until 1929 Norwegian whalers took at least 200 gray whales in Mexican waters. In the 1960s the gray whale population was considered to be increasing and estimated to be at least 12,000 animals (Rice and Wolman, 1971).

FORMAL PROTECTION OF GRAY WHALES IN MEXICO

History of gray whale conservation

The commitment of the Mexican government to the conservation of gray whales and their habitat in Baja California Sur is the result of: (1) the legacy of foreign overexploitation of natural resources including gray whales prior to the Mexican Revolution (1910), and the subsequent desire of the federal government to re-establish control over national territory and natural resources; (2) the work of policy makers and environmental advocates to protect two gray whale breeding/calving lagoons as sanctuaries and later as biosphere reserves; (3) cooperation between Mexican and US scientists and policy-makers interested in the conservation of gray whales and their habitat throughout their migratory range; and (4) the enactment of laws that provide government agencies in Mexico with the authorisation to protect gray whales and their habitat (Dedina and Young, 1994).

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[1] 1,440 barrels of oil, 35 barrels/gray whale.

Mexico recognised the Geneva Convention for the Protection of Whales in 1933, and gave its approval to the International Agreement for the Regulation of Whaling in 1938 (Diario Oficial, 1938). In 1949 Mexico became a member of the International Whaling Commission (Diario Oficial, 1949).

In 1965, the Secretariat of Fisheries (Pesca) proposed the opening of a whaling station to harvest gray whales off the Baja California coast (Bunker, 1965). As a result of an international outcry over the proposal, Mexico denied having made plans to resume whaling (Jones, H.Y., 1965; Dedina, 2000). Pressure to allow the hunting of gray whales continued. In 1970, gray whale researcher Raymond Gilmore argued that keeping the population near 10,000 would provide, '...whales for the whalers and the public and science'. He did suggest, however, that Mexico could '...make more money by having the herd conserved...where [the whales]...will breed unmolested and draw tourists' (Gilmore, 1970 cited by Dedina and Young, 1994).

Gray whale habitat protection

In December 1971, Mexican President Luis Echeverria signed legislation that established Laguna Ojo de Liebre as a whale refuge, the first of its kind in the world (Diario Oficial, 1972b; Jones, M.L. and Swartz, 1984). In June 1972, seven months after creating the Laguna Ojo de Liebre Whale Refuge, Echeverria declared both Laguna Ojo de Liebre and Laguna San Ignacio as Migratory Bird and Wildlife Refuges (Diario Oficial, 1972a). In 1979, President Jose Lopez Portillo declared Laguna San Ignacio as a Whale Refuge and Maritime Tourist Attraction Zone. The decree established a permitting mechanism for scientific research and tourism in the area, under the administration of the Ministry of Pesca (Diario Oficial, 1979). The vague wording of the 1971 Ojo de Liebre whale refuge decree prompted Lopez Portillo to revise it in 1980, to include reserve status for Laguna Manuela and Laguna Guerrero Negro (Diario Oficial, 1980).

In 1988, President Miguel De la Madrid signed a law creating the Vizcaino Biosphere Reserve within the frame of the National System of Protected Areas (SINAP) established in 1984 (Poder Ejecutivo Federal, 1984; SEDUE, 1986; Diario Oficial, 1988). In 1993 portions of El Vizcaino Biosphere Reserve consisting of Ojo de Liebre and San Ignacio lagoons were added to the World Heritage Site list of the United Nations Educational, Scientific, and Cultural Organisation (UNESCO).

International cooperation

An important aspect of efforts to protect gray whale habitat has been the international cooperation and research that involved sharing information regarding gray whale behaviour, migratory patterns, habitat, and conservation needs. In 1977, the Mexican government sponsored the First International Symposium on the Gray Whale in Guerrero Negro. During the meeting researchers and policy-makers from both Mexico and the USA discussed the most effective methods of assuring the continued growth of the gray whale population and the conservation of the Laguna Ojo de Liebre complex (Aurioles-Gamboa *et al.*, 1993).

Beginning in the late 1970s, the US National Oceanographic and Atmospheric Administration (NOAA) sponsored three joint meetings between Mexican and US researchers regarding gray whale research. Conferences on marine mammals held annually since the 1970s by the Mexican Society for the Study of Marine Mammals (SOMEMMA) have brought together researchers from various countries to discuss issues related to gray whale and other marine mammal research (Aurioles-Gamboa *et al.*, 1993; Urbán and Rojas, 1999).

Additional legislation

The 1988 General Law of Ecological Balance and Environmental Protection is the responsibility of the new Secretariat of the Environment and Natural Resources (SEMARNAT), established in December 2001. Articles 15 to 19 of the law provide SEMARNAT with a broad mandate to formulate policy and planning initiatives, and to implement management actions for the protection of the nation's natural resources (Estados Unidos Mexicanos, 1993).

One other piece of legislation, a 1991 addition to the Mexican Penal Code, Article 254 *bis*, later transformed into Article 420, imposes a prison term of between six months and six years plus a fine for the unauthorised capture of or injury to marine mammals and sea turtles (Diario Oficial, 1991; Cultura Ecológica, 1999).

The General Law of Wildlife, adopted on 27 April, 2000 (Diario Oficial, 2000a), added Article 60 *bis* on 10 January 2002, which states that: 'No marine mammal specimen of any species can be the subject of subsistence or commercial use, with the exception of captures with scientific research and educational purposes' (Diario Oficial, 2002b).

The Mexican Official Norm, NOM-59-ECOL-1994, defines those species and sub-species of terrestrial and aquatic wildlife flora and fauna that are in danger of extinction, threatened, rare and those subject to special protection, and established the specific provisions for their protection (Diario Oficial, 1994). This norm was updated on 6 March 2002 (NOM-59-ECOL-2001) (Diario Oficial, 2002c). Since 1994 gray whales have been listed under the category of 'special protection' which means that this species faces threats that could affect its survival.

The Mexican Official Norm, NOM-131-ECOL-1998 stipulates guidelines and specifications for whalewatching activities (Diario Oficial, 2000b). Whalewatching activities in Ojo de Liebre and San Ignacio lagoons, Santo Domingo Channel and Bahia Magdalena are included in this norm (Urbán and Gómez-Gallardo, 2000).

Finally, in May 2002 all the Mexican territorial seas and EEZ were declared a refuge for the protection of the large whales (Mysticeti and Odontoceti) (Diario Oficial, 2002a).

GRAY WHALE RESEARCH IN MEXICAN WATERS

Laguna Ojo de Liebre-Guerrero Negro

Since the account by Scammon (1874), no studies of gray whales on their winter grounds were conducted until 1952, when Raymond M. Gilmore made the first of a series of field trips to Baja California (Gilmore and Ewing, 1954; Gilmore, 1960a; b; 1976a; b). Subsequently, several researchers visited Laguna Ojo de Liebre, but their observations were mostly brief and opportunistic (Berdegué, 1956; Eberhardt and Evans, 1962; Eberhardt and Norris, 1964; Eberhardt, 1966; Hubbs and Hubbs, 1967; Spencer, 1973; Balcomb, 1974; Gard, 1974; 1978a; b; Samaras, 1974; White, 1975 and White and Griese, 1978). In 1978, representatives of Mexico's Departamento de Pesca and the US National Marine Fisheries Service's National Marine Mammal Laboratory met to develop a joint programme for the study of the gray whale for an initial period of five years

(1978-1983) (Rice *et al.*, 1981). The findings of this joint programme are available in published and unpublished papers (Fleischer, 1981; Rice *et al.*, 1981; 1982; Fleischer and Beddington, 1985).

In Laguna Guerrero Negro, Bryant *et al.* (1984) conducted vessel surveys from 1980-1982. In 1988, researchers from the new Biosphere Reserve El Vizcaíno began a monitoring programme of gray whales in Laguna San Ignacio and Laguna Ojo de Liebre (Sánchez P, 1991; 1998). In 2000, the Universidad Autónoma de Baja California Sur, began a project to document the current abundance, distribution, duration of residency and mortality of the gray whales in Laguna Ojo de Liebre (Urbán *et al.*, 2001).

Laguna San Ignacio

Aerial surveys to count gray whales wintering in Laguna San Ignacio were conducted between 1947 and 1965 by Gilmore (1960a; b), Hubbs and Hubbs (1967) and Gard (1978a). The first systematic study of gray whales utilising Laguna San Ignacio was conducted by Jones and Swartz (1984) with the twofold aim of providing baseline information on the demography and phenology of breeding whales, and to evaluate the effects of whalewatching activities within the lagoon on the whales. This field research continued for five consecutive winters from 1978 to 1982. It generated information on: (1) the seasonal timetable of lagoon occupation by whales; (2) the numbers and distribution of whales utilising the lagoon interior and inlet area; (3) the proportion of females with calves to whales without calves (singles) that utilise the lagoon throughout each winter season; (4) the location of specific nursery areas and the seasonal abundance of calves in these areas; (5) the seasonal mortality of adults, juveniles and calves; and (6) the number of whalewatching vessels and levels of tourism and other human activities that occur within the lagoon each winter. Between 1996 and 2000 a Mexican research team (Urbán *et al.*, 1997; 1998; 1999; 2001; Urbán and Gómez-Gallardo, 2000) continued the demographic studies of gray whales in Laguna San Ignacio based on the methods of Jones and Swartz (1984) to provide an update to the historical baseline information for this breeding lagoon and to evaluate the potential effects of building an industrial salt production facility on the northern shore of the lagoon.

Bahia Magdalena-Almejas and Santo Domingo Channel

Studies of gray whales in the Bahia Magdalena area have been conducted principally in the region of La Boca de la Soledad at the end of the Santo Domingo Channel. Hubbs and Hubbs (1967), Gard (1974), Rice *et al.* (1981; 1982) conducted aerial surveys to count gray whales. Fleischer and Contreras (1986) compared counts from different platforms. Norris *et al.* (1983) reported on the movements of whales in the mouth of Bahia Magdalena. Loreto *et al.* (1996) and Sánchez (1997) conducted studies to evaluate the magnitude of whalewatching activities in this region, and the effects of those activities on gray whales wintering there. Gardner and Chavez-Rosales (2000) documented changes in the relative abundance of gray whales in Bahia Magdalena during an El Niño event (1997-1999). During this time period the whale sightings were inversely related to temperature. In 1999 they registered 8.1 whales hr^{-1} with a sea surface temperature of 15.7 ± 0.9°C; and in 1998 0.55 whales hr^{-1} with a sea surface temperature of 21.5 ± 0.9°C. Péréz-Cortés *et al.* (2000) recorded the abundance variations of gray whales in Santo Domingo channel from the 1997 to 2000 winter seasons.

Bahía de Todos Santos

Bahía de Todos Santos is located on the northern coast of the Baja California Peninsula off the Port of Ensenada at 31°48’N 116°40’W. Heckel *et al.* (2001) investigated the influence of whalewatching boats on the behaviour of gray whales on their migratory route in Bahia Todos Santos, Baja California. They found significant differences in both speed and direction of the transit of gray whales with and without presence of whalewatching boats and made recommendations on the whalewatching regulations.

BIOLOGY POPULATION KNOWLEDGE

Winter abundance

The various research programmes conducted throughout the Pacific coastal waters and coastal lagoons and bays of Baja California provide minimum counts of gray whales that spend the winter breeding season in Mexican waters each year (Table 1). Although coverage has been fragmentary and less than synoptic over the past three decades, these counts do provide a rough index of the trends in the population of gray whales that winter in this portion of their breeding range.

Laguna Guerrero Negro

The abundance of gray whales in Guerrero Negro has varied dramatically since surveys began there in the 1950s (Fig. 2). Aerial surveys conducted in mid-February from 1952 to 1962 indicated that single whales predominated. The count in mid-February 1954 included 120 single whales and 22 mothers with calves (Gard, 1974). Subsequent aerial surveys conducted in 1964 and 1970 detected no whales inside this lagoon. Gray whales were again observed by aerial surveys in 1973 (34 singles and 35 mothers with calves), and in the ensuing three seasons (1974-1976) the numbers fluctuated from 12 to 82 singles and 23 to 34 mothers with calves (Gard, 1978a; b). In 1977, the first boat-based counts were made and included one single whale and 57 mother-calf pairs (Bryant *et al.*, 1984). From 1980 to 1982, Bryant *et al.* (1984) monitored gray whale abundance in Guerrero Negro lagoon during the breeding season. Boat-based counts during this study indicated a predominance of mothers with calves, with the highest count occurring in 1981 (43 singles and 164 mothers with calves). There were no surveys following this effort until 1997. Boat surveys conducted in 1997, 1998 and 2002 found low numbers ($>$ 13) of adult whales inside the lagoon.

Gard (1978a) stated that the decline of whale numbers between 1964 and 1970 was probably caused by the vessel activity associated with the commercial shipment of salt from Laguna Guerrero Negro, an operation that took place in that lagoon from 1957 to 1967 (Fig. 2). The constant dredging operation needed to keep the channel open may have been the main source of disturbance to the whales (Bryant *et al.*, 1984). Unfortunately there is no information on the use of the lagoon by gray whales between 1982 and 1997, but recent surveys suggest that the seasonal abundance of whales in the lagoon has decreased 90% since the 1980s. Local fishermen suggest that this decline could be due to the natural closure of the lagoon entrance as sand accumulates in the absence of any dredging operations. At this time there is no conclusive evidence concerning the cause of the extreme fluctuations in whale abundance in this lagoon over the years.

Table 1

Counts of gray whale cow-calf pairs (MC) and single adult or juvenile whales (S) along the Pacific coast and within the breeding lagoons at the peak of the breeding season in February. Key: BA = Bahia Almejas; BM = Bahia Magdalena; SDC = Santo Domingo Channel; LSI = Laguna San Ignacio; LOL = Laguna Ojo de Liebre; LGN = Laguna Guerrero Negro; C = west coast of Baja California Peninsula.

	BA		BM		SDC		LSI		LOL		LGN		C*	
Year	MC	S	MC	S	MC	S	MC	S	MC	S	MC	S	MC	S
1978							67	235						
1979							100	208						
1980	4	135	25	60			118	214	557	187	115	19	116	326
1981							141	207	525	477	164	43		
1982					106	33	137	270	553	483	101	23		
1983					123	36			463	299				
1984					151	7								
1985					173	15			502	283				
1987									534	336				
1988									95	369				
1989									91	178				
1996							92	115	377	245			21	206
1997	15	94	9	72	83	17	126	127	626	317	7	5		
1998	5	15	1	4	12	7	52	178	530	401	5	3	46	138
1999					32	26	17	144	213	324				
2000					16	21	45	182	256	209				
2001					25	44	29	108	333	153				
2002	44	201			97	0	43	170	475	248	6	2		

Sources: Laguna San Ignacio 1978-1982 from Jones and Swartz (1984); Bahia Almejas, Bahia Magdalena, Ojo de Liebre and west coast in 1980 from Rice *et al.* (1981); Laguna Guerrero Negro 1980-1982 from Bryant *et al.* (1984); Laguna Ojo de Liebre 1980-1983, and Santo Domingo Channel 1982-85 from Fleischer and Beddington (1985) and Fleischer and Contreras (1986); Laguna Ojo de Liebre 1985-1989 from Sánchez (1991).

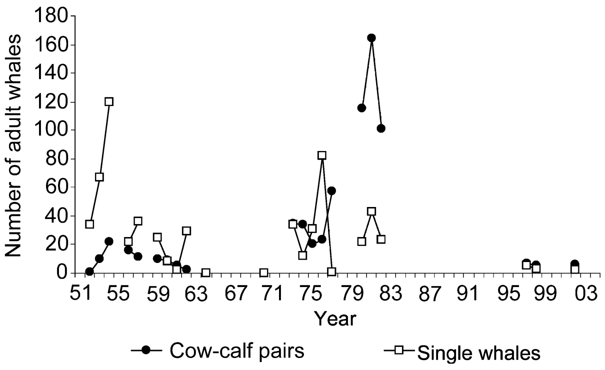

Fig. 2. Abundance of gray whales in Laguna Guerrero Negro.

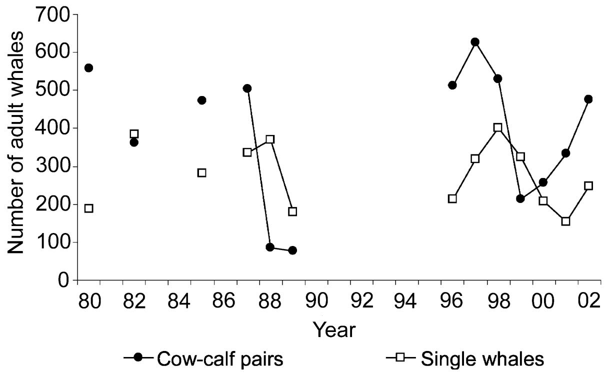

Fig. 3. Abundance of gray whales in Laguna Ojo de Liebre.

Laguna Ojo de Liebre

Historical surveys indicate that Laguna Ojo de Liebre is the most important breeding and calving lagoon in terms of the number of whales that occupy it during the winter breeding season. The maximum counts since the early 1980s are relatively constant with the exception of two drastic declines in recent years (Fig. 3).

During 1988, there was an extreme decline in the counts of mother-calf pairs from 503 in 1987 to 84 in 1988. The cause of this decline remains uncertain, however, apparently it was not related to Sea Surface Temperature (SST) anomalies observed during this period; the SST in the lagoon was the same (17.2°C) as the year before (Sánchez P, 1991). In 1989, low numbers of mothers with calves were observed again, along with lower than expected counts of single whales. The SST in the lagoon that year was 15.5°C (Sánchez P, 1991) and the general winter distribution of gray whales along the Pacific coast of Baja California appeared to have shifted further south, with some whales moving into the Gulf of California and up to Bahia de Banderas along the mainland coast (Urbán *et al.*, 1990). Unfortunately, there were no surveys during the next five years to monitor trends of gray whale occupancy in the lagoons. Surveys resumed in 1996, when winter counts of gray whales had returned to expected levels.

A similar decline in counts occurred in 1999, when the number of mother-calf pairs decreased from 530 in 1998 to 213. Again, the SST was lower than the average and the general whale distribution appeared to have shifted to the south (Urbán *et al.*, 2003). Counts during the 2000 and 2001 winter seasons indicated a slight increase in mothers with calves, but a decrease in single whales. Overall, surveys in 2002 suggest that both classes of whales are utilising this lagoon in expected numbers.

Laguna San Ignacio

Abundance records for Laguna San Ignacio come from two time-series of counts from small-boat transects during the peak of the gray whale winter breeding season in February

(Fig. 4). The first series, from 1978 to 1982, showed that winter occupation of Laguna San Ignacio began in December and reached its maximum by mid-February (Jones, M.L. and Swartz, 1984). The seasonal distribution was bi-modal: the major mode represented the maximum combined counts for each year and consisted of single whales and some mother-calf pairs. Following the February peak, the density of whales in the lagoon decreased as single whales departed and began their northward migration. During this five-year period mother-calf pairs increased in numbers during March and slowly declined through April each year. This late-season increase in mother-calf pairs appeared to be the result of an influx of mothers and calves from other areas, rather than of continuing births of calves. This was confirmed by the estimated length of the late-season calves indicating that they were not newly born, and by matching photographs of females indicating that some of them were coming to Laguna San Ignacio from other lagoons during the same winter season. The maximum combined mid-February counts of non-calf gray whales increased significantly at an average rate of 7.3% per year from 300 in 1978 to 407 in 1982 [$F(1,3) = 32.88$, $p < 0.025$, $r^2 = 0.916$]. Counts of single whales in Laguna San Ignacio reached a maximum in mid-February each year and averaged 226 whales (range 207-270), but did not show a significant trend [$F(1,3) = 0.52$, $p > 0.50$, $r^2 = 0.147$]. Mid-February counts of mothers and calves showed a significant increase each year [$F(1,3) = 16.13$, $p < 0.05$, $r^2 = 0.843$] and averaged 112 pairs (range 67-137). The greatest numbers of mother-calf pairs were observed during March following the mid-February maximum total counts, and averaged 225 pairs (range 186-282).

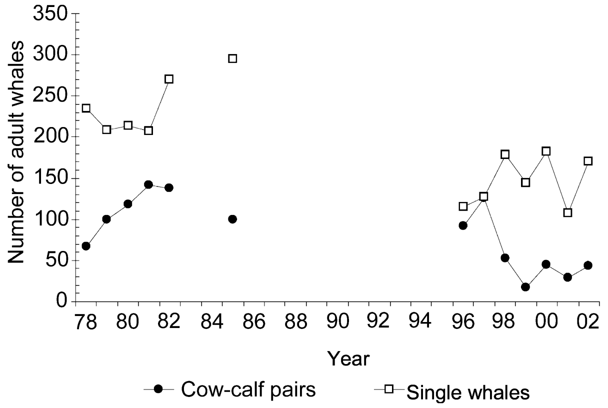

Fig. 4. Abundance of gray whales in Laguna San Ignacio.

The second time-series of whale counts from 1996 to 2000 was generated by Urbán *et al.* (2000) using basically the same survey and counting procedures as Jones and Swartz (1984). This series yielded total combined maximum counts that averaged 204 whales (range 137-253), suggesting an approximately 30% decrease in the mid-February counts of whales in the lagoon since the 1978-1982 time period. This decrease was seen in counts of single whales that averaged 146 whales (range 108-178), and in counts of mother-calf pairs that averaged 58 pairs (range 17-126). The late-season increase in mother-calf pairs observed in March in the years 1978-1982 was not evident during the 1996-2002 period. Counts of all whales decreased following the 1998 El Niño event, and these decreased counts may be the result of changes in the SST that persisted during 1999 and 2000 (Urbán *et al.*, 2003).

Bahía Magdalena Region

Although Magdalena Bay is frequently mentioned as a winter congregation area for the gray whale, the evidence shows that the different parts of this lagoon complex act as separate breeding sites. Whale counts in this region have been irregular and conducted from different platforms (Table 1). The most studied area has been the Santo Domingo Channel including the entrance, Boca de la Soledad. Two time-series of counts from small-boat transects along the channel during the peak of the gray whale winter breeding season in February are available. The first one from 1983 to 1985 documented the presence of gray whales from mid-January to mid-March (Fleischer and Beddington, 1985; Fleischer and Contreras U., 1986). Maximum counts were obtained in 1985 and included 173 mothers with calves and 15 single whales (Fig. 5). The second time series, from 1997 to 2002, documented abrupt changes in the abundance of both mothers with calves and single whales likely related to the influence of ENSO (Pérez-Cortés M. *et al.*, 2000; and this paper). Abundance decreased from 1997 to 1998, and then gradually recovered until 2002 when the number of mothers with calves was similar to 1997. Surprisingly, single whales were absent from this area in mid-February (Fig. 5). Thus, it seems that Santo Domingo Channel is used mainly as a calving/nursing area in contrast to the other parts of the lagoon complex (e.g. main Magdalena Bay and Almejas Bay) that apparently serve as mating areas or sites for congregation of young and immature gray whales.

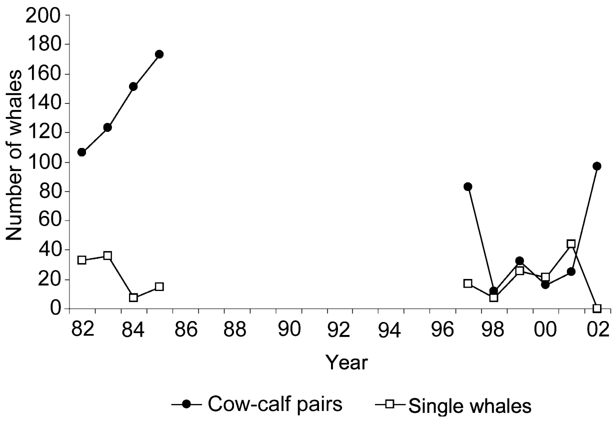

Fig. 5. Abundance of gray whales in Santo Domingo Channel.

Distribution among the breeding lagoons and coastal areas

The core of the winter breeding range of the eastern North Pacific gray whale stock lies along the west coast of the Peninsula de Baja California, from Morro de Santo Domingo (28°05'N) south to Isla Creciente (24°20'N). Some whales may be found north of this area all winter, but they are mostly transiting to and from the core winter breeding range. For example, in central California the earliest northbound migrants are seen before the last of the southbound whales have passed this area. In some years, a few whales also continue migrating south past the principal breeding lagoons and travel around Cabo San Lucas, the southern extremity of the peninsula, and enter the Gulf of California (Rice *et al.*, 1981). As noted above, the 'normal' winter distribution appears to be influenced by periodic SST anomalies; when the SST is higher the distribution shifts to the north, e.g.

1998 breeding season, and when is lower the winter distribution of gray whales shifts to the south, e.g. 1989 and 1999 breeding seasons (Urbán *et al.*, 1990; 2003; Gardner and Chávez-Rosales, 2000; Sánchez *et al.*, 2001).

Surveys for gray whales in different winter congregation and breeding areas during the same season were conducted in 1997 and 1998. The 1998 El Niño affected the whale distribution; therefore, the distribution of whales observed in 1997 is believed to best represent the usual distribution of gray whales in the winter range when no major SST anomalies are occurring.

With regard to the distribution of mothers with calves in the different breeding and calving aggregations, Laguna Ojo de Liebre is the most important, followed by Laguna San Ignacio and Santo Domingo Channel (Fig. 6). These three areas included 91% of all the mothers and calves counted in 1997. A comparison, counts of mother with calves obtained during the 1980 and 1997 breeding seasons indicates changes in the preference of the whales. Their proportional distribution increased in Laguna Ojo de Liebre from 53% in 1980 to 72% in 1997, decreased in Laguna Guerrero Negro from 10% to 1%, and decreased in Bahia Magdalena from 5% to 1% (Table 2) (see Rice *et al.*, 1981).

Laguna Ojo de Liebre also contains the highest number of single whales during the winter, followed by Laguna San Ignacio, Bahia Almejas and Bahia Magdalena (Fig. 7). Compared to the distribution of single whales observed during the 1980 breeding season (see Rice *et al.*, 1981), the main changes in the proportional distribution of single whales seen in 1997 include an increase of single whales in Laguna San Ignacio from 12% to 20%, a decrease in Laguna Laguna Guerrero Negro from 7% to 1%, and a decrease in the Santo Domingo Channel from 10% to 3% (Table 3).

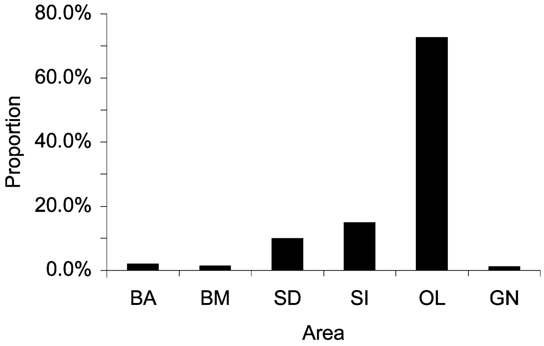

Fig. 6. Mothers with calf distribution in the 1997 winter season.

Table 2

Percentage of cow-calf pairs distribution during the 1980 and 1997 winter seasons. For key see Table 1.

Year	BA	BM	SDC	LSI	LOL	LGN	Total
1980	<1	5	13	13	58	10	100
1997	2	1	10	14	72	1	100

Table 3

Percentage of single whale distribution during the 1980 and 1997 winter seasons. For key see Table 1.

Year	BA	BM	SDC	LSI	LOL	LGN	Total
1980	19	8	10	12	44	7	100
1997	15	11	3	20	50	1	100

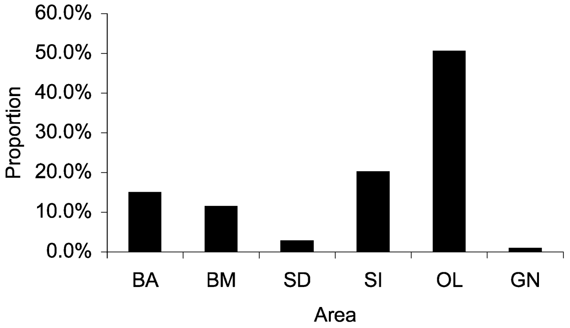

Fig. 7. Single whales distribution in the 1997 winter season.

Calf production and mortality in the lagoons

Jones and Swartz (1984) estimated the minimum calf mortality rate during the winter breeding seasons between 1978 and 1982 by dividing the number of dead calves discovered each season by the number of living and dead new-born calves counted each season. The mortality rates ranged from 2.8% in 1980 to 5.8% in 1978, with a five-year average of 3.5%.

Swartz and Jones (1983) estimated annual gray whale calf production and mortality from data collected in Laguna Guerrero Negro, Laguna Ojo de Liebre and Laguna San Ignacio between 1980 and 1982. A gross annual production of 1,185 calves with a 5.4% mortality based on lagoon strandings yielded a net production of 1,121 calves. This represented a 7.0% annual rate of production (no confidence intervals were reported) based on the best estimate of the 1981 population size of 15,942 whales. By comparison, the proportion of calves passing Pt Piedras Blancas in central California during the spring migration in 1980 and 1981 was 4.3% (679) and 4.8% (769) respectively (Poole, 1981 in Swartz and Jones, 1983), suggesting that a 31% calf decrease may have occurred during the northward spring migration between the breeding lagoons and central California. Based on these results, they postulated two periods critical to calf survival: the first period immediately follows birth, and the second corresponds to the calves' departure from the lagoons and the beginning of the northward migration when potentially some calves fall prey to sharks and killer whales (*Orcinus orca*), or become lost, disoriented and ultimately separated from their mothers prior to weaning (Swartz and Jones, 1983).

For the winter seasons 1997 to 2002 annual calf production was estimated using the assumption that counts of mother-calf pairs in Laguna Ojo de Liebre, Laguna San Ignacio and Santo Domingo Channel comprised 91% of the annual calf production in all of the winter breeding areas, based on the proportional distribution of mother-calf pairs counted during the 1997 winter season in all areas (Table 2). These estimates ranged from a low of 286 calves in 1999 to a high of 910 calves in 1997. Estimates based on counts of mother-calf pairs suggest a decrease in calf production from the 1997 high (910 calves estimated) to a low in 1999 (286 calves), followed by a gradual increase to 670 calves during the period 2000 to 2002 (Table 4).

Additional estimates of annual calf production are based on counts of northward migrating mother-calf pairs at Piedras Blancas in central California (Perryman, 2001; Perryman and Rowlett, 2002; Perryman *et al.*, 2002). These estimates peaked at 1,431 in 1997 and gradually declined to 256 calves in 2001. For the years 1997 to 1999 the estimates of calf production based on counts of mother-calf pairs in the breeding lagoons were lower, suggesting that counts made within the breeding lagoons were underestimating total calf production. It is possible that in those years additional calves were located outside of the lagoons along the coast of Baja California and thus were not counted in the lagoon surveys. If true, this would suggest that areas outside the breeding lagoons constitute important calving or nursery habitat that has been used to a greater extent as the population has increased. Estimates of the percentage of mothers with calves using areas outside the lagoons ranged from lows of 33% to 36% (1997 and 1999) to a high of 53% in 1998. This could be explained by changes in the winter distribution of whales as a result of higher than normal SST in their winter range. During such years, a larger percentage of gray whales can be expected to give birth and rear their newborn calves outside the lagoons and in the coastal waters of northern Baja California and southern California. In contrast, estimates of calf production based on mother-calf pairs migrating past central California in 2000 and 2001 were less than those based on counts within the lagoons (24% and 65% respectively) (Table 4). Assuming these differences are significant could suggest that for these years fewer calves were surviving during the northward spring migration from the lagoons to the summer feeding areas to the north. Increases in calf mortality could be caused by low body fat reserves of the adult females, which in turn are due to a decrease in their principal prey on their feeding grounds as suggested by Le Boeuf *et al.* (2000).

Calf mortality inside the lagoons was estimated using the same methodology described by Swartz and Jones (1983), and varied from 2.3% in 1999 to 0.5% in 2001, with an average of 2.0% (Table 5). These rates are lower than the 5.4% estimated by Jones and Swartz (1984). Between the 1999 and 2001 winter seasons estimated calf mortality declined from 2.2% to 0.005%, and then increased to 1.0% in 2001. Assuming these differences are significant, this trend in mortality may be due to the greater numbers of mother-calf pairs residing outside the breeding lagoons between 1997 and 1999, and thus, fewer dead calves were available to be discovered inside the lagoons.

Duration of stay within the breeding lagoons

Laguna San Ignacio

Resightings data from the photographic identification of 975 single whales and 519 mothers with calves during the winter seasons of 1996 to 2000 revealed that the mother-calf pairs remain within the area of Laguna San Ignacio approximately three times longer than single whales. (Urbán *et al.*, 1997; 1998) (Table 6; Fig. 8). The longest period between first and last sighting for a mother with calf was 61 days during the 1998 winter season. The average time between first and last sightings ranged from 25.5 days (95% CI = 20.1-30.9; *n* = 39) in 1999 to 19.1 days (95% CI = 14.3-23.9; *n* = 20) in 1996. In contrast, the average time between first and last sightings for single whales ranged from 6.8 days (95% CI = 3.6-10.0; *n* = 19) in 2000, to 2.6 days (95% CI = 1.7-3.5; *n* = 5) in 1996.

These results are consistent with findings by Jones and Swartz (1984), Harvey and Mate (1984) and Swartz (1986) who estimated from whale counts that the length of the winter season for mother-calf pairs is 16-18 weeks, whereas the length for single whales (males and females without calves) is 11.5 weeks. This difference can be attributed to the need for mothers to remain in the lagoon habitats for longer periods following the birth of their calves, while single adults gather at the lagoons during the period of highest whale densities to obtain mating opportunities. The longest period between the first and the last photographically documented mother with calf sighting within one season was 91 days (Swartz, 1986).

Laguna Ojo de Liebre

In the 2001 season, a total of 404 gray whales were photo-identified, 219 mothers and 182 single whales. Four of the mothers were first photographed without calves and a few days later with newborn calves. Similar to Laguna San Ignacio, different residency intervals were documented for each class based on re-sightings and photographs of identified individual whales. The photographic records suggest that mothers with calves stayed in the lagoon area for periods of one to at least 76 days with an average of 22.1 days (95% CI = 18.0-26.2; *n* = 69). Similarly, single whales stayed in the lagoon area for a period of one to at least 70 days with an average of 13.2 (95% CI = 4.7-21.7; *n* = 20).

Birth rate

Jones (1990) analysed approximately 6,000 photographs of at least 562 distinctively marked gray whales that were photographed in the breeding lagoons of Baja California. These included 55 mature females that were seen in two to six winter breeding seasons from 1977 to 1982. These females produced a total of 115 calves over the six-year

Table 5

Average calf mortality rate in the breeding lagoons. For key see Table 1.

Year	SDC	LSI	LOL	Total	Stranded calves	Gross calf production	Mortality (±SE)
1997	83	126	626	835	17	852	0.020 (0.0048)
1998	12	52	530	594	7	601	0.012 (0.0044)
1999	32	17	213	262	5	267	0.020 (0.0086)
2000	16	45	256	317	7	324	0.022 (0.0081)
2001	25	29	333	387	2	387	0.005 (0.0036)
2002	97	43	475	615	6	621	0.010 (0.0040)

Table 4

Estimated total annual calf production. For key see Table 1.

Year	SDC	LSI	LOL	Total	Estimate for all breeding areas	Calf estimate for California (±SE)*	Difference	Difference (%)
1997	83	126	626	835	910	1,431 (82.02)	521	36%
1998	12	52	530	594	647	1,388 (91.84)	741	53%
1999	32	17	213	262	286	427 (41.10)	141	33%
2000	16	45	256	317	345	279 (34.79)	-66	-24%
2001	25	29	333	387	422	256 (28.46)	166	-65%
2002	97	43	475	615	670			

* From Perryman and Rowlett (2002); Perryman *et al.* (2002).

Table 6

Duration of stay (days) in Laguna San Ignacio 1996-2000 (95% CI).

	1996		1997		1998		1999		2000	
	X	*n*	*X*	*n*	*X*	*n*	*X*	*n*	*X*	*n*
Single whales	2.6 ± 0.9	5	6.2 ± 3.2	4	5.6 ± 2	5	4.3 ± 2.0	11	6.8 ± 3.2	19
Cow-calf pairs	19.1 ± 4.8	20	19.6 ± 3.5	43	20.6 ± 4.1	43	25.5 ± 5.4	39	23.0 ± 6.6	25

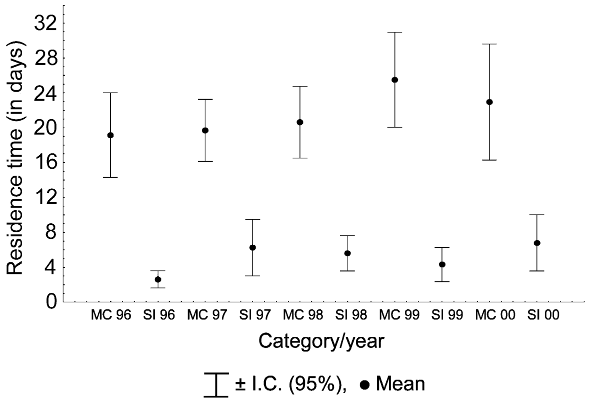

Fig. 8. Residency time of gray whales in Laguna San Ignacio Winter seasons 1996-2000. Key: MC = mothers with calf; SOL = single whales.

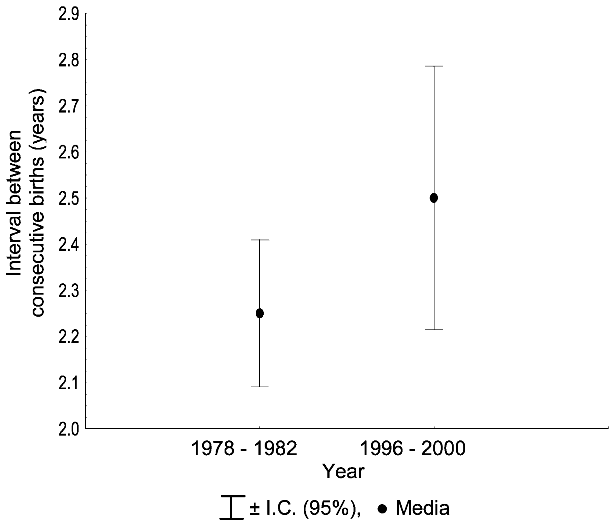

Fig. 9. Birth rate estimates in Laguna San Ignacio.

period. The length of time between birth and consecutive calves was documented for 42 of the females. Calving intervals ranged from 1-4 years but were predominantly 2 years (1 calf every other year). The observed calving intervals were: 1 year ($n = 1$), 2 years ($n = 48$), 3 years ($n = 6$) and 4 years ($n = 5$). The mean length of the calving interval, or breeding cycle, for the population from 1977 to 1982, was estimated as 2.11 (SD = 0.403) years.

Between 1996 and 2000, 1,494 gray whales were identified from photographs in Laguna San Ignacio. From these, 34 females were seen in more than one year, and 18 with calves in different winter seasons. Calving intervals ranged from 2-4 years: 2 years ($n = 11$), 3 years ($n = 7$), 4 years ($n = 1$). The mean length of the calving interval was estimated as 2.50±0.29 years (95% CI = 2.21-2.8; $n = 19$). This interval is significantly higher than 2.11 (SD = 0.403) years estimated for the period 1977 to 1982 (H (1, $n = 78$) = 4.165557 $p = 0.0413$) (Urbán and Gómez-Gallardo, 2000) (Fig. 9).

It is difficult to judge whether this increasing trend in the calving interval is a density-dependent response for a population approaching carrying capacity (Moore *et al.*, 2001), or related to the 1998-1999 change in SST associated with the ENSO events, which is believed to have caused changes in the distribution, abundance and mortality of this population, or a combination of these. It is also possible that some other factor(s) is increasing the calving interval (Brownell and Weller, 2001).

Mortality

Jones and Swartz (1984) summarised published records of dead gray whales found in the breeding lagoons from 1954 to 1983. They also reported on 194 dead gray whales that were discovered in the breeding lagoons between 1977 and 1982, including 57 males and 44 females for which the sex could be determined. Calves were the most frequent age-length class of dead whales averaging 91% (range 78%-100%). The percentage of immature whales ranged from 0% to 19.6% among the lagoons, while adults ranged from 0% to 5%.

Le Boeuf *et al.* (2000) summarised records of stranded gray whales in Laguna Ojo de Liebre, Laguna Guerrero Negro, Laguna Manuela and in the shoreline outside of these lagoons from 1984 to 1999. This compilation was based on the review by Sánchez Pacheco (1991; 1998), unpublished records from the Biosphere Reserve El Vizcaíno (1997-1999), and aerial surveys during 1999. Years with the highest mortality were 1991 with 45 stranded whales (37 adults, 2 yearlings and 6 calves), and 1999 with 71 stranded whales (14 adults, 10 yearlings, 5 calves and 42 unknown ege class).

During the winter season of 2000, relatively high numbers of stranded gray whales were again observed throughout the population's distribution. Along the Mexican coast there were 207 stranded whales, 61.8% adults, 3.9% yearlings, 12.6% calves and 21.7% unknown (Table 7). The number decreased to 10 whales (1 adult, 2 yearlings, 1 calf and 6 unknown) in 2001; and 13 whales in 2002 (4 adults, 6 calves and 3 unknown).

According to Le Boeuf *et al.* (2000), the apparently high mortality rate of gray whales in 1999 and 2000, the low calf production, shifts in the timing of winter occupation of the lagoons, changes in distribution and behaviour during migration and the reproductive season, are consistent with the hypothesis that the animals were suffering from low reserves of body fat and had insufficient energy to survive the regular period of fasting between feeding seasons. They argued that the most likely cause of this condition was a decrease in the gray whale's principal prey on the summer feeding grounds, a decrease brought about by increased predation and the depressing effect of increasing water temperature over the last decade on amphipod biomass.

Moore *et al.* (2001) argued that this event could be an indication that the Eastern gray whale population is reaching environmental carrying capacity. However, Brownell and Weller (2001) argued against the 'carrying capacity hypothesis' and suggested that some global or ocean basin change in the North Pacific may be influencing the availability of or access to primary prey for both the eastern and western populations of gray whales.

Movements, telemetry

Harvey and Mate (1984) and Mate and Harvey (1984) utilised VHF-radio tags to monitor the movements and behaviour of 18 gray whales in Laguna San Ignacio between 1979 and 1980. Ten of the whales tagged in February 1980 had mean dive duration from 1.0 to 2.6 mins (mean = 1.57 ± 0.02 min (SE)). Of the 11,080 dives recorded, 99% were less than 6 min and 49% less than 1 min in duration. The longest dive was 25.9 minutes. Tagged whales averaged 4.4 ± 0.6 sec (SE) at the surface per surfacing. Eight of the tagged whales averaged less than 2.9% of the time at the surface (range 1.56-16.3%). The tagged whales averaged 35.6 surfacing per hour. Three surfacing patterns were documented: regular-long, regular-short and clumped. These accounted for approximately one-half of all dive sequences analysed for two whales. Three radio-tagged whales were monitored for 4, 5 and 11 days, and moved into the ocean on 2, 2 and 7 occasions, respectively. Most oceanic movements were at night and 40% were against the tide. Seven of the tagged whales did not remain in the lagoon for more than 2 days. Those whales that left the lagoon travelled an average of 87km day^{-1} during the northward migration. No differences were found between maximum swimming speeds of single adults and those of mothers with calves. Some tagged whales moved both to the north and south of their tagging site in Laguna San Ignacio to adjacent breeding areas. Some tagged whales lingered around Laguna Ojo de Liebre and one whale was found apparently feeding with up to 60 other whales in an area along the northern coast of Baja California. One whale tagged in 1979 travelled 6,680km from San Ignacio to Unimak Pass, Alaska, which it reached 94 days after its tagging in Mexico.

Ludwig *et al.* (2001) investigated movements and diving of female gray whales in Laguna San Ignacio during the winter seasons of 1999-2001. Twenty-five VHF transmitters were successfully deployed with a crossbow on female gray whales with calves to investigate their preference for specific areas within and around the lagoon. Movements were documented for up to nine successive days, including night movements. Mother-calf pairs used the entire lagoon interior and periodically exited the lagoon. Most animals preferred the middle and lower lagoon, with mothers with older calves preferring the lower zone nearest the entrance. There was a trend for movements to the lower lagoon and to leave the lagoon area during night time (significant in six females). Some females with calves stayed outside the lagoon for extended periods of up to 2 to 3 days (i.e. in the Bahia Ballenas). It confirms the assumption that the Bahia Ballenas area is important to the whales, and should be included in any conservation plan for the lagoon area. During winter 1999 and 2001, Multi-Sensor/VHF tags were attached to female gray whales with calves, using suction cups with dissolvable magnesium release mechanisms. Data on depth, duration, tilt, temperature and light intensity were recorded. Tags were deployed successfully on 17 females with calves, recording a total of 40 hours of diving data, representing 1,080 dives. Overall mean dive duration was 1.54 min ± 0.27 SD (max. 10.5 min). It is interesting to note that there is no significant difference in average dive duration between the data recorded in 1999 and 2001, and those reported by Harvey and Mate (1984) in 1980 (U-test, U = 93.0, $n = 28$, $p = 0.98$). Regular long dives (> 60s) lasted 2.81 ± 0.85 min in 1999, and 2.58 ± 0.5 min in 2001. Two different dive profiles were distinguished: V- and U-shaped dives. Maximum dive depth was 27.4m. Mother-calf pairs used the whole depth profile of the lagoon. Bouts consisting of adjacent, extended U-shaped dives were recorded. There was a positive correlation between the durations of dives preceding and following a surfacing. Thus, a whale tended to make a series of dives of similar length rather than alternating short and long dives. Mean breathing rate was 0.61 breaths min^{-1} ± 0.10 SD. Resting females had significantly more breaths per surfacing than travelling whales (U-Test, $p < 0.01$). Resting was apparently an important part of the surface-dive characteristics of mother-calf pairs in the breeding grounds (Ludwig *et al.*, In prep).

Environmental and anthropogenic threats

Climate change

Although not a threat in Mexican waters, the major climatic regime shift in the Arctic region, probably coupled with a shortened feeding season due to extensive seasonal ice, lower overall food availability and El Niño and La Niña phenomena probably contributed to the mass mortalities, the emaciated whales and low calf production observed in Mexican waters, and all along the distribution range of gray whales (Le Boeuf *et al.*, 2000; Jones, M.L. and Swartz, 2002; Perryman *et al.*, 2002).

Mortality in passive fishing gear

Norris and Prescott (1961) documented the first gray whale taken in fishing gear. The whale was caught in April 1959 off the Palos Verdes Peninsula, California in a gillnet used for

Table 7

Gray whales stranded on the Mexican coast during the winter season of 2000. For key see Table 1.

		BA	BM	SDC	LSI	LOL	C	Total	%
Age class	Adults	0	10	2	34	34	48	128	62
	Yearlings	0	1	0		7	0	8	4
	Calves	1	5	0		1	19	26	12
	Unknown	0	3	1			41	45	22
	Total	**1**	**19**	**3**	**34**	**42**	**108**	**207**	**100**
Sex	Males	0	11	1	27	16	23	78	38
	Females	1	7	1	6	24	0	39	19
	Unknown	0	1	1	1	2	85	90	43
	Total	**1**	**19**	**3**	**34**	**42**	**108**	**207**	**100**

white sea bass (*Cynoscion nobilis*). Brownell (1971) reported four additional dead gray whales from California fisheries in the 1960s. Heyning and Lewis (1990) reported two dead gray whales and 61 more entangled gray whales during the 1980s in California fisheries. Forty of these 61 whales were observed alive but many of them were entangled in fishing gear and their survival was questionable in many cases. Most entangled whales were three years of age or younger. During the 1990s, two gray whales were observed dead in the offshore driftnet fishery off California (J. Carretta, pers. comm.). Thus, the minimum incidental bycatch in California fisheries is 48 whales over the past 43 years.

In Mexico, there have been six documented incidents of gray whales entangled in passive fishing gear. Two sub-adults (11-12m) were caught in a large nylon rope and steel chain in Playa Palmira, close to San Jose del Cabo at the southern end of Baja California Peninsula: one in 1989 and the other in 2000. Both whales were released by local fishermen, divers and scientists with at least superficial injuries to the rostrum and mouth. Two calves were observed dragging a buoy and line entangled around their peduncle: one in Santo Domingo Channel in 1992 and the other in Laguna San Ignacio in 1999. One gray whale, probably a yearling (10-11m) was caught by a 'curvinera' gillnet in Bahia de Ballenas, 15 miles NW of Laguna San Ignacio mouth. This whale was released by students of the UABCS after four days of entanglement with injuries to the peduncle. Finally, the only documented fatal incident was a calf found dead in a gillnet used, apparently illegally, for sea turtles in Laguna San Ignacio in 1996.

Angliss *et al.* (2001) reported additional human-caused mortality in fishing gear in Alaska, British Columbia and Washington but the data are very limited. Data on gray whales taken in other parts of their range (Russia) are not available.

Ship strikes

Gray whales are more vulnerable to being struck by ships because of their near-shore migration route (Laist *et al.*, 2001). Five deaths are known to have been caused by ship strikes in Californian waters between 1993 and 1998 and one in Alaskan waters in 1997 (Angliss *et al.*, 2001). It is believed that many ship strikes and subsequent mortality go unreported because the whale may not die when hit and may not strand when dead. According to fishermen in Santo Domingo Channel, a gray whale died during the 2002 season after being struck by a small, fast vessel.

During the winter season, when the whales are inside the lagoons, small fiberglass fishing boats (pangas) occasionally hit whales transiting to the fishing areas outside the lagoons. There are no records of strikes by large ships on gray whales in Mexican waters, but based on the photo-ID catalogue of the UABCS, at least 2% of the whales ($n = 1,600$) have injuries (scars) presumably produced by impact with a large keel or a propeller.

Escalera Naútica (Nautical steps)

Currently, in waters of the Baja California Peninsula, gray whales are relatively undisturbed due to the near absence of military exercises, coastal development and industries. However, this will change if the 'Nautical Steps' tourist development proceeds as proposed by Mexico's Bureau of Tourism. The project consists of a mega-development that would be distributed on more than 2,500 miles of coast. It is aimed at luring the 1.6 million boat owners in California and other nearby US states into a new system of harbours, wharves, hotels, restaurants, airports and airstrips. Marinas of the Nautical Steps network would link ports beginning in Ensenada, just south of San Diego, to marinas located along the entire western and eastern coasts of the Baja Peninsula. No more than 120 miles apart, some of the marinas would be built along the coasts of Sonora and Sinaloa states, which face Baja across the Gulf of California, on the mainland coast of Mexico. Only five such marinas or harbours currently exist; others would be expanded or built in new areas. If Nautical Steps is not carefully planned to be a low-impact development it could pose a major risk to gray whales and other large cetaceans in the area.

Major potential threats include: (1) increased whalewatching activities along the Baja California coast and outside the breeding lagoons; (2) increased noise associated with vessel traffic as much man-made noise in the ocean occurs in the lower frequency range and at high levels, which could interfere with or mask gray whale' sounds and possibly damage their hearing (Jones and Swartz, 2002); and (3) pollution from vessels and fuel stations, marinas, golf courses and hotels.

Whalewatching

Gilmore (1976b), who directed the first long-range marine mammal tourist ventures into Baja California waters in 1970, stated that the 'entry of man with his industrial or recreational activities into the calving and courting lagoons… could have only an adverse effect on the reproduction and survival of the newborn… the damage, if any as of now, has not been measured'.

Gard (1974), the first investigator to study the effects of human activities on the whales in the lagoons, concluded that the most serious threat was posed by San Diego-based excursion boats arriving to observe and photograph the whales. Rice (1975, in Reeves, 1977), claimed that 'considerable harassment is caused by commercial cruise boats which take people into the calving lagoons to see the whales'. He regarded this kind of activity, together with industrial development, as the 'greatest threat' to the whale population.

Kenyon (1973, in Reeves, 1977) described the observed effects on gray whales of close approach by outboard skiffs, but he, like Gard (1974), was unable to demonstrate unequivocally that such disturbances actually harmed the whales. 'It is unknown', he admitted, 'what effect this continued large-scale disturbance may have on the habits, behaviour, and population size of the gray whale. Certainly the effect is not beneficial'. Villa-Ramírez (1975), who was on the same cruise as Kenyon, wrote that 'the hundreds of tourists who want to view whales closely in the lagoons force the animals to seek other quiet areas far from their normal routes'.

Jones *et al.* (1994) noted that the primary, more frequent sources of potential human disturbance to the gray whales in Laguna San Ignacio from 1977 to 1982 were local fishing cooperatives inside the lagoon, US commercial whalewatching excursions (both ocean-going and overland groups) and scientific researchers. During the course of their study, they found no statistically significant evidence to substantiate the contention that whalewatching had a detrimental effect on the demography of gray whales in Laguna San Ignacio. They concluded that as of 1982, whalewatching activity in the lagoon did not seem to pose a serious threat to gray whales, but its potential for becoming a problem should be acknowledged. Urbán *et al.* (1997) detected a decrease in whale density in Laguna San Ignacio compared to earlier studies by Jones and Swartz (1984) and suggested that this variation was due to natural modification in timing and movements of the whales in response to changes in environmental factors or human activities such as whalewatching (Urbán and Gómez-Gallardo, 2000). Mosig (1998) reported an inverse relation between the average number of whalewatching boats and the average number of gray whales in Laguna San Ignacio in the winter of 1997, but she was not able to demonstrate a direct effect of the vessels on the whales. Heckel *et al.* (2001) found significant differences in both speed and direction of the transit of migrant gray whales with and without presence of whalewatching boats in Bahia de Todos Santos, Baja California.

Noise disturbance

The number of gray whales occupying Laguna San Ignacio declined in 1984 following a series of noise playback studies within the lagoon, but numbers appeared to return to previous levels the following year when no playback studies were conducted (Jones *et al.*, 1994). Other playback studies during the gray whales' migration past central California documented avoidance and disruption of their migration (Malme *et al.*, 1983; 1984). Many of the sounds produced by Outer Continental Shelf (OCS) activities of the Minerals and Management Service, USA, are within the frequency range of sounds produced by and, thus, probably heard by the California gray whale. The acoustical pulses used in seismic surveys off California are generated by air-guns or water-guns. If seismic-generated sound waves exceed the 'background' noise, they could interfere with gray whale communication or disturb behaviour. In controlled experiments, gray whales have exhibited startle responses, avoidance reactions, and other behavioral changes when exposed to seismic pulses at sound levels corresponding to a distance of 2-3 miles from an air-gun setup off the California coast. In recent biological opinions issued for OCS activities, the National Marine Fisheries Service, the Federal agency responsible for protecting the gray whale, has concluded that geophysical seismic activities may create a stressful situation for gray whales, but are not likely to inhibit their migration. In experiments conducted off central California, migrating gray whales have been exposed to underwater playbacks of drill-ship, semi-submersible, drilling platform and production platform sounds. Avoidance reactions to all sounds were observed at levels corresponding to distances of about 1,000m from a drill-ship and only 4-22m from the other three sources (Minerals Management Service, 2002). Limited observations also suggest that stationary industrial continuous noise results in less dramatic reactions by cetaceans than to moving sources of sound, particularly from ships (Richardson *et al.*, 1995).

LNG (Liquid natural gas) facilities

Five different energy consortiums have announced plans to build Liquefied Natural Gas (LNG) terminals at different locations along the northern Baja California coast. Sempra Energy and partner CMS Energy plan to build a $400-million (US) terminal about 75km (probably on Punta Salsipuedes) from the US-Mexico border. Another project with El Paso Corp., Royal Dutch/Shell, Chevron Texaco Corp and Marathon Oil Co. plans to build a terminal at Rosarito (Playas de Tijuana). The other three consortiums are: Marathon Oil, Chevron Texaco and El Paso Corporation and Conoco Phillips. These projects plan to re-gasify the super-cooled liquid gas and pipe it to California and other destinations in Mexico. The Sempra project will include a pier of a 300m or more from shore. Both projects hope to be operational around 2005 (Kraul, 2001a; b). Huge reservoirs of natural oil exist in the Tarija Province of Bolivia. The plan is to extract the gas and pipe it to a Pacific port, liquefy the gas and transport it by ship to the Mexican LNG terminals (Anon., 2002). First, however, Bolivia needs to find a port in either Peru or Chile.

The Sempra project, if established at Punta Salsipuedes, would be at an important point of the gray whale migration, especially for northbound females with their calves that pass very close to this prominent point of land.

FUTURE RESEARCH AND MONITORING NEEDS

Proportion of population utilising the breeding lagoons

The surveys conducted in the lagoons and coastal areas of Baja California during the winter breeding season have involved aerial and vessel-based counts to obtain an index of the density of gray whales. At best, these counts indicate the beginning, peak and end of the breeding season. To determine the relative importance of the coastal and lagoon areas as breeding habitats, it is necessary to determine the estimate of the population that congregates in these breeding habitats each winter, and the proportion of those that utilise specific areas. This will require the integration of the survey results with estimates of residency within specific lagoons, and the 'turn-over rates' or rate of exchange of whales in those sites. In addition, the timing and duration of the winter breeding season needs to be better documented. Previous surveys have not documented the arrival of the first gray whales in Baja California, or the departure of the last whales in the spring. Future surveys should begin early and continue for a sufficient time to document the 'tails' of the winter occupation of the lagoons by whales.

Photographic identification

To address residency times and inter-lagoon movements, individual reproductive rates, and fidelity to specific areas, photographic identification programmes should continue in all areas that gray whales congregate during the winter. The photographs provide a permanent record that contributes to numerous research objectives, including the identification of specific components of the population in other portions of their range (e.g. Northwest summer residents, Bering Sea feeding aggregations, etc.).

Radio telemetry

Radio tagging, both VHF and satellite-based, have great potential to improve understanding of gray whale migration paths, rates of travel, and yearly variation in the migration timing and residency in the breeding lagoons and coastal areas of Baja California. These data are valuable for addressing questions of the effects of seasonal variation in reproductive behaviour that may be the result of changes in environmental conditions.

Genetic research

Genetic research conducted in recent years suggests that groups of related gray whales preferentially use specific breeding lagoons for calving. Such a structure within the population could have implications for its resilience to perturbations from natural climate changes, or from disturbance by human activities (e.g. oil spills). Additional genetic sampling of gray whales in all the principal lagoon areas should be undertaken to increase the size of the genetic data base for this population. Larger samples will support statistically meaningful analyses and provide the basis for conclusions concerning population sub-structure.

Calf production

Calf counts during the northbound migration vary considerably from counts in the breeding lagoons. There is a reported loss of about 30% of the calves between the breeding lagoons and central California (Swartz, 1986). This needs to be investigated. An independent count of northward migrating mother-calf pairs in northern Baja California should be considered. This would allow comparisons with the counts from central California. An appropriate site for land surveys would need to be identified in northern Baja California.

Whalewatching

Assessments of long-term effects of whalewatching are aimed at measuring changes in population parameters, physical condition of individuals and habituation or tolerance (IFAW *et al.*, 1995). The population parameters that can be monitored in conjunction with whalewatching programmes and used to assess the long-term status of whale stocks could include:

(1) Those related to the behaviour of photo-identified whales such as: residency times, philopatry and fecundity/ calving rates.
(2) Those related to behaviour of the whales with or without the presence of tourist boats versus land based platforms.
(3) Those related to genetic studies using skin samples from living and stranded dead whales, including research on genetic diversity and relatedness.
(4) Mortality including the counting, measuring and determining the sex of dead whales found in the lagoons.

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