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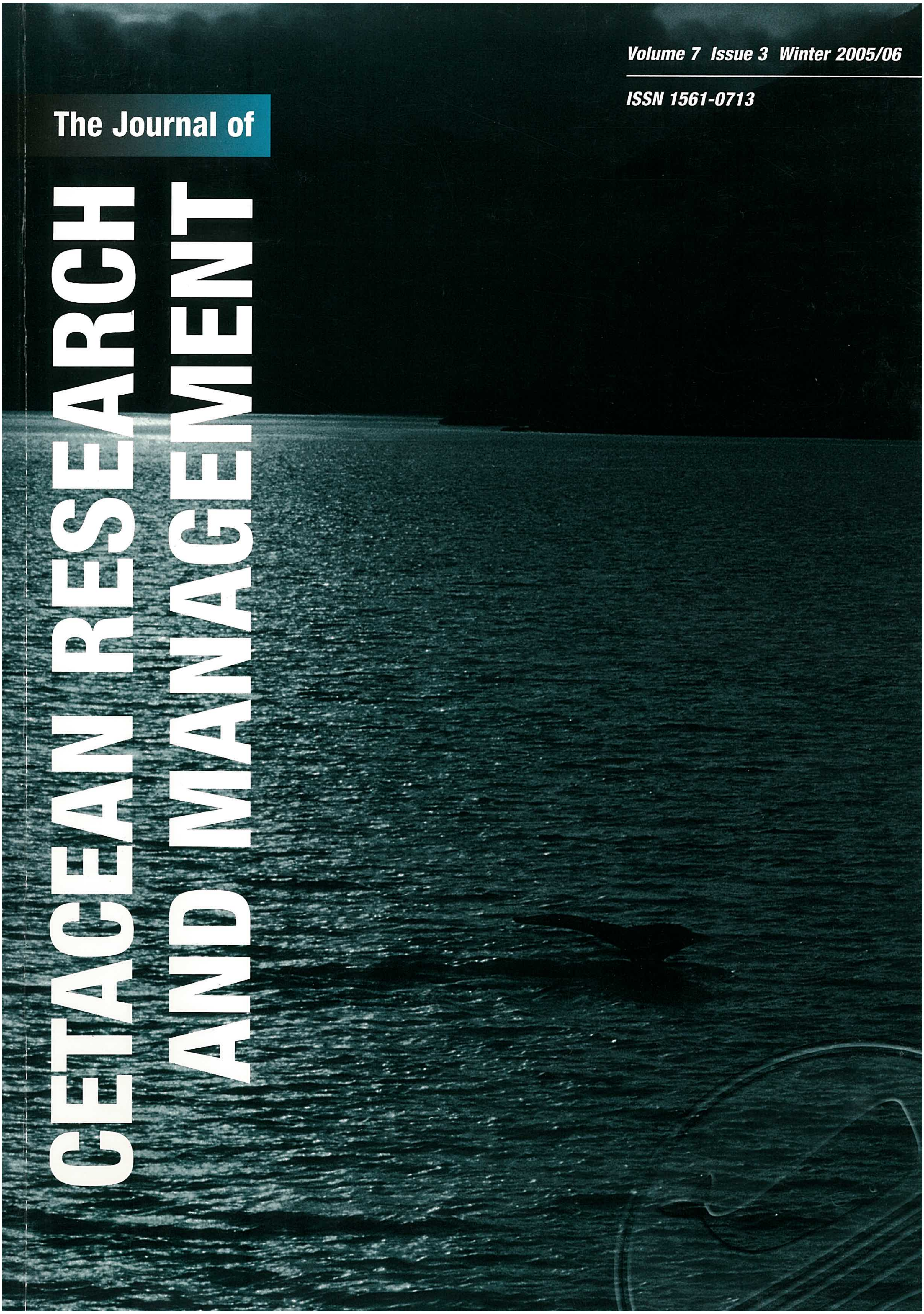

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Editorial

Welcome to this the final issue of Volume 7 of the *Journal of Cetacean Research and Management*. I must apologise that its appearance is later than usual, but this has been the result of certain logistical problems associated with the desire to dedicate the Winter Issue to one of the least known families of Cetacea, the beaked whales or Ziphiids. I hope that you will agree that the wait was worthwhile.

Ziphiids are particularly difficult to study, both as a result of their oceanographic distribution and the fact that they are long deep divers. Indeed, some species are known only from the bones of stranded specimens. Beaked whales have become particularly 'newsworthy' as a result of increasing evidence of their vulnerability to certain anthropogenic sounds, particularly those associated with airgun arrays and military mid-frequency sonar (2-10kHz). As a result of the temporal and spatial association of certain atypical 'mass' strandings of certain beaked whale species (e.g. Cuvier's and Blainville's) with certain naval manoeuvres in the last 15 years or so, the need to examine such cases in an objective and considered way has become more urgent.

Problems such as this require the co-operation of scientists from a wide number of disciplines. In April 2004, a group of experts in fields as diverse as acoustics, physiology, anatomy, ecology and veterinary medicine, met in Baltimore, USA under the auspices of the US Marine Mammal Commission. The meeting was important, not only in terms of its report but also as a means to develop research recommendations to address this important issue.

Many of the papers in this volume had their origin in the Baltimore meeting. The authors of the major review paper (Cox *et al.*, 'Understanding the impacts of anthropogenic sound on beaked whales') used the report of that meeting as its basis and it will be a valuable reference work for years to come. It reached a number of important conclusions that I would like to highlight here:

(1) it identified a plausible pathological mechanism for the observed mortality and morbidity of beaked whales that warrants further investigation (gas-bubble disease induced in supersaturated tissue by a behavioural response to anthropogenic noise);
(2) it identified important deficiencies in current mitigation and monitoring measures;
(3) it identified four major research priorities that need to be addressed to improve the situation.

The remaining ten papers review and present new information on a number of important topics concerning beaked whales and particularly in the context of better estimating the potential anthropogenic threats facing them at the population level and mitigating such threats as necessary.

Assessing and addressing any conservation issues requires fundamental information on distribution and abundance. These issues are considered in the papers by Macleod *et al.* (Known and inferred distributions of beaked whale species), Barlow *et al.* (Abundance and densities of beaked and bottlenose whales) and Ferguson *et al.* (Predicting Cuvier's (*Ziphius cavirostris*) and *Mesoplodon* beaked whale population density from habitat characteristics in the eastern tropical Pacific Ocean). The latter paper is especially interesting in using the relatively new techniques of spatial modelling to improve our understanding of beaked whale habitat and change some of the general impressions given by the biases arising from the fact that there are only a few areas in which good information is available. Finally, Macleod and Mitchell (Key areas for beaked whales worldwide) recognise the need to focus efforts on key areas and propose an approach to designating these around the world.

Assessing the level of any potential threats requires a better understanding of the nature of those threats and the possible cause-effect relationships. A number of papers examine aspects of this, including Rommel *et al.* (Elements of beaked whale anatomy and diving physiology and some hypothetical causes of sonar-related strandings), Macleod (How big is a beaked whale? A review of body length and sexual size dimorphism in the family Ziphiidae), Macleod and d'Amico (A review of beaked whale behaviour and ecology in relation to assessing and mitigating impacts of anthropogenic noise), d'Spain *et al.* (Properties of underwater sound fields during some well documented beaked whale mass stranding events) and Podesta *et al.* (A review of Cuvier's beaked whale strandings in the Mediterranean Sea).

I hope that the work represented in these papers provides the much needed stimulation to improve our knowledge of beaked whales, particularly with respect to the issue of anthropogenic noise. If we are to understand this problem sufficiently to properly assess its level and develop effective mitigation measures, it is essential that scientists, industry and the military co-operate and provide each other with necessary information. This is particularly true when incidences of atypical mass strandings occur, e.g. as recently occurred in Almeira, Spain at the end of January 2006. In that case, the veterinary scientists worked quickly and hard to perform full autopsies. It is important that relevant military and industrial organisations and authorities co-operate in providing information on any potentially damaging sound sources that may have occurred in the vicinity at the same time.

G.P. DONOVAN
Editor

Understanding the impacts of anthropogenic sound on beaked whales[1]

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This paper is dedicated to the memory of Dr. Edward Thalmann (1945-2004).

ABSTRACT

This review considers the effect of anthropogenic sound on beaked whales[2]. Two major conclusions are presented: (1) gas-bubble disease, induced in supersaturated tissue by a behavioural response to acoustic exposure, is a plausible pathologic mechanism for the morbidity and mortality seen in cetaceans associated with sonar exposure and merits further investigation; and (2) current monitoring and mitigation methods for beaked whales are ineffective for detecting these animals and protecting them from adverse sound exposure. In addition, four major research priorities, needed to address information gaps on the impacts of sound on beaked whales, are identified: (1) controlled exposure experiments to assess beaked whale responses to known sound stimuli; (2) investigation of physiology, anatomy, pathobiology and behaviour of beaked whales; (3) assessment of baseline diving behaviour and physiology of beaked whales; and (4) a retrospective review of beaked whale strandings.

KEYWORDS: BEAKED WHALES; ZIPHIIDAE; NOISE; MANAGEMENT; ACOUSTICS; CONSERVATION; STRANDINGS

INTRODUCTION

Beaked whales (family Ziphiidae) are among the least understood marine mammals. The family consists of approximately 21 species that spend relatively little time at the surface and occur almost exclusively in deep waters beyond the continental shelf. Most of our current knowledge of beaked whales is based on studies of stranded specimens. Reports of occasional mass strandings of beaked whales (i.e. strandings of two or more whales other than a cow-calf pair,

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[1] This paper arose out of a workshop convened in April 2004 by the US Marine Mammal Commission in Baltimore, Maryland, USA.

[2] Diverse fields (marine mammal ecology, medicine, behaviour, physiology, pathobiology and anatomy, human diving physiology and acoustics) were represented at the 2004 workshop and were brought together for an interdisciplinary discussion of various topics related to interactions between beaked whales and anthropogenic sound. These included sound propagation and acoustic exposure during specific stranding events, behaviour and ecology of beaked whales, beaked whale distribution, abundance and habitat, beaked whale anatomy and physiology and the efficacy of existing monitoring and mitigation efforts.

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Geraci and Lounsbury, 1993) date back to at least the early 1800s. Since 1960, however, 41 'mass' strandings of Cuvier's beaked whales (*Ziphius cavirostris*) have been reported worldwide (Brownell *et al.*, 2004; Taylor *et al.*, 2004). Furthermore, these probably represent only a small proportion of all beaked whale strandings. Some of these recent mass strandings were concurrent with naval manoeuvres and the use of active sonar (Frantzis, 1998[3]; Anon., 2001; Jepson *et al.*, 2003). The overall pattern of strandings has raised concerns that certain sounds from sonar could directly or indirectly result in the death or injury of beaked whales, particularly Cuvier's beaked whales. Additional concerns have been raised that sounds from seismic surveys might have similar effects (Taylor *et al.*, 2004).

Recent stranding events

Several recent mass strandings have led to suggestions that exposure to anthropogenic sounds negatively affects beaked whales. The temporal and spatial association of mass strandings of beaked whales and offshore naval manoeuvres was first noted in 1991 (Simmonds and Lopez-Jurado, 1991). Since then, a series of 'atypical' (Frantzis, 1998) beaked whale strandings, temporally (within hours or days) and spatially (less than 50km) associated with naval manoeuvres, have been better documented and are briefly summarised below. These strandings lend further support to the hypothesis that exposure to certain anthropogenic sounds may harm these animals.

Greece, May 1996

Frantzis (1998) reported an 'atypical' mass stranding of 12 Cuvier's beaked whales on the coast of Greece that was associated with acoustic trials by vessels from the North Atlantic Treaty Organisation (NATO). He was the first to hypothesise that these strandings were related to exposure to low-frequency military sonar. However, the sonar in question produced both low- and mid-frequency signals (600Hz, 228dB Sound Pressure Level (SPL) (re: 1μPa at 1m Root Mean Square (RMS))[4], 3kHz, 226dB SPL, D'Amico and Verboom, 1998). Frantzis's hypothesis prompted an in-depth analysis of the acoustic activity during the naval exercises, the nature of the strandings and the possibility that the acoustic source was related to the strandings (D'Amico and Verboom, 1998). Since full necropsies had not been conducted and no gross or histological abnormalities were noted, the cause of the strandings could not be determined unequivocally (D'Amico and Verboom, 1998). The analyses thus provided some support but no clear evidence for the hypothesised cause-and-effect relationship of sonar operations and strandings.

Bahamas, March 2000

When multiple beaked whales atypically stranded in the Bahamas in March 2000, researchers were aware of the possible link to anthropogenic sound sources and thus facilitated a more comprehensive examination of the dead animals. However, in most cases, analyses were performed on decomposed carcasses or tissues. Seventeen cetaceans (one spotted dolphin, *Stenella frontalis*, nine Cuvier's beaked whales, three Blainville's beaked whales, *Mesoplodon densirostris*, two minke whales, *Balaenoptera acutorostrata* and two unidentified beaked whales) stranded on 15-16 March 2000 on beaches of the Bahamas Islands. Eight beaked whales were returned to the water alive and one dead specimen was not readily accessible for necropsy. As a result, only five of the stranded beaked whales were examined *post mortem* and only two of these were marginally fresh enough to allow a more detailed pathological analysis of lesions. Initial gross necropsy of these five beaked whales indicated that the animals were in good body condition and that none presented any gross indication of debilitating infectious disease. Computerised tomography of two animals and detailed dissection of five heads indicated subarachnoid haemorrhages in the temporal region and haemorrhage in the cochlear duct of two of the animals. The *post mortem* time to examination varied from hours to several days, unfortunately compromising these analyses. The interim report of the investigation concluded that these findings were consistent with acoustic or impulse injuries that resulted in the animals stranding. The gross and histopathological evidence indicated cardiovascular collapse, which is often associated with other signs of extreme physiological stress observed in live, beach-stranded marine mammals (i.e. hyperthermia, high endogenous catecholamine release; Anon., 2001; see also Balcomb and Claridge, 2001). The role of intracranial and acoustic fat injuries in the strandings and mortalities was not clear. Analysis of acoustic sources used in the Bahamas naval exercises revealed that four of five ships were using mid-frequency sonar (AN/SQS-53C: 2.6-3.3kHz, ~235dB SPL, AN/SQS-56: 6.8, 7.5 and 8.2kHz, ~223dB SPL; Anon., 2001). The final report of the joint US National Oceanographic and Atmospheric Administration (NOAA) and US Navy investigation into the stranding event, including the full suite of pathological investigations is still pending. The event raised the question of whether the mid-frequency component of the sonar in Greece in 1996 was implicated in the stranding, rather than the low-frequency component proposed by Frantzis (1998).

Madeira, May 2000

The stranding in the Bahamas was soon followed by another atypical mass stranding of Cuvier's beaked whales in the Madeira Islands. Between 10 and 14 May 2000, three Cuvier's beaked whales stranded on two islands in the Madeira archipelago. NATO naval exercises involving multiple ships occurred concurrently with these strandings, although NATO has thus far been unwilling to provide information on the sonar activity during their exercises. Only one of the stranded animals was marginally fresh enough for a full necropsy (24 hours post-stranding). The necropsy revealed evidence of haemorrhage and congestion in the right lung and both kidneys (Freitas, 2004), as well as evidence of intracochlear and intracranial haemorrhage similar to that observed in the Bahamas beaked whales (D. Ketten, unpublished data).

Canary Islands, September 2002

In September 2002, a beaked whale stranding event occurred in the Canary Islands. On 24 September, 14 beaked whales (7 Cuvier's beaked whales, 3 Blainville's beaked whales, 1 Gervais' beaked whale, *M. europeaus*, and 3 unidentified beaked whales) stranded on the beaches of Fuerteventura and Lanzarote Islands, close to the site of an international naval exercise (called Neo-Tapon 2002) held that same day. The first strandings began about four hours after the onset of the use of mid-frequency sonar activity (3-

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[3] Frantzis (1998) cited the following references: Robinson *et al.* (1983); Miyazaki (1989); Simmonds and Lopez-Jurado (1991) and Tortonese (1963).

[4] Unless otherwise noted, all SPL values are RMS pressures referenced to 1μPa at 1m.

10kHz, D'Spain *et al.*, 2006; Jepson *et al*., 2003). Seven whales (1 female Blainville's beaked whale, 1 female Gervais' beaked whale and 5 male Cuvier's beaked whales) are known to have died that day (Fernández *et al.*, 2005). The remaining seven live whales were returned to deeper waters. Over the next three days, three male and one female Cuvier's beaked whales were found dead and a carcass of an unidentified beaked whale was seen floating offshore. A total of nine Cuvier's beaked whales, one Blainville's beaked whale and one Gervais' beaked whale were examined post mortem and studied histopathologically (one Cuvier's beaked whale carcass was lost to the tide). No inflammatory or neoplastic processes were noted grossly or histologically and no pathogens (e.g. protozoa, bacteria and viruses, including morbillivirus) were identified. Stomach contents were examined in seven animals and six of them had recently eaten, possibly indicating that the event(s) leading to their deaths had had a relatively sudden onset (Fernández *et al.*, 2005). Macroscopic examination revealed that the whales had severe, diffuse congestion and haemorrhages, especially in the fat in the jaw, around the ears, in the brain (e.g. multifocal subarachnoid haemorrhages) and in the kidneys (Fernandez, 2004; Fernandez *et al.*, 2004). Gas bubble-associated lesions were observed in the vessels and parenchyma (white matter) of the brain, lungs, subcapsular kidney veins and liver; fat emboli were observed in epidural veins, liver sinusoids, lymph nodes and lungs (Jepson *et al.*, 2003; Fernandez, 2004; Fernandez *et al.*, 2004; 2005). After the event, researchers from the Canary Islands examined past stranding records and found reports of eight other strandings of beaked whales in the Canaries since 1985, at least five of which coincided with naval activities offshore (Martín *et al.*, 2004).

Gulf of California, September 2002

In September 2002, marine mammal researchers vacationing in the Gulf of California, Mexico discovered two recently deceased Cuvier's beaked whales on an uninhabited island. They were not equipped to conduct necropsies and in an attempt to contact local researchers, found that a research vessel had been conducting seismic surveys approximately 22km offshore at the time that the strandings occurred (Taylor *et al.*, 2004). The survey vessel was using three acoustic sources: (1) seismic air guns (5-500Hz, 259dB re: 1μPa Peak to Peak (p-p); Federal Register, 2003); (2) sub-bottom profiler (3.5kHz, 200dB SPL; Federal Register, 2004); and (3) multi-beam sonar (15.5kHz, 237dB SPL; Federal Register, 2003). Whether or not this survey caused the beaked whales to strand has been a matter of debate because of the small number of animals involved and a lack of knowledge regarding the temporal and spatial correlation between the animals and the sound source. This stranding underlines the uncertainty regarding which sound sources or combinations of sound sources may cause beaked whales to strand.

Although some of these stranding events have been reviewed in government reports or conference proceedings (e.g. Anon., 2001; Evans and Miller, 2004), many questions remain. Specifically, the mechanisms by which beaked whales are affected by sound remain unknown. A better understanding of these mechanisms will facilitate management and mitigation of sound effects on beaked whales. As a result, in April 2004, the United States Marine Mammal Commission (MMC) convened a workshop of thirty-one scientists from a diverse range of relevant disciplines (e.g. human diving physiology and medicine, marine mammal ecology, marine mammal anatomy and physiology, veterinary medicine and acoustics) to explore issues related to the vulnerability of beaked whales to anthropogenic sound. The purpose of the workshop was to (1) assess the current knowledge of beaked whale biology and ecology and recent beaked whale mass stranding events; (2) identify and characterise factors that may have caused the strandings; (3) identify ways to more adequately investigate possible cause and effect relationships; and (4) review the efficacy of existing monitoring and mitigation methods. This paper arose out of the discussions at that workshop.

OVERVIEW OF RECENT FINDINGS

A number of scientists have prepared papers describing acoustic activities and propagation characteristics during some stranding events, beaked whale biology including behaviour and ecology, distribution, abundance, anatomy and physiology and mitigation and management (Barlow and Gisiner, 2006; Barlow *et al.*, 2006; D'Spain *et al.*, 2006; Ferguson *et al.*, 2006; MacLeod and D'Amico, 2006; MacLeod *et al.*, 2006 and Rommel *et al.*, 2006). These are briefly summarised here and where appropriate, we have made some general recommendations for further research topics.

Acoustic characteristics

D'Spain *et al.* (2006) described the acoustic sources and propagation parameters associated with several of the stranding events: Greece, 1996, the Bahamas, 2000 and the Canary Islands, 2002. The authors found that these three events shared three common features. One common environmental feature was deep water close to land (e.g. offshore canyons). Whether this feature influenced beaked whale distribution (e.g. species that stranded prefer this habitat), accentuated the effects of the sounds through reflection and reverberation from the bathymetry and/or acted in some other way is not clear. A second environmental feature common to all three events was the presence of an acoustic waveguide (see D'Spain *et al.*, 2006 for more details). Thirdly, the authors noted common transmission characteristics, including periodic sequences of transient pulses (i.e. rapid onset and decay times) generated at depths shallower than 10m (in the Bahamas and Canaries) by sound sources moving at speeds of 2.6m s^{-1} or more during source operation (see table 1 in D'Spain *et al.*, 2006 for more details).

The sound sources in use during the Gulf of California stranding event in September 2002 included both a sub-bottom profiler and multi-beam sonar system (Table 1). Air guns can neither be confirmed nor ruled out as a cause of these strandings and retrospective analyses are needed to investigate the possible role of these other sound sources in the stranding event.

It is not yet clear whether high-intensity sound sources alone are sufficient to trigger beaked whale strandings, or whether certain acoustic, biological or environmental characteristics must co-occur with these stimuli. A more complete understanding of the source characteristics and propagation of anthropogenic sounds associated with beaked whale strandings would be extremely useful in predicting and preventing future incidents of this nature, but it is often difficult to obtain such specific information, which may be sensitive for many of the parties involved.

Based on the available data, we recommend research to: (1) identify key characteristics of sound (e.g. frequency, amplitude, energy, directional transmission pattern, use of arrays vs. single sources, etc.) that may affect beaked whales; (2) identify characteristics of anthropogenic sounds associated with historic stranding events; (3) estimate the possible range of sound levels the animals received prior to stranding; (4) characterise environmental parameters that influence sound propagation and model site-specific sound propagation (on *post hoc* and predictive basis), especially where detailed environmental data are not immediately available; and (5) measure the behavioural responses of beaked whales in the presence of sound.

Behaviour and ecology

MacLeod and D'Amico (2006) reviewed the behaviour and ecology of beaked whales and their relevance to the impacts of sound on beaked whales. Specifically, they reviewed beaked whale social structure, life history, ecology, sound production and function and the characteristics of their habitat. Multiple strandings of beaked whales that occur concurrently with sound-generating anthropogenic activities often include a large proportion of immature and juvenile animals. However, it is not known whether juveniles are disproportionately affected, the age structure observed in the strandings is representative of that in beaked whale populations, or the strandings indicate geographic separation of demographic groups. If juveniles are disproportionately affected, it might suggest a relationship between the dimensions of some part of the anatomy and the wavelength of the sound involved or, alternatively, an age-specific behavioural response.

Recent tagging data from Cuvier's and Blainville's beaked whales from the Mediterranean Sea and Canary Islands (Tyack, unpub. data) have revealed several notable features of their dive profiles: (1) dives to depths near 2km and lasting nearly 1.5hrs; (2) slow ascent rates; and (3) a series of 'bounce' dives to 100-400m between the deeper, longer dives. The implications of this dive pattern are discussed below. We recommend a combination of short- (hours to days) and long-term studies (weeks to months) on the behaviour of beaked whales using multiple methods (e.g. D-tags which measure received sound levels as well as other movement data, time-depth recorders and visual observations) to better describe 'normal' behaviour.

Distribution, abundance and habitat

Barlow *et al.* (2006), Ferguson *et al.* (2006) and MacLeod *et al.* (2006) reviewed global distributions and abundance of beaked whales. Our understanding of the distribution of many beaked whales is very limited and based primarily on observations of strandings and a limited number of at-sea sightings. The identification of important habitat is generally compromised by insufficient and inconsistent observation effort. It is clear that research effort must focus on: (1) population structure, possibly using genetic data from archived samples (bone, skin, etc.) housed in museums and other collections around the world; and (2) population distributions.

Estimates of abundance and density are hindered by the typical surfacing behaviour of beaked whales at sea: their blows are generally not visible, they have low surfacing profiles and they spend the majority of their time at depth (Hooker and Baird, 1999; Baird *et al.*, 2004; Barlow and Gisiner, 2006). In addition, beaked whales tagged by Johnson *et al.* (2004) vocalised only when they were deeper than 200m, an observation that has important implications for passive acoustic monitoring. The importance of identifying, classifying and understanding vocalisations of beaked whales and the potential utility of passive acoustic monitoring must be noted. For such monitoring to be effective, future research must (1) develop and test detection algorithms; (2) ground-truth detection methods by coupling visual and passive acoustic studies and by monitoring vocalisations in areas for which there are good density estimates; and (3) investigate the behavioural context of vocalisations. In addition, it is important that effort be expended on: (1) estimation of abundance and densities of beaked whale species, especially in those areas where sound-producing activities are planned or regularly carried out; (2) systematic surveys that include oceanographic data to help identify key habitat characteristics; and (3) increase understanding of movement patterns via multiple methods (e.g. telemetry).

An improved understanding of basic beaked whale biology will advance the potential for predictive habitat modelling and may help managers and sound-producers predict which areas support high densities of beaked whales

Table 1

Acoustic characteristics of sound sources and propagation during stranding events.

Name	Centre frequency	SPL	Beam direction	Model propagation?
Greece[1], May 1996				
TVDS	600Hz	228dB re: 1μPa at 1m (RMS)	Horizontal	Yes
TVDS	3kHz	226dB re: 1μPa at 1m (RMS)	Horizontal	Yes
Bahamas[2], March 2000				
AN/SQS 53C	2.6kHz; 3.3kHz	~235dB re: 1μPa at 1m (RMS)	3° down from horizontal	Yes
AN/SQS 56	6.8kHz; 7.5kHz; 8.2kHz	223dB re: 1μPa at 1m (RMS)	Horizontal	Yes
Madeira, May 2000				
Unknown	Unknown	Unknown	Unknown	Unknown
Canary Islands, September 2002				
Unknown	Unknown	Unknown	Unknown	Unknown
Gulf of California, September 2002				
Air gun[3]	Broadband	236-262dB re: 1μPa at 1m (p-p)	Vertical	No
Multi-beam sonar[4]	15.5kHz	237dB re: 1μPa at 1m (RMS)	Omnidirectional	No
Sub-bottom profiler[3]	3.5kHz	204dB re: 1μPa at 1m (RMS)	Vertical	No

Sources: [1]D'Amico and Verboom (1998); [2]Anon. (2001); [3]Federal Register (2003); [4]Federal Register (2004). For more details, please see D'Spain *et al.* (2006).

and how this density may vary with season. However, we advocate a cautious approach when applying habitat models to regions that have not been thoroughly studied (i.e. extrapolating behaviour or habitat usage from one area to another) due, for example, to documented differences between known high density areas of beaked whales in different ocean basins (Barlow *et al.*, 2006; Ferguson *et al.*, 2006).

Anatomy and physiology

Rommel *et al.* (2006) reviewed the limited information available on anatomy and physiology of beaked whales. Given the scarce knowledge and the important conservation and mitigation implications, it is important that much more research be conducted on the anatomy and physiology of beaked whales, as well as the pathological changes caused by exposure to sound. We agree that emerging evidence supports the hypotheses that: (1) normal beaked whale diving patterns may lead to chronic tissue accumulation of nitrogen; and (2) chronic tissue accumulation of nitrogen may make beaked whales particularly vulnerable to diving related pathologies when their diving patterns are disrupted by exposure to intense sound. Research is needed in two key areas to further evaluate these hypotheses: (1) the factors contributing to nitrogen supersaturation, including normal and acoustically altered dive profiles and the depth at which complete lung collapse occurs; and (2) the potential for *in vivo* bubble nucleation and/or growth within tissues as a result of exposure to sound and/or disruption of normal diving patterns. In addition, the following are required: (1) better descriptions of normal gross and normal microscopic anatomies of healthy beaked whales (e.g. from incidental fishery takes and from ‘normal’ strandings); (2) investigations of the direct impacts of sound on tissues (*ex vivo*) presumed to be most susceptible to anthropogenic sound; (3) better descriptions of pathological changes in stranded beaked whales exposed to sound; (4) standardisation of gross and histopathological examination protocols for all beaked whale strandings, with special emphasis on the occurrence of gas and fat emboli and methods to prevent introduction of gas emboli during necropsies; (5) better descriptions of blood flow patterns in the vicinity of tissues potentially sensitive to sound; and (6) better descriptions of the anatomy and function of tissues and organs involved in hearing in beaked whales.

Comparative studies involving multiple beaked whale species and surrogate species (e.g. *Kogia*) may be useful. However, caution is required when extrapolating from other species to beaked whales. We therefore believe that when feasible, attempts should be made to rehabilitate live stranded beaked whales to provide opportunities for research not possible or more difficult with animals in the wild. However, it should be noted that an animal being held in rehabilitation will not experience the physiological challenges or adaptations associated with diving to depths of more than 500m; clearly observations made of a sick animal at the surface must be interpreted with caution.

Monitoring and mitigation

Barlow and Gisiner (2006) discussed the effectiveness of current monitoring and mitigation practices and described promising new tools for improving monitoring and mitigation in the near future. Current monitoring often involves a single observer using low-power (7×) binoculars searching for beaked whales and other marine mammals in all sea states during both day and night. Although it has been suggested that monitoring after dark may be aided with recent night-vision technologies, this would require appropriate testing before being considered practical. Barlow and Gisiner (2006) provided a crude estimate that the visual methods currently employed may result in as little as a 1-2% chance of detecting beaked whales (the actual value will vary considerably depending on *inter alia* sea state and experience of observers). The present authors concur that these methods are ineffective in appreciably reducing interactions between beaked whales and potentially hazardous sound sources. Even using current best practices in visual surveys, such as those employed in line-transect abundance surveys with highly experienced observers, the probabilities of detecting beaked whales are 20-50% at best (Barlow and Gisiner, 2006). Passive acoustic sensors have not been used as part of beaked whale noise risk mitigation because little was known about their vocal behaviour. Recent data (Johnson *et al.*, 2004) indicate that passive acoustics may increase the probability of detecting beaked whales when the sensors are deployed at greater than 200m depth. However, any use of passive acoustic sensors at the surface must be tested carefully before being considered appropriate; it is possible beaked whales do not echolocate at shallower depths (Johnson *et al.*, 2004; Zimmer *et al.*, 2005). Other new sensing technologies such as active acoustics and radar have also not yet been tested sufficiently to assess their potential for detecting beaked whales.

Both long- and short-term research projects would help to better assess and mitigate the effects of anthropogenic sound on beaked whales. Important long-term studies include: (1) descriptions of population structure; (2) assessment of distribution and abundance for stocks and species; (3) development and testing of habitat use models; (4) assessment of population trends in local areas (e.g. in Abaco, Bahamas); and (5) systematic collection of information from live stranded and dead beaked whales. These studies would help to better identify sites of known or likely beaked whale occurrence, enable better assessment of the likely effects on individuals and populations from a given sound regime and lead to improved understanding of the clinical signs and pathologies of sound exposure. We also recommend the following short-term strategies: (1) detect and evaluate impacts of anthropogenic sound activities on beaked whales whenever a potential incident that may be a result of sound occurs; (2) conduct surveys for strandings and/or floating carcasses during and after anthropogenic sound activities; (3) determine the probability of detecting a floating carcass; (4) determine whether beaked whales avoid or approach vessels; and (5) incorporate behavioural reactions of beaked whales to anthropogenic sources of sound into monitoring measures.

POTENTIAL MECHANISMS

Although a number of beaked whale stranding events coincided with naval activities and active sonar use (e.g. Simmonds and Lopez-Jurado, 1991; Frantzis, 1998; Anon., 2001; Jepson *et al.*, 2003), the mechanism(s) by which sonar may lead to stranding and sometimes the death of beaked whales is not well understood. Determining such mechanisms is not only of scientific interest, but important in terms of mitigation. If, for example, the primary cause of strandings is a behavioural response in which whales avoid sound by moving into shallow water, then perhaps only those sound producing activities in close proximity to land need to be managed. Similarly, if these events resulted from abnormal acoustic propagation due to unusual environmental conditions (e.g. waveguides – D'Spain *et al.*, 2006), then producers of sound need to monitor environmental conditions prior to introducing sound and mitigate when certain conditions occur. However, the available evidence is not currently sufficient to reach such conclusions.

Several possible mechanistic pathways through which sonar may lead to stranding and/or death of beaked whales are shown in Fig. 1. The first potential pathway entails a behavioural response to sound that leads directly to stranding, such as swimming away from a sound into shallow water. An alternative scenario involves a behavioural response leading to tissue damage. Such responses could include: a change in dive profile; staying at depth longer than normal; or remaining at the surface longer than normal. All of these responses could contribute to gas bubble formation, hypoxia, cardiac arrhythmia, hypertensive haemorrhage or other forms of trauma. Another pathway is through a physiological change such as a vestibular response leading to a behavioural change or stress induced hemorrhagic diathesis leading to tissue damage. Finally, beaked whales might also experience tissue damage directly from sound exposure, such as through acoustically mediated bubble formation and growth or acoustic resonance of tissues. Each of these potential mechanisms is described in detail below and at present it is not possible to rule out any of these.

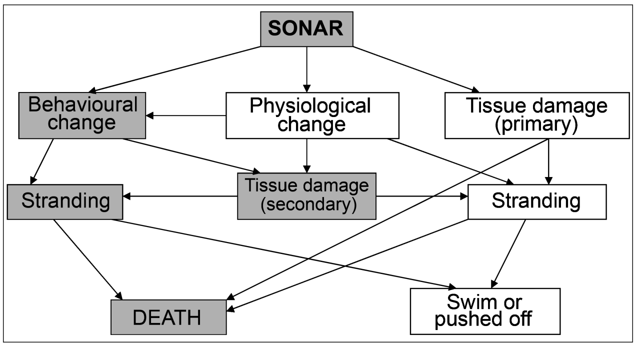

Fig. 1. Potential mechanistic pathways by which beaked whales are affected by sonar. Whereas we are unable to eliminate any pathways as implausible given current data, most of our discussions focus on the left side (shaded boxes) of the diagram. Note that death will not necessarily be the end result of sonar exposure in every case and that behavioural change, physiological change, primary tissue damage, secondary tissue damage, or stranding may occur without leading to death. This figure is intended to outline potential mechanisms of only those exposures which do lead to observed effect.

Behavioural response

Beaked whales may respond to sound by changing their behaviour, which could lead to a stranding event prior to the onset of physical trauma (Fig. 1, left). For example, in areas where deep waters occur in close proximity to shallow waters (e.g. 'canyon areas' of the Bahamas, oceanic islands), beaked whales may swim into shallow waters to avoid certain sounds and could strand if they are unable to navigate back to deeper waters. The end result of stranding may be that animals swim away, are pushed off, or die of hyperthermia or other stress-related causes resulting from the actual stranding. Evidence that some of the stranded beaked whales in the Bahamas succumbed to cardiovascular collapse due to hyperthermia (Anon., 2001) is consistent with this mechanism, although the final pathology report for this stranding event is still pending and the proposed mechanism does not account for some of the trauma observed in that event (e.g. subarachnoid haemorrhage). The array of pathologies (Anon., 2001; Fernandez, 2004) observed in the beaked whales from the Bahamas and Canary Islands mass stranding in 2002 suggest injuries in addition to those typical of the physical effects of stranding itself.

Behavioural response leading to tissue damage

Acoustically induced behavioural responses may lead to tissue damage prior to stranding. Such responses may include altered dive profiles, remaining at the surface for prolonged periods or remaining at depth. Physiological responses could include hypoxia (from longer than normal time at depth or increased energy or oxygen use at a given time) or elevated nitrogen supersaturation of tissues, leading to formation of gas bubbles (from altered dive profiles).

One potential mechanism that deserves particular consideration is an acoustically induced behavioural change (dive response) that leads to formation of significant gas bubbles, which damage multiple organs or interfere with normal physiological function. Such a mechanism would be similar to decompression sickness in human divers and would have two parts: a dive response precipitating adverse gas bubble formation and pathology. Because many species of marine mammals make repetitive and prolonged dives to great depths, it has long been assumed that marine mammals have evolved physiological mechanisms to protect against the effects of rapid and repeated decompressions. To date, two physiological adaptations have been identified that may afford protection against nitrogen gas supersaturation: lung alveolar collapse at depths of 20-70m and 'elective circulation' involving vasoconstriction to the peripheral circulation during diving (Kooyman *et al.*, 1972; Ridgway and Howard, 1979; Zapol *et al.*, 1979; Davis *et al.*, 1983). However, Ridgway and Howard (1979), the only researchers who have assessed nitrogen gas accumulation in a diving cetacean, trained bottlenose dolphins (*Tursiops truncatus*) to dive repeatedly to 100m and found that the muscle of the dolphin was substantially supersaturated with nitrogen gas. From nitrogen washout curves, they estimated that this species experienced lung collapse at approximately 70m of depth, thus making it susceptible to nitrogen gas accumulation when making repetitive dives shallower than 70m. Houser *et al.* (2001) used the data from Ridgway and Howard (1979) to model the accumulation of nitrogen gas within the muscle tissue of other marine mammal species. The model was limited in that it necessarily assumed similar depths of lung collapse for all cetaceans and that exchange of nitrogen gas between tissue compartments ceased below the depth of lung collapse. The model predicted that those cetaceans that dive deep and have slow ascent/descent speeds would have tissues that are more supersaturated with nitrogen gas than other marine mammals. While the predictions for beaked whales were in excess of 300% supersaturation at the surface, this should be viewed cautiously because of the limitations of the model used and the problems of using extrapolations from other species.

Dive profiles of three species (Cuvier's and Blainville's beaked whales and bottlenosed whales, *Hyperoodon ampullatus*; Hooker and Baird, 1999; P. Tyack, unpub. data) suggest that at least some species of beaked whales have dive profiles not previously observed in other marine mammals. These led to the suggestion that some beaked whales may chronically accumulate nitrogen in a manner not dissimilar to human 'saturation divers'. The critical components of this dive sequence include: (1) very deep and long foraging dives (to as deep as 2km and lasting as long as 90mins); (2) relatively slow, controlled ascents, followed by (3) a series of 'bounce' dives to between 100-400m depth (Hooker and Baird, 1999; P. Tyack, unpub. data). Thus, if any part of this dive sequence was affected by a behavioural response to sound (e.g. extended time at surface without the requisite bounce dives), it could induce excessive levels of nitrogen supersaturation in tissues, driving gas bubble and emboli formation in a manner similar to decompression sickness in humans.

It is clear that long-term studies on the behaviour of beaked whales to better define a baseline of 'normal' behaviour are needed. Obtaining baseline dive profiles via several methods over extended periods (e.g. D-tags, time-depth recorders) is especially important. We unanimously agree that highest priority should be given to designing controlled-exposure experiments to investigate the responses of beaked whales to anthropogenic sounds. Nowacek *et al.* (2004) conducted a controlled exposure experiment in northern right whales (*Eubalaena glacialis*) responding to a novel alerting stimulus. This study demonstrated that whales responded to stimuli at received sound levels as low as 133dB (re: 1μPa), with an immediate ascent followed by an extended surfacing interval. It was hypothesised that abnormal changes in dive behaviour in beaked whales could precipitate pathologic bubble formation in tissues. By applying innovative technology, researchers can further investigate behavioural responses and begin to examine physiological responses to sound. Designing exposure studies that are acceptable from both a scientific and animal welfare perspective is difficult. We recommend that the best way to design such experiments is through a workshop of appropriate experts.

Determining whether beaked whales are susceptible to developing gas bubbles due to changes in behaviour or physiological condition may prove to be even more difficult. To date, while there is no evidence of *in vivo* bubble formation in any marine mammals (but see Jepson *et al.*, 2003; 2005; Fernandez *et al.*, 2004), it is also true that no studies have been conducted to specifically look for the formation of intravascular bubbles during or following repetitive diving. Although it is possible to conduct such studies with shallow diving species such as bottlenose dolphins, until such work is conducted with deep-diving species such as beaked whales, it will not be possible to gain an insight into this possibility. As noted above, marine mammals have long been thought to have evolved anatomical, physiological and possibly behavioural adaptations to their marine environment to mitigate the risk of bubble formation (e.g. Harrison and Tomlinson, 1956; Ridgway and Howard, 1979; 1982; Falke *et al.*, 1985; Ponganis *et al.*, 2003). Despite these adaptations, recent theoretical and pathological evidence suggests that cetaceans can produce *in vivo* bubbles or experience tissue injury as a result (Jepson *et al.*, 2003; 2005; Fernandez *et al.*, 2004; 2005). These data and interpretations are the subject of continuing scientific debate (Fernandez *et al.*, 2004; Piantadosi and Thalmann, 2004).

Modelling predictions (Houser *et al.*, 2001) support the hypothesis that beaked whale tissues could be greater than 300% saturated with nitrogen. *Post mortem* evidence of acute and chronic gas emboli-associated lesions in liver, kidney, spleen, and lymph nodes of eight dolphins, one harbour porpoise (*Phocoena phocoena*) and one Blainville's beaked whale that stranded in the United Kingdom (Jepson *et al.*, 2003; 2005) also support this hypothesis. In addition, gas and fat emboli and widely disseminated microvascular haemorrhages were found in ten beaked whales examined in the Canary Islands mass strandings event in September 2002 (Jepson *et al.*, 2003; Fernandez *et al.*, 2004; 2005). In humans and experimental animals, such gas and fat emboli released into the venous system and deposited in the pulmonary capillary beds may travel through arterio-venous shunts into the systemic circulation. Prior to, or concomitant with this, respiratory and cardiovascular dysfunctions may occur with a biphasic response at the brain-spinal cord level, an initial, venous embolic obstruction and vasoconstriction, followed by secondary vasodilatation and prolonged (reactive) hyperaemia (Shigeno *et al.*, 1982). This haemodynamic process may explain the widespread cerebral congestion and edema, with spongiosis, intracranial perivascular haemorrhages and subarachnoid and intraventricular haemorrhages described in the beaked whale mass strandings.

A number of areas of research are required to further investigate whether beaked whales are susceptible to gas bubble formation, either as a function of altered behaviour or as the direct impact of sound on existing bubble nuclei. It is important that detailed necropsies are conducted of all freshly dead beaked whales, especially those whose deaths are correlated in both space and time with sound events. These necropsies should be conducted under laboratory procedures with rigorous protocols, e.g. opening the braincase underwater before the head is separated from the body or tying off primary vessels prior to removal, so as to avoid introducing bubbles during the necropsy. A standardised protocol for beaked whale necropsies is being developed to address these needs.

Experimental studies are needed to determine whether marine mammals can develop *in vivo* gas bubbles due to alterations in their dive profiles and to document precise levels of nitrogen supersaturation necessary to invoke such bubble formation. Specifically, ascertaining the onset of lung collapse and its impact on nitrogen gas kinetics is critical to determining what physiological effects any changes in dive profile might have on tissues. In the absence of live beaked whales for such studies, comparative studies could be conducted using marine mammals that are accessible and trainable. Physiological effects in shallow diving cetaceans and deep divers should be compared cautiously as deep divers will experience different physiological demands from environmental conditions at 1-2km and will likely have different adaptations and responses to those conditions. The depth at which lung collapse occurs is key to any modelling of nitrogen supersaturation because lung collapse prevents gas exchange and nitrogen absorption by the blood. The depth at which the lung collapses might be estimated using bottlenose dolphins with arterial blood sampling and blood nitrogen analyses. These results could then be compared to *post mortem* determination of lung collapse by compression testing of the lungs of a bottlenose dolphin carcass. Comparable results would support the use of *post mortem* testing of beaked whale lungs to determine the depth at which lung collapse occurs in those species. To test the hypothesised scenario that adverse gas bubble formation may result from a change in dive behaviour, it will be necessary to determine whether beaked whale tissues supersaturate with nitrogen and if so, to combine that information with dive profiles and potential changes in dive profiles. The scenario of gas bubble formation secondary to a behavioural response is plausible and merits rigorous investigation.

Physiological change

Haemorrhagic diathesis

The Bahamas beaked whale report listed twelve possible causes for the lesions observed and one proposed mechanism was haemorrhagic diathesis (Anon., 2001; 2002). Haemorrhagic diathesis is a tendency to bleed that results from one or more of several conditions, including: (1) depletion of clotting factors (disseminated intravascular coagulation (DIC); (2) a hereditary deficiency in one or more of a suite of blood clotting factors; or (3) platelet dysfunction or thrombocytopenia. Humans with the hereditary deficiency develop haemorrhages in regions similar to those of the beaked whales (i.e. subarachnoid spaces and the inner ear; Palva *et al.*, 1979) and hypertension increases the likelihood of such patients suffering intracranial bleeds (Hart *et al.*, 1995). If beaked whales are subject to haemorrhagic diathesis, stress caused by exposure to sound may cause them to haemorrhage. Similar haemorrhages in human patients can cause headache, nausea and vomiting, confusion, ataxia, dizziness, loss of consciousness and even death (Hart *et al.*, 1995). By analogy, intracranial haemorrhages observed in beaked whales may have resulted in disorientation, a subsequent inability to navigate and eventual stranding (Anon., 2001).

While nothing is known currently about clotting abilities or DIC in beaked whales, a lack of clotting factors has been noted in some cetacean and pinniped species, which may be related to diving adaptations. Northern elephant seals (*Mirounga angustirostris*) have platelets that are less prone to triggering clotting at high pressure, such as at depth (Field *et al.*, 2001) and they are prone to DIC (Gulland *et al.*, 1996). Lack of certain clotting factors, specifically Hageman's factor, Fletcher factor activity and Factor IX, are common to all of the limited number of cetacean species studied to date (Lewis *et al.*, 1969; Robinson, A.J. *et al.*, 1969; Saito *et al.*, 1976). If all cetaceans lack multiple clotting factors, it is not clear why beaked whales exposed to sonar might be more susceptible to the effects of haemorrhage than other species. However, the fact that few other species stranded simultaneously in cases involving sonar may in part be a reflection of differences amongst species' perceptions of an event as stressful, fundamental susceptibilities to stress, or differences in subsequent responses to the event. Future studies are needed on the haematology and physiology of coagulation in beaked whales to determine whether they are predisposed to haemorrhaging. In addition, future studies should investigate differences in behavioural responses of beaked whales to stressful stimuli.

Vestibular response

Marine mammals could become disoriented due to a vestibular response to sounds. Tullio's phenomenon, or dizziness induced by sound, has long been known of in humans (Tullio, 1929). The peripheral vestibular system of beaked whales may be affected by sound, affecting their ability to navigate. Beaked whales, which are usually found in deep waters, might, if disoriented, move into shallow waters and be unable to navigate back to deeper waters. However, Balcomb and Claridge (2001) observed that when pushed towards deep water, several animals swam away without the characteristic rolling or turning movements typical of animals with vestibular pathology. Furthermore, disorientation can result from a number of phenomena, making it difficult to detect and attribute a vestibular response to sound exposure in the presence of other potentially contributing factors.

Primary tissue damage leading to behavioural response

Sound may damage tissue directly through acoustically mediated bubble growth or tissue shear. A scientific workshop organised by the US NOAA/National Marine Fisheries Service was held in 2002 to consider the potential for resonant effects of sound to induce tissue injury in cetaceans (Anon., 2002). Modelling of acoustic resonance in lungs of cetaceans and comparative data from other animal systems (e.g. humans, dogs, pigs) suggested that only minimal tissue injury is likely to result from such a mechanism because tissue displacements are minute (Anon., 2002). The only exception is the large excursions of tissue that could occur where two dramatically mismatched tissue boundaries intersect in which there was minimal damping by associated tissues. Discussions also occurred on the possibility of a mechanism of sonar-related tissue injury in cetaceans from acoustically mediated bubble growth, particularly in tissues supersaturated with nitrogen, as may occur towards the end of a dive (Anon., 2002). This concept was primarily based on the work of Crum and Mao (1996) and Houser *et al.* (2001). Crum and Mao (1996) modelled the likelihood of acoustically driven bubble growth in humans and marine mammals by the process of rectified diffusion. The model assumed modest levels of nitrogen tissue (super)saturation and predicted that relatively high sound pressure levels (>210dB re:1μPa) would be necessary to induce significant bubble formation in human divers or marine mammals at 300-500Hz. Houser *et al.* (2001) estimated that levels of nitrogen supersaturation in some tissues of some deep-diving species, such as the northern bottlenose whale, could exceed 300% near the surface, raising the possibility that acoustically mediated bubble formation might occur at received sound pressures and sound durations lower than those predicted by Crum and Mao (1996). The workshop therefore recommended that the Crum and Mao model (1996) be used to estimate the threshold sound pressure levels for the higher levels of nitrogen tissue supersaturation predicted to occur from typical beaked whale dive profiles (Anon., 2002).

Isolated porcine liver tissue, polyacrylamide gels and human blood that have been compressed 4-7 atmospheres for 1-3hrs and then decompressed to ambient show extensive bubble development when exposed to high intensity (230dB SPL re:1μPa) ultrasound of 37kHz (Crum *et al.*, 2005). The authors postulated that the underlying mechanism might be destabilisation of pre-existing bubble nuclei by the ultrasound exposure, resulting in bubble growth by static diffusion in supersaturated tissue. Although these experiments demonstrated a possible mechanism by which bubble growth might occur, it did so under conditions that are different from those to which beaked whales may have been exposed during the stranding events. Thus, it is premature to judge acoustically mediated bubble growth as a potential mechanism and we recommend further studies to investigate this possibility. Further exposure studies should be conducted on marine mammal tissues by saturating them, exposing them with frequencies and amplitudes of interest and testing for minimum levels that could result in tissue damage.

Acoustic resonance

Anon. (2002) also considered the possibility that beaked whales are susceptible to effects of acoustic resonance (see discussion above). Most participants agreed that the best available models indicated that acoustic resonance is highly unlikely in the lungs of beaked whales, but recommended further studies to fully eliminate this hypothesised mechanism. They did not evaluate the possibility of resonance in other organs or structures and therefore recommended further modelling to determine if those would be susceptible to resonance. Given the full discussion in Anon. (2002), this mechanism is not discussed in depth here. The authors do, however, endorse the three areas of study recommended in Anon. (2002): (1) the possibility of resonance in the lung throughout the dive profile of beaked whales; (2) the potential for other organs or structures to be affected by acoustic resonance (either through modelling or empirical observation); and (3) the possibility that animals experience tissue shear (and determine how such injuries might appear).

Primary tissue damage leads to death

Some of the above mechanisms (i.e. gas bubble disease, haemorrhagic diathesis, acoustic resonance) could lead to lethal tissue damage. For example, the intracranial haemorrhage seen in the Bahamas and Canary Islands animals could have been caused by a stress response and associated haemorrhagic diathesis or bubble formation rupturing local capillaries. Although some of the stranded beaked whales were found dead, it is not clear whether these animals were alive when they first stranded. Several animals in all the events stranded alive and some either swam away or were pushed offshore. Even though their eventual fate is unknown, they did not die immediately. Determining whether sound exposure causes tissue damage that leads directly to death will be difficult and likely will require a process of elimination regarding other possible mechanisms. Testing the hypothesis that death results directly from sound-related tissue damage will be facilitated greatly by access to freshly stranded specimens that have been exposed to sound.

EDUCATION AND COORDINATION

As discussed below, education, communication and co-ordination will all facilitate the investigation of the effects of sound on beaked whales and mitigation measures to avoid adverse effects.

Education

Greater public outreach and education can be achieved through: (1) improved communication with environmental non-governmental organisations; (2) established links among scientists, the public and local and state policymakers; and (3) increased dissemination of stranding response information to the general public.

Co-ordination and communication

Improved co-ordination and communication is required among: (1) stranding responders to develop an international standardised protocol for necropsy; (2) sound producers, stranding responders and researchers to facilitate planning and preparation prior to sound exposure events and to monitor animal behaviour opportunistically; (3) sound producers and researchers to conduct retrospective analyses; (4) stranding responders to provide comprehensive databases to the public; (5) scientists and museums to obtain genetic samples from museum collections to evaluate population structure; and (6) terrestrial mammal and marine mammal physiologists to increase understanding of beaked whale physiology. Interaction across scientific disciplines (e.g. human dive physiology, terrestrial mammalogy, marine mammal behaviour, etc.) is critical to an improved understanding of this problem and broad research co-ordination and co-operation are needed.

CONCLUSIONS

Monitoring and mitigation

Current visual survey efforts to detect beaked whales in areas of acoustic activity are probably ineffective as a mitigation aid. Key limiting factors include sea state, amount of daylight, experience of observers and the diving and surfacing behaviour of beaked whales, which makes them either difficult to see or unavailable for visual observation at the surface for long periods of time. For the same reasons, surveys to determine distribution and abundance are also difficult and limited in their reliability. However, additional sensing technologies, such as passive acoustics, active sonar and radar, are currently in development that may increase scientists' abilities to detect beaked whales. Improved baseline data on distribution, abundance and habitat preferences of beaked whales are needed, in addition to increased effort in detection and recovery of dead and injured animals for improved understanding of the effects of anthropogenic sound.

Research

Although no potential mechanisms can be eliminated at this stage, we highlight gas bubble formation mediated through a behavioural response as plausible and in need of intensive study. Intensive research is needed to eliminate or confirm this hypotheses. The following four research priorities will provide better insights into its possible role.

(1) Controlled exposure experiments should be the top research priority. These experiments are critical for investigating beaked whale responses to sound. A multi-disciplinary workshop is needed to co-ordinate and design these experiments.
(2) There is an urgent need for studies of anatomy, physiology and pathology of beaked whales, particularly in situations where there is a known cause of death (e.g. bycatch). A comprehensive, standardised necropsy protocol is needed to make the best possible use of animals that become available through stranding or fisheries interactions.
(3) Baseline descriptions of diving behaviour and physiology of beaked whales are required to be able to better evaluate the potential for beaked whales to experience gas bubble disease from changes in dive behaviour.
(4) Finally, a retrospective review of all stranding records is necessary, as well as new studies in areas beaked whales are concentrated and exposed to anthropogenic sounds. To the greatest extent possible, retrospective analyses should: (1) describe and compare pathologies from all stranding events; (2) model the received sound level at sites where sound-related stranding occurred; (3) document all anthropogenic sound sources during stranding events; (4) assess population level effects in areas where sufficient data are available (e.g. the Bahamas); (5) evaluate distribution of all strandings relative to surrounding oceanographic/topographic features and possibly-related anthropogenic sound activities; and (6) identify areas where beaked whales are present and naval exercises have occurred, but strandings have not been documented and compare those situations with documented stranding events.

> Reviews should not interpret lack of strandings as sufficient evidence of no effect, because animals that die offshore may not wash ashore, animals that strand may not remain on the beach for more than one tidal cycle (Taylor *et al.*, 2004) and observation effort can vary markedly by location. Furthermore, whether or not strandings occur, activities involving anthropogenic sounds that may affect beaked whales should be documented to identify common features of habitat, species present or involved and acoustic properties to facilitate management and mitigation of such activities.

Understanding and evaluating potential mechanisms will aid managers in knowing when, where and how to best mitigate interactions between anthropogenic sound and beaked whales. The interdisciplinary approach of the workshop greatly facilitated exchanges of knowledge among scientists of disparate disciplines. The importance of interdisciplinary co-ordination and communication in solving this environmental problem cannot be overemphasised.

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Elements of beaked whale anatomy and diving physiology and some hypothetical causes of sonar-related stranding

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ABSTRACT

A number of mass strandings of beaked whales have in recent decades been temporally and spatially coincident with military activities involving the use of midrange sonar. The social behaviour of beaked whales is poorly known, it can be inferred from strandings and some evidence of at-sea sightings. It is believed that some beaked whale species have social organisation at some scale; however most strandings are of individuals, suggesting that they spend at least some part of their life alone. Thus, the occurrence of unusual mass strandings of beaked whales is of particular importance. In contrast to some earlier reports, the most deleterious effect that sonar may have on beaked whales may not be trauma to the auditory system as a direct result of ensonification. Evidence now suggests that the most serious effect is the evolution of gas bubbles in tissues, driven by behaviourally altered dive profiles (e.g. extended surface intervals) or directly from ensonification. It has been predicted that the tissues of beaked whales are supersaturated with nitrogen gas on ascent due to the characteristics of their deep-diving behaviour. The lesions observed in beaked whales that mass stranded in the Canary Islands in 2002 are consistent with, but not diagnostic of, decompression sickness. These lesions included gas and fat emboli and diffuse multiorgan haemorrhage. This review describes what is known about beaked whale anatomy and physiology and discusses mechanisms that may have led to beaked whale mass strandings that were induced by anthropogenic sonar.

Beaked whale morphology is illustrated using Cuvier's beaked whale as the subject of the review. As so little is known about the anatomy and physiology of beaked whales, the morphologies of a relatively well-studied delphinid, the bottlenose dolphin and a well-studied terrestrial mammal, the domestic dog are heavily drawn on.

KEYWORDS: BEAKED WHALES; STRANDINGS; BOTTLENOSE DOLPHIN; ACOUSTICS; DIVING; RESPIRATION; NOISE; METABOLISM

INTRODUCTION

Strandings of beaked whales and other cetaceans that are temporally and spatially coincident with military activities involving the use of mid-frequency (1-20kHz) active sonars have become an important issue in recent years (Nascetti *et al.*, 1997; Frantzis, 1998; Anon., 2001; 2002; Balcomb and Claridge, 2001; Jepson *et al.*, 2003; Fernández, 2004; Fernández *et al.*, 2004; 2005; Crum *et al.*, 2005). This review describes the relevant aspects of beaked whale anatomy and physiology and discusses mechanisms that may have led to the mass strandings of beaked whales associated with the use of powerful sonar. The anatomy and physiology of marine mammals are not as well studied as are those of domestic mammals (Pabst *et al.*, 1999) and within the cetacean family of species even less is known about the beaked whales than about the more common delphinids (e.g. the bottlenose dolphin, *Tursiops truncatus*). Furthermore, many of the morphological and physiological principles that are applied to pathophysiological evaluations of marine mammals were developed on small terrestrial mammals such as mice, rats and guinea pigs (e.g. Anon., 2001). Predictions and interpretations of functional morphology, physiology and pathophysiology must therefore be handled cautiously when applied to the relatively large diving mammals (Fig. 1). Interpolation is a relatively accurate procedure, but extrapolation, particularly when it involves several orders of magnitude in size, is less so (K. Schmidt-Nielsen, pers. comm. to S. Rommel).

Beaked whales are considered deep divers based on their feeding habits, deep-water distribution and dive times (Heyning, 1989b; Hooker and Baird, 1999; Mead, 2002). Observations from time-depth recorders on some beaked

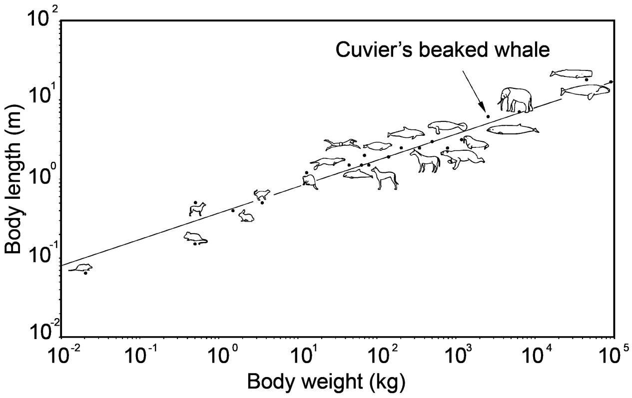

Fig. 1. Body size, expressed as weight and length for a variety of mammals. Marine mammals are large when compared to most other mammals and beaked whales are relatively large marine mammals.

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whales have documented dives to 1,267m and submergence times of up to 70min (Baird *et al.*, 2004; Hooker and Baird, 1999; Johnson *et al.*, 2004). Notably, beaked whales spend most of their time (more than 80%) at depth, typically surfacing for short intervals of one hour or less. Virtually no physiological information on beaked whales exists and information on any cetacean larger than the bottlenose dolphin is rare. Given this paucity of data this review relies on information obtained from both terrestrial mammals and other marine mammal species. In particular it draws heavily from the morphology of a well-studied terrestrial mammal, the domestic dog (*Canis familiaris*) and a relatively well-studied cetacean, the bottlenose dolphin, referred to herein as *Tursiops* (Fig. 2). Beaked whale morphology is illustrated using Cuvier's beaked whale (*Ziphius cavirostris*), further referred to as *Ziphius*. *Ziphius*, based on stranding records (they are rarely identified at sea), is the most cosmopolitan of the 21 beaked whale species (within 6 genera: *Berardius*, *Hyperoodon*, *Indopacetus*, *Mesoplodon*, *Tasmacetus* and *Ziphius*) (Baird *et al.*, 2004; Dalebout and Baker, 2001; Mead, 2002; Rice, 1998).

ANATOMY/PHYSIOLOGY

Before considering the potential mechanism by which sounds may affect beaked whales, it is important to review what is known and can be inferred of their anatomy and physiology.

External morphology

Aside from dentition and conspecific scarring between males, there are few external morphological differences between the genders of *Ziphius* (Mead, 2002). The head is relatively smooth (Figs 2 and 3) and the average adult total body length is 6.1m (Heyning, 2002). The throats of all beaked whales have a bilaterally paired set of grooves associated with suction feeding (Heyning and Mead, 1996). *Ziphius* bodies are robust and torpedo-like in shape, with small dorsal fins approximately 1/3 of the distance from the tail to the snout. The relatively short flippers can be tucked into shallow depressions of the body wall (Heyning, 2002).

Specialised lipids

Marine mammals have superficial lipid layers called blubber (Fig. 3). Blubber in non-cetaceans is similar to the subcutaneous lipid found in terrestrial mammals; in contrast, the blubber of cetaceans is a thickened, adipose-rich hypodermis (reviewed in Pabst *et al.*, 1999; Struntz *et al.*, 2004). Cetacean blubber makes up a substantial proportion (15-55%) of the total body weight (Koopman *et al.*, 2002; McLellan *et al.*, 2002) and the lipid content can vary depending upon the species and the sample site (Koopman *et al.*, 2003a). Blubber is richly vascularised to facilitate heat loss (Kanwisher and Sundes, 1966; Parry, 1949) and is easily bruised by mechanical insult. Since blubber has a density that can be different from those of water and muscle, it may respond to ensonification differently, particularly if conditions of vascularisation (i.e. volume and temperature of blood) vary. The roles blubber (and other lipids) may play in whole-body acoustics should be the subject of further research.

As in other odontocetes, the hollowed jaw is surrounded by acoustic lipids[1], although the beaked whale acoustic lipids are chemically different from those of other odontocetes (Koopman *et al.*, 2003b). These acoustic lipids conduct sound to the pterygoid and peribullar sinuses and ears (Koopman *et al.*, 2003a; Norris and Harvey, 1974; Wartzog and Ketten, 1999) and may function as an acoustical amplifier, similar to the pinnae of terrestrial

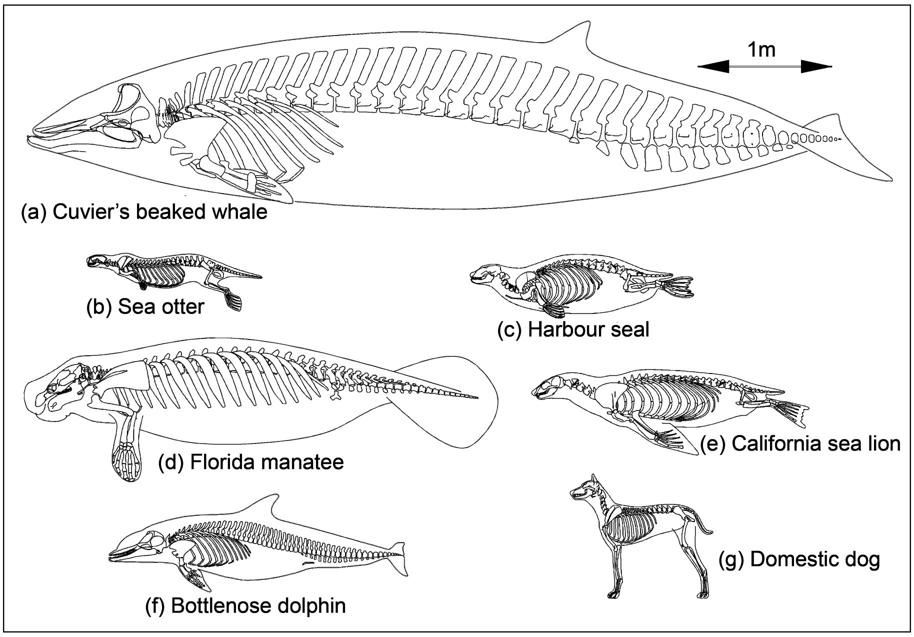

Fig. 2. The skeleton of a Cuvier's beaked whale, (a) compared to selected marine mammal skeletons: sea otter, *Enhydra lutris* (b); harbour seal, *Phoca vitulina* (c), Florida manatee, *Trichechus manatus latirostris* (d); California sea lion, *Zalophus californianus* (e); bottlenose dolphin (f) and the domestic dog, *Canis familiaris* (g). Each skeleton was scaled proportionately to the beaked whale. The *Ziphius* skeleton was drawn from photographs of Smithsonian Institution skeleton #504094 and from photographs courtesy of A. van Helden; other skeletons were re-drawn from Rommel and Reynolds (2002).

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[1] Evidence from anatomical, morphological, biochemical and behavioural studies all support the role of the melon and mandibular lipids in the transmission and reception of sound by odontocetes (Norris and Harvey, 1974; Koopman *et al.*, 2003b; Ketten *et al.*, 2001;Varanasi *et al.*, 1975; Wartzog and Ketten, 1999). Thus, these fats are collectively referred to here as the 'acoustic lipids'.

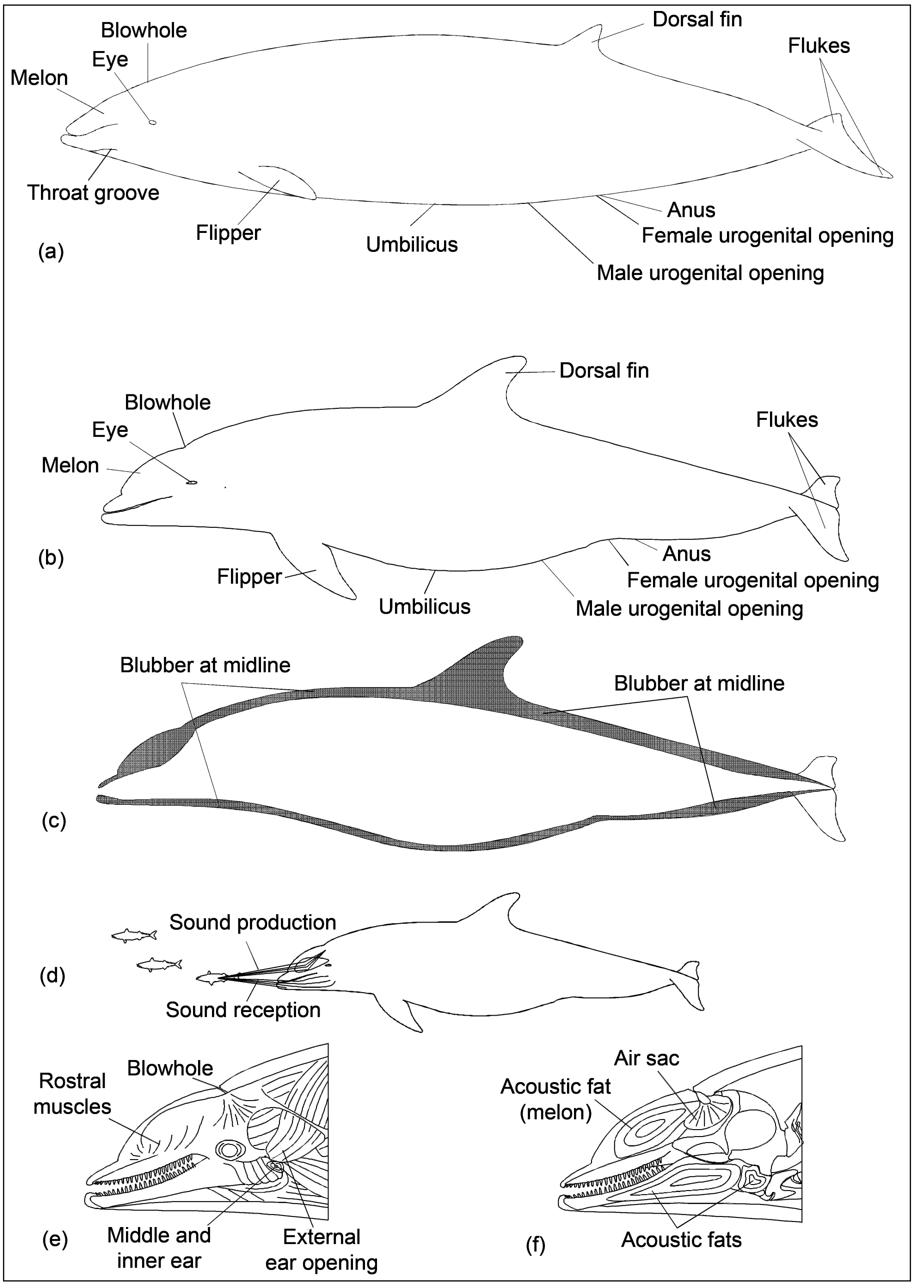

Fig. 3. The external morphology of a Cuvier's beaked whale (a) compared with that of the bottlenose dolphin (b). When compared to terrestrial mammals, Odontocetes have extensive and atypical fat deposits and fat emboli have been implicated in some beaked whale mass strandings; thus, their potential sources (such as well-vascularised fat deposits) are of special interest. Skin lipids (or blubber) perform several functions: for example, buoyancy, streamlining and thermoregulation. (c) This drawing illustrates the thickness of the blubber of a dolphin along the midline of the body. (d-f) Odontocetes have specialised acoustic lipids, represented by contours in f, which are found in the melon and lower jaw. These lipids have physical characteristics that guide sound preferentially.

mammals (Cranford *et al.*, 2003). The ziphiid melon is similar in size, shape and position to that of other odontocetes (Heyning, 1989b), but Koopman *et al.* (2003b) have shown that like the jaw fat, the acoustic lipids of the ziphiid melon are also chemically different. This suggests potential differences in sound propagation properties and perhaps in response to anthropogenic ensonification. Thus, understanding the role and composition of acoustic lipids may be important in interpreting lesions in mass stranded beaked whales.

Extensive fat deposits are also found in the skeleton. Most cetacean bones are constructed of spongy, cancellous bone, with a thin or absent cortex (de Buffrenil and Schoevaert, 1988). Like the fatty marrow found in terrestrial mammal bones, the medullae of cetacean bones are rich in lipids and up to 50% of the wet-weight of a cetacean skeleton may be attributed to lipid. Since it has been demonstrated that individual lipids within the same, as well as different, parts of the cetacean body may be structurally distinct, it may be of value to analyse the composition of fat emboli to determine if the sources are from general or specific lipid deposits. Thus, lipid characterisation of fat emboli may help pinpoint the source of lipids and therefore the site of injury.

The skeletal system

There is a pronounced sexual dimorphism in the skulls of *Ziphius*; the species name (*cavirostris*) is derived from the deep excavation (prenarial basin) on the rostrum that occurs in mature males (Heyning, 1989a; Heyning, 2002; Kernan, 1918; Omura *et al.*, 1955). The bones of male beaked whale rostra (the premaxillaries, maxillaries and vomer) may become densely ossified (in the extreme, up to 2.6g cm^{-3} in Blainville's beaked whale, *Mesoplodon densirostris*), thought to be an adaptation for conspecific aggression (de Buffrenil and Zyberberg, 2000; MacLeod, 2002). Both genders have homodont dentition (teeth are all the same shape) and a caudally hollowed, lipid-filled, lower jaw, as do other odontocetes.

The premaxillary, maxillary and vomer bones are elongated rostrally and the premaxillaries and maxillaries are also extended dorsocaudally over the frontal bones (Fig. 4b; *telescoping*, Miller, 1923). The narial passages are essentially vertical in all cetaceans and the nasal bones are located at the vertex of the skull, dorsal to the braincase. In *Tursiops*, the nasal bones are relatively small vestiges that lie in shallow depressions of the frontal bones (Rommel, 1990). Conversely, the nasal bones of beaked whales are robust and are part of the prominent rostral projections of the skull apex (Fig. 4; Kernan, 1918; Heyning, 1989a).

Odontocetes have larger, more complex pterygoid bones than terrestrial mammals. In delphinids, the pterygoid and palatine bones form thin, almost delicate, medial and lateral walls lining the bilaterally paired pterygoid sinuses. The pterygoid sinuses of *Tursiops* are narrow structures that are constrained by the margins of the pterygoid bones. In contrast, the pterygoid bones of beaked whales are thick and robust (Figs 4 and 5) and their pterygoid sinuses are very large (measured by Scholander (1940) each to be approximately a litre in volume in the northern bottlenose whale, *Hyperodon ampullatus*). Beaked whale (and physeteroid) pterygoid sinuses lack bony lateral laminae (Fraser and Purves, 1960). These morphological characteristics of the pterygoid region imply differences in mechanical function and perhaps response to ensonification by anthropogenic sonar, and thus may be important in interpreting lesions found in beaked whales.

In most mammals, there is a temporal 'bone', which is a compound structure made up of separate bony elements and/or ossification centres (Nickel *et al.*, 1986). In many mammals, the squamosal bone is firmly ankylosed to the periotic (petrosal, petrous), tympanic (or parts thereof) and mastoid bones to form the temporal bone (Kent and Miller, 1997). However, this is not the case in fully aquatic marine mammals (cetaceans and sirenians), where the squamosal, periotic and tympanic bones (there is some controversy over the nature of the mastoid as a separate 'bone') remain separate (Rommel, 1990; Rommel *et al.*, 2002). Unlike the skulls of most other mammals in which the periotic bones are part of the inner wall of the braincase, the cetacean tympano-periotic bones are excluded from the braincase (Fig. 5; Fraser and Purves, 1960; Geisler and Lou, 1998). The beaked whale tympano-periotic is a dense, compact bone (as in other cetaceans), whereas its mastoid process (caudal process of the tympanic bulla) is trabecular[2] (like most other cetacean skull bones). The *Ziphius* mastoid process, unlike that of the delphinids (and some other beaked whales), is relatively large and interdigitates with the mastoid process of the squamosal bone (Fraser and Purves, 1960).

The beaked whale basioccipital bone is relatively massive, with thick ventrolateral crests, in contrast to the basioccipital crests in delphinids, which are relatively tall but thin and laterally cupped (Fig. 5). In odontocetes, there are large, vascularised air spaces (peribullar sinuses) between the tympano-periotics and basioccipital crests. In *Tursiops*, the pathway from the braincase for the 7th and 8th cranial nerves is a short (parallel to these nerves), open cranial hiatus (Rommel, 1990) bordered by relatively thin bones. In *Ziphius*, this path is a narrow, relatively long channel through the basioccipital bones (Fig. 5). It is similar in position, but not homologous to the internal acoustic (auditory) meatus of terrestrial mammals. The morphology of the pterygoid and basioccipital bones and the size and orientation of the cranial hiatus likely contribute to differences in acoustical properties and mechanical compliance of the beaked whale skull. These bony structures are therefore of potential importance in the effects of acoustical resonance.

The vertebral column supports the head, trunk and tail (Figs 2 and 6). In *Tursiops* the first two cervical vertebrae are fused, but the rest are typically unfused (Rommel, 1990); in contrast, the first four cervicals of *Ziphius* are fused. There is more individual variation in the numbers of vertebrae in each of the postcervical regions of cetaceans than in the dog. The numbers of thoracic vertebrae vary between *Tursiops* and *Ziphius*: there are 12-14 thoracics in *Tursiops* and 9-11 in *Ziphius*. In cetaceans, the lumbar region has more vertebrae than that of many terrestrial mammals, significantly more so in *Tursiops* (16-19) than in *Ziphius* (7-9), however the lumbar section of *Ziphius* is greater in length than that of *Tursiops*. As in all other cetaceans, there has been a substantial reduction of the pelvic girdle and subsequent elimination (by definition) of the sacral vertebrae. The caudal regions have also been elongated to varying degrees. The vertebral formula that summarises the range of these numbers for *Tursiops* is C7:T12-14:L16-19:S0:Ca24-28 and for *Ziphius* is C7:T9-11:L7-9:S0:Ca19-22 (Figs 6b and 6c).

There is a bony channel, the neural canal (Fig. 6b), located within the neural arches, along the dorsal aspects of the vertebral bodies of the spinal column. In most mammals the neural canal is slightly larger than the enclosed spinal cord (Nickel *et al.*, 1986). In contrast, some marine mammals (e.g. seals, cetaceans and manatees) have considerably larger (i.e. 10-30X) neural canals, which accommodate the relatively large masses of epidural vasculature and/or fat (Rommel and Lowenstein, 2001; Rommel and Reynolds, 2002; Rommel *et al.*, 1993; Tomlinson, 1964; Walmsley, 1938). These epidural vascular masses are largest in deeper diving cetaceans (Ommanney, 1932; Vogl and Fisher, 1981; Vogl and Fisher, 1982; S. Rommel, pers. obs. in beaked whales and sperm whales). In the tail, there is a second bony channel formed by the chevron bones, which is located on the ventral aspect of the spinal column (Pabst, 1990; Rommel, 1990). The chevron bones form a chevron (hemal) canal, which encompasses a vascular countercurrent heat exchanger, the caudal vascular bundle (Figs 6b and 6c; Rommel and Lowenstein, 2001).

The ribs of cetaceans are positioned at a more acute angle to the long axis of the body than those of terrestrial mammals in order to accommodate decreases in lung volume with depth. The odontocete thorax has costovertebral joints that allow a large swing of the vertebral ribs, which substantially increases the mobility of the rib cage (Rommel, 1990). This extreme mobility of the rib cage presumably accommodates the lung collapse that accompanies depth-related pressure changes (Ridgway and Howard, 1979). In cetaceans, the single-headed rib attachment is at the distal tip of the relatively wide transverse processes instead of the centrum as it is in other mammals (Rommel, 1990). In contrast to *Tursiops*, in which 4-5 ribs are double-headed, 7 of the ribs in *Ziphius* are

[2] A trabecular mastoid is also observed in some physeteroids.

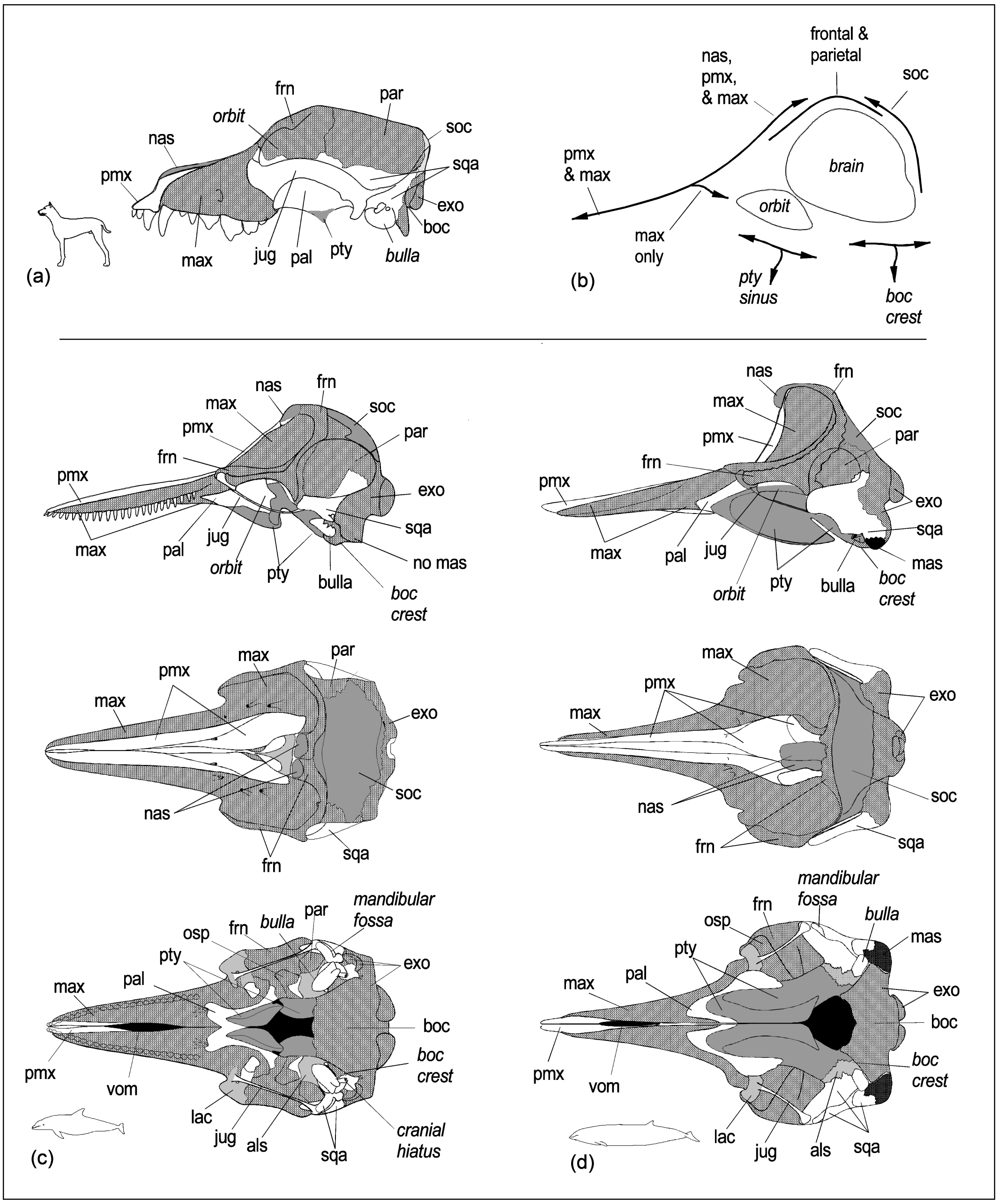

Fig. 4. Bones of the domestic dog skull (a) compared with a schematic illustration (b) showing telescoping in odontocetes and with the skull bones of *Tursiops* (c) and *Ziphius* (d). Telescoping refers to the elongation of the rostral elements (both fore and aft in the case of the premaxillary and maxillary bones), the dorso-rostral movement of the caudal elements (particularly the supraoccipital bone) and the overlapping of the margins of several bones. One major consequence of telescoping is the displacement of the external nares (and the associated nasal bones) to the dorsal apex of the skull. One of the most striking differences between the *Tursiops* and *Ziphius* skulls is the relatively massive pterygoid bones of the latter. The nasal bones of beaked whales are more prominent and extend from the skull apex. *Tursiops* has extensive tooth rows; in contrast *Ziphius* has no maxillary teeth. The dog and *Tursiops* skulls are adapted from Rommel *et al.* (2002). The *Ziphius* skull was drawn from skulls S-95-Zc-21 and SWF-Zc-8681-B (courtesy of N. Barros and D. Odell), from photographs of Smithsonian Institution skull #504094 and from photographs courtesy of A. van Helden and D. Allen.

double-headed. This arrangement may contribute to the function (e.g. mechanical support or pumping action) of thoracic retia mirabilia located on the dorsal aspect of the thoracic cavity (Fig. 7) by placing the costovertebral hinges closer to the lateral margins of the retia. Delphinids have bony sternal ribs, whereas those of beaked whales are cartilaginous. The sternum of *Tursiops* is composed of 3-4 sternabrae, whereas that of *Ziphius* is 5-6. These morphological differences might produce different dynamics during changes of the thorax in response to diving and thus alter some of the physical properties of the air-filled spaces. This is an area requiring further research, particularly because we do not know at what depth beaked whale lungs collapse.

The air-filled spaces

In addition to the flexible rib cage, cetacean respiratory systems possess morphological specialisations supportive of an aquatic lifestyle (Pabst *et al.*, 1999). These specialisations involve the blowhole, the air spaces of the head, the larynx and the terminal airways of the lung.

The single blowhole (external naris) of most odontocetes is at the top of the head (Fig. 7). During submergence, the air passages are closed tightly by the action of the nasal plug that covers the internal respiratory openings (Fig. 8). The nasal plug sits tightly against the superior bony nares and seals the entrance to the air passages when the nasal plug muscles are relaxed (Lawrence and Schevill, 1956; Mead, 1975).

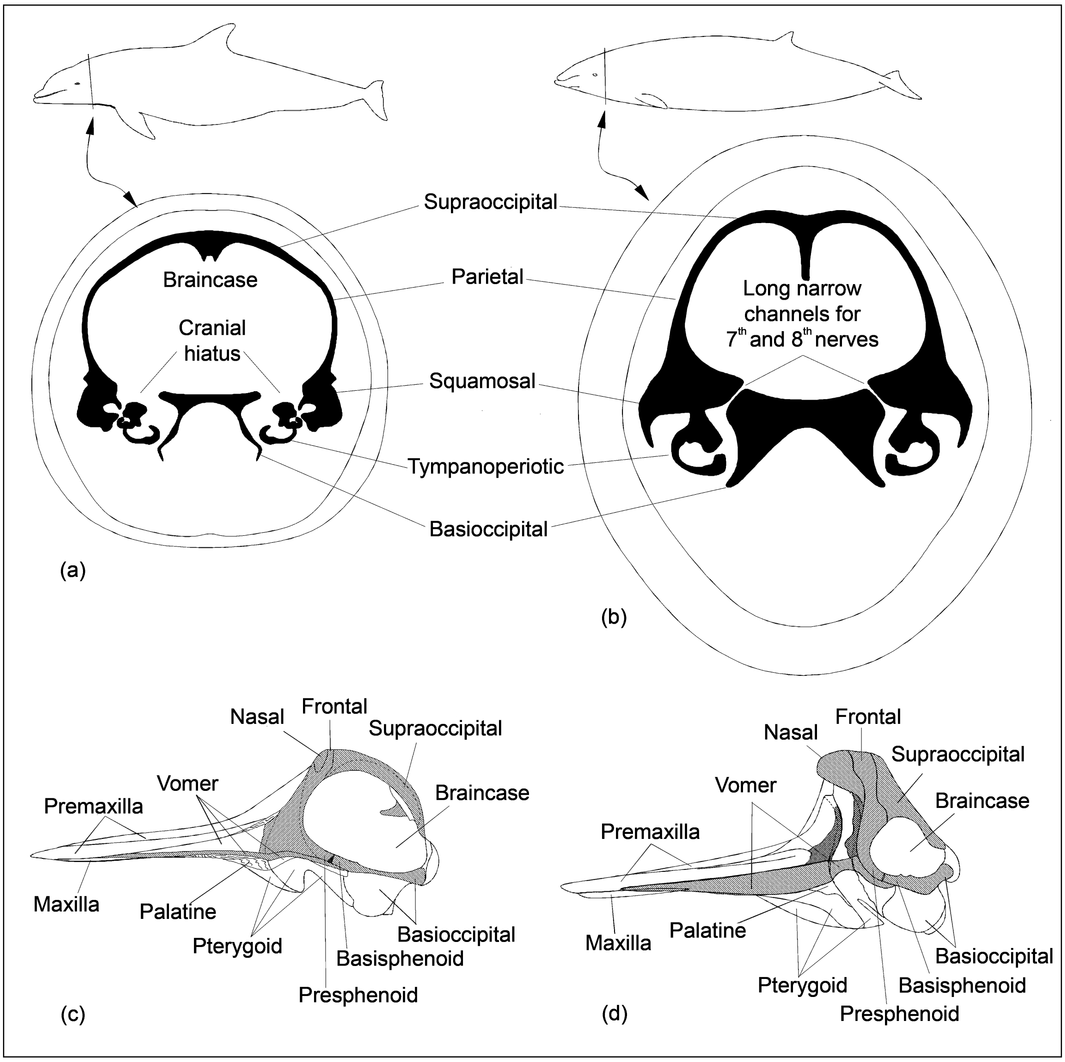

Fig. 5. Cross-sections of the skulls of *Tursiops* (a) and *Ziphius* (b). The cross sections (at the level of the ear) are scaled to have similar areas of braincase. In *Tursiops*, the pathway out of the braincase for the VIIth &VIIIth cranial nerves is a short open cranial hiatus (Rommel, 1990) bordered by relatively thin bones, whereas in *Ziphius* it is a narrow, relatively long channel. The ziphiid basioccipital bones are relatively massive with thick ventrolateral crests; in contrast, delphinid basioccipital bones are relatively long and tall, but thin and laterally cupped. Note that in contrast to the *Ziphius* calf cross-section, the adult head would have a greater amount of bone and the brain size would be different. The cross section of an adult *Tursiops* is after Chapla and Rommel (2003) and that of *Ziphius* is after a scan of a calf (courtesy of T. Cranford). Midsagittal sections of an adult *Tursiops* (c; after Rommel, 1990) and an adult *Ziphius* (d; drawn from photographs of a sectioned skull at the Museum of New Zealand Te Papa Tongarewa).

The anatomy of the blowhole vestibule and its associated air sacs varies within, as well as between, odontocete species (Mead, 1975), yet the overall echolocating functions are believed to be similar. In *Ziphius*, the vestibule is longer and more horizontal than in *Tursiops* (Fig. 8) and *Ziphius* has no vestibular sacs, no rostral components of the nasofrontal sacs and the right caudal component of the nasal sacs extends up and over the apex of the skull (Heyning, 1989a). In some *Ziphius* males, there are relatively small, left (caudal) nasal sacs, which are vestigial or absent in females (Heyning, 1989b). The premaxillary sacs, which lie on the dorsal aspect of the premaxillary bones, just rostral to the bony nares, are asymmetrical, the right being several times larger than the left. In adult *Ziphius* males, there is a rostral extension of the right premaxillary sac that is (uniquely) not in contact with the premaxillary bone (Heyning, 1989a). In *Tursiops*, there are small accessory sacs on the lateral margins of the premaxillary sacs (Schenkkan, 1971; Mead, 1975). In contrast, *Ziphius* has no well-defined accessory sacs (Heyning, 1989a). Based on simple physics, these differences in air sac geometry may influence the mechanical responses of the head to anthropogenic ensonification.

Odontocetes have air sinuses surrounding the bones associated with hearing; the peribullar and pterygoid sinuses (Figs 8 and 9). These air sinuses are continuous with each other (Chapla and Rommel, 2003) and have been described by Boenninghaus (1904) and Fraser and Purves (1960) as highly vascularised (see below; Fig. 9) and filled with a coarse albuminous foam, which may help these air-filled structures resist pressures associated with depth as well as with acoustic isolation. The odontocete larynx is very specialised – its cartilages form an elongate goosebeak (Reidenburg and Laitman, 1987). The laryngeal cartilages fit snugly into the nasal passage and the palatopharyngeal sphincter muscle keeps the goosebeak firmly sealed in an almost vertical intranarial position (Lawrence and Schevill, 1956). These morphological features effectively separate the respiratory tract from the digestive tract to a greater extent than is

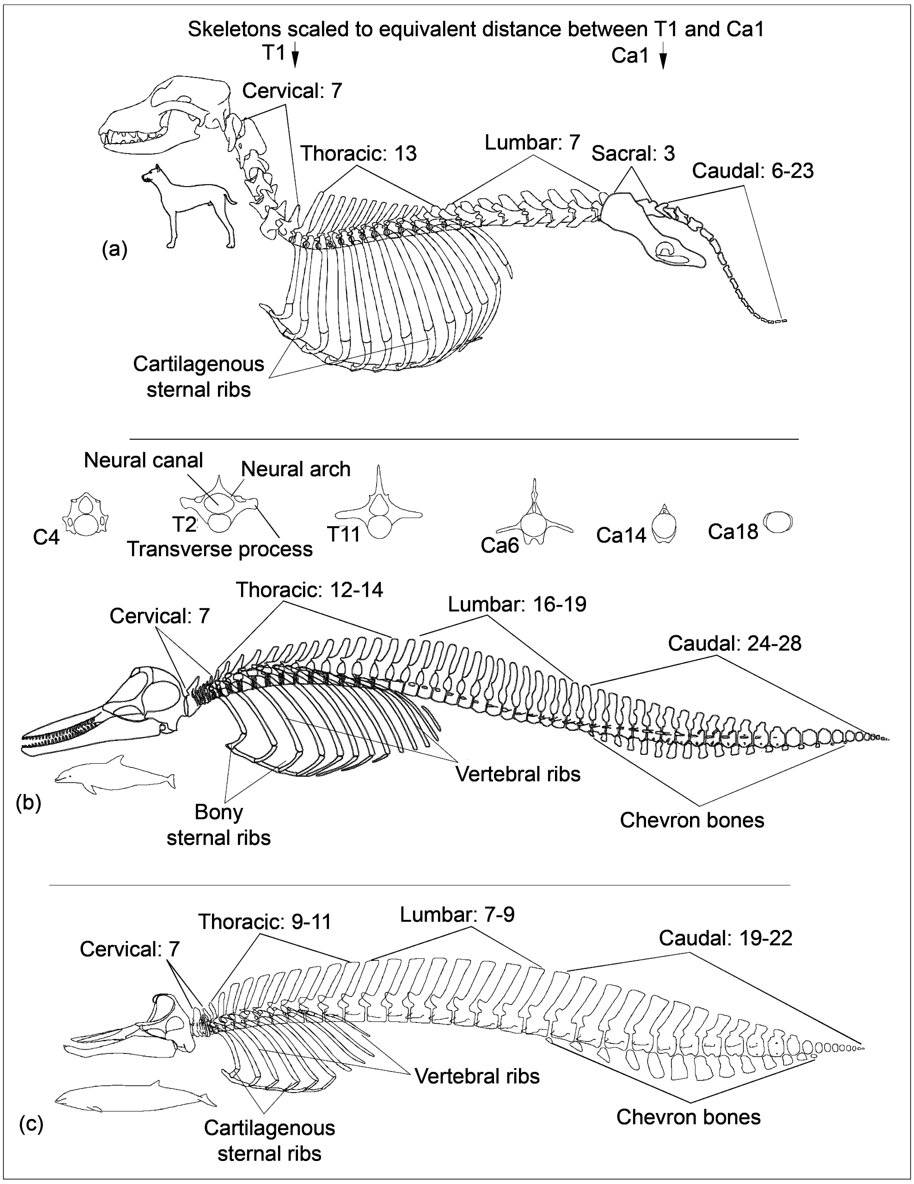

Fig. 6. The axial skeletons and rib cages of the domestic dog (a) compared to those of *Tursiops* (b) and *Ziphius* (c). The caudal region of *Tursiops* has 24-28 vertebrae while that of *Ziphius*, 19-22, depending on the individual. The neural canals are the dorsal, vertebral bony channels extending from the base of the skull to the tail, in which are contained the spinal cord and associated blood vessels. The ventrally located chevron bones enclose the chevron canal, in which are found the arteries and veins of the caudal vascular bundle. (Redrawn after Rommel and Reynolds, 2002).

found in any other mammal (Figs 7b and 7c; Reidenburg and Laitman, 1987). The complex head and throat musculature manipulates the gas pressures in the air spaces of the head and thus can change the acoustic properties of the air spaces and the adjacent structures (Coulombe *et al.*, 1965).

The thoracic cavity (Figs 7a and 7b) contains (among other structures) the heart, lungs, great vessels and in cetaceans and sirenians, the thoracic retia (McFarland *et al.*, 1979; Rommel and Lowenstein, 2001). In *Tursiops*, the cranial aspect of the lung extends significantly beyond the level of the first rib (Fig. 7a), in close proximity to the skull (McFarland *et al.*, 1979). The terminal airways of cetacean lungs are reinforced with cartilage up to the alveoli (Fig. 7d; e.g. Ridgway *et al.*, 1974). Additionally, the cetacean bronchial tree has circular muscular and elastic sphincters at the entrance to the alveoli (Fig. 7d; Drabek and Kooyman, 1983; Kooyman, 1973; Scholander, 1940). It has been hypothesised that bronchial sphincters regulate airflow to and from the alveoli during a dive (reviewed in Drabek and Kooyman, 1983). Under compression, the alveoli in the cetacean lung collapse and gas from them can be forced into the reinforced upper airways of the bronchial tree. Thus, nitrogen is isolated from the site of gas exchange, reducing its uptake into tissues and mitigating against potentially detrimental excess nitrogen absorption (reviewed in Pabst *et al.*, 1999; Ponganis *et al.*, 2003). The microanatomy of beaked whale lungs has not been described and is therefore an area requiring future research.

In cetaceans, the ventromedial margins of the lungs embrace the heart (Fig. 7e), so the heart influences the geometry of the lungs. These single-lobed lungs change shape with respiration and depth and the heart affects the size and shape of the lungs because gas distribution in the lungs changes, but the shape of the heart remains relatively unchanged. Additionally, because of the mobility of the ribs, the size and shape of the lungs change in a manner different than do those of a terrestrial animal with a rigid rib cage and multilobed lung (Rommel, 1990). Since respiratory systems contain numerous gas-

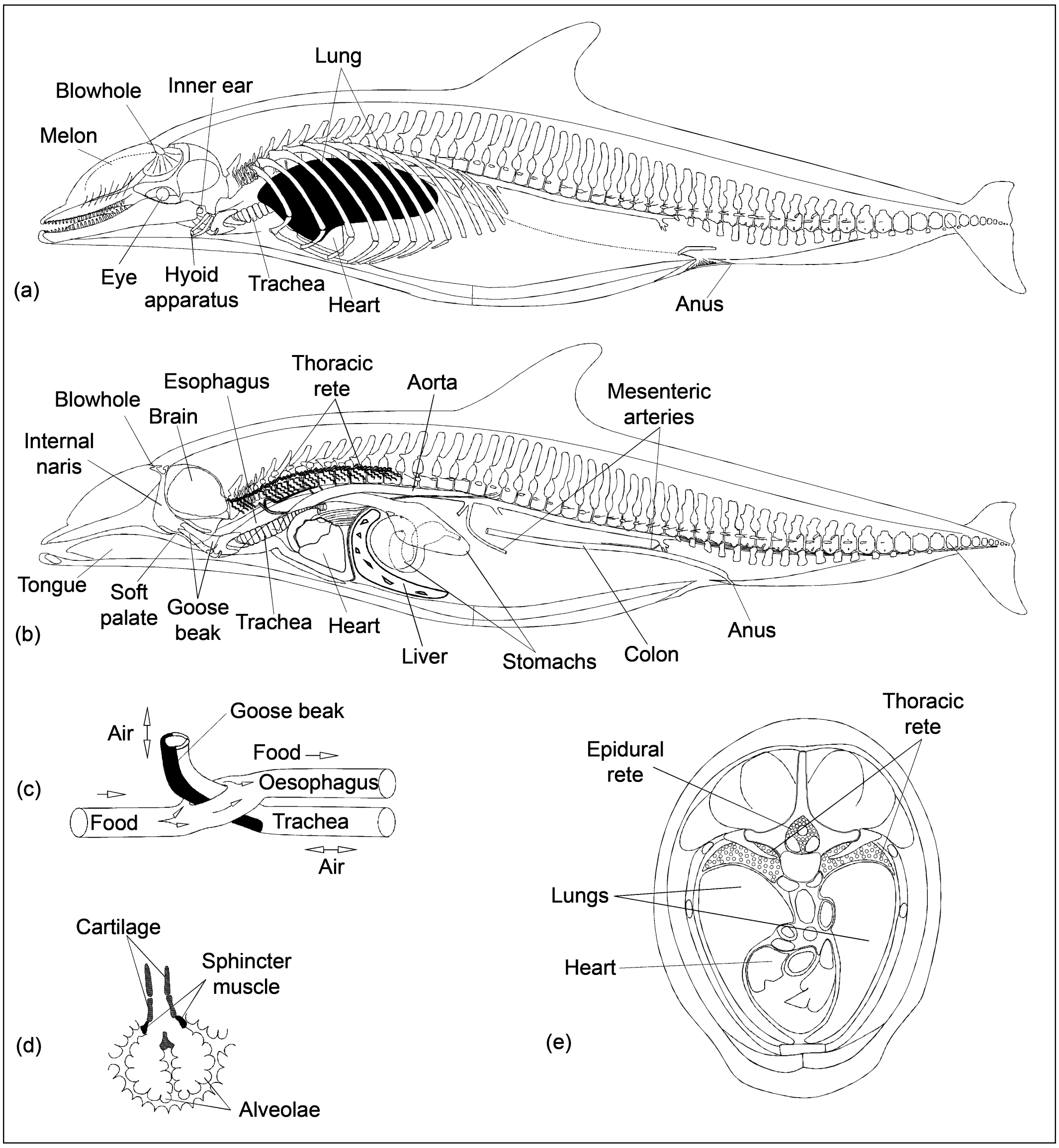

Fig. 7. The major respiratory and thoracic arterial pathways are illustrated for *Tursiops* (a, b). Note the structure of the oesophagus and trachea (b, c) and the reinforced terminal airways of the cetacean lung with sphincter muscles surrounding the distal bronchioles (d). The lungs with a heart in between (e) are a complex shape that will have different resonant responses to ensonification from a simple spherical model. (a-b adapted from Rommel and Lowenstein, 2001; c-d adapted from Pabst *et al.*, 1999; e adapted from Rommel *et al.*, 2003).

filled spaces, the pressure exerted on them at depth affects their volume, shape and thus their resonant frequencies. The shapes of compressed cetacean lungs and the thorax are also influenced by small changes in blood volume within the thoracic retia mirabilia (Figs 7e and 10c-e; Hui, 1975). Although the thoracic retia have not yet been described in beaked whales, it has been assumed (because they are deep divers and their retia are relatively large) that filling these retia with blood may have a noticeable influence on internal thoracic shape, particularly with depth.

The actions of the liver and abdominal organs pressing against the diaphragm, in concert with abdominal muscle contractions, affect gas pressure in and the distribution of mechanical forces on the lungs. Appendicular-muscle-dominated locomotors (such as the dog) couple different sorts of respiratory and locomotory abdominal forces (Bramble and Jenkins, 1993) compared to axial-muscle-dominated locomotors (such as the cetaceans; Pabst, 1990). This action has not been investigated in cetaceans, but it is likely that it plays some role in altering the physical properties of the pleural cavity and the flow of venous blood and therefore may be important in any mechanical analysis of this region.

The vascular system

The mammalian brain and spinal cord are sensitive to low oxygen levels, subtle temperature changes and mechanical insult (Baker, 1979; Caputa *et al.*, 1967; McFarland *et al.*, 1979). The vascular system helps avoid these potential problems. Mammalian brains are commonly supplied either solely by, or by combinations of the following paired vessels: internal carotid, external carotid and vertebral arteries and less commonly by the supreme intercostal arteries (Fig. 10; Nickel *et al.*, 1981; Rommel, 2003; Slijper, 1936). In cetaceans, the internal carotid terminates within the tympanic bulla but contributes blood to the fibro-venous plexus (FVP), which is associated with the pterygoid and peribullar sinuses (Fig. 9, Fraser and Purves, 1960). These FVPs do contain some arteries (Fraser and Purves, 1960) but

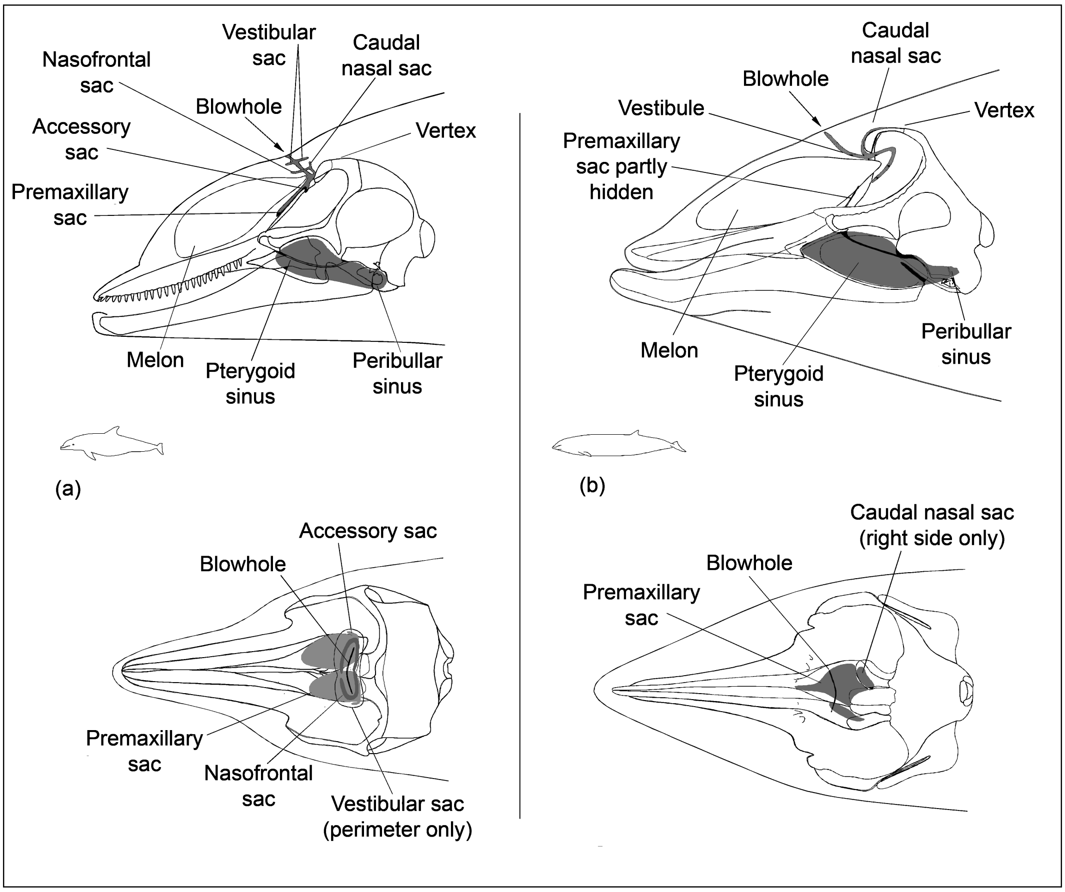

Fig. 8. Left lateral and dorsal views of the extracranial sinuses in *Tursiops* (a) and *Ziphius* (b). Arrows point to the blowholes and are parallel to the vestibules. The dorsocranial/supraorbital air sacs and sinuses associated with vocalisation and echolocation are much more extensive and convoluted in delphinids than in ziphiids. The pterygoid and peribullar sinuses of ziphiids are much larger than those of delphinids. The dorsal and lateral views of the air sacs of *Tursiops* are adapted from Mead (1975), those of *Ziphius* from Heyning (1989a).

are mostly venous vascular structures[3]. The cetacean brain is supplied almost exclusively by the epidural retia via the thoracic retia (Breschet, 1836; Boenninghaus, 1904; Fraser and Purves, 1960; Galliano *et al.*, 1966; Nagel *et al.*, 1968; McFarland *et al.*, 1979). These vascular structures have not yet been fully described for beaked whales.

In most cetaceans, the blood delivered to the brain leaves the thoracic aorta via the supreme intercostal arteries and supplies the thoracic retia from their lateral margins (Figs 10d and 10e). The blood then flows towards the midline and into the epidural (spinal) retia mirabilia of the neural canal (Wilson, 1879; McFarland *et al.*, 1979) and is directed towards the head to supply the brain (Fig. 10c). Interestingly, it has been suggested that the sperm whale (*Physeter macrocephalus*) brain may be supplied in a slightly different manner (Melnikov, 1997) and because of their phylogenetic proximity (Rice, 1998), it is reasonable to assume that beaked whale morphology approximates that of the condition in *Physeter*. This is a potentially important area for future research.

In the cetaceans for which thoracic and epidural retia have been described, the right and left sides of these vascular structures have little or no communication and there is an incomplete circle of Willis, potentially supplying the right and left sides of the brain independently (McFarland *et al.*, 1979; Nakajima, 1961; Vogl and Fisher, 1981; 1982; Walmsley, 1938; Wilson, 1879). This bilateral isolation of paired supplies may have profound implications on hemispherical sleep (Baker, 1979; Baker and Chapman, 1977; McCormick, 1965; Oleg *et al.*, 2003; Ridgway, 1990) and other important physiological processes.

Blood flow is not only separated at the brain. In general, mammals possess two venous returns from their extremities: one deep and warmed; one superficial and cooled (Fig. 11). In the deep veins, which are adjacent to nutrient arterial supplies, countercurrent heat exchange (CCHE) occurs if the temperature of the arteries is higher than that of the veins (Figs 11-13; Schmidt-Nielsen, 1990; Scholander, 1940; Scholander and Schevill, 1955); warmed blood is returned and body heat is trapped in the core. Arteriovenous anastomoses (AVAs), can bypass the capillaries and bring relatively large volumes of blood close to the skin surface to

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[3] FVPs have been described as retia mirabilia but should be classed by themselves. Retia mirabilia (singular- rete mirabile) in the thoracic and cranial regions have been studied by many workers (Breschet, 1836; Wilson, 1879; Boenninghaus, 1904; Ommanney, 1932; Slijper, 1936; Walmsley, 1938; Fawcett, 1942; Fraser and Purves, 1960; Nakajima, 1961; Hosokawa and Kamiya, 1965; Galliano *et al.*, 1966; McFarland *et al.*, 1979; Vogl and Fisher, 1981; 1982; Shadwick and Gosline, 1994; they were reviewed by Geisler and Lou, 1998), but they are still poorly understood, in part because of the variety of terms (e.g. basicranial rete, opthalmic rete, orbital rete, fibro-venous plexus, carotid rete, internal carotid rete, rostral rete, blood vascular bundle) used to describe them; in some references (e.g. McFarland *et al.*, 1979), several different terms are used to label the same structure; conversely, the same term has been used to describe different structures in different individuals. The pterygoid and opthalmic venous plexuses and the maxillary arterial rete mirabile of the cat and the palatine venous plexus of the dog (Schaller, 1992), which are involved with heat exchange, could be homologous to the FVP. The arterial plexuses of the cetacean braincase may be homologous to the rostral internal carotid arterial plexus of terrestrial mammals (Geisler and Lou, 1998).

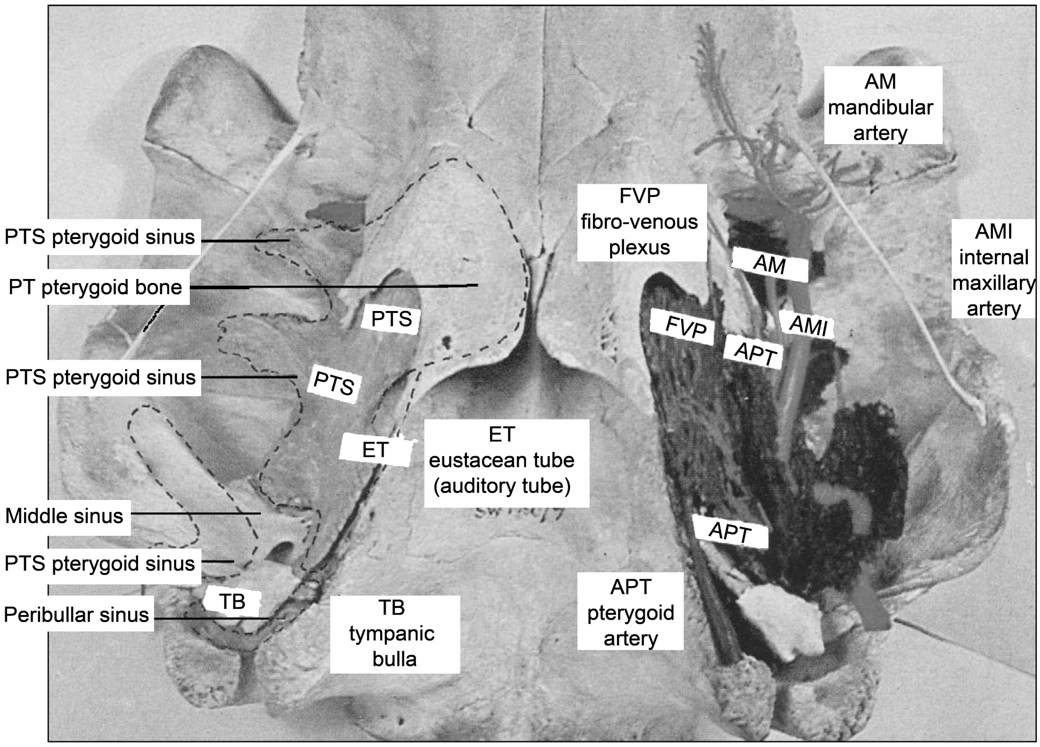


Fig. 9. Skull of a young pilot whale in which the peribullar and pterygoid air sinus system (left) and its vascular system have been injected (on the right) with polyester resin (Fraser and Purves, 1960). The peribullar and pterygoid sinuses extend from the hollow cavity of the pterygoid bone caudally to the region surrounding the tympanic bulla. The FVP is a mostly-venous plexus that surrounds these air sinuses. Both the air sinuses and the FVP are surrounded by a mass of acoustic lipids that extend from the hollow channel of the mandible to the pterygoid and tympano-periotic bones medially. Beaked whale pterygoid sinuses and associated fat structures are massive (Cranford *et al.*, 2003; Koopman *et al.*, 2003b) and their FVPs are presumed to be correspondingly larger than those of the delphinids.

maximise heat exchange with the environment (Fig. 11b; Bryden and Molyneux, 1978; Elsner *et al.*, 1974). Blood returning in these veins is relatively cool (Hales, 1985). In most mammals, the warmed and cooled venous returns are usually mixed at the proximal end of the extremity. In some cases, such as the brain coolers of ungulates and carnivores, evaporatively cooled blood from the nose is used to reduce the temperature of blood going to the brain (Fig. 11c) before joining with the central venous return, thereby allowing the brain to operate at a temperature lower than that of the body core (reviewed in Baker, 1979; Schmidt-Nielsen, 1990; Taylor and Lyman, 1972).

In mammals, CCHEs have many configurations in addition to the venous lake surrounding the arterial rete at the base of the brain (Caputa *et al.*, 1967; Caputa *et al.*, 1983; Taylor and Lyman, 1972; illustrated for the antelope in Fig. 11c). Increasing the surface area of contact between the arteries and veins in different ways optimises these CCHEs. Three examples of CCHEs found in cetaceans are illustrated in Fig. 11d. On the left is a flat array of juxtaposed arteries and veins found in the reproductive coolers of cetaceans (Rommel *et al.*, 1992; Pabst *et al.*, 1998), in the middle is a vascular bundle, an array of relatively straight, parallel channels, an optimum configuration for CCHE (Scholander, 1940), such as is found in the chevron canals of cetacea (Fig. 13c; Rommel and Lowenstein, 2001). On the right (Fig. 11d) is a periarterial venous rete (PAVR), which is a rosette of veins surrounding an artery. These CCHEs are found in the circulation of cetacean fins (Figs 13d and 13e), flukes and flippers (Scholander, 1940; Scholander and Schevill, 1955).

Superficial veins of a cetacean can supply cooled blood to the body core (Fig. 12a). The veins carrying this blood feed into bilaterally paired reproductive coolers (Figs 12d-g) (Rommel *et al.*, 1992; Pabst *et al.*, 1998). In addition to providing thermoregulation for the reproductive system, cooled blood from the periphery is also returned to the heart via large epidural veins (Figs 12d; Figs 13 and 14), which perform some of the functions of the azygous system in other mammals (Rommel *et al.*, 1993; Tomlinson, 1964). In deep divers, such as beaked whales and sperm whales, these epidural veins are even larger than those observed in delphinids (S. Rommel, pers. obs.). In *Tursiops*, the epidural venous blood may return to the heart via five very enlarged, right intercostal veins to join the cranial vena cava (Figs 13a; 14b and 14c). Alternatively, during a dive, epidural blood may continue to flow in a caudal direction beyond the intercostal veins so that blood from the brain pools as far away from the brain as possible, as has been hypothesised for seals (Rommel *et al.*, 1993; Ronald *et al.*, 1977).

Cooled blood supplied by superficial veins to the epidural veins could potentially exchange heat with the epidural (arterial) retia and/or return cooled blood to the cranial thorax. Additionally, it may cause a change in the local temperature of the spinal cord and juxtaposed veins (Rommel *et al.*, 1993). This hypothesis is supported by the regional heterothermy observed in colonic temperature profiles for seals, dolphins and manatees (Rommel *et al.*, 1992; 1994; 1995; 1998; 2003; Pabst *et al.*, 1995; 1996; 1998). Additionally, superficial veins cranial to the dorsal fin (Fig. 12a) may provide cooled blood that can be juxtaposed to the arterial retia in the head and neck. This morphology has not been described in sufficient detail in

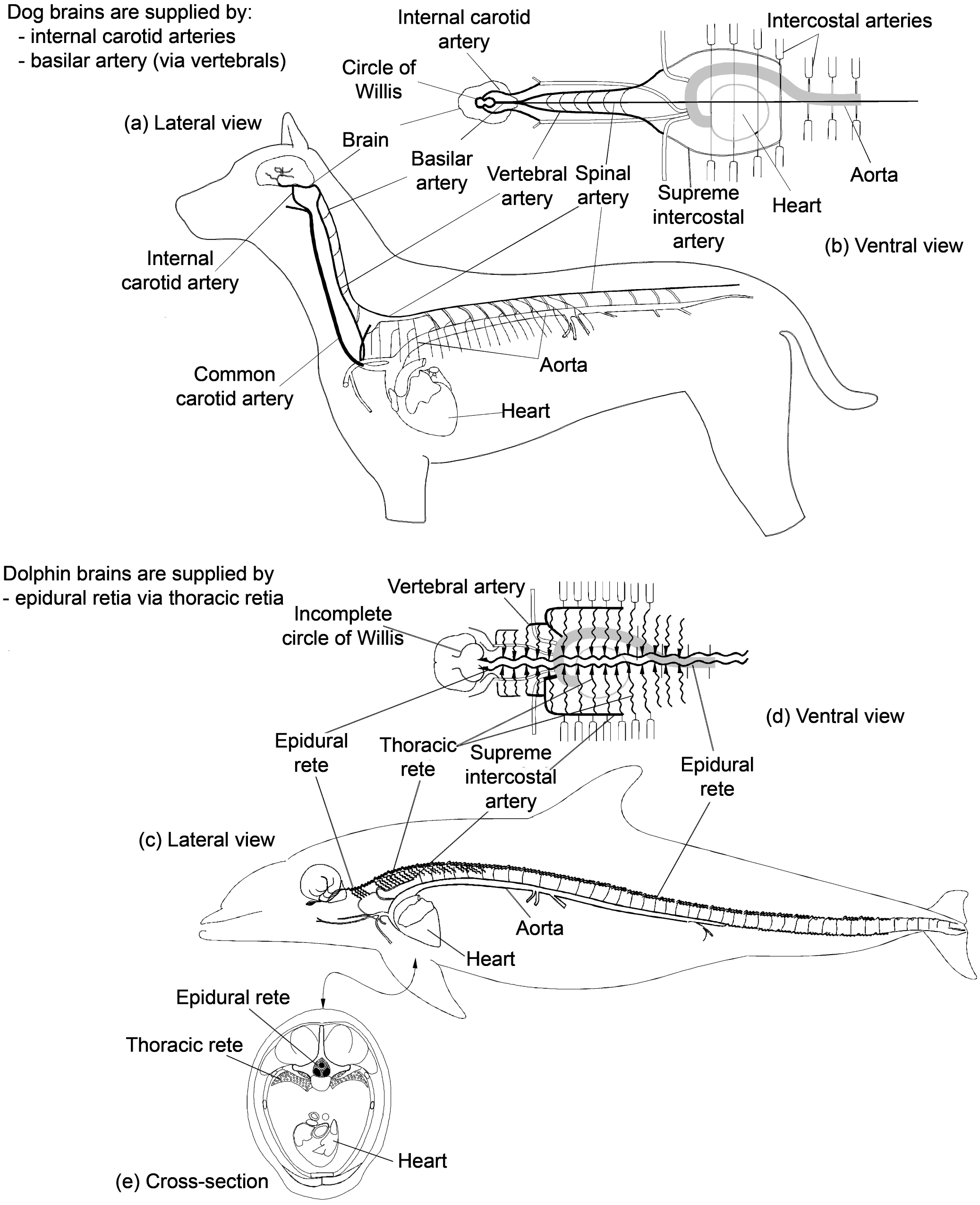
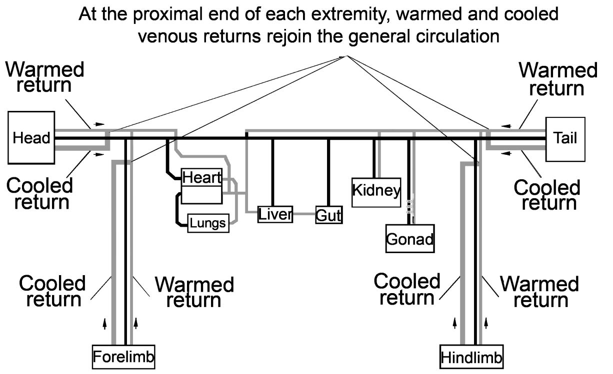


Fig. 10. Schematic of arterial circulation in the domestic dog (a-b) compared with that of the bottlenose dolphin (c-e). The arterial circulation in *Tursiops* is assumed to be representative of brain circulation of most cetacea. The cross section, e, which is at the level of the heart, illustrates the positions of the epidural retia around the cord and the thoracic retia dorsal to the lungs. Illustration adapted from Rommel (2003).

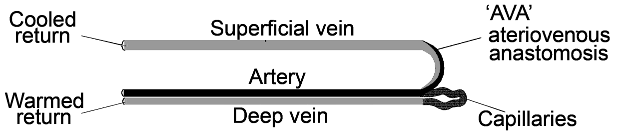
any cetacean and should be considered to be an important area of future research due to the significant implications of spinal cord heterothermy.

The morphology of the vascular system allows us to speculate on some functions that might be important in interpreting strandings of deep divers. It is clearly possible that cooled blood deep within the body may change some of the physical parameters, (e.g. viscosity, solubility and pH) of tissues and fluids. Cooled blood could possibly change physiological parameters e.g. nervous response time, balance (because of temperature changes in fluid density within the semi-circular canals) and acoustic and resonant properties of tissues. The epidural and thoracic retia may also provide some control of central nervous system (CNS) temperature. This hypothesis was rejected by previous workers (e.g. Harrison and Tomlinson, 1956; McFarland *et al.*, 1979) but those investigations lacked the current knowledge of superficial venous return (Pabst *et al.*, 1998; Figs 12a and 12b; Rommel *et al.*, 1992). It is well known that epidural cooling protects against ischaemic spinal cord damage in humans and terrestrial mammals (Marsala *et al.*, 1993) and we now know that it is possible for cooled blood to flow in the epidural veins. Since ischaemia is an important part of deep and prolonged dives, it is reasonable to assume that cooling of the CNS may occur in diving mammals in order to limit the consequences of reduced perfusion (Rommel *et al.*, 1995).

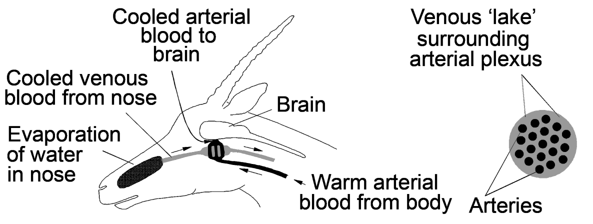
In mammals, the temperature of the CNS is also important in regulating tissue activity (Blumberg and Moltz, 1988; Caputa *et al.*, 1983; 1991; Chesy *et al.*, 1983; 1985; Miller and South, 1979; Wunnenberg, 1973) and contributes to prolonging dives in marine mammals by reducing metabolic demands (Cossins and Bowler, 1987; Elsner, 1999; Hochachka and Guppy, 1986; Ponganis *et al.*, 2003).



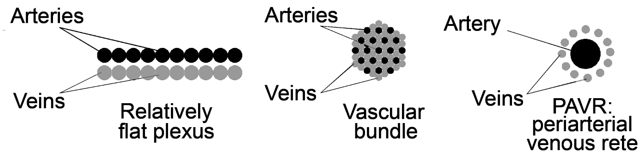
(a) Two venous returns:
one deep and warmed, one superficial and cooled



(b) CCHE: countercurrent heat exchange



(c) Brain cooling mechanism in antelope (Taylor and Lyman,1972)



(d) Cetacean countercurrent heat exchanges

Fig. 11. a. Simplified schematic of the mammalian circulatory system, showing alternate warmed and cooled venous returns, which typically mix with each other and the central venous return at the proximal end of each extremity. b. Warmed venous return is achieved by CCHEs. Cooled venous return is achieved when veins are allowed to lose heat to the environment. AVAs allow blood to bypass capillary beds to increase the rate of blood flow in the superficial veins and increase heat loss. c. In some mammals, such as the antelope illustrated here, cooled venous blood from the nose reduces the temperature of arterial blood to the brain via a venous lake, which surrounds the arterial supply of the brain. d. Cetaceans have elaborate CCHEs, three of which are illustrated here.

The superficial venous returns from the skin and evaporatively cooled blood at or near respiratory structures provide cooled blood that could modify deep body temperatures and extend dive capabilities (Rommel *et al.*, 1995); deeper divers (such as beaked whales) could conceivably have excellent control of this thermoregulation mechanism. As previously mentioned, the concept of evaporative coolers is not unique to dolphins; they have also been described in seals (Costa, 1984; Folkow *et al.*, 1988) and are responsible for brain cooling in terrestrial mammals (Baker, 1979; Baker and Chapman, 1977; Blumberg and Moltz, 1988). The structure involved in the CNS coolers of terrestrial mammals (rostral plexus, pterygoid plexus, opthalmic plexus) may be homologous to some of the plexuses supplying the heads of cetaceans (Geisler and Lou, 1998).

Both the internal and external jugular veins of *Tursiops* drain the caudal margin of the FVP and there are several robust anastomoses between the internal and external jugular veins (Fig. 14a) at the base of the skull. In this region, the facial, lingual and maxillary branches join the external jugular vein and the mandibular, pterygoid and petrosal branches join the internal jugular vein. These anastomoses are located near the caudal margin of the FVP, close to where the hyoid apparatus joins the skull on the ventrolateral aspects of the basioccipital bones (tympanohyal of Ridgway *et al.*, 1974). We have been unable to find a complete description of these vascular structures for the cetacean head.

The brain is surrounded by three connective tissue layers: the dura mater (which is adherent to the bones of the braincase), the arachnoid and the pia maters (which enclose the cerebrospinal fluid [CSF] and brain, respectively). The veins of the odontocete braincase (Fig. 14c), like those of terrestrial mammals, are divided into two groups: the meningeal veins on the surface of the brain, which are deep to the dura matter and the dural sinuses, which are veins found between the dura and the braincase and which may create grooves in the skull bones.

The venous system draining the braincase and skull base is extremely complex (Fraser and Purves, 1960). The bilaterally paired FVPs consist of small-caliber, thin-walled veins extending onto the bones of the orbit, the peribullar sinus and the pterygoid sinus (Fig. 14b). Each FVP appears to also extend into the mandibular acoustic fat body, which is juxtaposed to the pterygoid and peribullar sinuses and is continuous with the acoustic fat of the mandible (Fig. 9; Boenninghaus, 1904; Fraser and Purves, 1960). The structure of this special plexus should be the focus of further work.

According to Fraser and Purves (1960), there are anastomoses (e.g. emissary veins) between the veins of the braincase and those from the FVP. The only emissary vein observed thus far (in *Tursiops*) is between the basilar dural sinus on the floor of the braincase and the internal jugular (Figs 13a and 14c). In *Tursiops*, this emissary vein exits the skull via the cranial hiatus and joins the jugulars near the jugular notch between the basioccipital crest and the paroccipital process. The geometry of these veins is likely to be very important because this is the region of the haemorrhage described for a Bahamas beaked whale head (labelled 'internal auditory canal/cochlear aquaduct' in Anon., 2001). Interestingly, there is a robust plexus of branches from each internal jugular vein that surrounds each proximal carotid artery, giving the proximal internal jugular the appearance of a very large vein or venous plexus – part of this plexus is illustrated as a vasa vasorum of the external carotid in Ridgway *et al.* (1974), but our injections of *Tursiops* showed it to be much more robust than illustrated by them.

In the dog and other domestic mammals, the external jugular vein is significantly larger than the internal jugular vein (Ghoshal *et al.*, 1981; Nickel *et al.*, 1981). In contrast, the internal jugular vein may be equal to or larger than the external jugular in cetaceans (S. Rommel, pers. obs.; Fraser and Purves, 1960; Ridgway *et al.*, 1974; Slijper, 1936). The relatively large size of the delphinid internal jugular vein

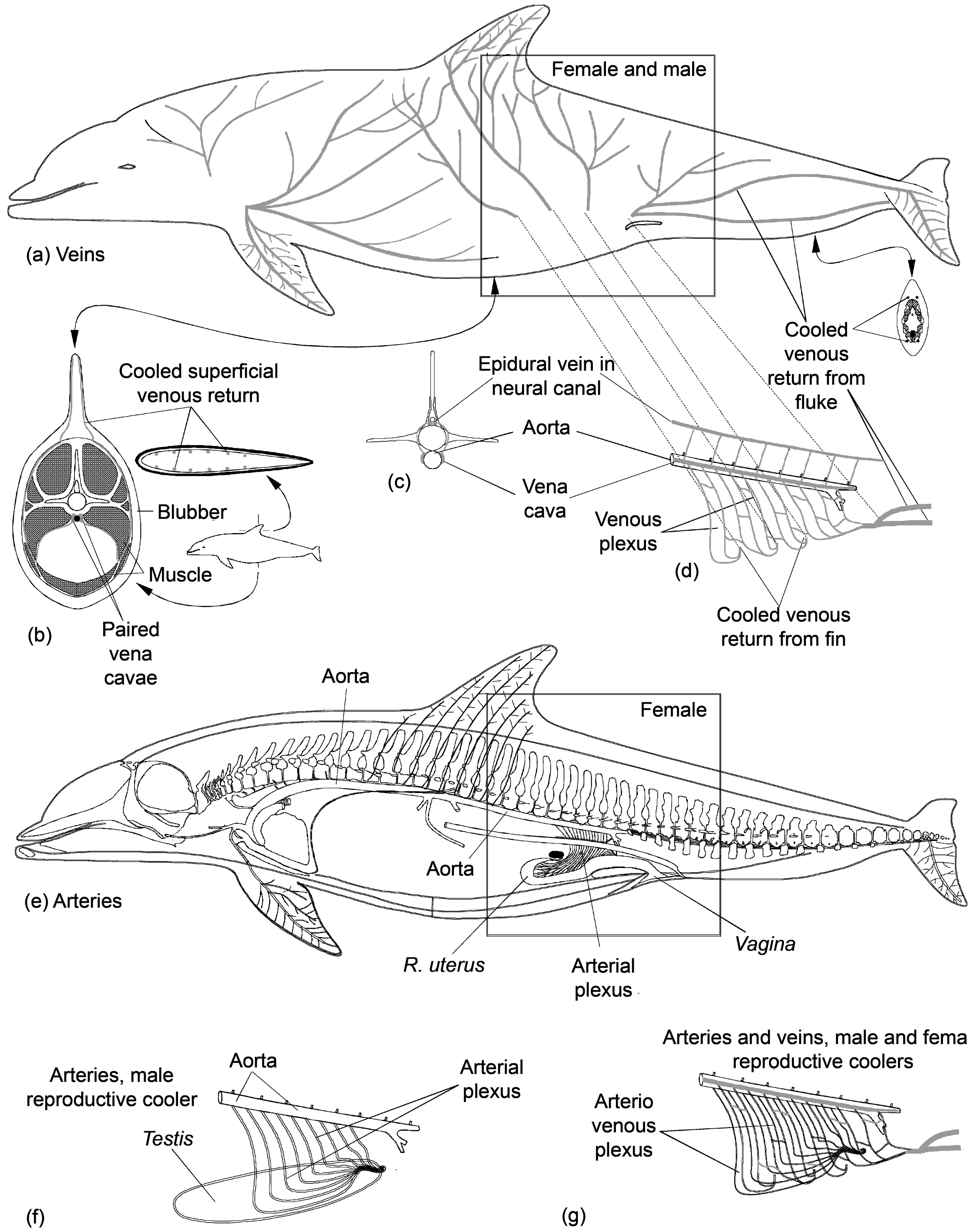


Fig. 12. Superficial veins (a-b) supply large amounts of cooled venous blood to different parts of the *Tursiops* body. In the caudal half of the body, cooled blood is supplied to a CCHE (e-f) deep within the abdomen. Note the arteriovenous reproductive plexus in which arteries are juxtaposed to cooled, superficial venous return from the dorsal fin and flukes. Heat can be transferred from the warm arteries to the cooled veins so that arterial blood does not damage the temperature sensitive reproductive tissues. In the cranial half of the body there are also superficial veins returning cooled blood; the potential for deep body cooling in this region has yet to be investigated. (Rommel *et al.*, 1992; Pabst *et al.*, 1998).

may be due to the large drainage field of the FVP(s) and the vasa vasorum of the carotid artery, as well as input of the emissary vein draining the caudal ventrolateral basilar dural sinuses within the braincase.

Other vascular structures

Typically, most cetaceans have small spleens (Rommel and Lowenstein, 2001), in contrast to the deep-diving pinnipeds, which have relatively large spleens that provide storage of red blood cells to increase haematocrit during dives (Elsner, 1999; Zapol *et al.*, 1979). Increasing hematocrit alters blood properties such as viscosity (Elsner *et al.*, 2004). Interestingly, beaked whales have much larger spleens than delphinids (Nishiwaki *et al.*, 1972) and beaked whale livers may be relatively larger as well. Both organs filter blood and may therefore be important in the management of emboli. The large venous sinuses and muscular portal sphincters in cetacean livers (reviewed in Simpson and Gardener, 1972) may increase the hepatic entrapment of otherwise fatal portal gas emboli, which have been described in the Canary Islands (Fernández *et al.*, 2004; 2005) and UK (Jepson *et al.*, 2003) cetacean strandings. The kidney, another organ that filters blood, has been reported to have DCS-like (gas bubble) lesions in the same Canary Islands and UK strandings. Capillary fenestrae may allow fat and gas emboli to pass through them. Unfortunately, the specifics of the vascular anatomy describing these functions are inadequate.

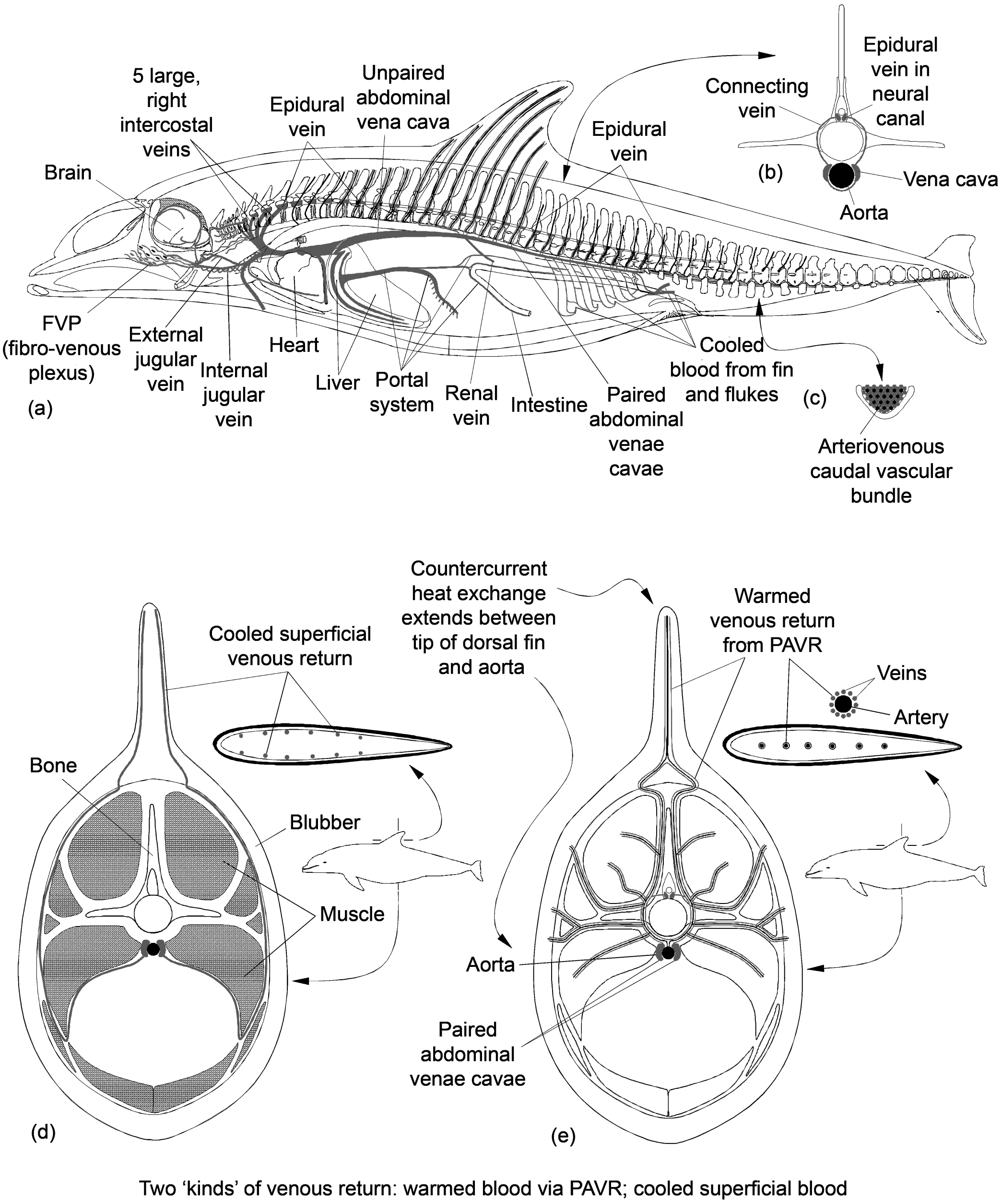


Fig. 13. Deep (a-c, e) and superficial (d) venous return in *Tursiops*. To expend heat, blood is routed through superficial veins in the dorsal fin (d); the blood in the superficial veins is cooled prior to entering general circulation. In contrast, to conserve heat, deep veins surrounding the arteries of the dorsal fin (e) are recruited in order to return the blood to the vena cava. The portal vein, which may be a source of gas emboli, drains the intestines and delivers blood to the liver (a). The abdominal vena cava brings venous blood from the abdominal region to the heart at the dorsocranial aspect of the liver. There is little evidence for an azygous vein in cetaceans. Due to abdominal pressures that may invoke the Valsalva phenomenon, an alternate venous return may be necessary to prevent elevated abdominal pressures from collapsing the large veins and preventing blood from returning to the heart. This return is achieved via the epidural veins (a-b), the relatively large bilaterally paired veins adjacent to the spinal cord within the neural canal. This part of the venous system may be supplied by the same cooled venous blood that regulates temperature of the reproductive system. Thus cooled blood may be located in several regions of the body and may affect physical properties (e.g. viscosity, solubility, pH) in the tissues it comes in contact with.

Finally, a number of cetacean cardiovascular adaptations, such as the large venous sinuses (Harrison and Tomlinson, 1956; Tomlinson, 1964) and convoluted pathways for blood flow (e.g. Nakajima, 1967; Slijper, 1936; Vogl and Fisher, 1981; Walmsley, 1938), may have relevance to the mitigation of gas emboli and DCS. For example, the double capillary network in the lung alveoli (reviewed in Simpson and Gardener, 1972) may help prevent transpulmonary passage (arterialisation) of venous gas emboli. The extensive meshwork of small arteries (the retia mirabilia) that perfuse the entire CNS (Viamonte *et al.*, 1968) might efficiently filter any arterialised gas emboli (Ridgway and Howard, 1979). It is notable that the retia are most developed in the deeper divers (Vogl and Fisher, 1981). Autochthonous or venous-gas bubbles and epidural venous thrombosis have been proposed as mechanisms of spinal DCS lesions in humans (Hallenbeck *et al.*, 1975; reviewed in Francis and Mitchell, 2003). The large epidural venous spaces (Harrison and Tomlinson, 1956) and the lack of Hageman and other clotting factors and more potent heparin in cetacean blood (reviewed in Ridgway, 1972) may therefore also reduce the risk of cetacean spinal cord bubble injury.

Dive physiology

The numerous diving challenges (e.g. DCS, shallow-water blackout, nitrogen narcosis) are probably overcome by a number of anatomical, physiological and behavioural

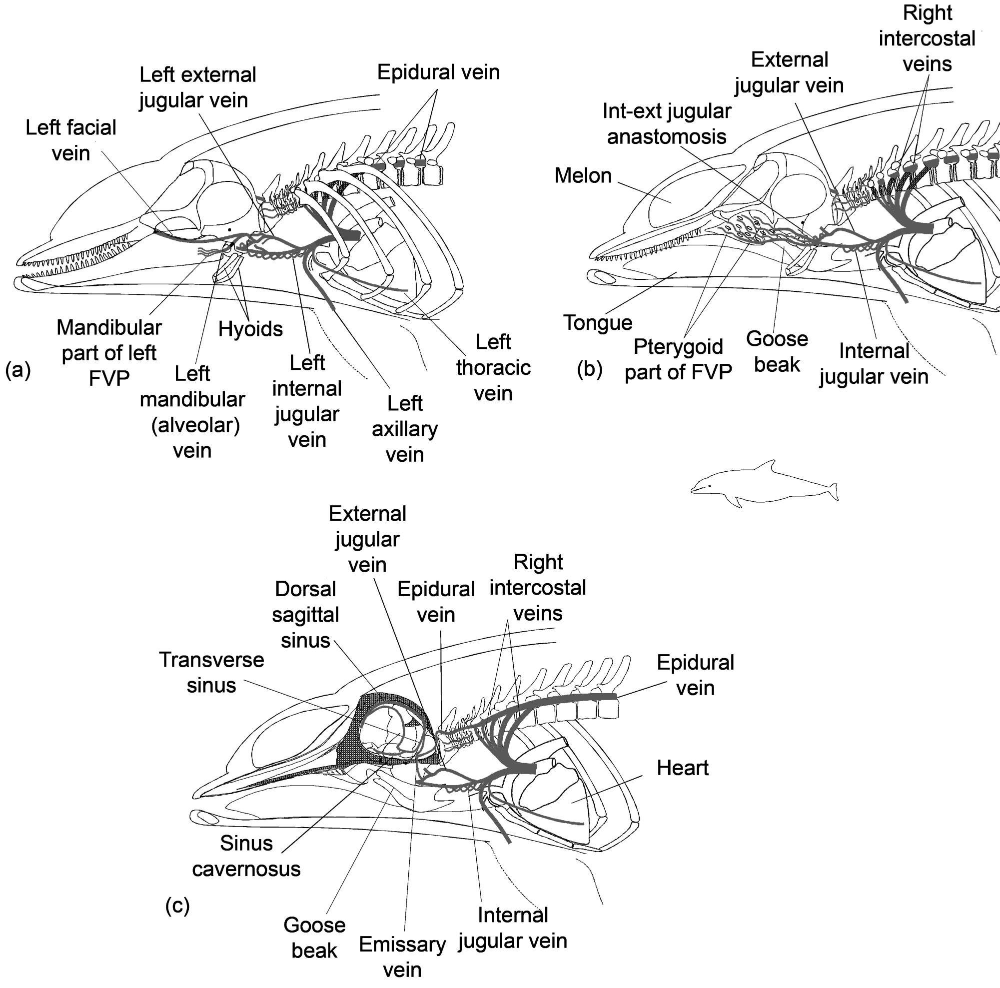


Fig. 14. Illustrations of the venous return from the head of *Tursiops.* Skull with mandible, zygomatic arch and hyoid apparatus illustrating the more superficial veins of the head (a). The internal and external jugular veins anastomose via a robust plexus near the caudal margin of the mandible. These veins drain the FVP. There is a small mandibular part of the FVP that lies near the medial aspect of the mandible. (b) Skull with hyoid apparatus and goosebeak present and the mandible and zygomatic arch removed. The largest part of the FVP is illustrated here and corresponds to that in Fig. 9. Mid-sagittal section of a skull (c), illustrating the dural sinuses and veins exiting the braincase. The emissary vein carries blood from the ventral braincase to the jugular veins.

adaptations, such as the dive response, lung collapse, controlled ascent from deep dives and surface interval (e.g. Baird *et al.*, 2004; Elsner, 1999; Ponganis *et al.*, 2003). The dive response includes a slowing heart rate (reduction in cardiac output) and a change in the distribution of peripheral resistance (change in blood flow). While diving, this response helps ensure that oxygen-sensitive tissues (e.g. the CNS and heart) maintain a supply of oxygen, while those with lower metabolic rates or that are tolerant to hypoxia receive less blood flow. Lung collapse obviates the exchange of lung gas with blood and most likely serves to minimise the uptake of nitrogen by tissues. Most studies of diving adaptation have been performed on pinnipeds (e.g. Davis *et al.*, 1983; 1991; Elsner, 1999; Kooyman *et al.*, 1981; Ponganis *et al.*, 2003), with relatively few being conducted on cetaceans (e.g. Scholander, 1940; Ridgway and Howard, 1979). Although it is generally accepted that these physiological responses to diving are shared across both cetacean and pinniped taxa, none of these phenomena or their physiological impacts have been quantified in beaked whales.

Research on freely diving seals suggests that the redistribution of blood flow during diving is a graded response, with restriction of blood flow to certain organs occurring only as oxygen stores become depleted (e.g. Davis *et al.*, 1991; Ponganis *et al.*, 2003; Ronald *et al.*, 1977; Zapol *et al.*, 1979). Nonetheless, in forced dives, peripheral vasoconstriction redistributes blood so that the brain maintains constant vascular flow at the expense of other tissues, which is similar to results observed during unrestrained deep dives (Kooyman, 1985; Ponganis *et al.*, 2003). Few similar lines of forced-dive research have been conducted on cetaceans (Scholander, 1940).

During a dive, if the pressure exerted on a gas is doubled, its volume is halved. Water exerts approximately one atmosphere of pressure for every 10m of depth, so a marine mammal at 10m experiences twice the hydrostatic pressure it would at the surface and the air within its lungs will occupy one half of its volume. Hydrostatic pressures experienced by diving marine mammals, in conjunction with anatomical structures supporting the respiratory system, influence the depth at which lung collapse occurs (Hui, 1975). Without differentiating between lung and alveolar collapse, dive experiments suggest that nitrogen exchange ceases at depths of approximately 70m in bottlenose dolphins (Ridgway and Howard, 1979) and 30-50m in seals (Falke *et al.*, 1985; Kooyman, 1985; Zapol *et al.*, 1979). A contributory factor to the different depths may be that seals exhale before diving (Kooyman *et al.*, 1970; Scholander, 1940), whereas dolphins dive on a lung full of air (Ridgway *et al.*, 1969).

The effects of increased hydrostatic pressure are not limited to volume and geometry of the thoracic cavity and its contents. Increased hydrostatic pressure also acts on lung air (before complete collapse), by increasing the amount of nitrogen that dissolves into the blood across the alveolar membrane. Additionally, raising the pressure also increases the absolute amount of gas that can be dissolved into other tissues and fluids. As nitrogen is biologically inert and lipophilic, it readily accumulates in lipid-rich tissue (e.g. lipids, bone marrow). If tissues become nitrogen supersaturated during rapid ascent, nitrogen can rapidly come out of solution, potentially forming bubbles in lipid-rich tissues and regions supportive of cavitation (e.g. localised negative pressure sites associated with the motion of joints). If large enough and in sufficient quantities, bubbles may result in vascular emboli, cause haemorrhage in capillary dense tissues and create localised regions that apply pressure to nervous tissue. If severe enough, the presence of the bubbles in humans may cause symptoms of DCS, including pain, disorientation, nausea and neurological impairment. Accumulation of gas emboli in joints and the associated pain is termed ‘the bends’. Additionally, bubbles may damage lipid tissues (where dissolved nitrogen gas concentrations may be relatively high) and release fat emboli into circulation (Ponganis *et al*., 2003).

In cetaceans, the extensive arrangement of extracranial arterial retia is an adaptation to diving and is more extensive in deeper divers (Vogl and Fisher, 1982); however, a lack of these structures does not preclude deep diving or extended breath-holds, because they are not found in seals or sea lions (Pabst *et al.*, 1999; Rommel and Lowenstein, 2001). Unlike seals and sea lions, cetaceans have short necks, which reduces the distance between the heart and the brain. This presumably increases the potential for mechanical injury from the systolic pulse of the heart. The brain supply of cetaceans may act as a *windkessel*, dampening pressure fluctuations resulting from the pulsatile flows produced by the heart (Galliano *et al.*, 1966; Nagel *et al.*, 1968; Shadwick and Gosline, 1994). Additionally, this vascular structure may have a function in the management of emboli. Interestingly, the short-necked sirenians also have retia similar to those of cetaceans as part of their brain blood supplies (Murie, 1872; Rommel *et al.*, 2003).

HYPOTHESISED FACTORS INVOLVED IN SONAR-RELATED STRANDING EVENTS

Gas and fat emboli

Emboli are clots, globular obstructions or gas bubbles that occlude blood vessels or damage tissues by expansion. Gas emboli are typically formed by uncontrolled dysbaric changes. When hydrostatic pressure is decreased rapidly (such as during rapid ascent from a dive), high partial pressures of gases in a saturated medium (such as blood and interstitial fluid) force gases out of solution. If the ascent rate is fast enough, gases leaving a saturated tissue form bubbles, which continue to grow with decreasing hydrostatic pressure (Boyle’s Law). The growing bubbles are either trapped in tissues and cause physical damage by way of their expansion, or they can be transported by the circulatory system to sensitive tissues and cause a blockage. Obstruction of blood flow to the heart or CNS is the most severe manifestation of gas embolism, although numerous other forms of gas emboli of varying severity exist (Francis and Mitchell, 2003).

Fat emboli were originally seen in human patients with long-bone and pelvic fractures but are now associated with a range of conditions including dysbaric osteonecrosis (DiMaio and DiMaio, 2001; Jones and Neuman, 2003; Kitano and Hayashi, 1981; Saukko and Knight, 2004). Fat emboli are believed to be formed when fatty tissue is injured, resulting in release of fat droplets into circulation. Fat emboli have been the proximal cause of death in human bone-fracture cases. The beaked whales that mass stranded in the Canary Islands in 2002 had widely disseminated fat emboli in numerous tissues. Although not diagnostic of DCS, these findings are consistent with a DCS-like or acoustically mediated mechanism of gas-bubble formation (Fernández *et al.*, 2005; Jepson *et al.*, 2003).

Acoustically mediated bubble growth

Even though marine mammals are believed to be protected from the formation of gas emboli through behavioural or physiological means, Crum and Mao (1996) produced a model suggesting that a sufficient level of acoustic exposure might cause bubbles to form and grow. One form of this is called rectified diffusion (Crum, 1980). During the compression phase of each sound wave, each bubble is reduced in size, pressure within the bubble is increased and gas diffuses out of the bubble. In the rarefaction phase of the sound wave, bubble diameter increases, pressure is reduced and gas diffuses into the bubble. Since the amount of gas moving into and out of the bubble is related to its surface area and there is a greater surface area during the rarefaction phase, the result is a net gain of gas within a bubble during each cycle of the applied sound.

Within a gas-supersaturated medium, the threshold for rectified diffusion was predicted to be lower and gas bubbles were predicted to grow, once activated, without the continued presence of an acoustic field (Crum and Mao, 1996). Houser *et al.* (2001) modelled the accumulation of gaseous nitrogen within the muscles of various cetacean species based upon known dive profiles. The results suggested that species that descend slowly and deeply, beyond the depth of lung collapse, were those likely to accumulate the most nitrogen in their muscles. This process is augmented if surface intervals of sufficient length to allow nitrogen washout are not performed regularly. Beaked whales and sperm whales were predicted to accumulate the most nitrogen, as high as 300% supersaturation, after a typical dive sequence. Thus, if such a mechanism were possible, the likelihood of gas emboli growing, when ensonified by midrange military sonar, was predicted to be greater for these types of divers (Crum *et al.*, 2005; Houser *et al.*, 2001).

Dysbaric Osteotrauma (DOT)

Osteonecrosis refers to bone and bone marrow death brought on by ischaemia. In dysbaric osteonecrosis, disruption or cessation of oxygen and/or blood supply to the bone and bone marrow brought on by harmful pressure changes, are believed to be the primary pathogenic mechanism (Hutter, 2000; Jones *et al.*, 1993). Hyperbaric exposure causing tissues to become saturated with gasses, makes individuals prone to hypobaric outgassing and outgassing due to supersaturation is believed to result in gas emboli. These emboli may expand and thus damage bone marrow, thereby releasing fatty thromboses and indirectly causing ischaemic necrosis. Alternatively, the gas emboli may directly obstruct vascular pathways. Dysbaric osteonecrosis typically produces chronic lesions in bones and therefore does not fit with the very short time period between sonar exposures to beaked whale mass strandings. Nonetheless, chronic lesions found in the bones of sperm whales imply that even under normal circumstances, deep diving whales are vulnerable to DOT (Moore and Early, 2004). This potential vulnerability of deep diving whales, in concert with other pathogenic circumstances such as abbreviated ascent rates and prolonged surface intervals, could conceivably be the cause of severe and acute manifestations of DOT.

Such bone trauma may release fat emboli from the damaged marrow into the circulation, thereby resulting in acutely and widely disseminated thromboses and rapid death. The fat emboli suggested by Jepson and Fernández (Fernández *et al.*, 2004; 2005; Jepson *et al.*, 2003) may therefore have a far more important role than has previously been assumed. The 'standard' histological techniques applied to the Bahamian beaked whales were presumably inadequate to assess the presence of fat and gas emboli.

Behavioural alterations

Under the hypothesis of behavioural alteration, acoustic exposure is not the primary pathogenic mechanism; rather, it causes a behavioural response that induces beaked whales to forgo natural diving protocols in response to the sound field. Prior to lung collapse, an increased hydrostatic pressure of air within the lung causes more nitrogen to dissolve into the blood across the alveolar membranes of the lungs. An animal that has a substantial amount of nitrogen gas absorbed in its tissues and which may be frightened by sonar could be forced to alter its dive profile and ascend faster than normal. This may result in the supersaturated tissues exceeding the threshold for bubble formation in these animals (Crum *et al.*, 2005). We have learned from human divers that even slight modifications to ascent rate can be damaging or fatal. Under such a condition, rapid ascent or extended surface interval may exceed acceptable rates and/or quantities of nitrogen offloading to the extent that nitrogen bubbles evolve, forming gas emboli (Jepson *et al.*, 2003; Fernández *et al.*, 2004; 2005). Extended surface intervals are likely, perhaps even more likely, to be a critical factor influencing nitrogen tissue supersaturation and bubble pathogenesis, given that beaked whales appear to spend most of their time at depth and only limited surface intervals have been recorded (Hooker and Baird, 1999). Although these mechanisms of pathogenesis are plausible in light of recent pathobiological discoveries, conclusive evidence is elusive. Future research should therefore be open to other potential mechanisms of pathogenesis.

Resonance

Air-containing spaces in diving mammals create media interfaces with tissues and act as boundaries at which acoustic energy may be reflected and/or absorbed. These air spaces may resonate if ensonified at the appropriate frequency and amplitude. At a meeting organised by NOAA Fisheries in 2002, scientists were invited to evaluate the potential for resonance to cause damage in diving marine mammals (Anon., 2002). Resonance was modelled using a free, spherical bubble model, which should predict the maximum vibratory response during ensonification at the sphere's resonant frequency. Results from this simplified model (Anon., 2002) suggested that displacement due to vibration at resonance, even without the damping provided by adjacent biological tissues, may be insufficient to cause significant damage at gas-tissue boundaries. Furthermore, resonant frequencies predicted for various air spaces were below those used by the midfrequency sonar systems implicated in a previous stranding event.

Although useful, the spherical lung model may be an oversimplification. Complex structures such as lungs likely have more modes of resonance than simple structures and although the displacement of tissues at those modes should be less than at the fundamental frequency of resonance, it may still be harmful. A compressible, air-filled (there are also blood, mucus and connective tissues) lung-pair with an incompressible heart at its midline is a complex shape (Fig. 11). Such a structure will have complex modes of vibration that change as the volume and shape of the lung-pair changes with depth (damaged or diseased lungs will resonate differently). However, it is unknown how the dimensions of the lungs change with depth, how many modes of vibration there are and how the modes change with depth, blood viscosity and temperature.

Further examination of other resonance models may lead to a more accurate representation of the complex geometry of mammalian lungs and the physical properties that govern their resonant characteristics. A good understanding of the effects of size, shape, function and composition on resonance would improve our understanding of the etiology of acoustically induced lesions. Furthermore, additional measurements of vibrations on living marine mammals may provide insight into how resonance changes with depth in animals that have collapsible lung cavities.

Disseminated Intravascular Coagulation (DIC) – coagulopathy, bleeding diathesis

Another hypothesis proposed for the causes of beaked whale strandings is that of diathetic fragility, or the tendency to bleed. It has been proposed that this may occur in concert with resonance in such a way that bleeding becomes associated with the tissues of resonating structures or air spaces. It may also result from a stress response initiated by acoustic exposure. Identifying whether blood components known to be related to diathesis are found in beaked whales has been suggested as a means to investigate this possibility. Coagulopathies are caused by any process that substantially activates the clotting cascade for prolonged periods. Activation of the clotting cascade within the blood vessels causes the ordinarily liquid blood to clot. Sustained activation of the clotting cascade leads to depletion of clotting factors and a subsequent inability of the remaining blood to coagulate in response to tissue injury. Cetaceans are missing one of the usual clotting factors (Hagman and Fletcher factors; Bossart *et al.*, 2001) and may therefore be prone to some forms of coagulopathy even without extensive depletion of clotting factors (see also Gulland *et al.* (1996), for this disorder, termed DIC, in seals).

DIC is variable in its clinical effects and can result in either systemic clotting symptoms or, more often, uncontrolled bleeding. Bleeding can be severe. DIC may be stimulated by many factors, including blood infection by bacteria or fungi, severe tissue injury from burns or head injury, cancer, reactions to blood transfusions, shock and dystocia. Although DIC is a hypothetical mechanism that has been proposed as a factor in cetacean strandings, there are few data to support it.

REVIEW OF NECROPSY FINDINGS

In the Bahamian beaked whale strandings, massive ear injuries were seen (bilateral intracochlear and unilateral subarachnoid haemorrhages) and blood clots on the ventrolateral aspects of the braincase along the path of the acoustic nerve (in most mammals, the internal auditory meatus) and extending into the ear. The *Ziphius* braincase is robust (Fig. 5) with a long, narrow channel, which is in contrast to the short, wide cranial hiatus of *Tursiops*. The mechanical properties (e.g. compliance) of these two skull types and their surrounding tissues is probably dramatically different and may help account for the appearance of the lesions described in the Bahamian stranded beaked whales (Anon., 2001). In these carcasses, postcranial lesions (other than contraction band necrosis of the heart) were not found, possibly due in part to the degree of tissue autolysis.

In contrast, tissues from the Canary Islands beaked whales were much better preserved, enabling a more detailed pathological investigation. The Canary Islands beaked whales had acute systemic haemorrhages within the lungs, CNS and kidneys; systemic fat emboli; and the gross and/or histological appearance of gas emboli in vessels from a range of tissues including the brain, choroid plexus, visceral/parietal serosa and kidney. These acute, systemic and widely disseminated lesions were considered consistent with, although not diagnostic of, DCS (Jepson *et al.*, 2003; Fernández *et al.*, 2004; 2005).

In the UK, a small number of cetaceans with acute and chronic gas-bubble lesions have been found (Jepson *et al.*, 2003; 2005; Fernández *et al.*, 2004). The lesions, exclusive to these UK-stranded cases, included large (0.2-6cm diameter), hepatic, gas-filled cavities associated with extensive pericavitary hepatic fibrosis and involved several dolphins, a porpoise and only one beaked whale. These chronic hepatic lesions were found alongside extensive portal and sinusoidal gas emboli, many of which were associated with acute tissue responses, including marked tissue compression and vessel distension, focal haemorrhages, acute hepatocellular necrosis and fibrin thrombi. To date, two UK-stranded common dolphins (*Delphinus delphis*) also had clearly demarcated bilateral acute coagulative renal necrosis (consistent with infarcts) associated with gross and microscopic gas bubbles and (arterial) gas emboli. Additional cavities formed by gas bubbles were also seen in lymphoid tissue and other parenchymatous organs. Of all the UK-stranding cases, the brains from three carcasses were examined, spinal cord sections in only two cases (most were either grossly and microscopically normal or showing signs of autolysis) and the skeletal material was examined in none. It was therefore not possible to confirm or refute the presence of lesions consistent with DCS-like symptoms or other causes of gas embolism in either CNS or bone for most UK-stranded cases (Jepson *et al.*, 2003; 2005). Although the lesions found in the UK-stranded animals cover a wide range of acute and chronic pathologies related to diving and pressure changes, they may be useful in understanding beaked whale lesions. It should be noted that these odontocetes all stranded singly and their histories in terms of acoustic exposure are unknown.

CONCLUSION

It is important to note that no current hypothesis of pathogenic mechanisms resulting in acoustically-related strandings is proven. Even the most widely accepted and supported ideas have a number of unanswered questions. Additionally, the diversity of beaked whale species affected, in conjunction with the variety of geographic locations and hydrographic features where incidents have occurred, limit the certitude of interpretations that can be gleaned from current findings.

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A review of beaked whale behaviour and ecology in relation to assessing and mitigating impacts of anthropogenic noise

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ABSTRACT

Little is known about the ecology and behaviour of species within the family Ziphiidae. In this paper, five aspects of beaked whale ecology and behaviour are reviewed in relation to possible anthropogenic impacts upon them: social structure; life history; foraging/diving ecology; form and function of beaked whale sounds; and habitat characteristics. Differences in social structure within and between species may affect how anthropogenic activities affect local populations. Life history parameters may likewise vary within and between species and may influence the extent of and ability to recovery from population level impacts. Foraging and diving ecology determine where beaked whales spend most of their time and therefore, where in the water column they are most likely to encounter anthropogenic activities. The form and function of beaked whale sounds may be important in determining whether and how beaked whales are affected by anthropogenic noise. Finally, habitat characteristics determine whether beaked whales are likely to occur in a specific area where anthropogenic activities are to be undertaken and may also determine exactly how beaked whales are affected by it within a local area. To help fill the gaps in our knowledge of beaked whale behaviour and ecology, available opportunities for data collection must be maximised. This includes greater levels of co-operation between research groups to build up large datasets, the use of platforms of opportunity to study beaked whales in areas where little research has previously been undertaken and maximising the amount of information that can be learned from each possible source of data, such as stranded animals, through co-ordinated national and international research programmes.

KEYWORDS: BEAKED WHALES; NOISE; SOCIAL; REPRODUCTION; FEEDING; ECHOLOCATION; DISTRIBUTION; DIVING; COMMUNICATION; HEARING; HABITAT

INTRODUCTION

Beaked whales have been recognised as distinct from other cetaceans from at least as early as 1850 (Gray, 1850). However, until the 1980s, most research on beaked whales had concentrated on anatomy, morphology and the identification of species. In the last two decades this has changed and there has been an increasing amount of research into other aspects of beaked whale biology, such as ecology and behaviour. Recently, this has, in part, been driven by a number of mass strandings of Cuvier's beaked whale (*Ziphius cavirostris*) and other beaked whales, coinciding temporally and spatially with naval manoeuvres (e.g. Simmonds and Lopez-Jurado, 1991; Frantzis, 1998; Anon., 2001; Martin-Martel, 2002). These events have increased interest in the potential impacts of human activities, particularly those that transmit sounds into the water column, on beaked whales. The exact mechanisms by which anthropogenic sound production may affect beaked whales are currently unclear (see review in Cox *et al.*, 2006) and investigations into potential mechanisms have been limited by a lack of information on beaked whale biology, particularly behaviour and ecology.

Studying behaviour and ecology generally requires long-term *in situ* studies. In terms of beaked whales, the first such detailed investigation was the study of northern bottlenose whales (*Hyperoodon ampullatus*) at The Gully, a submarine canyon that penetrates the continental shelf edge east of Nova Scotia, Canada (e.g. Whitehead *et al.*, 1997). This study has shown that long-term studies of living beaked whales in the wild are feasible, as well as greatly enhancing our knowledge of this species. However, such studies of beaked whales remain rare and many published accounts of beaked whale behaviour and ecology are based on short-term observations of a few groups of individuals (e.g. Ritter and Brederlau, 1999).

This paper provides a brief overview of current knowledge of beaked whale ecology and behaviour, and highlights research needs to understand and address interactions between beaked whales and anthropogenic activities. Five general aspects of beaked whale ecology and behaviour are reviewed: social structure, life history, foraging/diving ecology, form and function of beaked whale sounds and habitat characteristics.

SOCIAL STRUCTURE

Social structure can be defined as the content, quality and patterning of relationships among individual animals within a species or population (Hinde, 1976). Possible social structures include solitary animals that meet only to reproduce, animals that maintain strong social bonds with small numbers of related (or unrelated) members of the same, opposite or both sexes and animals that form large groups of unrelated animals composed of smaller sub-units of related individuals (Hinde, 1976; Connor, 2000; Connor *et al.*, 2000). Social structures can vary between sub-populations within a population, between populations of the same species and in space and time within a population. As a result, determining the exact social structure of a species or population and making comparisons between them can be difficult. In particular, it is often necessary to follow a large number of individually-identified animals over long periods of time before the social structure of a population or species becomes reasonably well understood. For example, the social structure of some populations of killer whales (*Orcinus orca*) in the northwest Pacific has been studied by following known individuals for over 30 years, allowing a clear and detailed understanding of their social biology (Bigg *et al.*, 1990; Connor *et al.*, 2000). Such studies of beaked whales are rare and relatively recent. Even the

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longest study, that of northern bottlenose whales in the Gully, has only been running for about 15 years. However, despite this some general aspects of beaked whale social structure are known, as well as some specific aspects of social structures for some populations.

Group size

Group size may appear to be one of the most easily obtained measures of beaked whale social structure. However, there are a number of difficulties in determining group size. Firstly, there is the definition of what constitutes a group. For example, does it consist of all individuals observed within a few body lengths of each other and engaged in the same activities, or does it consist of all individuals in visual or acoustic contact with one another (Connor, 2000)? Secondly, there is a question of what a group represents. For example, does it represent a long-term and well-defined social unit or a temporary aggregation of individuals that will never associate again? Finally, due to long dive times and unobtrusive surfacing behaviour, it is not always possible to determine whether all members of a group of beaked whales are counted during an encounter or sighting.

Given the limitations of the available data, for the purposes of this review, a group is defined as all individuals found in the same location at the same time and it is assumed that all published or recorded records of beaked whale group size fit this definition. While this assumption is almost certainly biologically invalid, it provides a useful starting point for more detailed consideration of these issues in future analyses and emphasises the need for researchers to specify what they mean by the term 'group' or 'school' in their work. From published and unpublished sources available to the authors, reported group sizes ranged from 1-100 individuals (Table 1). A simple consideration of this table suggests that there are two different group size categories. The first is observed in species such as northern and southern bottlenose whales (*H. ampullatus* and *H. planifrons*), Cuvier's beaked whales and Blainville's beaked whales (*Mesoplodon densirostris*). In these species, reported group sizes have a maximum of around 20 animals, with the average ranging in size from 2.5 and 3.5 individuals (standard deviations (SDs) range 1.7-2.4). The second category is for larger (in both cases up to a maximum of 100 animals) groups and comprises *Berardius* species (mean 7.87 and SD 9.21) and Longman's beaked whales, *Indopacetus pacificus*[1] (mean 19.4, SD 22.23).

The suggested differences are further supported by a chi-square contingency test of these data. The frequency of occurrence of three group sizes (1-5 individuals, 6-10 individuals and 11 or more individuals) in six taxonomic groups (Longman's beaked whale, *Berardius* species, the southern bottlenose whale, the northern bottlenose whale, Cuvier's beaked whale and *Mesoplodon* species – there was insufficient data to include Blainville's beaked whale as a separate species in the analysis) differed significantly from expected (chi sq.= 443.6, df=10, p<0.0001). *Berardius* species and Longman's beaked whale were recorded in groups of 11 or more significantly more frequently than expected (chi sq.=120.9, df=1, p<0.0001; chi sq.=140.3, df=1, p<0.0001 respectively) and in groups of one to five significantly less frequently than expected (chi sq.=28.8, df=1, p<0.0001; chi sq.=12.9, df=1, p=0.0003 respectively). In contrast, the southern bottlenose whale, the northern bottlenose whale, Cuvier's beaked whale and *Mesoplodon* species were all recorded significantly less frequently than expected in groups of 11 or more (southern bottlenose: chi sq.=8.5, df=1, p=0.0036; northern bottlenose: chi sq.=18.4, df=1, p<0.0001; Mesoplodon: chi sq.=14.0, df=1, p=0.0002; Cuvier's beaked whale: chi sq.=6.0, df=1, p=0.0143). Therefore, Longman's beaked whale and *Berardius* species occur more often in larger groups than Cuvier's beaked whale *Hyperoodon* species and *Mesoplodon* species which primarily occur in relatively small groups (Fig. 1). This suggests that there may be at least two different social structures exists in the family Ziphiidae.

Table 1

Group sizes of various taxonomic groupings of beaked whales from published and unpublished sources (contact C.D. MacLeod for full details). Range: Represents the minimum and maximum group sizes recorded for a taxonomic grouping; N: Total number of groups used to calculate the mean and SD for each taxonomic grouping.

	Group size			
Taxonomic grouping	Range	Mean	SD	N
Northern bottlenose whales	1-22	3.6	2.4	895
Southern bottlenose whales	1-20	2.4	2.2	201
Cuvier's beaked whales	1-15	2.3	1.7	189
Blainville's beaked whales	1-8	3.5	1.7	31
Mesoplodon spp.	1-15	2.9	1.8	354
Longman's beaked whales	1-100	19.38	22.32	36
Berardius spp.	1-100	7.87	9.21	335

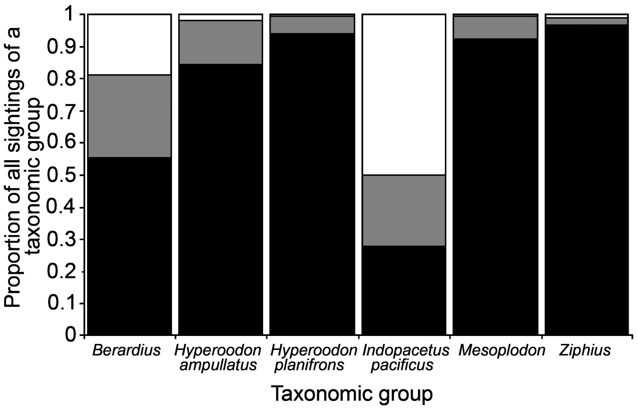

Fig. 1. The frequency of occurrence of groups in three size classes for sightings of Longman's beaked whale, *Berardius* spp., the southern bottlenose whale, the northern bottlenose whale, Cuvier's beaked whale and *Mesoplodon* spp. Dark grey=Percentage of total sightings for a taxonomic group with group sizes of 1-5 individuals; Light grey=Percentage of total sightings for a taxonomic group with group sizes of 6-10 individuals; White=Percentage of total sightings for a taxonomic group with group sizes of eleven or more individuals.

To date, all mass strandings associated in time and space with anthropogenic noise sources have involved species in the first category (Cuvier's beaked whale, various *Mesoplodon* species and the northern bottlenose whale – Simmonds and Lopez-Jurado, 1991; Frantzis, 1998; Anon., 2001; Martin-Martel, 2002). However, whether this is truly representative is unknown. For example it may reflect a geographic bias towards the Atlantic Ocean, where most of these strandings events have been reported and where neither *Berardius* spp. or Longman's beaked whales are known to occur. It is also noteworthy that for several mass

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[1] For the purpose of this review, the sightings reviewed in Pitman *et al.* (1999) are considered to represent Longman's beaked whale based on the evidence presented in that paper and on the recent morphological and genetic evidence published by Dalebout *et al.* (2003).

strandings with suggested links to anthropogenic noise, the number of individuals involved was several times the average reported group size for that species (e.g. 19 Cuvier's beaked whales in the Canaries in October 1989 – Simmonds and Lopez-Jurado, 1991; 12 Cuvier's beaked whales in Greece in May 1996 – Frantzis, 1998; 9 Cuvier's beaked whales in the Bahamas in March 2000 – Anon., 2001; 9 Cuvier's beaked whales in the Canaries in September 2002 – Martin-Martel, 2002; Average reported group size for sightings at sea: 2.3 – see Table 1). This suggests that either more than one group was involved in these strandings events or that 'biologically meaningful' group size of beaked whales is larger than that detected at sea.

A more thorough investigation of 'group' size, including a thorough investigation of how the various investigators defined a 'group' and possible regional and temporal variations in group size, is needed.

Group composition

Good information on group composition is only available for northern bottlenose whales and to a much lesser extent, Blainville's and Baird's beaked whales. For northern bottlenose whales in the Gully, groups may consist of individuals of different ages and sex classes. However, while females appear to form a loose network of social partners with no obvious long-term associations, some males have been repeatedly recorded together over many years and may form long-term coalitions (Gowans *et al.*, 2001). For Blainville's beaked whales in the northeastern Bahamas, groups usually (18 out of 20, CDM own data) consisted of a number of females, calves and/or juvenile animals. In some groups, a single mature male with fully erupted tusks and/or a single pubescent (sub-adult) male was present, but never more than one of each of these classes. Single animals were observed twice, one was a pubescent male and one an adult male (C.D. MacLeod, own data). In other *Mesoplodon* species, there have been incidental sightings of groups with two or more adult males (e.g. Hooker and Baird, 1999b). Baird's beaked whales are also known to occur in multi-male groups and the large groups observed in this species can consist of adults of both sexes. This, along with a longer life-span in adult males, suggests that Baird's beaked whale may have a different social structure to the northern bottlenose whale and Blainville's beaked whale (Kasuya *et al.*, 1997; Connor *et al.*, 1998; Connor *et al.*, 2000).

Mass strandings of beaked whales that have occurred in spatial and temporal concordance with anthropogenic activities have often consisted of a large proportion of immature, juvenile or probable cow-calf groupings (e.g. up to 66% of individuals that stranded in the Bahamas in March 2000 – Anon., 2001; 100% of individuals that stranded in Greece in 1996 – Frantzis and Cebrian, 1998; 45% of individuals in the 2002 Canaries stranding – Martin-Martel, 2002). While little is known about group composition of the main species involved (Cuvier's beaked whales), this does not reflect an equal representation of all length classes as revealed by strandings data (see Fig. 2). While strandings events may not be representative of the structure of living populations (in particular there may be biases towards the youngest and oldest age classes in the general strandings data due to higher natural mortalities), the information available suggests differences in mortality rates for different age classes between 'normal' strandings and atypical mass strandings associated with anthropogenic noise. These differences may include one, or more, of the following:

(1) Some age and sex classes within individual groups may be more susceptible to intense noise exposure, for example due to physiological differences, differences in body size, differences in responses to perceived threats (e.g. younger individuals or groups of younger animals may be preferentially attracted to, or fail to avoid, sources of anthropogenic noise) or differences in 'experience';
(2) naturally occurring age- and sex segregation in populations where mass strandings have occurred;
(3) there is an uneven age or sex ratio in these beaked whale populations; and/or
(4) behavioural responses to noise exposure results in the fragmentation of groups into individual animals or age/sex segregated sub-units, some of which are subsequently more likely to strand.

Further detailed work on group composition, both in terms of instantaneous group sampling and long-term associations between individually-identifiable animals and on different reactions towards human activities between groups of different compositions, are required to understand which, if any, of these are correct and exactly how the actual group composition of beaked whales species relates to the composition of individuals in mass stranding events. This will be particularly important for investigating possible mechanisms underlying anthropogenic noise-related mass stranding events, specifically to investigate the hypothesis of socially-facilitated panic.

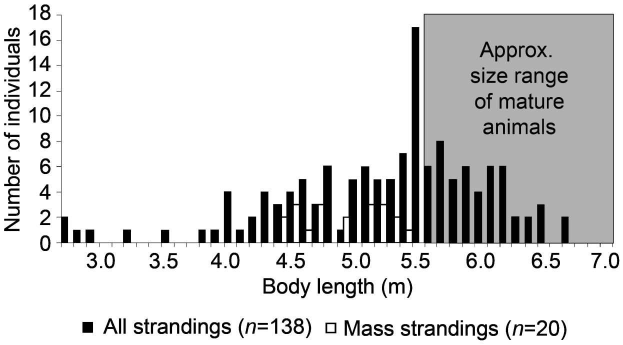

Fig. 2. A comparison of body lengths of Cuvier's beaked whales from two mass strandings events associated with anthropogenic noise (Greece 1996 and Canaries 2002, *n*=20) with those of Cuvier's beaked whales from all types of strandings events around the world (*n*=138).

LIFE HISTORY

Relatively little is known about the life history of beaked whales. The survey by Mead (1984) is currently the only published work dedicated to this topic and concentrates primarily on reproductive data from stranded animals and whale fisheries. Even within this study, detailed information is only available for Baird's beaked whale and the northern bottlenose whale, both of which had been targeted by whalers. For other species the information is either limited, in terms of the number of individuals examined or reproductive aspects investigated or non-existent. The oldest beaked whale recorded is 84 years (if each tooth layer relates to one year) for a male Baird's beaked whale (Kasuya *et al.*, 1997). However, the oldest recorded female Baird's beaked whale is only 54 years (Kasuya *et al.*, 1997). For all other beaked whales where it has been examined, the maximum recorded age is between 27 and 39 (Mead, 1984).

For species where it has been examined (Baird's beaked whale and the northern bottlenose whale), the age at sexual maturity is between seven and 15 years (Mead, 1984; Kasuya *et al.*, 1997). Mead (1984) noted that gestation is 17 'lunar months' for Baird's beaked whale and 12 months for the northern bottlenose whale. Benjaminsen and Christensen (1979) gave lactation length as one year and birth interval as two years for the northern bottlenose whale. For Blainville's beaked whales encountered during a study of habitat preferences, a calf initially thought to be in its first year, was subsequently seen in the next two years still associated with the same adult female and was also observed to nurse in the second year, when it would have been between one and two years old (C.D. MacLeod, pers. obs.). This suggests that for some individuals and/or species, lactation and birth interval may be longer than that cited by Benjaminsen and Christensen (1979). No data are available on reproductive rates, although crude approximates of calf production per mature female per year can be obtained by using the calving interval value.

Natural causes of mortality for beaked whales are poorly understood, but will likely include predation, disease and 'old age'. Anthropogenic mortality may be caused by direct hunting, bycatch, plastic ingestion, stranding associated with sound-generating activities and perhaps pollution. There is potential for anthropogenic causes of mortality to interact additively or synergistically with natural ones to adversely affect populations or species. Further information is needed to address whether there may be population level effects, including information on abundance, levels of anthropogenic mortality and life history parameters. This will allow modelling (e.g. population viability analysis) efforts to investigate possible scenarios. Obtaining such information will require a major co-operative research effort (involving both examination of strandings and long-term studies of live animals); this should initially be concentrated on 'key' areas (MacLeod and Michell, 2006).

FORAGING AND DIVING ECOLOGY

Some aspects of beaked whale foraging ecology are amongst the best known aspects of beaked whale biology, while others remain amongst the most poorly known. For example, dietary information is available from stomach contents analyses of stranded animals and from whaling operations, while there has been no opportunity to directly observe prey pursuit or capture at the depths beaked whales are thought to forage. Here, five aspects of foraging ecology are considered: prey species; position of foraging in the water column; diving behaviour; alloparental care of young at the surface during deep dives; and the pursuit of and capture of prey.

Prey species

MacLeod *et al.* (2003) reviewed the information on the diet of beaked whales available from stomach contents analysis, recognising that there may be biases associated with using stomach contents data for analysing prey preferences (see MacLeod *et al.*, 2003). In general, cephalopods were the most commonly recorded prey for almost all beaked whale species which have been examined, although in some individuals fish and even crustaceans were also found to be important (MacLeod *et al.*, 2003). Similarities in dentition with other fish-eating odontocetes and a very limited number of prey remains from a single specimen (Mead and Payne, 1975; Mead, 1989) infer that Shepherd's beaked whale may be the only beaked whale species that routinely preys on fish rather than cephalopods but clearly more evidence is required to confirm or deny this. In general, the prey found in stomach contents are deep-water species with almost all recorded prey are found at depths below 200m for at least part of their lives. There appears to be no obvious bias towards bioluminescent prey, muscular or neutrally buoyant squid, vertically migrating species or any other ecological characteristics other than water depth (MacLeod *et al.*, 2003). However, the fish and squid species from beaked whale stomach contents usually differ in one specific way. While squid species recorded are mainly mesopelagic, although they may have been associated with the seabed for part of their lives, the fish species recorded are primarily benthic or benthopelagic. In terms of differences between beaked whale species, *Ziphius* and *Hyperoodon* spp. were found to consume much larger prey than *Mesoplodon* spp., both in general and when individuals from the same location were compared (MacLeod *et al.*, 2003). However, three species in the northeast Atlantic Ocean (Cuvier's beaked whale, the northern bottlenose whale and Sowerby's beaked whale) preferentially consume prey within a range of 1-5% of their own body length, suggesting that prey size differences between species at the same location may be related to differences in body length (MacLeod, 2006). This differences in prey size between these genera are, to some extent, confirmed by stable isotope analyses, which although has its own set of limitations and biases, is independent of stomach contents data (Ostrom *et al.*, 1993; Hooker *et al.*, 2001; MacLeod *et al.*, 2003; MacLeod, 2005).

Position of foraging in the water column

There is little information on the position that beaked whales forage in the water column. The only published directly-measured diving data for a series of sequential probable foraging dives is for northern bottlenose whales in the Gully, where two individuals repeatedly dived to, or close to, the seabed in waters depths of up to approximately 1.5km (Hooker and Baird, 1999a). A single deep and presumed foraging dive recorded from a second species, Blainville's beaked whale, in Hawaii was also found to be at or close to the seabed (Baird *et al.*, 2004). The picture from stomach contents analyses is somewhat mixed, with cephalopods suggesting foraging in deep mid-water areas away from the seabed, while fish species suggest a more benthic diet (MacLeod *et al.*, 2003). Clearly more information is required.

Dive patterns, duration and depth

Although few detailed data exist, beaked whales are generally considered to be long and deep divers. Surface observations can provide some information and in general, beaked whale dive patterns consist of a long dive followed by a series of surfacings before another long dive. However, this pattern is not always followed, for example, under some conditions animals may spend up to an hour or more at or close to the surface breathing at regular intervals. Similarly, while all individuals within a 'group' often surface synchronously, on some occasions asynchronous surfacings are observed.

Barlow and Sexton (1996) estimated the number of breaths within each surfacing series to be approximately 10-30 for pygmy beaked whales (*M. peruvianus*) and Cuvier's beaked whales. Barlow (1999) found the median duration of long dives to be 20.4min for *Mesoplodon* spp., 28.6min for Cuvier's beaked whales and 15.5min for Baird's beaked whales, with median durations of surfacing series of 150s and 126s, respectively. Kasuya (1986) noted than for Baird's beaked whales off Japan, the time at the surface for individual schools varied in the range 1-14min, but was usually less than 5min. Dive times recorded ranged 1-67min, with a median dive time of 19.8min, excluding dives between 1-2min in length.

Three types of surfacing patterns in Blainville's beaked whales in the Bahamas are observed (C.D. MacLeod, own data – 20+ at intervals of a few 10s of seconds): (1) a long (8.4hrs of observations from 18 groups) series of shallow dives where the animals remain visible from the surface for much of the time with no sustained movement over ground and no apparent direction of travel; (2) a series (10-20 at intervals of a few 10s of seconds) of surfacings followed by a longer dive of 12-15min, where all individuals within a group remain in close proximity while moving in a definite direction and at an almost constant speed for periods of up to an hour or more; and (3) a series (20+ at intervals of a few 10s of seconds) of surfacings, with or without an apparent direction of travel, followed by a long dive of up to 20min or more, when an animal or group of animals return to a point on the surface close (usually within 500m) to where the long dive started. These three dive patterns are thought to be related to socialising/curiosity about the research vessel, travelling and foraging respectively.

Direct measurement of dive depth and dive profile have only been specifically investigated in two locations and for a small number of animals. The dives of two individual northern bottlenose whales in the Gully (Hooker and Baird, 1999a) could be separated into 'short duration and shallow' and 'long duration and deep', where northern bottlenose whales dived approximately every 80min to depths of over 800m and probably foraged at or close to the seabed. For a single individual Blainville's beaked whale in Hawaii, most dives were of short duration to relatively shallow depths (an average of 7.47min, to 58.6m) during a social period, with a single deep dive to 890m for at least 23.3min (Baird *et al.*, 2004). This long dive was probably to the depth of, or close to the seabed.

Alloparental care during deep water foraging

For sperm whales, another deep-diving cetacean, young whales are often accompanied at the surface by a number of different adult or larger individuals. Whitehead (1996) suggested that this represents alloparental care of calves, while their mothers are engaged in deep foraging dives. A possible function of this may be that adult females dive to depths that are too great and for too long for their young calves to accompany them. Alloparental care may help to reduce the likelihood of predation of a calf left at the surface while its mother forages (Whitehead, 1996). As deep-diving species, beaked whales may have similar limitations on calves accompanying adult females during foraging dives and may be expected to also exhibit alloparental care of small calves. Any such social behaviour would have implications for interpreting both the effects of anthropogenic sounds and on population level effects of sounds, however, there is currently little evidence either for or against the occurrence of alloparental care in beaked whales. Gowans (1999) found possible, but equivocal, evidence for alloparental care for the northern bottlenose whale. During a much shorter amount of observation time (8.4hrs of observations from 18 groups) on habitat use of Blainville's beaked whales in the northern Bahamas, noted no observations consistent with alloparental care i.e. no observations of individual calves being observed at the surface with a number of different larger individuals during an encounter (C.D. MacLeod, own data). Further research is required to determine (1) whether alloparental care does indeed occur in beaked whales; and (2) if so, what implications this may have for assessing and mitigating the potential impacts of anthropogenic noise on beaked whale species both in terms of individuals and of populations.

Pursuit of prey and prey capture

The feeding strategies (e.g. whether they are 'ambush' or 'pursuit' hunters) of beaked whales are unknown. Heyning and Mead (1996) suggested that the white areas inside and around the mouths of beaked whales may become covered in bioluminescent slime and micro-organisms following successful capture of prey, that then act as bait for the next prey. Such a strategy suggests a fairly passive approach to foraging. However, prey pursuit is the strategy adopted by most other odontocetes and certainly the bodies of beaked whales are sufficiently hydrodynamic to suggest they are capable of the fast movements and rapid turns required of pursuit predators (Bose *et al.*, 1990). Based on morphology, prey ingestion is via suction feeding e.g. the presence of expandable throat grooves, a large piston-like tongue and associated large hyoid apparatus and greatly reduced dentition in comparison with many other toothed whales (Heyning and Mead, 1996). However, suction feeding could form part of both an ambush and a pursuit foraging strategy.

Based on currently available data, beaked whales are thought to spend much of their lives below the surface (for example, the Hooker and Baird study using tagged northern bottlenose whales showed that they spent around 67% of the time at depth (Hooker and Baird, 1999b)). Therefore, understanding the behaviour of beaked whales while they are underwater is of great importance. Given daily energy demands, foraging is probably the most important aspect beaked whale behaviour at depth and thus understanding this may be an important component of understanding beaked whale-anthropogenic noise interactions. Potentially important factors include: the depths to which animals dive; the proportion and absolute amount of time spent at depth; the usual ascent and decent rates; the shape of the dive profiles; and the movements while underwater both vertically and horizontally. In particular, vertical movements may have a greater effect on received sound levels from near surface-generated sound sources for individual animals than horizontal movements, particularly in areas where there is strong ducting of sound, resulting in large vertical variations in sound levels (e.g. in the Bahamas, March 2000 – Anon., 2001). For example, an animal surfacing vertically from a depth of 1.5km at the end of a foraging dive may pass vertically through varying received sound levels from near-surface sound sources. Due to limited remaining oxygen supplies at the end of a long dive, under such conditions an animal may have limited abilities to display any 'normal' avoidance behaviour. Instead, it may be required to continue to move towards the surface regardless of changes in received sound levels due to its need to replenish its diminished oxygen stores before it can undertake any avoidance measures. This is an area in which more research is required to fully understand the impacts of anthropogenic noise on beaked whales. The recent work of Jepson *et al.* (2003) suggesting that the animals which stranded during a naval exercise in the Canaries in

September 2002 may have suffered from dive-related injuries emphasises the importance of understanding normal foraging and diving.

FORM AND FUNCTION OF BEAKED WHALE SOUNDS

At present, information on sounds produced by beaked whales is only available for six species. These are the northern bottlenose whale (Winn *et al.*, 1970; Hooker and Whitehead, 2002), Blainville's beaked whale (Caldwell and Caldwell, 1971), Hubbs' beaked whale (*M. carlhubbsi* – Lynn and Reiss, 1992; Marten, 2000), Cuvier's beaked whale (Manghi *et al.*, 1999; Frantzis *et al.*, 2002), Arnoux's beaked whale (*B. arnuxii* – Rogers and Brown, 1999) and Baird's beaked whale (Dawson *et al.*, 1998). Sounds produced by Blainville's and Hubbs' beaked whales have only been examined for stranded animals, while for the other species, sounds were recorded from free-ranging animals. However, these recordings are from a limited number of locations and individuals. In addition, sounds have also been recorded in the field from an unidentified *Mesoplodon* spp. and there are sound recordings attributed to southern bottlenose whales recorded during acoustic surveys in Antarctica (Dawson *et al.*, 1998; Leaper and Scheidat, 1998; Leaper *et al.*, 2000).

The northern bottlenose whale

There are two published reports on sound production by northern bottlenose whales (Winn *et al.*, 1970; Hooker and Whitehead, 2002), both from the Gully east of Nova Scotia (approximately 44°N, 59°W). Hooker and Whitehead (2002) recorded two distinct classes of click series. The first class were heard at low amplitude when the whales were submerged (termed 'deep-water' clicks). Deep-water clicks were usually regular in inter-click interval, with an average click duration of 0.35ms, an average inter-click interval of 0.40s and an average peak frequency of 23.88kHz, with the mean value in any one session varying from 20.86kHz to 25.50kHz. The second class were heard at much greater amplitude, usually while the whales were at the surface (named 'surface' clicks by Hooker and Whitehead, 2002). Surface clicks were often emitted in rapid succession in the form of click trains over a period of up to 20s or more. Surface clicks differed significantly from deep-water clicks in inter-click interval and peak frequencies, but not click duration. In addition, surface clicks differed significantly in the inter-click interval between recording sessions, which was not the case for deep-water clicks. The average click duration for surface clicks was 2.02ms and the average click interval was 0.07s. The average peak frequency was 10.79kHz, with the mean value in any one session varying from 4.36 to 21.32kHz.

Winn *et al.* (1970) recorded two types of sounds they believed were produced by a group of northern bottlenose whales in the Gully (at 43°50'N, 58°56'W) in 1969. The first type comprised clicks in the frequency range from below 500Hz to above 26kHz, with some having most of their energy from 8-12kHz and others having peak energies at lower frequencies. Click trains recorded varied 3-50 clicks per train, with click repetition rates as high as $82s^{-1}$. The amplitude of the clicks was so low that they could not usually be detected if the animals were more than about 30m from the boat. The second type were whistles in the frequency range 3-16kHz and duration 115-850ms. While some whistles varied in frequency, others remained at constant frequency. Constant frequency calls had a frequency of around 4kHz, while the constant frequency sections of varying frequency calls were generally in the ranges of 3-5kHz, 7-9kHz or 12-14kHz. A few short (70-90ms) chirp-like calls were also detected which started at around 4kHz and swept up to 13kHz.

However, pilot whales (*Globicephala melas*) were recorded around the same location as Winn *et al.*'s study was conducted and it has been suggested that the whistles did not originate from northern bottlenose whales, but another odontocete species, such as pilot whales (Hooker and Whitehead, 2002). Indeed, the lack of whistles which could definitively be attributed to northern bottlenose whales in the recordings made by Hooker and Whitehead (2002) seems to support this, or at least suggest that if northern bottlenose whales do produce whistles it may not be a common feature of their sound repertoire.

The southern bottlenose whale or Arnoux's beaked whale

Leaper and Scheidat (1998) describe recording of sounds which they attribute to beaked whales. During a survey of the Southern Oceans one detection was made of several high frequency click trains from an unknown species (at 61°45'S, 57°53'W). Leaper and Scheidat (1998) describe these sounds as '...several short bursts of rapid clicks with a repetition rate of around 200kHz and a longer sequence with a repetition rate around 17kHz'. The main energy of the clicks was around 18kHz, with little variation between individual clicks. Leaper and Scheidat (1998) noted the similarities between these clicks and those recorded by Hooker and Whitehead in the Gully (see above) and suggest they were produced by either southern bottlenose whales or Arnoux's beaked whales (see below). However, in a more recent paper (Leaper *et al.*, 2000) 'rapid click trains' were again reported to correspond with a sighting identified visually as southern bottlenose whales, suggesting that this species may be the origin of the sounds reported above.

Hubbs' beaked whale

Lynn and Reiss (1992) reported sounds produced by two juvenile (2.87m and 2.99m in length) male beaked whales which stranded alive at Ocean Beach, San Francisco, USA, one of which was *post mortem* identified as a Hubbs' beaked whale. Pulses were categorised into two types. Type 1 were mainly lower frequency pulses with some wide band components going beyond the capabilities of the recording system used (over 40kHz). The majority of energy was confined to a narrow bandwidth between 300Hz and 2kHz. Type 2 pulses were broader band pulses with energy from 300Hz to over 40kHz (the limit of the recording system) and were similar to the echolocation signals used by many small odontocetes. Sequences had an average of seven pulses per group lasting for an average of 60ms, with an average of 142ms between groups. The average number of groups per sequence was 4.2. Sequences were composed entirely of type 1 or type 2 pulses. Ungrouped pulses of both types were also recorded, and grouped and ungrouped pulses were recorded within the same sequence. Six whistles were also recorded, with frequency ranges of 2.6-10.7kHz and lasting 156-450ms. Individual whistles varied in their dynamic range from 1-7kHz and each whistle occurred discretely from other whistles and from pulse sequences.

Blainville's beaked whale

Caldwell and Caldwell (1971) recorded sounds produced by a sub-adult (389.5cm total length) male Blainville's beaked whale stranded at Crescent Beach, Florida, USA. Sounds were recorded while the animal was still in the surf. At least some of the sounds were pulsed and all had fundamental frequencies between slightly less than 1kHz to almost 6kHz.

Unidentified *Mesoplodon* species

In a paper on sounds recorded from Baird's beaked whale (see below), Dawson *et al.* (1998) refer to an unpublished account by Ljungblad of sounds from a free-swimming Mesoplodont and note that it produced ultrasonic clicks. No further details are given.

Cuvier's beaked whale

Manghi *et al.* (1999) recorded sounds from two separate groups of Cuvier's beaked whales encountered during a survey along the continental shelf off the Greek islands of Corfu and Paxos. Each group consisted of a pair of animals. Sounds recorded consisted of a number of weak modulated whistles, with minimum variation between them. The whistles ranged from 8-12kHz, with a constant sweep up and lasted about 1s.

Dawson *et al.* (1998) also tried to record sounds from a group of Cuvier's beaked whales off Baja California, Mexico. However, and despite recording for 15min in close proximity to the animals, no sounds were recorded.

Frantzis *et al.* (2002) recorded sounds from Cuvier's beaked whales off southwest Crete in Greece. These sounds were pulsed, with each click lasting about 1ms. Sequences of 35-105 clicks lasting 15-44s in duration, with pauses of 3-10s between sequences were recorded. These clicks had a relatively narrow peak at 13-17kHz.

Arnoux's beaked whale

Rogers and Brown (1999) recorded sounds from Arnoux's beaked whale in an ice-free coastal polynya off the east Antarctic coast at 66°56'S, 61°54'E. Over a three day period, the number of animals varied from 23 to 47, with an average pod size of 6.7 individuals. The whales were highly vocal, with the most common call being pulsed tones with wavering frequency modulation. The maximum and minimum frequencies were 8.5kHz and 1kHz respectively and the mean duration was 0.77s. Pulse rates varied depending on whether they were broad-band clicks, click trains or burst pulses. Click trains lasted an average of 1.18s and contained an average of 25 clicks. Within click trains, the average repetition rate was $34s^{-1}$. Burst pulses had a mean duration of 0.53s with maximum and minimum frequencies of 10.91kHz and 3.135kHz respectively. Whistles were also recorded and had wavering frequency modulation, with a mean starting frequency of 5.222kHz, ending frequency of 4.283kHz and fundamental frequency of 4.896kHz. The mean duration was 0.65s.

Baird's beaked whale

Dawson *et al.* (1998) report recordings of sounds from a group of 30-35 Baird's beaked whales encountered off the Oregon coast (44°10'N, 129°10'W). Frequency modulated whistles with fundamental frequencies of 4-8kHz and with 2-3 harmonics were recorded, as well as broadband clicks and tonal sounds apparently generated by clicks at high repetition rates. Further recordings were made from Baird's beaked whales by Dawson *et al.* (1998) off the coast of Baja California (28°10'N, 11°45'W). Sounds were sorted into three categories (clicks, irregular pulse sequences and click bursts). The ten best recordings of clicks had an average duration of 636ms and contained 1-9 pulses. The mean inter-click interval was 141.7ms and individual clicks ranged in length from 122 to 953μs. The largest spectral peak was between 22 and 25kHz for most clicks, with the second largest peak usually between 35 and 40kHz. Of four largest spectral peaks for each click, the highest recorded for any click was 129.5kHz. For all clicks there was a significant inverse relationship between click duration and dominant frequency. Irregular pulse sequences from the ten best recordings averaged 320ms and obtained an average of 11.9 individual pulses. There was a strong spectral peak for most pulses around 23kHz, with a second harmonically unrelated peak at approximately 42kHz. The maximum largest peak for any pulse was 134kHz and again, dominant frequency and pulse duration were significantly inversely related. Click bursts from the ten best recordings lasted an average of 269ms and contained 17 click bursts in total. The dominant frequency for 94% of these click bursts was between 23 and 24.6kHz and there were no click bursts with appreciable energy over 90kHz.

Possible functions of sounds produced

Odontocete sounds have been hypothesised to have a number of functions (e.g. Norris and Mohl, 1983; Ford, 1989; Whitehead and Weilgart, 1990; Smolker *et al.*, 1993; Thompson and Richardson, 1995; Cranford, 1999). Some of these have been proven (e.g. use of echolocation pulses for navigation and foraging – Moore, 1980; Thompson and Richardson, 1995), while others remain hypothetical (e.g. prey stunning – Norris and Mohl, 1983; signalling during male/male competition – Cranford, 1999). Between these two extremes are hypothesised functions for which there are differing levels of evidence (e.g. contact calls – Smolker *et al.*, 1993). The sounds recorded from beaked whales can be divided into two categories; whistles and pulsed sounds or clicks, which, based on inferences from other odontocetes, may have different functions.

Whistles, such as those associated with Hubbs', Baird's, Arnoux's and Cuvier's beaked whale recordings, are most likely to serve some sort of social function. These could include social communication, group cohesion, individual identification and contact calls. However, too little is known about the social ecology of beaked whales to suggest which, if any, are true. However, between the four species from three genera where whistles have been recorded, there is a high level of consistency in the frequencies (Hubbs' beaked whale: 2.6-10.7kHz, Baird's beaked whale: 4-8kHz, Arnoux's beaked whale: mean fundamental frequency 5.2 kHz, Cuvier's beaked whale: 8-12kHz). This may be the result of conservation of an ancestral pattern, or a convergence in frequency as an adaptation to life in a common niche (deep-diving in oceanic waters). Whichever is the case, it suggests that most beaked whale species may use similar types and frequencies of sounds for social functions. One possible exception to this is the northern bottlenose whale, for which no whistles have been recorded which can definitively be assigned to this species despite over seven hours of recordings (Hooker and Whitehead, 2002).

Pulsed sounds have been recorded for all species of beaked whales where sound recordings have been analysed. While such sounds are most likely to serve in foraging or navigation, is should be noted that pulsed sounds are also used by sperm whales for social functions (Watkins and Schevill, 1977; Weilgart and Whitehead, 1988). There is no evidence of the coda-like structures thought to be used for social functions in sperm whales (see Weilgart and Whitehead, 1993; Weilgart and Whitehead, 1997 for details), in any of the beaked whale recordings and unlike whistles, pulsed sounds of beaked whales vary considerably within and between species in frequency and inter-click intervals. Therefore, it is likely that pulsed sounds in beaked whales function as echolocation for foraging and/or navigation. Frequencies range 300Hz to 135kHz, however, the upper limit may have been limited by the equipment rather than reflecting the highest frequencies produced. For several species, different types of pulsed sounds have been detected, which may be associated with different functions. For example, Hooker and Whitehead (2002) suggested that 'deep-water' clicks may be used to search for prey and that the peak frequency of such clicks may reflect the size of prey being searched for. Other classes could be associated with prey tracking while chasing individual animals, prey stunning, close investigation of other individuals or objects or navigation.

Anthropogenic sounds may disrupt or interfere with sounds produced by beaked whales. These impacts could include disruption of navigation, which could result in strandings and interference with social communication, which could lead to a breakdown in group cohesion and confusion, particularly during deep foraging dives. The latter is consistent with the apparent bias in age classes of animals that strand concurrently with human noise production. However, the exact characteristics and uses of sounds produced by beaked whales will need to be better understood before any possible mechanism involving disruption of or interference with sound functions can be identified.

HABITAT CHARACTERISTICS

Specific studies into the habitat preferences of beaked whales are rare (and indeed such studies can be difficult e.g. IWC, 2006). Whitehead and his colleagues have studied those of northern bottlenose whales in the Gully off Nova Scotia as part of a long-term research project into this population (e.g. Hooker *et al.*, 2002), Cuvier's beaked whales have been studied in the Bay of Biscay (Williams *et al.*, 1999) and the Gulf of Genoa (Biassoni *et al.*, 2003) and Blainville's beaked whales have been studied in the northern Bahamas (MacLeod and Zuur, 2005). Information on beaked whale habitats has also been obtained during surveys aimed at calculating the abundance and distribution of cetaceans in several parts of the world, particularly in US territorial waters (e.g. Waring *et al.*, 2001).

In many of the above areas, beaked whale occurrence has been linked to the seabed topography, particularly to features such as slopes, canyons, escarpments and oceanic islands. For example, in the waters off Nova Scotia the distribution of northern bottlenose whales was found to be closely associated with the Gully and this species preferentially occurs in this marine canyon rather than the neighbouring shelf, slope and abyssal areas (Hooker *et al.*, 2002). In the Bay of Biscay, the Cuvier's beaked whales studied by Williams *et al.* (1999) primarily occurred around the Cap Breton Canyon and in the Gulf of Genoa; this species distribution is also associated with a marine canyon (Azzellino *et al.*, 2001; D'Amico *et al.*, 2003). East of Great Abaco, in the northeastern Bahamas, Blainville's beaked whales were found to preferentially occur over the upper reaches of the Little Abaco Canyon (MacLeod and Zuur, 2005). In the northwest Atlantic, beaked whales are generally sighted along the continental shelf-edge break in waters 200-2,000m in depth, with sightings rates significantly higher within canyon areas than non-canyon, shelf edge areas (Waring *et al.*, 2001).

Of course, correlation with a physical variable or feature such as seabed topography does not mean that it is the only explanatory factor or show whether the link is direct or indirect (i.e. it serves as proxy for other more biologically important factors). For example, surface and deep water currents, levels of local productivity and distribution of preferred prey species may all exert a more direct influence on whether beaked whales occur at a specific location. In the Genoa canyon, the occurrence of Cuvier's beaked whales has been linked to apparent downwelling in the local water currents, which coupled with the canyon environment, may form a trap for suspended particulate matter of high biomass (D'Amico *et al.*, 2001). This, in turn, may lead to a relatively high local concentration of prey species. Similarly, the occurrence and patterns of habitat utilisation of Blainville's beaked whales around Little Abaco Canyon have been linked to the interactions between local deep-water currents and the seabed, which may result in the accumulation of prey species in the benthic boundary layer at specific locations (MacLeod and Zuur, 2005)

From these studies, it is tempting to conclude that beaked whales primarily utilise waters over certain topographic features with possible links to other factors, such as currents and frontal regions. However, little research has been conducted in abyssal areas of the North Atlantic and it is unclear whether beaked whales also occur in such areas and, if so, under what conditions. Certainly, in the eastern tropical Pacific (ETP), where detailed surveys have been conducted over abyssal areas away from the shelf edges, beaked whales are sighted well away from such areas (e.g. fig. 1 in Pitman *et al.*, 1999; fig. 1 in Pitman and Lynn, 2001). These may reflect either differences in effort in different habitat types, or differences in habitat use by beaked whales between oceanic areas. More research is required into such apparent differences in habitat use to establish whether and how information on habitat preferences from one area can be applied to other areas.

Within some areas, individual animals have been resighted over time, suggesting some level of residency. For example, in the Gully, individual animals were found to be resident in the area for an average of around 20 days at a time (SE: 10-17 days – Gowans *et al.*, 2000). Similarly, in the northeastern Bahamas, although the majority of animals identified over two consecutive summers were seen only once (*n*=29 out of 36), a small proportion (*n*=7 out of 36) were repeatedly seen in the same location within and between years (C.D. MacLeod, own data). However, to date there have been too few studies to draw any general conclusions on residency and habitat use.

A better understanding of beaked whale habitat and distribution is particularly important in the context of potential interactions with anthropogenic noise. Obviously, beaked whales can only be affected by anthropogenic noise if they are present in the same area. However, levels of impact from the same anthropogenic sounds may vary by habitat due to regional sound propagation characteristics affecting received sound levels. To examine this, it is important to understand habitat preferences both in areas where previous mass strandings linked to anthropogenic sounds have occurred and in areas where both beaked whales are known to occur and where sounds similar to those linked to mass strandings have been regularly generated, but where no similar mass strandings have been recorded. Of course, a lack of reported mass strandings in an area can not necessarily be interpreted as meaning that beaked whales in that area are unaffected by anthropogenic sounds. It may simply be that, for a variety of reasons (e.g.

distance from shore, displacement offshore, water depth, currents, sinking of the carcase) the affected animals did not strand.

Such a comparative approach will also benefit greatly from better information on levels of residency within specific areas/habitats in relation to repeated occurrence of anthropogenic noise within individual areas. This will allow an investigation of whether there is the potential for cumulative effects of repeated exposure to anthropogenic sounds and/or what proportion of a population may be affected in a single location, which will have implications for population level impacts and mitigation strategies.

To better understand the factors that determine the spatio-temporal distribution of beaked whales, further studies dedicated to investigating habitat use and temporal variations in occurrence are required. Such studies need to investigate beaked whale local distribution, in relation to physical and biological explanatory variables, for example using appropriate spatial and modelling approaches (e.g. see IWC, 2006). Obtaining appropriate data will require interdisciplinary research including the simultaneous collection of sightings (and absence of sightings) data and potential explanatory variables (both at sea and via remote sensing), the use of autonomous acoustic monitoring of areas where beaked whales may occur, the use of tags to study the behaviour of individual animals throughout the dive cycle (e.g. Johnson and Tyack, 2003).

CONCLUDING REMARKS

It is clear from the above review that for most, if not all species, little is known about many key aspects of beaked whale behaviour and ecology. Until further information is obtained, it is tempting to extrapolate between populations of the same species and between different beaked whale species. However, the available information suggests that special care should be taken before making any such inferences. While it appears that for some features, comparison among species may be reasonable (e.g. where there are data, beaked whales have been found to use relatively high frequency echolocation (up to 120kHz or more) and non-echolocation sounds in the region of 1-16kHz), this is certainly not true for all features. Three examples of this can be found in this review. Firstly, despite apparently occupying very different positions in the phylogenetic tree (see Dalebout *et al.*, 2002), *Berardius* species and Longman's beaked whale appear to form similar group sizes and these two groupings differ from other beaked whale species in this aspect. Secondly, northern bottlenose whales and Blainville's beaked whales appear to have very different patterns of male-male associations with the former forming male coalitions while in the latter adult males may not associate. Finally, based on sightings around oceanic islands, Blainville's beaked whale appear to occur in much shallower waters than other *Mesoplodon* species. Even within a species there may be differences, for example, Blainville's beaked whales in the Bahamas and in the ETP appear to occupy very different habitats; in the former occupying specific habitats around an oceanic island (MacLeod and Zuur, 2005), while in the latter being distributed over deeper waters and away from oceanic islands (Pitman and Lynn, 2001). Before extrapolations can be made between populations, both within and between beaked whale species, appropriately detailed intra- and inter-specific comparative studies must be undertaken to determine which, if any, aspects of their biology can reliably be extrapolated. However, as yet, no such studies have been undertaken for beaked whales.

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Properties of the underwater sound fields during some well documented beaked whale mass stranding events

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ABSTRACT

Recent mass strandings of marine mammals, mostly Cuvier's beaked whales (*Ziphius cavirostris*) from the family of ziphiidae, have occurred coincident in space and time with human production of high levels of underwater sound. Three of these events, the May 1996 mass stranding along the Greek coast, the Bahamas mass stranding event in March 2000 and the September 2002 event in the Canary Islands, were selected for consideration here since pertinent information was readily available. The purpose of this paper is to summarise the probable characteristics of the sound fields during these events and to search for common features. The acoustic sources in all three cases moved at speeds of 5 knots or greater and generated periodic sequences of high amplitude, transient pulses 15-60s apart that contained significant energy in the 1-10kHz frequency band. The environmental conditions included water depths exceeding 1km close to land. In addition, the depth dependence of the ocean sound speed created an acoustic waveguide whose lower boundary was formed by refraction within the water column. The anthropogenic sources in all cases were located within such waveguides. Under these conditions, sound levels decrease more slowly with increasing range after a certain transition range than otherwise, due to sound focusing and to decreased attenuation because of isolation over extended ranges from the ocean bottom. In addition, the frequency dispersion is such that pulses tend to remain as pulses during propagation. For those events involving near-surface sources in surface ducts, weather conditions were calm leading to minimal sound attenuation and scattering by near-surface bubbles and ocean surface roughness. Quantitative prediction of the actual sound field properties during these events is limited primarily by the lack of knowledge of prevailing environmental conditions. Results from simple numerical modelling show that received sound level increases of up to 20dB occur after the transition range for sources and receivers within refractive waveguides. Data-based semi-empirical models of surface duct propagation provide simple, realistic, quantitative estimates of the mean acoustic field in the duct and the effects of changes in environmental conditions. Numerical modelling of total sound exposure (pressure squared integrated with respect to time) illustrates the importance of the relative velocity and minimum range between source and receiver, indicating that realistic animal motion models are required to obtain representative results. Although several features of the sound fields during these three mass stranding events are very similar, their actual relationship to the strandings is unknown.

KEYWORDS: NOISE; STRANDINGS; MODELLING; ACOUSTICS; BEAKED WHALES

INTRODUCTION

Several authors (e.g. Frantzis, 1998; Anon., 2001; Department of the Environment, 2002) have suggested in recent years that high sound level sonars may be responsible for mass strandings of beaked whales (family Ziphiidae), defined as the strandings of two or more whales other than a cow-calf pair (Cox *et al.*, 2006). Other sources of anthropogenic sound also have been implicated (e.g. Gentry, 2002). Although a cause-and-effect relationship has not been firmly established, several of these human activities are temporally and spatially correlated with mass strandings of Cuvier's beaked whales (*Ziphius cavirostris*) alone or with members of the genus Mesoplodon (e.g. *Mesoplodon densirostris*, *M. europaeus*). Over the past decade, the public and the scientific community have become increasingly aware that some historical mass strandings of beaked whales also may be associated, both spatially and temporally, with military use of sonar (e.g. Frantzis, 1998; Department of the Environment, 2002; Cox *et al.*, 2005).

Three of the best documented stranding events, for which some information is readily available, are the focus of this paper. These events are: (1) the strandings along the west coast of Greece in May 1996 (D'Amico and Verboom, 1998; Frantzis, 1998); (2) the Bahamas stranding event in March 2000 (Anon., 2001; Fromm and McEachern, 2000); and (3) the Canary Islands stranding event in September 2002 (Department of the Environment, 2002). The 1996 Greek strandings occurred during the same time period that the North Atlantic Treaty Organisation (NATO) SACLANTCEN Undersea Research Centre performed an acoustic experiment called Shallow Water Acoustic Classification in Kyparissiakos Gulf, close to the Greek Coast. The majority of the dozen or so animals stranded in a two-day period (12-13 May) over approximately 35km of coastline (D'Amico and Verboom, 1998).

The Bahamas event consisted of a mass stranding of 16 cetaceans, comprised of both beaked and common minke whales (*Balaenoptera acutorostrata*), over a 240km arc of coastline bordering the Northeast and Northwest Providence Channels of the Bahamas Islands. The strandings occurred over a 36-hour period, 15-16 March 2000 and corresponded simultaneously with the transit of five US Navy surface ships through the channels, operating mid-frequency hull-mounted sonar systems as part of a training exercise. Only detailed information on four of the five US ships is provided by Anon. (2001) and Fromm and McEachern (2000). Based on the way in which the strandings coincided with this naval activity, it was concluded that the tactical mid-range sonars were the most plausible cause of the trauma observed in the autopsies of stranded animals (Anon., 2001).

Over 24-27 September 2002, a mass stranding of approximately 14 cetaceans, all beaked whales (for those animals where species identification was made), occurred along the southeast side of the island of Fuerteventura and the northeast side of Lanzarote in the Canary Islands. This stranding was temporally and spatially coincident with an international naval exercise called Neo Tapon. The exercise

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involved ships and aircraft from 11 NATO countries (Socolovsky, 2002). Six mass strandings of beaked whales had previously taken place along these same sections of coastline over the six-year period 1985-1991, many of which were coincident in time with naval exercises in the area (Department of the Environment, 2002). The specifics of the naval activities during Neo Tapon are not readily available. However, military hull-mounted sonar systems similar to those used during the Bahamas event were likely in operation given that surface ships and submarines were participating in 'acoustic exercises' at the time (Department of the Environment, 2002; Table 2).

A common aspect of these three stranding events is that they were coincident in time and space with exercises involving the operation of mid-frequency sonar systems (the Greek event was the only one known to have involved a low frequency sonar in addition to a mid-frequency sonar). Some people have also suggested a link between beaked whale strandings and seismic air gun operations (Gentry, 2002; Cox *et al.*, 2006). For completeness, the general properties of the acoustic signals generated by seismic air gun arrays operated by the oil and gas industry are included in this paper, along with those of the mid-frequency sonars and the low frequency sonar used in Greece.

This paper summarises the probable characteristics of the sound fields during these events and searches for common features. In any discussion of underwater sound fields and marine life, distinctions must be made between the properties of the acoustic source, the properties of the environment (the medium through which the sound travels), the received acoustic field properties at a specified location and the characteristics of an animal's perception of the sound. First, the properties of the acoustic sources that were in operation during these stranding events are summarised followed by a discussion of what is known about the characteristics of the environments in which the strandings occurred. The lack of knowledge of the environmental conditions during the events probably is the source of greatest uncertainty in the prediction of the received acoustic field at a given location. Some of the relevant features of sound propagation in these environmental settings are outlined in this paper. Background information on acoustic propagation modelling and some examples of acoustic propagation modelling to illustrate some of the main points in the paper are also presented. The perception of sound fields by marine mammals is beyond the scope of this paper.

PROPERTIES OF THE ACOUSTIC SOURCES

Greece, 1996

The Towed Vertically Directive Source (TVDS) used in the 1996 Shallow Water Acoustic Classification experiment was towed by the NATO Research Vessel *Alliance* at various depths from 60 to 93m, but primarily in the 70-85m depth interval. It differs in this regard from the other sources discussed herein in that it operated at depths greater than 10m. The source transmitted for 2.5 to 3.75hrs during each run, with three runs per day over four consecutive days (D'Amico and Verboom, 1998). Acoustic signals were generated simultaneously in two different frequency bands with centre frequencies of 600Hz and 3kHz and at source levels of 228 and 226dB re: 1µPa at 1m, respectively (Table 1). Both continuous wave (CW) signals (i.e. a tone at a constant, single frequency) and hyperbolic frequency-modulated (HFM) waveforms (where the frequency of the tone being transmitted varies continuously over time with a temporal dependence given by a hyperbola) were used in the tests. CW signals are sensitive to the motion of an acoustic reflector, whereas HFM signals are invariant to reflector motion but instead provide information on the distance to the reflector. The TVDS had a vertical beamwidth of 23° at 600Hz and 20° at 3kHz. These two beams were oriented in the horizontal direction to focus the radiated sound along the axis of the sound channel (discussed later).

Given that the pulses in both frequency bands always were transmitted simultaneously (probably in a phase coherent way) and that the main beams of the vertical source array components for the two frequency bands were oriented in the same direction (horizontal) at all times, then the combined pulses can be considered as one pulse. In this case,

coherent (amplitude) addition = $20\log_{10}\left(10^{228/20}+10^{226/20}\right)$

therefore, the overall source level = 233dB re: 1µPa at 1m.

For incoherent (energy) addition = $10\log_{10}\left(10^{228/10}+10^{226/10}\right)$

therefore, the overall source level = 230db re: 1µPa at 1m.

Bahamas, 2000

The sonars used in the Bahamas event were types AN/SQS 53C and AN/SQS 56 hull-mounted systems. The 53C was used on two ships and transmitted at centre frequencies of 2.6kHz and 3.3kHz. They operated for most of the time at a source level of 235dB re: 1µPa at 1m. The 56 sonars transmitted signals with centre frequencies of 6.8kHz, 7.5kHz and 8.2kHz at 223dB re: 1µPa at 1m source level. During the exercise, these sonars each transmitted pulses of 1-2s in duration once every 24s. Pulse transmissions from each ship were staggered in time to prevent overlap. This 24s interpulse interval allowed reflections from surfaces and objects out to distances approaching 20km from the ship (40km round trip) to be received before the next pulse was transmitted. The pulses had rise times of 0.1-0.4s and typically were comprised of three consecutive waveform types (Table 1), with nominal bandwidths up to 100Hz. Both 53C and 56 sonars are vertically directional. The 53C has a nominal 40° vertical beamwidth (depending upon frequency) centred at 8m depth and which was steered 3° down from horizontal direction. The SQS 56 has a somewhat narrower main lobe of 30°, centred at 6m depth and steered horizontally. Both sonars create acoustic fields that are omnidirectional in azimuth, although the 53C also can create beams covering 120° azimuthal sectors that can be swept from side to side during transit.

Canary Islands, 2002

Information is not readily available on the types of naval sonars employed during the 2002 Neo Tapon exercise. However, given that at least one aircraft carrier, 50 surface vessels, 6 submarines and 30 aircraft were participating in 'acoustic exercises' at the time of the strandings (Department of the Environment, 2002), it can be reasonably assumed that tactical hull-mounted sonar systems similar to those used during the 2000 Bahamas stranding event were in operation. Table 2 lists the types of surface ship sonar systems used by the navies of the 11 NATO countries reported to have participated in the Canary Islands exercise.

Table 1

Summary of acoustic source properties.

	TVDS low frequency	TVDS mid frequency	AN/SQS 53C	AN/SQS 56	Air gun array
Waveform	HFM/CW[1]	HFM/CW	FM/CW[1]	FM/CW	BB pulse[2]
Source level[3]	228dB[4]	226dB[4]	235dB	223dB	260dB[5]
Pulse duration	4sec	4sec	1-2sec	1-2sec	0.02sec
Inter-pulse time	1min	1min	24sec	24sec	10-12sec
Centre frequency	600Hz	3,000Hz	2,600Hz 3,300Hz	6,800Hz 7,500Hz 8,200Hz	Broadband[6]
Bandwidth	250Hz	500Hz	100Hz	100Hz	Wideband[7]
Source depth	70-85m	70-85m	8m	6m	6-10m
Beamwidth	23°	20°	40°	30°	Function of freq
Beam direction	Horizontal	Horizontal	3° down from horizontal	Horizontal	Vertical

[1] Hyperbolic frequency modulated (HFM), continuous wave (CW), and frequency modulated (FM).

[2] Broadband (BB).

[3] The source level is the estimated acoustic pressure level of the radiated sound from a source as measured in the far-field and then back-propagated to a reference distance, usually 1m, from the acoustic center of the source. Source levels (rms for sonars and 0-pk for the air gun array are in units of dB re 1 μPa @ 1m).

[4] The simultaneous low frequency and mid frequency transmissions considered as one pulse have a source level of 233dB re: 1 μPa @ 1m (coherent addition) and 230dB re: 1 μPa @ 1m (incoherent addition).

[5] 0-pk source level for an equivalent point source along the main beam in the far field.

[6] Peak levels in the 5-300Hz band.

[7] Radiated acoustic energy extending up to several kHz.

Seismic airgun arrays

Air gun arrays are used in seismic reflection surveys to search for oil and gas deposits under the ocean floor. These arrays typically are composed of 12 to 48 air guns that are towed by the survey vessel at 5-10m depth in a horizontally oriented and rectangular geometry with dimensions of approximately 20 × 20m (National Research Council, 2003). The air guns release compressed air simultaneously to create a high level, short duration (20-30ms) sound pulse that is focused in the vertical direction. The air guns are 'fired' once every 10-12s during a survey. The pulse rise times are a few ms and the source levels for an equivalent point source measured in the main beam direction in the far field (i.e. at distances significantly greater than the dimensions of the array) approach 260dB re: 1μPa at 1m zero-to-peak. The pulses usually have maximum energy in the 5-300Hz range, with energy decreasing with increasing frequency. However, it appears that they still contain appreciable energy up to several kilohertz (Fontana, 2002; Diebold *et al.*, 2003).

A summary of the salient features of the sonars used during the 1996 Greek event (the TVDS source described in D'Amico and Verboom, 1998) and during 2000 Bahamas event (the AN/SQS 53C and 56 sonars; Anon., 2001), as well as the air gun arrays reported in National Research Council (2003) is given in Table 1. All ships involved in these events travelled at speeds of 5kt (2.6m s^{-1}) or greater during operation.

PROPERTIES OF THE ENVIRONMENT

The first obvious environmental similarity between these stranding events is that the acoustic source(s) was operated in a region inhabited by beaked whales and within tens of kilometres of land. These regions contain areas with complex, steeply-sloping bathymetry and places where water depths of 1km or greater exist. The ocean regions overlying these types of bathymetric features may be desirable habitats for beaked whales. However, the characteristics of the ocean bottom are of secondary importance in determining the properties of the acoustic fields. The interactions of the sound fields with the ocean bottom appear to have been minimal, except possibly at short ranges from the source(s) and very close to land (where the bathymetry begins to shoal), because of the depth dependence of the water column sound speed. For the case of the sonar systems, bottom interaction also was reduced by the source radiation pattern, which focused the sound in the horizontal direction. For each stranding event, the dependence of the speed of sound on depth (Figs 1 and 2; discussed below) appears to have created a waveguide, or acoustic lens, that focused sound from sources within the waveguide to long ranges, i.e. ranges that approach the distance of the sound source(s) from land. As discussed below, one aspect of waveguide focusing is the change in the rate of geometrical spreading of the sound field from spherical to cylindrical spreading after the transition range, r_t, resulting in a decrease in transmission loss in decibels equal to $10\log_{10}(r/r_t)$.

During the 1996 Greek stranding event, the acoustic waveguide was centred at a depth of 85m (Fig. 2, right hand panel), corresponding to the depth of the TVDS deployment (D'Amico and Verboom, 1998). The type of acoustic waveguide present in this environment is formed by the same physical processes that form the acoustic waveguide throughout the deep oceans of the world. That is, it is formed by the combined depth dependence of water temperature and ambient pressure. Temperature typically decreases or remains constant with increasing depth (unless the salt content increases to compensate for the effects on density). In contrast, the ambient pressure, caused by the weight of the overlying water column, monotonically increases with depth. The speed of sound in water decreases with decreasing temperature but increases with increasing pressure, so that the interplay of these two factors creates a deep ocean acoustic waveguide. This deep ocean waveguide, or sound channel, is so important to deep water acoustic propagation that it has been assigned two acronyms, the SOFAR (sound fixing and ranging) channel and the DSC (deep sound channel). The depth of the centre of the deep sound channel is a function of latitude, being deepest in equatorial regions where the surface waters are warm, and ascending to the surface at high latitudes (e.g. Medwin and Clay, 1998). The acoustic waveguide at 85m in

Table 2

Surface ship sonar systems of the 11 NATO countries reportedly participating in Neo Tapon 2002 (Jane's Underwater Warfare Systems, 2004; Friedman, 1989).

Country	System	Frequency (kHz)	Type[1]	Installed on (class)	Number of units[2]
Belgium	AN/SQS 510	4.3-8	HM	Wielingen	3
Canada	AN/SQS 510	4.3-8	HM	Halifax	12
			VDS/HM	Iroquois	4
France	DUBA 25	8-10	HM	Type A69	9
				Cassard	1
	DUBV 23	4.9-5.4	HM	Suffren	1
				Tourville	2
				Georges Leygues	4
	DUBV 24	4.9-5.4	HM	Cassard	1
				Georges Leygues	3
				Jeanne d'Arc	1
	DUBV 25	4.9-5.4	HM	Cassard	1
	DUBV 43B/C	5	VDS	Suffren	1
				Georges Leygues	7
Germany	DSQS 21	In the band 3-14	HM	Bremen	8
				Lutjens	1
Greece	1 BV	Greater than 14	HM	Thetis	5*
	AN/SQS 56	6.7 - 8.4	HM	HYDRA	4
	(DE 1160[#])				
	(DE 1164)				
	AN/SQS 505	7	HM	Kortenaer	8
	DE 1191	5-7	HM	Charles F. Adams	2
Norway	TSM 2633	6-8	HM	Oslo	3
	(Spherion)				
Portugal	DUBA 3A	22.6-28.6	HM	Cdt Joao Belo	3
	AN/SQS 510	4.3-8	HM	Cdt Joao Belo	3
			HM	Vasco da Gama	3
Spain	AN/SQS 35	13	VDS	Baleares	5
	AN/SQS 56	6.7-8.4	HM	Baleares	5
	(DE 1160[#])			Descubierta	6
	(DE 1164)			FFG 7	6
Turkey	AN/SQS 26	3	HM	Knox	5
	AN/SQS 56	6.7-8.4	HM	Barbaros	4
	(DE 1160[#])			FFG7	7
	(DE 1164)			YAVUZ	4
	DUBA 25	8-10	HM	Type A69	6
UK	Type 2016	4.5-7.5	HM	Invincible	3
				Type 42	7
	Type 2050	4.5-7.5	HM	Type 22	5
				Type 23	16
				Type 42	11
USA	AN/SQS 53	3	HM	Spruance	10
				Ticonderoga	27
				Arleigh Burke I/II/IIIa	38
	AN/SQS 56	6.7-8.4	HM	FFG 7	33
	(DE 1160[#])				
	(DE 1164)				

[1] HM: hull-mounted; VDS: variable-depth sonar.

[2] Number of units is the total number in each country's navy, NOT the number of those units in the exercise.

*May actually be an acoustically passive, rather than active, sonar system; not clear from the references.

[#] The DE 1160 and DE 1164 systems are very similar to the SQS 56 sonar.

the Mediterranean Sea is atypical of those found at mid to low latitudes in other parts of the world's oceans, where the depth of the waveguide centre is several hundred metres.

The acoustic waveguide that appears to have been present in the other mass stranding events discussed here is of a different type than the SOFAR channel. It existed in the uppermost part of the water column, again corresponding to the depths where the acoustic sources were operating (8m and 6m for the AN/SQS 53C and 56 sonars, respectively, and 5-10m for the typical deployment depths of seismic air gun arrays). These waveguides at the surface, called surface ducts, are fairly common features throughout the world's oceans, particularly during the winter and spring months (Urick, 1983). They are formed by mixing of the near-surface waters by convection and by ocean surface wave activity generated by atmospheric winds. This mixing forms a surface layer with nearly constant temperature so that sound speed increases with depth in the layer solely due to an increase in pressure. For purely isothermal conditions, the sound speed gradient is expected to be $0.016\text{m s}^{-1}\text{ m}^{-1}$ (Jensen *et al.*, 1994, p.25). A smaller positive sound speed gradient can occur due to very slight decreases in temperature with depth, as appears to have occurred during the March 2000 Bahamas event (Anon., 2001; Fromm and McEachern, 2000).

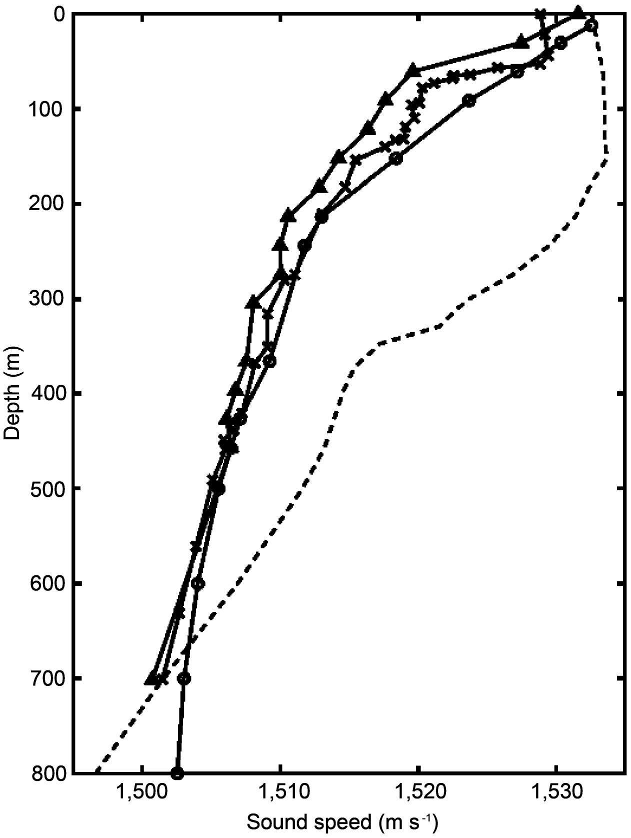

Fig. 1. Sound speed profiles derived from 3 XBTs collected in the vicinity of the Canary Islands around the time of the 2002 stranding event (plotted as circles, triangles and 'x's) along with the XBT-derived sound speed profile from the Bahamas 2000 event (dashed curve). An XBT measures temperature as a function of time after its deployment. The temperature data were converted into sound speed using an empirical equation of state for seawater and a salinity profile representative of the location of interest, typically extracted from an oceanographic database. An assumed descent rate for the XBT was used to derive depth. Deviations of the true descent rate from that assumed can lead to distortions in the derived sound speed profile, therefore, the surface duct depths of about 50m in the Canary Islands and about 150m in the Bahamas 2000 XBT are only approximations.

Fig. 1 shows the sound speed profiles derived from three expendable bathythermograph (XBT) profiles taken in the vicinity of the Canary Islands around the time of the 2002 naval exercise along with an XBT-derived sound speed profile from the Bahamas 2000 event (dashed curve). Two of the Canary Islands profiles show downward-refracting conditions near the surface (i.e. a steady decrease in sound speed with increasing depth), but one profile (denoted by 'x's) indicates the presence of a surface duct of about 50m thickness. The surface duct in the Bahama 2000 profile is about three times this thickness. This feature effectively traps mid to high frequency sound radiated by acoustic sources within the duct, such as surface ship sonars, so that the properties of the water column at greater depths and the ocean bottom are of secondary importance except at close range or close to land. At low frequencies, the sound is no longer effectively trapped by the duct because the acoustic wavelength (equal to the medium sound speed divided by the frequency) is too large in comparison to the duct thickness. The minimum frequency, f_{min}, in kilohertz, trapped by a surface duct of thickness H, in metres (Urick, 1983, p.151) is,

$$f_{\min} \simeq 176 / H^{3/2}$$

As an example, the minimum frequency for a 50m duct is 500Hz.

The physical processes of surface layer mixing that create and maintain surface ducts at mid and lower latitudes also tend to decrease the acoustic transmission efficiencies of these ducts. That is, the roughness of the ocean surface due to wave activity scatters sound out of the duct. Note that a weak sound speed gradient in the duct, as apparently existed in the Bahamas incident, can help reduce the scattering effects due to surface roughness by causing the sound field to interact at more grazing incidence with the surface. In addition, wave breaking injects bubbles into the water column that significantly scatter and absorb sound at mid-frequencies and above (i.e. above 1kHz). Without these mixing processes, the near-isothermal mixed layer conditions necessary for surface ducts are soon lost through

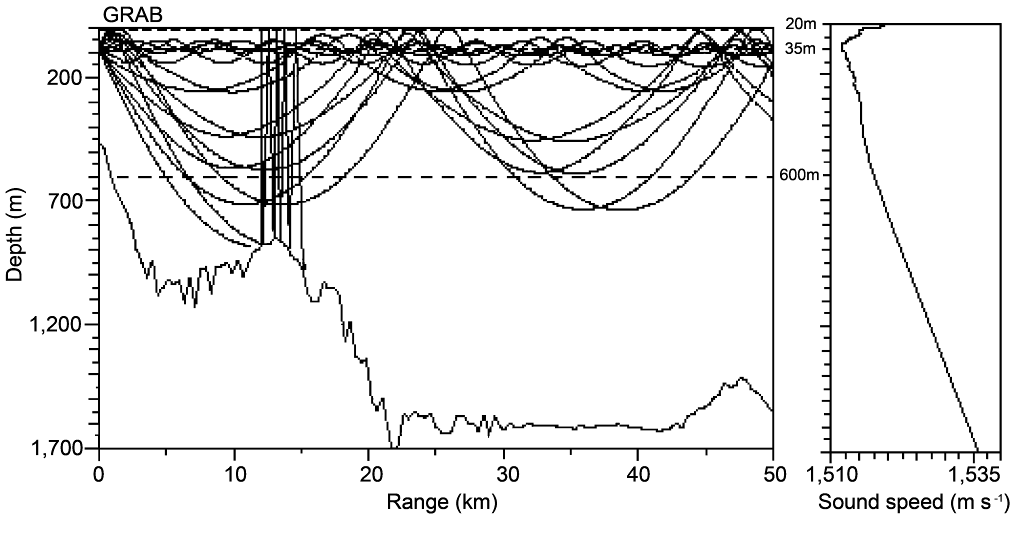

Fig. 2. Ray-trace for the sound field from the TVDS source at 85m depth in the 1996 Greek mass stranding event along with the sound speed profile. Rays were launched from the source at 0km range in the angular interval about the horizontal direction corresponding to the vertical beam pattern of the TVDS source (Table 1). Horizontal dashed lines are placed at 20, 85 and 600m depth in the left panel (fig. 8.2.1 of D'Amico and Verboom, 1998).

solar heating. In fact, the diurnal variability of surface ducts has been recognised for over a half century and is referred to as the 'afternoon effect' (Urick, 1983). These and other properties of surface ducts have been extensively studied due to their importance in surface ship tactical sonar performance (e.g. Schulkin, 1968; Baker, 1975; Urick, 1979; 1983; Hall, 1980).

Therefore, the most acoustically efficient surface duct conditions exist shortly after medium to strong winds (sufficient to cause wave breaking) have subsided and solar heating of the surface layer is minimised, e.g. by cloud cover or night. Since the pitching/rolling motion of a surface ship is reduced, calm sea conditions also help keep the main beam of hull-mounted sonar systems directed into the surface duct. In addition, the naturally-occurring background noise levels in the ocean (predominantly associated with ocean surface wave activity; Wenz, 1962) generally decrease under calm conditions so that the signal-to-noise ratio (SNR) of man-made signals correspondingly increases. Calm sea conditions with a pronounced surface duct prevailed in the New Providence Channel during the March, 2000 event (Anon., 2001; Fig. 1). Likewise, an anomalous weather pattern that led to the absence of trade winds existed during the 2002 Canary Islands event. In addition, the situation that resulted in the strandings appears to have occurred at night, since the initial discovery of the stranded animals occurred in the morning (Department of the Environment, 2002).

Enclosed basins may also present special conditions for the existence of surface ducts. Under open ocean conditions, white caps, which indicate the presence of bubbles, typically begin to occur when the wind speed exceeds 7-10kts i.e. 3-5m s^{-1} (Wenz, 1962). This white-capping activity is modulated by open ocean swell (Phillips, 1977). In enclosed basins, where deep ocean swell activity is reduced by bathymetric/topographic blockage, the onset of white-capping may be suppressed.

A further environmental factor that plays a role in the efficiency of sound propagation at higher frequencies is the average water temperature. Sound absorption increases with decreasing temperature above 3kHz so that, whereas the received sound levels at 30km range at 3kHz are less than 1dB lower in waters at 4°C than in 24°C waters, they are 10dB lower at 8kHz and 15dB lower at 10kHz. A near-surface water temperature of 24°C is representative of the conditions in the Bahamas 2000 event (Anon., 2001; Fromm and McEachern, 2000). The temperature dependence of sound absorption is discussed later.

PROPERTIES OF PROPAGATION

Several textbooks describe the properties of acoustic fields in detail (e.g. Brekhovskikh and Lysanov, 1991; Jensen *et al.*, 1994; Kinsler *et al.*, 1982; Medwin and Clay, 1998; Richardson *et al.*, 1995; Tolstoy and Clay, 1987; Urick, 1979; 1983). Only brief comments on one aspect of acoustics, that of sound propagation in waveguides, are provided here given its potential significance to the stranding events discussed in this paper.

An important aspect of the acoustic focusing effects of waveguides is the change in the rate of geometrical spreading after a certain transition range, r_t. In a waveguide, the decrease in sound pressure amplitude with increasing range due to geometrical spreading occurs at the rate of the inverse square root of the range ('cylindrical' spreading) after the transition range (because the sound field has now filled the waveguide), rather than decreasing inversely with the range itself ('spherical' spreading). Note that arrays of sources, properly oriented, can fill a waveguide with sound more effectively than individual sources, thereby decreasing geometrical spreading loss. The net result of the difference in geometrical spreading is that the acoustic energy in a duct (proportional to the square of the pressure amplitude, on average) decreases at a rate that is the range times smaller than in spherical spreading, at ranges greater than the transition range. An equivalent statement is that the transmission loss (TL) due to cylindrical spreading increases with the range, r after the transition range, r_t, as

$$20\log\frac{r_t}{r_{ref}}+10\log_{10}\left(r/r_t\right)$$

where r_t is the transition range, compared to:

$$20\log_{10}\left(r/r_{ref}\right)$$

for spherical spreading (r_{ref} typically is 1m), so that the difference between the two in decibels after r_t equals:

$$10\log_{10}\left(r/r_t\right)$$

Therefore, received sound fields in waveguides created by sources within them have significantly higher levels than otherwise at ranges greater than the transition range. The numerical modelling results presented later quantify this difference for some simple environments.

The waveguide boundaries are more important in determining the sound propagation characteristics than the interior of the waveguide itself. In shallow water (e.g. near the coast) and at low frequencies, a waveguide is often formed by reflection from the underside of the sea-surface and reflection from the ocean bottom. In these cases, the water depth and its spatial variation have a significant effect on the propagation properties. In addition, interaction with the bottom causes loss of energy from the sound field. This loss is due both to sound penetration into the bottom, which usually is much less efficient at transmitting acoustic energy than the ocean, and to scattering from bottom roughness. Broadband propagation in shallow water waveguides is also quite dispersive. Dispersion occurs when the speed at which energy is transferred down the waveguide, called the group speed, is a function of frequency. This frequency dependence causes the time spreading of a broadband pulse to increase with increasing propagation distance. In shallow water, the energy at higher frequencies is transferred at higher group speeds than at lower frequencies (that is, until the frequency becomes so low that most of the energy is effectively travelling within the ocean bottom). Therefore, the received waveform in shallow water from a source such as an air gun or an explosion will not be a pulse. Instead, it generally will begin with the highest frequencies and evolve to lower frequencies with increasing time. The total duration of the arriving signal increases with increasing range and the received signal duration can be used to estimate the range of the source.

A waveguide boundary also can be formed by refraction due to the increase in water sound speed with increasing distance from the central axis of the waveguide. Sound propagating in acoustic waveguides formed by refraction in the water column usually attenuates at a much lower rate than in shallow-water-type waveguides because it is isolated from interaction with the ocean boundaries. The effect is particularly pronounced when isolated from the sound-attenuating ocean bottom. In fact, ocean acoustic waveguides formed by refraction within the water column are some of the most efficient waveguides for energy transmission found in nature. The frequency dispersion of broadband pulses in these types of waveguides can be negligible. Group speeds can either increase or decrease with frequency, but typically at significantly lower rates than in shallow water. The reason is that, from a ray theory point of view, the increase in propagation distance of more steeply propagating rays is compensated for (partially to fully depending upon the sound speed gradients) by the increase in medium sound speeds with increasing vertical distance from the waveguide axis (depth of minimum sound speed). In effect, pulses tend to remain as pulses during propagation. One consequence is that rapid signal rise times are not degraded appreciably by frequency dispersion during propagation, but change only as a result of frequency-dependent attenuation mechanisms.

PREDICTION OF SOUND FIELD PROPERTIES

The issues that need to be addressed to accurately predict the properties of the underwater sound field during mass stranding events are: (1) the transmission characteristics of the sources (e.g. signal types, levels, frequency content, duty cycle, directionality, etc.) and times of transmission and locations of the sources over the course of the event; (2) the important environmental phenomena that need to be included in the modelling; (3) the capability of the propagation codes to accurately model the important environmental phenomena (i.e. how well do the models capture the relevant physics); and (4) the availability and quality of the environmental information required as input to the propagation models. Each of these topics will be discussed in turn.

Regarding the first issue, the properties of the TVDS source and the nominal characteristics of the hull-mounted sonar systems are well known, as described earlier (although changes in hull-mounted sonar performance over time due to aging and use are not accounted for since frequent system calibrations are not performed; Anon., 2001). However, the actual output levels and directionality of seismic air-gun arrays at higher frequencies are presently active areas of investigation (e.g. Diebold *et al.*, 2003). Information on source location over time typically is recorded in a ship's log(s), although that information may not be openly available.

The environmental property of greatest relevance in these events is probably the spatial dependence of the ocean sound speed; primarily on depth, but also on range and azimuth. This sound speed information determines the existence and spatial extent of any ducts or sound channels and dictates the overall propagation characteristics. A second important environmental property is the intrinsic sound absorption of the ocean. At the frequencies of interest here, this is due primarily to endothermic reactions associated with magnesium sulphate and boric acid (Fisher and Simmons, 1977). It increases approximately at the rate of the square of the frequency and so becomes increasingly important with increasing frequency in limiting the spatial extent of propagation (see later). Note that wind-generated ocean ambient noise in the mid to high frequency band also decreases approximately at the rate of the square of the frequency (Wenz, 1962), so the received signal-to-noise ratios from sources with frequency-independent source levels also are roughly frequency independent. For sound fields that interact with the ocean surface as in surface duct propagation, the roughness of the sea-surface and the near-surface bubble content of the water column are important features. For waveguides formed by refraction within the water column, the temporal and spatial variability of the water column in the refraction region, for example due to internal wave activity, may play an important role. Significant factors for sound fields that interact with the ocean bottom (including those in shallow water and at short range to the source unless the directional characteristics of the source reduce bottom interaction as with the TVDS and hull-mounted sonars) are the bathymetry, interface roughness and sub-bottom geoacoustic properties.

Other phenomena that pertain to propagation at mid frequencies such as the presence of fish schools, precipitation, and nonlinear internal waves (e.g. solitons), may also be significant in certain situations.

Once the relevant environmental phenomena have been identified, numerical propagation codes that incorporate the physics of sound field interactions with these phenomena must be used in the modelling effort. The physics of sound propagation is based upon the laws of conservation of mass, linear momentum and energy. The equations expressing these laws are typically combined to obtain the acoustic wave equation, a second order partial differential equation that expresses the relationship between changes in space and time of acoustic pressure. Equations can be derived for other acoustic field variables, e.g. acoustic particle velocity, acoustic density and vector acoustic intensity, but acoustic pressure is almost always the quantity of interest. One of the prominent achievements of the acoustics community over the past few decades has been the development of more accurate numerical modelling techniques for acoustic propagation in increasingly complex environments.

Numerical models for ocean sound propagation mainly fall into one of four categories, ray-based codes, normal mode codes, those based on the parabolic equation (PE) approximation to the wave (elliptical) equation and wave number integration codes (Jensen *et al.*, 1994). Propagation codes of each type, as well as others are freely available at the Ocean Acoustics Library website *http://oalib.saic.com*. Methods such as finite element and finite difference techniques can be applied in highly complex and variable environments, but typically require high computing power and long run times. In any case, each of these modelling approaches is based on certain approximations and assumptions in order to calculate the fields in a computationally efficient way. As a result, a given approach is applicable only for a certain realm of propagation conditions. In addition, most codes are not numerical solutions to the acoustic wave equation itself, but rather its frequency-domain analogue (the Helmholtz equation) and so must be run several times to model broadband propagation. Results from an advanced ray-based code (Gaussian Ray Bundle, GRAB; Weinberg and Keenan, 1996) are reported by D'Amico *et al.* (1998). Codes based on all four approaches were used to predict the received fields in the Bahamas, 2000 incident for a small subset of environments (Fromm and McEachern, 2000), although reported results for a wide range of environmental conditions were obtained using a PE-based code (Collins, 1995). Recent enhancements to the PE approach incorporate many of the environmental complexities found in surface duct propagation (Norton *et al.*, 1998).

Accurate predictions of the acoustic field properties require not only the inclusion of the relevant physics in the numerical model, but also availability of accurate information on the environmental inputs. In most cases, collection and/or availability of measured environmental data for a stranding event is very limited. In some instances, a few *in situ* profiles of water temperature may have been collected to derive the dependence of water sound speed on depth. The spatial dependence of the sound speed profiles throughout the area of interest typically must be inferred from historical databases, or possibly from fine-scale oceanographic models (e.g. Fox, 1996). Historical databases also provide information on the pH of the water column, which provides a measure of the amount of boric acid present and is required for accurate estimates of intrinsic sound absorption. At the least, approximate absorption estimates can be obtained from *in situ* measurements of water temperature alone (see later). Sea-surface roughness, particularly important in surface duct propagation situations, can be estimated using a model of the ocean surface wave spectrum (e.g. Pierson and Moskowitz, 1964) if the wind speed is known or possibly from visual observations. The bubble content and distribution in the near-surface layer and the degree of internal wave activity are only estimates. In contrast, large-scale ocean bathymetric information is readily available for situations in which bottom interaction is important (Sandwell *et al.*, 1998). However, the geoacoustic properties of the bottom and its roughness must often be inferred from the geological setting. In any case, uncertainty in the environmental inputs is probably the source of greatest error in predicting sound fields. Lack of knowledge of the animals' locations over time is an even greater source of error if an attempt is made to use the acoustic modelling results to estimate the animals' maximum received levels and 'unweighted sound exposure' (defined as the integral of pressure squared over time; American National Standards Institute (ANSI, 1994)).

An example of a numerical modelling output for one of these events is presented in Fig. 2. This ray tracing result, from the SACLANTCEN report of the 1996 Greek stranding event (fig. 8.2.1 of D'Amico and Verboom, 1998), was calculated using the GRAB propagation code (Weinberg and Keenan, 1996). The input sound speed profile and ocean bathymetry are plotted in the right panel. The profile shows a sound channel with a sound speed minimum (axis) at 85m, corresponding to the depth of the TVDS source. The main beam of the source was directed horizontally along the sound channel axis. The ray traces in the left panel provide a picture of the paths of acoustic energy flow as a function of range and depth. They show that two types of waveguides dictated the propagation characteristics. One waveguide, spanning the upper 800m or so, was formed by reflection from the ocean surface and refraction in the mid water column. The second was formed purely by refraction, which confines the acoustic energy to a relatively narrow depth interval centred at 85m at all ranges. The received sound levels at a given range are highest (by around 10dB; D'Amico and Verboom, 1998) within this depth interval (see below). The vertical directionality of the source minimised the interaction of the sound field with the ocean bottom at close range (Fig. 2). Significant interaction did not occur until the 10-15km range and the resulting reflection and scattering of the field to shallower depths likely did not contribute significantly to the received levels.

Several additional examples of numerical modelling results specific to the 1996 Greek event and the Bahamas 2000 event can be found in D'Amico *et al.* (1998) and Fromm and McEachern (2000) respectively. An overall comparison of the results for the two events shows that the received levels at 3kHz at a given range differ by about 10dB due to the difference in the sonar source levels in this frequency band (Table 1). Some of the important aspects of waveguide propagation, particularly propagation in surface ducts, are presented below.

GENERAL MODELLING RESULTS

Simple numerical modelling

The importance of waveguides in underwater sound propagation, as discussed previously, can be illustrated with some simple examples. Two cases have been considered, one that is representative of the environmental conditions in the 1996 Greek event and one that illustrates the focusing effects of surface ducts. In both cases, the environmental properties are independent of range and azimuth, including the water depth which was fixed at 1.5km. Also, the source frequency was 3kHz in both cases. Calculations were performed using the GRAB ray tracing code that uses a Gaussian ray bundle approach for deriving the sound field amplitudes (Weinberg and Keenan, 1996).

Fig. 3 shows the ray tracing results over depth and range out to 30km for a sound speed profile representative of those collected in the 1996 Greek event (the profile in the left panels is nearly identical to that in Fig. 2). The source is placed at 8m depth for the upper right panel whereas it is at 85m in the lower panel. The source depths are indicated by the horizontal dotted lines in the sound speed profile plots. For an 8m source in this environment, a 'shadow zone' – i.e. a region that contains no rays and thus has very low sound levels – exists in a semi-circular region that extends approximately 1-26km in range. This shadow zone is partly filled by energy that reflects off the bottom (rays requiring more than one bottom reflection to reach the 30km range have been suppressed in this plot for clarity), but bottom interaction significantly lowers the sound levels received by shallow receivers. In contrast, the sound field created by a source at 85m depth, corresponding to the depth of the waveguide axis, fills in this shadow zone at depths below the source to a large extent. Sound is also focused in a depth interval centred at 85m at all ranges.

These observations from the ray-trace plots are further illustrated in the corresponding transmission loss versus range plots at 3kHz presented in Fig. 4. These plots were obtained by incoherently summing the individual ray energy to obtain the total field at a given range, equivalent to incoherently averaging the field over small range intervals centred on the range. The solid curve in each panel on the right is for a source at 8m and the dotted curves are for a source at 85m. The receiver depth is 8m in the upper right panel and 85m in the lower right panel. The straight portion of the two curves in the upper right panel and the solid curve in the lower panel (i.e. for an 8m source/8m receiver, 8m source/85m receiver and 85m source/8m receiver), extending from a few kilometres to 25-26km represent the shadow zones for these source/receiver combinations. The received levels in these regions are determined by bottom-reflected energy and therefore show large transmission loss. Over a range interval of 25-30km, the change with depth in the sound speed profile at depths greater than 100m causes a focusing of the refracted rays and the received levels to increase by 20dB or so. This focusing effect clearly illustrates the impact of the sound speed profile on the character of ocean-borne sound fields.

An even more dramatic focusing effect is shown by the dotted curve in the lower right panel of Fig. 4, corresponding to the transmission loss versus range for a receiver at the waveguide axis depth of 85m due to a source at this same depth. The sound field levels are 20dB greater

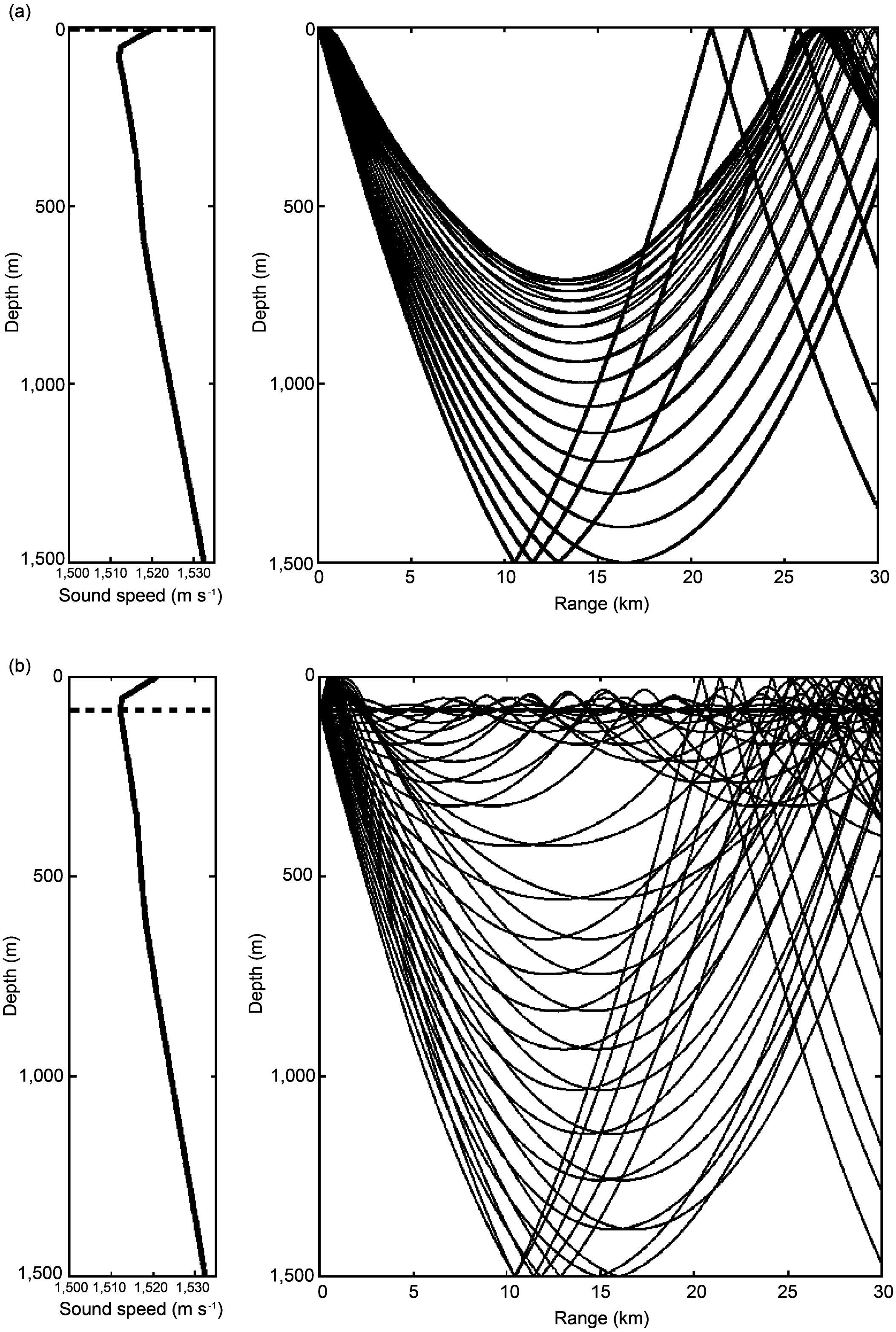

Fig. 3. Ray-trace in range and depth for a Mediterranean-like sound-speed profile (left) for a source depth of 8m (upper plot) and 85m (lower plot).

than the other source/receiver combinations at almost all ranges greater than the 1-2km transition range because of the focusing effects of the waveguide.

In the next example, presented in Figs 5 and 6, the source depth remains fixed at 8m. However, the sound speed profile in the uppermost 100m is modified from downward-refracting conditions (the sound speed steadily decreases with increasing depth) to surface ducting conditions (the two profiles in the leftmost panels). The corresponding ray-tracing plots show how the ray paths are altered by the surface duct, causing a focusing of sound in the near-surface waters. These effects are quantified in the transmission loss as a function of range plots in Fig. 6, where the levels received at 8m depth in the presence of a surface duct (the

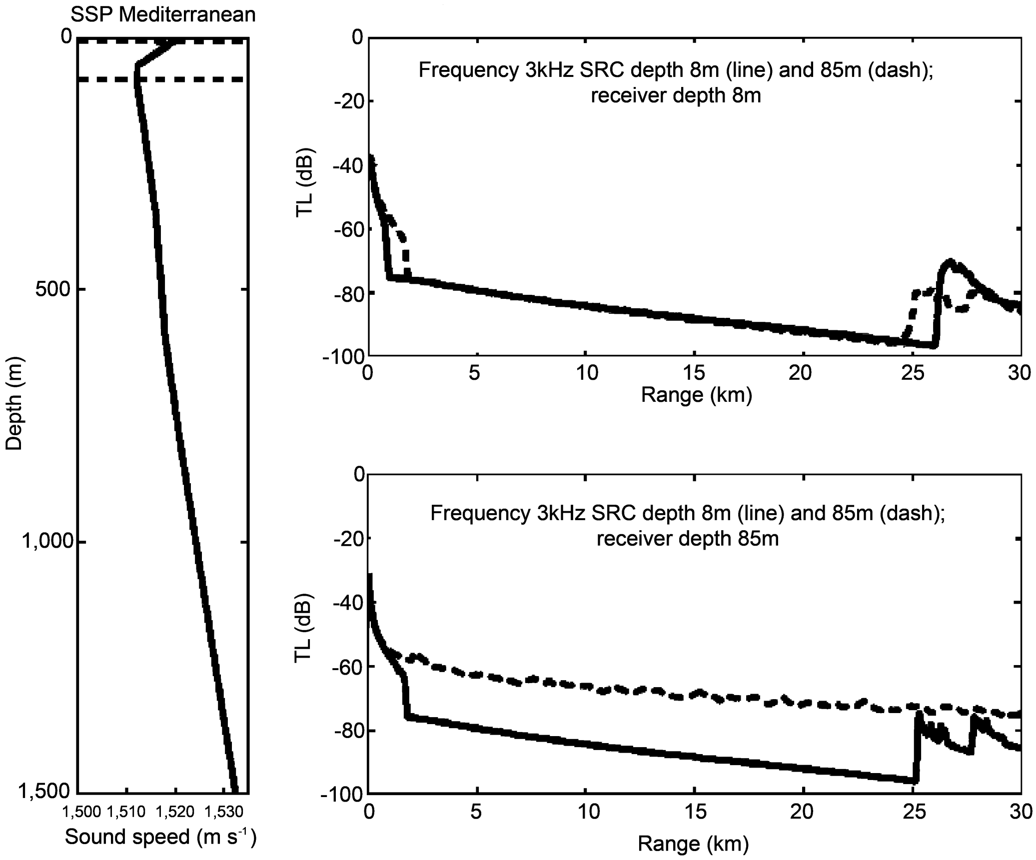

Fig. 4. TL as a function of range for a Mediterranean-like sound speed profile (left) with source depths of 8m (solid lines) and 85m (dashed lines) and receiver depths of 8m (upper right) and 85m (lower right). The estimated received levels as a function of range for a specific source can be easily determined by adding the source's source level from Table 1 to the TL values in the plots. For example, at 5km in the upper plot where the TL is 80dB, the estimated received level for the TVDS mid-frequency source is 146dB re: 1μPa (= 226dB – 80dB).

solid curve in the upper right panel) are 15-20dB greater than otherwise past the 1km transition range. The reason for choosing a receiver depth of 300m for comparison was so that it was significantly deeper than the base of the duct.

The main conclusion to draw from these examples is that the depth-dependence of the sound speed profile can have a dramatic effect on the properties of an underwater sound field. In particular, the sound levels inside an acoustic waveguide created by a source within the waveguide are significantly greater at almost all ranges greater than the transition range than when a waveguide does not exist or when either the source or receiver is not within the waveguide.

A semi-empirical model of surface duct propagation

The previous examples are simplified representations of naturally-occurring propagation conditions. For example, no rough surface scattering, interaction with near-surface bubbles, or horizontal variability of the environment was included. Because of the importance of surface ducts in hull-mounted sonar system performance, extensive measurements of surface duct propagation have been made throughout the world's oceans (Urick, 1979; Urick, 1983). Before the advent of modern computers, the measurements were fitted with simple semi-empirical equations to give a prediction capability. These equations account for transmission loss due to geometrical spreading, intrinsic absorption and duct 'leakage'. This latter term includes the effects of all physical processes not taken into account by the other two terms. These equations provide a simple, data-based method of evaluating the changes in propagation conditions due to changes in environmental properties. The semi-empirical surface duct propagation model discussed in this subsection is that given in Baker (1975). In the Baker model, the transmission loss, TL, in decibels is given by:

for short ranges, $r < 0.204\sqrt{H}$

$$\mathrm{TL} = 20\log_{10}(r) + 60.8 + (A+B)r$$

for long ranges, $r > 0.204\sqrt{H}$

$$\mathrm{TL} = 10\log_{10}(r) + 5\log_{10}(H) + 53.9 + (A+B)r$$

In truth, the transition between short and long range in Baker (1975) is given as $\sqrt{0.122H}$, but the value above is used so that the transmission losses given by the two expressions are equal at the transition range. Units for the quantities in these expressions are; r in units of km, the surface duct thickness, H, in metres, and the attenuation coefficients, A and B, with units of dB km^{-1}. The constants 60.8 and 53.9 provide the necessary corrections so that transmission loss in dB referenced to 1m is obtained. The terms involving the logarithm express the loss due to geometric spreading and are derived from the conservation of acoustic energy. The coefficient A is due to sound absorption in the water column. In the Baker model, it is a function of frequency

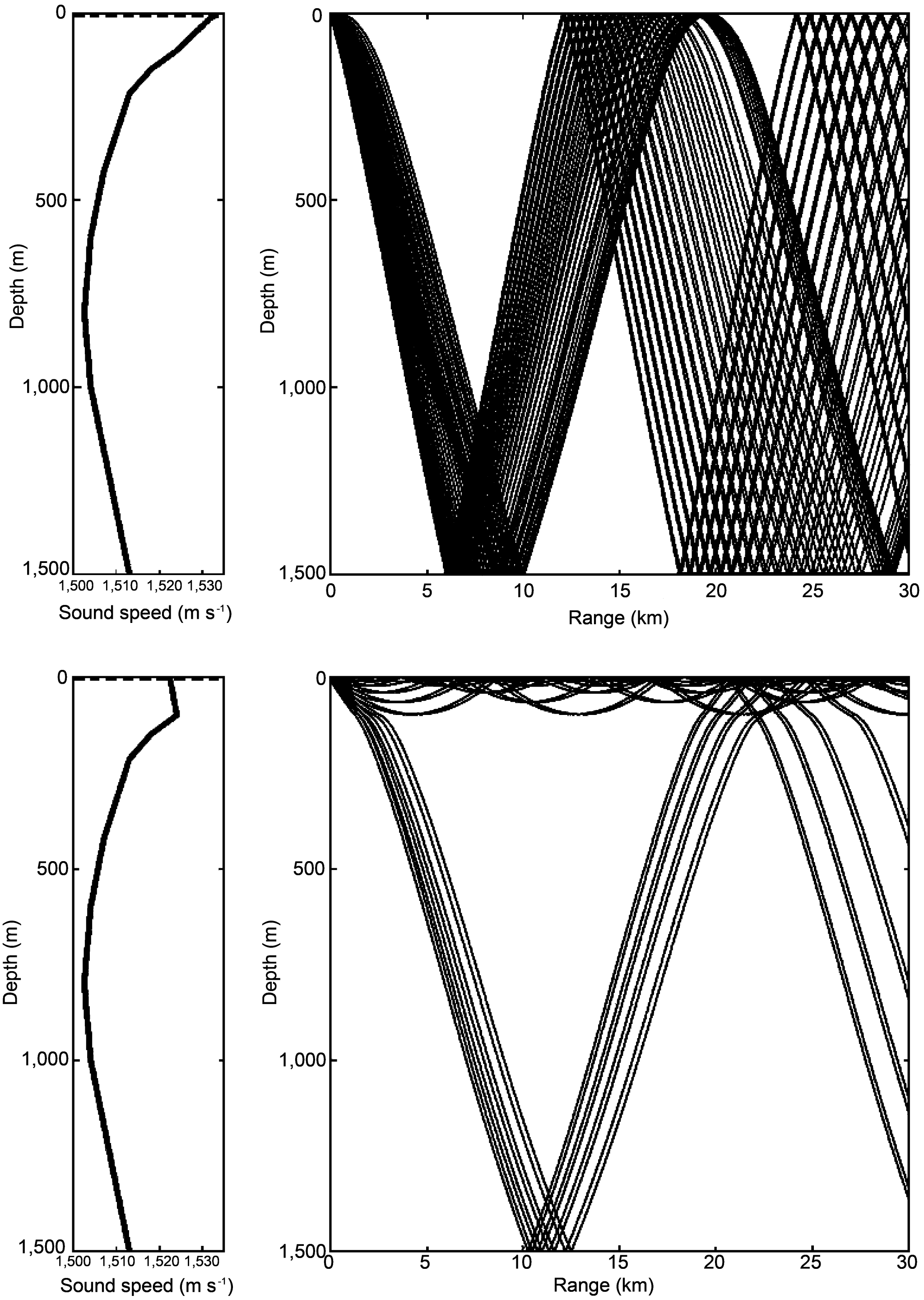

Fig. 5. Ray-trace in range and depth for an omni-directional point source at 8m depth in two eastern Atlantic-like environments that are identical except in the uppermost 100m (left). One has a monotonically decreasing sound speed profile with increasing depth (upper plot) whereas the other one has a 100m thick surface duct (lower plot).

and water temperature only. The expression for A (obtained from work by H.R. Hall at the Naval Undersea Warfare Centre) is:

$$A = \frac{1}{0.9144}\left[\frac{1.776 f^{1.5}}{32.768 + f^{3}} + \frac{1}{1 + 32.768\big/ f^{3}}\left(\frac{0.65053 f^{2} f_{T}}{f^{2} + f_{T}^{2}} + \frac{0.026847 f^{2}}{f_{T}}\right)\right] dB\ km^{-1}$$

where the frequency, f, is in kHz, f_r = 21.9 × $10^{[(6T + 118)/(T + 273)]}$, and T is the water temperature in °C.

The duct leakage coefficient, B, is a function of duct thickness and sea-state as well as frequency and temperature, i.e.:

$$B = \frac{29.1 f}{\sqrt{\left[\left(1452 + 3.5T\right)H\right]}}\left(1.4\right)^{\mathrm{SS}}\ dB\ km^{-1}$$

where SS is the sea-state (see Wenz, 1962 for descriptions of sea-states).

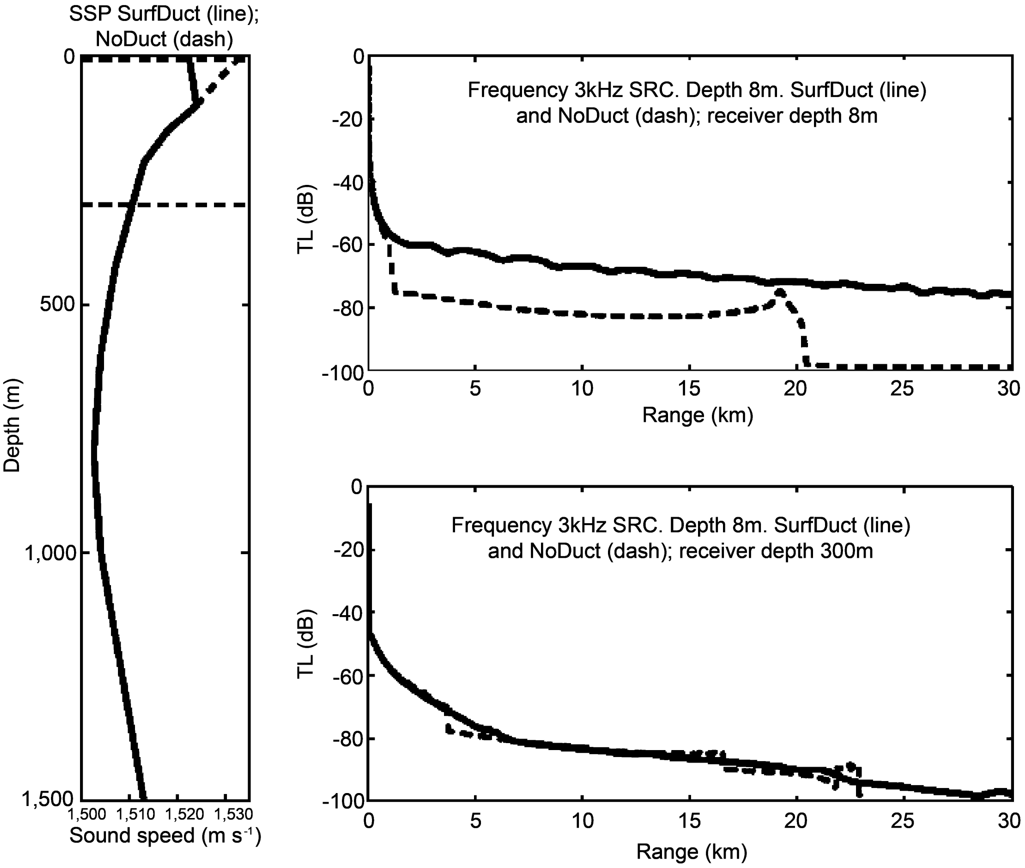

Fig. 6. TL as a function of range for two eastern Atlantic-like sound speed profiles (left) with a source depth of 8m and receiver depths of 8m (upper right) and 300m (lower right). The dashed curves are for a profile with a monotonically decreasing sound speed with increasing depth over the uppermost 100m and the solid curves are for a profile with a 100m thick surface duct. Refer to the caption for Fig. 4 to determine how to convert these TL values versus range into estimated received levels for a given source.

The Baker model was obtained by curve-fitting to a total of 438 open-ocean measurements where all the free parameters in the fit were contained in the coefficient B. The mean errors of the fit were ± 2dB with a standard deviation of 7dB. The result is strictly valid for the range of environmental conditions and experimental geometries in which the data were collected. These were:

Environmental:	
duct depth	24 – 67m
water temperature	15 – 25°C
sea-state	2 to 5
Geometry:	
source, receiver depths	9.1 – 18.3m
source/receiver range	1 – 31km
frequency	3.25 – 7.5kHz

The near-surface water temperatures in the Bahamas and Canary Islands events are at the upper end of the interval of temperatures in Baker’s data sets. Also, although the surface ship sonar depths were slightly less than the source depths in Baker’s data sets and some of the transmitted frequencies may be slightly outside the 3.25-7.5kHz band, the deviations are not large and the Baker model predictions should provide representative results for these events.

The attenuation coefficients A and B in the Baker model contain all of the frequency dependence of the transmission loss of acoustic fields in surface ducts. Whereas A is a complicated function of frequency, the expression for B shows that duct leakage increases in a simple linear way with increasing frequency. The expressions for these coefficients also quantify the effects of changes in environmental conditions on transmission loss. For example, the value of the sea-state appears as a power law exponent in the expression for B so that for each step increase in sea-state, the duct leakage increases by a factor of 1.4. In addition, B is inversely proportional to the square root of the duct depth. To illustrate the effects of changes in these properties, Fig. 7 provides a plot of the duct leakage coefficient in units of dB km^{-1} for duct thicknesses of 60m and 100m at sea-states 2, 3, 4 and 5. The plot shows that a doubling of the duct thickness has the same effect on B as a decrease by one in the sea-state (note that the constant of 1.4 in the expression for B approximately equals $\sqrt{2}$. Similarly, Fig. 8 provides plots of A (dotted curves), B (dashed curves) and the sum of the two (solid curves) as a function of frequency for the three water temperatures of 4°C, 15°C and 24°C. The duct thickness and sea-state are fixed at 60m and sea-state 2. Although duct leakage is only very weakly dependent upon water temperature, intrinsic absorption decreases with increasing temperature at frequencies above 3kHz. At 10kHz, the coefficient decreases from about 1dB km^{-1} at 4°C to 0.5dB km^{-1} at 24°C. Therefore, the 10kHz absorption loss at 30km decreases from 30dB to 15dB due to this 20°C increase in water temperature. Clearly warmer surface waters provide more favourable propagation conditions at the higher frequencies. Note that almost all of the sonar systems in Table 2 operate at these higher frequencies. An interesting question is whether or not lower absorption at higher temperatures is in any way related to

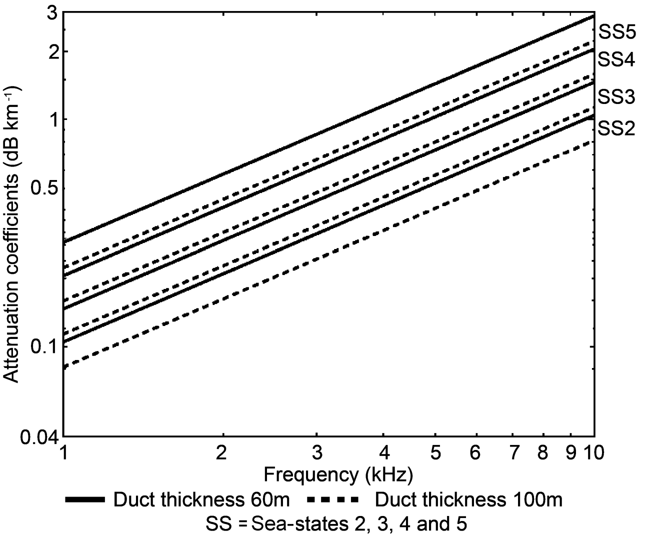

Fig. 7. Duct 'leakage' attenuation coefficients from the Baker model for duct thicknesses of 60m and 100m for four different sea-states.

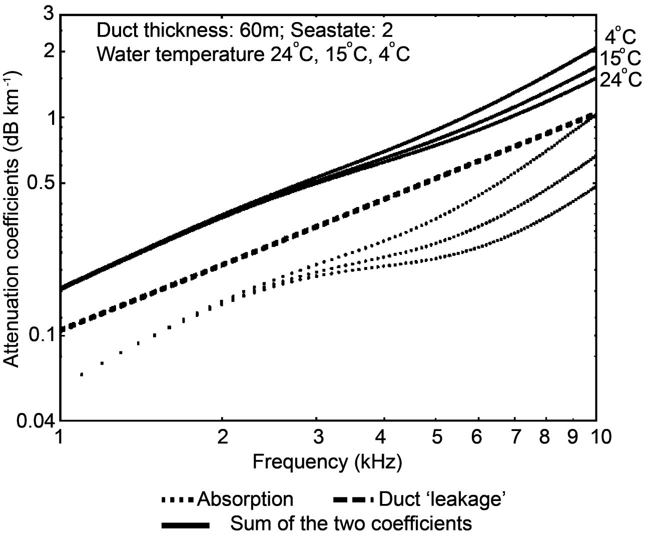

Fig. 8. Effect of changes in average water temperature on the two attenuation coefficients and their sum in the Baker model.

the observation that the number of animals involved in historical Canary Islands stranding events is greatest in the autumn, as reported on the Department of the Environment, Government of the Canary Islands website (2002).

Fig. 7 shows that thicker ducts have less leakage loss than shallower ducts. However, because of the difference in the range where the transition from spherical to cylindrical spreading occurs, thicker ducts also have greater geometrical spreading loss. The difference in TL for two ducts of thicknesses H_2 and H_1 (with all other conditions remaining the same) is:

$$\mathrm{TL}(H_2)-\mathrm{TL}(H_1)=5\log_{10}\left(\frac{H_2}{H_1}\right)-\beta\left(\frac{1}{\sqrt{H_1}}-\frac{1}{\sqrt{H_2}}\right)r$$

where:

$$\beta\equiv\frac{29.1f}{\sqrt{\left[\left(1452+3.5T\right)\right]}}\left(1.4\right)^{SS}$$

Since the second term on the right hand side depends on range whereas the first does not, the transmission loss for a thicker duct changes from being greater than to being less than that of a shallower duct at some crossover range. As an illustration, Fig. 9 shows the TL versus range curves predicted from the Baker model for two duct depths of 60m and 100m at a frequency of 3kHz, a water temperature of 24°C and a sea-state of 2. The crossover range is 16km, as can be determined by setting the TL difference above to zero and solving for range. However, the difference between the two curves is not significant. Therefore, the dependence of the received sound levels on duct thickness is probably negligible. This result holds for frequencies that are appreciably greater than the low frequency cut-off for the duct.

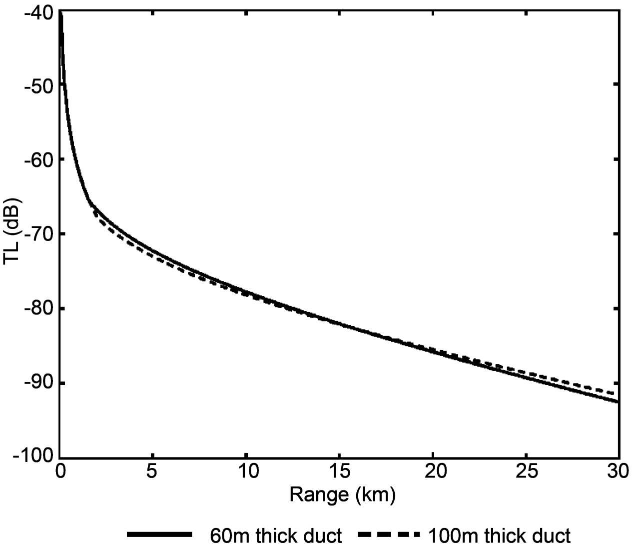

Fig. 9. Transmission loss as a function of range for two different duct thicknesses as predicted by the Baker model. The solid curve is for a duct thickness of 60m and the dashed curve for 100m. Sound frequency 3kHz, water temperature 24°C and sea-state 2.

Calculation of unweighted sound exposure

Sound exposure, SoE, defined as the integral of acoustic pressure, *p*, squared over time (ANSI, 1994), may be an important measure of a sound field's potential to cause temporary threshold shift (National Research Council, 2003). This quantity can be calculated in a straightforward way using a model for the transmission loss (e.g. the Baker model), knowledge of the source transmission properties and its motion and a model of the receiver motion.

The sound exposure for a single pulse of duration T_s, is defined as:

$$\mathrm{SoE(1\ pulse)}=10\log_{10}\left[\int_0^{T_s}p^2(t)dt\right]$$

$$=10\log_{10}[T_s]+10\log_{10}\left[\frac{1}{T_s}\int_0^{T_s}p^2(t)dt\right]$$

$$=10\log_{10}[T_s]+\mathrm{RL}$$

The received level, RL, from the sonar equation (Urick, 1983) is determined by the difference between the source level, SL, and transmission loss as a function of range, TL(*r*), so that:

$$\mathrm{SoE(1\ pulse)} = \mathrm{SL} - \mathrm{TL}(r)+10\log_{10}[T_s]$$

The root mean square (rms) source levels for the sonar systems of interest are listed in the second row of Table 2, along with the pulse durations in the third row. The total sound exposure due to N pulses where the source/receiver range changes from one pulse to the next is:

$$\mathrm{SoE(total)} = 10\log_{10}[T_s] + 10\log_{10}\left[\sum_{i=1}^{N} 10^{\frac{\mathrm{SL\text{-}TL}(r_i)}{10}}\right]$$

The values of r_i in this expression can be obtained from knowledge of the source (ship) tracks and a model of the receiver motion. For example, assume that the source and the receiver travel at constant horizontal velocities with components of relative speed between them of v_x and v_y in the east/west and north/south directions, respectively. At the time of the first pulse, the initial source/receiver distances in the east/west and north/south directions are d_x and d_y and given that the interpulse time, τ (given on the fourth row of Table 1) is constant, then $t = (i-1)\tau$ and the range between source and receiver at the time of the ith pulse is simply:

$$r_i = \sqrt{\left(d_x + v_x(i-1)\tau\right)^2 + \left(d_y + v_y(i-1)\tau\right)^2}$$

In the following example, the environmental properties are those of a duct 100m thick, a water temperature of 24°C and a sea-state of 2, similar to the conditions preceding the Bahamas, 2000 event. Also, the frequency of the source is 3kHz and its signals have an interpulse time, pulse duration and source level equivalent to those listed in Table 1 for the AN/SQS 53C sonar (i.e. 24s, 2s and 235dB re: 1μPa at 1m, respectively). Only pulses with a received level above 160dB re: 1μPa were included in the calculation of the total sound exposure. The motions of the source and receiver were assumed to be such that their range was determined only by an initial range and a constant relative speed. Results for various combinations of starting source/receiver ranges and relative speeds are presented in Figs 10 and 11. The number of pulses that were received above the 160dB re: 1μPa threshold is presented in Fig. 10 and the resulting total sound exposure is shown in Fig. 11. Both quantities are plotted as a function of the relative speed between the source and receiver for positive values from 1-10m s^{-1} in 1m s^{-1} increments (positive relative speeds indicate that the source/receiver range monotonically increases with time). Each figure contains six curves pertaining to six starting source/receiver distances of 1km (uppermost curve in each figure) to 6km (lowermost curve) in 1km increments. The number of received pulses above the threshold (Fig. 10) shows a dramatic rise as the relative speed decreases below a few metres per second. A small relative speed occurs, for example, when the source and receiver tracks are co-linear and the receiver is ahead of the source and travelling at a slightly greater speed. The total sound exposure (Fig. 11) displays the corresponding change in values with the most rapid changes (slopes of the curves) occurring for changes in small relative speeds. The sound exposure values increase by nearly 10dB for a 10-fold decrease in relative speed from 10-1m s^{-1} at all starting ranges. The effect of decreasing starting range is even greater, with a 15dB increase from 6-1km at all relative speeds. This sensitivity is indicative of the importance of the contributions of the pulses at the closest ranges.

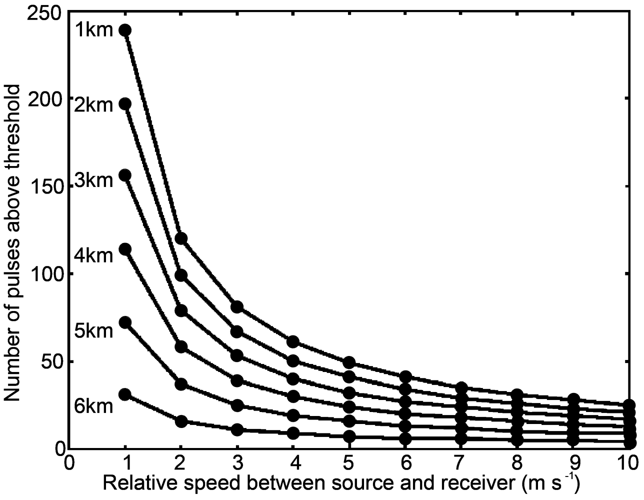

Fig. 10. Number of pulses with a received level above 160dB re: 1 μPa as a function of the assumed relative speed between the source and receiver for 6 starting source/receiver distances of 1-6km in 1km increments.

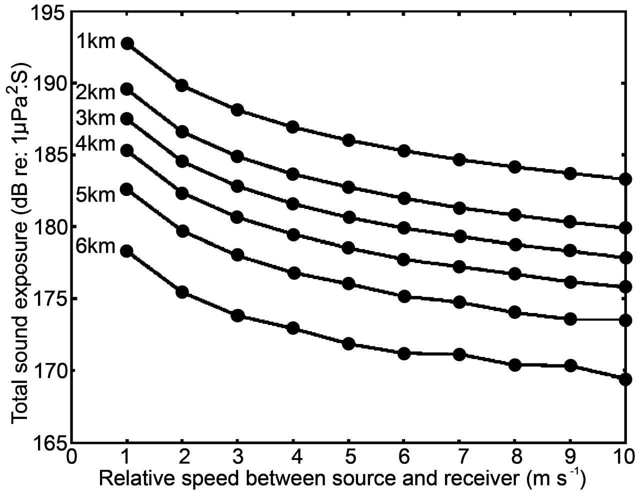

Fig. 11. Total unweighted sound exposure from pulses with received levels above 160dB re: 1μPa as a function of the assumed relative speed between the source and receiver for 6 starting source/receiver distances of 1-6km in 1km increments.

CONCLUSIONS

The acoustic signals transmitted by the sonar systems during these stranding events and seismic air gun arrays have several features in common. The temporal character of each type of signal is a periodic sequence of transient pulses where the time interval between the pulses is on the order of tens of seconds (15-60s). The individual sonar pulses have a time duration of order a few seconds (1-4s) and contain similar types of waveforms (frequency-modulated 'chirps' and continuous-wave 'pings'), whereas a seismic air gun pulse is a short-duration (tens of milliseconds) impulse. In the frequency domain, all sources generate appreciable energy in the mid-frequency (1-10kHz) band (although the radiated spectral levels of seismic air guns in the mid-frequency band is a topic of investigation at present), with TVDS sources and air-gun arrays also generating significant amounts of lower frequency energy. The systems creating the sounds were all designed as source arrays to focus acoustic energy in a specific direction. Arrays of sources also allow the equivalent far-field source level to be much greater than the water column's cavitation limit, which is about 230dB re: 1μPa at the depth of the hull-mounted sonar systems (Urick, 1983). All except the source in the 1996 Greek event were deployed at depths less than 10m. Finally, all sources moved at speeds of 5kts (2.6m s^{-1}) or more during operation.

The environmental settings for all cases was relatively deep water (1km or more) located close to land. Proximity to land is a requisite feature for strandings to occur. It is uncertain whether the environment accentuated the effects of the sounds through reflection and reverberation from the bathymetry. Very close to land, the shoaling bathymetry can focus the sound by a process called upslope conversion. In the cases involving sonar, the horizontal orientation of the source beams helped to minimise bottom interactions. These environmental settings may simply be the preferred habitats for beaked whales. In any case, most, if not all, water column conditions supported ducted waveguide propagation where at least one boundary of the waveguide (the lower one) was formed by refraction in the water column. In most, if not all, cases, the sound source(s) was located within the waveguide.

Sound propagation in acoustic waveguides formed by refraction in the water column has four features of potential significance to the events discussed here. (1) The sound radiated by sources within the waveguide is focused after a certain transition range so that geometrical spreading then occurs at the rate of cylindrical spreading, rather than the more rapidly decreasing spherical spreading. (2) The attenuation of the sound field with increasing range is minimised due to isolation from interaction with the ocean boundaries, particularly with the ocean bottom, which tends to scatter and absorb sound. In fact, ocean acoustic waveguides formed by refraction are some of the most efficient waveguides for energy transmission found in nature. For those events involving surface duct conditions, the weather conditions were calm, thereby decreasing the roughness of the sea-surface and the near-surface bubble content and increasing sound propagation efficiency of the duct. These conditions can also cause an overall decrease in the sound levels for receivers below the duct. Under calm conditions, the decrease in the pitching and rolling of the surface ships helps keep the main beams of their hull-mounted sonars focused within the duct and the decrease in wind-generated ambient noise levels results in an increase in the SNR of the transmitted signals. The average water temperature during the stranding event was relatively warm, thereby decreasing intrinsic absorption at frequencies above 3kHz. (3) The spatial gradients of the sound field amplitude with depth in the water column may be significant in the refractive boundary region. (4) The frequency dispersion of broadband pulses usually is minimal so pulses tend to remain as pulses and signal rise times do not increase appreciably during propagation.

The ability to predict the acoustic propagation characteristics during a given event is limited by the lack of knowledge of the environmental inputs, not by an inability to incorporate the relevant physics (once identified from the environmental conditions) into the numerical models. Unavailability of information on the location of source(s) with time also is a limiting factor in some cases.

Simple numerical models illustrate the focusing effects of waveguides. They show that 20dB increases in received sound levels can occur over extended range intervals after the transition range (typically 1km in extent in the examples presented here) when waveguide propagation conditions exist and both source and receiver are located in the waveguide. Data-based, semi-empirical models of surface duct propagation are useful in providing simple, realistic, quantitative estimates of the mean acoustic field in the duct and changes in the mean field due to changes in environmental conditions. As an example, the effect on the transmission loss due to duct leakage from an increase in sea-state by one value (a change from sea-state 2 to sea-state 3 etc) is equivalent to a nearly 50% increase in source/receiver range. However, changes in duct thickness have a negligible impact (as long as the sound frequency is significantly above the duct cut-off frequency), due to its competing effects on geometrical spreading and duct leakage. Numerical calculations of sound exposure using a semi-empirical surface duct model and simple models of the source and receiver motion indicate the importance of relative source/receiver speed and minimum source/receiver range to the total exposure.

In conclusion, the underwater sound fields created by human activities simultaneously and in the same region as the mass strandings of beaked whales examined in this paper appear to have several features in common. The actual relationship of these features with the strandings is unknown. A critical piece of information, the locations of the animals as a function of time, is missing for these events.

ACKNOWLEDGEMENTS

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Mitigating, monitoring and assessing the effects of anthropogenic sound on beaked whales

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ABSTRACT

Certain anthropogenic sounds are widely believed to cause strandings of beaked whales, but their impacts on beaked whale populations are not known and methods for mitigating their effects are largely untested. The sound sources that have been coincident with beaked whale strandings are military, mid-frequency sonar (2-10kHz) and airgun arrays, both of which are used widely throughout the world for defence and geophysical exploration, respectively and for which alternative technologies are not readily available. Avoidance of beaked whale habitats is superficially a straightforward means of reducing the potential effects, but beaked whales are widely distributed and can be found in virtually all deep-water marine habitats that are free of ice. Some areas of high beaked whale abundance have been identified, but the geographic distribution is poorly known for most species. Beaked whales are both visually and acoustically difficult to detect. Commonly used mitigation measures (e.g. 'ramp-up' and 'detection-modification-avoidance') have not been assessed for their effectiveness. Surveys to detect population-level impacts would likely require many years of regular monitoring and for most areas where beaked whale strandings have occurred, there are no pre-exposure estimates of population sizes. Risk assessment models can be used to estimate the sound levels to which beaked whales might be exposed under a variety of scenarios, however, the lack of information on the causal mechanism for sound-related beaked whale strandings makes it difficult to identify exposure levels that would warrant mitigative actions. Controlled exposure experiments, which measure the behavioural responses of animals to fully characterised sound sources, may hold the greatest potential for understanding the behavioural responses of beaked whales to sound and for designing mitigation methods to avoid future impacts.

KEYWORDS: MONITORING; POPULATION ASSESSMENT; BEAKED WHALE; ACOUSTICS; NOISE; STRANDINGS; SURVEY-AERIAL; SURVEY-ACOUSTIC; SURVEY-VESSEL

INTRODUCTION

Recent observations of beaked whale strandings coincident with loud, anthropogenic sounds (e.g. Frantzis, 1998; Anon., 2001; Jepson *et al.*, 2003; Peterson, 2003) have focused attention on the potential impact of such sounds on beaked whale individuals and populations. This paper provides a brief overview of the technologies and methods available for monitoring and mitigating the effects of man-made sound on beaked whales. Four subject areas are covered: (1) methods to detect beaked whales; (2) methods to mitigate the potential impact of anthropogenic sound on beaked whales; (3) methods to monitor the impact of sound on beaked whale individuals and populations; and (4) methods of risk assessment. The efficacy of measures currently taken to mitigate the impacts of anthropogenic sounds on marine mammals are reviewed, focusing on two common sources of loud anthropogenic sound: military, mid-frequency sonar and airgun arrays used for seismic surveys.

BEAKED WHALE DETECTION METHODS

Some acoustic mitigation strategies are based on detecting marine mammals before they are exposed to potentially dangerous sound levels and either avoiding the mammals or modifying the sound sources. Current detection methods and some new technologies that may assist in detecting beaked whales in the future are reviewed in the Section.

Visual detection

Visual surveys for beaked whales are typically conducted from ships or aircraft. Of all cetaceans, beaked whales are among the most difficult to detect and identify, posing problems for both types of survey (Barlow *et al.*, 2006). Beaked whales dive for long periods of time and are at or near the surface for very short periods. For Cuvier's beaked whales (*Ziphius cavirostris*), the median dive time is 29min and the median surface time is 2min; for *Mesoplodon* beaked whales the corresponding times are 20min and 2.5min (Barlow, 1999). The probability of detecting most beaked whales is thus low even in the best survey conditions and drops rapidly in sub-optimal survey conditions.

On ship line-transect surveys, two observers typically search using 7×50 handheld or 25×150 pedestal-mounted binoculars and one observer/data recorder searches by naked eye as the ship travels along specified tracklines at approximately 10kts (18.5km hr^{-1}). Observers scan forward of the ship from the highest stable deck, often the flying bridge deck or top of the pilothouse, though occasionally the bridge wings are used on larger ships. From ships, beaked whales are detected only when they surface to breathe. The effective search width for beaked whales is typically 1-2km for observers using 25× binoculars in excellent or good sighting conditions (Barlow *et al.*, 2006, table 2). Accounting for both submerged animals and animals that are otherwise missed by the observers in excellent survey conditions, only 23% of Cuvier's beaked whales and 45% of *Mesoplodon* beaked whales are estimated to be seen on ship surveys if they are located directly on the survey trackline (Barlow, 1999). The encounter rate of beaked whales decreases by more than an order of magnitude as survey conditions deteriorate from Beaufort 1 sea state to sea state 5 (Barlow *et al.*, 2006, table 1). Most estimates of beaked whale density from ship surveys are based only on search effort in excellent (Beaufort 0-2) or excellent to good (Beaufort 0-4) survey conditions (Barlow *et al.*, 2006, table 2). The beaked whale sighting rates of experienced observers are approximately twice those of inexperienced observers (Barlow *et al.*, 2006).

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On aerial line-transect surveys, teams of 2-3 observers typically search without binoculars from an altitude of 600-1,000ft (183-305m) and at a speed of approximately 100kts (185km hr^{-1}). 'Bubble' side windows are typically used to allow direct downward visibility, and ideally, a 'belly' window is also used to improve downward visibility. Aerial observers can see beaked whales only when the whales are at or near the sea-surface (typically within 5m of the surface). During aerial surveys, the ability to see submerged animals is adversely affected by sea state and cloud cover (e.g. Forney *et al.*, 1991). Most estimates of beaked whale density from aerial surveys are based only on search effort during survey conditions of Beaufort sea state 0-4 (Barlow *et al.*, 2006, table 2). Accounting for animals that are not detected because they are diving, approximately 7% of Cuvier's beaked whales and 11% of *Mesoplodon* beaked whales would be seen on aerial surveys if they are located directly on the survey trackline (Barlow *et al.*, 2006). The fraction that would be seen decreases rapidly with distance from the trackline; the effective search width is typically only 250-500m (on each side of the aircraft) for aerial observers searching by naked eye in good to excellent sighting conditions (Barlow *et al.*, 2006, table 2).

Passive acoustic detection

Passive acoustic detection refers to the detection of animals by listening for the sounds that they produce. There has been a rapid growth in the application of passive acoustic detection and monitoring of marine mammals in the last decade (e.g. Clark and Fristrup, 1997; Leaper *et al.*, 2000; Watkins *et al.*, 2000; Charif *et al.*, 2001; Clark and Gagnon, 2002; Mellinger *et al.*, 2004; Nieukirk *et al.*, 2004). Cetacean sounds can be detected with towed hydrophone arrays, stationary hydrophones monitored from ships or from land, autonomous-recording sea-floor hydrophones or drifting radio-linked sonobuoys deployed and monitored from ships, aircraft or land. Each monitoring system has distinct advantages and disadvantages, and the optimal choice depends on the frequency structures of the sounds of interest, the depth at which animals produce sounds and the logistics of mitigation (a stationary hydrophone might be inappropriate for a moving sound source, and a sea-floor recorder is not appropriate for real-time monitoring). Acoustic localisation of cetaceans typically requires more than one hydrophone. A Directional Fixing and Ranging (DIFAR) sonobuoy can give a compass bearing to a low-frequency sound source (<2.5kHz) and two such buoys can be used to localise that source (Greene *et al.*, 2003). Long towed arrays (1-5km) with 16 or more elements can determine the bearing and distance to a sound source, but typically cannot resolve whether the source is to the left or the right of the array. Short towed arrays with two or more elements can also provide a bearing angle (again with the left/right ambiguity) and a sound source can be localised by the convergence of a series of bearing angles measured from different locations as the array is towed behind a ship (Leaper *et al.*, 1992).

Most cetacean species produce sounds and one advantage of acoustic detection methods over visual methods is that these sounds can often be detected when animals are submerged or out of range for visual observations. One disadvantage is that sound production is voluntary and many cetaceans may be silent for long periods of time. At present there are no reports of the relative incidence of sound production by beaked whales.

Species identification from vocalisations is easier for some cetacean species than others. Baleen whales, in particular, appear to make stereotypical calls that can be used to distinguish species (Thomson and Richardson, 1995) and, in some cases, populations (Stafford *et al.*, 2001; Mellinger and Barlow, 2003). Dolphin whistles are more variable and species identification from whistles is difficult, with 30-50% error rates in species classification (see review by Oswald *et al.*, 2003). Echolocation clicks can be used to identify sperm whales (*Physeter macrocephalus*) with certainty and frequency can be used to distinguish clicks made by porpoises and *Cephalorhynchus* spp. from other odontocetes (Au, 1993; Cranford and Amundin, 2004; Nakamura and Akamatsu, 2004).

All beaked whales are believed to produce echolocation clicks and some or all may also produce whistles (Dawson *et al.*, 1998; MacLeod and D'Amico, 2006). The larger beaked whales (*Hyperoodon* and *Berardius* spp.) are very vocal and their vocalisations have been frequently recorded using surface hydrophones (Hobson and Martin, 1996; Dawson *et al.*, 1998; Hooker and Whitehead, 2002). In contrast, there have been many unsuccessful attempts to record sounds from Cuvier's and *Mesoplodon* beaked whales using surface hydrophones (Dawson *et al.*, 1998; Barlow and Rankin, unpubl. data) and relatively few successes (Frantzis *et al.*, 2002). Recent studies using acoustic recorders attached to individual animals (Johnson *et al.*, 2004) have shown that Cuvier's and Blainville's (*M. densirostris*) beaked whales frequently produce echolocation clicks when diving, but only when they are several hundred metres below the surface. The tendency for these smaller beaked whales to produce sounds primarily at great depth may explain the difficulty researchers have had in recording them. Past experience with other species has shown that the likelihood of acoustic detection improves tremendously if one knows what to listen for, so we anticipate improvements in passive acoustic monitoring as we learn more about beaked whale vocalisations. The echolocation clicks of beaked whales appear to be more narrow-banded than those of many other species in the same frequency range (Dawson *et al.*, 1998; Johnson *et al.*, 2004) and therefore, may be easier to distinguish using electronic filtering methods (as has been done for porpoise clicks, Chappell *et al.*, 1996).

Active acoustic detection – sonar

Commercially available sonar has been used to monitor the underwater movements of marine mammals for research purposes (Papastavrou *et al.*, 1989; Watkins *et al.*, 1993) and more recently, active sonar systems have been designed specifically to detect and track marine mammals under water (Miller, 2004; Stein, 2004). Active sonar has an advantage over passive acoustic or visual survey methods because it does not rely on the animal producing sound or being visible at the surface. In practice, effective mitigation will require a high probability of beaked whale detection. However, high detection rates can result in unacceptably high levels of false detections (mistaking entrained air bubbles, fish, other whales, or other phenomena for the object of interest). This trade-off between correct detections and false detections is referred to as the Receiver Operating Characteristics (ROC). At present there are no published ROC data for sonar systems used to detect marine mammals. Target (or species) identification is also a potential problem for active sonar. Although signal processing can improve data interpretation, the return signal varies with the animal's orientation, volume of respiratory air spaces (which change with depth) and other factors. False detections may be too common to allow active sonar to be a practical mitigation tool.

The ability to detect and identify beaked whales is not the only parameter for assessing the use of active sonar. Since active sonar releases acoustic energy into the environment, it must also be assessed for possible adverse effects. The operating frequencies of sonar for detection of marine mammals will likely fall within the hearing range of many species of small cetaceans, pinnipeds and fish. If animals can hear the sound source, they may react to it and that reaction may be beneficial if the animals move away from a potentially harmful sound. However, any sound within an animal's hearing range has the potential for causing auditory damage if received levels are too high. The use of active sonar for whale detection has been strongly opposed by some environmental groups and has resulted in threatened or actual litigation in the US.

New detection technologies

A variety of technologies (radar, infrared and hyper-spectral imagery, satellite imagery, and Light Detection and Ranging (LIDAR)) may hold promise for detecting beaked whales. LIDAR is a raster-scanned laser light source and receiver used from aircraft to 'see' subsurface objects up to depths of 30m or more and can reveal objects that would not be visible in ambient sunlight. Recent tests of radar systems showed that humpback whales (*Megaptera novaeangliae*) could be detected at distances that were equal to or greater than the distance at which these whales can be seen. Given the difficulty in detecting beaked whales using visual and passive acoustic methods, these new technologies should be evaluated. However, these methods only detect whales that are at or near the sea-surface, so the long, deep dives and short surface times of beaked whales will pose similar problems as those associated with visual survey. None of these technologies have been evaluated for detection of beaked whales.

Probabilities of visually detecting beaked whales for typical mitigation/monitoring efforts

The probabilities of detecting beaked whales have not been previously estimated for typical mitigation monitoring. For Cuvier's and *Mesoplodon* beaked whale species, detection probabilities have been estimated for research surveys utilising three observers and two 25× binoculars in excellent conditions (Beaufort 0-2 during daylight hours). These estimated values from research surveys are compared to the expected detection probabilities for mitigation monitoring. Mitigation associated with seismic surveys (Appendices 1 and 2) was chosen because the monitoring protocols for this type of survey are well defined. The average detection probabilities for mitigation efforts on seismic surveys would be less than on research surveys since: (1) seismic surveys are also conducted at night; (2) seismic surveys are not limited to calm sea conditions; (3) mitigation observers are primarily searching with unaided eyes and 7× binoculars; and (4) typically only one or possibly two observers are searching.

A crude estimate of the detection probabilities for beaked whales for typical mitigation monitoring can be made by reducing the probability estimates for research surveys (0.23 to 0.45 respectively for Cuvier's and *Mesoplodon* beaked whales, Barlow, 1999) by several independent factors to account for the differences in survey efficiency. These factors include a roughly two-fold reduction in efficiency because beaked whales cannot be seen at night, a two- to four-fold reduction to account for searches in rougher sea states (detection probabilities decrease by a factor of two for every increment in Beaufort sea state – Barlow *et al.*, 2006), a three-fold reduction to account for the image size difference in 7× vs 25× binoculars and a two-fold reduction to account for the lower number of observers used in mitigation surveys. Therefore, the overall probability of detecting beaked whales is likely to be 24 to 48 times lower for mitigation monitoring than for research vessel surveys. Based on this, mitigation monitoring detects fewer than 2% of beaked whales if the animals are directly in the path of the ship. This approach does not include factors to account for training or experience in identifying beaked whales, but Barlow *et al.* (2006) showed that experience can account for a two-fold difference in the likelihood of detecting beaked whales. The probability of detecting a beaked whale with 7× binoculars drops to zero approximately 1km from a ship.

MITIGATION METHODS

Removal or modification of the sound source

The simplest mitigation method would be to discontinue use of sound sources that pose a potential risk to beaked whales; however, this approach is not feasible. Mid-frequency sonar is widely used by the navies of the world as a critical part of their anti-submarine defence and it is unlikely that any would willingly abandon sonar use. Airguns are widely used in seismic surveys by the marine geophysical exploration industry to locate potential offshore deposits of oil and natural gas. Airguns are also used in a variety of research applications, including the detection and mapping of offshore fault zones. It is unrealistic to think that industrial and research use of airguns will stop in the near future.

While complete cessation of sonar operations might pose unacceptable risks to naval personnel and vessels, restricted or modified use may be acceptable in some circumstances. Sonar is used mostly during training and equipment testing, rather than in combat. One option might be the regional or seasonal closures of areas with high beaked whale population densities for all training and test exercises (see below). Another option might be to increase the use of simulations for sonar training in place of ship-based training. However, *in situ* training is considered critical to maintaining a combat-ready fleet, so it is unlikely that all training will ever be shifted to simulators.

Other acceptable modifications might include changes in the frequency or amplitude characteristics of the sonar signals. If adverse effects seen in beaked whales are caused by a narrow range of frequencies or by a particular waveform, other signal types might work just as well for locating submarines. Improvements in the processing of the received signals might enable sonar to achieve current performance standards, with reduced source levels. However, advances in signal processing would not necessarily lead to reduced source levels because there would still be an advantage in using both improved signal processing and the maximum achievable source levels.

Low Frequency Active (LFA) sonar (operating below 2kHz) is being developed by several nations to address the need to increase the range at which sonar can detect modern, quiet, diesel-fuelled submarines. There have been no reported beaked whale strandings associated with LFA sonar alone; however, the beaked whale stranding in Greece in 1996 occurred in conjunction with testing of a sonar possessing both low frequency (300Hz, 228dB re:1μPa) and typical mid-frequency (3kHz, 226dB re:1μPa) sound sources (D'Amico and Verboom, 1998). LFA sonar has been the subject of considerable attention because its low frequency sounds travel greater distances than sounds from mid-frequency sonar, but the potential of LFA sonar to cause strandings or produce other adverse effects on beaked whales is still uncertain. If the impact on beaked whales is frequency-specific, LFA sonar might have fewer adverse effects than mid-range sonar.

Another anthropogenic sound of potential concern for beaked whales is produced by airguns used for seismic exploration. The inferred association between airgun use and beaked whale strandings (Peterson, 2003) is based largely on one stranding of two Cuvier's beaked whales in the Gulf of California. In that instance, the ship that was towing the airgun array was also using two active sonar systems, including a sub-bottom profiler with a frequency (3.5kHz) similar to military mid-frequency sonar but with a 20dB lower source level (204dB re:1μPa) and a much shorter ping duration (1-4msec) (Federal Register, 2003). Regardless of what caused that particular stranding event, airguns produce some of the loudest manmade sounds in the ocean, with source levels of up to 259dB re:1μPa (Richardson *et al.*, 1995) and the potential for causing harm to marine mammals has long been recognised. Alternative sources of acoustic or vibrational energy for imaging geological structures have been substituted for airguns in some cases, but are not widely used. Again, improved signal processing methods may allow for use of lower source levels for airguns without loss of performance.

Avoiding beaked whale habitat

Another mitigation option is simply to avoid beaked whale habitat. Beaked whales occur in virtually all deep-water habitats that are not ice-covered (MacLeod *et al.*, 2006). Previous studies of sightings and strandings (Waring *et al.*, 2001; D'Amico *et al.*, 2003; MacLeod, 2004) identified continental slopes, canyons and seamounts as areas of particularly high beaked whale abundance. MacLeod (2004) presented lists of known 'hot spots' or areas with high densities of beaked whales. Ferguson *et al.* (2006) show that the habitat preferences of beaked whales in the Northeast Atlantic Ocean and Mediterranean Sea appear to differ from those in the eastern tropical Pacific, where beaked whales are found in more pelagic waters, far from continental slopes. While there is little doubt that 'hot spots' of high beaked whale density do occur, the areas identified to date are based on limited data and caution is recommended in extrapolating habitat preferences to unsurveyed areas (Ferguson *et al.*, 2006). Consideration should also be given to the potential sound impacts on other marine animals if sound production is shifted away from beaked whale habitat; for example, the densities of dolphins and baleen whales are often much higher in shelf waters where beaked whale densities are low.

Ramp-up procedures

Perhaps the most widely used mitigation method is 'ramp-up' or 'soft start'; the stepwise increase of the sound-level over a period of several minutes or hours, to enable animals to detect the sounds at low levels and presumably, move away before harmful effects occur. This is practical in some cases (for example, air gun arrays, see Appendices 1 and 2), but not in others (such as tactical use of sonar in anti-submarine combat). Ramp-up mitigation is based on the assumption that animals will locate the source of the low-level sound and will react appropriately to avoid exposure. However, the effectiveness of this mitigation method has not yet been tested (Stone, 2003). The potential remains that ramp-up may not have the desired effect, and may even create greater risk by causing animals to approach the sound-source. Another premise of ramp-up mitigation is that when a sound-source is at its maximum amplitude, animals that are newly exposed to the sound by relocation of the sound source will experience a gradual ramp-up as it approaches. Although the theory seems sensible, the sound-related beaked whale strandings in the Bahamas (Anon., 2001) occurred with moving sound sources that had been active for some time.

Detection of beaked whales and modification of sound-producing activities

Many mitigation plans include a strategy for detecting marine mammals (visually or acoustically) and modifying activities to avoid the detected animals, decrease amplitude, or turn off the sound source if the animals are within a critical distance. These methods depend on the detection of animals before they are exposed to potentially dangerous levels of sound.

Mitigation plans for seismic surveys or experimental sound sources usually require searching by ship-based marine mammal observers during daylight hours and in some cases, at night using nightvision devices (Appendix 1). Typically, mitigation observers search using the naked eye and 7× binoculars during daylight hours. Mitigation plans often provide no guidelines for 'acceptable' survey conditions and in some cases, searching may continue in Beaufort sea states of 7 or 8 (Appendix 1). In some mitigation plans, such as those for the ship-shock trials of the destroyer USS *John Paul Jones* in the Pacific Ocean, aerial observations made in front of a moving vessel may augment visual surveys from a ship (Department of the Navy, 1994). Given the difficulty in detecting and identifying beaked whales using even experienced observers in optimal conditions (see above), mitigation observers from either ships or aircraft will likely detect only a small fraction of the animals that are within their range of vision.

Passive acoustic detection has been used in some mitigation plans. Sonobuoys dropped from aircraft were used to detect whales during the *John Paul Jones* ship-shock trials in the Pacific Ocean and resulted in several detections of baleen whales. A towed hydrophone array was used experimentally in a recent seismic test (Appendix 1), but no marine mammals were acoustically detected during this short experiment.

Active sonar has been used to detect marine mammals as part of the mitigation plan for the Surveillance Towed Array Sensor System (SURTASS) LFA sonar, and active sonar could potentially be used in other mitigation contexts to detect marine mammals. The Environmental Impact Statement for SURTASS LFA (Department of the Navy, 2001) and Johnson (2004) describe the design, tested effectiveness and usage of active sonar in mitigation.

Currently, none of the available detection methods (visual search and passive acoustic monitoring) has a high probability of detecting and identifying beaked whales. Improvements in passive acoustic detection methods are anticipated, but the tendency for smaller beaked whales to only make sounds at depth may limit the degree to which detection distances can be improved, at least with surface hydrophones.

Sound screening procedures

Mitigation measures for stationary sound sources such as pile-driving or explosives include the use of bubble screens or material screens that impede sound propagation from its source (Vagle, 2003). For typically mobile sources, such as ship sonars and airgun arrays, this form of mitigation is unlikely to be an option.

Alerting stimuli and alarms

Alarm signals have been proposed as a means of moving animals away from a potentially dangerous situation. Acoustic Deterrent Devices (ADDs or 'pingers') are low-amplitude sound sources (<150dB re:1μP) that are commonly used on gillnets to reduce cetacean bycatch. Acoustic Harassment Devices (AHDs) are higher amplitude sound sources (>180dB re:1μP) typically used to keep seals and sea lions away from aquaculture pens, fish ladders and other locations where they could cause damage to resources or property. ADDs have been shown to be effective at reducing gillnet bycatch of harbour porpoises (*Phocoena phocoena*) (Kraus *et al.*, 1997; Gearin *et al.*, 2000) and other cetaceans species (Barlow and Cameron, 2003); however, the mechanism by which they work is not clear (Kraus *et al.*, 1997). The sound from ADDs appears to be aversive to many cetaceans (Anderson *et al.*, 2001), thus the difference between 'deterrent' and 'harassment' devices may be artificial. Since California-based drift gillnet vessels began to use pingers in 1996 no beaked whales have been observed entangled in nets with pingers (Carretta *et al.*, 2005), whereas, 26 beaked whales were observed caught in nets from 1991-95 (Julian and Beeson, 1998).

To evaluate the effectiveness of an alarm signal, it will be necessary to assess the type of alarm response elicited and its likelihood of reducing risk. Some responses to alarms may not reduce the risk of harm, as Nowacek *et al.* (2004) showed, when the behavioural response of right whales (*Eubalaena* spp.) to an alarm signal (reduced diving and increased surface time) probably increased their vulnerability to vessel collisions. It should be noted that the risks associated with vessel collisions may be completely different to those associated with sonar.

MONITORING THE IMPACT OF SOUND ON BEAKED WHALES

In general, monitoring for impacts of sound on beaked whales has received less emphasis than mitigation measures to prevent impacts. Although it is clearly better to prevent impacts, the efficacy of all current mitigation methods remains untested. It is therefore important to develop monitoring tools to directly evaluate impacts when they occur.

Surveys for dead or injured whales

The most direct method of monitoring beaked whale injury or death is to conduct surveys to detect dead or injured whales during and after exposure to a sound source. To date, all beaked whale strandings associated with anthropogenic sound have been detected by chance, without dedicated search efforts. Instead of relying on accidental detections, ship or aerial surveys could be used to detect dead or injured whales at sea and aerial or ground-based surveys could be used to detect stranded whales onshore. Whales are likely to be identified as injured only if their surface behaviour is grossly changed, so there are some limitations to the effectiveness of this approach, but those limitations may be minor relative to the advantages of prompt detection. Such surveys have been used before, for example in the *John Paul Jones* ship shock trials (Department of the Navy, 1994). The merit of directed survey for dead or injured animals would depend on the probabilities of mortality or injury occurring and being detected, the survey effort needed to effectively cover an area of concern and its cost. Direct impact assessment by detecting dead and injured whales is best for measuring the impact on individuals, but cannot easily be used to infer population-level impacts, unless the population sizes and structures are already well known. Implementation of such surveys may require a public education component, since several recent proposals to monitor for mortality and injury have been construed as anticipation that mortality would certainly occur, leading to public opposition and cancellation of the activities that had otherwise been deemed low risk.

Uncertainties in directly monitoring impacts include the probability that a dead whale will float and if it does, the probability that it will strand on a beach. The probability that a dead beaked whale will float is at least partially dependent on the depth at which it dies. Experiments with freshly stranded beaked whales and buoyancy modelling may help resolve these uncertainties.

Special methods for the collection, preservation and analysis of specimen materials are required for stranded dead and injured beaked whales associated with anthropogenic sounds (Jepson *et al.*, 2003). As hypotheses are developed about the possible causal mechanisms of the observed physiological effects, new collection and analytical methods may be needed when stranded beaked whales are detected. At present, few investigators are sufficiently trained to perform these and such response personnel are needed to mount effective stranding responses.

Surveys to detect changes in abundance

Ship or aerial surveys can be used to estimate the abundance of beaked whales (Barlow *et al.*, 2006) and such estimates, if repeated over time, can be used to estimate changes in beaked whale abundance. A significant, population-wide decline in abundance may indicate anthropogenic impacts from sound or other factors (such as bycatch). This approach does not hold much promise in the short term due to the lack of precision in estimates of beaked whale population sizes. Taylor and Gerrodette (1993) discussed the problems associated with detecting changes in population size for rarely seen species and showed that they could become extinct before a statistically significant decline is detected. The coefficients of variations in beaked whale abundance estimates from a single survey are typically high (40-100%, Barlow *et al.*, 2006, table 2). This lack of precision means that many years of annual surveys would be required to detect any change. The lack of any baseline abundance information for the vast majority of the world's oceans adds further to the problem of detecting changes.

Individual identification and mark-recapture studies

Many species of beaked whale are well marked with scars on their bodies or nicks in their dorsal and caudal fins and individuals can be recognised from those marks. Most individual identification studies are based on photographs; however, individuals can also be identified genetically. Individual identification studies have proven to be a valuable tool for the study of many cetacean populations (e.g. Hammond *et al.*, 1990; Calambokidis and Barlow, 2004) and can be used to determine residency patterns, population size, mortality rates and reproductive parameters. Individual identification studies benefit most from a continuous series of observations over many years. However, valuable information can be gathered over shorter time periods and abundance estimates can often be made with two seasons of fieldwork (typically separated by a year to allow random mixing of the marked animals within the population).

The only long-term, photo-identification study of Cuvier's and *Mesoplodon* beaked whales is based on Abaco Island in the area of the Bahamas where a beaked whale mass-stranding coincided with a Navy sonar exercise in March 2000 (Anon., 2001). This study began prior to the strandings and has since continued (Claridge and Balcomb, 1993; 1995; Claridge *et al.*, 2001). A complete analysis of the data from this study may provide a more precise estimate of the population size than would line-transect surveys. Continued studies in the area might provide a unique insight into the long-term effects of sound on marine mammals. A similar long-term study of northern bottlenose whales, *H. ampullatus* (Whitehead *et al.*, 1997; Gowans *et al.*, 2000) also provides behavioural and ecological information that is relevant to monitoring sound impacts on beaked whales. Additional opportunities for long-term photo-identification studies exist in other locations and should be explored.

Controlled exposure experiments

One way to monitor the effect of sound on beaked whales would be to deliberately expose whales to a known sound source while studying their behaviour. Such controlled exposure experiments (CEEs) are amongst the most powerful tools for monitoring the responses of animals to sound (Tyack *et al.*, 2004). Changes in behaviour in response to a sound are difficult to detect from opportunistic observations because uncontrolled variables often mask any response. However, CEEs may put some animals at risk and individuals and organisations have previously objected to and attempted to block such experiments and objections are likely to be again voiced in the future.

The behavioural responses of beaked whales to sound are difficult to directly observe because of their long dive times. Recently, acoustic data-logging tags (Burgess *et al.*, 1998; Johnson and Tyack, 2003) have been developed that allow measurement of the sound levels received by individual animals. Depth and detailed behaviour (orientation, roll, pitch, acceleration, fluke stroke-rate, sound production, etc.) can also be recorded. The deployment of such tags on beaked whales is a critical first step in measuring underwater behavioural responses and hence enabling CEEs with beaked whales. CEEs without data-logging tags are already possible, but provide much less information. The logistical problems of reliably finding and tagging beaked whales with appropriate instruments need to be resolved. Recently, researchers have succeeded in tagging Cuvier's and *Mesoplodon* beaked whales (Baird *et al.*, 2004; Johnson *et al.*, 2004) and as expertise is gained in using acoustic data-logging tags, direct CEE assessment of beaked whale response to sound may become possible.

RISK ASSESSMENT MODELS

Risk assessment is a powerful but under-used tool in conservation biology (Harwood, 2000). Risk assessment models can be used to evaluate the possible exposure of marine mammals to specific sound sources, given different sound production scenarios and sound propagation conditions. The number of marine mammals exposed to any anthropogenic sound source and their levels of exposure will depend on the characteristics of the source, the local abundance of marine mammals, their diving behaviour, their distance from the source and the local sound propagation characteristics. Simple risk models assume a cylindrical or spherical sound propagation and assume that all individuals are at the depth of highest sound levels. More complicated models use simulations to reduce the number of simplifying assumptions. At least two such models have been developed and used to model risks from underwater sound. The first is the Acoustic Integration Model (AIM) developed by Marine Acoustics Inc. and now marketed in a variety of versions (Ellison *et al.*, 1999). The second is the Effects of Sound on the Marine Environment (ESME) programme, sponsored by the US Office of Naval Research, which is attempting to bring together state-of-the-art science in all the relevant fields of information to create an integrated mathematical model of risk. The ESME model accounts for uncertainty within its components and thus allows sensitivity analyses for any of the parameters.

Risk assessment models are, themselves, valuable tools in assessing research/data needs. For example, one might be faced with the choice of investing a million dollars and three years in improving the accuracy of the sound field prediction in reverberant environments only to find that it only alters the outcome by 1%, whereas a much smaller investment in improved beaked whale density estimates for the same site might produce a much larger difference in the estimated outcome of the model. Model sensitivity therefore becomes a good guide in how to best allocate limited resources to achieve the greatest gains in certainty.

Understanding the sound exposure experienced by a diving animal is critical to risk assessment. However, until we have improved population data and improved understanding of the physical, physiological, and/or behavioural mechanisms by which sound is adversely affecting beaked whales, we will not be able to confidently assess risk.

CONCLUSIONS

We have briefly reviewed a range of options for mitigating, monitoring and assessing the potential impacts of human acoustic activities on beaked whales. Clearly, this is extremely complex. Beaked whales are difficult to detect by any available method and given their wide distribution, are difficult to avoid. The effectiveness of all mitigation methods that are currently in use has not been established for beaked whales. The number of animals exposed and the sound exposure levels can be estimated with risk assessment models, but actual risk to populations or individuals cannot be confidently estimated without knowing the causal relationship between anthropogenic sounds and beaked whale strandings. We hope that by focusing attention on the problems associated with mitigating and monitoring the effects of sound on beaked whales, research will be directed to solve these problems.

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Appendix 1

SEISMIC MITIGATION AND MONITORING ON ACADEMIC RESEARCH SURVEYS

Airguns produce some of the loudest sounds made by humans (Richardson *et al.*, 1995) and some of the most powerful airgun arrays are used in geophysical research on the structure of the earth's crust. Marine mammal monitoring and mitigation reports are available for four seismic surveys and tests conducted in 2003 by the Lamont-Doherty Earth Observatory on the research vessel *Maurice Ewing* (LGL, 2003; Smultea and Holst, 2003; MacLean and Haley, 2004 and Holst, 2004). The monitoring and mitigation methods used on these four projects and the results of their monitoring efforts are briefly reviewed below.

All the mitigation and monitoring described here were associated with the use of airgun arrays configured with 2-20 airguns. Following guidance from the US National Marine Fisheries Service (NMFS), it was assumed that some marine mammals could be 'taken by harassment' (disturbed) if exposed to a received sound level of greater than 160dB re:1μPa. The potential for injury occurs at a higher sound level; the NMFS standard at that time was that cetaceans and pinnipeds should not be exposed to pulsed sounds at received levels greater than 180dB and 190dB, respectively. For the projects described here, 'precautionary safety radii' were defined as 1.5× times the distance at which sounds were predicted to diminish to 180dB for cetaceans and 190dB for pinnipeds. The factor of 1.5× was introduced to account for uncertainty in estimating safe distances via a propagation model that was, at the time, not yet validated by empirical measurements. The safety radius used for cetaceans (1.5× the predicted 180dB radii) varied from as low as 75m (with two airguns) to as high as 1,350m (with 20 airguns).

The mitigation plan for each survey included: (1) changing vessel heading and speed, when feasible, to avoid marine mammals ahead of the ship; (2) 'ramp-ups' whenever arrays with more than two guns started firing after a period without operation; and (3) 'power-downs' (turning off the array) whenever marine mammals were detected within, or about to enter the applicable safety radius. In general, if all airguns were shut down for an extended period at night, airgun operations did not resume until daylight. Marine mammal monitoring was also part of the mitigation plan and was critical to mitigation strategies (1) and (3) above.

Monitoring was normally the responsibility of three biological observers, who were trained to identify marine mammals and sea turtles. Typically, when the array was active during daylight hours, two observers searched with 7×50 binoculars and with naked eyes, while the third observer rested. Given the limited ability to sight marine mammals at night even when night vision devices (NVDs) were used, observers did not search at night except prior to and during ramp-ups; at those times, they searched with 3rd generation, 3× NVDs. Tests on one cruise (Holst, 2004) indicated that three white milk jugs tied together were generally visible out to 50-65m, but were only visible to one of three observers at 150m (on a bright night in Beaufort 4 conditions). During night periods when the airguns were active, bridge crew watched for marine mammals and sea turtles near the vessel as part of their normal watch duties. One marine mammal observer was on-call incase the bridge crew saw a marine mammal at night. One project (LGL, 2003) had eight observers (extras were aboard for another project) and two 25×150 *Big-Eye* binoculars. On that project, daytime monitoring was done by four observers, two searching with 25× binoculars and two searching with 7×50 binoculars and naked eyes and there were no night time airgun activities.

Table A1 gives the hours of monitoring effort when the airgun arrays were active (including power-up time), stratified by Beaufort sea state. Marine mammal sightings when the arrays were active are summarised in Table A2. The mitigation and monitoring reports also detail the monitoring effort and marine mammal sightings during transit to the study area and at other times that the array was not active. During night time operations, no marine mammals were seen by the observers or reported to the observers by bridge crew.

Passive acoustic monitoring was attempted in the Gulf of Mexico project (LGL, 2003). The Seamap Cetacean Monitoring System (Seamap, 2002) consisted of a towed hydrophone array capable of detecting signals between 8Hz and 24kHz. One person aurally monitored signals and visually monitored spectrographs. Monitoring occurred for 32hrs, mostly when the array was not firing. Three visual sightings were made during periods of acoustic monitoring, but no marine mammals were detected acoustically.

Table A1

Hours of monitoring effort by marine mammal observers when airgun arrays were active (including ramp-up periods) stratified by Beaufort sea state. Average Beaufort is a time-weighted average.

	Beaufort sea state											
Project area	0	1	2	3	4	5	6	7	8	Average Beaufort	Reference	Total hours
Northern Gulf of Mexico	0.0	0.0	8.8	7.8	0.8	0.0	0.0	0.0	0.0	2.5	LGL (2003)	17.4
Hess Deep/eastern tropical Pacific	0.5	0.0	0.0	13.3	38.0	38.8	8.4	0.0	0.0	4.4	Smultea and Holst (2003)	99.1
Storegga Slide/Norway	0.5	8.7	25.2	33.2	56.7	59.6	61.8	18.3	1.9	4.5	MacLean and Haley (2004)	265.9
Mid-Atlantic Ridge	0.0	0.0	0.0	1.3	6.0	7.2	7.7	0.1	0.0	5.0	Holst (2004)	22.4

Table A2

Total monitoring effort and marine mammal sightings made when airguns were active (including ramp-up periods). Animal actions are relative to the vessel, but are not necessarily reactions to the vessel or airgun array. Airguns were powered down in response to marine mammal sightings in five instances. Beaufort sea state for sightings off Norway from LGL (B. Hayley, pers. comm.).

Project area	Monitoring (hrs)	Species	Group size	Date (dd/mm)	Distance (m)	Beaufort sea-state	Animal action	Array power down?
Northern Gulf of Mexico	17.4	Dwarf sperm whale	2	30/05	5,000	2	Dive	No
		Bottlenose dolphin	8	02/06	1,125	3	Swim away	No
Hess Deep/eastern tropical Pacific	99.1	Unidentified beaked whale (probable)	1	17/07	1,000	4	Breaching	Yes
Storegga Slide/Norway	265.9	Fin whale	1	01/09	3,306	3	Swim away	No
		Unidentified whale	3	01/09	2,074	3	Swim away	No
		Unidentified whale	2	01/09	3,306	3	Swim away	No
		Minke whale	2	01/09	3,306	3	Swim away	No
		Minke whale	2	01/09	3,306	3	Swim away	No
		Unidentified beaked whale	2	01/09	2,074	3	Swim away	No
		Unidentified dolphin	10	01/09	1,519	3	Milling	No
		Minke whale	1	04/09	533	4	Swim toward	No
		Minke whale	1	05/09	847	5	Swim parallel	No
		Minke whale	1	05/09	200	5	Swim toward	Yes
		Unidentified whale	1	05/09	2,074	5	Swim away	No
		Long-finned pilot whale	7	06/09	200	6	Swim toward	Yes
		Long-finned pilot whale	25	06/09	277	5	Swim parallel	Yes
		Long-finned pilot whale	15	06/09	4,500	6	Swim toward	No
		Unidentified whale	1	07/09	4,813	4	Swim parallel	No
		Unidentified whale	3	07/09	847	4	Swim toward	Yes
		Unidentified whale	1	11/09	654	2	Swim away	No
Mid-Atlantic Ridge	22.4	None	n/a	n/a	n/a	n/a	n/a	n/a

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Appendix 2

SEISMIC MITIGATION AND MONITORING FOR OIL AND GAS EXPLORATION

Airguns are in common use worldwide for oil and natural gas exploration. Most commercial users of airguns have instituted some form of mitigation to reduce the potential for marine mammal injury. Pierson *et al*. (1998) and Stone (2003) have summarised the mitigation methods used by the seismic exploration industry and a very brief synopsis of these methods based on those papers is detailed below.

Mitigation measures for seismic surveys are not required by any international agreement, but are required by national laws in the waters of many countries (Pierson *et al.*, 1998). Commonly, mitigation measures required under national laws include closures of certain regions, or a combination of regional and seasonal closures to protect areas of known high density of marine mammals, or to protect migrating marine mammals. Examples include seasonal limitations to protect migrating gray whales in US waters off California, a temporary moratorium on seismic exploration in the 'Gully' off eastern Canada, a closure of nearshore waters to night time seismic surveys in Italy and many others. Even where no national closed areas are established, permit applications are often reviewed on a case-by-case basis and season/area limitations are sometimes applied. Countries requiring permits for seismic exploration include the US, Canada, the UK, Italy, Norway and Brazil.

Other commonly applied mitigation measures include 'ramp-up' (also known as 'soft start' in the UK and elsewhere) and the use of safety zones in conjunction with real-time monitoring. 'Ramp-up' criteria may be based on the rate at which output is increased (such as 6dB min^{-1} above 160dB in the US), or may be based on absolute time duration (a slow build-up over 20 minutes in the UK). A safety zone is defined as a region where there is at least some potential for temporary auditory damage in marine mammals and may range 100-1,000m from an airgun array, depending on the source levels and propagation conditions. This safety zone may be monitored prior to and during ramp-up, or may be monitored during any seismic operation. In their guidelines for minimising disturbance to marine mammals, the UK Joint Nature Conservation Committee sets this safety zone at 500m and recommends surveys beginning at least 30mins before the use of seismic sources and during ramp-up (Stone, 2003). In some cases an airgun array is powered down if a marine mammal is seen within the safety zone, but an exception is sometimes made for marine mammals, especially pinnipeds, that appear to voluntarily approach the source. The application of safety zones requires some form of real-time monitoring, typically visual shipboard monitoring. Observers generally search by naked eye or 7 × 50 binoculars. If monitoring occurs only during and prior to ramp-up, one observer may be required, but for longer periods, two or three observers alternate to avoid fatigue. Many of the companies operating seismic survey vessels have instituted voluntary standards for ramp-up, safety zones and visual monitoring in countries where mitigation is not required.

Stone (2003) conducted the largest study to date on the results of marine mammal monitoring efforts in conjunction with seismic surveys in UK and adjacent waters. Her analysis included almost 45,000 hours of visual monitoring in 1998-2000 and the detection of 1,652 groups of marine mammals. She found that the effect of airguns varied between species. Sighting rates were generally lower and detection distances greater for small odontocetes when the airguns were firing, compared to period when they were silent and small cetaceans showed the most conspicuous avoidance response. Killer whales (*Orcinus orca*) were seen further from the airguns when they were firing and pilot whales (*Globicephala*, spp.) oriented away from the survey vessel. Sperm whales showed no apparent changes. Baleen whales showed fewer responses to airguns than small cetaceans, but were found at greater distances when airguns were firing compared to control periods when airguns were silent. Only three of the 1,652 sightings included beaked whales (two with northern bottlenose whales and one with a Sowerby's beaked whale (*M.bidens*)) and consequently no analyses were presented for beaked whale. Thirty-minute, pre-shot surveys were completed in approximately 80% of the 5,343 recorded startups, with much higher compliance when a dedicated marine mammal observer was aboard (Stone, 2003, table 17). Marine mammals were detected in the safety zone during 27 of these pre-shot surveys, and start-up was delayed only 14 times (and only when a dedicated marine mammal observer was aboard) (Stone, 2003, table 17).

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Appendix 3

MITIGATION AND MONITORING FOR NAVY OPERATIONS

All US Naval operations and exercises are planned using available data on beaked whale sightings and strandings, as well as the most recent predictive habitat correlative studies. Single-ship sonar exercises use dedicated observers to search for marine mammals from the ship's bridge. Watchstanders receive special training, including methods for detecting, identifying and reporting marine mammals. All vessels are equipped with 7× handheld binoculars and 20× *BigEye* binoculars, although the 20× binoculars are not usually used on bridge watches due to the narrow field of view of these higher power binoculars. All ships have standardised marine mammal and sea turtle reporting forms and observers are strongly encouraged to complete forms for all sightings. If marine mammals are sighted prior to planned sonar use, sonar usage is deferred until the area is determined to be clear of marine mammals. For multi-ship exercises, aerial and shipboard surveys are conducted in the area prior to the exercise. The commander of the exercise must determine that the area is 'clear' prior to initiating sonar usage. If marine mammals or sea turtles are detected in the area during the exercise, the sonar is shut down and not resumed until the area is determined to be clear. Use of active sonar requires prior deployment and checking of the passive receiving array. During that time, a minimum of 2 mins, the sonar operator monitors the passive listening arrays for marine mammal sounds. Training of Navy sonar operators has traditionally included the identification of marine mammal sounds and other 'biologics'. Current training is providing a greater emphasis on the understanding of marine mammal sounds and their significance. Active sonar is not turned on if marine mammal sounds are detected on the passive arrays prior to active sonar operations.

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A review of Cuvier's beaked whale strandings in the Mediterranean Sea

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ABSTRACT

Cuvier's beaked whale (*Ziphius cavirostris*) is the only species of beaked whale commonly found in the Mediterranean Sea, a deep, semi-enclosed basin. Beaked whales are generally an offshore family often found in association with the canyons and steep escarpments common to the area. Much of the current knowledge of this species has been derived from strandings data. Historically, strandings data for the Mediterranean Sea has been collected by individual researchers and more recently, over the last two decades, by national strandings networks. We reviewed strandings data collected by strandings networks from Italy, Greece, Spain and France. Additionally, we compiled strandings information gleaned from the literature, personal communications, regional newspapers and the world wide web from countries that border the Mediterranean Sea. While this review is certainly not exhaustive, it has allowed the creation of an extensive geo-referenced basin wide database using a geographic information system (GIS) of over 300 stranding events. The acquired data permit documentation of the number of mass stranding events, allow general observations about distribution and chronology of stranding events dating back to 1803 and enables evaluation of strandings based on several different criteria. The first recorded mass stranding event was in 1963 off Genova, Italy. Analysis shows that specific geographic stranding areas can be identified, even though the level of effort undertaken in the different countries may vary.

KEYWORDS: CUVIER'S BEAKED WHALE; STRANDINGS; EUROPE; MEDITERRANEAN SEA; DISTRIBUTION

INTRODUCTION

Cuvier's beaked whale (*Ziphius cavirostris*) is a pelagic, deep-diving species and the only beaked whale commonly found in the Mediterranean Sea (Notarbartolo di Sciara and Demma, 1994). The species was first described by G. Cuvier, using a partial skull collected in 1803 near Fos-sur-Mer, on the Mediterranean coast of France (Cuvier, 1823). Beaked whales generally live offshore (although see Ferguson *et al.*, 2006) and are often associated with regions characterised by canyons or steep escarpments (Heyning, 1989), as typically found in this basin.

In recent years, sightings of Cuvier's beaked whales have been reported more frequently in some areas of the Mediterranean, such as the Ligurian Sea (Ballardini *et al.*, 2005), where studies of habitat use and diving behaviour have also been carried out (Azzellino *et al.*, 2003; Johnson *et al.*, 2004).

The Mediterranean Sea is an elongated semi-enclosed deep basin that is virtually landlocked. It is divided into two sub-basins, linked via the Sicilian Channel, whose shallow depth separates the hydrological and ecological conditions of the two sub-basins. The external exchanges of the sub-basins are with each other, with the Atlantic Ocean via the Straits of Gibraltar on the western side and with the Black Sea via the Dardanelles and Bosphorus Straits on the eastern side. Elevated chlorophyll-a concentrations related to coastal upwelling and mesoscale features characterise the western basin, while the eastern basin is influenced by cyclonic and anticyclonic patterns (Crise *et al.*, 1999).

Although mass strandings of this species are not usual (e.g. Heyning, 1989; Brownell *et al.*, 2006), in the last fifteen years, several authors have suggested that some atypical beaked whale mass stranding events have been associated with naval activities (Simmonds and Lopez-Jurado, 1991; D'Amico and Verboom, 1998; Frantzis, 1998 and Frantzis, 2004; Anon., 2001; Martín, 2002; Freitas, 2004; Martín *et al.*, 2004, Fernàndez *et al.*, 2004). Assessing the cause and mitigating against any impacts is currently limited by the lack of scientific knowledge of beaked whale physiology, behaviour, distribution and habitat use (Cox *et al.*, 2006).

This paper reviews and documents Cuvier's beaked whale stranding events recorded in the Mediterranean Sea, including those that may not have been previously reported in the literature, i.e. those only available in relatively inaccessible sources (e.g. national stranding networks, local museums archives and newspapers). Inconsistencies between references for the same event reported in different papers are discussed in order to give certainty and avoid errors and duplication of data. Anomalous stranding patterns for the Mediterranean Sea have been identified, but the causes of these strandings are beyond the scope of this paper. Cox *et al.* (2006) provide a good review of that subject.

While this review has probably not resulted in a definitive list, given the limited verification available for some records, we believe it is the most complete list of Cuvier's beaked whale strandings now available for the Mediterranean Sea. This database is a subset of the

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Mediterranean and Black Sea Cetacean database developed within the North Atlantic Treaties Organisation (NATO) Undersea Research Centre's (NURC), Sound Ocean and Living Marine Resources (SOLMAR) project, which contains sighting and stranding data for all species commonly found in the Mediterranean Sea (Fossati *et al.*, 1999).

METHODS

Data collection and georeferencing

Stranding data were acquired from a variety of sources. A review was conducted of stranding data collected by the Italian (CSC – Centro Studi Cetacei: yearly reports 1986-2003), Greek (ARION – Cetacean Rescue and Rehabilitation Research Society and DELPHIS – Hellenic Cetacean Research and Conservation Society: Drougas, 1996; 1998; Drougas and Komnenou, 2001; unpublished data for years 2001-03) and French (CRMM – Centre de Recherche sur les Mammifères Marins, La Rochelle: 1971-2003) national stranding networks. Additionally, stranding information was compiled from scientific literature, personal communications and archives, regional newspapers and the World Wide Web from the 20 countries that border the Mediterranean Sea. The data listed in Table 1 contain stranding information until December 2003. Bycaught and dead animals found floating in the open sea are also included.

The database includes information (when available) about the number of animals, the species, size and sex, the status observed when the animals were found (alive, dead, level of decay), any injuries observed on bodies, the presumed cause of death and the treatment and release condition in cases of animals found alive. Additional information related to the location of biological samples (tissue, skeletons, etc.) and the final disposition of the bodies is included. The Italian historical literature was verified with additional information available from the Italian Museums.

All data have been georeferenced; in many cases the exact latitude and longitude was not known so the geo-referenced location of the beach, village, or town where the stranding occurred was used. Datasets were then transferred to a Geographic Information System (*ESRI ArcView 8*) for validation of locations and display. The coastline and bathymetric data used for the Mediterranean Sea is the IBCM bathymetric contours distributed by the British Oceanographic Data Centre (BODC, UK).

Data analysis

Mass strandings are defined as two or more animals that are not a cow-calf pair (Geraci and Lounsbury, 1993). Potential mass strandings may often be recorded as isolated events if animals do not come ashore in close proximity. Mass strandings in the last decade, however, have demonstrated that a single mass stranding event may occur over several days and be spread over many miles of coastline (Simmonds and Lopez-Jurado, 1991; Frantzis, 1998 and Frantzis, 2004; Anon., 2001; Martín, 2002; Freitas, 2004).

For this analysis, each mass stranding originally reported as one event, even if carcasses were found spread over many miles of coast, was retained (e.g. Tortonese, 1963). In some cases, some 'single' stranded animals were reclassified into one mass stranding event, based on the spread of the May 1963 mass stranding described by Tortonese (1963), the morphology of the coastline and the direction of the surface currents.

Mass stranding events were separated into two categories, stranding events with two animals and stranding events with three or more animals. Distances between stranded animals were calculated based on the GIS display. Strandings resulting from fishery bycatches were identified and were not included in the calculation of mass stranding of three or more animals. Due to the unreliability of data on level of decay, in only a few cases were we able to use this information to increase the confidence that the single strandings were likely related or not.

RESULTS

A total of 232 stranding events representing 316 animals was reported, based on analysis of the accumulated beaked whale stranding records (Table 1), with eight events (9 animals) lacking sufficient documentation and not included in the other tables and maps. For all the stranding events combined, 132 animals were able to be categorised by sex (71 females, 61 males). Table 1 contains a chronological list of all stranding events with mass stranding events indicated by total number of animals (≥ 2) and date range, where applicable. Original source references documenting each stranding event are also included. The corresponding locations of all Cuvier's beaked whale strandings in the Mediterranean Sea are shown in Fig. 1.

In addition to Cuvier's beaked whale, four *Mesoplodon* specimens have been reported stranded in the Mediterranean Sea. One animal reported as Sowerby's beaked whale (*M. bidens*) stranded in Italy in 1927 (Brunelli and Fasella, 1928) but it was not preserved, and no clear species description was given. Based on the morphological description provided, it was certainly not a Cuvier's beaked whale ['the teeth are not on the tip of the lower jaw']. Another stranding that occurred in Italy in 2001 was the first finding of a Gervais' beaked whale (*M. europaeus*) for Mediterranean waters (Podesta *et al.*, 2005). A Sowerby's beaked whale stranded in Greece in 1989 (Drougas and Komnenou, 2001) and a Blainville's beaked whale (*M. densirostris*) stranded in Spain in 1980 (Casinos and Filella, 1981; Grau *et al.*, 1986). Given the focus of this paper and their limited presence, all *Mesoplodon* spp. events have been excluded from the present analysis and are not incorporated into Table 1.

Stranding events were reported for Albania, Algeria, Croatia, Egypt, France, Greece, Israel, Italy, Malta, Spain and Turkey. No strandings are known for Cyprus, Lebanon, Libya, Monaco, Morocco, Slovenia, Syria, Tunisia or Yugoslavia. Table 2 shows the number of events, number of animals, and associated percentages by country, with 15 stranding events of two animals (three of which were bycatch) and 12 events of three or more animals. Mass strandings of three or more animals by area and date are listed in Table 3 and the detailed location of each event is shown in Figs 2 and 3. Fig. 4 shows the number of animals stranded in five years intervals along with the total number of strandings of three or more animals. Fig. 5 shows the monthly distribution of the individual strandings.

The analysis of historical literature performed for this paper, together with cross-referencing and examining specimens held by regional museums, clarified a number of inconsistent reports from earlier papers. For example, Paulus (1962) described a stranding event that occurred in Livorno around 1871, reporting that the skeleton was preserved in the Pisa Museum. Richiardi (1873), cited in Paulus (1962) was never published, but two unpublished tables from Richiardi with specimen drawings were

Table 1

Chronological list of Cuvier's beaked whale strandings. *Indicates bycatch.

ID	Date range	No. of animals	Country	References	ID	Date range	No. of animals	Country	References
1	1803	1	France	Cuvier (1823); Vinciguerra (1926); Paulus (1962)	114	6 Jul. 1989	1*	Italy	Centro Studi Cetacei (1991)
2	19 Sep. 1823	1	Italy	Richiardi (1875)	115	15 Jul. 1989	1	Italy	Centro Studi Cetacei (1991)
3	23 Sep. 1840	1	Italy	Cocco (1846); Bauer (1978)	116	29 Jul. 1989	1*	Italy	Centro Studi Cetacei (1991)
4	1842	1	France	Vinciguerra (1926); Paulus (1962)	117	13 Aug. 1989	1*	Italy	Centro Studi Cetacei (1991)
5	15 May 1850	1	France	Vinciguerra (1926); Paulus (1962)	118	14 Aug. 1989	1*	Italy	Centro Studi Cetacei (1991)
6	1866	1	France	Vinciguerra (1926); Paulus (1962)	119	13 Mar. 1990	1	Italy	Centro Studi Cetacei (1992)
7	1867	1	Italy	Giglioli (1880); Carruccio (1913)	120	1 Jun. 1990	1	Spain	Borrell *et al.* (2000)
8	4 Sep. 1878	1	France	Giglioli (1880); Vinciguerra (1926); Paulus (1962)	121	5 Jul. 1990	1*	Italy	Centro Studi Cetacei (1992)
9	15 Aug. 1879	1	France	Paulus (1962)	122	13 Dec. 1991	1	Spain	Borrell *et al.* (2000)
10	15 Oct. 1889	1	France	Paulus (1962)	123	24 Jan. 1992	3	Italy	Centro Studi Cetacei (1995)
11	24 Sep. 1900	1	Italy	Mezzana (1900); Vinciguerra (1926); Paulus (1962)	124	4 Feb. 1992	1	Italy	Centro Studi Cetacei (1995)
12	9 Sep. 1913	1	France	Vinciguerra (1926); Paulus (1962)	125	21 May 1992	1	Italy	Centro Studi Cetacei (1995)
13	15 Dec. 1918	1	Spain	Aguilar-Amat (1918); Casinos and Vericad (1976)	126	26 Aug. 1992	1*	Italy	Centro Studi Cetacei (1995)
14	3 Mar. 1919	1	Spain	Cabrera (1919); Casinos and Vericad (1976)	127	12 Oct. 1992	1	Italy	Centro Studi Cetacei (1995)
15	25 May 1919	1*	Spain	Cabrera (1919); Casinos and Vericad (1976)	128	7 Dec. 1992	1	Greece	Drougas and Komnenou (2001)
16	13 Nov. 1925	1	Italy	Vinciguerra (1926); Paulus (1962); Arbocco (1969)	129	21 Mar. 1993	1	Greece	Drougas and Komnenou (2001)
17	21 Aug. 1927	1	France	Paulus (1962)	130	20 Apr. 1993	3	Greece	Drougas and Komnenou (2001)
18	1930-1940	1	Italy	Littardi *et al.* (2004)	131	15 Jun. 1993	1	Italy	Centro Studi Cetacei (1996)
19	24 Nov. 1931	1	France	Paulus (1962)	132	10 Nov. 1993	1	Italy	Storelli *et al.* (1999)
20	1933	1*	Algeria	Boutiba (1994)	133	11 Nov. 1993	1	Greece	Drougas and Komnenou (2001)
21	11 Dec. 1934	1*	Italy	Tortonese (1957); Paulus (1962); Arbocco (1969)	134	19-20 Nov. 1993	2	Greece	Drougas and Komnenou (2001)
22	1938	1	Algeria	Boutiba (1994)	135	8-9 Feb. 1994	2	Greece	Drougas and Komnenou (2001)
23	8 Oct. 1939	1	Croatia	Hirtz (1940); Holcer *et al.* (2004)	136	28 Feb. 1994	1	Italy	Centro Studi Cetacei (1996)
24	5 Jun. 1940	1	Spain	A. Canadas (Alnitak) (pers. comm.)	137	13 Apr. 1994	1	Italy	Centro Studi Cetacei (1996)
25	18 Nov. 1940	1	Spain	Casinos and Vericad (1976)	138	15 Jul. 1994	1	Turkey	Ozturk and Ozturk (1998)
26	16 Mar. 1943	1	Spain	Casinos and Vericad (1976)	139	6 Aug. 1994	1*	Italy	Centro Studi Cetacei (1996)
27	29 Jan. 1944	1	Spain	Casinos and Vericad (1976)	140	11 Aug. 1994	1*	Italy	Centro Studi Cetacei (1996)
28	5 Jun. 1944	1	Spain	Casinos and Vericad (1976)	141	21 Nov. 1994	1	Algeria	Boutiba *et al.* (1997)
29	5 Sep. 1944	1*	Spain	Casinos and Vericad (1976)	142	14 Jan. 1995	1	Greece	Drougas and Komnenou (2001)
30	1945	1	Israel	Marchessaux (1980)	143	8 Feb. 1995	1	Greece	Drougas and Komnenou (2001)
31	15 Sep. 1954	1	Greece	Kinzelbach (1985)	144	1 Jun. 1995	1*	Italy	Centro Studi Cetacei (1997)
32	18 Sep. 1955	1	Italy	Tortonese (1957); Paulus (1962)	145	3 Jun. 1995	1*	Italy	Centro Studi Cetacei (1997)
33	28 Dec. 1956	1*	Italy	Tortonese (1957); Paulus (1962); Arbocco (1969)	146	5 Jun. 1995	1*	Italy	Centro Studi Cetacei (1997)
34	9 Feb. 1957	1	Italy	Tortonese (1957); Paulus (1962); Arbocco (1969)	147	15 Jun. 1995	1	Turkey	Ozturk and Ozturk (1998)
35	9 Mar. 1957	1*	Italy	Tamino (1957)	148	3 Dec. 1995	1	Malta	F.Bowman and S. Muscat (pers. comm.)
36	1958	1	Italy	Littardi *et al.* (2004)	149	3 Feb. 1996	1	Greece	Drougas and Komnenou (2001)
37	16 Mar. 1961	1	France	Paulus (1962)	150	3 Feb. 1996	1	Italy	Centro Studi Cetacei (1997)
38	30 Mar.-2 Apr. 1961	2	Italy	Paulus (1962)	151	25-26 Feb. 1996	2	Spain	Blanco *et al.* (1997); Blanco and Raga (2000)
39	10 Jun. 1961	1	France	Paulus (1962)	152	12 Apr. 1996	2	Greece	Drougas and Komnenou (2001)
40	15 Jul. 1961	1	Italy	Paulus (1962)	153	19 Apr. 1996	1	Italy	Centro Studi Cetacei (1997)
41	15-20 Jul. 1961	2	France	Paulus (1962)	154	12-13 May 1996	14	Greece	Frantzis (1998); Lefkaditou and Poulopoulos (1998); Drougas and Komnenou (2001)
42	7 Nov. 1961	1	Spain	Casinos and Vericad (1976)					
43	24 Nov. 1961	1	France	Paulus (1962)	155	15 May 1996	2*	Greece	Drougas and Komnenou (2001)
44	5 Jan. 1963	1	Italy	Littardi *et al.* (2004)	156	28 May 1996	1	Greece	Drougas and Komnenou (2001)
45	13 Jan. 1963	1	Italy	Littardi *et al.* (2004)	157	12 Jun. 1996	1	Greece	Drougas and Komnenou (2001)
46	Jan.-Feb. 1963	5	Italy	Tortonese (1963)	158	16 Aug. 1996	2	France	Oliver *et al.* (1997); Van Canneyt *et al.* (1998)

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ID	Date range	No. of animals	Country	References
47	11 May 1963	15	Italy	Tortonese (1963)
48	9 Nov. 1963	15	Italy	Anon. (1963); Littardi *et al.* (2004)
49	10 Nov. 1963	1	Israel	Marchessaux (1980)
50	1963	2*	Greece	Marchessaux and Duguy (1978); Marchessaux (1980)
51	8 Mar. 1964	1	Turkey	Marchessaux and Duguy (1978); Marchessaux (1980)
52	20 Apr. 1964	1	Italy	Cagnolaro (1965); Arbocco (1969)
53	15 Aug. 1964	1	Spain	Casinos and Vericad (1976)
54	1964-1965	1	Italy	Littardi *et al.* (2004)
55	7 Apr. 1965	1	Spain	Casinos and Vericad (1976)
56	10 Apr. 1965	1	Greece	Kinzelbach (1985)
57	26 Dec. 1965	1*	Greece	Kinzelbach (1985)
58	15 Jul. 1966	1	Israel	Marchessaux (1980)
59	15 Nov. 1966	3	Italy	Littardi *et al.* (2004)
60	1968	1	Greece	Kinzelbach (1985)
61	1968	1	Greece	Marchessaux and Duguy (1978); Marchessaux (1980)
62	20 Mar. 1970	1*	Spain	Filella Cornado (1971); Casinos and Vericad (1976)
63	22 Nov. 1971	1	France	Duguy and Budker (1972)
64	15 Mar. 1972	1	Italy	Progetto Cetacei 1972-1985 (unpublished data)
65	2 Jul. 1972	1	Spain	Casinos and Vericad (1976)
66	29 Jan. 1973	1	Spain	Casinos and Filella (1975)
67	15 Mar. 1973	1	Italy	Progetto Cetacei 1972-1985 (unpublished data)
68	25 Mar. 1973	1	Spain	Casinos and Filella (1975); Filella Cornado (1976)
69	13 Jun. 1973	1	Spain	Casinos and Filella (1975)
70	19 Dec. 1973	1	Spain	Casinos and Filella (1975)
71	16-22 Dec. 1974	4	France	Duguy (1975); Viale (1975)
72	23 Oct. 1975	1	Albania	Lamani *et al.* (1976)
73	15 Nov. 1975	1	France	Duguy (1976); Besson (1976)
74	1975	1	Greece	Bauer (1978)
75	15 Jul. 1976	1	Italy	Progetto Cetacei 1972-1985 (unpublished data)
76	10 Apr. 1977	1	Algeria	Lloze (1980); Boutiba *et al.* (1997)
77	6 Oct. 1977	1*	France	Duguy (1978)
78	22 May 1978	1	Algeria	Lloze (1980); Boutiba *et al.* (1997)
79	15 Jun. 1979	1	Israel	Marchessaux (1980)
80	10 Nov. 1979	1	Algeria	Lloze (1980); Boutiba *et al.* (1997)
81	10 Nov. 1979	1	Algeria	Lloze (1980); Boutiba *et al.* (1997)
82	2 Dec. 1979	1	Spain	Grau *et al.* (1980)
83	16 May 1981	1	Italy	Progetto Cetacei 1972-1985 (unpublished data)
84	9 Aug. 1981	1	Spain	Grau *et al.* (1986)
85	11 Oct. 1981	1	Spain	Grau *et al.* (1986)
86	4 Nov. 1981	1	Spain	A. Cañadas (Alnitak) (pers. comm.)
87	15 Feb. 1982	1	Italy	Progetto Cetacei 1972-1985 (unpublished data)
88	22 Apr. 1982	1	Spain	Raga *et al.* (1991)
89	8 Jul. 1982	1	Algeria	Boutiba (1994); Boutiba *et al.* (1997); Boutiba *et al.* (2001)
90	13 Sep. 1982	1	Turkey	Kinzelback (1985)
91	18 May 1983	1	Italy	Cagnolaro *et al.* (1986)
92	10 Nov. 1983	1	France	Duguy (1984); Oliver (1990)
93	22 Aug. 1984	1*	Italy	Progetto Cetacei 1972-1985 (unpublished data)
94	2 Oct. 1984	1	France	Duguy (1985)
159	18 Aug. 1996	1	Italy	Centro Studi Cetacei (1997)
160	18 Dec. 1996	1*	Italy	Centro Studi Cetacei (1997)
161	22 Dec. 1996	1	France	Oliver *et al.* (1997); Van Canneyt et al. (1998)
162	27 Jan. 1997	1	France	Oliver and Rigollet (1998); Collet *et al.* (1999); Frodello *et al.* (2002)
163	18 Mar. 1997	1	Greece	Drougas and Komnenou (2001)
164	12 Apr. 1997	1	Spain	A. Cañadas (Alnitak) (pers. comm.)
165	14 Apr. 1997	1*	Greece	Drougas and Komnenou (2001)
166	15 Apr. 1997	1	Turkey	Ozturk and Ozturk (1998)
167	24 Apr. 1997	1	Greece	Drougas and Komnenou (2001)
168	27 May 1997	1	Spain	A. Cañadas (Alnitak) (pers. comm.)
169	18 Jun. 1997	1	Greece	Drougas and Komnenou (2001)
170	28 Jul. 1997	1	Greece	Drougas and Komnenou (2001)
171	26 Aug. 1997	3	Greece	Drougas and Komnenou (2001)
172	24 Sep. 1997	1	Italy	Centro Studi Cetacei (1998)
173	26 Sep. 1997	1	Spain	A. Cañadas (Alnitak) (pers. comm.)
174	2-5 Oct. 1997	8	Greece	Drougas and Komnenou (2001)
175	3 Oct. 1997	4	Greece	Drougas and Komnenou (2001)
176	4 Oct. 1997	1*	Italy	Centro Studi Cetacei (1998)
177	6-14 Oct. 1997	2	Greece	Drougas and Komnenou (2001)
178	14 Oct. 1997	1	Greece	Drougas and Komnenou (2001)
179	20 Oct. 1997	1	Italy	Centro Studi Cetacei (1998)
180	25 Nov. 1997	1	Greece	Drougas and Komnenou (2001)
181	13 Jan. 1998	1	Greece	Drougas and Komnenou (2001)
182	17 May 1998	1	Spain	A. Cañadas (Alnitak) (pers. comm.)
183	2 Oct. 1998	1	Greece	Drougas and Komnenou (2001)
184	5 Oct. 1998	1	Greece	Drougas and Komnenou (2001)
185	26 Nov. 1998	1	Spain	A. Cañadas (Alnitak) (pers. comm.)
186	14-16 Jan. 1999	3	Greece	Drougas and Komnenou (2001)
187	12 Mar. 1999	1	Italy	Centro Studi Cetacei (2001)
188	15 Mar. 1999	1	Israel	Goffman *et al.* (2000) (and ECS Newsletter)
189	12 May 1999	1	Greece	Drougas and Komnenou (2001)
190	21 May 1999	1	Italy	Centro Studi Cetacei (2001)
191	17 Jun. 1999	1	Spain	A. Cañadas (Alnitak) (pers. comm.)
192	23 Jun. 1999	1	Greece	Drougas and Komnenou (2001)
193	30 Oct. 1999	1	Greece	Drougas and Komnenou (2001)
194	3 Jan. 2000	1	Italy	Centro Studi Cetacei (2002)
195	13 Feb. 2000	2*	Greece	Drougas and Komnenou (2001)
196	15 Feb. 2000	1	Italy	Centro Studi Cetacei (2002)
197	23 Feb. 2000	1	Greece	Drougas and Komnenou (2001)
198	30 Mar. 2000	1	Spain	A. Cañadas (Alnitak) (pers. comm.)
199	1 Jun. 2000	1*	Greece	Drougas and Komnenou (2001)
200	7 Feb. 2001	2	Algeria	Boutiba *et al.* (2001)
201	5 Apr. 2001	1	Italy	Centro Studi Cetacei (2003)
202	12 Apr. 2001	1	Croatia	Holcer *et al.* (2004)
203	19 Apr. 2001	2	Turkey	A.C. Gucu (pers. comm.)
204	17 May 2001	1	Italy	Centro Studi Cetacei (2003)
205	14 Jun. 2001	1	Italy	Centro Studi Cetacei (2003)

cont.

ID	Date range	No. of animals	Country	References	ID	Date range	No. of animals	Country	References
95	6 Nov. 1984	1	France	Duguy (1985)	206	Jun. 2001	1	Israel	Goffman O. (ECS Newsletter on line, Jun. 2001)
96	21 Nov. 1984	1	France	Duguy (1985)	207	12 Jul. 2001	1	Italy	Centro Studi Cetacei (2003)
97	8 Mar. 1985	1	Italy	Progetto Cetacei 1972-1985 (unpublished data)	208	23 Jul. 2001	2	Algeria	Boutiba *et al.* (2001)
98	30 Mar. 1985	1	Italy	Progetto Cetacei 1972-1985 (unpublished data)	209	25 Oct. 2001	1	Greece	Drougas and Komnenou (2001)
99	10 Sep. 1985	1	France	Duguy (1986)	210	2001	1	Spain	A. Cañadas (Alnitak) (pers. comm.)
100	12 Feb. 1986	1	Italy	Progetto Cetacei 1972-1985 (unpublished data)	211	7 Feb. 2002	1	Croatia	Holcer *et al.* (2004)
101	22 May 1986	1*	Italy	Centro Studi Cetacei (1987)	212	3 Mar. 2002	1	Greece	Drougas and Komnenou (2001)
102	30 Jun. 1986	1	Spain	Raga *et al.* (1991)	213	26 Mar. 2002	1	Italy	Centro Studi Cetacei (2004)
103	15 Jan. 1987	1	Italy	Centro Studi Cetacei (1988)	214	12 Apr. 2002	1	Italy	Centro Studi Cetacei (2004)
104	10 Feb. 1987	2	Italy	Centro Studi Cetacei (1988); Podestà and Meotti (1991)	215	16 Apr. 2002	1	Greece	Arion/Delphis (Greece)
105	14 Feb. 1987	1	Italy	Centro Studi Cetacei (1988)	216	27 Apr. 2002	1	Greece	Arion/Delphis (Greece)
106	22 May 1987	1	Italy	Centro Studi Cetacei (1988)	217	17 May 2002	1	Greece	Arion/Delphis (Greece)
107	23 Sep. 1987	1	Algeria	Boutiba (1994); Boutiba *et al.* (1997)	218	1 Jun. 2002	1	Spain	A. Cañadas (Alnitak) (pers. comm.)
108	9 May 1988	1	France	Duguy (1989)	219	3 Oct. 2002	1	Greece	Arion/Delphis (Greece)
109	15 Jul. 1988	1	Italy	Centro Studi Cetacei (1990)	220	14 Apr. 2003	1	France	Van Canneyt *et al.* (2004)
110	25 Jul. 1988	1*	Italy	Centro Studi Cetacei (1990)	221	24 Apr. 2003	1	France	Van Canneyt *et al.* (2004)
111	27 Sep. 1988	1*	Italy	Centro Studi Cetacei (1990)	222	24 Jun. 2003	1	Greece	Arion/Delphis (Greece)
112	22 Nov. 1988	1	Italy	Centro Studi Cetacei (1990); Carlini *et al.* (1992)	223	5 Nov. 2003	1	Greece	Arion/Delphis (Greece)
113	22 Jan. 1989	1	Spain	Borrell *et al.* (2000)	224	24 Dec. 2003	1	Italy	Centro Studi Cetacei Onlus e Museo Civico di Storia Naturale di Milano (2004)
Total = 307									
Incomplete data:									
		1	Greece	Kinzelbach (1985)					
		1	Greece	Kinzelbach (1985)					
		1	Egypt	Marchessaux (1980)					
	1913	2	Spain	Vinciguerra (1926)					
	1962	1	France	Viale					
	1963	1	Israel	Marchessaux (1980); Kinzelbach (1985)					
	1968	1	France	Viale					
	2001	1	Algeria	Boutiba *et al.* (2001)					

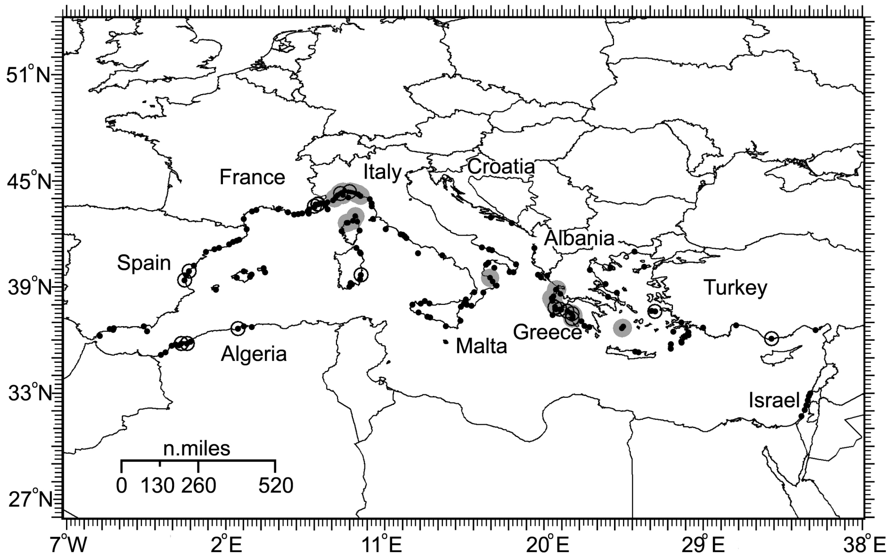

Fig. 1. Strandings recorded in the Mediterranean Sea (1803-2003). Open circles show strandings of two animals, grey circles show strandings of three or more animals.

Table 2

Number of animals and number of stranding events by Country. Numbers marked with (x) include bycatch. For stranding events with three or more animals, total animals are given in brackets. Other than those reported here, nine more animals have been found with incomplete data and were not included in the table.

Country	Total animals	Strandings (1 animal)	% of total	Strandings (2 animals)	% of total	Strandings (≥3 animals)	% of total
Italy	118	73 x	61.9	2	3.4	5 (41)	34.7
Greece	86	37 x	43	7 x	16.3	6 (35)	40.7
Spain	38	36 x	94.7	1	5.3		
France	34	26 x	76.5	2	11.8	1 (4)	11.8
Algeria	13	9 x	69.2	2	30.8		
Turkey	7	5	71.4	1	28.6		
Israel	6	6	100				
Croatia	3	3	100				
Albania	1	1	100				
Malta	1	1	100				
	307	197	64.2	15 (30)	9.8	12 (80)	26.1

available at the Pisa Museum. Physical verification of the skeleton confirmed that it belongs to an 1823 stranding reported by Richiardi in 1875 (Table 1, # 2). Paulus (1962) also reported a stranding in Beaulieu, Villafranca (France) on 23 June 1878. This stranding actually occurred on 4 September 1878 (Table 1, #8), as first published by Giglioli (1880) and Vinciguerra (1926).

In another example, Mezzana (1900) reported a specimen stranded in Varazze (Genova, Italy) (Table 1, # 11) as a '*Hyperoodon bidens'*, and this report was subsequently repeated in Vinciguerra (1926) and Paulus (1962). However, both the description given, and examination of the skull preserved at the Museum of Natural History of Calci (Pisa) (Cagnolaro, 1996) confirm that this was a Cuvier's beaked whale.

A short report concerning historical strandings of Cuvier's beaked whales in the Ligurian Sea was presented to the International Commission for the Study of the Mediterranean Sea (ICSM-CIESM) by Littardi *et al.* (2004). In this paper, few original source references for these strandings were cited, with a significant amount of information derived from unlisted newspaper accounts. When possible, original source references were obtained to validate the events presented. This comparison of the data presented in Table 1 and in Littardi *et al.* (2004) highlights some reporting inconsistencies. Two strandings reported in 1956 over two subsequent days (28 and 29 December) at two different locations very close to each other, were actually the same animal (Table 1, # 33). Tortonese (1957) described the mistake made by a newspaper journalist at the time (dated 29 December) that reported the stranding at the incorrect location. Two strandings were listed for 1964, one of which was reported in Cagnolaro (1965) (Table 1, # 52), while the other was from a newspaper with no date. The

Table 3

Mass strandings of three or more animals. ID numbers refer to Table 1. Bycatch is not included.

ID	Map	Year	Date	Location	Country	Animals
46	A	1963	Jan.-Feb.	Ligurian Sea (Liguria)	Italy	5
47	B	1963	11 May	Ligurian Sea (Liguria)	Italy	15
48	C	1963	9 Nov.	Ligurian Sea (Liguria)	Italy	15
59	D	1966	15 Nov.	Ligurian Sea (Liguria)	Italy	3
71	E	1974	16-22 Dec.	Ligurian Sea (N. Corsica)	France	4
123	F	1992	24 Jan.	Ionian Sea (Calabria)	Italy	3
130	G	1993	20 Apr.	Ionian Sea (Kephalonia and Zakynthos Islands)	Greece	3
154	H	1996	12-13 May	Ionian Sea (Kyparissiakos Gulf)	Greece	14
171	I	1997	26 Aug.	Ionian Sea (Assos Island)	Greece	3
174	J	1997	2-5 Oct.	Ionian Sea (Kephalonia Island)	Greece	8
175	K	1997	3 Oct.	Ionian Sea (Lefkas Island)	Greece	4
186	L	1999	14-16 Jan.	Aegean Sea (Mylos Island)	Greece	3

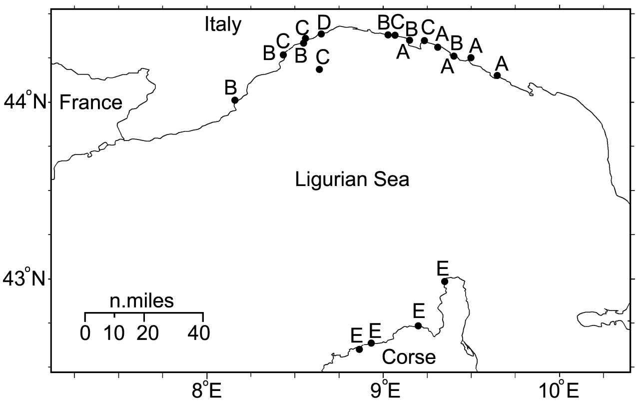

Fig. 2. Strandings occurred in the Ligurian Sea in years 1963-74. See Table 3 for details.

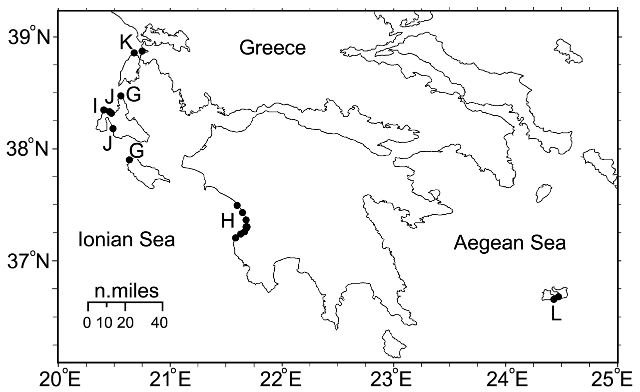

Fig. 3. Strandings occurred in Greek waters in years 1996-99. See Table 3 for details.

second reference source was rejected since it was felt that this was a duplicate report. Three live animals that stranded in Cogoleto (Genova) in 1966 were described as 'disoriented' (Table 1, # 59). Two were able to swim back toward the open sea, while the third was caught by fishermen, but eventually escaped after being wounded. This particular animal might have died and stranded later, but this cannot be confirmed (M. Rosso, pers. comm.). Furthermore, the authors postulate that five strandings could be correlated with the presence of military ships in the area. Two of these five events involved a single specimen (5 and 13 January 1963: Table 1, #44, #45). For the mass stranding events listed in Littardi *et al.* (2004), some specimens were described as disoriented and others showed evidence of firearms wounds, although this cannot be confirmed as the cause of death (Anon., 1963).

Of the three Italian mass stranding events in 1963 (Table 1, #46, #47, #48), only two have been documented in the scientific literature (Tortonese, 1963). In addition, Tortonese provided some details of another mass stranding event that occurred in the same area earlier that year during 'the end of January, the beginning of February' (Table 1, #46). While searching newspaper accounts for reports about the 1963 stranding events, an additional mass stranding event was discovered in this same region on 9 November 1963 (Anon., 1963; Littardi *et al.*, 2004; Table 1, #48), probably after Tortonese's paper was published. The newspaper account (Anon., 1963) describing this event contained pictures of the animals, which confirm these as Cuvier's beaked whales.

DISCUSSION AND CONCLUSION

This review of Cuvier's beaked whale strandings in the Mediterranean Sea has facilitated the creation of a comprehensive, geo-referenced database.

The geographic distribution of the data may suggest an abundance of this species in particular areas, such as the Ligurian and the Ionian Seas. However, the study effort along the Mediterranean coast is extremely variable by area and this must be taken into account in any analysis. While national networks have been operating in France and Italy for many decades, other countries also have historical reports, even if not organised at a national level (e.g. Spain). Many southern Mediterranean nations have only sporadic reports of strandings, with no methodical monitoring of their coasts. Stranding records date back to the beginning of the 19th century in Italy and France, while the first record in Spain is nearly a hundred years later. For other countries, records started within the first half of the 20th century.

Geo-referencing of the data shows that most strandings of Cuvier's beaked whales occur near regions with steep bathymetry. This is consistent with sightings data for the same areas (Ballardini *et al.*, 2005; Azzellino *et al.*, 2003) for the Ligurian Sea. Despite the obvious limitations, the use

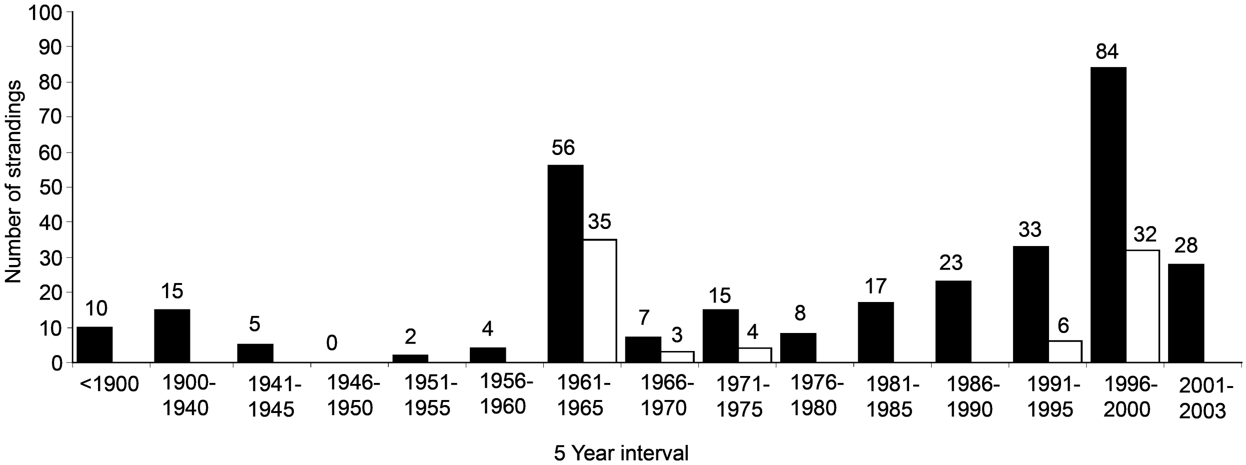

Fig. 4. Cuvier's beaked whale strandings in the Mediterranean in five-year intervals, earliest year – 2003. Shaded columns show the total number of animals; white columns show the number of animals stranded in groups of 3 or more.

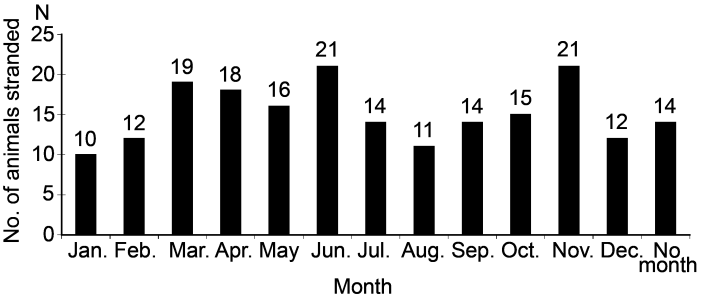

Fig. 5. Distribution of individual strandings by month.

and reliability of stranding records as a source of information on the occurrence of certain species in certain areas has been shown in a paper on the Hawaiian Islands Odontocetes (Maldini *et al.*, 2005).

The absence of strandings along the Italian Adriatic Sea coastline, despite relatively consistent effort along the Italian coast, may indicate that this is an area which these whales do not frequent; its shallow water depth is typically not considered a beaked whale habitat. However, the pronounced lack of strandings along the North African coast may be more likely connected to scarce effort than the steep bathymetry here, which suggests that it may be a suitable Cuvier’s beaked whale habitat.

The first reported mass stranding in the Mediterranean area was in 1963 near Genova, Italy. We are confident that this event is the first mass stranding event for the Ligurian Sea, since single stranding events have been recorded in this region since 1823.

From the analysis of the percentages reported in Table 2, it can be shown that for Greece, strandings of three or more animals are nearly as likely as individual strandings. However, for Spain single strandings make up the majority (94.7%) and mass strandings of three or more have never been reported.

All mass strandings of three or more animals (Table 3) have occurred in the Ligurian Sea (Italy and France, Fig. 2), the Ionian Sea and the Aegean Sea (Greece, Fig. 3), accounting for 80 animals and representing 26% of the total number of the animals recorded for the whole Mediterranean area. Note that the May 1963 stranding in Italy (#B, Table 3) extends over more than 50 n.miles of coastline; however, this stranding was described as a single event in the first report by Tortonese (1963). Furthermore, since these strandings occurred on the same day along a coastline that forms a wide gulf on which carcasses can be spread out by counterclockwise currents documented for the Ligurian Sea, they have been maintained as a single mass stranding event.

The majority of the mass stranding events of three or more animals have occurred in the Ligurian Sea (Italy 4 events, France 1 event) and in the Ionian Sea (Greece 5 events). The mass stranding in the Ligurian Sea in 1963 is one of the first events reported worldwide. Notably, events in the Ligurian Sea occurred in the period 1963-74, while events in Ionian Sea occurred in years 1993-97.

The Greek mass stranding event in Kyparissiakos Gulf (# H, Table 3) of May 1996, consisting of 14 animals, was the first case reported in the Mediterranean Sea that was identified as being correlated in both space and time with sonar activities (D’Amico and Verboom, 1998; Frantzis, 1998 and Frantzis, 2004). Two more specimens found on 15 May were not included in the total for this mass stranding event because although the location of these animals was close to Kyparissiakos Gulf, the stranding report documents that they were entangled alive in a fishing net and subsequently released.

The two Greek mass strandings in October 1997, listed as #J and #K in Table 3, totalled 12 animals, and could be considered a single event given that they took place in the same area (approximately 34 n.miles apart) and in the same time frame (within four days), with the majority of carcasses slightly decomposed. The data were directly collected by two of the authors of this paper (Drougas and Komnenou, 2001). Frantzis (2004) reported nine animals stranded in ten days for this event.

The analysis of the number of animals stranded in five-year intervals (Fig. 4) indicates an increase in the number of stranded animals during the last two decades. Given the increased worldwide interest in marine mammal stranding events, it cannot be determined whether this apparent trend is the result of improved reporting and record keeping, or an actual increase in stranding occurrence. The inclusion of infrequent mass stranding events that contain a large number of animals can influence the overall stranding trend suggested in Fig. 4. For instance, the anomalous peak in 1963 is due to three mass stranding events on the Ligurian coast (Tortonese, 1963; Anon., 1963), while another peak in 1996 and 1997 is due to two mass stranding events in Greece (D’Amico and Verboom, 1998; Frantzis, 1998 and Frantzis, 2004; Drougas and Komnenou, 2001).

The monthly distribution of individual strandings (Fig. 5) shows peaks in spring/early summer and in November. Unfortunately, these strandings data cannot be compared with sightings data because studies at sea of this species are primarily conducted in summer.

In recent years there has been increasing concern, in both the scientific and military communities, about the potential impacts of anthropogenic acoustic activities on beaked whales (Simmonds and Lopez-Jurado, 1991; Frantzis, 1998 and Frantzis, 2004; Anon., 2001; Martín, 2002; Freitas, 2004; Brownell *et al.*, 2004; Evans and Miller, 2004; Fernàndez *et al.*, 2004; Cox *et al.*, 2006). In the Mediterranean Sea, only one mass stranding out of a total of 12 can be unequivocally associated with naval activity, as the sonar activity and corresponding ship’s tracks have been well documented (D’Amico and Verboom, 1998; Frantzis, 1998 and Frantzis, 2004). For other ‘atypical’ (sensu Frantzis and Cebrian, 1998) mass stranding events there is only anecdotic information about the presence of military ships in the same region (Anon., 1963; Littardi *et al.*, 2004). Better information would be valuable, if it could be provided by appropriate military authorities.

Further study is required to investigate the context of the mass strandings described here and to possibly link them to specific human activities. Nevertheless, the analyses presented here and the validated geo-referenced database may be useful for predicting areas of Cuvier's beaked whale habitat in the Mediterranean Sea, in order to mitigate potential impacts of man-made noise, as recommended by ACCOBAMS Resolution 2.16 (ACCOBAMS, 2004).

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Abundance and densities of beaked and bottlenose whales (family Ziphiidae)

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ABSTRACT

Estimating the abundance and density of beaked whales is more difficult than for most other cetacean species. Consequently few estimates appear in the published literature. Field identification is problematic, especially for the smaller species, and visual detection rates decrease dramatically with Beaufort sea state; prior experience is very important to an observer's ability to detect beaked whales. Passive acoustics may hold future promise for detecting beaked whales from their vocalisations, especially for the larger species. Most published estimates of abundance or density are based on visual line-transect studies that found narrower effective strip widths and lower trackline detection probabilities for beaked whales than for most other cetaceans. Published density estimates range from 0.4-44 whales per 1,000km^2 for small beaked whales and up to 68 whales per 1,000km^2 for large beaked whales. Mark-recapture methods based on photo-identification have been used to estimate abundance in a few cases in limited geographical areas. Focused research is needed to improve beaked whale abundance and density estimates worldwide.

KEYWORDS: ABUNDANCE ESTIMATE; *g*(0); MARK-RECAPTURE; SURVEY-VESSEL; SURVEY-AERIAL; SURVEY-ACOUSTIC; BEAKED WHALE; MODELLING; DISTRIBUTION; ACOUSTICS; PHOTO-ID

INTRODUCTION

Despite their nearly ubiquitous distribution in the world's oceans, there are few estimates of the density or absolute abundance of beaked whales. In part, this is because many surveys have concentrated on continental shelf waters, where beaked whales are rare. However the lack of estimates largely reflects the general rarity and difficulty in detecting and identifying beaked whales under typical survey conditions. There is a growing recognition that mass strandings of beaked whales have been associated with loud anthropogenic sounds, such as military sonar (e.g. Anon., 2001) and possibly geophysical research (Peterson, 2003). Consequently, there is a growing need for information about the abundance and density of beaked whales to allow us to better (1) evaluate the risks that anthropogenic sounds pose to specific beaked whale populations and (2) monitor and mitigate those effects at the population level.

In this paper, some of the problems encountered when making quantitative estimates of abundance or density for beaked whales are examined, studies where abundance or density was estimated are reviewed and recommendations for research to help fill gaps in current knowledge are made.

Field identification

Throughout this paper, large (6-13m) beaked whales (*Berardius* spp., *Hyperoodon* spp., and *Indopacetus pacificus*) and small (4-7m) beaked whales (*Ziphius cavirostris, Mesoplodon* spp. and *Tasmacetus shepherdi*) are differentiated between because their detectabilities differ markedly. Field identification is a major problem in estimating the abundance of small beaked whales. Although Cuvier's beaked whales (*Z. cavirostris*), Tasman beaked whales (*T. shepherdi*), and *Mesoplodon* spp. are physically distinctive at close range, all three genera appear similar at distance; medium-sized, brown to grey in colour, with dorsal fins located closer to flukes than to head. The elusive behaviour of small beaked whales in the presence of survey ships often prevents close approaches to verify species identification. The typical duration of a surfacing series for Cuvier's and *Mesoplodon* beaked whales is only 2-3mins (Barlow, 1999), leaving little time for observation. Their long dives (typically 15-40mins; Barlow and Sexton, 1996) substantially reduce the opportunity to relocate groups and to verify species under average survey conditions. Within the genus *Mesoplodon*, field identification of species is even more problematic. For many species, field identification is impossible for juveniles or females, therefore only groups with mature males may be identified to species. To further compound problems, three to five species of *Mesoplodon* may be sympatric in a given area (MacLeod *et al.*, 2006). Finally, the taxonomy of the genus *Mesoplodon* is still being resolved, with two new species described in the last 15 years (Reyes *et al.*, 1991; Dalebout *et al.*, 2002). Consequently, most *Mesoplodon* sightings are identified only to genus, and many sightings of small beaked whales may be field-classified as 'unidentified ziphiid'.

Species identification is less of a problem for the large beaked whales because the species are physically more distinctive and are often easier to approach. Of the five species, only the southern bottlenose whale (*H. planifrons*) and Arnoux's beaked whale (*B. arnuxii*) overlap in distribution (MacLeod *et al.*, 2006), which eliminates potential confusion in tropical and northern latitudes. However, the external morphology of Longman's beaked whale (*I. pacificus*) was described only recently and many previous sightings of this species were attributed to *Hyperoodon* spp. (Pitman *et al.*, 1999; Dalebout *et al.*, 2003). Although Longman's beaked whales overlap in size with adult Cuvier's beaked whales, we have included the

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former with the large beaked whales because their larger group sizes and conspicuous blows make them more similar in detectability to the other large beaked whales.

Detecting beaked whales

Small beaked whales are more difficult to visually detect in the field than most other cetaceans, with the exception of *Kogia* spp. and some porpoises. They typically surface inconspicuously, usually without a splash or visible blow and seldom breach or display other aerial activities. In addition, small beaked whales rarely display their flukes when they dive and they occur in small groups, typically 1-5 individuals. Finally, they spend very little time at the surface and then dive for extraordinarily long periods (Barlow, 1999). In contrast, the visual detection of large beaked whales is easier because they have a conspicuous blow and are physically larger. However, large beaked whales also have relatively long dive times compared to other cetaceans (Kasuya, 1986; Barlow, 1999; Hooker and Baird, 1999), which reduces their detectability by visual observers.

Sea state

The group encounter rate (number of groups seen per unit of search effort) can be used as a rough measure of how the ability to visually detect beaked whales changes with sighting conditions. Sea state is the most commonly used measure of sighting conditions for cetacean surveys. Encounter rates can change dramatically with increasing sea states (Table 1), decreasing more than 10-fold from Beaufort 0-1 (glassy or with a few ripples, wind speed 0-3kts) to Beaufort 5 (moderate waves with many whitecaps, wind speed 17-21kts). Visual surveys for cetaceans are generally not conducted above Beaufort 5.

Table 1

Changes in the encounter rates (ER = number of sightings per 1,000 km of survey effort) with Beaufort sea state for small beaked whales (genera *Mesoplodon* and *Ziphius*). Survey effort consisted of a team of at least three observers in all cases*.

	SWFSC: 1986-2002		SEFSC: 1991-2003		NEFSC: 1998	
Beaufort sea state	No. sightings	ER (per 1,000 km)	No. sightings	ER (per 1,000 km)	No. sightings	ER (per 1,000 km)
0	16	9.8	11	16.8	n/a	n/a
1	122	10.1	45	7.2	32	145.0
2	169	4.9	18	1.4	44	23.9
3	175	2.4	26	1.2	18	7.2
4	180	1.5	5	0.2		
5	76	0.9	6	0.5		

*Data are from Southwest Fisheries Science Center surveys in the eastern Pacific (SWFSC: Ballance, Barlow, and Gerrodette, unpubl. data); Southeast Fisheries Science Center surveys in the Gulf of Mexico, Caribbean, and North Atlantic (SEFSC: Hansen, Hoggard, Garrison and Mullin, unpubl. data); and Northeast Fisheries Science Center surveys in slope and offshore waters of the North Atlantic (NEFSC: Palka and Waring, unpubl. data).

Experience

The importance of observer experience in detecting beaked whales has not been examined previously. This paper examines data from Southwest Fisheries Science Center (SWFSC) surveys in the eastern tropical Pacific (ETP) to quantify the effect of experience. The surveys from 1986-1990 and 1998-2000 were used since these covered almost exactly the same study area (Fig. 1), and thus geographic differences in sighting rates is not a confounding factor. Observers were classified by previous experience on SWFSC or Southeast Fisheries Science Center (SEFSC) line-transect surveys as follows: (1) first-time observers; (2) observers with at least four months of previous at-sea experience as a marine mammal observer; and (3) observers with at least 12 months of at-sea experience. Note, however, that even first-time observers had some previous cetacean research experience and in some cases, had considerable at-sea experience (e.g. as fishery observers). Ability to detect beaked whales was estimated as the number of beaked whales (i.e. sightings identified as Cuvier's beaked whales, *Mesoplodon* beaked whales and unidentified ziphiid whales) detected by each observer per 1,000km of transect surveyed by that observer in a given survey year. Analysis of variance (ANOVA) was used to test whether *experience*, *survey year*, or *observer* were significant factors in explaining variation in beaked whale sighting rates, which were weighted by the length of transect surveyed by an observer in a given year.

Results of the ANOVA indicate that *experience* was a significant factor in explaining differences in sighting rates among observers ($p<0.0001$). The effects of *year* ($p=0.90$) and *observer* ($p=0.22$) were not significant when *experience* was included in the model. Mean sighting rates were 0.54 per 1,000km for first-time observers, 0.67 per 1,000km for observers with 4-11 months prior experience and 0.93 per 1,000km for observers with at least 12 months prior experience. The analysis only considered the ability of an observer to detect a beaked whale and not necessarily his/her ability to identify one. Since observers work in teams of three and each team has at least one very experienced observer (the identification expert), the difficult species were often identified by someone other than the observer who made the initial sighting. There were only 20° of overlap in search angles between the right and left observers, so the presence of a more experienced observer should not have appreciably affected the sighting rate of the observer on the opposite side of the vessel. However, this lack of complete independence may have exaggerated the p-value in the above comparison of sighting rates, if more experienced observers were also more likely to see beaked whales first.

Acoustic detection

Although visual detection has been used on all previous surveys, passive acoustic detection (listening for sounds produced by beaked whales) offers the potential to detect submerged whales. The value of acoustic detection will depend on how frequently the whales vocalise and how easily those vocalisations can be detected. Until recently, very little was known about beaked whale vocalisations. Studies of captive and stranded whales suggested that beaked whales are capable of producing both pulsed sounds (clicks) and whistles (Dawson *et al.*, 1998). Ljungblad (cited in Dawson *et al.*, 1998) recorded ultrasonic clicks in the vicinity of a *Mesoplodon* whale. Frantzis *et al.* (2002) recorded narrow-banded, 13-17kHz clicks in close proximity to Cuvier's beaked whales and Johnson *et al.* (2004) recorded clicks ranging from 20kHz to over 40kHz using recorders that were physically attached to Cuvier's beaked whales. However, many efforts to record sounds in the vicinity of free-ranging Cuvier's and *Mesoplodon* beaked whales have been unsuccessful (Barlow *et al.*, 1997; Barlow and Rankin, unpubl. data), indicating that sound production may not be common in the smaller beaked whales, or that their sounds do not propagate well to surface hydrophones. Large beaked whales in the genera *Berardius* and *Hyperoodon* make more consistent vocalisations that can be detected at the surface (Hobson and Martin, 1996;

Dawson *et al.*, 1998; Hooker and Whitehead, 2002). Passive acoustics may add appreciably to our ability to detect *Berardius* and *Hyperoodon* species when they are submerged. Two attempts to record Longman's beaked whales (in mixed groups with short-finned pilot whales, *Globicephala macrorhynchus*) failed to detect sounds that could unambiguously be attributed to that species (Rankin and Barlow, unpubl. data). The narrow-banded characteristic of clicks from Cuvier's beaked whale (Frantzis *et al.*, 2002; Johnson *et al.*, 2004), Baird's beaked whale (*B. bairdii*; Dawson *et al.*, 1998), and the northern bottlenose whale (*H. ampullatus*; Hooker and Whitehead, 2002) distinguish them from clicks of many other species and if this pattern holds elsewhere, digital filters could be designed to greatly improve our ability to acoustically detect beaked whales. Currently, however, methods to routinely incorporate acoustic detections into abundance estimation surveys are not well developed (Mellinger and Barlow, 2003) and have never been used for beaked whales.

Line-transect abundance estimation

Most previous abundance or density estimates for small beaked whales have been based on visual line-transect methods. The basic line-transect equation for estimating density, D, in a defined study area is:

$$D = \frac{n \cdot S}{2 \cdot L \cdot ESW \cdot g(0)} \qquad (1)$$

where:
n = number of sightings;
S = expected (or mean) group size;
ESW = effective strip half-width;
L = total length of transects in the study area; and
$g(0)$ = probability of detecting an animal on the trackline.

Abundance, N, is estimated by multiplying density by the size of the study area, A.

ESW is estimated by fitting an empirical function, the detection function, to the distribution of perpendicular sighting distances. A minimum sample size of 60 sightings is recommended for estimating a detection function (Buckland *et al.*, 2001), and ~15 sightings is an absolute minimum. As the encounter rate is typically low for small beaked whales and decreases rapidly with increasing sea state, sample size is often an impediment to estimating beaked whale abundance. Although it is recommended that detection functions are fitted to data from each specific survey (a combination of ship, area, personnel, and sea conditions), 15 beaked whale sightings would not be made during most surveys. As a result, most estimates of beaked whale abundance or density have pooled data from multiple surveys to estimate *ESW*. To obtain an adequate sample size for estimating *ESW*, some authors have used pooled sighting distributions of several species, such as Cuvier's and *Mesoplodon* beaked whales (Forney *et al.*, 1995), all beaked whales (Kasamatsu and Joyce, 1995) or small beaked whales with other small whale species (Barlow, 1995; Mullin and Fulling, 2003). There is a trade-off between the improved precision obtained by pooling species and the potential biases that could result from pooling. Barlow *et al.* (2001) showed that when modelling perpendicular distance (a surrogate for *ESW*) a species-pooling scheme that combined Cuvier's beaked whales, *Mesoplodon* beaked whales and minke whales (*Balaenoptera acutorostrata*) resulted in a more parsimonious model based on Akaike's Information Criterion (AIC) than a model that included all species separately. Thus, at least in some cases, the trade-off appears to favour pooling species of similar size, behaviour and sighting characteristics.

Estimating the probability of detecting an animal on the trackline, $g(0)$, is also critical for estimating abundance or density for most beaked whales. Animals can be missed on the trackline either because they were at the surface and were not seen (i.e. perception bias) or because they were never at the surface within the visual range of the observers (i.e. availability bias) (Marsh and Sinclair, 1989). Both types of bias affect beaked whale density estimates. As discussed above, beaked whales are difficult to detect and to identify, leading to perception bias. They also have long dive times (Kasuya, 1986; Kasamatsu and Joyce, 1995; Barlow, 1999), leading to availability bias. To minimise these biases, line-transect data for the small beaked whales are often limited to the best survey conditions (e.g. Beaufort sea state ≤ 2; Barlow, 1995). However, even under these conditions and using 25X binoculars to extend sighting distances, many trackline animals may be missed. Two methods have been used to estimate $g(0)$ for beaked whales: independent observer methods using multiple observation locations from a single ship or aircraft (to estimate perception bias only) and model-based methods (to estimate perception and/or availability bias). Barlow (1995) pooled beaked whales with other small whales to obtain an estimated $g(0)$ value of 0.84, using conditionally independent observer methods. Miyashita (1986) estimated a $g(0)$ value of 0.84 to correct availability bias for Baird's beaked whales based on a dive-time simulation model. Kasamatsu and Joyce (1995) and Barlow (1999) made model-based estimates of $g(0)$ for beaked whales that included diving and detection models, thereby accounting for both availability and perception bias during shipboard surveys. Based on the use of 7X binoculars in sea states of Beaufort ≤ 5, Kasamatsu and Joyce (1995) estimated that $g(0)$ for southern bottlenose whales was approximately 0.27 (CV=0.04). Based on SWFSC surveys using 25X binoculars, Barlow (1999) estimated that $g(0)$ was approximately 0.23 (CV=0.35) for Cuvier's beaked whales and 0.45 (CV=0.23) for *Mesoplodon* whales in Beaufort 0-2 survey conditions and was 0.96 (CV=0.23) for Baird's beaked whales in Beaufort 0-5 conditions. Values of $g(0)$ for Cuvier's and *Mesoplodon* beaked whales have not been estimated for sea states of Beaufort ≥ 3, but based on the decline in encounter rates, we can infer that values would be dramatically lower in rougher conditions.

Values of $g(0)$ for beaked whales on aerial surveys have only been estimated once and then only to account for perception bias ($g(0)$=0.95; Forney *et al.*, 1995). Given their long dive times and short surface times, availability bias is likely to be an even bigger problem for beaked whale abundance estimates derived from aerial surveys than from vessel-based surveys. A crude estimate of $g(0)$ for availability bias in beaked whales can be made by estimating the fraction of time they spend in surfacing series, assuming that animals are visible from the air during the entirety of a surfacing series. Based on published dive and surface times (Barlow, 1999), these crude $g(0)$ values would be 0.11 for *Mesoplodon* beaked whales, 0.07 for Cuvier's beaked whales and 0.18 for Baird's beaked whales. These small values still probably overestimate the $g(0)$ values for beaked whales on aerial surveys because they do not include corrections for perception bias.

Reactive movement of beaked whales in response to survey vessels can also bias line-transect estimates of density and abundance. Small beaked whales are often referred to as 'shy' (Leatherwood *et al.*, 1988) and may avoid vessels by diving (Heyning, 1989). The perceived shyness and avoidance behaviour may be an erroneous interpretation of their normal short surface and long dive times. Recently, both Bainville's (*M. densirostris*) and Cuvier's beaked whales have been approached by small boats for photo-identification and suction-cup tagging (Johnson *et al.*, 2004; R. Baird, pers. comm.). Northern bottlenose whales are often described as 'curious' and may be attracted to stationary vessels (e.g. Whitehead *et al.*, 1997). Currently it is not possible to say whether movement in response to survey vessels is introducing any appreciable bias in line-transect estimates.

The difficulty in identifying species of beaked whales at sea and the resulting high incidence of 'unidentified beaked whales' on most surveys poses other problems for abundance estimation. The sightings of unidentified beaked whales can be treated as an independent category for estimating *ESW* and *g*(0), or they can be pooled with other sightings that were identified to species or genus for estimating these line-transect parameters. In either case, the abundance of unidentified beaked whales can be prorated into other species categories based on the relative abundance of the other categories, or the abundance of unidentified beaked whales can be reported separately. One problem with separate analysis of *ESW* and *g*(0) is that beaked whales that are seen at greater distance may be more likely to remain unidentified. Barlow *et al.* (2001) showed that unidentified small beaked whales were seen on average at greater perpendicular sighting distances than Cuvier's or *Mesoplodon* beaked whales. Consequently, the line-transect assumption that animals are uniformly distributed relative to the trackline may be violated. For this reason, it may be best to pool all small beaked whales (including unidentified small beaked whales) when estimating line-transect parameters.

Previous line-transect abundance estimates for beaked whales are summarised in Table 2. Estimates from three major ocean basins are discussed below.

Pacific Ocean

Miyashita (1986) and Miyashita and Kato (1993) estimated the abundance of Baird's beaked whales in slope waters west of Japan based on ship surveys in 1984, 1991 and 1992. They used a *g*(0) estimate from Miyashita (1986) to correct for diving whales that were missed. In both of these studies, abundance was only estimated for strata that contained sightings of Baird's beaked whales, so the density estimates in Table 2 (40 to 68 animals per 1,000km^2) are higher than the density would be for the entire study area. Wade and Gerrodette (1993) estimated the abundance of Cuvier's and *Mesoplodon* beaked whales in the eastern tropical Pacific based on 1986-90 SWFSC ship surveys. However, their study assumed that *g*(0) was 1.0 and included Beaufort sea states of 0 to 5, so abundances and densities were certainly underestimated. Barlow (1995) estimated the abundance of Cuvier's beaked whales, *Mesoplodon* beaked whales, unidentified small beaked whales and Baird's beaked whales based on a 1991 summer/fall ship survey within 556km (300 n.miles) of the coast of California and Forney *et al.* (1995) estimated the abundance of unidentified small beaked whales based on winter 1991 and 1992 aerial surveys within 185km (100 n.miles) of the coast of California. Both Barlow (1995) and Forney *et al.* (1995) used estimates of *g*(0) to account for perception bias but did not account for availability bias. Barlow (2003b) re-estimated beaked whale abundance in California waters and expanded estimates to Oregon and Washington waters based on new survey data. In this analysis and all subsequent analyses of the Pacific surveys, observations were limited to Beaufort sea states 0-2 and model-based estimates of *g*(0) (Barlow, 1999) were used to account for both perception and availability biases. Ferguson and Barlow (2001) re-analysed all SWFSC ship survey data from 1986-96 (using the new *g*(0) estimates) and estimated abundances and densities stratified by 5° (latitude and longitude) rectangles for the eastern tropical Pacific, Gulf of California, and US west coast study areas. Barlow (2006) estimated the abundance of beaked whales in the US Exclusive Economic Zone (EEZ) around Hawaii using multiple-covariate methods, with *ESW* and *g*(0) estimates that were based on previous SWFSC surveys in the eastern Pacific. For Cuvier's beaked whale in the Pacific, the highest densities were found in the southern Gulf of California (38 animals per 1,000km^2). For *Mesoplodon* beaked whales in the Pacific, densities were again highest in the southern Gulf of California (6.4 animals per 1,000km^2).

Atlantic Ocean and Gulf of Mexico

Beaked whale abundance and density were estimated from ship surveys around Iceland (Gunnlaugsson and Sigurjónsson, 1990), from aerial surveys along the US northeastern coast (Winn, 1982), from ship surveys along the US eastern coast (Mullin and Fulling, 2003) and from ship and aerial surveys in the Gulf of Mexico (Hansen *et al.*, 1995; Mullin and Hoggard, 2000; Mullin and Fulling, 2004; Mullin *et al.*, 2004). Study areas included shelf, slope and deep waters. In the study around Iceland, abundance was estimated only for northern bottlenose whales; the other researchers estimated abundance only for small beaked whales. All small beaked whales were pooled for estimating *ESW*, and for some studies, beaked whales were also pooled with other 'cryptic species' to estimate *ESW*. In the Atlantic and Gulf of Mexico, the highest beaked whale densities were estimated from aerial surveys in the Gulf of Mexico (1.5 animals per 1,000km^2; Mullin *et al.*, 2004).

Southern Ocean

In Antarctic waters, Kasamatsu and Joyce (1995) estimated the pooled abundance of all beaked whales based on ship-based sighting surveys conducted in 1976-88 in Beaufort sea state $\leq$5. The study area ranged from the Antarctic pack ice edge or continental edge northward, with most survey effort being south of 60°S latitude. The majority of identified beaked whale sightings were southern bottlenose whales (*H. planifrons*). They estimated *g*(0) using a model of dive times and a simulation of the sighting process. Overall densities in this enormous study area were very high (20 animals per 1,000km^2).

Mark-recapture abundance estimation

Photo-identification coupled with mark-recapture can also be used to estimate beaked whale population sizes. Many species of beaked whales are highly marked with scars and should be readily identifiable. Extensive photo-identification catalogues have been developed for small beaked whales in the Bahamas (Claridge *et al.*, 2001) and for northern bottlenose whales in 'The Gully' – a submarine canyon off Nova Scotia (Whitehead *et al.*, 1997). To date, mark-recapture abundance estimates have been made only for the Gully population of northern bottlenose whales. In one study (Gowans *et al.*, 2000), 66% of animals were estimated to have reliable long-term marks and the population size was estimated to be about 130 (95% CI=106-166). The range of this population outside the Gully

Table 2

Summary of line-transect abundance and density estimates for beaked whales. Average densities are estimated by dividing the total abundance by the size of the total study area. The basis for $g(0)$ estimates include independent observer (IO) and model-based methods and can include corrections for perception bias (PB) and/or availability bias (AB).

Study region	Total area km^2	Overall abundance	Overall density per 1,000km^2	CV	Beaufort sea state range used	*ESW* km	$g(0)$	$g(0)$ basis	Notes
NORTH PACIFIC									
Japanese eastern slope waters, 1983 (Miyashita, 1986)									
B. bairdii	61,970	4,220	68.1	~0.30	0-5	2.49	0.84	Model, AB	1
Japanese eastern slope waters, 1991-92 (Miyashita and Kato, 1993)									
B. bairdii	124,606	5,029	40.4	~0.56	0-5	1.35	0.84	Model, AB	1
Eastern tropical Pacific ship surveys, 1986-90 (Wade and Gerrodette, 1993)									
Z. cavirostris	19,148,000	20,000	1.0	0.27	0-5	0.86	1.00	Assumed	
Mesoplodon spp.	19,148,000	25,300	1.3	0.20	0-5	1.26	1.00	Assumed	
California ship surveys, 1991 (Barlow, 1995)									
Z. cavirostris	815,000	1,621	2.0	0.82	0-2	1.63	0.84	IO, PB	
Mesoplodon spp.	815,000	250	0.3	0.83	0-2	1.63	0.84	IO, PB	
Unid. sm. ziphiid	815,000	1,322	1.6	0.89	0-2	1.63	0.84	IO, PB	
B. bairdii	815,000	38	0.0	1.02	0-5	3.90	1.00	IO, PB	
California aerial surveys, 1991-92 (Forney *et al.*, 1995)									
Unid. sm. ziphiid	264,270	392	1.5	0.41	0-4	0.40	0.95	IO, PB	
Eastern North Pacific ship surveys, 1986-96 (Ferguson and Barlow, 2001)									
Z. cavirostris	25,000,000	90,725	3.6	N/A	0-2	Various	0.23	Model, PB+AB	
Mesoplodon spp.	25,000,000	32,678	1.3	N/A	0-2	Various	0.45	Model, PB+AB	
Unid. sm. ziphiid	25,000,000	51,365	2.1	N/A	0-2	Various	0.35	Model, PB+AB	
B. bairdii	N/A	1,104	0.1 to 1.2	0.5 to 1.0	0-5	Various	0.96	Model, PB+AB	1
I. pacificus	N/A	291	0.2 to 0.4	1.00	0-5	Various	0.96	Assumed	1,3
US West coast ship surveys, 1996 and 2002 (Barlow, 2003)									
Z. cavirostris	1,142,500	1,884	1.6	0.68	0-2	1.76	0.23	Model, PB+AB	
Mesoplodon spp.	1,142,500	1,247	1.1	0.92	0-2	1.76	0.45	Model, PB+AB	
Unid. sm. ziphiid	1,142,500	432	0.4	1.06	0-2	1.76	0.34	Model, PB+AB	
B. bairdii	1,142,500	228	0.2	0.51	0-5	2.82	0.96	Model, PB+AB	
Hawaii ship surveys, 2002 (Barlow, 2006)									
Z. cavirostris	2,452,916	15,242	6.2	1.43	0-2	1.64	0.23	Model, PB+AB	
M. densirostris	2,452,916	2,872	1.2	1.25	0-2	2.55	0.45	Model, PB+AB	
Unid. sm. ziphiid	2,452,916	371	0.2	1.17	0-2	2.02	0.35	Model, PB+AB	
I. pacificus	2,452,916	1,007	0.4	1.26	0-6	2.24	0.96	Assumed	3
NORTH ATLANTIC									
Northeastern Atlantic high latitudes - NASS-87 (Gunnlaugsson and Sigurjonsson, 1990)									
H. ampullatus	2,284,095	5,827	2.6	0.16	0-4	N/A	1.00	Assumed	
U.S. NE coast CETAP summer aerial surveys, 1978-82 (Winn, 1982)									
Z. cavirostris	278,350	25	0.1	0.94	0-3	0.29-0.52	1.00	Assumed	
Mesoplodon spp.	278,350	121	0.4	0.70	0-3	0.29-0.52	1.00	Assumed	
U.S. SE coast ship survey, 1998 (Mullin and Fulling, 2003)									
Mesoplodon spp.	573,000	348	0.6	0.76	0-4	1.78	1.00	Assumed	
Unid. sm. Ziphiid	573,000	193	0.3	0.71	0-4	1.78	1.00	Assumed	
Gulf of Mexico ship surveys, 1991-94 (Hansen *et al.*, 1995)									
Z. cavirostris	398,960	30	0.1	0.50	0-5	1.79	1.00	Assumed	
Unid. sm. ziphiid	398,960	117	0.3	0.38	0-5	1.78	1.00	Assumed	
Gulf of Mexico ship surveys, 1996-2001 (Mullin and Fulling, 2004)									
Z. cavirostris	380,432	95	0.2	0.47	0-4	1.67	1.00	Assumed	
Mesoplodon spp.	380,432	106	0.3	0.41	0-4	1.67	1.00	Assumed	
Unid. sm. ziphiid	380,432	146	0.4	0.46	0-4	1.67	1.00	Assumed	
Gulf of Mexico aerial surveys, 1992-1994 (Mullin *et al.*, 2004)									
Z. cavirostris	85,815	11	0.1	0.71	0-3	0.23	1.00	Assumed	
Mesoplodon spp.	85,815	52	0.6	0.30	0-3	0.23	1.00	Assumed	
Unid. sm. ziphiid	85,815	71	0.8	0.53	0-3	0.23	1.00	Assumed	
Gulf of Mexico aerial surveys, 1996-1998 (Mullin and Hoggard, 2000)									
Z. cavirostris	70,470	22	0.3	0.83	0-4	0.35	1.00	Assumed	
Mesoplodon spp.	70,470	59	0.8	0.51	0-4	0.35	1.00	Assumed	
ANTARCTIC/SOUTHERN OCEAN									
Southern Ocean ship surveys, 1976-88 (Kasamatsu and Joyce, 1995)									
All ziphiid whales	29,179,839	599,300	20.5	0.15	0-5	0.80	0.27	Model, PB+AB	2

1. Range of this species is smaller than entire study area; density is estimated for strata which include at least one sighting. 2. Most sightings were of *H. planifrons*. Estimate of $g(0)$ was based on that species. 3. $g(0)$ estimated based on similar diving patterns of *B. bairdii.*

is not known, but only 34% of the population is estimated to be using the Gully at any one time (Gowans *et al.*, 2000). Work is in progress to estimate abundance of small beaked whales in the Bahamas using mark-recapture methods applied to photo-identification data (Claridge, Durban, Parsons and Balcomb, pers. comm.).

Review of abundance and density estimation

Line-transect surveys using visual detection methods are currently the only reliable method for estimating density and abundance of beaked whales over broad areas. From previous estimates, average pooled densities of all small beaked whales fall within the range of 0.4-44 animals per

1,000km², with the *g*(0)-corrected estimates falling in the upper part of that range (2.7-44 animals per 1,000km²). All of these studies include a combination of shelf (less than 200m), slope (200-2,000m), and deep (greater than 2,000m) waters and additional insight could be obtained if estimates were stratified to include only the slope and deep-water habitats of beaked whales. There are no estimates of density from oligotrophic deep-water regions that are far from continents or islands. Areas such as the southern Gulf of California have densities of small beaked whales that are an order of magnitude higher (44 animals per 1,000km²) than the averages found in other study areas. This appears to validate the concept of 'hot spots' with much higher than average beaked whale abundance. The densities of southern bottlenose whales in the Southern Ocean (20 animals per 1,000km²) and Baird's beaked whales in slope waters of Japan (40-68 animals per 1,000km²) are higher than the typical density estimated for the smaller beaked whales. For comparison, global estimates of sperm whale (*Physeter macrocephalus*) densities (0.8-17.4 animals per 1,000km²; Whitehead, 2002) fall within the same range as density estimates for small beaked whales.

Mark-recapture abundance estimates based on photo-identification appear to have limited utility for estimating the population sizes of smaller beaked whales over broad areas, because animals are rarely seen and are difficult to approach and the overall populations appear to be large. There are several locations, however, where beaked whales are more easily approached. Photo-identification studies in those areas may be valuable for estimating local population sizes and for obtaining a wealth of other data, such as residency patterns and social structure (Claridge *et al.*, 2001). Mark-recapture appears to have greater potential for estimating the abundance of entire populations of the larger beaked whales such as northern bottlenose whales and Baird's beaked whales. For both of these species, animals are well marked and easily approached.

When considering current densities of beaked whales, it is important to remember that these may be less than the historic levels of abundance. Northern bottlenose whales have been depleted, perhaps multiple times, by whaling in the Atlantic Ocean (Mitchell, 1977; Christensen and Ugland, 1983) and Baird's beaked whales have been subject to whaling off Japan. Bycatch of small beaked whales has occurred off the US west coast (Julian and Beeson, 1998) and elsewhere, but population-level effects have not been assessed. The potential population-level effects of anthropogenic sounds on beaked whales are poorly understood. Balcomb and Claridge (2001) found that none of the Cuvier's beaked whales that were photo-identified near their Abaco study site in the Bahamas were ever seen again after the beaked whale stranding incident in March 2000, indicating the potential for at least local population-level effects.

RESEARCH RECOMMENDATIONS

(1) Virtually nothing is known about the population structure within most species of beaked whales. Genetic, morphometric, photo-identification and long-term tagging studies are needed to evaluate how populations are structured.

(2) There are many gaps in our knowledge of the worldwide distribution of beaked whales. Emphasis should be placed on training observers for at-sea identification of beaked whales for all cetacean surveys and on the collection of genetic and other specimen material for the accurate identification of stranded beaked whales.

(3) The estimation of correction factors (*g*(0)) for missed animals is critical for accurately estimating abundance or density for line-transect surveys. Additional research is needed on methods, and additional data (such as dive times) are needed.

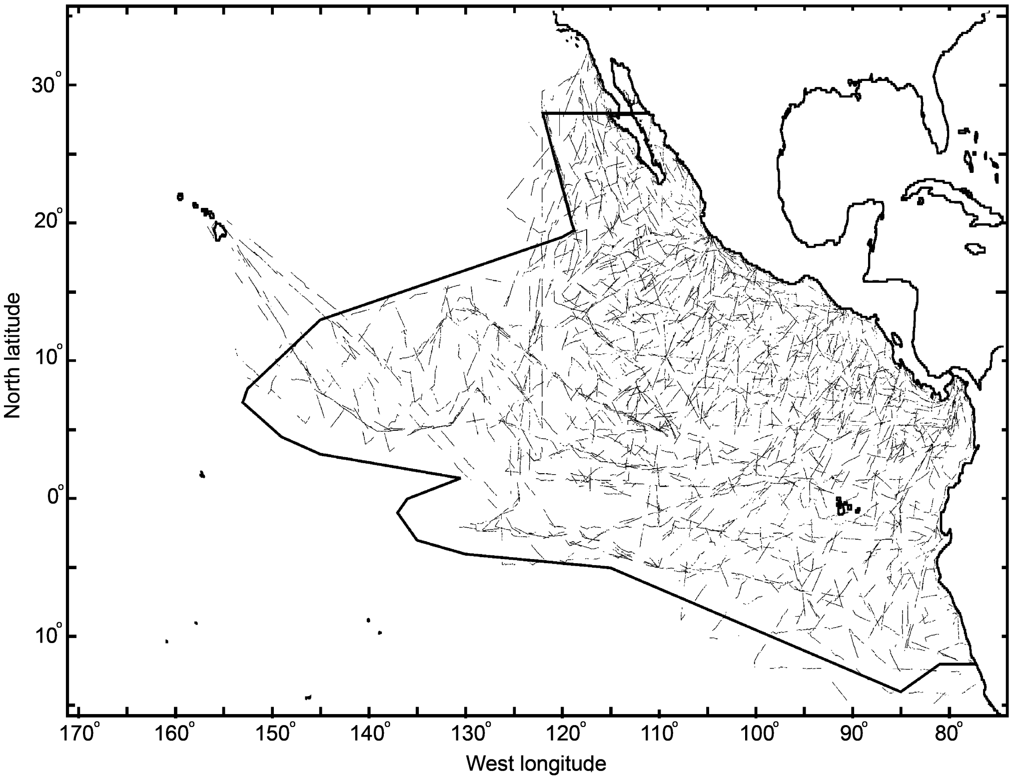

Fig. 1. Transect lines covered during the 1986-1990 and 1998-2000 shipboard cetacean surveys conducted by the SWFSC. Bold line indicates the boundary of the eastern tropical Pacific (ETP) study area.

(4) Most abundance and density estimates for beaked whales exist only where cetacean surveys have been conducted for other reasons, such as for whale stock assessment or where fishery bycatch problems exist (Fig. 1). Densities have not been estimated for vast areas of beaked whale habitat, particularly those areas that are far from shore. Additional surveys are needed to characterise beaked whale densities in these other habitats.

(5) Since beaked whales spend so much of their time submerged and unavailable to visual observers, acoustic detection methods should be investigated. Additional information is needed to characterise the vocal behaviour of beaked whales and to detect those vocalisations from a surface vessel.

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Known and inferred distributions of beaked whale species (Cetacea: Ziphiidae)

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ABSTRACT

Information regarding beaked whales is so sparse that even the most basic aspects of their biology, such as their distribution, remain poorly defined for some species. We have reviewed the known distribution of each beaked whale species and where possible, used this information to infer its global distribution. While for some species, such as the relatively commonly recorded Cuvier's beaked whale, the inferred distribution is likely to be an accurate reflection of the species' actual distribution, for other lesser known species, such as the spade-toothed whale, the inferred distribution is more tentative. However, even such limited distribution information is essential when assessing and mitigating potential anthropogenic impacts on beaked whales and serves to highlight gaps in our knowledge that need to be filled if assessment and mitigation are to be successfully conducted.

KEY WORDS: DISTRIBUTION; NORTHERN HEMISPHERE; SOUTHERN HEMISPHERE; CONSERVATION

INTRODUCTION

To understand the extent to which beaked whales may be affected by anthropogenic activities, it is essential to know where they occur. The spatial distribution of a species has two closely-related aspects: the global range and the way individuals are distributed throughout that range. Individuals may be clumped in space and time, occurring in higher numbers or more regularly in some areas and at some times than others. The global range of a species is defined by the limits outside which individuals of a species cannot survive, for example where it is too warm or too cold, while the distribution within that range is defined by the preference for particular conditions, for example, certain habitats and the presence of food. This paper reviews what is known about the range of each beaked whale species and, where possible, the total range is inferred. This inferred range defines where the species may occur, but it does not necessarily identify where the highest densities or abundance occurs.

The family Ziphiidae is one of the most wide-ranging families of cetaceans, occurring from the ice edges at both poles, to the equator in all the world's oceans. However, knowledge of individual species ranges varies greatly. For some species the range is fairly well known (e.g. Sowerby's beaked whale (*Mesoplodon bidens*) – MacLeod, 2000), while for others it is almost completely unknown (e.g. the spade-toothed beaked whale (*M. traversii*) – van Helden *et al.*, 2002). This variation in knowledge exists for a number of reasons. Firstly, while for some species there are many distribution records, for others our entire understanding comes from a very small number of widely scattered records. In addition, while some species are regularly sighted at sea (e.g. Cuvier's beaked whale, *Ziphius cavirostris* – see below), giving us a picture of where living animals actually occur, others are mostly, or only, known from strandings (e.g. Andrews' beaked whale, *M. bowdoini*). Stranded animals may have drifted, either incapacitated or as dead carcasses, for long distances before making landfall, meaning that such evidence may not reflect the actual distribution of the species. Finally, while a great deal of cetological research has been conducted in some parts of the world, in terms of sightings surveys (Fig. 1) and recording of strandings (e.g. in US and European waters), there has been little or no such effort in other parts of the world (e.g. the tropical eastern Atlantic). Therefore, apparent discontinuities in species distribution may reflect patchy data collection rather than true gaps in occurrence.

Defining beaked whale ranges is further confounded by uncertain taxonomy. On occasion, morphologically similar species have initially been considered as a single species and only later identified as separate species, causing major shifts in the perceived distribution of the species. For example, Hubbs' beaked whale (*M. carlhubbsi*) was initially identified as Andrews' beaked whale and the recently described Perrin's beaked whale (*M. perrini*) from California, USA, was originally identified as Hector's beaked whale, *M. hectori* (Hubbs, 1946; Moore, 1968; Mead, 1981; Dalebout *et al.*, 2002). In both cases, the lumping of separate species under a single name resulted in falsely perceived anti-tropical distributions. Species identification of beaked whales, particularly of living animals at sea, has been difficult, either because the external morphology of a species has been unknown, as in the case of the spade-toothed whale, or because of a poor understanding of species-specific field marks and/or a lack of obvious morphological differences between species.

This paper describes the known range of each currently recognised species of beaked whale based on a review of published information and from unpublished sighting and stranding records collected by the authors or obtained from other sources. As many specific locations as possible (i.e. those with available latitude and longitude or details of a species location) were plotted to show their geographic

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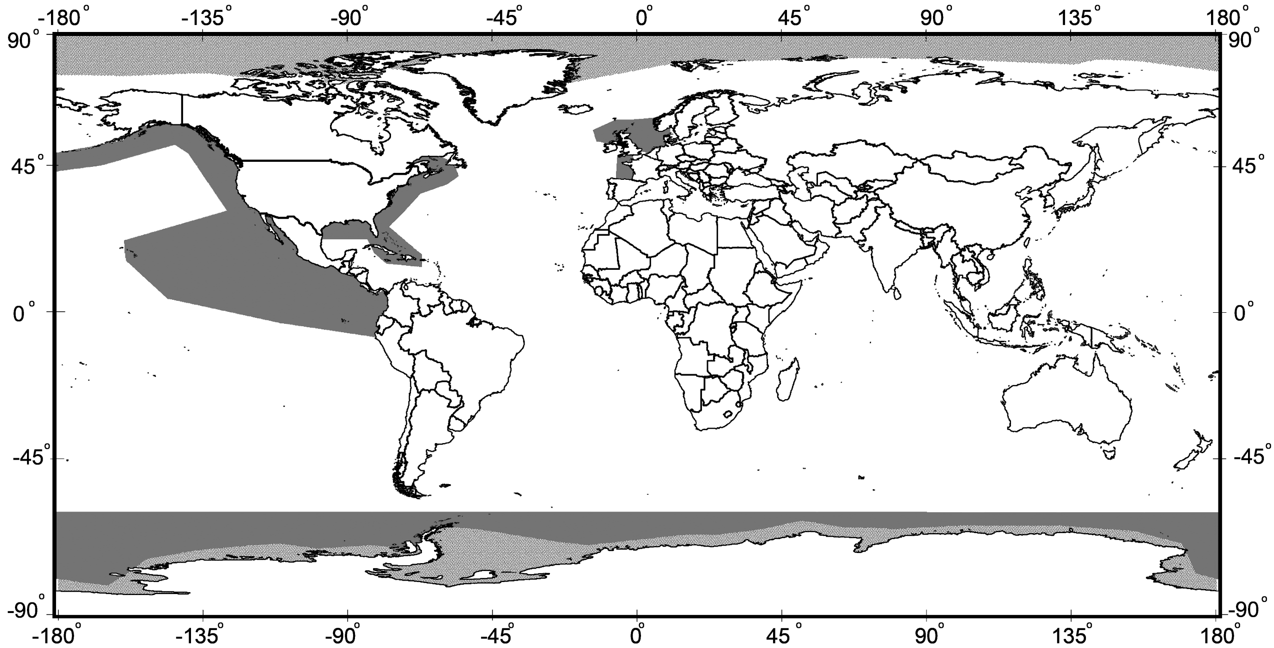


Fig. 1. Areas where dedicated surveys for cetaceans have been conducted and where sightings data may be more representative of actual at-sea distribution. However, these surveys have been conducted from different research platforms and using different methodologies, and so levels and types of effort are not directly comparable between surveyed areas. Therefore, this figure should not be used to make comparisons between different survey areas in terms of densities and/or abundance of beaked whales or different beaked whale species.

spread and these are the records plotted as individual locations on species distribution maps (Fig. 2). However, to provide a full understanding of species distribution, these records were then augmented by a detailed investigation of the available literature to identify additional general areas where a species has been recorded, but where available information is insufficient to allow a specific location to be plotted (e.g. published catch records from the whaling industry and species occurrence lists for countries or areas). As a result, a lack of specific point locations on a distribution map should not be interpreted as a lack of occurrence of a species in a specific area. Both specific locations and more general distribution information were then used, where possible, to infer a global range for each species. For some species the data are relatively sparse, meaning that there is significant risk that the inferred distributions do not accurately reflect the actual distributions. For species or areas where the range has been inferred from stranding records, it should be remembered that the transportation of dead or incapacitated animals by ocean currents and winds may lead to inaccuracies in the inferred distributions. Finally, this review has used beaked whale records going back as far as the early 1800s to infer current species ranges to increase the amount of available data. Species ranges are not static and can change over time. Therefore, the historical presence of a species at a specific location does not necessarily mean that it still occurs there, nor does the current range necessarily reflect the future range of a species. These limitations should be borne in mind when interpreting the figures and using them to assess and mitigate human impacts on beaked whales.

GENUS *BERARDIUS*

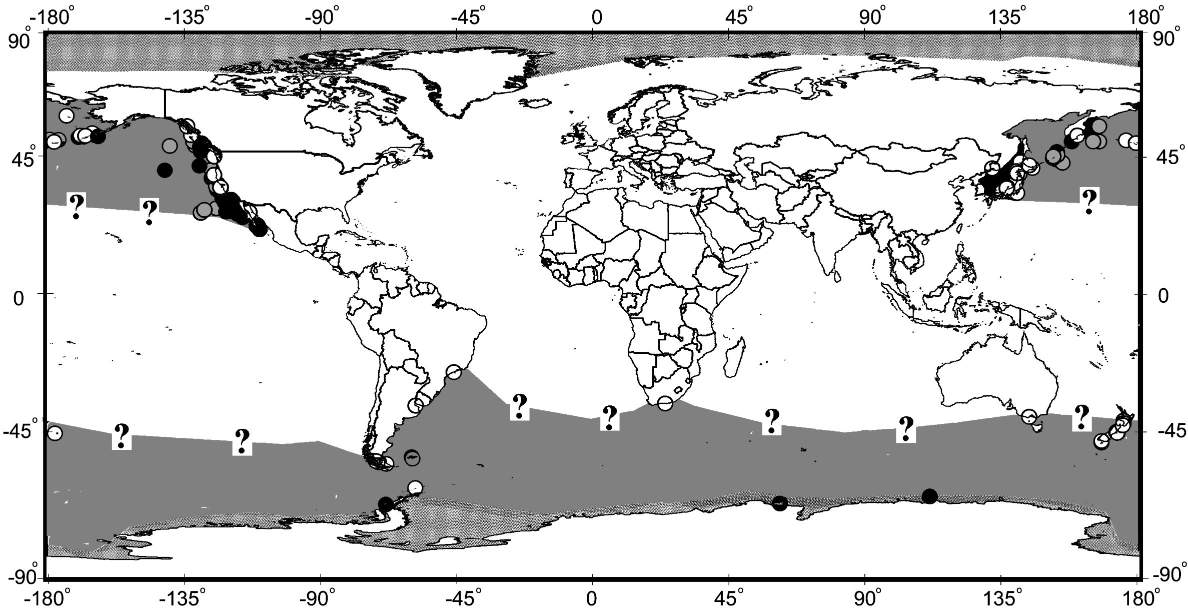
Arnoux's beaked whale (*Berardius arnuxii*)

This species has been recorded throughout the colder waters of the Southern Hemisphere, with strandings as far north as southern Brazil (Martuscelli *et al.*, 1995), South Africa (Ross, 1984), southern Australia, New Zealand and the Chatham Islands (McCann, 1975). In addition, strandings have been recorded in northern Argentina (McCann, 1975), Tierra del Fuego (Goodall, 1978), the Falkland Islands (Lichter, 1986) and Antarctica (e.g. McCann, 1975; Ponganis *et al.*, 1995; Hobson and Martin, 1996; Rogers and Brown, 1999) (Fig. 2a). Based on sightings, the southern limit for this species is the ice edge and the continental shore of Antarctica. It has also been recorded in polynyas inside the ice edge (e.g. Kasamatsu *et al.*, 1988; Ponganis *et al.*, 1995; Hobson and Martin, 1996). The distribution along the western coast of South America is unclear, with no definite records known from this region. The northern limit of Arnoux's beaked whale is unclear throughout much of its range, but most records are from latitudes south of approximately 40°S (Fig. 2a).

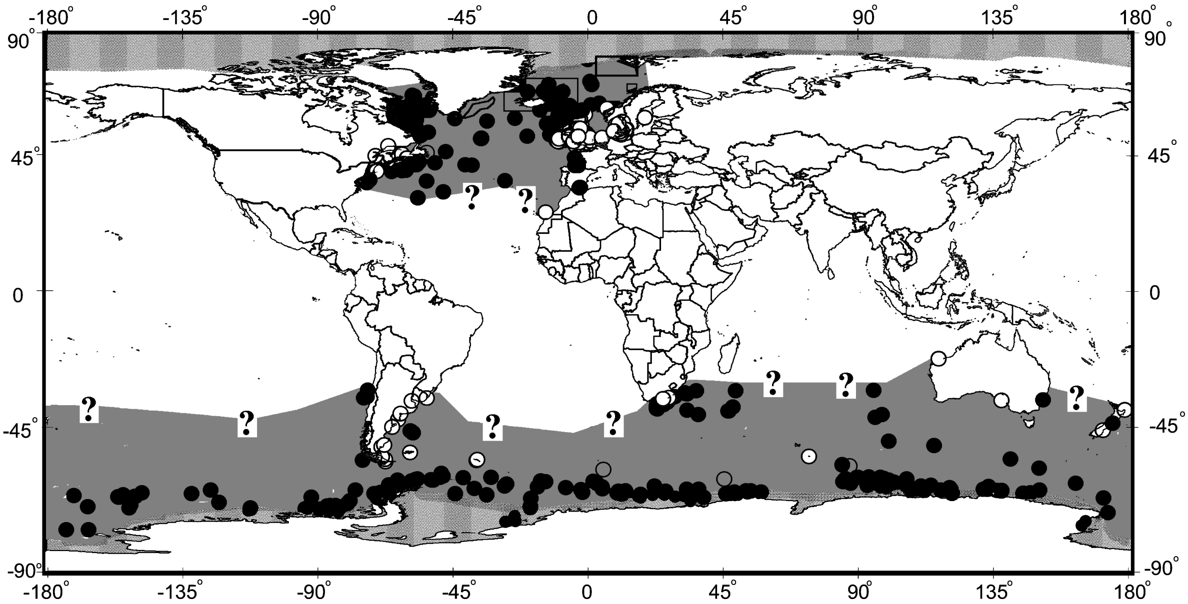
Baird's beaked whale (*B. bairdii*)

This species is endemic to the colder waters of the North Pacific Ocean (Fig. 2a). In the eastern North Pacific it is known from strandings as far south as La Paz at the southern tip of Baja California, Mexico (Aurioles-Gamboa, 1992) and as far north as mainland Alaska and the Aleutian Islands (Scheffer, 1949; Reeves and Mitchell, 1993). In the western Pacific it is known from whaling data to occur along both the eastern and western coasts of Japan (Omura *et al.*, 1955; Nishiwaki and Oguro, 1971; Nishiwaki and Oguro, 1972; Kasuya and Miyashita, 1997; Marine Mammal Database, National Museum of Science, Tokyo) and from strandings to occur as far north as the Kamchatka Peninsula in Russia (Reeves and Mitchell, 1993). Around Japan, the southern limit appears to be 34°N. The distribution in the central North Pacific is unclear. These whales appear to be relatively common around Japan, with evidence of seasonal movements into and out of the shelf-edge regions (Kasuya and Miyashita, 1997). Reports of Baird's beaked whales from farther south in the Pacific Ocean (e.g. Miyashita *et al.*, 1996) may represent sightings of Longman's beaked whales

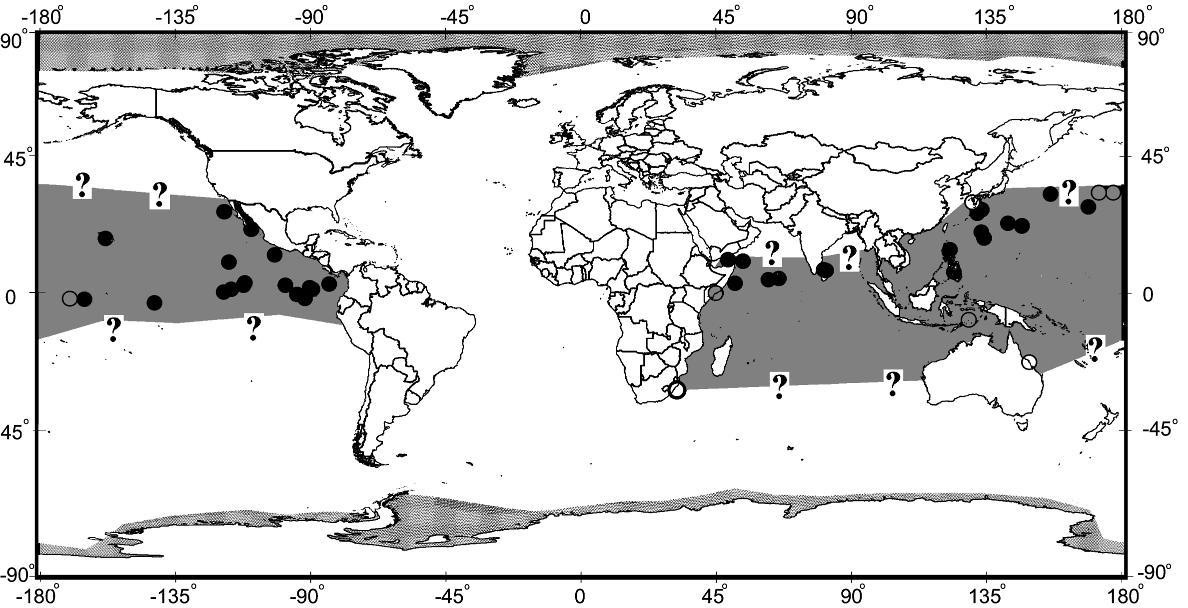
(a) *Berardius* spp.



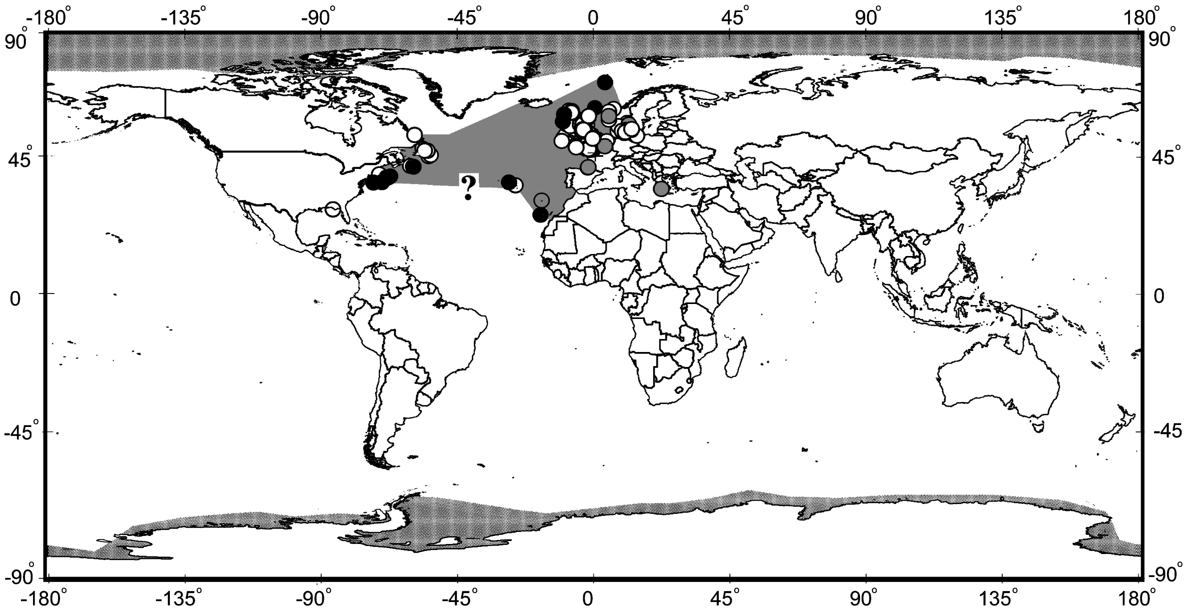
(b) *Hyperoodon* spp.



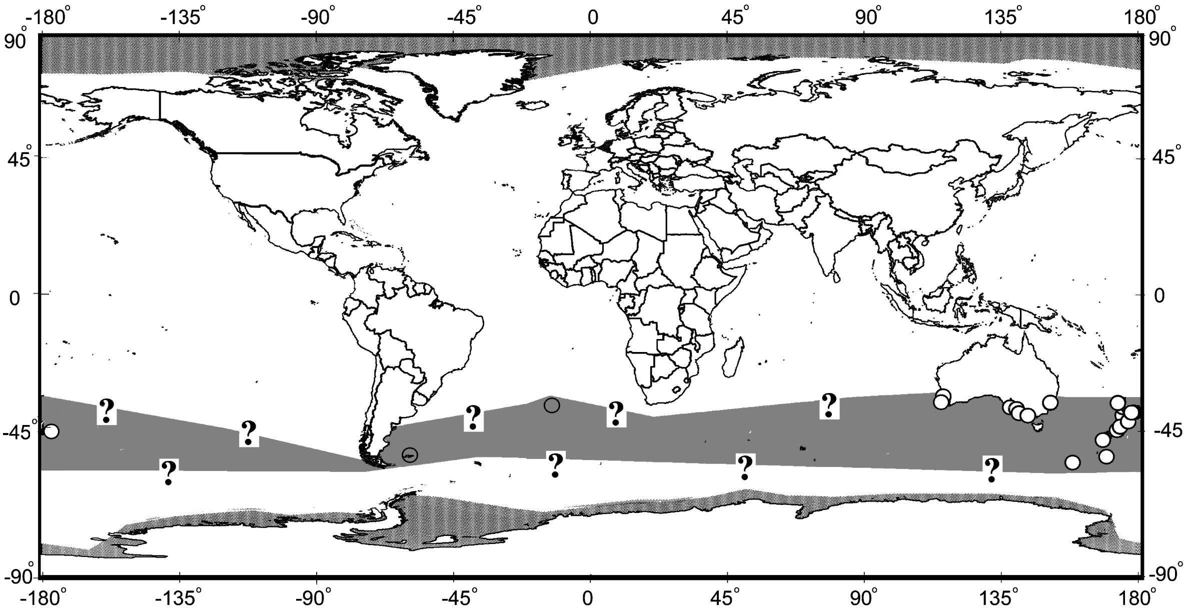
(c) Longman's beaked whale



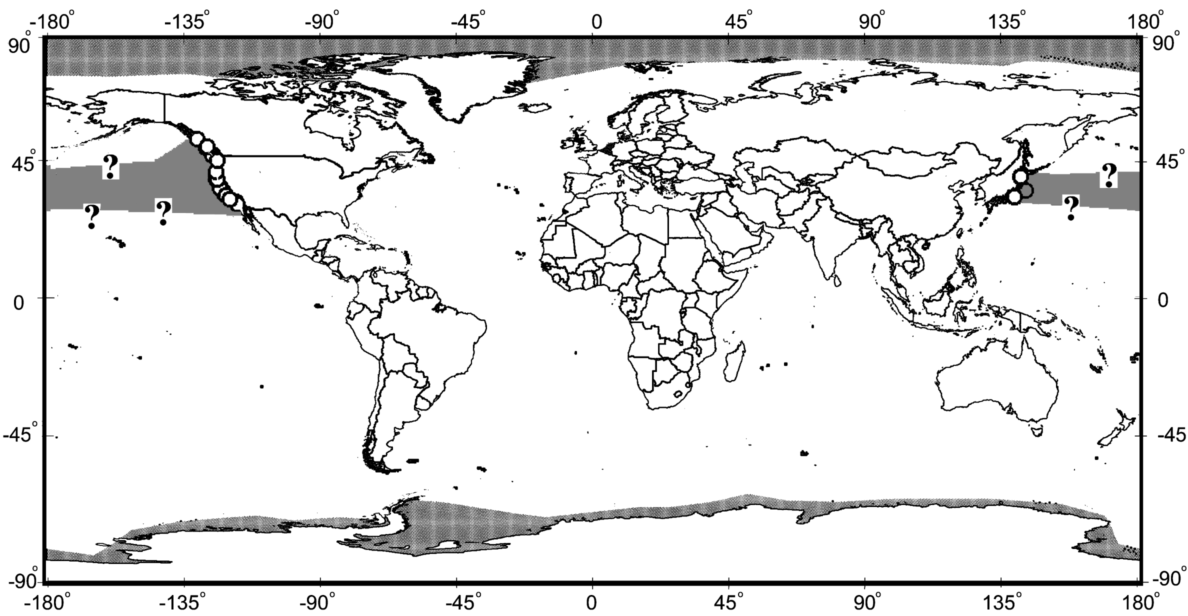
(d) Sowerby's beaked whale



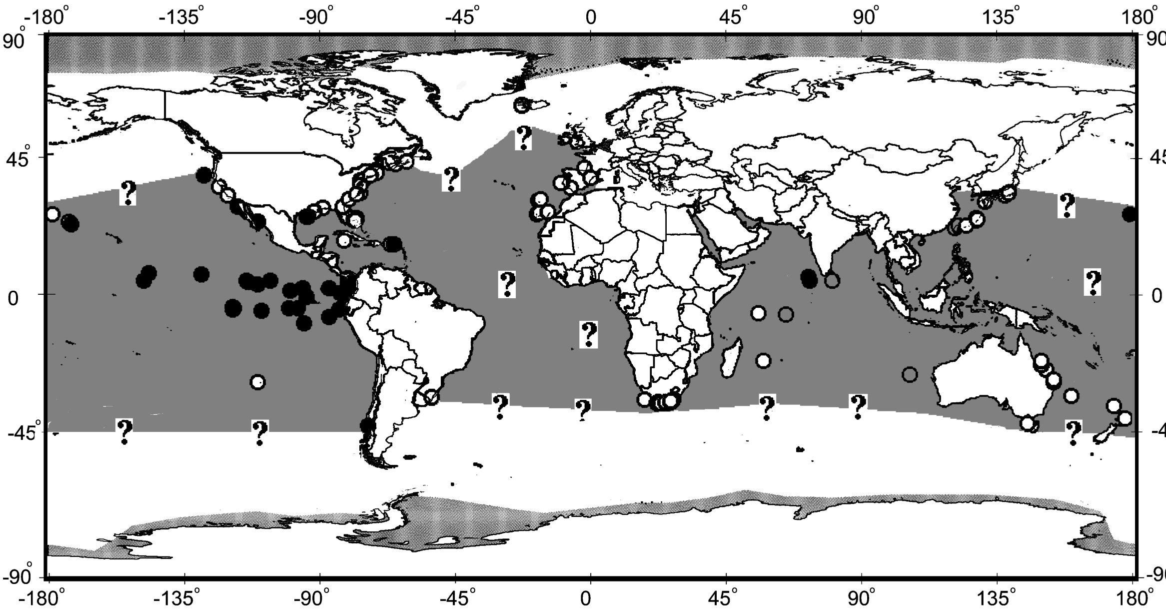
(e) Andrews' beaked whale



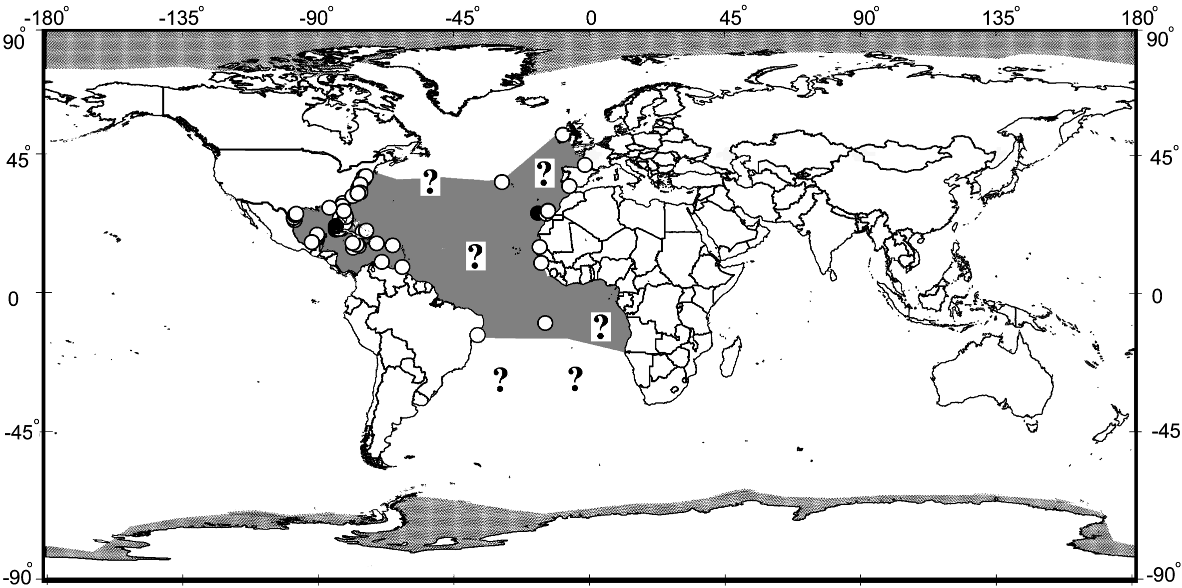
(f) Hubbs' beaked whale



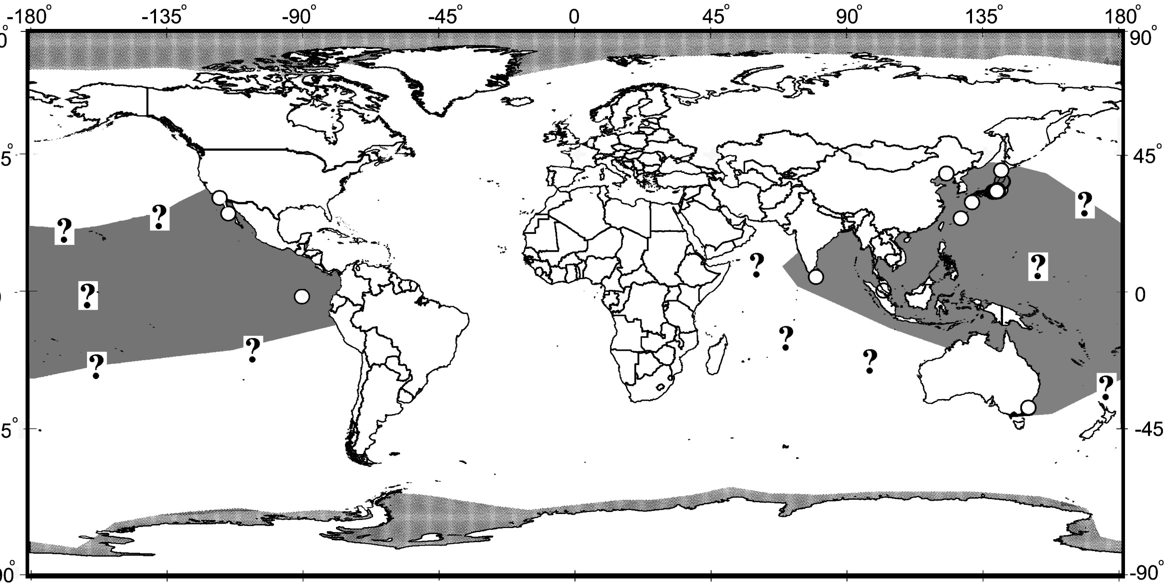
(g) Blainville's beaked whale



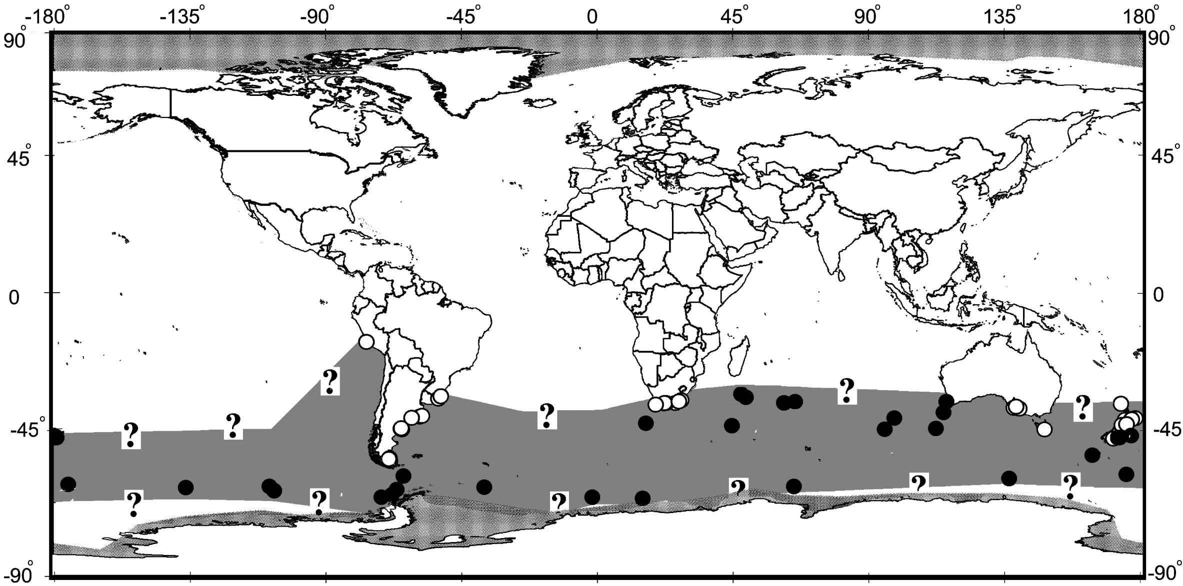
(h) Gervais' beaked whale



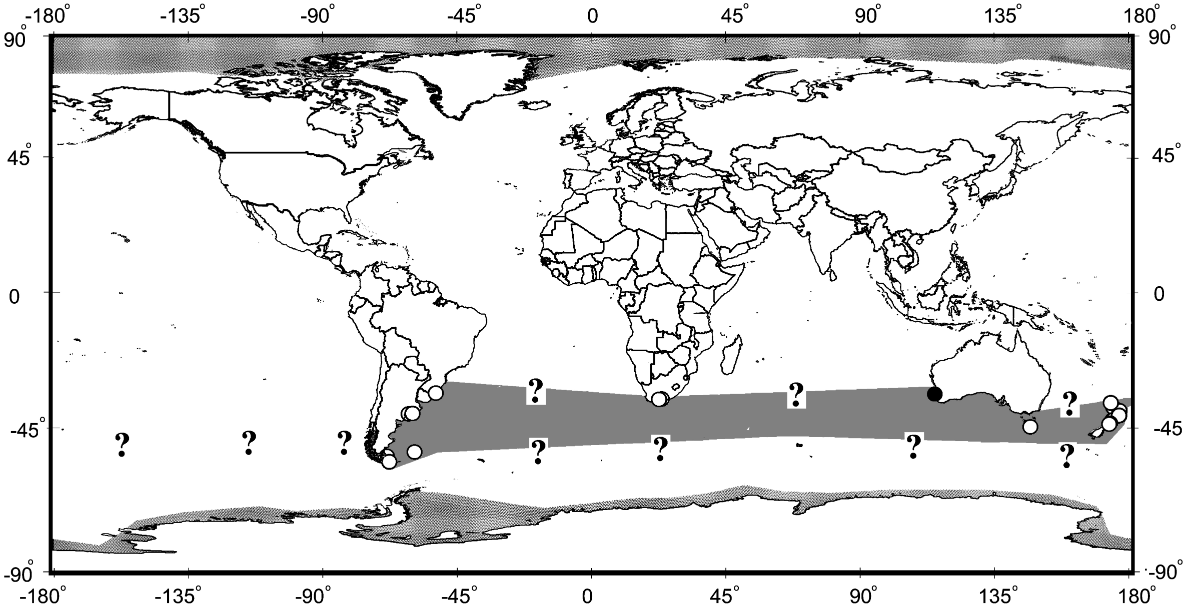
(i) Ginkgo-toothed beaked whale



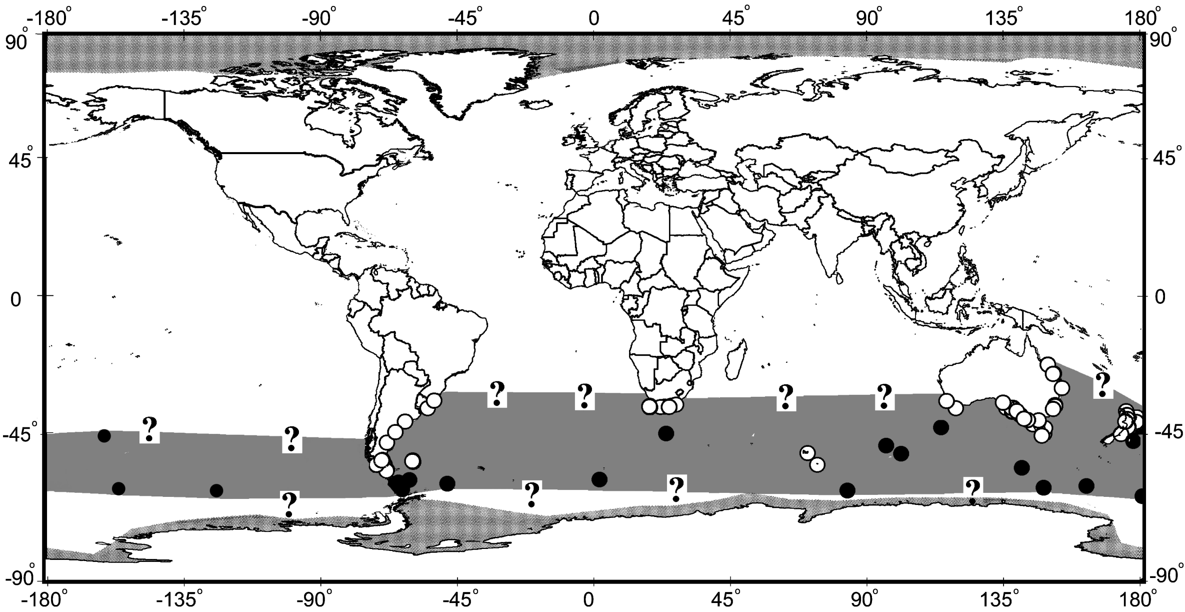
(j) Gray's beaked whale



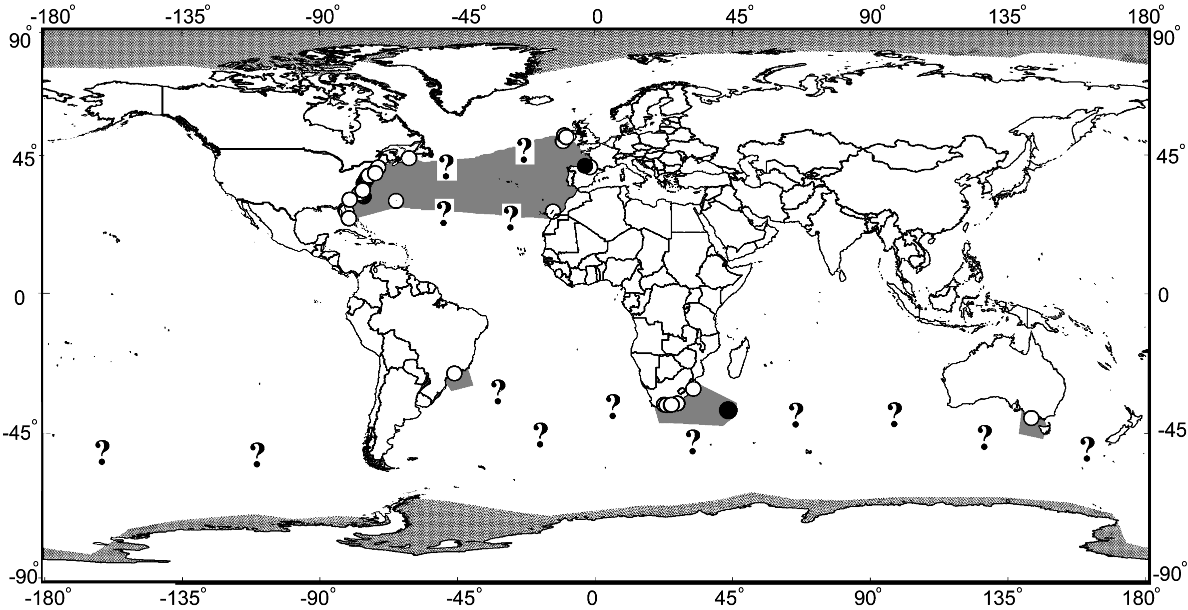
(k) Hector's beaked whale



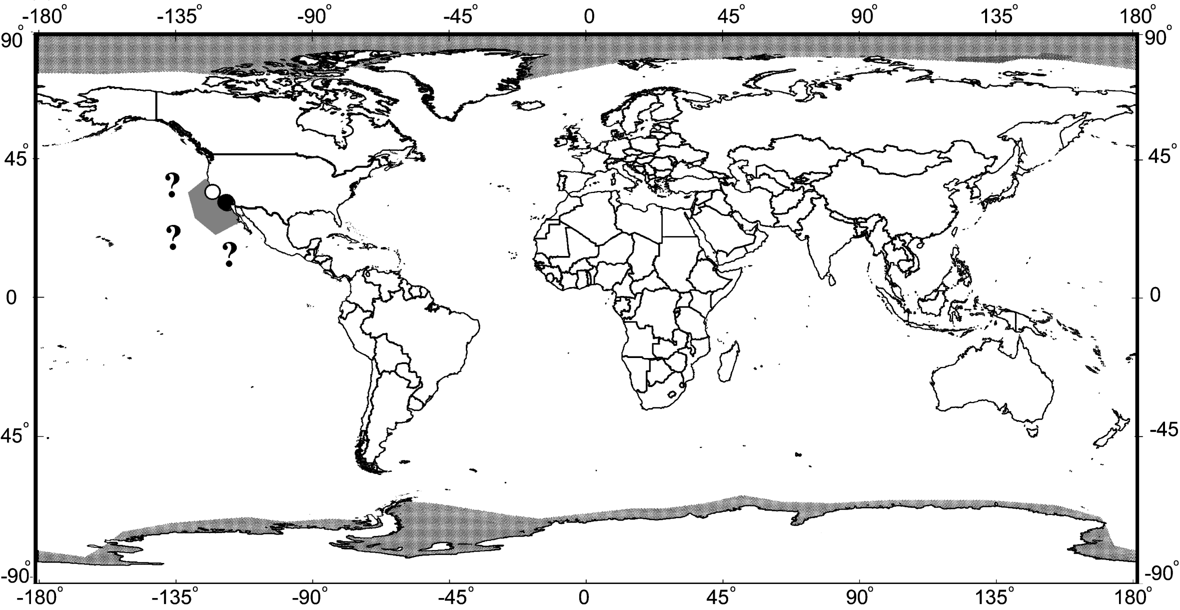
(l) Strap-toothed whale



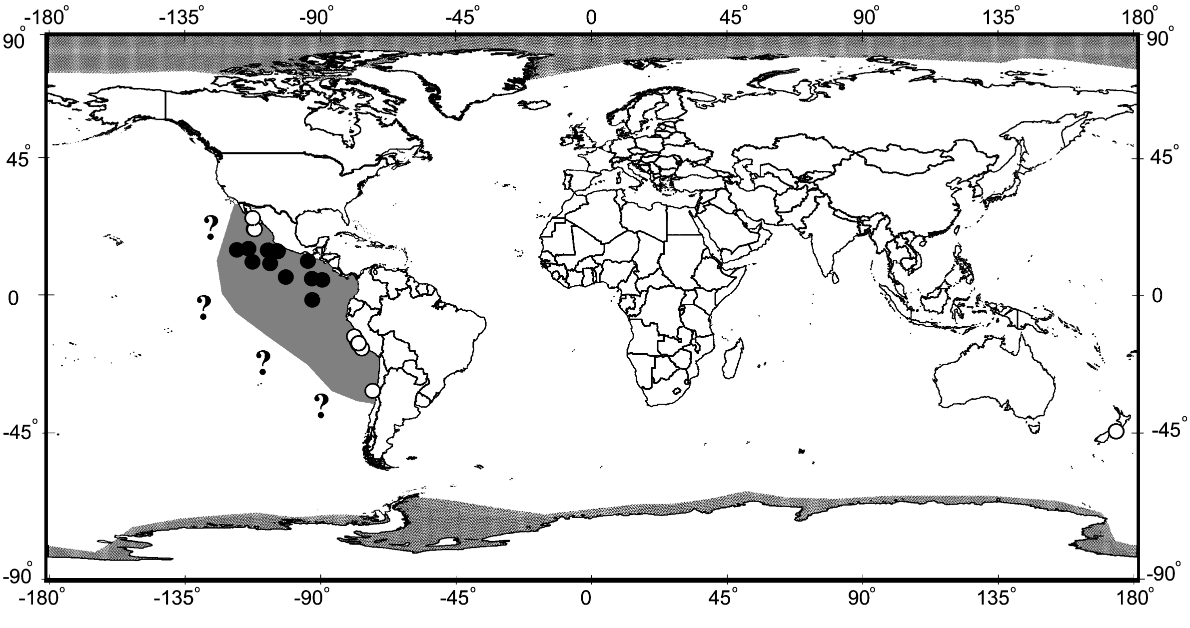
(m) True's beaked whale



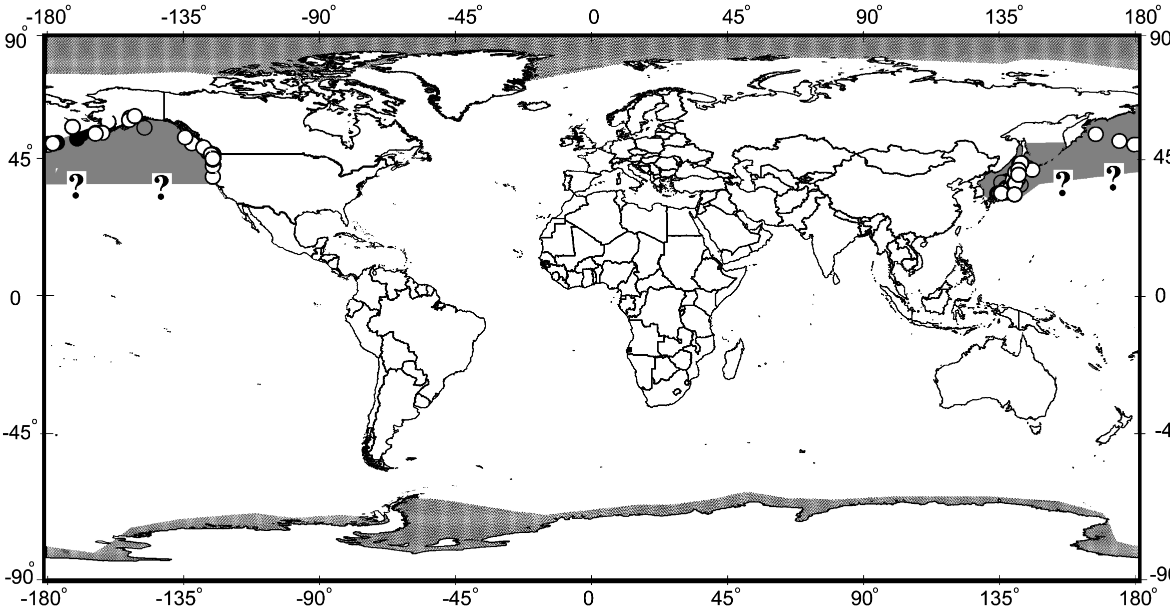
(n) Perrin's beaked whale



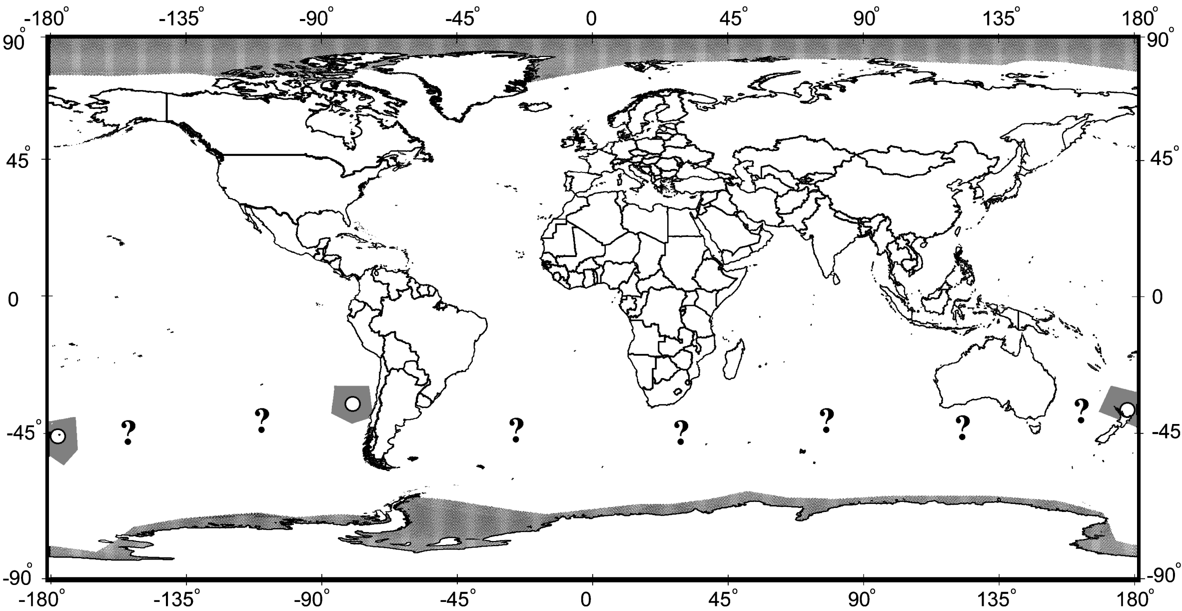
(o) Pygmy beaked whale



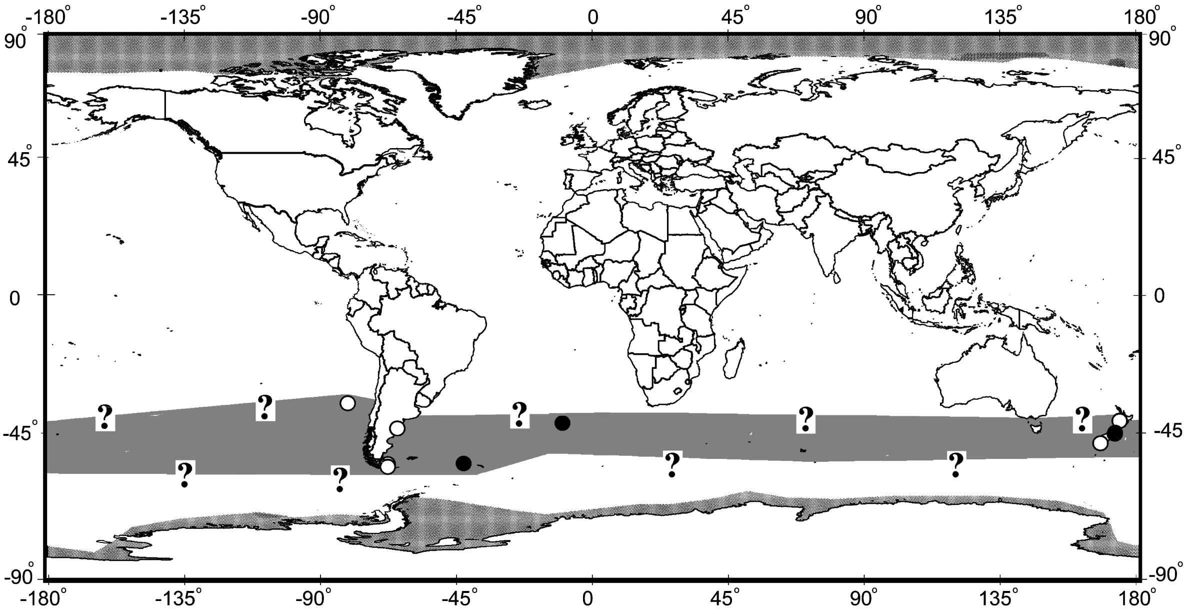
(p) Stejneger's beaked whale



(q) Spade-toothed whale



(r) Shepherd's beaked whale



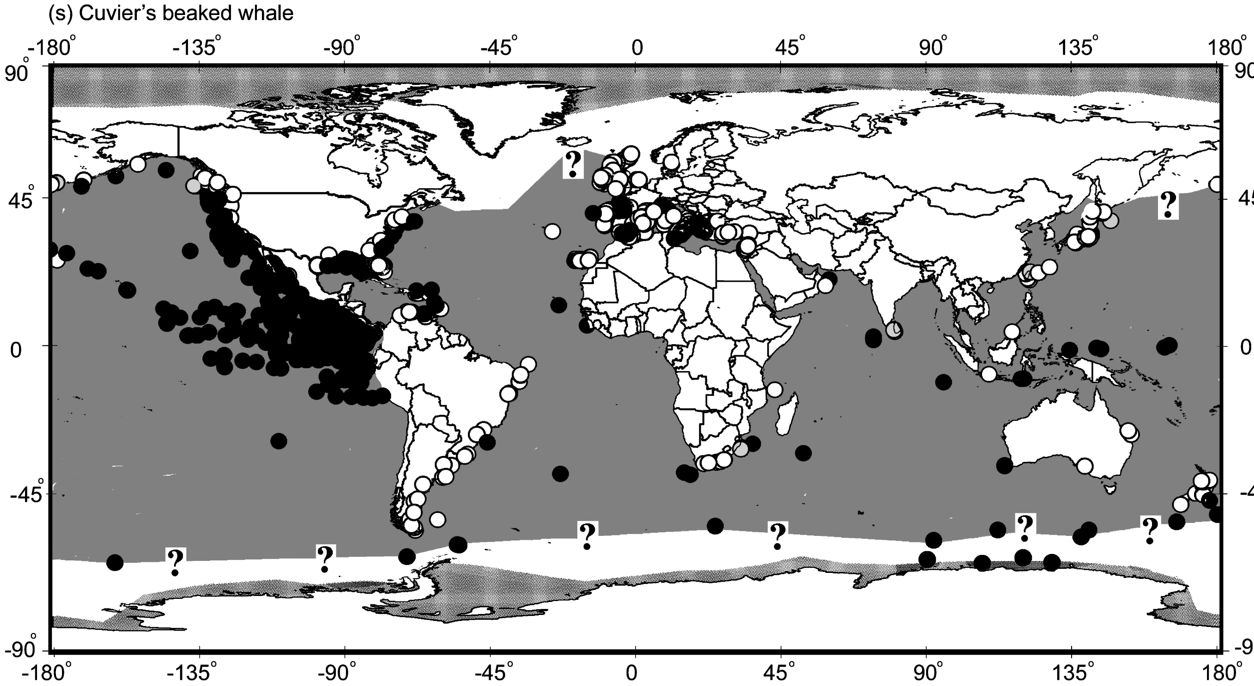


Fig. 2. Known and inferred distributions of beaked whales by species. Shaded areas indicate inferred distribution, ? indicates probable but unconfirmed areas/limits of occurrence. Stippled area indicates average minimum ice cover. Circles represent known records for which positions were available. Black circles – sightings; white circles – strandings; grey circles – other/unknown record types. PLEASE NOTE: Plotted records originate from a number of sources and are NOT corrected to take into account differences in levels of effort between different areas. Therefore, the densities of plotted at-sea sightings ARE NOT representative of the actual densities of these species NOR is absence of records indicative of a lack of occurrence at a specific location. (a) Arnoux's beaked whale (Southern Hemisphere) and Baird's beaked whale (North Pacific); (b) The northern bottlenose whale (North Atlantic) and the southern bottlenose whale (Southern Hemisphere). For northern bottlenose whales, main areas where this species was killed by whalers are marked with a black box (extent taken from Benjaminsen 1972); (c) Longman's beaked whale; (d) Sowerby's beaked whale; (e) Andrew's beaked whale; (f) Hubbs' beaked whale; (g) Blainville's beaked whale; (h) Gervais' beaked whale; (i) The ginkgo-toothed beaked whale; (j) Gray's beaked whale; (k) Hector's beaked whale; (l) strap-toothed whale; (m) True's beaked whale; (n) Perrin's beaked whale; (o) pygmy beaked whale; (p) Stejneger's beaked whale; (q) The spade-toothed whale; (r) Shepherd's beaked whale; (s) Cuvier's beaked whale.

(*Indopacetus pacificus*), a species for which the external morphology has only recently become known (Dalebout *et al.*, 2003).

GENUS *HYPEROODON*

Northern bottlenose whale (*Hyperoodon ampullatus*)

This species is endemic to the North Atlantic Ocean. It has been recorded from sightings and whaling data as far north as the Davis Strait, Iceland and the Norwegian Sea, south to the northeastern USA, the Azores and the western Mediterranean and from a stranding in the Canaries (Mitchell and Kozicki, 1975; Christensen *et al.*, 1977; 1992; Benjaminsen and Christensen, 1979; Clarke, 1981; Vonk and Martel, 1989; Reeves *et al.*, 1993; Dalebout *et al.*, 2001; Leal *et al.*, 2004; Cañadas, pers. comm.) (Fig. 2b). Although strandings have been recorded in the North and Baltic Seas (e.g. Fraser, 1953; Aguayo L, 1978; Kinze, 1995), these waters are generally too shallow for northern bottlenose whales. In fact, the North Sea may act as a trap for oceanic cetaceans, such as northern bottlenose whales and other beaked whales, as they migrate southward from higher-latitude areas such as the Norwegian Sea (Smeenk, 1997; MacLeod, 2000).

Southern bottlenose whale (*H. planifrons*)

Southern bottlenose whales have a circumpolar distribution throughout the Southern Hemisphere, with strandings as far north as southern Brazil (at 33.7°S – Gianuca and Castello, 1976), South Africa (Sekiguchi *et al.*, 1993) north-western Australia (at 20.6°S – Flower, 1882), south-eastern Australia (34.3°S – Hale, 1931), and northern New Zealand (37.7°S – Gianuca and Castello, 1976) and sightings off central Chile (sighting at 31.2°S – Clarke *et al.*, 1978) and off the west coast of South Africa (31.2°S – IWC, unpublished data). Observations, either sightings or whaling records, have been made at sea off South Africa, Chile, around the Falkland Islands and throughout Antarctic waters as far south as the ice edge (Clarke *et al.*, 1978; Kasamatsu *et al.*, 1988; White *et al.*, 2002; IWC, unpublished data) (Fig. 2b). Most at-sea records are from 57-70°S, however this may be due to higher levels of research effort at these latitudes. The southern bottlenose whale appears to be one of the most abundant beaked whales and indeed one of the most abundant cetacean species in Antarctic waters (Kasamatsu and Joyce, 1995). It is worth noting that two specimens at the northern end of this species range in South Africa originally identified as southern bottlenose whales have since been re-identified as Longman's beaked whales (Dalebout *et al.*, 2003).

GENUS *INDOPACETUS*

Longman's beaked whale (*I. pacificus*)

Very poorly known, this is the only species in the genus *Indopacetus*. Until recently it was known from only two skulls, one from Queensland, Australia (Longman, 1926), and another from Somalia (Azzaroli, 1968). However, additional specimens have been identified from South Africa, the Maldives and Japan, providing the first description of the species' external morphology (Press Release, National Museum of Science, Tokyo, 25th December 2002; Dalebout *et al.*, 2003). This has given weight to the suggestion by Pitman *et al.* (1999) that a number of sightings of unidentified beaked whales in the tropical Indo-Pacific may have been of this species. Those sightings occurred off the coast of Mexico, from the eastern tropical Pacific to the western Pacific and into the Indian Ocean all the way to eastern Africa (Fig. 2c). These sightings were made in surface water temperatures of 21-31°C, with most of them in waters warmer than 26°C (Pitman *et al.*, 1999). Pitman *et al.* (1999) suggested that Longman's beaked whale is more common in the western than the eastern Pacific. To date, this species has not been recorded in the Atlantic Ocean.

GENUS *MESOPLODON*

Sowerby's beaked whale (*M. bidens*)

This species is endemic to the North Atlantic and has a well described distribution due to its occurrence in the waters off North America and Europe. It has been sighted at 71.5°N in the Norwegian Sea (Carlström *et al.*, 1997) and strandings have been documented in Iceland and in Double Mer, Labrador, Canada (Lien and Barry, 1990). The southernmost records are strandings in Madeira in the east (Maul and Sergeant, 1977), the Azores in the mid-Atlantic (Reiner, 1986) and Port Saint Jose, on the Gulf of Mexico coast of Florida, USA (Bonde and O'Shea, 1989) in the west (Fig. 2d). The majority of stranding records are from northern Europe, particularly around the British coasts and in other countries bordering the North Sea (Mead, 1989a), with some also in the Baltic Sea (e.g. Aguayo L, 1978). However, the North and Baltic Seas are not thought to be areas of regular occurrence (MacLeod, 2000). There are fewer records from the western than the eastern Atlantic. All but one stranding (from the Gulf of Mexico coast of Florida, USA) have occurred between Labrador and New England (Bonde and O'Shea, 1989). Sowerby's beaked whale was the principal *Mesoplodon* species killed in the former large-pelagic driftnet fishery along the southern edge of Georges Bank (NOAA Fisheries, NEFSC, unpublished data). The Florida specimen is generally considered to have been a stray and the species is not thought to inhabit the Gulf of Mexico (Bonde and O'Shea, 1989; Jefferson and Schiro, 1997). There is some debate as to whether Sowerby's beaked whale occurs in the Mediterranean Sea (Mead, 1989a) but Van Bree (1975) found no evidence to support their presence in this area. However, Frantzis *et al.* (2003) reported a dead adult male *Mesoplodon* floating two miles off Cape Tainaro (36.4°N, 22.6°E) off the southern coast of Greece. The description, including the position of a large pair of teeth approximately in the middle of the lower jaw, is consistent with the characteristics of an adult male Sowerby's beaked whale (Frantzis *et al.*, 2003). However, as with the Florida specimen, this animal is most likely to represent a stray individual and not a regular occurrence in this area.

Andrews' beaked whale (*M. bowdoini*)

Andrews' beaked whale is known from 35 records, all of which are from strandings (Baker, 2001). Of these, 21 come from New Zealand and its surrounding islands. Of the remaining 14 records, most come from the southern coasts of Australia, with two from Tristan da Cunha and two from the Falkland Islands (Fig. 2e). There is also an additional record from Tierra del Fuego (N. Goodall, pers. comm.). These records range in latitude from 35.2°S (western Australia) south to 54.5°S (Macquarie Island). Baker (2001) surmised from these records that the species has a circumpolar distribution north of the Antarctic Convergence to 32°S. However, as Baker (2001) emphasised, there is a gap in the distribution from Chatham Island (176.57°W) east to the South American Coast (approximately 66°W in Tierra del Fuego) that may either represent a real break in distribution, or only reflect a general shortage of cetacean records for this part of the world.

Hubbs' beaked whale (*M. carlhubbsi*)

This species is endemic to the North Pacific, with most records consisting of strandings from the western seaboard of North America. The strandings ranged from 54.3-32.7°N (Mead *et al.*, 1988; Willis and Baird, 1998). A small number of stranded animals have been recorded on the Pacific coast of Japan, 41.7°N-35.0°N (Marine Mammal Database, National Museum of Science, Tokyo) (Fig. 2f). These records suggest a pan-North Pacific distribution, at least at these latitudes, although no records are available from the central North Pacific and it is possible that separate western and eastern populations exist. Mead *et al.* (1982) suggested that the distribution of Hubbs' beaked whale is related to the deep sub-Arctic current system.

Blainville's beaked whale (*M. densirostris*)

Blainville's beaked whale is the most widely distributed *Mesoplodon* species. Although it has not been recorded in some areas, it is thought to have a continuous distribution throughout the tropical, sub-tropical and warm-temperate waters of the world's oceans, with occasional occurrences in cold-temperate areas (Fig. 2g). The only apparent exception is the eastern Mediterranean, where it has yet to be recorded. In the North Atlantic, strandings have been recorded in Iceland, south to the Canaries in the east and Puerto Rico and into the Gulf of Mexico in the west (Mead, 1989a; Ritter and Brederlau, 1999; Rosario-Delestre *et al.*, 1999; A. Petersen, unpublished report). In the South Atlantic, strandings have been recorded in Brazil (Lichter, 1986) and South Africa (Ross, 1984). It is presumed that the distribution is continuous across the equator in the North Atlantic, particularly in the light of cross-equatorial distributions in other oceans, but this is as yet unconfirmed. In the Indian Ocean, there have been strandings off South Africa (Ross, 1984), the Seychelles (Besharse, 1971), and Mauritius (Michel and van Bree, 1976) and the species has been taken accidentally by fisheries off Sri Lanka (Ilangakoon, 2002) and sighted in the Maldives (Ballance *et al.*, 2001) and west of Australia (McCann, 1964). In the western Pacific, strandings have been recorded from Japan (Kasuya and Nishiwaki, 1971) to Tasmania, Australia (Guiler, 1966). In the central Pacific there have been strandings in Hawaii (Galbreath, 1963) and at Easter Island (Aguayo *et al.*, 1998), with sightings from the Society Islands (Gannier, 2000) and the Cook Islands (N. Hauser, pers. comm.). In the eastern Pacific strandings and sighting records range 37.3°N-41.5°S (Mead *et al.*, 1988; Pastene *et al.*, 1990; Pitman and Lynn, 2001).

Gervais' beaked whale (*M. europaeus*)

This species is endemic from the warm-temperate to tropical Atlantic (Fig. 2h). Strandings records range from Ireland (Berrow and Rogan, 1997) in the north, to southeast Brazil in the south (de Oliveira Santos *et al.*, 2004), with records from the Gulf of Mexico (e.g. Reynoso and Pimienta, 1989), the Caribbean (e.g. Debrot and Barros, 1994), the Canaries (e.g. Martin *et al.*, 1990), Mauritania (Robineau and Vely, 1993) and Guinea-Bissau (Reiner, 1980). The distribution in the South Atlantic remains unclear, but Gervais' beaked whales have stranded at Ascension Island (Mead, 1989a; White, pers. comm.) and in Brazil (23.97°S – de Oliveira Santos *et al.*, 2004). Based on its distribution in the North Atlantic, it would be expected that it occurs as far south as Uruguay in the west and Angola in the east. However, further data are needed to confirm or deny this possible distribution.

Ginkgo-toothed beaked whale (*M. ginkgodens*)

There are approximately 23 known records of the ginkgo-toothed beaked whale, all of which are from strandings and are restricted to the Pacific and Indian Oceans (Fig. 2i). Most records (15) are from Japan (Nishiwaki and Kamiya, 1958; Nishiwaki *et al.*, 1972; Marine Mammal Database, National Museum of Science, Tokyo). Strandings have also been recorded in China (Mead *et al.*, 1988), Taiwan (Nishiwaki *et al.*, 1972), Malaysia (Mead, 1989a), Guam (K. Robertson, pers. comm.), Sri Lanka (Deraniyagala, 1963), south-eastern Australia (Tidemann, 1980; Mead, 1989a), California (Moore and Gilmore, 1965), Mexico (Mead, 1989a) and the Galapagos Islands (Palacios, 1996). These locations range from 42.0°N-36.4°S in the western Pacific and 32.9°N-00.3°N in the eastern Pacific. The extent to which this reflects the actual distribution of this species is unknown and its range could include other areas of the Pacific and Indian Oceans. For example, Ballance and Pitman (1998) reported possible sightings in the Arabian Sea. However, this species is almost impossible to identify with certainty at sea and there have been as yet no confirmed sightings.

Gray's beaked whale (*M. grayi*)

Gray's beaked whale has been recorded in the temperate South Atlantic and Indian Oceans, with additional records eastward into the Pacific as far as New Zealand and south to Antarctic waters where the distribution is circumpolar (Fig. 2j). Along the eastern coast of South America, Gray's beaked whale has stranded from the southern tip of Brazil (31.8°S – Pinedo *et al.*, 2002a), south to Tierra del Fuego (53.3°S – Goodall, 1978). Strandings have occurred as far north as 31.1°S in South African waters (Ross, 1984), 33.6°S in Australia (Gales *et al.*, 2002), 34.4°S in New Zealand (Mead, 1989a) and 13.8°S in Peru (Reyes, 1990). The record from Peru is significantly farther north than all other Southern Hemisphere records, which are south of 30°S, and may represent an extension of this species into lower latitudes along the western South American coast in the cooler waters of the Humbolt current. Gray's beaked whale has been seen close to the Antarctic Peninsula and other Antarctic coastlines in summer months (IWC, unpublished data). A single stranding was reported from the Dutch coast in the North Sea (Boschma, 1951). Geographically, this is so far from all other records of this species that it is presumed to be extralimital rather than representing the normal presence of this species in the North Atlantic.

Hector's beaked whale (*M. hectori*)

Hector's beaked whale is known of from 25 published strandings, mostly from the southeast coast of South America or New Zealand (Fig. 2k). In South America, the species has been recorded from southern Brazil (32.0°S – Zerbini and Secchi, 2001), to Tierra del Fuego (55.1°S – Siefeld, 1979), while in New Zealand records range from 35.2°S-42.4°S (Mead, 1981; 1989a). Additional records come from Tasmania (Guiler, 1967), Western Australia (Gales *et al.*, 2002) and South Africa (Ross, 1984), giving a range of 68.5°W-176.9°E. There are no records from the southern Pacific between New Zealand and South America. Whether this represents a break in distribution or a lack of cetological effort in this area is unknown. Stranded animals previously identified as Hector's beaked whale from the eastern North Pacific (e.g. Mead, 1981; 1989a) have now been reclassified as Perrin's beaked whale (*M. perrini*) and Hector's beaked whale is no longer thought to occur in the Northern Hemisphere (Dalebout *et al.*, 2002).

Strap-toothed whale (*M. layardii*)

This species is endemic to the Southern Hemisphere and has a circumpolar distribution (Fig. 2l). It has stranded in southern Brazil (32.1°S – Pinedo *et al.*, 2002b), Uruguay (Lichter, 1986), Argentina (Goodall, 1978), the Falkland Islands (Lichter, 1986), South Africa (33.48°S – Ross, 1984), Kerguelen Island (Robineau, 1989), Heard Island (Guiler *et al.*, 1987), the southern coast of Australia and as far north as 20.3°S (Dixon, 1980; Paterson and van Dyck, 1990) and New Zealand (Mead, 1989a). With the exception of records in Western Australia, all known records are south of 32°S. The southernmost record is a sighting at 63.3°S (IWC, unpublished data). While it is assumed here that all reported records are accurately identified, it is possible that some older osteological records previously identified as strap-toothed whales are actually referable to the spade-toothed whale (*M. traversii*), a species which is morphologically similar and which has recently been classified as distinct (van Helden *et al.*, 2002).

True's beaked whale (*M. mirus*)

True's beaked whale is apparently the only species of *Mesoplodon* with isolated populations in separate hemispheres (Fig. 2m). This species has been recorded only in the temperate North Atlantic and South America, southern Africa and southern Australia. In the North Atlantic, it apparently occurs only in temperate waters and possibly only in warm temperate waters. In the western Atlantic, stranded animals have been recorded from Nova Scotia (46.3°N) to Florida (26.7°N – Mead *et al.*, 1988), with additional records along the length of the eastern seaboard (e.g. True, 1913) and in Bermuda (MacLeod, 2000). There have also been sightings off the northeast US coast (e.g. Tove, 1995). In the eastern Atlantic, the species has stranded from Ireland (53.7°N – Berrow and Rogan, 1997) south to the Canaries (28.9°N – Vonk and Martel, 1988), with sightings in the Bay of Biscay (Weir *et al.*, 2004). As yet, True's beaked whale has not been recorded in the Gulf of Mexico, the Caribbean, the Mediterranean or farther south in the North Atlantic. In the Southern Hemisphere, this species has stranded in southern Brazil (de Souza *et al.*, 2004), on the Indian Ocean coasts of South Africa at around 34°S, 22.6-25.3°E (Ross, 1984) and in southern Australia at around 38.4°S (Dixon and Frigo, 1994). Sightings have been recorded at approximately 33°S, 44°E in the Indian Ocean off Madagascar. The full extent of the range of True's beaked whale in the Southern Hemisphere is currently unclear and it is worth noting that for other *Mesoplodon* species which were previously thought to have anti-tropical distributions (Andrews' beaked whale and Hector's beaked whale), it has since been discovered that the putative populations in separate hemispheres represent distinct species. Therefore, the possibility that the anti-tropical populations of True's beaked whales may represent distinct species needs to be investigated.

Perrin's beaked whale (*M. perrini*)

Perrin's beaked whale was first described in 2002 through genetic analysis of skeletal material originally identified as Hector's beaked whale, a species now known to be restricted to the Southern Hemisphere (Dalebout *et al.*, 2002). Currently, there are five confirmed records of this species, all of stranded animals (Fig. 2n). All of these records are from the waters of the state of California, USA (Dalebout *et al.*, 2002). Whether this species is restricted to these waters or actually has a more widespread distribution is unknown.

Pygmy beaked whale (*M. peruvianus*)

The pygmy beaked whale was first described in 1991 from bycaught and stranded specimens from Peru (Reyes *et al.*, 1991). Since then there have been identified strandings along the coasts of North and South America 29.2°S-27.9°N (Reyes *et al.*, 1991; Pitman and Lynn, 2001) (Fig. 2o). Sightings at sea have been difficult to interpret due to possible mis-identifications of living animals based on descriptions of stranded ones, particularly in relation to pigmentation patterns. However, prior to the description of the pygmy beaked whale, Pitman *et al.* (1987) had reported sightings of an unidentified beaked whale in the eastern tropical Pacific and suggested it may represent an undescribed species referred to as '*Mesoplodon* sp. A' (Pitman *et al.*, 1987). Pitman and Lynn (2001) provided evidence that the pygmy beaked whale and *Mesoplodon* sp. A. are in fact the same species. Based on the sightings of *Mesoplodon* sp. A., Pitman and Lynn (2001) concluded that the pygmy beaked whale is probably endemic to the eastern tropical Pacific. A recent stranding record from New Zealand (Baker and van Helden, 1999) may represent either an extralimital stray or be indicative of a wider distribution.

Stejneger's beaked whale (*M. stejnegeri*)

Stejneger's beaked whale is endemic to the northern North Pacific where it is found in cold-temperate and sub-polar waters (Fig. 2p). It has stranded as far north as the Gulf of Alaska (55.0°N – Willis and Baird, 1998), the Aleutian Islands (around 52°N – Mead, 1989a; Walker and Hanson, 1999) and northern Russia (57.4°N – Moore, 1963) and been sighted around the Aleutian Islands (51.8°N – Loughlin *et al.*, 1982). The southernmost records are strandings from central California (36.6°N – Henshaw *et al.*, 1997) and the southern coast of Japan (35.1°N – Marine Mammal Database, National Museum of Science, Tokyo). The southern limit in the central Pacific is unknown.

Spade-toothed beaked whale (*M. traversii*)

The spade-toothed beaked whale is currently known of from three stranding records in the south-western Pacific; in New Zealand, the Chatham Islands and the Juan Fernandez Archipelago (van Helden *et al.*, 2002) (Fig. 2q). These three records suggest a Southern Hemisphere distribution in temperate waters approximately 33-44°S in the South Pacific. Morphological similarities between the spade-toothed and strap-toothed whales may mean that some osteological records assigned to the latter species actually represent the former and an investigation of this possibility may alter the perceived distributions of these two species.

GENUS *TASMACETUS*

Shepherd's beaked whale (*T. shepherdi*)

This species is known only from a small number of strandings in New Zealand (Oliver, 1937; Sorensen, 1940; Smith, 1965; Mead, 1989b), the Juan Fernandez Archipelago (Brownell *et al.*, 1976), Tierra del Fuego (Goodall, 1978) and Peninsula Valdez in central Argentina (Mead and Payne, 1975) and Tristan da Cunha, and a few probable or possible sightings at sea. A probable sighting was reported by Laughlin (1996) at approximately 53°45'S, 42°30'W in the western South Atlantic. Possible sightings have been reported near Christchurch, New Zealand (Watkins, 1976) and at 40.32°S, 9.88°W (Pym, pers. comm.). From these records it has been presumed that this species has a circumpolar distribution in the colder waters of the Southern Hemisphere, but the records are sufficiently sparse that this should be treated as unconfirmed (Fig. 2r).

GENUS *ZIPHIUS*

Cuvier's beaked whale *(Ziphius cavirostris)*

This species is the most widely distributed beaked whale, with a cosmopolitan distribution throughout almost all temperate, sub-tropical and tropical waters of the world as well as sub-polar and even polar waters in some areas (Fig. 2s). It is the only beaked whale regularly recorded in the eastern Mediterranean Sea (e.g. Politi *et al.*, 1994). In the Atlantic Ocean, Cuvier's beaked whales have stranded as far north as northeast USA (Backus and Schevill, 1961), Iceland (Petersen, pers. comm.) and northern UK (Fraser, 1953; MacLeod *et al.*, 2004), south to Tierra del Fuego (Goodall, 1978), the Falkland Islands (Lichter, 1986) and South Africa (Ross, 1984). A sighting was reported 37.5°S in the central South Atlantic (Findlay *et al.*, 1992). In the Indian Ocean, animals have stranded in South Africa (Ross, 1984), Oman (Alling, 1986), the Comoros (Robineau, 1975), Sri Lanka (Deraniyagala, 1965) and Indonesia (Dammerman, 1926) and been sighted in the Arabian Sea (Ballance and Pitman, 1998), the Maldives (Ballance *et al.*, 2001), and eastern Australia (IWC, unpublished data). In the western Pacific, records range from Japan in the north to southern New Zealand in the south (Fordyce *et al.*, 1979; Marine Mammal Database, National Museum of Science, Tokyo). In the eastern Pacific, this species has stranded as far north as the Aleutians (Kenyon, 1961) and Alaska (Foster and Hare, 1990) and been sighted as far south as 27.3°S (Aguayo *et al.*, 1998). It has also been sighted in the Southern Ocean as far south as 64.9°S (Kasamatsu *et al.*, 1988; IWC, unpublished data).

CONCLUDING REMARKS

For almost every beaked whale species, there are areas where it is suspected or presumed to occur, but where it has not as yet been recorded. In particular, data are generally scarce for offshore areas away from the continental shelf. Except in the eastern tropical Pacific, little systematic research has been conducted in such areas and even opportunistic records are rare. In other regions, data are not available even for nearer-shore areas, including the continental slope, due to a generally low level of cetological research or monitoring. This is true, for example, in the eastern tropical Atlantic, where little information is available on the occurrence of any cetacean species. Therefore, it can be difficult to produce, with any certainty, a complete beaked whale species list for specific locations. Such lists can be an important first step in the assessment and mitigation of potential anthropogenic impacts on beaked whales, particularly if different species are affected by anthropogenic activities to different degrees or in different ways. The inferred ranges outlined here provide a starting point for understanding which species are likely to occur at a given location, but further work is required to clarify and evaluate these inferred ranges. In addition, we need to understand whether and how these distributions may change in the future, e.g. with respect to global climate change (Harwood, 2001).

The best way to clarify the distribution of beaked whale species, and to monitor changes in distribution over time, is to conduct dedicated sightings surveys on a regular and continuous basis. However, to do this effectively at a global level would be expensive, and it would take many years to achieve a reasonable level of baseline coverage. Therefore, in the short term, and with less cost, it is important that full advantage is taken of currently available data and specimens, as well as existing opportunities to collect new information. At least three approaches should be considered. Firstly, improvements are needed in methods for accurately identifying beaked whales, whether dead (e.g. stranded, in fish markets, bycaught etc.) or alive. It is now possible to identify beaked whales from their DNA, including DNA extracted from biopsies, stranded animals and osteological specimens in museums (e.g. Dalebout *et al.*, 2002; 2003). Genetic identification should be applied when there is a possibility of confusion between morphologically similar but poorly known species to help clarify species ranges. In addition, more effort should be made to ensure that tissue samples are procured from as many future strandings, bycaught or killed animals as possible, as well as sightings (where feasible), to help to ensure that animals are identified correctly. In terms of sightings data, a definitive guide to field marks of species would prove useful, particularly for species that are more difficult to identify in the field or about which less is known. Such a guide would prove invaluable for the training purpose and for observers on general cetacean sightings cruises to allow beaked whales to be identified to species level rather than simply noted as an unidentified beaked whale species.

Secondly, survey effort should be directed at areas where little research has previously been conducted. In particular, where available, ‘platforms of opportunity’ can be used to achieve survey coverage of such areas at relatively low costs. If possible, networks of opportunistic surveys should be arranged, using a standardised methodology, to enable the most to be achieved from such surveys.

Finally, the underlying factors that determine species ranges need to be investigated. Once our knowledge of these has improved, it may be possible to predict the occurrence of species in locations where little direct information exists and to predict how ranges may change in response to environmental flux. Once species ranges have been defined, it may be possible to predict the finer-scaled distribution of individuals using models of habitat preferences and of factors related to local variations in species density and/or abundance.

In summary, there are still many gaps in our knowledge of beaked whale distribution that need to be resolved to allow potential impacts on beaked whales around the world to be adequately assessed and mitigated. While these gaps may not be filled in the near future, by making the most of available data and future data collection opportunities it may be possible to expand our knowledge of the distribution of beaked whale species in the near future at relatively little cost.

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Predicting Cuvier's (*Ziphius cavirostris*) and *Mesoplodon* beaked whale population density from habitat characteristics in the eastern tropical Pacific Ocean

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ABSTRACT

Temporally dynamic environmental variables and fixed geographic variables were used to construct generalised additive models to predict Cuvier's (*Ziphius cavirostris*) and *Mesoplodon* beaked whale encounter rates (number of groups per unit survey effort) and group sizes in the eastern tropical Pacific Ocean. The beaked whale sightings and environmental data were collected simultaneously during the Southwest Fisheries Science Center's cetacean line-transect surveys conducted during the summers and autumns of 1986-90 and 1993. Predictions from the encounter rate and group size models were combined with previously published estimates of line-transect sighting parameters to describe patterns in beaked whale population density (number of individuals per unit area) throughout the study area. Results provide evidence that the previously proposed definition of beaked whale habitat may be too narrow and that beaked whales may be found from the continental slope to the abyssal plain, in waters ranging from well-mixed to highly stratified. Areas with the highest predicted population densities were the Gulf of California, the equatorial cold tongue and coastal waters, including the west coast of the Baja Peninsula and the Costa Rica Dome. Offshore waters in the northern and southern subtropical gyres had the lowest predicted *Mesoplodon* densities, but density predictions were high for Cuvier's beaked whales in the waters southeast of the Hawaiian Islands. For both encounter rate and group size models, there was no geographic pattern evident in the residuals as measured by the ratio of pooled predicted to pooled observed values within geographic strata.

KEYWORDS: OCEANOGRAPHY; PACIFIC OCEAN; MODELLING; CUVIER'S BEAKED WHALE; MESOPLODON BEAKED WHALES; HABITAT; DISTRIBUTION

INTRODUCTION

Recent scientific efforts to describe and quantify beaked and bottlenose whale (family Ziphiidae) habitats have been primarily motivated by an interest in mitigating, minimising or eliminating harmful effects of human activities on ziphiid whales for conservation or management purposes. Concerns regarding the association of beaked whale mass strandings with loud anthropogenic noise in the marine environment (e.g. Anon., 2001; Peterson, 2003; Cox *et al.*, 2006) have placed an ecological imperative on the quest for basic knowledge about these cetaceans.

Beaked whales are particularly difficult cetaceans to study because they are infrequently encountered (Houston, 1990a; Ostrom *et al.*, 1993; Weir *et al.*, 2001; Mead, 2002). Furthermore, when human observers are in close proximity, beaked whales may go unnoticed because they have long dive times, surface without a visible blow or splash (Barlow, 1999; Weir *et al.*, 2001) and are relatively silent when they are within 200m of the surface (Johnson *et al.*, 2004). As a result, most knowledge about many beaked whale species comes only from stranded specimens (Houston, 1990a; b; Palacios, 1996; Dalebout *et al.*, 2002). New species have recently been identified and described (Reyes *et al.*, 1991; Pitman *et al.*, 1999; Pitman and Lynn, 2001; Dalebout *et al.*, 2002). Dalebout *et al.* (2002) noted that, 'Of the twelve cetacean species described in the last 100 years, eight have been ziphiids, primarily of the genus *Mesoplodon*'. Nevertheless, progress is ongoing in efforts to understand the ecology of beaked whales.

It is conventionally thought that beaked and bottlenose whales prefer deep-water habitats (Jefferson *et al.*, 1993; Mead, 2002; Reeves *et al.*, 2002). Beyond this basic preference, several authors have described beaked and bottlenose whale habitat preferences for specific study areas based on qualitative or correlation studies (reviewed by Ferguson, 2005). In the Gulf of Mexico, beaked whales were found in the deepest average water depths of any cetacean species (Davis *et al.*, 1998). Most studies have reported that beaked whales are commonly seen in waters over the continental slope (in waters 200-2,000m depth) (Waring *et al.*, 2001; Hooker *et al.*, 2002; Wimmer, 2003; MacLeod *et al.*, 2004) and submarine canyons (D'Amico *et al.*, 2003; Wimmer, 2003; Wimmer and Whitehead, 2004). MacLeod *et al.* (2004) also found that Cuvier's (*Ziphius cavirostris*) and *Mesoplodon* beaked whales were most often sighted over seafloors with greater slopes than the remainder of the study area in the Bahamas. Several authors have speculated that the distribution of beaked whales (or cetaceans in general) is likely to be primarily determined by prey availability (Davis *et al.*, 1998; Cañadas *et al.*, 2002; Hooker *et al.*, 2002; MacLeod, 2005).

Various methods have been used to quantitatively model the habitat preferences of beaked whales (reviewed by Ferguson, 2005). The most commonly used method has been logistic regression or generalised linear models (GLMs) with a logistic link function to model beaked whale distribution as a function of habitat variables. Using GLM, Waring *et al.* (2001) and Hamazaki (2002) found that Cuvier's and *Mesoplodon* beaked whales off the northeastern coast of the US were associated with the outer shelf edge. Cañadas *et al.* (2002) used GLMs to examine beaked whale distributions in the Mediterranean Sea and found that functions of depth were better predictors than those of seafloor slope. Another quantitative method applied to beaked whale habitat studies is ecological niche factor

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analysis (ENFA; MacLeod, 2005), which has shown that beaked whales in the North Atlantic Frontier (from west of the Hebrides in Scotland to the west and north of Shetland) tend to occupy deeper waters in areas with higher slopes than average, and prefer southward and westward facing slopes. MacLeod and Zuur (2005) used generalised additive models (GAMs) and classification and regression trees (CART) to examine beaked whale habitat associations in the Bahamas and found that depth, seabed slope and seabed aspect were all important factors.

Few of the previous attempts to model beaked whale distribution have been based on data collected over broad geographic areas and few included substantial areas of deep-water habitat with low seafloor slope (abyssal plains). None of the previous studies included variation in beaked whale group size with habitat variables. Only the recent studies by MacLeod and Zuur (2005) allowed for nonparametric, nonlinear responses to habitat gradients. In this paper, beaked whale habitat preferences and distributions were modelled from ship line-transect surveys conducted in a vast area of the eastern tropical Pacific Ocean (ETP) that included continental shelf, slope and abyssal plain habitats. Geographic variation in the population densities (number of individuals per unit area) of two genera of beaked whales, Cuvier's beaked whales and *Mesoplodon* beaked whales (*M. densirostris, M. peruvianus,* and *Mesoplodon* spp.), were quantified by modelling variation in encounter rates (number of sightings per unit of survey effort) and group sizes using GAMs. The results suggest that some of the generalities that have been inferred from previous, more limited studies do not appear valid for these species in the ETP.

METHODS

Study area

The study area encompassed 19.6 million km^2 of the ETP (Fig. 1). Circulation patterns in the surface waters of the region are dominated by the zonal equatorial current system between the anticyclonic North and South Pacific subtropical gyres (Kessler, 2005). The California Current and the Peru Current form the eastern boundaries of the North and South Pacific gyres, respectively (Fig. 2). The California Current flows into the North Equatorial Current and the Peru Current flows into the South Equatorial Current. The North Equatorial Countercurrent flows towards the east in the latitudes between the North and South Equatorial Current. Three primary surface water masses exist in the ETP: the warm, low-salinity Tropical Surface Water (TSW), which includes the eastern Pacific warm pool and underlies the Intertropical Convergence Zone (ITCZ), a zonal band between 5 and 10°N where rainfall is high as a result of the north and south trade winds converging; the higher-salinity Equatorial Surface Water (ESW) (the coldest surface water mass) with the equatorial cold tongue projecting from its eastern boundary; and the cool, Subtropical Surface Waters (SSW) located towards the poleward edges of the ETP, where the highest salinities are found (Fiedler and Talley, 2005) (Fig. 2). The thermocline is strongest beneath the TSW and weakest beneath the SSW (Fiedler and Talley, 2005). Although not considered part of the ETP, but included in the analysis nonetheless, the Gulf of California is a region in which evaporation largely exceeds precipitation, resulting in highly saline surface waters. Physical and biological processes in the study area interact to yield highly productive waters in the upwelling regions of the California Current, Peru Current, equatorial cold tongue and Costa Rica Dome, in contrast to the low productivity of the oligotrophic SSWs (Ryther, 1969; Fiedler and Philbrick, 2002; Fiedler, 2002) (Fig. 2). In general, both coastal and oceanic upwelling regions are characterised by relatively weak and shallow thermoclines and high levels of chlorophyll. In comparison, the oligotrophic regions have stronger and deeper thermoclines and lower levels of chlorophyll.

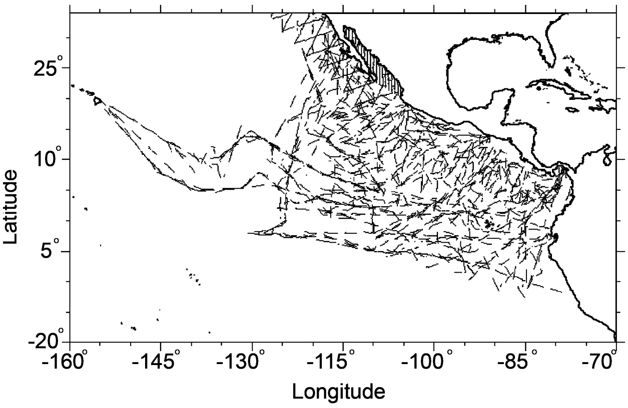


Fig. 1. Transect lines covered during the 1986-90, and 1993 shipboard cetacean line-transect surveys conducted by the SWFSC in the ETP.

Field methods

Cetacean sightings data and *in situ* oceanographic data were collected on Southwest Fisheries Science Center (SWFSC) research cruises conducted during the summer and autumn of each year 1986-90 and 1993. Two National Oceanic and Atmospheric Administration (NOAA) research vessels, *David Starr Jordan* and *McArthur*, followed standard line-transect protocols (Buckland *et al.*, 2001) to survey cetaceans in the ETP, while concurrently collecting a suite of oceanographic data over the length of the trackline.

Kinzey *et al.* (2000) provide a complete description of the SWFSC cetacean data collection procedures followed during the ship-based line-transect surveys. In brief, two teams of three visual observers rotated through three positions located on the flying bridge of the ship. Starboard and port observers used 25 × 150 'big eye' binoculars, scanning an arc of approximately 100° extending from the starboard and port beams, respectively, to 10° on the opposite side of the trackline. A third observer, the designated data recorder, searched by naked eye and occasionally 7 × 50 binoculars across the entire 180° arc in front of the ship. All cetaceans sighted were identified to the lowest taxonomic level possible. Group size estimates were recorded independently by each observer.

The *in situ* oceanographic data collected during the line-transect surveys and considered as potential predictor variables in the encounter rate and group size models were: sea surface temperature (SST); sea surface salinity; thermocline depth; thermocline strength; and the natural logarithm of surface chlorophyll concentration (hereinafter simply referred to as surface chlorophyll concentration). Details of the oceanographic data collection methods for each ship and each year 1986-90 are available in Thayer *et al.* (1988a; b; c; d), Lierheimer *et al.* (1989a; b; 1990a; b), and Philbrick *et al.* (1991a; b). Oceanographic methods and results from the 1993 cruise have not yet been published. The temperature and salinity of the sea surface were recorded continuously using a thermosalinograph and then

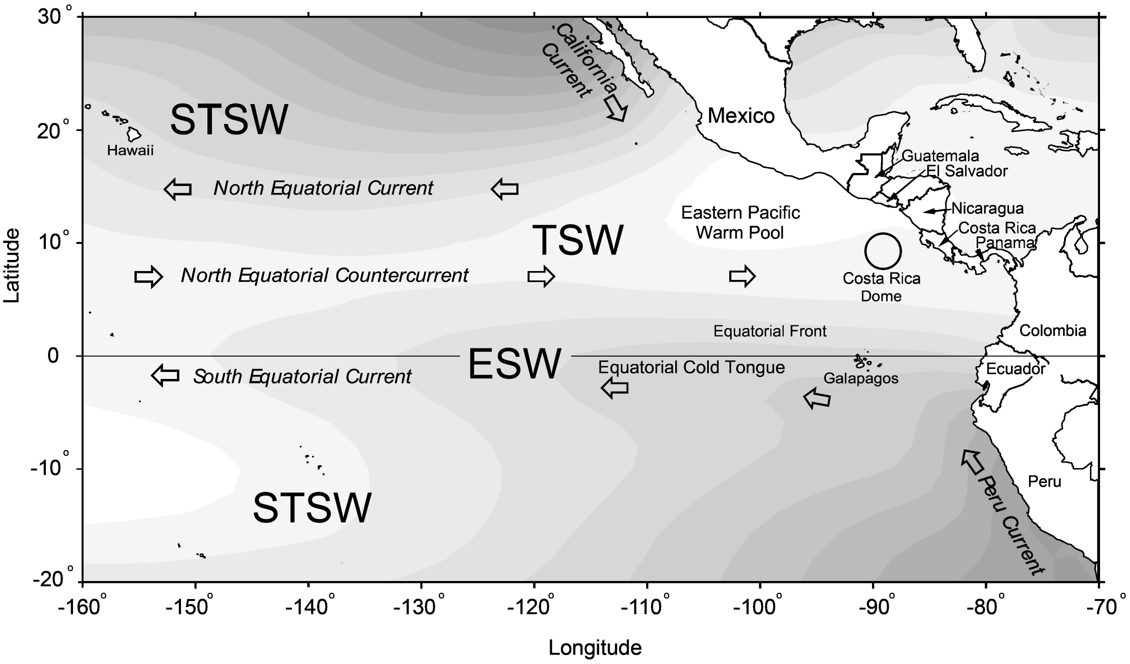


Fig. 2. Oceanography of the ETP study area. STSW: Subtropical Surface Water; TSW: Tropical Surface Water; ESW: Equatorial Surface Water.

summarised into hourly means, resulting in a spatial resolution of approximately 18.5km (Table 1). Thermocline depth and strength were derived from conductivity temperature depth (CTD) stations and expendable bathythermograph (XBT) probes, having a spatial resolution of approximately 40-110km (Table 1). Surface chlorophyll concentrations have a spatial resolution of approximately 15-130km (Table 1). Beaufort sea state was recorded while the marine mammal observers were on-effort and was updated whenever conditions changed. Beaufort sea state is a dominant factor affecting the visibility of cetaceans; therefore it was included in all models to account for potential biases due to visibility. Although it might be possible to account for the sea state visibility bias elsewhere in the density analysis, including Beaufort sea state as a predictor variable in the generalised additive model automatically accounts for correlations among other predictor variables, thereby providing a better assessment of each predictor variable's individual effects on the response variable (Hastie and Tibshirani, 1990).

Additional environmental data that were considered in the models include distance from shore, depth and slope of the ocean bottom, latitude and longitude. Offshore distance was calculated as the shortest distance between a given point on the trackline and the closest point on the North, Central or South American mainland. Depth data were obtained from the National Geophysical Data Center's TerrainBase data set, which had a spatial resolution of 5 × 5 minutes (approximately 9 × 9km). The slope was derived from the depth data in the two-step process described below.

Analytical methods

In preparation for building the models, the beaked whale sighting data and oceanographic data were summarised into 9km segments of on-effort trackline, corresponding roughly to the finest resolution of environmental data. The 9km distance for each segment was measured directly along the trackline; therefore, the start and end points of a given segment may have been less than 9km apart as measured by straight-line distance if the trackline in the segment followed bends or curves. Conversely, the straight-line distance between segment start and end points could have been greater than 9km if off-effort sections of trackline intervened between contiguous on-effort sections in a given segment. In those instances when off-effort sections separated contiguous on-effort sections, data from the discontinuous sections of on-effort trackline were summarised together if the distance between sequential sections of on-effort trackline was less than 9km. Otherwise, the on-effort section before observers went off effort was omitted and the start point for the new segment was located at the beginning of the on-effort section following the lag in effort. Due to the relatively small scale of the analysis, autocorrelation undoubtedly exists in the sighting and oceanographic data on neighbouring 9km segments. Nevertheless, the primary goal was prediction rather than explanation of ecological relationships or hypothesis testing; therefore, the problems associated with inflated sample size and autocorrelation are largely irrelevant because they do not add appreciable bias to the parameter estimates required for prediction (Neter *et al.*, 1990; Hamazaki, 2004).

Oceanographic values for each segment were calculated as weighted averages of the data from the oceanographic stations immediately before and after each segment midpoint, where the midpoint was defined as the point at which 4.5km of on-effort trackline had been covered. Inverse distance weighting (distance^{-1}) was used for thermocline depth, thermocline strength, and surface chlorophyll, whereas time^{-1} weighting was used for SST and sea surface salinity. This difference in weighting methods was necessary because the latter oceanographic data were recorded with only a time stamp. Nevertheless, the ships travelled at approximately a constant speed, so the inverse distance and inverse time weighting methods are roughly comparable. Depth values for each segment were calculated as the inverse distance weighted average depth of the four closest nodes in the TerrainBase 5 × 5 minute grid to the segment midpoint. Assigning slope values to each segment required two steps. First, slope values were calculated for each node on the 5 × 5 minute grid as the magnitude of the depth gradient:

Table 1

Temporal and spatial resolution of *in situ* oceanographic data collected during SWFSC cetacean line-transect survey cruises in 1986-90 and 1993.

Variable	Resolution
Sea surface temperature	Recorded every five minutes; summarised into hourly means (approx. 18.5km)
Sea surface salinity	Recorded every five minutes; summarised into hourly means (approx. 18.5km)
Thermocline depth*	40-110km
Thermocline strength*	40-110km
Surface chlorophyll concentration	15-130km

*These variables were derived from CTD (conductivity, temperature, and depth) and XBT (expendable bathythermographs) data.

$$\text{Slope} = \sqrt{\left(\frac{\partial z}{\partial x}\right)^2 + \left(\frac{\partial z}{\partial y}\right)^2} \qquad (1)$$

Using compass-based grid notation and representing the slope angle in degrees yields the following equation:

$$\text{Slope} = \left(\frac{180}{\pi}\right) \bullet \arctan\left\{\sqrt{\left(\frac{Z_E - Z_W}{2\Delta x}\right)^2 + \left(\frac{Z_N - Z_S}{2\Delta y}\right)^2}\right\} \qquad (2)$$

where Z_E, Z_W, Z_N, and Z_S refer to the grid nodes to the east, west, north and south of the desired node. Second, the slope for the segment midpoint was assigned the value of the slope of the node closest to the segment midpoint.

Beaked whale sightings data for each segment were summarised as the total number of groups sighted and the average group size in the segment. Prior research has shown that individual observers' estimates of group size can be biased when compared to counts made from aerial photographs and that group size estimates can be improved by applying individual-specific calibrations to correct this bias (Gerrodette *et al.*, 2002). Computing the average group size for each segment required three steps: (1) calculation of the bias-corrected group size estimate for each observer for each sighting in the segment based on individual calibration coefficients; (2) calculation of the mean group size estimate, averaged over all observers, for each sighting in the segment; and (3) calculation of the mean group size estimate, averaged over all sightings, for each segment. For (1) one of three methods was used; all methods were derived by comparing the observers' uncalibrated group size estimates with group size estimates obtained from photographs of cetacean groups taken during the surveys. Direct calibration with quasi-maximum likelihood bias correction was the preferred method and was used if the group size estimates and Beaufort sea state data necessary for the observer's calibration were available (Gerrodette *et al.*, 2002). Directly calibrated observers have two types of direct calibrations, one that is year-specific and one that is a general calibration to be used in any year (Gerrodette *et al.*, 2002). If data were not available to use the direct calibration model that was specific to a given year, the next option was to use the general direct calibration model for the observer. If neither direct calibration model could be used due to lack of data, indirect calibration with a quasi-maximum likelihood bias correction was considered (Barlow *et al.*, 1998). The indirect calibration method could be used only if an observer's best estimate of group size was available and if an indirect calibration model existed for the observer. At this stage in the selection of a calibration method, if a best estimate was not available, that observer's data was not included in the mean group size estimate for the sighting. If the indirect calibration method could not be used but a best estimate was available for the observer, then the ratio method was used (Gerrodette *et al.*, 2002):

$$\hat{s} = \frac{s_b}{\left[\sum_{i=1}^{n} m_i\right]^{-1} \left[\sum_{i=1}^{n} \sum_{j=1}^{m_i} \left(\frac{s_{b_{i,j}}}{s_{p_i}}\right)\right]} \qquad (3)$$

where,

$\hat{s}$ = observer's calibrated group size estimate,
$s_{b_{i,j}}$ = observer *j*'s best estimate of size for group *i*, and
s_{p_i} = size of group *i* estimated from photographs of group *i*.

Thus, in the ratio method, the observer's best estimate (s_b) was corrected by the ratio of observer best estimates to photographic counts, averaged over all *n* photographic calibration groups, each having *m* observer estimates. Once each observer's group size estimate was calibrated, the mean group size was calculated for each sighting as the weighted mean of the natural logarithm of the calibrated group size estimates, resulting in a weighted geometric mean group size. The calibrated group size estimates were weighted by variance^{-1}, where the value for the variance for each observer was the mean square error (MSE) reported for directly calibrated observers and observers calibrated with the ratio method (Gerrodette *et al.*, 2002) or the average square prediction error (ASPE) reported for indirectly calibrated observers (Barlow *et al.*, 1998). Finally, the mean group size estimate for each segment was calculated as the arithmetic mean of the weighted geometric mean group size estimates for all sightings in the segment.

GAMs were used to relate beaked whale sightings to the summarised fixed geographic variables and temporally dynamic *in situ* oceanographic data described above. A GAM (Hastie and Tibshirani, 1990) may be represented as:

$$g(\mu) = \alpha + \sum_{j=1}^{p} f_j\left(X_j\right) \qquad (4)$$

As in GLMs, the function $g(\mu)$ is known as the link function, and it relates the mean of the response variable given the predictor variables, $\mu = E(Y|X_1,\ldots,X_p)$, to the additive predictor $\alpha+\Sigma_j f_j(X_j)$. GAMs are nonparametric extensions of GLMs: the components $f_j(X_j)$ in the additive predictor may include nonparametric smooth functions of the predictor variables, allowing GAMs to be considerably more flexible than GLMs, which are restricted by the constraints of the linear predictor, $\alpha+\Sigma_j\beta_j X_j$. Separate GAMs were built to describe and predict beaked whale encounter rates and average group sizes. The encounter rate data were essentially clustered counts; therefore, the number of sightings in each segment were modelled using a quasi-likelihood error distribution with variance proportional to the mean and a logarithmic link function (approximating an over-dispersed Poisson distribution). Encounter rate models were built using all 9km segments, regardless of whether they contained sightings. Observed distributions of cetacean group sizes in the ETP region typically have long tails and are restricted to positive, real values. Furthermore, after correcting for bias and averaging group sizes across individuals and sightings in each segment, group size estimates are likely to be non-integer valued. Therefore, GAMs were built using the natural logarithm of group size as the response variable and a Gaussian error distribution with the identity link function. Group size models were built on only the 9km segments that contained Cuvier's or *Mesoplodon* beaked whale sightings with valid group size estimates.

The encounter rate and group size GAMs were built using *S-PLUS 6 for Windows*. Forward/backward stepwise selection of variables, with linear terms or smoothing splines having two and three degrees of freedom (df) in the scope of predictor variables, was implemented using the function *step.gam*. Models built using a maximum of four df for each variable in the scope of *step.gam* were considered, but resulting models were qualitatively similar to those limited to three df and the added complexity of the four df models appeared to have no ecological justification. Akaike's Information Criterion (AIC) was used to determine the best model at each step. Stepwise selection of variables occurred twice for each model. The first stepwise selection process started with the null model, did not contain terms for latitude or longitude and linear terms were excluded from the scope. Latitude and longitude were excluded from the first call to try to explain the observed variation in the beaked whale data using the more informative environmental data before considering fixed geographic co-ordinates. Linear functions were excluded from the first call because a few instances were found in which AIC was lower for a linear fit than for a quadratic smoothing spline, but a cubic smoothing spline was better than a linear fit. In those instances, the stepwise fitting algorithm would not go beyond the quadratic and test the AIC value resulting from splines with higher df. The second call to *step.gam* began with the best model from the first call, and included latitude, longitude and linear functions of all variables in the scope of predictor variables. It is advantageous to call *step.gam* twice because, by default, the function uses the dispersion parameter of the original gam object (Chambers and Hastie, 1993) and the estimated dispersion parameter associated with the best model from the first call to the function is likely to better represent the underlying process than that associated with the null model.

The above stepwise selection of variables finds the model that provides the best fit to the given data as judged by AIC, but it does not provide any information about the predictive power of the resulting model. To assess the predictive power of a number of models, the stepwise building procedure was performed on all combinations of the years 1986-90 with one year left out; 1993 was also included in all trials because it was a relatively small data set. This modified procedure resulted in five 'best' encounter rate models and five 'best' group size models. To evaluate which encounter rate and group size models performed best according to predictive power, cross-validation methods were applied, testing each model on the excluded year. The model with the lowest average squared prediction error (ASPE) was selected as the model with the best predictive performance. The model selected by the cross-validation process was rebuilt using the specified df and all years of data to fine-tune the smoothing splines.

The final *Mesoplodon* encounter rate model and Cuvier's group size model included latitude. To determine how the fixed geographic variable affected the predictive performance of the models, the stepwise selection and cross-validation procedures were repeated, excluding latitude and longitude from the scopes of both calls to *step.gam*. The ASPE values of the final models built without geographic variables in the scopes were compared to the final models built with geographic variables; the models with the lowest ASPE values were selected as the best overall *Mesoplodon* encounter rate and Cuvier's group size models.

To estimate beaked whale density, *D*, the encounter rate (*n/L*) and group size (*S*) model results were incorporated into the standard line-transect equation:

$$D = \left(\frac{n}{L}\right) S \left(\frac{1}{2 \cdot ESW \cdot g(0)}\right) \quad (5)$$

where,

n/L = encounter rate (number of sightings per unit length of trackline),

S = expected (or mean) group size,

ESW = effective strip half-width, or $1/f(0)$, where $f(0)$ is the sighting probability density at zero perpendicular distance, and

$g(0)$ = probability of detecting an animal on the trackline.

The values of $f(0)$ and $g(0)$ were those for Cuvier's and *Mesoplodon* beaked whales in the ETP and Gulf of California from Ferguson and Barlow's (2001) analysis. It was necessary to apply a bias-correction factor to the group size predictions from the GAMs because the models were built in log space and then the results were transformed back to arithmetic space, converting the group size estimate to a geometric mean in the process (Finney, 1941; Smith, 1993). The ratio estimator was used to correct for this back-transformation bias (Smith, 1993). Density estimates for each segment were smoothed to give a geographic representation of average density over the study period by using an inverse distance weighting interpolation to the first power, with the anisotropy ratio set to 1.0 in *Surfer* software (version 7.0).

To evaluate the models' fit to the observed data, the following error analysis was conducted. Encounter rate models were fitted to the observed oceanographic and geographic data for all segments in the study area and the differences between predicted and observed values for each segment (ΔER_i) were calculated:

$$\Delta ER_i = ER_{i_{predicted}} - ER_{i_{observed}} \quad (6)$$

for segment *i* in the study area. In addition, the ratio (R_{ER}) between pooled predicted values and pooled observed values was calculated:

$$R_{ER} = \frac{\sum_{i=1}^{n} ER_{i_{predicted}}}{\sum_{i=1}^{n} ER_{i_{observed}}} \quad (7)$$

where the summation is over the total number of segments used to build the models or the number of segments in a given geographic stratum, as described below. Group size was predicted from GAMs based on the subset of data comprised of only the segments with either Cuvier's or *Mesoplodon* beaked whale sightings, as appropriate. This subset of predictions was used to test how well the model predicted group size for each segment (ΔSS_i) and for the study area as a whole (R_{SS}) because the group size model was built on the same subset of data upon which the predictions were based. The group size predictions were corrected for the bias due to back-transforming from the log space and the computations for ΔSS_i and R_{SS} were analogous to the respective encounter rate statistics (Eqs 6 and 7). To qualitatively determine whether spatial patterns existed in the predictions for encounter rate and group size, a spatially stratified analysis was conducted in which values of R_{ER} and R_{SS} were calculated for geographic strata of approximately 5° latitude × 5° longitude.

RESULTS

In total, 90 Cuvier's beaked whale sightings and 106 *Mesoplodon* sightings were included in the models. Cuvier's and *Mesoplodon* beaked whales were sighted in groups of approximately two individuals, on average, with maximum group sizes of six and five individuals, respectively. The mean water depth where Cuvier's beaked whales were sighted in the ETP was approximately 3.4km with a maximum depth of over 5.1km; similarly, the mean depth of *Mesoplodon* beaked whale sightings was just over 3.5km and the maximum depth was approximately 5.75km (Table 2; standard deviations (SD) for all environmental variables and summary statistics for the entire study area are also presented in Table 2). Cuvier's beaked whale was found over seafloors with a mean slope of 0.732° (range: 0.003-6.425°), and *Mesoplodon spp.* were found over a mean slope of 0.673° (range: 0.006-4.935°). In addition, beaked whales in the ETP were found in waters that ranged from well-mixed to stratified, with a continuum of weak to strong thermoclines. Both species were sighted an average of 1,000km offshore, with a range of approximately 40-3,750km. The concentration of chlorophyll at the surface associated with the Cuvier's and *Mesoplodon* sightings ranged from 0.048-0.649mg m^{-3} (mean=0.203mg m^{-3}) and 0.047 to 2.26mg m^{-3} (mean=0.255mg m^{-3}), respectively.

Models for both genera predicted highest densities in the highly productive coastal and equatorial waters (Figs 3 and 4). The mean predicted Cuvier's beaked whale density resulting from the overall best encounter rate and group size models was 4.55 individuals 1,000km^{-2} (SD=1.96). The best Cuvier's beaked whale encounter rate and group size

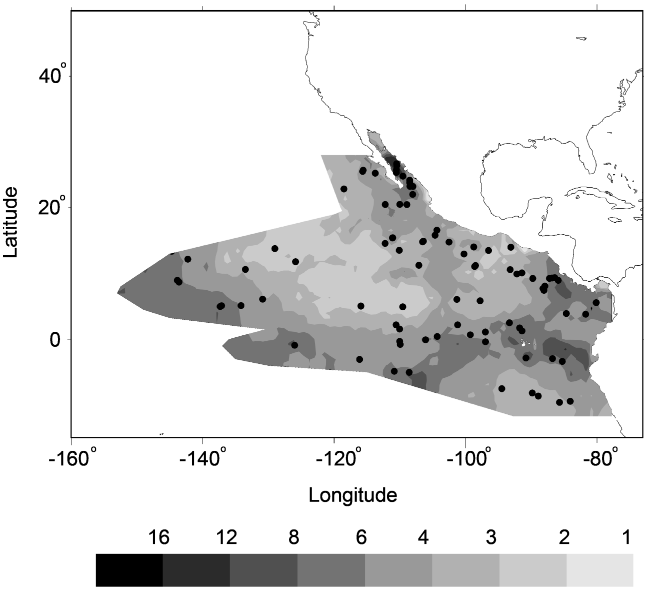
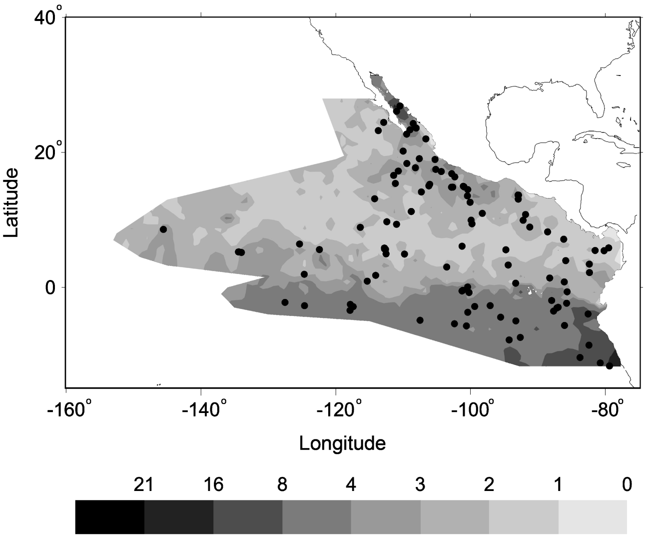


Fig. 3. Predicted Cuvier's beaked whale density (no. individuals 1,000km^{-2}) in the ETP. Predictions are for Beaufort sea state of 1. Black circles mark locations of all transect segments with on-effort Cuvier's beaked whale sightings and oceanographic data from SWFSC surveys 1986-90 and 1993.



`Fig. 4. Predicted *Mesoplodon* beaked whale density (no. individuals 1,000km^{-2}) in the ETP. Predictions are for Beaufort sea state of 1. Black circles mark locations of all on-effort *Mesoplodon* sightings and oceanographic data from SWFSC surveys 1986-90 and 1993.

Table 2

Summary statistics of environmental variables for the ETP study area and the segments in which *Ziphius* and *Mesoplodon* (*Mesop.*) beaked whale sightings occurred.

	Minimum			Mean			Maximum			Standard deviation		
	Ziphius	*Mesop.*	Study area	*Ziphius*	*Mesop.*	Study area	*Ziphius*	*Mesop.*	Study area	*Ziphius*	*Mesop.*	Study area
Beaufort*	0.8	0.2	0.2	2.9	2.9	3.7	5.0	5.0	6.0	1.3	1.3	1.1
Distance offshore (km)	42.5	36.0	3.8	1,097.8	1,052.0	1,249.7	3,670.6	3,844.6	3,851.8	1,064.5	970.0	942.2
Depth (m)	1,167.5	717.7	46.2	3,445.8	3,513.6	3,573.8	5,197.6	5,749.9	5,873.0	902.7	878.5	917.1
Slope (°)	0.003	0.006	0.000	0.732	0.673	0.504	6.425	4.935	10.487	1.145	1.097	0.935
Sea surface temperature (°C)	19.7	18.5	16.6	26.8	26.3	26.1	30.6	31.3	31.7	3.2	3.6	2.8
Sea surface salinity (psu)	30.1	30.3	16.3	33.9	34.0	33.9	35.3	35.3	35.7	0.8	1.0	1.0
Surface chlorophyll concentration (mg/m^3)	0.048	0.047	0.015	0.203	0.255	0.220	0.649	2.260	8.976	0.110	0.306	0.270
Thermocline depth (m)	15.0	15.0	11.0	53.9	56.2	61.4	151.0	126.0	211.7	24.0	23.9	28.0
Thermocline strength (°/m)	0.149	0.108	0.068	0.367	0.391	0.393	0.795	0.795	0.973	0.140	0.154	0.155

*Beaufort sea state was treated as a continuous variable in the analysis.

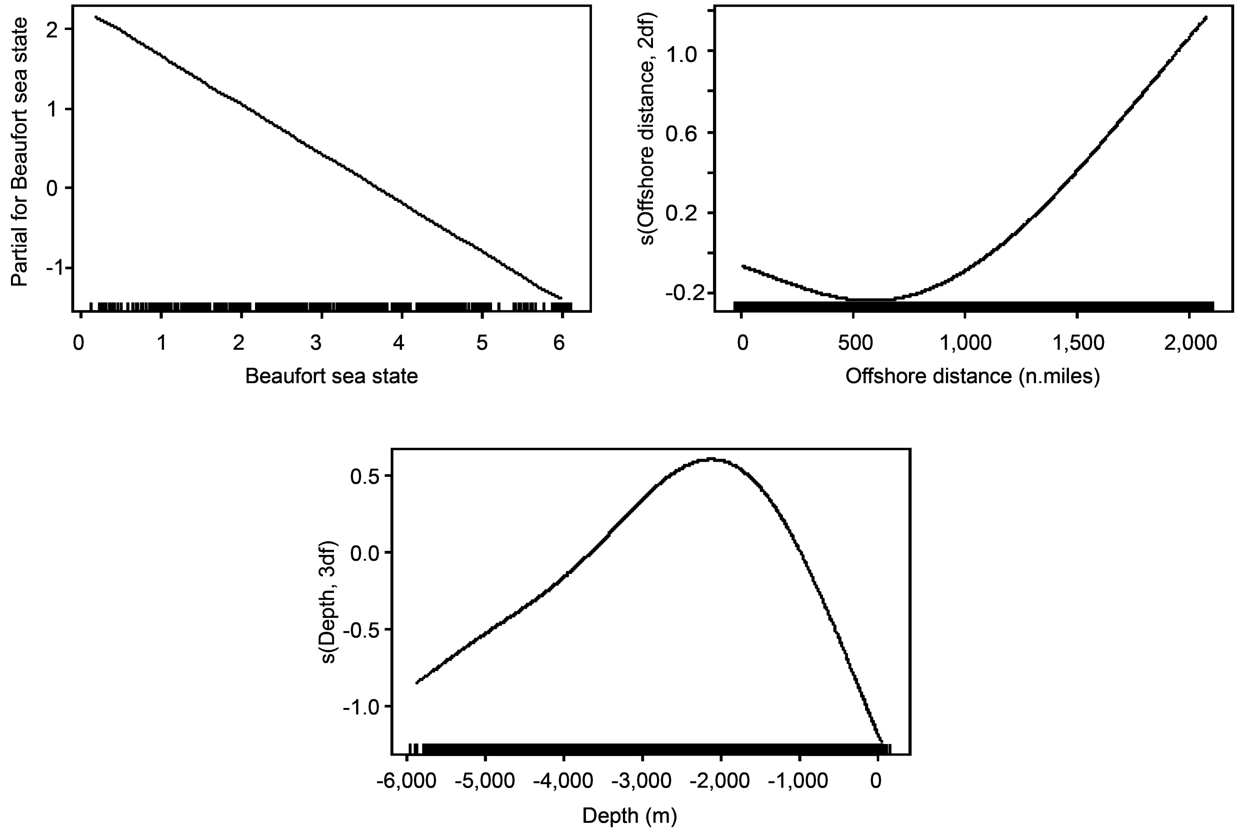


Fig. 5. Smooth spline functions of the predictor variables incorporated into the final Cuvier's beaked whale encounter rate (no. sightings/unit survey effort) GAM. Degrees of freedom for nonlinear fits are in the parentheses on the *y*-axis. Tick marks above the *x*-axis indicate the distribution of observations in all segments (with and without Cuvier's beaked whales).

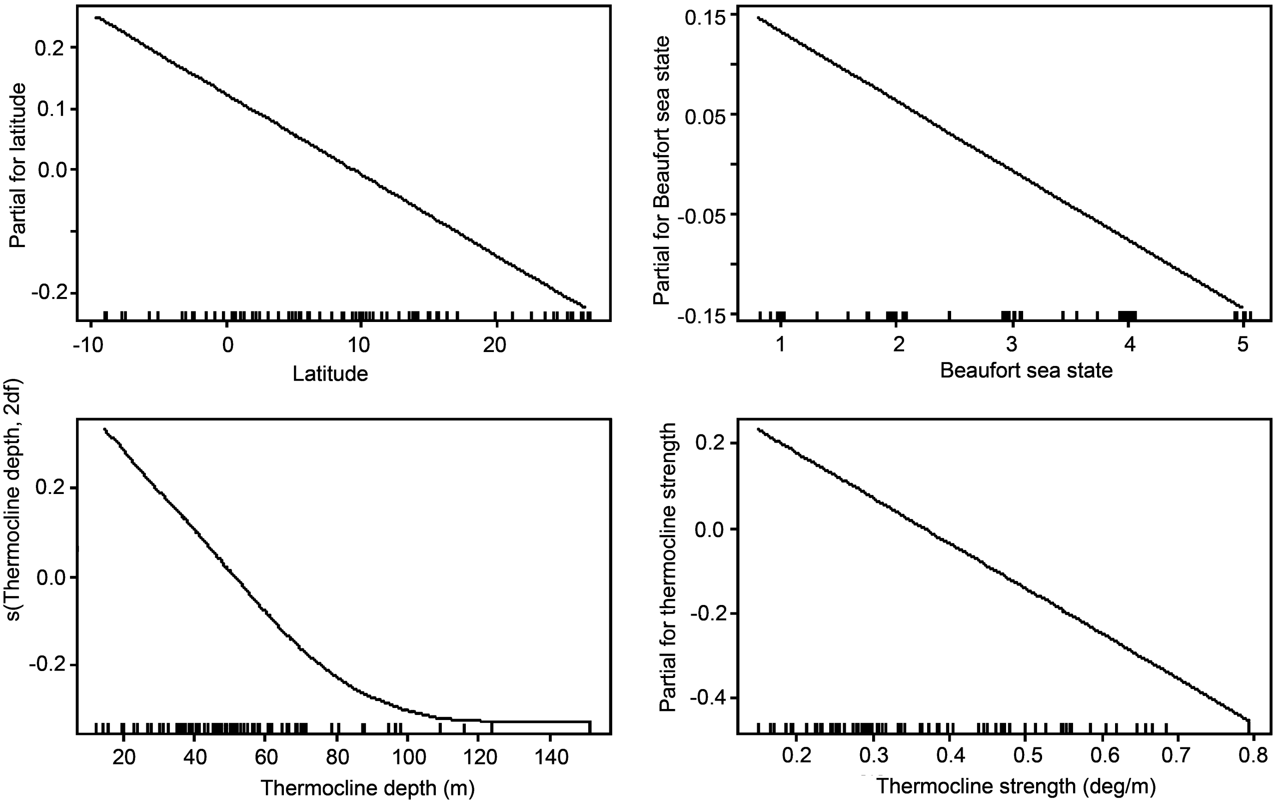


Fig. 6. Smooth functions of the predictor variables incorporated into the final Cuvier's beaked whale group size GAM. Degrees of freedom for nonlinear fits are in the parentheses on the *y*-axis. Tick marks above the *x*-axis indicate the distribution of observations in all segments with Cuvier's beaked whales.

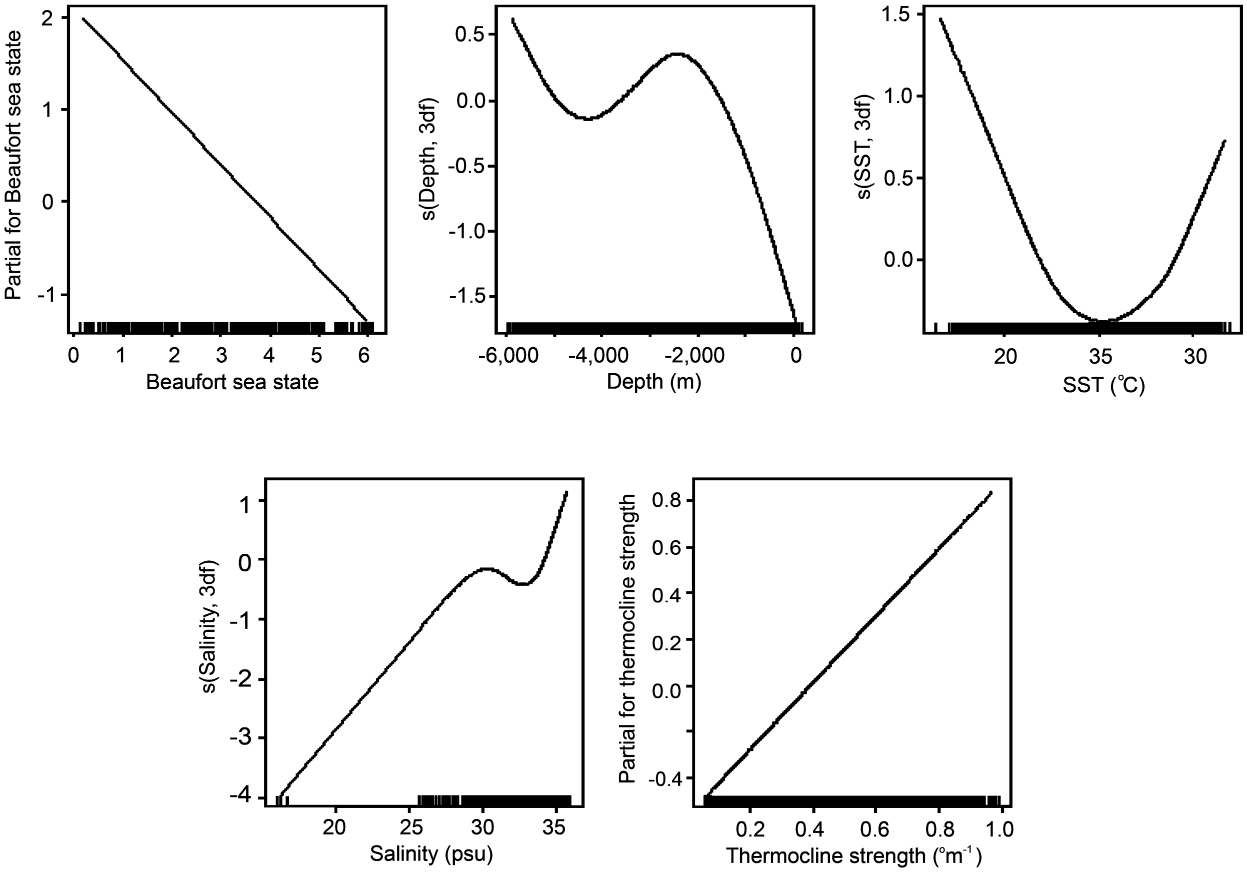


Fig. 7. Smooth functions of the predictor variables incorporated into the final *Mesoplodon* beaked whale encounter rate GAM. Degrees of freedom for nonlinear fits are in the parentheses on the *y*-axis. Tick marks above the *x*-axis indicate the distribution of observations in all segments (with and without *Mesoplodon* beaked whales).

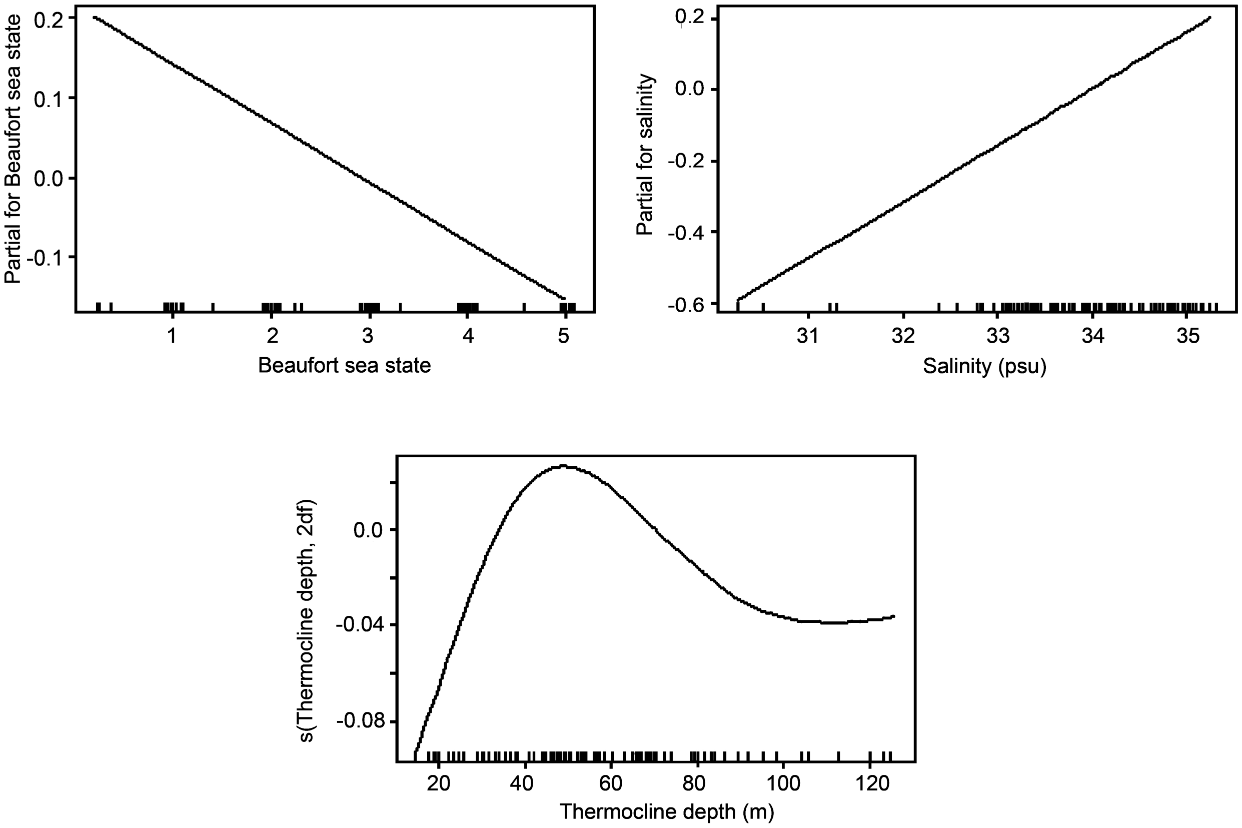


Fig. 8. Smooth functions of the predictor variables incorporated into the final *Mesoplodon* beaked whale group size GAM. Degrees of freedom for nonlinear fits are in the parentheses on the *y*-axis. Tick marks above the *x*-axis indicate the distribution of observations in all segments with *Mesoplodon* beaked whales.

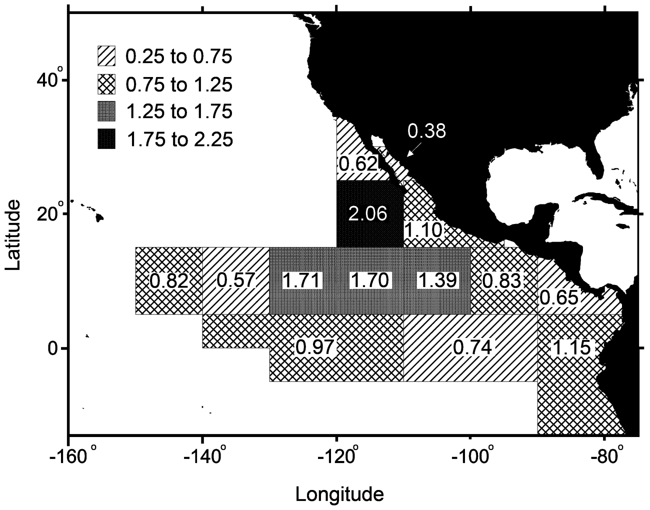


Fig. 9. Geographic distribution of residuals for Cuvier's beaked whale encounter rates measured as the ratio: R_{ER}=[Σ(predicted)/Σ(observed)]. R_{ER} values are shown in each stratum. Predictions were based on observed oceanographic data from SWFSC survey cruises in 1986-90 and 1993.

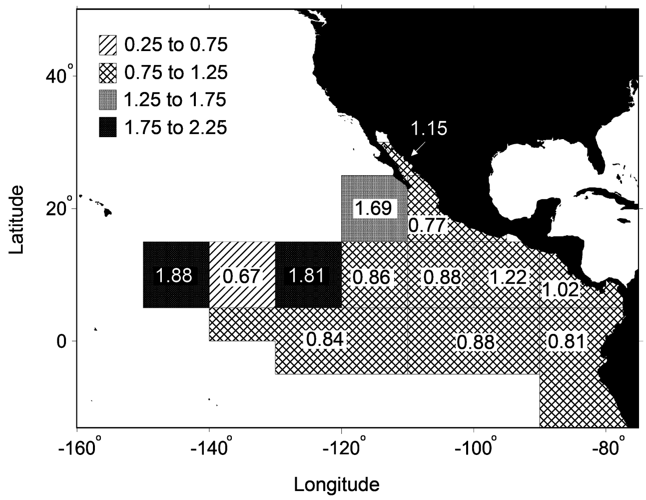


Fig. 10. Geographic distribution of residuals for *Mesoplodon* beaked whale encounter rates measured as the ratio: R_{ER}=[Σ(predicted)/Σ(observed)]. R_{ER} values are shown in each stratum. Predictions were based on observed oceanographic data from SWFSC survey cruises in 1986-90 and 1993.

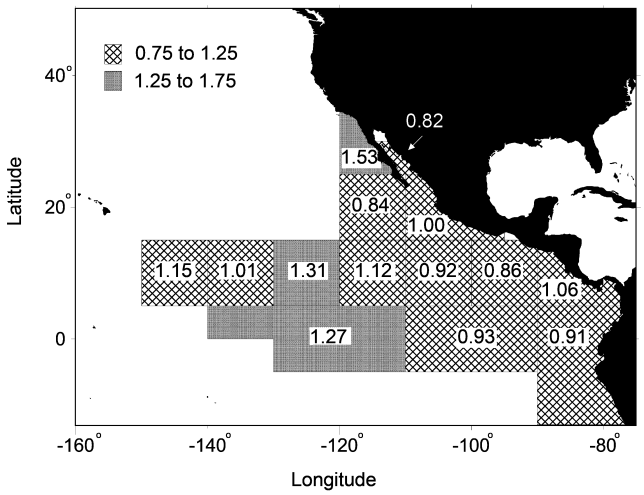


Fig. 11. Geographic distribution of residuals for Cuvier's beaked whale group sizes measured as the ratio: R_{SS}=[Σ(predicted)/Σ(observed)]. R_{SS} values are shown in each stratum. Predictions were based on observed oceanographic data from SWFSC survey cruises in 1986-90 and 1993.

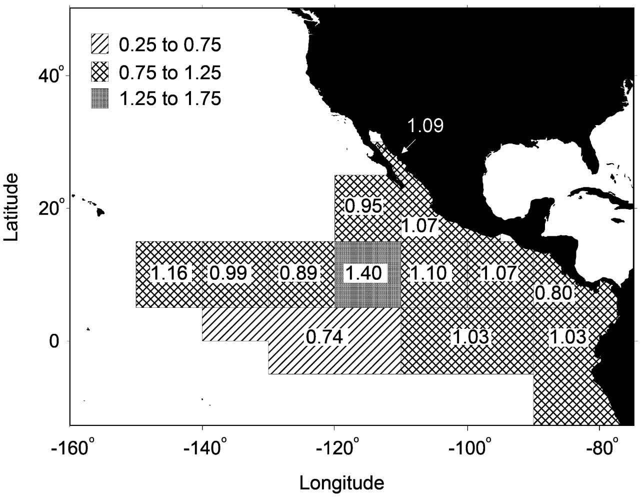


Fig. 12. Geographic distribution of residuals for *Mesoplodon* beaked whale group sizes measured as the ratio: R_{SS}=[Σ(predicted)/Σ(observed)]. R_{SS} values are shown in each stratum. Predictions were based on observed oceanography data from SWFSC survey cruises in 1986-90 and 1993.

models reduced deviance by 7.15% and 15.07% respectively, compared to the null models (Table 3). The Cuvier's beaked whale encounter rate model used only Beaufort sea state and the fixed geographic variables offshore distance and depth (Fig. 5 and Table 3), and the group size model incorporated latitude, Beaufort sea state, thermocline depth, and thermocline strength (Fig. 6 and Table 3). Beaufort sea state entered both Cuvier's models as a linear fit with negative slope, indicating smaller observed encounter rates and group sizes with increasing sea states (Figs 5 and 6). Offshore distance was included in the encounter rate model as a smoothing spline with 2df, showing a minimum around 926km (500 n.miles) and the highest rates further offshore (Fig. 5); the slight increase in encounter rate very close to shore is likely due to the cluster of sightings in the Gulf of California and along the Baja Peninsula (Fig. 3). In addition, the encounter rate model incorporated depth as a smoothing spline with 3df, and implies that Cuvier's beaked whales tended to be sighted most often in waters approximately 2km deep (Fig. 5), corresponding to the offshore edge of the continental slope. In the Cuvier's group size model, linear fits for latitude and thermocline strength suggest smaller groups at higher latitudes and in waters with stronger thermoclines (Fig. 6). Thermocline depth entered the Cuvier's group size model as a smoothing spline with 2df, with larger groups observed over shallower thermoclines, although there were few observations at deeper thermoclines and therefore, the tail of the smooth function should be interpreted with caution (Fig. 6).

Mesoplodon beaked whales were predicted to have a mean density of 2.96 individuals $1{,}000\text{km}^{-2}$ (SD=2.06). The decrease in deviance between the best *Mesoplodon* encounter rate model and the null encounter rate model was 8.39%, whereas the best group size model resulted in an 11.18% decrease in deviance (Table 4). The *Mesoplodon* encounter rate model without latitude resulted in a lower ASPE value than the model with latitude (Table 4). The *Mesoplodon* encounter rate model included Beaufort sea state, depth, SST, salinity and thermocline strength and the group size model contained Beaufort sea state, salinity and thermocline depth. The effects of Beaufort sea state were similar for both *Mesoplodon* models, suggesting that more animals were observed in calmer waters, as expected (Figs

Table 3

Summary of Cuvier's beaked whale encounter rate and group size GAMs for the ETP. Linear fits are represented by 'L1', whereas smoothing splines are represented by 'S#', where # is the associated degrees of freedom. Final selected model is indicated by **bold** font. Percent change in deviance was calculated for final selected model, rebuilt using all years' data, as: ((null deviance - residual deviance)/null deviance) x 100.

			Predictor variables										
Model	Year omitted	% change in deviance	Lat.	Long.	Beaufort	Offshore distance	Depth	Slope	SST	Salinity	Log surface chlorophyll	Thermocline depth	Thermocline strength
Cuvier's encounter rate													
	1986	-	-	L1	L1	S2	S3	-	L1	-	S2	L1	S3
	1987	-	-	-	L1	-	S3	-	-	L1	-	L1	-
	1988	**7.15**	**-**	**-**	**L1**	**S2**	**S3**	**-**	**-**	**-**	**-**	**-**	**-**
	1989	-	-	L1	L1	S2	S3	-	S3	L1	S3	L1	L1
	1990	-	-	L1	L1	S2	S3	-	S3	L1	-	L1	L1
Cuvier's group size													
	1986	**15.07**	**L1**	**-**	**L1**	**-**	**-**	**-**	**-**	**-**	**-**	**S2**	**L1**
	1987	-	-	-	-	S2	-	-	S3	-	-	-	-
	1988	-	-	L1	-	-	-	-	-	-	-	S3	-
	1989	-	-	-	-	S3	-	-	-	S2	-	L1	L1
	1990	-	-	L1	-	-	-	-	-	-	-	-	-

Table 4

Summary of *Mesoplodon* beaked whale encounter rate and group size GAMs for the ETP. Linear fits are represented by 'L1', whereas smoothing splines are represented by 'S#', where # is the associated degrees of freedom. 'NLL' designates model built without latitude or longitude. Final selected model is indicated by **bold** font. Percent change in deviance was calculated for final selected model, rebuilt using all years' data, as: ((null deviance - residual deviance)/null deviance) x 100.

			Predictor variables										
Model	Year omitted	% change in deviance	Lat.	Long.	Beaufort	Offshore distance	Depth	Slope	SST	Salinity	Log surface chlorophyll	Thermocline depth	Thermocline strength
***Mesoplodon* encounter rate**													
	1986	-	L1	-	L1	-	S3	-	S3	S2	S3	-	-
	1987	-	S3	-	L1	-	S3	-	S3	-	-	-	-
	1988	-	-	-	S3	-	S3	-	-	L1	S3	-	S2
	1989	-	L1	-	S3	-	S3	-	S3	S3	-	-	-
	1990	-	S3	-	L1	-	S3	-	S3	-	S3	-	-
	NLL	**8.39**	**-**	**-**	**L1**	**-**	**S3**	**-**	**S3**	**S3**	**-**	**-**	**L1**
***Mesoplodon* group size**													
	1986	-	-	-	L1	-	-	-	-	S2	-	-	-
	1987	**11.18**	**-**	**-**	**L1**	**-**	**-**	**-**	**-**	**L1**	**-**	**S2**	**-**
	1988	-	-	-	L1	S3	-	-	-	-	S3	-	-
	1989	-	-	-	L1	-	-	S3	-	S2	-	-	-
	1990	-	-	-	-	-	-	-	-	S2	-	-	-

7 and 8). *Mesoplodon* encounter rates and group sizes displayed positive associations with sea surface salinity (a smoothing spline with 3df in the encounter rate model and a linear term in the group size model; Figs 7 and 8, respectively), a trend that is likely due to the sightings in the Gulf of California and stretching out from the coast along 10°S (Fig. 4), both of which are regions of relatively high salinity waters (Fiedler, 1992). Similar to the Cuvier's beaked whale encounter rate model, the *Mesoplodon* encounter rate model selected depth as a smoothing spline with 3df, showing a peak at approximately 2km depth, with a secondary increase from about 4km to the maximum depth at which the genus was observed (Fig. 7). The smooth fit of SST to *Mesoplodon* encounter rate suggests a relative minimum in waters of 25°C (Fig. 7). The linear fit for thermocline strength in the *Mesoplodon* encounter rate model, showing higher encounter rates with stronger thermoclines (Fig. 7), is likely produced by the numerous sightings centred near the coast around 10°N in the TSW (Fiedler, 1992). The *Mesoplodon* group size model fits a smoothing spline with 2df to thermocline depth (Fig. 8), indicating larger groups in waters with 60m deep thermoclines, which is close to the mean value for the study area (Table 2).

The error analysis showed that the mean differences (averaged across all years and all segments used to build the models) between predicted and observed values of encounter rate and group size were zero for both Cuvier's and *Mesoplodon* beaked whales. The SDs in the differences between predicted and observed values were similar for both genera, with $SD(\Delta ER) \simeq 0.085$ and $SD(\Delta SS) \simeq 1.00$. In addition, for both Cuvier's and *Mesoplodon* beaked whales, when pooling all segments used to build the models, the ratios between the pooled predicted encounter rates and the pooled observed encounter rates (R_{ER}) equalled unity out to at least two decimal places, and R_{SS} was also equal to 1.0. The geographically stratified analysis of residuals in the encounter rate for Cuvier's (Fig. 9) and *Mesoplodon* (Fig. 10) beaked whales showed that, in approximately half of the strata, the ratio of pooled predicted to observed values, R_{ER}, was close to unity (1.0 ± 0.25). Values of R_{ER} departed considerably from unity in some strata (from 0.38 to 2.06 for

Cuvier's beaked whale), but the distribution of residuals did not show much geographic pattern. Residuals in the group size estimates for pooled strata, R_{SS} , were near unity (1.0 ± 0.25) for the majority of strata for both species (Figs 11 and 12), and again there was little geographic pattern to the residuals.

DISCUSSION

The beaked whale models presented here are the first to estimate population densities. In addition, they were based upon a large study area with a substantial amount of survey effort over the abyssal plain. Although it is clear that some species of ziphiid whales are associated with continental slopes or topographic features such as seamounts, ridges and canyons in some areas, this association pattern may not hold for all species throughout their distributions. The ETP Cuvier's and *Mesoplodon* beaked whale analyses appear to expand the definition of what is considered suitable beaked whale habitat. Beaked whales in the ETP were sighted in considerably deeper waters than in any of the other studies discussed. In addition, beaked whales in the ETP were found in waters that ranged from well-mixed to stratified. High population densities of beaked whales were predicted in the southern Gulf of California, in coastal waters and in the equatorial cold tongue of the ETP study area, but beaked whales did not appear to be narrowly restricted to the highly productive waters typified by these coastal and upwelling systems and they were not limited to the continental slope and shelf waters, which is where the majority of beaked whale field studies have been conducted (Ferguson, 2005).

These analyses have shown that the extent and location of the study area can considerably affect the interpretation of results from beaked whale habitat studies. Two additional aspects of such studies with power to influence the results are the type of analytical method chosen for the analysis and the scale of the analysis. The analytical methods used in previous studies to examine beaked whale habitats ranged from hypothesis tests such as the Kruskall-Wallis one-way ANOVA (Davis *et al.*, 1998), Kolmogorov-Smirnov (Hooker *et al.*, 2002; Wimmer, 2003) and Chi-square (Cañadas *et al.*, 2002; Wimmer, 2003; MacLeod *et al.*, 2004) goodness of fit tests and the Wilcoxin signed rank test (Waring *et al.*, 2001), which determine whether a given environmental variable is related to beaked whale distribution patterns, to multivariate tools such as GLMs (Waring *et al.*, 2001; Cañadas *et al.*, 2002; Hamazaki, 2002), GAMs (MacLeod and Zuur, 2005), ENFA (MacLeod, 2005) and CART (MacLeod and Zuur, 2005), which can quantify the magnitude of the effect (i.e. how much a given environmental variable affects beaked whale distribution).

Generalised additive models were chosen for the ETP analysis because of their flexibility. One weakness of GAMs, however, is that they are data-intensive. All species of *Mesoplodon* sighted in the ETP study area were modelled together because small sample sizes of individual species (n=17 *M. peruvianus*, n=11 *M. densirostris*) prevented construction of separate models and there was a need to include a large number (n=78) of 'unidentified *Mesoplodon* beaked whales'. Grouping all *Mesoplodon* spp. together undoubtedly obscured the species-specific differences in habitat (Pitman and Lynn, 2001), thereby lowering explanatory or predictive power in the final models; this could potentially account for the low percent explained deviance in the GAMs. Other potential reasons for the relatively small reduction in deviance between the null and best GAMs exist: (1) the signal-to-noise ratio in the environment might be too high relative to the number of observations in the data set; (2) the environmental predictors used to build the models might not be strongly associated with beaked whale habitat; or (3) the error distributions specified for the encounter rate and group size models might be inappropriate. Addressing these questions and the issue of understanding and enumerating the various sources of uncertainty in the models are active areas of research. Nevertheless, as noted above, a dominant strength of GAMs is their flexibility, which manifested itself in the error analyses for Cuvier's and *Mesoplodon* encounter rates and group sizes. The error analyses found small differences between observed and predicted values, and found that the ratios of pooled predicted to pooled observed values were close to 1.0. Furthermore, in the geographically stratified residual analyses, predictions in the majority of the strata for both genera and both response variables (encounter rate and group size) were within 25% of the observed values and there was no evidence of a spatial pattern.

The spatial or temporal scale at which data are analysed in habitat studies is likely to have profound effects on the results. Ecological mechanisms affecting beaked whale distribution may be scale-specific and there may be a hierarchy of such mechanisms operating on different scales that influence where beaked whales are found. The slope of the seafloor is one variable that may be especially sensitive to the spatial scale of the analysis. For example, the steep wall of a submarine canyon is a feature that would appear in analyses conducted on scales of a few hundred meters to a few kilometres, but it would almost disappear in larger scale analyses such as that described for the ETP. Such small-scale features are likely to be important to the success of localised beaked whale foraging. Nevertheless, the animals may incorporate information from larger spatial scales, as exemplified by upwelling regions such as the Costa Rica Dome, California Current, Peru Current and equatorial cold tongue, to guide them to larger regions of enhanced foraging success. In the time domain, small scale patches with high densities of prey are likely to be temporally dynamic; therefore, instantaneous information about the present environment is most relevant for determining foraging success at a specific point and place in time. To arrive in the general vicinity of patches with high densities of prey, however, successful predators might have processed time-lagged information, averaging their foraging experiences in different regions over the past week, month, year, or decade, for example. Time lags are particularly important when proxies such as chlorophyll data are used to indicate beaked whale habitat because it is not the primary producers themselves, but the squid and mesopelageic fishes several trophic levels higher, that beaked whales eat and time lapses before energy and nutrients from the primary producers climb the food chain up to cetacean prey species (Jaquet, 1996). It is noteworthy that the ETP analysis found no associations between beaked whales and surface chlorophyll concentration, which is a biological variable commonly used as a proxy for cetacean prey. Ultimately ecologists are left with a conundrum: to determine which environmental predictors define beaked whale habitat it is important to know the scale at which to observe the ecology of the system; simultaneously, to determine the scale at which to observe the ecology of the system, it is important to know which environmental predictors define beaked whale habitat. This suggests that an iterative approach may be the best way to increase ecological understanding of these animals.

Understanding of ziphiid whale habitats may be enhanced by conducting more surveys in a greater diversity of potential habitats, thoughtfully selecting the types of environmental data collected and the scale at which they are collected, investigating the effects of scale on habitat models and explicitly accounting for detection bias (e.g. by incorporating Beaufort sea state and availability bias correction) in occurrence, density and abundance models.

RESEARCH RECOMMENDATIONS

(1) Accurate habitat models for ziphiid whales will not be possible unless surveys cover a broader range of potential habitats, including deep waters over the abyssal plains. Surveys that only cover the suspected habitat, such as slope waters, cannot be used to confirm this habitat preference.
(2) Oceanographic data should be collected in conjunction with cetacean surveys to improve the data available for habitat modelling. There is a particular need to identify the prey of ziphiid whales and to develop methods to measure their abundance.
(3) To reconcile apparent differences in results among different habitat studies, the influences of observation scale (including total survey area and the sample size used to partition that area into smaller units), detection bias (the effect of sea state on apparent density) and suite of predictor variables, must be addressed.

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How big is a beaked whale? A review of body length and sexual size dimorphism in the family Ziphiidae

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ABSTRACT

There is a paucity of data on the family Ziphiidae (the beaked whales) and even basic information, such as body length, is not available for some species. This review examines published records of body length for 20 of the 21 currently recognised species of beaked whale. It considers maximum, median and modal body lengths, where possible by sex. For Cuvier's, Blainville's and Gray's beaked whales, modal and median lengths were much shorter than the maximum reported lengths; this may reflect misidentification of the largest animals. Although males of some species reached a greater maximum size, there was only a significant difference in median body length for three species: True's beaked whale; the strap-toothed whale; and Gervais' beaked whale. In all three cases, females had a significantly larger median length. The apparent lack of consistent sexual dimorphism in body length suggests that, while male beaked whales use their tusks as weapons to compete aggressively for access to receptive females, large size does not give a competitive advantage. This may be a result of the way the sexually dimorphic tusks are used during combat. The only exception to this rule appears to be the northern bottlenose whale, for which males consistently reach greater body lengths than the largest females. Male-male combat appears to take a different form in this species.

KEYWORDS: MORPHOMETRICS; REPRODUCTION; AGGRESSION; BEAKED WHALES; STRANDINGS; WHALING

INTRODUCTION

Beaked whales (Family Ziphiidae; Order Cetacea) remain the least well understood family of cetaceans and for several species even basic biological information, such as pigmentation and external morphology, is unknown (e.g. the spade-toothed whale, *Mesoplodon traversii*, is only known from three partial skeletons – van Helden *et al.*, 2002). Even for better known species, information on biological characters, such as body length, is often dispersed throughout the scientific literature with only small sample sizes. This review brings together and analyses as much of the information on body length in beaked whales as could be found. Previous studies examining body length have generally only considered the maximum body length (e.g. Mead, 1984; 1989a; b) although Mead (1984) tried to obtain additional data on, for example, mean length at sexual maturity. For most species, modal and median lengths have not previously been reported.

Body size is an important component of an animal's biology, influencing a variety of aspects of its life including metabolic requirements, prey size selection, locomotory abilities, habitat utilisation and competitive abilities (Guyton, 1974; Andersson, 1982; Cox *et al.*, 1982; Warner and Hall, 1988; Miquelle *et al.*, 1992; Poole, 1994; Whitehead, 1994; Olsson and Shine, 1996; Radloff and Du Toit, 2004). Understanding the body length (both as a characteristic of a species in its own right and as a proxy for mass) reached by the majority of individuals within a species, rather than just the largest, is thus important. This review addresses two questions: (1) what are the maximum and most common body lengths for each beaked whale species and (2) are beaked whale species sexually dimorphic in terms of body length?

MATERIALS AND METHODS

Beaked whale data from published accounts of stranded animals, strandings databases and personal communications from other researchers have been collated into a global database (see D'Amico *et al.*, 2003 for details). In almost all cases, the measurements came from stranded animals with the associated potential problems this brings (see 'Results and Discussion'). The only exceptions to this were measurements of pygmy beaked whales (*M. peruvianus*) made from aerial photographs (Pitman and Lynn, 2001). Data from whaling records have been considered separately. Any records where the species identification was known to be uncertain, or where the body length was estimated or approximated, were not included in this analysis.

Due to problems associated with identifying beaked whales to the species level, even for experienced observers (e.g. see Dalebout *et al.*, 1998), it is not possible to rule out that some animals that have been misidentified may have been included in this analysis; if so, this could cause a bias when investigating body length. To address this potential problem, three different parameters were examined: maximum recorded body length; modal body length (for 10cm increments); and median body length. Maximum body length reflects the largest length a species reaches, but could be biased if large animals have been misidentified. When the maximum reported length was more than 0.5m larger than the next largest measurement, then both are given (Table 1). Modal body length shows the most common body length of stranded animals and is not greatly affected by erroneous identifications of larger animals. Modal lengths were identified only when there was a clear increase in the frequency of records at specific body lengths. However, the mode could potentially be affected by misidentifications of a significant proportion of the animals in a specific length class. In addition, when sample sizes are relatively small, the mode may be influenced by a small number of individuals within one length class that may not be representative of the species as a whole.

Three approaches have been adopted to investigate whether sexual dimorphism in body length occurs in beaked whales. Firstly, the percentage body length of the largest female to the largest male was calculated. Secondly, where there were a sufficient number of individuals, the Mann-Whitney test was used to compare the median length of males and females of the same species; the null hypothesis investigated was that the sexes did not differ in median body length. However, in this case it must be recognised that males and females may have similar median lengths but still be sexually dimorphic. For example, in sperm whales (*Physeter macrocephalus*) only the oldest males reach the greatest lengths (Rice, 1989) and therefore, a difference between males and females is only noticeable in the largest size classes. To try to account for this a third approach was used in which the frequency distributions were divided into length classes and the frequency of occurrence of males and females in the largest were compared using a chi square test. In this case, the null hypothesis was that there was no difference in the frequency of occurrence of males and females in the largest recorded length classes. The length classes chosen varied by species (0.4-1.0m) and the number of classes varied from two to three to ensure that the expected values were sufficiently large to avoid violating the requirements of the statistical test used.

RESULTS AND DISCUSSION

The body lengths of 805 individual beaked whales from 20 of the 21 currently recognised species (Table 1) were found (excluding the whaling data). The final species, the spade-toothed beaked whale, is only known from skeletal remains, so no length data are available (van Helden *et al.*, 2002). Sufficient (n>10) data to estimate a modal length were available for 17 species. An investigation of possible sexual dimorphism was possible for 15 species although the length class approach could only be used for seven due to sample size considerations.

Maximum and modal lengths

Strandings data

The longest beaked whale species is Baird's beaked whale (*Berardius bairdii*), with a maximum reliably reported length of 11.0m in our database (original source: Marine Mammal Strandings Database, National Museum of Science, Tokyo, Japan). The aptly-named pygmy beaked whale is the smallest beaked whale species, with a maximum reported length of 3.9m (Pitman and Lynn, 2001).

Modal lengths were notably smaller than the maximum reported lengths for all species. This suggests that the maximum length may not be the most suitable parameter to use when investigating how body size interacts with and influences other aspects of a species' biology. For some species the differences between maximum and modal length was sufficiently large to suggest that there are biases or errors within the data (Fig. 1). The greatest difference was in Hubbs' beaked whale (*M. carlhubbsi*), where the primary mode was at 2.5-2.6m, compared with a maximum reported length of 5.32m (Mead *et al.*, 1988). Mead (1984) estimated the average length at birth of Hubbs' beaked whale to be 2.5m, and the mode around this body length may represent a high proportion of juveniles in the relatively small total number of animals for the species (n=26). Secondary modes occurred at 4.9-5.0m and 5.3-5.4m and may be more reflective of typical adult length.

There were also large differences between maximum and modal length of northern bottlenose whales (*Hyperoodon ampullatus*), Blainville's beaked whale (*M. densirostris*), Gray's beaked whale (*M. grayi*) and Cuvier's beaked whales (*Ziphius cavirostris*). In these cases, these differences may represent a small number of unusually large individuals in the dataset, or errors in species identification or measurements. For example, Heyning (1989) considered all Cuvier's beaked whales measuring over 7m to represent misidentified individuals. The vast majority (93%) of Cuvier's beaked whale records examined here were under 7m and all larger records come from higher latitudes where Cuvier's beaked whale is sympatric with other larger beaked whale species (*Hyperoodon* and *Berardius* spp.), with which it could be confused. Heyning (1989) noted that the largest unquestionable length recorded for a stranded Cuvier's beaked whales is only 6.93m. Therefore, it is unlikely that the actual maximum length of Cuvier's beaked whales is greater than 7m (and see below).

Similarly, based on field observations of this species, the author does not consider Blainville's beaked whales to reach the maximum reported length (6.4m – Rosario-Delestre *et al.*, 1999) with any regularity. In fact, since the next largest record is only 4.725m (Ross, 1984) and the modal length classes are 3.9-4.0m and 4.3-4.4m (Fig. 1), it appears that this species rarely, if ever, reaches lengths over 4.8m and that most individuals are under 4.5m in length. The maximum reported length of Shepherd's beaked whale, *Tasmacetus shepherdi*, may also represent an error of some kind (Mead, 1989c), as at 9.1m this animal was 30% larger than the next longest individual. However, there are insufficient data to calculate a modal or median length for comparison. For the remaining animals, all measurements of body length that could be calculated were sufficiently similar to suggest they all may be an accurate indicator of actual values for the species.

Comparison with whaling data (see Table 2)

BAIRD'S BEAKED WHALE

Balcomb (1989) presented data on lengths of Baird's beaked whales caught off Japan (n=26) and California (n=14). He reported two modes for the California fishery, one at 10.6-10.7m and one at 10.9-11.0m. He also reported a maximum length of 11.2m off California and one of 'about 12.8m' for Japan. The latter animal was reported as being 42ft in Nishiwaki and Oguro (1971). The next largest they reported was 39ft (11.9m). A more recent extensive study by Kasuya *et al.* (1997) for whales off Japan examined by biologists reported that males ranged from 7.8-10.7m (n=88) and females from 8.2-11.1m (n=47). For both sexes, there was a single modal peak at 10.2-10.3m. The modal lengths of animals reported by Kasuya *et al.* (1997) were slightly larger than the modal lengths of the stranded animals analysed in this study (10.0-10.1m). The Kasuya *et al.* (1997) study incorporated the Japanese data from Balcomb (1989) and three stranded animals and does not make direct reference to the 'about 12.8m' animal. However, the authors noted that measurements taken by industry personnel may differ in methods and not be strictly comparable. This may explain the generally larger values in the Omura *et al.* (1955) study.

NORTHERN BOTTLENOSED WHALE

Data from whaling on body length are also available for northern bottlenose whales caught by Faroese and Norwegian whalers. Bloch *et al.* (1996) compared the lengths of 109 northern bottlenose whales caught off the Faroes by whaling vessels and in the local shore-based drive fishery. In the offshore fishery, males ranged from 3.41-11.16m and females from 3.41-8.47m, while animals caught in the drive fishery ranged from 3.98-8.81m for males and 3.66-7.62m for females. As Bloch *et al.* (1996) noted, the lengths for both sexes are thus greater for animals shot offshore than taken in the drive fishery. The authors suggest that this reflects a tendency for larger, more experienced

Table 1

Minimum, maximum, modal and median body lengths for each beaked whale species, with comparison of body length between males and females of each species, where possible. Whaling data are not included (see text and tables). For modal length, '-' indicates that there was no clear modal value (see Fig. 1). Median values were only calculated for sample sizes greater than five. Percentage column refers to the percentage of largest female to largest male. Where there is doubt about the largest size, the value in parentheses is for the next largest individual of that sex. *W* and *P* refer to Mann-Whitney test for comparing median values for males and females. Significantly different median values are indicated in bold with an asterisk after the letter denoting the larger sex. Records of Cuvier's beaked whale over 7m are considered unreliable (Heyning, 1989) and a 9.1m record of Shepherd's beaked whale possibly inaccurate (Mead, 1989c). All lengths are in metres.

	All individuals (incl. unknown sex)					Females				Males				Females vs. males			Larger sex		
Species	Min.	Max.	Mode	Median	*n*	Max.	Mode	Median	*n*	Max.	Mode	Median	*n*	%	*W*	*P*	Max.	Mode	Median
B. arnuxii	6.00	9.30	-	-	7	-	-	-	-	-	-	-	-	-	-	-	-	-	-
B. bairdii	5.80	11.00	10.0-10.1	10.0	22	11.00	-	10.50	10	11.00	-	9.60	5	100	84.5	0.624	M=F	-	F
H. ampullatus	2.70	10.00	6.1-6.2; 6.4-6.5	6.40	116	8.60	-	6.51	23	10.00 (8.70)	6.5-6.6	6.40	32	86 (99)	667.0	0.701	M	-	F
H. planifrons	4.63	7.50	-	6.50	15	7.45	-	6.50	5	6.93	-	6.425	5	108	29.0	0.834	F	-	F
M. pacificus	2.91	6.50	-	-	4	6.00	-	-	2	-	-	-	-	-	-	-	-	-	-
M. bidens	2.59	5.50	4.5-4.6; 4.8-4.9	4.50	95	5.10	4.8-4.9	4.49	40	5.50 (4.95)	4.7-4.8	4.50	34	93 (103)	1505.5	0.957	M	F	M
M. bowdoini	2.30	4.41	3.9-4.0; 4.2-4.3	4.03	15	4.36	-	4.075	6	4.41	-	4.22	7	100	36.0	0.3922	M	-	M
M. carlhubbsi	2.49	5.32	2.5-2.6	4.76	26	5.32	-	4.85	12	5.30	-	4.72	13	100	157.5	0.956	F	-	F
M. densirostris	2.30	6.40 (4.725)	3.9-4.0; 4.3-4.4	4.15	63	4.71	3.9-4.0 4.5-4.6	4.135	34	6.4 (4.725)	4.3-4.4; 4.6-4.7	4.10	26	74 (100)	1028.0	0.899	M (M)	M	F
M. europaeus	2.17	4.85	4.2-4.3	4.23	72	4.85	4.5-4.6	4.32	35	4.57	-	4.09	29	106	1318.0	0.015	F	-	**F***
M. ginkgodens	3.29	5.28	4.7-5.0	4.64	16	4.90	4.8-4.9	4.45	9	5.10	-	4.86	4	96	54.0	0.190	M	-	F
M. grayi	2.42	5.64 (4.80)	4.7-4.8	4.56	14	4.80	-	4.67	5	5.64 (4.80)	-	4.50	8	85 (100)	42.0	0.340	M (M=F)	-	F
M. hectori	1.90	4.34	3.7-3.8	3.425	16	4.15	-	4.00	3	4.34	3.7-3.8	3.73	8	96	19.0	0.918	M	-	F
M. layardii	4.55	6.25	-	5.37	18	6.25	-	5.765	8	5.84	-	5.145	10	107	104.0	0.0145	F	-	**F***
M. mirus	2.25	5.40	4.8-4.9	4.76	34	5.26	4.8-4.9	4.87	13	5.335	-	4.56	21	99	304.5	0.0067	M	-	**F***
M. perrini	2.10	4.43	-	-	5	4.43	-	-	1	3.90	-	-	3	114	-	-	F	-	-
M. peruvianus	1.59	3.90	3.2-3.3; 3.6-3.7; 3.7-3.8	3.385	15	3.90	-	-	3	3.72	-	-	4	105	-	-	F	-	-
M. traversii	-	-	-	-	-	-	-	-	-	-	-	-	-		-	-	-	-	-
M. stejnegeri	2.13	5.74	5.0-5.1	4.83	99	5.44	4.8-4.9	4.88	45	5.74	4.6-4.7; 5.0-5.1	4.76	48	95	2152.5	0.776	M	M	F
T. shepherdi	4.80	9.10 (6.97)	-	-	5	6.60	-	-	1	9.1 (6.97)	-	-	2	73 (95)	-	-	M	-	-
Z. cavirostris	2.50	9.80 (9.10)	5.4-5.5	5.50	148	8.50 (7.60)	5.5-5.6	5.47	53	9.80 (7.92)	5.5-5.6	5.50	53	87 (96)	2830.5	0.977	M (M)	M=F	M

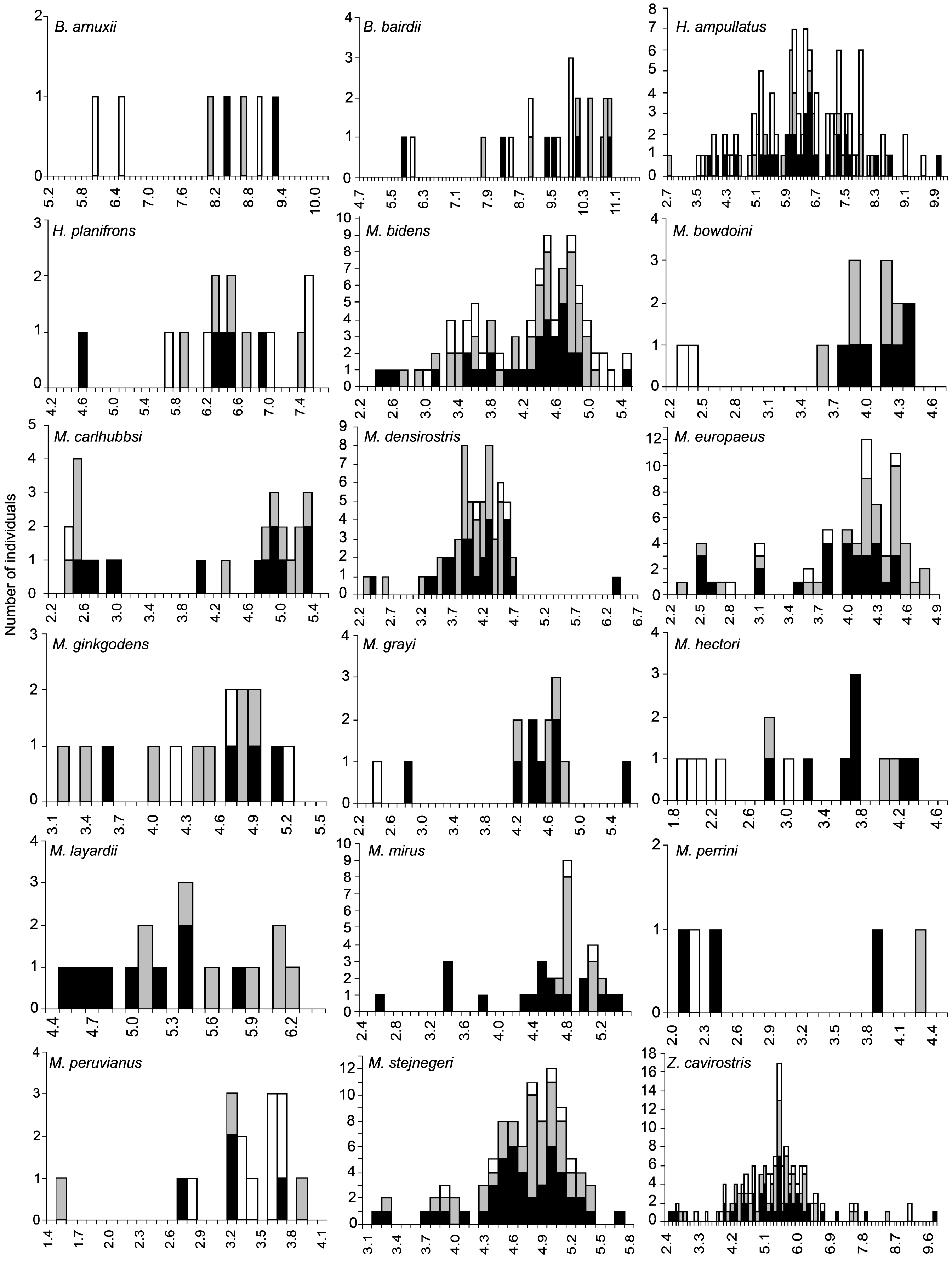

Fig. 1. Frequency distribution at 0.1m intervals of body length of stranded individuals of 17 beaked whale species (with the exception of photogrammetric measurements of pygmy beaked whales from Pitman and Lynn, 2001). Black bars – male, grey bars – female, white bars – sex unknown.

Table 2

Comparison of information from whaling data and strandings data.

	Males (M)			Females (F)			F:M
	Max (m)	Mode (m)	*n*	Max (m)	Mode (m)	*n*	% maximum
B. bairdii							
Strandings (this paper)	11.00	10.0-10.1[1]	5	11.00	10.0-10.1[1]	10	100
Whaling (Kasuya *et al.*, 1997) - 1975; 1985-88	10.70	10.2-10.3	88	11.10	10.2-10.3	47	104
Whaling (Nishiwaki and Oguro, 1971)* - 1965-69	11.88	10.1-10.4	400	12.80	10.1-10.4	301	108
Whaling (Omura *et al.*, 1955)* - 1948-52	11.60	10.4-10.7	631	12.20	10.7-11	293	105
H. ampullatus							
Strandings (this paper)	10.00(8.70)[2]	6.5-6.6	32	8.60	Not given	23	86(99)[2]
Whaling (Bloch *et al.*,1996 - offshore)	11.16	7-7.5[3]	20	8.47	6.5-7[3]	22	76
Whaling (Bloch *et al.*,1996 - drive)	8.81	7-7.5[3]	36	7.62	6.5-7[3]	31	86
Whaling (Benjaminsen, 1972)*	10.97		5,043[3]	8.80		5,043[4]	80
Z. cavirostris							
Strandings (this paper)	9.80(7.92)[2]	5.5-5.6	53	8.50 (7.60)[2]	5.5-5.6	53	87(96)[2]
Whaling (Nishiwaki and Oguro, 1972)* - 1965-70	7.00	6.10	132	6.70	6.10	57	96
Whaling (Omura *et al.*, 1955)* - 1948-52	6.71	5.50	51	7.00	5.80	34	104

*Original measurements in feet. [1]Given the small sample size, the mode is for all individuals (including those of unknown sex) combined. [2]The values in parenthesis are for the second largest animals (see text). In the case of the northern bottlenose whale, the length of the largest whale in the strandings sample is not inconsistent with the whaling data. However, for Cuvier's beaked whale, the maximum lengths for both sexes for the strandings data are considerably larger than those for the whaling data. [3]It was not possible from the paper to determine the precise number of males and females so the total for all animals of known sex is given here.

animals to stay further from shore, particularly when accompanied by small calves. If true, this may also result in a bias in the body lengths of stranded animals. For males included in the database, the range (3.7-10m) was less than that for the 'offshore' Faroese fishery but greater than for the Faroese drive fishery. The same was not true for adult females (2.7-8.6m), although this can be assigned to the one extremely small individual and one female that was somewhat larger than others in this study (Fig. 1). For all the Faroese data combined, males had a modal length of 7-7.5m and females 6.5-7m. Data for the same species are also available for animals taken by Norwegian whalers in the North Atlantic Ocean (Benjaminsen, 1972). For all five main whaling areas (Labrador, Iceland, Svalbard, Andenes and Møre) there is a clear modal length for females at 7.3m with a maximum length rarely over 8.5m. For males, the modal length varied from 7.3m to 8.3m across these areas, with a maximum length rarely greater than 9.7m. These data from whaling compare to a modal length of 6.5-6.6m for males and 6.4-6.5m overall obtained in this study, and maximum lengths of 8.6m for females and 10m for males.

CUVIER'S BEAKED WHALE

Nishiwaki and Oguro (1972) reported that the modal length of Cuvier's beaked whales of each sex (132 males and 57 females) caught by whalers in the North Pacific was 20ft (6.1m). The maximum lengths for males and females were 23ft (7.0m) and 22ft (6.7m) respectively. In this study, the modal values were 5.5-5.6m for each sex and 5.4-5.5m for the species as a whole, whilst the maximum values of over 7.0m were probably a result of misidentification according to Heyning (1989; see above).

Limitations of whaling and strandings data

For both strandings and whaling data, the primary question is how representative are the data of the true 'population'? In the context of this study, the 'population' refers to the species as a whole. The examples above illustrate the potential strengths and limitations of both data sources.

In general, whalers will tend to select for larger individuals in the 'available' population. Exceptions to this might be expected if, for example (1) the animals are at low densities such that being overly selective is uneconomic or (2) the species being taken is not the primary target of the fishery (i.e. it is largely opportunistic). Bias may also occur if there is geographical and/or temporal segregation in the whale population by sex- and/or age-class and the whaling operations are limited in their geographical and/or temporal scope. The overall length distribution in a population may also vary due to exploitation. Given the propensity for selecting for large individuals, one might expect that the maximum length data are more 'representative' of the species than the modal lengths. Where whaling data are only recorded by whalers, there may be either deliberate inaccuracies due to possible commercial pressures to exaggerate length, e.g. due to higher bonus payments for large animals or to comply with length regulations or accidental inaccuracies due to carelessness, or different methods of measuring or stretching as the animal is hauled from the sea. It should be noted that no length limits were in force for the beaked whale operations considered here and that for many of the samples, measurements were taken by biologists (e.g. Kasuya *et al.*, 1997). Sample sizes are usually larger than for strandings data.

Strandings data also have a number of limitations and potential biases. For example, the likelihood of stranding may be indirectly length-related due to (1) differential survival by age-class, (2) geographical and/or temporal segregation by age-class in relation to prevailing currents and/or the efficiency/existence of the stranding scheme or (3) the nature of the stranding (e.g. mass stranding, individual stranding, stranding due to illness, stranding due to bycatch etc.). As a result, certain length classes may be over- or under-represented in databases constructed from strandings records. Inaccuracies may also occur due to lack of experience in identifying species, taking standard measurements or the decomposition state of the carcase.

For the three species where a comparison can be made animals killed by whalers tended to be larger than animals that stranded, as reflected in the modal lengths. This tends to suggest that the whalers were selecting for larger animals although it may also reflect under-representation of larger animals in the strandings record. Further investigation is required to determine which, if either, most accurately reflects the true modal lengths of the species concerned.

Such considerations must also be borne in mind in the discussion of sexual dimorphism below.

Sexual dimorphism

Strandings data

The maximum recorded length of females ranged from 74-114% of that for males (Table 1).

In six species, the percentage was less than 95% (i.e. females were smaller). However, as noted above, there are doubts over the maximum lengths recorded for males for four species (Blainville's, Gray's, Shepherd's and Cuvier's beaked whales); this is also true for the female Cuvier's beaked whale (see above). If for each of these, the largest female (or second largest for Cuvier's) is compared to the second largest male, the values all become between 95% and 103% (Table 1). For one of the remaining two species, Sowerby's beaked whale (*M. bidens*), the largest known sex animal is a male of 5.5m (there is also one of unknown sex at the same length), then three animals of unknown sex between 5.2-5.3m, followed by four of the next six animals being females (the other two being of unknown sex). For the final species (northern bottlenosed whale), there were three animals of unknown sex after the largest 10m male before the next known sex animals which were a male and a female, both around 8.6-8.7m. Mead (1989a) reported that the largest recorded male is 9.8m and the largest female 8.7m; similar to the results given here.

In five species, the percentage was 105% or greater (i.e. females were larger). However, for three of these species, the sample sizes were very small (5 or less, for either sex). For the remaining two species, Gervais' beaked whale (*M. europaeus*) and strap-toothed whale (*M. layardii*), there were several females larger than the largest male (Fig. 1). Therefore, from the strandings data, these are the only two species for which there is a clear and unequivocal difference between males and females in terms of the maximum size reached; in both of these species females reach a consistently larger size than males.

Turning to median values, there were only three species for which there were significant differences between the sexes and in each case, the females had the significantly larger value (Table 1). These species were Gervais' beaked whale, the strap-toothed whale and True's beaked whale (*M. mirus*).

In terms of the comparison of body lengths in the largest length classes, in only one of the seven species where this could be examined was there a significant difference (Table 3). For Gervais' beaked whales, males and females were found to differ significantly in their frequency of occurrence in the three longest classes (χ^2 = 6.136, d.f.=2, *p*=0.047). In the longest class (4.4-4.8m) there were more females (14) and fewer males (4) than expected. The overall results concur with the examination of median values, i.e. there was no evidence of sexual dimorphism in length for most species and where there was evidence, females were larger in those three species. Of course, it should be remembered that this analysis does not take into account the animals of unknown sex which may be important in some cases (e.g. see the comments on northern bottlenosed and Sowerby's beaked whales above).

Therefore, Gervais' beaked whale is the only species in our database that shows a consistent sexual dimorphism in body length, when unknown sex animals are excluded for the three measures investigated. For this species, females were found to have a clear difference in maximum length, a greater median length and a greater occurrence in the largest size category.

Table 3

Comparison of male and female beaked whales in largest length categories for seven beaked whale species. In only one species, *M. europaeus*, was there a significant difference between the number of males and females in these categories. In this case, there were more females than expected in the largest length category.

Length categories (m)	No. males	No. females	d.f.	χ^2	Probability
H. ampullatus					
6.0-7.0	14	6			
7.0-8.0	5	7			
>8.0	3	2	2	2.498	0.287
M. bidens					
4.0-4.4	4	4			
4.4-4.8	15	8			
>4.8	5	13	2	5.668	0.059
M. mirus					
4.6-5.0	9	9			
5.0-5.4	5	4	1	0.018	0.892
M. europaeus					
3.6-3.99	4	2			
4.0-4.39	14	11			
4.4-4.8	4	14	2	6.136	**0.047**
M. densirostris					
3.6-3.99	4	8			
4.0-4.39	10	12			
4.4-4.8	5	9	2	0.601	0.741
M. stejnegeri					
4.4-4.8	18	8			
4.8-5.2	15	22			
>5.3	6	6	2	5.059	0.080
Z. cavirostris					
5.0-5.5	15	11			
5.5-6.0	11	10			
>6.0	6	7	2	0.475	0.788

However, questions of sample size for some analyses, the treatment of animals of unknown sex and the possible biases arising out of strandings data referred to above must temper any conclusions that can be drawn.

Comparison with whaling data (see Table 2)

For Baird's beaked whales, whaling data appear to suggest little sexual dimorphism but with a tendency to slightly larger females. In the study by Nishiwaki and Oguro (1971) for catches between 1965 and 1969, they found similar modal lengths in the catches for each sex (33-34ft; 10.1-10.4m) although noting that 'roughly, larger lengths are of females'. The largest animal was a 42ft female (12.8m) while the largest male was 39ft (11.9m) – the female to male percentage is thus 108%. In the more recent Kasuya *et al.* (1997) study, the largest animal was an 11.1m female while the largest male was 10.7m – the percentage was thus 104%. Kasuya *et al.* (1997) also calculated growth curves and estimated asymptotic lengths of 10.45m for females 10.10m for males. An earlier study by Omura *et al.* (1955) for catches between 1948-52 also fitted this pattern (the percentage was 105%). The lengths for both sexes were generally larger than the later studies – this may reflect a real difference or different measuring methods.

For Cuvier's beaked whale, Heyning (1989) reported that whaling data indicated no significant difference in length between the sexes. The studies of Omura *et al.* (1955) and Nishiwaki and Oguro (1972), show the percentage of female maximum length to male maximum length vary from 96-104% and similar modes for both sexes (although lower in the earlier period).

The above whaling data are thus consistent with a general hypothesis of either a lack of sexual dimorphism in body length or with females being slightly larger in the family Ziphiidae.

Within the literature there is one species, the northern bottlenose whale, that has consistently been reported as being sexually dimorphic in terms of length (e.g. see Mead, 1989a). For the Faroese operations (*n*=109), males had both a larger modal body length than females and a larger maximum size (11.16m for males and 8.47m for females – Bloch *et al.*, 1996). For Norwegian operations, males had a greater modal length than females in all but one area and a greater maximum length in all areas (Benjaminsen, 1972). However, in the Faroese (Bloch *et al.*, 1996, fig. 6) and Norwegian whaling data (Benjaminsen, 1972, fig. 6), it is a relatively small proportion of males that are larger than the largest females. While the difference in maximum size was also apparent from the strandings data, there were only two known males that exceeded the maximum size of females (although an additional three animals of unknown sex exceeded this length) and there were no significant differences between males and females in terms of body length. The strandings data are more similar to the Faroese drive fishery data, supporting the view of Bloch *et al.* (1996) that the larger animals may be more common offshore.

The evidence therefore supports the view of limited sexual dimorphism with the largest males being somewhat larger than the largest females. Bloch *et al.* (1996), noted a change in the shape (from bulbous to flat) and colour (from grey to white) of the melon of males with length that may be related to sexual and physical maturity. Of 32 males examined, changes in head shape and colour began to be noticed between 6.54-6.92m, becoming more pronounced between 6.94-7.55m (grey but flat) and becoming fully white and flat from 8.33m. Benjaminson (1972) reported from a histological analysis that males became mature at 24-25ft (*n*=32) or about 7.3-7.6m. Thus it may be that males reach sexual maturity at around this length and physical and/or social maturity at around 8.3m. Differences in the length at attainment of sexual and physical and/or social maturity are not uncommon in cetaceans (e.g. sperm whales; Best *et al.*, 1984).

CONCLUSION

Whilst recognising the limitations of the available data as discussed above, I believe that the analyses presented here are sufficient to propose that, as a family, most beaked whale species show either no sexual dimorphism in body length or have slightly larger females (e.g. Gervais' beaked whale). The only exception to this within the family Ziphiidae (for which there are sufficient data) appears to be for the northern bottlenose whale where a small proportion of males may be consistently larger than the largest adult females. Whether the same is true for the closely-related southern bottlenose whale (*H. planifrons*) is currently unclear due to a lack of sufficient data (*n*=5 for each sex).

In many marine mammal species where males compete aggressively for females, males are often significantly larger (e.g. elephant seals, *Mirounga* species – Modig, 1996; sperm whales – Rice, 1989). This is also the case for many terrestrial mammals, including those that use teeth as weapons (e.g. anthropoid primates – Leutenegger and Kelly, 1977). In most beaked whale species, males are thought to compete for females and use their tusks as weapons (Heyning, 1984). While a lack of sexual dimorphism in body length or having larger females might be thought unexpected, in the case of beaked whales, such dimorphism would only be expected if having a larger body size gave a competitive advantage (Ralls, 1976; Brownell and Ralls, 1986).

Scarring patterns indicate that in most species of beaked whale, males fight by making a series of passes at their opponents, analogous to humans jousting on horseback (MacLeod, 2002). The turning radius of a cetacean is related to its body length, thus when all else is equal a longer animal will have a greater turning radius (Fish, 2002; Fish *et al.*, 2003). As a result, shorter males might have an advantage since they can mount a new run at a larger opponent before the opponent can turn fully and be ready to re-engage. In this context, therefore, the selection pressure would be for shorter and more manoeuvrable males, all other things being equal. Other selective pressure may then either maintain a similar length between males and females, as seems to be the case in most beaked whales, or even be for larger females, as is apparently the case in Gervais' beaked whale.

Bottlenose whales appear to be the only beaked whale species that fight in a different manner, with males using their foreheads and their large underlying maxillary crests as battering rams (Gowans and Rendell, 1999). While repeated turning and re-engaging is also employed during such fights, it may be that body size also gives some competitive advantage. This could explain why the northern bottlenose whale is the only species for which there is evidence that some adult males are consistently larger than adult females.

In summary, this paper presents the first published modal and median values of body length for many beaked whale species. Analysis of these data revealed no clear evidence of sexual dimorphism in body length in most species for which there are sufficient data. Where clear sexual dimorphism in body length was found, this might be related to the nature of competition among males.

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[1] *http://www.iwdg.ie/strandings.*

[2] *http://svrsh1.kahaku.go.jp/database_english/frameset.html.*

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Key areas for beaked whales worldwide

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ABSTRACT

Beaked whales represent one of the groups of large mammals about which relatively little is still known. Many beaked whale species are known of from less than 50 records and one is known only from three partial skeletons. Beaked whales are subject to bycatch by fisheries, ingestion of plastics, accumulation of biocontaminants and adverse effects from anthropogenic noise. However, the inadequacy of knowledge about their biology means that developing effective conservation strategies can be difficult. We suggest that beaked whale conservation can best be achieved if, in consort with other approaches, key areas for beaked whales around the world can be identified. We suggest five criteria that can be used to identify key areas for beaked whales where, if human impacts were to occur, they would cause conservation concerns for beaked whales at a regional or global level. Using these criteria, 23 beaked whale key areas have been identified, based on existing knowledge contained in a database created from published and unpublished beaked whale records. In total, these 23 key areas covered the locations of almost 70% of all the beaked whale records in the database. However, for the identification of key areas to provide a useful tool for beaked whale conservation it is important not only that they are identified but that appropriate assessment and mitigation strategies are implemented within them to ensure that beaked whales are not adversely affected by human activities.

KEYWORDS: CONSERVATION; DISTRIBUTION; MONITORING; ATLANTIC OCEAN; BEAKED WHALES; HABITAT; GEOGRAPHY

INTRODUCTION

Less is known about many extant beaked whale species than about some mammals that became extinct thousands of years ago (e.g. mammoths) and most of what is currently known about the 21 species recognised by the International Whaling Commission (IWC) has been gleaned from beached animals, sometimes discovered far from the deep-water habitats in which they lived (Heyning, 1989; Mead, 1989a; MacLeod, 2000). Although beaked whales occur in all major seas and both hemispheres, some species are known from fewer than 50 published records worldwide (see MacLeod *et al.*, 2006). One species, the spade-toothed whale (*Mesoplodon traversii*), is known from only three partial skeletons (van Helden *et al.*, 2002) and several others have yet to be seen alive (Dalebout *et al.*, 2002). Directed studies of live animals are few (MacLeod, 2000) although that number has grown in recent years (e.g. Claridge and Balcomb, 1995; Whitehead *et al.*, 1997b; MacLeod and Claridge, 1999; Williams *et al.*, 1999; MacLeod and Zuur, 2005).

The lack of knowledge about beaked whales is primarily due to their oceanic distribution and their preferences for deep waters beyond the shelf edges where relatively few research vessels venture (MacLeod, 2000). However, there are also problems in identifying animals to species level at sea and even stranded animals can be mis-identified (Dalebout *et al.*, 1998; 2002; 2003; Barlow *et al.*, 2006). Beaked whales can be affected by human activities and known or suspected mortalities occur as a result of whaling, bycatch in fisheries for other marine species, ingestion of plastics, accumulation of biocontaminants and anthropogenic noise (e.g. Mitchell, 1977; Knap and Jickells, 1983; Simmonds and Lopez-Jurado, 1991; Law *et al.*, 1997; Frantzis, 1998; Poncelet *et al.*, 2000; Balcomb and Claridge, 2001; Waring *et al.*, 2002; Cox *et al.*, 2006).

The premise of this paper is that beaked whale conservation can best be achieved in the short-term if the traditional approaches for conserving large mammals (such as calculating and monitoring population sizes, investigating habitat requirements, monitoring habitat loss, fragmentability and connectivity, increasing community awareness, identifying potential threats and implementing appropriate mitigation measures) are focussed on identified areas of regional or global importance for beaked whales. Such ‘key’ areas are identified using relatively simple criteria and available knowledge. The list and the criteria can be revised in the future to take these advances in knowledge into account.

Despite this approach, it is important to stress that, particularly given current knowledge, it should not be taken to mean that beaked whales do not occur outside these areas. All beaked whales may be affected by anthropogenic activities and appropriate mitigation measures must be taken both within and outside key areas.

IDENTIFICATION OF KEY AREAS FOR BEAKED WHALES

Central to the identification of ‘key’ areas is a clear definition of what comprises a key area and how it is identified. In this paper, a key area is defined as any area where, if anthropogenic impacts were to occur, they might give rise to conservation concerns at a regional or global level. Four criteria are used to identify such key areas:

(A) areas where one or more beaked whale species have been regularly recorded at sea;
(B) areas used during movements between two or more key areas identified in criterion (A);
(C) areas with a high diversity of beaked whales where ‘high’ means records of more than 25% of all beaked whale species and at least 50% of all beaked whale genera;
(D) relatively small areas that cover a large portion, or all, of the known range of a species or isolated population.

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A fifth criterion (E), that can be used in additional support in the context of the above four, is for areas where beaked whales have already been affected by human impacts and where conservation concerns may exist or where they may be more vulnerable to future anthropogenic interference.

CONSTRUCTION OF A DATABASE TO IDENTIFY KEY AREAS FOR BEAKED WHALES

A global database containing 4,857 beaked whale records was constructed using all information available about sighting, bycatch, whaling, strandings and other types of records that, within the data, contained specific locations (Fig. 1). The data sources varied widely in content and included reviewed literature, published and unpublished reports, public and private datasets and on-going research. These records were collated into a single GIS database with a standardised format and were plotted using *ArcView 3.2* GIS software. Each record was examined for transcription errors (e.g. sightings on land), suspect information within specific records (e.g. where measurements or estimated size greatly exceeded published maximums for species or taxonomic group) and possible mis-identification (e.g. more refined identification than photographs could confirm). Problem records were isolated and original sources consulted for resolution. Resolution included assignment of lowest certain taxonomic level (e.g. *Mesoplodon* sp.) or removal from the database. After these quality control procedures, data were re-plotted and sorted using the criteria presented above to identify and define key areas for ziphiids. Finally, literature, unpublished reports and manuscripts that contained information (but not precise locations) about beaked whales' distribution were examined. These often described more general areas, for example around specific bathymetric features or in specific geographic areas.

While primary literature was the preferred resource, 'grey' literature often contained valuable and relevant information about distribution and occurrence. Accuracy of records found in grey literature was validated wherever possible. The entire process formed the basis for the key areas for beaked whales identified below. However, it should be noted that there was clearly a patchy distribution of data available for this study, which reflects inadequate sighting or survey effort in some places (e.g. throughout the west coast of Africa) and this limited the power of this study to identify all key areas for beaked whales that may exist.

PROPOSED KEY AREAS FOR BEAKED WHALES

Twenty-three areas were identified from the collated data and a review of published literature (Table 1; Fig. 2). In the summaries below, the limits were set based on the available data, details of which are provided afterwards. The number of records refers to the number for each key area which are currently held in the beaked whale database, rather than the total of all records in a key area. Where additional information has also been used, the appropriate references are provided.

1. The Atlantic Frontier

Limits: From the Scottish coasts between the southern Outer Hebrides, to Shetland, north to 62.30°N and the Faeroe Islands and as far west as 59.85°W (based on 120 records).

Three species of beaked whale from three genera have been recorded in this area (Table 2) and there are two specific areas which are important for beaked whales (Table 1). These are the region around the northern end of the Rockall Trough, particularly around the eastern end of the Wyville-Thompson Ridge and the Faeroe-Shetland Channel (Pollock *et al.*, 2000). Migration, at least for northern bottlenose whales (*Hyperoodon ampullatus*), is thought to occur through this area in late summer/early autumn and in late winter/early spring (MacLeod *et al.*, 2004b). However, this has not been confirmed by tracking the movements of individual animals.

The Atlantic Frontier therefore qualifies as a key area under criterion (A) and potentially (B).

2. The Bay of Biscay

Limits: From the European coast, out to a line between 48.53°N, 4.77°W-43.53°N, 5.84°W based on 131 records[1].

The Bay of Biscay has records for all six species of beaked whales (from three genera) that regularly occur in the North Atlantic, making it an area of high beaked whale

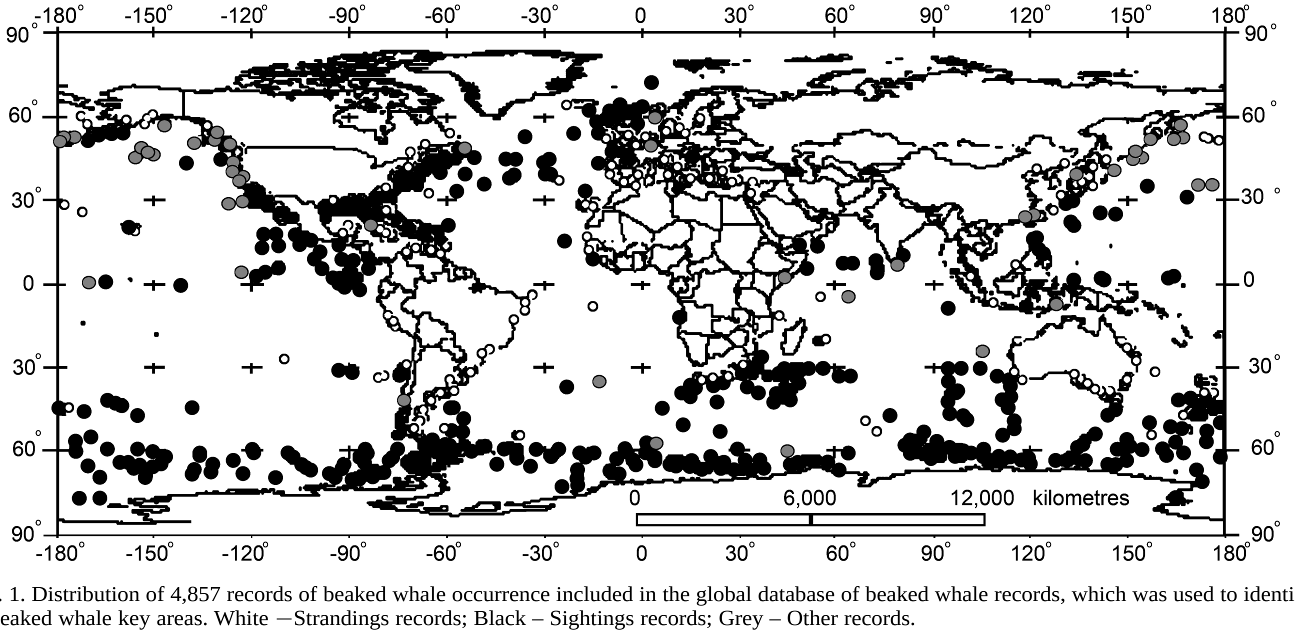

Fig. 1. Distribution of 4,857 records of beaked whale occurrence included in the global database of beaked whale records, which was used to identify beaked whale key areas. White —Strandings records; Black – Sightings records; Grey – Other records.

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[1] With additional information from D. Walker (Organisation Cetacea), and A. Williams (Biscay Dolphin Research Programme).

Table 1

Known key areas for beaked whales identified using the five criteria outlined in this study; (+) means criterion is probably met.

Known beaked whale key areas	Criteria					Specific areas known to be of importance in key area (criteria)	References
	A	B	C	D	E		
1. Atlantic Frontier	+	(+)				Northern end of the Rockall Trough (particularly around the eastern end of the Wyville-Thompson Ridge, approximately 59.4°N, 007.9°W (A), and the Faeroes-Shetland Channel, centred at approximately 61.7°N, 003.0°W (A, B).	Pollock *et al.* (2000); Weir (2000); MacLeod *et al.* (2004a).
2. Bay of Biscay	+		+			Southern Bay of Biscay around Cap Breton Canyon and along continental shelf edge (A).	Barriety (1962); Castells and Mayo (1992); Mead *et al.* (1988); Gannier *et al.* (2000); Poncelet *et al.* (2000); Williams *et al.* (1999); A. Williams (Biscay Dolphin Research Project) (pers. comm.); D. Walker (Organisation Cetacea) (pers. comm.).
3. Genoa Canyon	+						Azzellino *et al.* (2001).
4. Eastern Alboran Sea	+	(+)		(+)		Triangle between 36.34°N, 003.00°W, 36.51°N 002.52°W and 36.26°N, 002.79°W (A).	Sagarminaga and Cañadas (2003).
5. Western Greece	+				+	Ionian Sea (A) Kyperissiakos Gulf (E).	Politi *et al.* (1992); Politi *et al.* (1994); Pulcini and Angradi (1994); Frantzis (1998).
6. Azores	+		+			Around the island of Pico (A).	Richard (1936); Bruyns (1968); Clarke (1981); Reiner *et al.* (1993); Steiner *et al.* (1998); Leal *et al.* (2001).
7. Canaries	+		+		+	South of La Gomera (A), south-west of Tenerife 28.3°N, 16.9°W; 28.1°N, 16.8°W (A), Fuertaventura and Lanzarote (E).	Mead *et al.* (1988); Vonk and Martin (1988; 1989); Martin *et al.* (1990); Simmonds and Lopez-Jurado (1991); Montero and Martin (1992); Politi *et al.* (1992); Carrillo and Lopez-Jurado (1998); Carrillo and Martin (1999); Ritter and Brederlau (1999); Evans *et al.* (2001); Vidal Martin (pers. comm.).
8. The Gully, Nova Scotia	+			+		43.5-44.5°N, 058.5-060.0°W (A, D).	Whitehead *et al.* (1997a); Gowans *et al.* (2000); Dalebout *et al.* (2001); Hooker *et al.* (2002a); Hooker *et al.* (2002b).
9. North-eastern North America continental shelf margins	+		+		+		Ulmer (1941); Backus and Schevill (1961); Mitchell and Kozicki (1975); Leatherwood *et al.* (1976); CETAP (1982); Bane and Zullo (1980); Mead *et al.* (1988); Mead (1989a); Lien and Barry (1990); Waring *et al.* (1993); Nawojchik (1994); Tove (1995); Waring *et al.* (2001); Waring *et al.* (2002).
10. Northern Bahamas	+				+	Little Abaco Canyon, centred at approximately 26.6°N, 076.9°W (A), southern edge of Little Bahama Bank from 26.6°N 078.5°W to 25.9°N 077.3°W (E).	Claridge and Balcomb (1995); Balcomb and Claridge (2001); Evans *et al.* (2001); MacLeod *et al.* (2004b); MacLeod and Zuur (in press).
11. Northern Gulf of Mexico continental shelf margins	+					25.9-27.6°N and 96.0-90.8°W (A), an area bordered by the following co-ordinates: 26.6°N, 90.0°W; 27.0°N, 90.4°W; 27.7°N, 90.6°W; 28.0°N, 90.6°W; 29.2°N, 87.4°W 28.9°N, 87.1°W; 27.7°N, 88.0°W (A).	Jefferson and Shiro (1997); NOAA CD-ROM NODC-72.
12. Puerto Rico and the Virgin Islands	+						Varona (1964); Varona (1970); Erdman *et al.* (1973); Varona (1985); Mattila and Clapham (1989); Mignucci-Giannoni (1989); Mignucci-Giannoni (1996); Mignucci-Giannoni (1998); Rosario-Delestre *et al.* (1999); Roden and Mullin (2000); Swartz and Burks (2000); Swartz *et al.* (2001).
13. Californian shelf margins, USA	+		+	+		Waters 32.9-36.6°N (D).	Hubbs (1946); Houck (1958); Roest (1964); Mitchell (1968); Sullivan and Houck (1979); Dohl *et al.* (1981, 1983); Mead *et al.* (1988); Hill and Barlow (1992); Lynn and Reiss (1992); Carretta and Forney (1993); Forney (1994); Barlow and Gerrodette (1996); Carretta *et al.* (2000, 2002); Dalebout *et al.* (2002).
14. Hawaii	+						Shallenberger (1981); Mobley *et al.* (2000); Baird (pers. comm.).
15. Eastern Tropical Pacific	+		+	+		From the central and northern South American coast west to approximately 135.0°W (A, C). From the South American coast westward around 30°S (A).	Vidal *et al.* (1993); Dawson *et al.* (1998); Perrin *et al.* (1999); Pitman and Lynn (2001); H. Whitehead (Dalhousie University) (pers. comm.).
16. Galapagos	+					1.6°N-1.3°S, 92.6-89.9°W.	Robinson *et al.* (1983); Palacios (1996); Perrin *et al.* (1999); Daniel Palacios, unpublished data); H. Whitehead (Dalhousie University) (pers. comm.)
17. Falkland Is./Tierra del Fuego	+		+				Goodall (1978); White *et al.* (2002).

Cont.

Table 1 cont.

Known beaked whale key areas	Criteria					Specific areas known to be of importance in key area (criteria)	References
	A	B	C	D	E		
18. Indian Ocean around South Africa	+		+	(+)			Talbot (1960); Ross (1969); Gambell *et al.* (1975); Nemoto *et al.* (1980); Ross (1984); Findlay *et al.* (1992).
19. Japan	+	+	+			34.0-36.0° N, 139.0-143.0°E (designated Area I); 37.0-38.0°N, 141.0-144.0°E (designated Area II); off the coast of Hokkaido, particularly around 44.0°N, 145.0°E. Areas I (particularly in an area centred at approximately 34.5°N, 139.5°E) II and VII.	Omura *et al.* (1955); Nishiwaki and Oguro (1971); Nishiwaki and Oguro (1972); Nishiwaki and Kamiya (1958); Nishiwaki *et al.* (1972); Miyashita (1986); Miyazaki *et al.* (1987); Kasuya and Miyashita (1997); Marine Mammal Stranding Database (National Museum of Science, Tokyo, Japan).
20. Southwestern Australia	+						Gales *et al.* (2002); IWC (unpublished data).
21. Tasmania and southeastern Australia			+	+			Hale (1931); Guiler (1966); Guiler (1967); Aitken (1971); McCann (1975); Gianuca and Castello (1976); Dixon (1980); Lewis (1988); Mead (1989a); Dixon and Frigo (1995).
22. New Zealand	+		+	(+)		To the east and south of South Island (A).	Oliver (1937); Gaskin (1971); McCann (1975); Gianuca and Castello (1976); Fordyce *et al.* (1979); Mead and Baker (1987); Mead (1989a, b); Baker and van Helden (1999); Baker (2001); van Helden *et al.* (2002); IWC (unpublished data).
23. Southern Ocean and Antarctic waters	+					Antarctic Peninsula from 65.2°S, 066.2°W-70.3°N, 094.6°W (A).	Gianuca and Castello (1976); Miyazaki and Kato (1988); Kasamatsu *et al.* (1993); Bowles *et al.* (1994); Ponganis *et al.* (1995); Hobson and Martin (1996); Pankow *et al.* (1997); Pierpoint *et al.* (1997); Leaper and Scheidat (1998); Branch and Butterworth (2001).

diversity (Table 2). The Bay of Biscay also has had repeated sightings of beaked whales at sea, including Cuvier's beaked whales (*Ziphius cavirostris*), northern bottlenose whales and various *Mesoplodon* species (e.g. Castells and Mayo, 1992; Williams *et al.*, 1999; D. Walker, pers. comm.). Sightings of Cuvier's beaked whales are particularly common around the Cap Breton Canyon, where Williams and colleagues have been studying them and have seen some individuals on a number of occasions (A. Williams, pers. comm.). Preliminary research also suggests that *Mesoplodon* species are distributed throughout the deep waters areas of this key area (A. Williams, pers. comm.).

The Bay of Biscay therefore qualifies as a key area under criteria (A) and (C).

3. The Genoa Canyon

Limits: From 43.51°N, 9.68°E, due west to the French coast and due north to the Italian coast (based on 75 records).

The Genoa Canyon lies in the north west of the Ligurian Sea, an area of the Mediterranean between Italy, France and northern Sardinia. Although Cuvier's beaked whale is the only species that has been recorded in this area, it is one of the few areas in the Mediterranean where they are regularly sighted (e.g. D'Amico *et al.*, 2001; Azzellino *et al.*, 2004).

The Genoa Canyon therefore qualifies as a key area under criterion (A).

4. Eastern Alboran Sea

Limits: A pentagon with corners at 36.52°N, 3.10°W; 35.98°N, 3.10°W; 36.08°N, 2.87°W; 36.52°N, 2.13°W and 36.47°N, 2.80°W (based on 27 records and Sagarminaga and Cañadas, 2003[2]).

Sagarminaga and Cañadas (2003) have recorded many sightings of Cuvier's beaked whales in the eastern Alboran Sea, as well as occasional sightings of northern bottlenose whales. The area represents an area of regular sightings of beaked whales and is the only known area outside the North Atlantic Ocean where northern bottlenose whales have been observed. In addition, its position between the North Atlantic and the main body of the Mediterranean means that it is potentially important for exchange of genetic information between these two areas, although it is not currently known whether such mixing occurs.

The eastern Alboran Sea therefore qualifies as a key area under criterion (A) and possibly (B) and (D).

5. Western Greece

Limits: Waters west of Greece and southern Albania from 39.92-36.41°N (based on 29 records and additional information from Frantzis, 1998).

Cuvier's beaked whale is the only beaked whale species regularly recorded in the eastern Mediterranean and it is regularly sighted in the deep waters around western Greece (e.g. Politi *et al.*, 1992; 1994; Pulcini and Angradi, 1994). In addition, an 'atypical' mass stranding of 13 Cuvier's beaked whales occurred in this region in 1996. This stranding has been linked to the use of naval sonars in the local area (Frantzis, 1998; Cox *et al.*, 2006).

Western Greece therefore qualifies as a key area under criterion (A) augmented by (E).

6. The Azores

Limits: 35.50-43.75°N, 23.50-32.25°W (based on 10 records and additional information from Clarke, 1981; Reiner *et al.*, 1993; Steiner *et al.*, 1998 and Leal *et al.*, 2004).

The Azores are situated on the border between the colder waters of the northern North Atlantic and the warmer waters of the Gulf Stream. These productive waters have a relatively high abundance and diversity of cetaceans in general and beaked whales in particular. Six beaked whale species from three genera have been recorded in the Azores (Table 2). The Azores also has a very high number of beaked

[2] With additional information from A. Cañadas (SMRU).

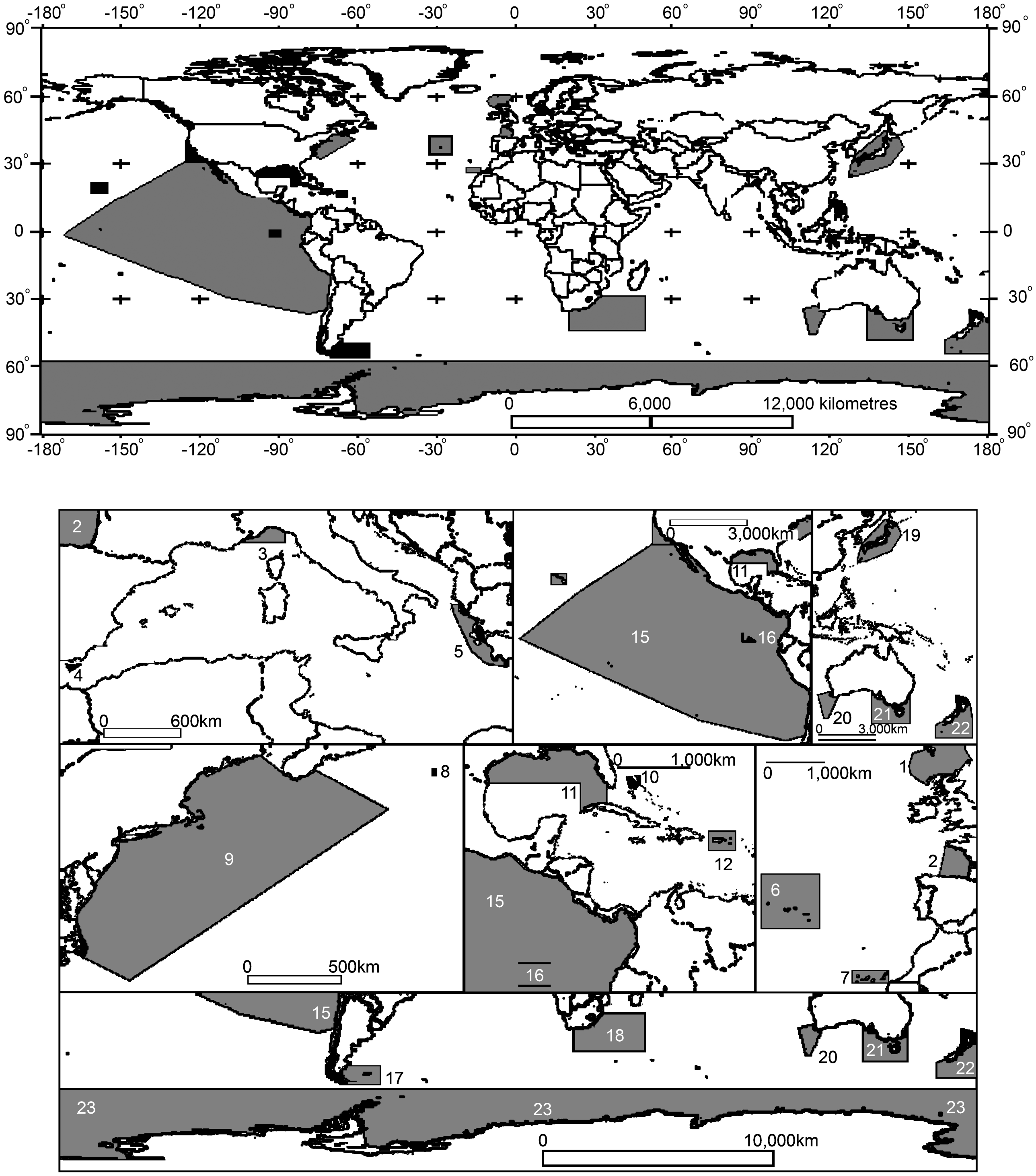

Fig. 2. A. (top) Global distribution of the 23 areas of the world which fulfil one or more of the criteria used to define a beaked whale key area based on the currently available information. B. (bottom) Detailed views of each key area by oceanic region. (1) The Atlantic Frontier; (2) The Bay of Biscay; (3) The Gulf of Genoa; (4) The eastern Alboran Sea; (5) Western Greece; (6) The Azores; (7) The Canaries; (8) The Gully, Nova Scotia; (9) North-eastern North American continental shelf margins; (10) Northern Bahamas; (11) Northern Gulf of Mexico continental shelf margins; (12) Puerto Rico and the Virgin Islands; (13) The Californian shelf margins; (14) Hawaii; (15) The eastern tropical Pacific; (16) The Galapagos; (17) Tierra del Fuego and the Falkland Islands; (18) The Indian Ocean around South Africa; (19) Japan; (20) South-western Australia; (21) Tasmania and south-eastern Australia; (22) New Zealand; (23) Southern Ocean and Antarctica.

whale sightings relative to other parts of the world, for example Leal *et al.* (2004) reported 147 sightings of beaked whales made between June-October 2000. Of particular interest are regular sightings of northern bottlenose whales and Sowerby's beaked whales (*M. bidens*), which may represent the southernmost populations of these species in the eastern Atlantic.

The Azores therefore qualify as a key area under criteria (A) and (C).

7. The Canaries

Limits: 27.50-29.50°N, 13.25-18.75°W (based on 60 records).

Five beaked whale species from three genera have been recorded in the Canaries (Table 2). Blainville's beaked whales (*M. densirostris*) and Cuvier's beaked whales have been repeatedly sighted (e.g. Carrillo and Lopez-Jurado, 1998; Ritter and Brederlau, 1999; F. Ritter, pers. comm.) and there have been at least five atypical mass strandings involving four beaked whale species in the Canaries; several of these have been linked to military activities in the local area (e.g. Simmonds and Lopez-Jurado, 1991; Brownell *et al.*, 2006; Cox *et al.*, 2006; V. Martin, pers. comm.).

The Canaries therefore qualify as a key area under criteria (A) and (C) augmented by (E).

8. The Gully, Nova Scotia

Limits: 43.7-44.0°N, 58.8-59.0°W (based on 950 records).

The Gully, a submarine canyon off Nova Scotia, is home to a resident population of approximately 133 northern bottlenose whales (95% CI: 111-166, Gowans *et al.*, 2000). The Gully population is the most intensively studied population of beaked whales in the world and is thought to be relatively isolated and genetically separate from its nearest neighbouring populations of this species (Dalebout *et al.*, 2001). The Gully covers a relatively small area, around 200km² that is the core area for this population and where it would be extremely vulnerable to anthropogenic impacts. Individuals may remain resident in the Gully for an average of 20 days at a time and continually enter and leave it (Hooker *et al.*, 2002b). The population may have previously been depleted by whaling activity and thus may be vulnerable to further disturbances (Gowans *et al.*, 2000). This population is classified as 'endangered' by the Committee on the Status of Endangered Wildlife in Canada (COSEWIC 2002[3]) and the Gully is classified as a 'Pilot Marine Protected Area' (Hooker *et al.*, 2002a).

The Gully therefore qualifies as a key area under criteria (A) and (D).

9. Northeastern North America Continental Shelf Margins

Limits: From Cape Hatteras to southern Nova Scotia and east to the start of the Abyssal plain (based on 498 records and additional information from Waring *et al.* (2001).

This key area covers an area between the edge of the continental shelf and the start of the abyssal plains from Cape Hatteras, North Carolina to the vicinity to Nova Scotia, Canada and has a high diversity of beaked whale species (six species from three genera, Table 2). Sightings data suggests that beaked whales have a widespread distribution along the shelf edge and over the continental slope and rise, with some emphasis on Cape Hatteras and Georges Bank offshore areas (CeTAP, 1982; Waring *et al.*, 1993; Waring *et al.*, 2001). For *Mesoplodon* species and Cuvier's beaked whale, the minimum population of these two combined is estimated to be 2,419 (CV=0.34, Waring *et al.*, 2002). Past human impacts on beaked whales in this area include bycatch in pelagic driftnet fisheries and Waring *et al.* (2002) estimated annual fisheries-related mortalities at 4-60 individuals during 1989-1998.

This region therefore qualifies as a key area under criteria (A) and (C) augmented by (E).

10. Northern Bahamas

Limits: Northwest and northeast Providence Channels from a line between Freeport and northern Andros east to northern Eleuthra and southern Abaco and along the eastern side of Little Bahama Bank to 26.75°N, 76.80°W (based on 47 records).

There are two areas which are known to be of particular importance for beaked whales: (1) around Little Abaco Canyon (centred at approximately 26.6°N, 76.9°W), where Blainville's beaked whales are regularly seen, including repeated sightings of the same individuals within and between years (Claridge and Balcomb, 1995; MacLeod *et al.*, 2004a; MacLeod and Zuur, 2005); and (2) south and west of the southern tip of Great Abaco. Blainville's and Cuvier's beaked whales have been recorded in this latter area (Claridge and Balcomb, 1995) and both species were involved in a mass stranding incident there in March 2000; military sonar in the Northeast and Northwest Providence Channels has been implicated (Claridge and Balcomb, 1995; Balcomb and Claridge, 2001; Cox *et al.*, 2006).

The northern Bahamas therefore qualifies as a key region under criterion (A) augmented by (E).

11. Northern Gulf of Mexico Continental Shelf Margins

Limits: North of a line from the US/Mexican border, east to 84.87°W, south to the western end of Cuba, east to 81.34°W and North to Florida (based on 170 records).

Four different species of beaked whales (Table 2) and a relatively high number of sightings have been recorded in the Gulf of Mexico area (NOAA). Most of these sightings occurred in two adjacent areas (Table 1).

This region therefore qualifies as a key region under criterion (A).

12. Puerto Rico and the Virgin Islands

Limits: 16.75-19.50°N, 64.0-67.75°W (based on 69 records and Erdman *et al.*, 1973; Mattila and Clapham, 1989; Mignucci-Giannoni, 1998 and Swartz *et al.*, 2002).

Three species of beaked whales have been recorded around Puerto Rico and the Virgin Islands (Table 2). Cuvier's beaked whales have been regularly sighted in the deep waters surrounding the Puerto Rico Bank, with most to the south of the Bank especially around the deep waters leading into and including the Anegada Passage (Erdman *et al.*, 1973; Mattila and Clapham, 1989; Mignucci-Giannoni, 1998; Swartz *et al.*, 2002). *Mesoplodon* species have been sighted to the south of the Puerto Rico Bank, to the north of St. Croix including the Anegada and Mona Passages and to the east towards the Dominican Republic and Cuba (Varona, 1964; 1970; 1985; Mattila and Clapham, 1989; Roden and Mullin, 2000; Swartz *et al.*, 2002).

This region therefore qualifies as a key area under criterion (A).

13. Californian Shelf Margins

Limits: From the Californian coast, west to 125.0°W (based on 70 records and Dohl *et al.*, 1983; Hill and Barlow, 1992; Carretta and Forney, 1993; Forney, 1994; Barlow and Gerrodette, 1996; Carretta *et al.*, 2000; 2002).

Perrin's beaked whale (*M. perrini*), one of the least known species of beaked whale is currently only known from Californian waters. It was first described in 2002 and is only known of from a total of five stranded animals and one possible sighting at sea ranging from 32.9°-36.6°N (Dalebout *et al.*, 2002). The known range is thus restricted to a small area off the Californian coast. Six other species of beaked whales have been recorded in Californian waters (Table 2). Several of these species, including Baird's beaked whales, Blainville's beaked whales, *Mesoplodon* species and Cuvier's beaked whales have been observed repeatedly in Californian waters, particularly in the southern California Bight. The latter species is probably the most numerous, with an estimated population of over 4,000 (Carretta *et al.*, 2000; 2002).

[3] *www.cosewic.gc.ca/eng/sct1/searchform_e.cfm.*

Table 2

Diversity of beaked whale species in each beaked whale key area. Key areas highlighted in bold are those classified as high diversity in terms of number of species (more than 25% of known species) and genera (at least 50% of all known genera).

Known beaked whale key areas (in order of diversity)	**Total number of beaked whale species**	**Total number of beaked whale genera**	Arnoux's beaked whale	Baird's beaked whale	Northern bottlenose whale	Southern bottlenose whale	Longman's beaked whale	Andrews' beaked whale	Sowerby's beaked whale	Hubbs' beaked whale	Blainville's beaked whale	Gervais' beaked whale	Ginkgo-toothed beaked whale	Gray's beaked whale	Hector's beaked whale	Layard's beaked whale	True's beaked whale	Perrin's beaked whale	Pygmy beaked whale	Spade-toothed beaked whale	Stejneger's beaked whale	Shepherd's beaked whale	Cuvier's beaked whale	References
22. New Zealand	**11**	**5**	+			+		+			+			+	+	+			+	+		+	+	Oliver (1937); Gianuca and Castello (1976); McCann (1975); Fordyce *et al.* (1979); Mead and Baker (1987); Mead (1989a, b); Baker and van Helden (1999); Baker (2001); van Helden *et al.* (2002).
21. Tasmania and South-eastern Australia	**10**	**4**	+			+		+			+		+	+	+	+	+						+	Hale, (1931); Guiler (1966); Guiler (1967); Aitken (1971); McCann (1975); Dixon (1980); Dixon and Frigo (1995); Mead (1989a); Baker (2001).
15. Eastern Tropical Pacific	**9**	**5**		+		+	+				+		+						+	+		+	+	Brownell *et al.* (1976); Mitchell (1968); Clarke *et al.* (1978); Vidal *et al.* (1993); Palacois (1996); Aguayo *et al.* (1998); Pitman *et al.* (1999); Pitman and Lynn, (2001); van Helden *et al.* (2002).
18. Indian Ocean around South Africa	**9**	**5**	+			+	+				+			+	+	+	+						+	McCann and Talbot (1963); Ross (1969); Gambell *et al.* (1975); Ross (1984); Dalebout *et al.* (2003).
17. Falkland Islands and Tierra del Fuego	**8**	**5**	+			+								+	+	+					+	+	+	Gianuca and Castello (1976); Goodall (1978); Mead and Baker (1987); Baker (2001).
13. Californian Shelf Margins	**7**	**3**		+						+	+		+					+					+	Hubbs (1946); Houck (1958); Roest (1964); Mitchell (1968); Mead *et al.* (1988); Lynn and Reiss (1992); Dalebout *et al.* (2002).
19. Japan	**7**	**4**		+			+			+	+		+								+		+	Omura *et al.* (1955); Nishiwaki and Kamiya (1958); Nishiwaki and Oguro (1972); Nishiwaki *et al.* (1972); Miyazaki *et al.* (1987); Marine Mammal Stranding Database (National Museum of Science, Tokyo, Japan).
2. Bay of Biscay	**6**	**3**			+				+		+	+					+						+	Barriety, (1962); Mead *et al.* (1988); Gannier *et al.* (2000); Poncelet *et al.* (2000); Williams (pers. comm.).
6. Azores	**6**	**3**			+				+		+	+					+						+	Reiner *et al.* (1993); Steiner *et al.* (1998).
9. North-eastern North American Shelf Margins	**6**	**3**			+				+		+	+					+						+	Ulmer, (1941); Mitchell and Kozicki (1975); Bane and Zullo (1980); Mead (1989a); Lien and Barry (1990); Nawojchik (1994).
20. South-western Australia	5	2																						Dixon (1980); Baker (2001); Gales *et al.* (2002); IWC (unpublished data).
23. Southern Oceans and Antarctic Waters	5	4	+			+								+		+							+	Gianuca and Castello (1976); Miyazaki and Kato (1988); Hobson and Martin (1996); IWC (unpublished data).
7. Canaries	5	3			+						+	+					+						+	Vonk and Martel (1988, (1989); Martin *et al.* (1990); Montero and Martin (1992); Ritter and Breberlau (1999).
11. Northern Gulf of Mexico Shelf Margins	4	2							+		+	+											+	Jefferson and Shiro (1997).
16. Galapagos	4	3					+						+						+				+	Robinson *et al.* (1983); Palacois (1996); Pitman *et al.* (1999); Palacios (unpublished data).
1. Atlantic Frontier	3	3			+				+														+	Pollock *et al.* (2000); MacLeod *et al.* (2006).
12. Puerto Rico	3	2									+	+											+	Mignucci-Giannoni (1989); Mignucci-Giannoni (1996); Rosario-Delestre *et al.* (1999).
14. Hawaii	3	3					+				+												+	Mitchell, (1968); Shallenberger, (1981); Pitman *et al.* (1999).
10. Northern Bahamas	2	2									+												+	Claridge and Balcomb (1995); MacLeod *et al.* (2004b).
4. Eastern Alboran Sea	2	2			+																		+	Sagarminaga and Cañadas (2003).
8. The Gully, Nova Scotia	2	2			+				+															Whitehead *et al.* (1997a, b); Hooker and Baird (1999b).
3. Genoa Canyon	1	1																					+	Azzellino *et al.* (2001).
5. Western Greece	1	1																					+	Frantzis (1998).

The California shelf margins therefore qualify as a key area under criteria (A), (C) and (D).

14. Hawaii

Limits: 18.5-22.5°N, 154.5-160.25°W (based on three records and additional information from Shallenberger, 1981; Mobley *et al.*, 2000; Anon., 2003; Baird *et al.*, 2003; R. Baird, pers. comm.).

Three species of beaked whale have been recorded in Hawaiian waters (Table 2). Anon. (2003) reported sightings of 30 groups of beaked whales, while Baird *et al.* (2003) reported six sightings from a survey in May/June 2003. The information from these surveys suggest regular occurrences of beaked whales in this area. The main species involved in these sightings, and other published accounts, are Blainville's beaked whales and Cuvier's beaked whales around the Hawaiian archipelago (Shallenberger, 1981; Mobley *et al.*, 2000; Anon., 2003; Baird *et al.*, 2003; R. Baird, pers. comm.).

Hawaii therefore qualifies as a key area under criterion (A).

15. Eastern Tropical Pacific (ETP)

Limits: From the coasts of the Americas between the US/Mexican border and 35.0°S, west to a maximum of 170.0°W and including the Gulf of California (based on 105 records and data from Pitman and Lynn, 2001).

Within this area, sightings of beaked whales are relatively common and six species have been recorded in the ETP (Table 2). The vast majority of sightings (and indeed strandings) of the pygmy beaked whale (*M. peruvianus*) have been in the ETP and as a result, Pitman and Lynn (2001) consider this species to be endemic to this area. Sighting of other species include Blainville's beaked whale, Longman's beaked whale (*M. pacificus*) and Cuvier's beaked whale (Vidal *et al.*, 1993; Dawson *et al.*, 1998; Pitman *et al.*, 1999; Pitman and Lynn, 2001; H. Whitehead, pers. comm.).

The ETP therefore qualifies as a key area under criteria (A), (C) and (D).

16. Galapagos

Limits: 1.25°S-1.50°N, 89.0-93.25°W (based on 48 records).

The Galapagos Islands represent a sub-division of the ETP key area and are considered separately due to the different oceanographic conditions provided in comparison with the surrounding oceanic waters. Four species of beaked whales are known to occur around the Galapagos Islands (Table 2). Beaked whales have regularly been sighted around the Galapagos Islands, e.g. Palacios (1999; unpublished data) recorded sightings of 34 groups of beaked whale, including six sightings of Cuvier's beaked whales totalling 21 animals and three groups of *Mesoplodon* species (including one group of pygmy beaked whales) totalling 13 animals. These sightings have all been recorded 1.6°N-1.3°S, 92.6-89.9°W.

The Galapagos therefore qualifies as a key area under criterion (A).

17. The Falkland Islands and Tierra del Fuego

Limits: From Tierra del Fuego and the South American coast, from 48.5-59.5°S east to 54.50°W (based on 61 records).

Eight species of beaked whale of five genera have been recorded in this area, giving it a high diversity of species (Table 2). Southern bottlenose whales (*H. planifrons*) and a lesser number of *Mesoplodon* species, have been regularly sighted around the Falkland Islands (White *et al.*, 2002).

This region therefore qualifies as a key area under criteria (A) and (C).

18. Indian Ocean around South Africa

Limits: 28.25-41.25°S, 21.25-49.25°E (based on 127 records).

The Indian Ocean east of South Africa has a relatively high diversity of beaked whale species, with nine species from five genera having been recorded in this area (Table 2). Of particular interest are records of True's beaked whale (*M. mirus*). This species is only known to exist in three areas in the Southern Hemisphere; Australia, South Africa and South America (McCann and Talbot, 1963; Ross, 1969; Dixon and Frigo, 1994; Bannister *et al.*, 1996; de Souza *et al.*, 2004). Whether these represent three separate populations, or parts of the same population is unknown. Until this is clarified, it may be wise to consider each as a separate population. Under such an assumption, South Africa may represent a large portion of the area inhabited by one population. The waters around South Africa, particularly in the Indian Ocean to the east, have had relatively high numbers of sightings and have whaling records of southern bottlenose whales, with additional sightings of Cuvier's beaked whales and *Mesoplodon* species (Gambell *et al.*, 1974; Nemoto *et al.*, 1980; Ross, 1984; Findlay *et al.*, 1992).

This region therefore qualifies as a key area under criteria (A) and (C) and possibly (D).

19. Japan

Limits: All waters surrounding Japan out to the abyssal plain, including the East China Sea (based on 188 records and Omura *et al.*, 1955; Nishiwaki and Oguro, 1972; Miyashita, 1986 and Kasuya and Miyashita, 1997).

Japan has a high diversity of beaked whales, with seven species of five genera recorded in the area (Table 2). The majority of known records (15 out of 23) of the ginkgo-toothed beaked whale (*M. ginkgodens*), come from Japanese waters (Nishiwaki and Kamiya, 1958; Nishiwaki *et al.*, 1972; Miyazaki *et al.*, 1987; Marine Mammal Stranding Database, Tokyo, Japan). The Japanese have hunted Baird's beaked whales (*Berardius bairdii*) in deep waters off their coasts for many years (e.g. Omura *et al.*, 1955; Nishiwaki and Oguro, 1971; Kasuya *et al.*, 1997). Cuvier's beaked whales were also taken opportunistically but are no longer hunted (Nishiwaki and Oguro, 1972; Anon., 2004). Coastal whaling is active in Chiba, Miyagi and Hokkaido and the annual quota for Baird's beaked whale was 62 animals in 2004 (Anon., 2004). Miyashita (1986) estimated the 1984 summer population of Baird's beaked whales off the Pacific coast of Japan at a minimum of 4,220 animals. Kasuya and Miyashita (1997) reviewed the distribution of Baird's beaked whales off Japan using sightings data obtained during cruises from 1982-1984, resulting in 320 school being studied. They reaffirmed the hypothesis of three stocks, i.e. Sea of Japan, Pacific Coast and Okhotsk Sea, with some seasonal migration of the last stock off eastern Hokkaido.

Japan therefore qualifies as a key area under criteria (A), (B) and (C) augmented by (E).

20. Southwestern Australia

Limits: Along the southwestern Australian coast from 32.08°S, 115.74°E-34.54°S, 118.90°E to as far as 44.75°S and 109.25°E (based on 19 records).

Five species of beaked whale have been recorded in southwestern Australia (Table 2). These include the poorly known Hector's (*M. hectori*) and Andrews' (*M. bowdoini*) beaked whales. In addition, there have been regular sightings of beaked whales at sea, particularly to the south of the Australian coast. These include sightings of *Mesoplodon* species and Cuvier's beaked whales (Gales *et al.*, 2002; IWC, unpublished data).

Southwestern Australia therefore qualifies as a key area under criterion (A).

21. Tasmania and Southeastern Australia

Limits: Along the Australian coast from 134.0-151.5°E, 47.0°S (based on 48 records).

Tasmania and southeastern Australia has the second highest diversity of beaked whale species for any of the key areas identified here, with records of ten species (Table 2). As noted above it is also one of the three areas of the Southern Hemisphere where True's beaked whale has been recorded. Following the approach for key area 18, it may be wise to consider the animals in this area as a separate population.

The region therefore qualifies as a key area under criterion (C) and possibly (D).

22. New Zealand

Limits: Waters surrounding New Zealand, south to 53.5°S and east to 180°E (based on 119 records).

New Zealand has the highest diversity of beaked whales of any of the key areas identified here, with records of eleven species from five genera (Table 2). These waters may be globally important for four poorly known species, of which no live sightings have been confirmed. The majority of known records for Andrews' beaked whales (21 out of 35) come from New Zealand, or the nearby Chatham Islands, Campbell Islands and Macquarie Island (Baker, 2001). Similarly for Hector's beaked whales, 11 out of the 25 published records come from this area (Mead, 1989a; Baker *et al.*, 2001). For the spade-toothed whale, only three records are known around the world and one of these records comes from New Zealand and a second from the neighbouring Chatham Islands (van Helden *et al.*, 2002). Finally, for Shepherd's beaked whale (*Tasmacetus shepherdi*) five of the nine published records come from New Zealand (Mead, 1989b). There have been numerous beaked whale sightings in waters around New Zealand, mainly *Mesoplodon* species and Cuvier's beaked whales. The majority of these have been to the east and south of South Island (Gaskin, 1971; IWC, unpublished data).

New Zealand therefore qualifies as a key area under criteria (A), (C) and probably (D).

23. Southern Ocean and Antarctic Waters

Limits: South of 57.5°S to the ice edge and beyond (based on 347 records).

Arnoux's beaked whale (*B. arnuxii*) and the southern bottlenose whale are commonly recorded in the Southern Ocean, particularly around the Antarctic convergence (60.0-70.0°S) and as far south as the ice edge, and indeed in polynas within the ice itself (Cherry-Garrard, 1922; Gianuca and Castello, 1976; Miyazaki and Kato, 1988; Hobson and Martin, 1996). In addition, *Mesoplodon* species, such as Gray's beaked whale (*M. grayi*), the strap-toothed beaked whale, and Cuvier's beaked whale have also been recorded in these waters (e.g. Gianuca and Castello, 1976; Miyazaki and Kato, 1988; Kasamatsu *et al.*, 1993; Bowles *et al.*, 1994; Ponganis *et al.*, 1995; Hobson and Martin, 1996; Pankow *et al.*, 1997; Pierpoint *et al.*, 1997; Leaper and Scheidat, 1998; Branch and Butterworth, 2001). Branch and Butterworth (2001) estimated a population of about 72,000 southern bottlenose whales in the Antarctic south of 60.0°S. The surveys from which this estimate was obtained were designed to obtain Antarctic minke whale (*Balaenoptera bonaerensis*) population estimates and as a result, did cover the entire range of the beaked whale species in the Southern Ocean, but did not correct for animals missed on the trackline.

DISCUSSION

The key areas identified here cover the locations of almost 70% of the beaked whale records included in the database constructed for this analysis. They range from relatively small and discrete geographic areas, such as the Gully off Nova Scotia, to entire regions, such as the ETP or Southern Ocean and Antarctica. Such differences in scale reflect two factors. Firstly, they may reflect different levels of survey effort. For example, in the Gully, research has been specifically targeted at studying the northern bottlenose whales known to be found there (Whitehead *et al.*, 1997a), whereas for the Southern Ocean and Antarctic waters, most data come from wide-ranging surveys undertaken to estimate abundance of minke whales (Kasamatsu *et al.*, 1993; Branch and Butterworth, 2001). Furthermore, some key areas are based on strandings data, which at best provide only a low resolution view of patterns in beaked whale occurrence as they are heavily dependent on the prevailing conditions, with animals potentially travelling great distances before stranding (MacLeod, 2000); such data can thus only be used to identify very general areas of occurrence. Secondly, they may reflect real differences in distribution at different scales and in different oceans. For example, on a broad scale, there is a high abundance of beaked whales throughout the Southern Ocean and Antarctic (Branch and Butterworth, 2001). In other locations, beaked whale distribution is related to fine-scale factors with relatively low levels of occurrence outside key areas (e.g. in one part of the northeastern Bahamas, beaked whale distribution is closely tied to the presence of a marine canyon and few groups are encountered away from this specific location; MacLeod and Zuur, 2005). Further data are required to investigate whether there are specific fine-scale areas that beaked whales preferentially use within broad-scale areas and whether fine-scale areas are part of larger networks of areas of high beaked whale abundance. This is particularly important for key areas such as the Southern Ocean and Antarctic, for which current fine-scale knowledge is limited.

Applying the identification of key areas to beaked whale conservation

Identifying key areas is not an aim in itself but rather a way of providing a focus for appropriate assessment, mitigation and regulatory strategies. However, there is little available information appropriate on mitigation and regulatory strategies for some of the identified potential anthropogenic threats, especially related to noise. Determination of the mechanisms behind such threats will only be possible if many currently isolated fields begin to collaborate (Cox *et al.*, 2006). Current work aimed at understanding how naval sonars may result in mass strandings of beaked whales includes researchers working in areas as diverse as auditory anatomy, sound propagation, physical oceanographic modelling, diving behaviour, ecology and pathology (Gisiner, 2003). A similar multi-disciplinary approach is required to determine whether other potential threats are real. For example, although some biologists may suspect that particular activities, such as over-fishing of preferred prey, adversely affect beaked whales in some regions, it will require input from a number of disciplines to confirm or deny this, and where appropriate develop and implement appropriate mitigation strategies. In the absence of conclusive knowledge of anthropogenic impacts and appropriate mitigation strategies, a precautionary approach should be implemented in key areas.

The marine environment is a dynamic system with major changes occurring over relatively short time periods that can affect species distribution and habitat preferences, e.g. in the ETP during El Niño-Southern Oscillation events (Lu *et al.*, 2001; Richards and Engle, 2001), an increasing North Atlantic Oscillation Index (Kroencke *et al.*, 2001) or changes in local water temperatures in northwest Scotland (MacLeod *et al.*, 2005). It is thus important to recognise that the identified key areas may not be (and probably are not) static entities. This is perhaps particularly important for key areas that cover relatively small, discrete areas and that are based on fine-scale data, where small geographical shifts in oceanographic conditions could result in local changes in beaked whale distributional patterns. Consequently, the key areas should be regularly monitored for changes in beaked whale distribution and occurrence. This information can then be used to increase the understanding of how key areas may change over time and with certain environmental changes, which can then be taken into account in future identification of key areas.

It is almost certain that further research will identify additional key areas as well as leading to the modification of existing ones. For example, a similar analysis carried out a decade ago would have identified only eight of the current key areas. Even in this study a number of other areas went close to fulfilling our criteria. From the strandings evidence and a limited number of sightings, the Aleutian Islands, particularly around Adak (51.9°N, 176.6°W), seem a likely future key area (Loughlin *et al.*, 1982; Walker and Hanson, 1999). However, more data, particularly on distribution at sea and the causes of a number of mass strandings of Stegneger's beaked whale (*M. stegnegeri*) on Adak (Walker and Hanson, 1999), are required. This reinforces the fact that absence of evidence should not be taken as evidence of absence. Simply because an area is not identified as a key area in this paper, it does not mean that beaked whales are not present, locally important or susceptible to anthropogenic impacts in other areas.

To identify or modify key areas requires the undertaking of dedicated research projects and surveys; many areas of the world remain unsurveyed, e.g. the eastern tropical Atlantic. However, undertaking dedicated surveys and research projects for oceanic species is complex, expensive and may take several years. In order to help focus this effort therefore, it would be valuable to use newly developed techniques of spatial modelling with the available data on beaked whale occurrence to predict areas of suitable beaked whale habitat (e.g. Hedley *et al.*, 1999; Cañadas *et al.*, 2005; IWC, 2006). These areas can then be the focus of dedicated surveys to confirm or deny the presence of beaked whales, as well as highlighting further areas where a precautionary approach to anthropogenic disturbance is warranted.

The use of key areas as proposed here combined with a spatial modelling approach should allow suitably precautionary conservation measures to be applied despite the relatively poor knowledge of beaked whales in many areas of the world, as well as focussing efforts to improve our knowledge.

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