

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).

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).

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.

Taxonomic grouping	Group size			N
	Range	Mean	SD	
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
<i>Mesoplodon</i> spp.	1-15	2.9	1.8	354
Longman's beaked whales	1-100	19.38	22.32	36
<i>Berardius</i> spp.	1-100	7.87	9.21	335

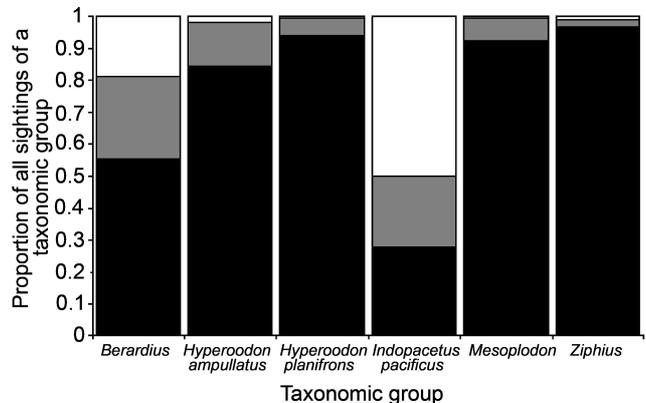


Fig. 1. The frequency of occurrence of groups in three size classes for sightings of Longman's beaked whale, *Berardius* spp., the southern bottlenose whale, the northern bottlenose whale, Cuvier's beaked whale and *Mesoplodon* spp. Dark grey=Percentage of total sightings for a taxonomic group with group 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

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.

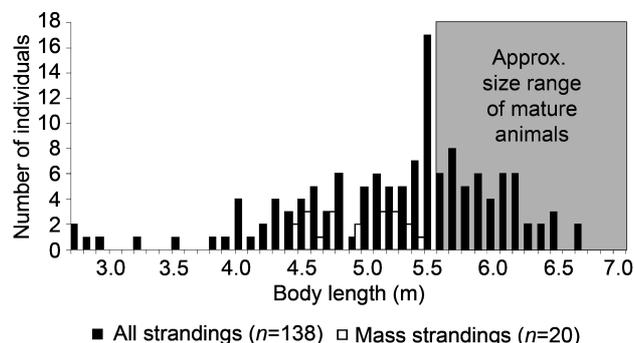


Fig. 2. A comparison of body lengths of Cuvier's beaked whales from two mass strandings events associated with anthropogenic noise (Greece 1996 and Canaries 2002, $n=20$) with those of Cuvier's beaked whales from all types of strandings events around the world ($n=138$).

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 that 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 953 μ s. 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 Muhl, 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 Muhl, 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, it 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 carcass) 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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REFERENCES

- Anon. 2001. Joint interim report on the Bahamas marine mammal stranding event of 15–16 March 2000 (December 2001). NOAA unpublished report. 59pp. [Available from http://www.nmfs.noaa.gov/prot_res/overview/Interim_Bahamas_Report.pdf].
- Azzellino, A., Airdoli, S., Gaspari, S., Patti, P. and Sturlese, A. 2001. The physical habitat of cetaceans along the continental slope of the Western Ligurian Sea. Poster presented at the 15th Annual Meeting of the European Cetacean Society, 6–10 May 2001, Rome.
- Baird, R.W., McSweeney, D.J., Ligon, A.D. and Webster, D.L. 2004. Tagging feasibility and diving of Cuvier's beaked whales (*Ziphius cavirostris*) and Blainville's beaked whales (*Mesoplodon densirostris*) in Hawaii. SWFSC Admin. Report prepared under Order No. AB133F-03-SE-0986 to the Hawaii Wildlife Fund, Volcano, HI. 15pp. [Available from: [swfsc.nmfs.noaa.gov](http://www.swfsc.nmfs.noaa.gov)].
- Barlow, J. 1999. Trackline detection probability for long-diving whales. pp. 209–21. In: G.W. Garner, S.C. Amstrup, J.L. Laake, B.F.J. Manly, L.L. McDonald and D.G. Robertson (eds.) *Marine Mammal Survey and Assessment Methods*. Balkema Press, Rotterdam, Netherlands. 287pp.
- Barlow, J. and Sexton, S. 1996. The effect of diving and searching behavior on the probability of detecting track-line groups, $g(0)$, of long-diving whales during line-transect surveys. SWFSC Admin. Rep. No. LJ-96-14. 21pp. [Available from: www.st.nmfs.gov/tm/swfsc].
- Benjaminsen, T. and Christensen, I. 1979. The natural history of the bottlenose whale, *Hyperoodon ampullatus* Forster. pp. 143–64. In: H.E. Winn and B.L. Olla (eds.) *Behavior of Marine Animals*. Vol. 3. *Cetaceans*. Plenum Press, New York and London. i–xix+438pp.
- Biassoni, N., Miller, P.J.O., Podesta, M., Johnson, M., Sturlese, A., Tyack, P. and Bocconcelli, A. 2003. Behavioural observations and non-invasive tagging of Cuvier's beaked whales, *Ziphius cavirostris*, in the Ligurian Sea. *European Cetacean Society Conference Guide and Abstracts* 17:138. Paper presented to the 17th Conference of the European Cetacean Society, Las Palmas de Gran Canaria, March 9–13 2003.
- Bigg, M.A., Olesiuk, P.F., Ellis, G.M., Ford, J.K.B. and Balcomb, K.C. 1990. Social organization and genealogy of resident killer whales (*Orcinus orca*) in the coastal waters of British Columbia and Washington State. *Rep. int. Whal. Commn* (special issue) 12:383–405.
- Bose, N., Lien, J. and Ahia, J. 1990. Measurements of the bodies and flukes of several cetaceans species. *Proc. R. Soc. Lond. Ser. B*. 242(1305):163–73.
- Caldwell, D.K. and Caldwell, M.C. 1971. Sounds produced by two rare cetaceans stranded in Florida. *Cetology* 4:1–6.
- Connor, R.C. 2000. Group living in whales and dolphins. pp. 199–218. In: J. Mann, R.C. Connor, P.L. Tyack and H. Whitehead (eds.) *Cetacean Societies: Field Studies of Dolphins and Whales*. University of Chicago Press, Chicago. 433pp.
- Connor, R.C., Mann, J., Tyack, P.L. and Whitehead, H. 1998. Social evolution in toothed whales. *Trends Ecol. Evol.* 13:228–32.
- Connor, R.C., Read, A.J. and Wrangham, R. 2000. Male reproductive strategies and social bonds. pp. 247–69. In: J. Mann, R.C. Connor, P.L. Tyack and H. Whitehead (eds.) *Cetacean Societies: Field Studies of Dolphins and Whales*. University of Chicago Press, Chicago. 433pp.
- Cox, T.M., Ragen, T.J., Read, A.J., Vos, E., Baird, R.W., Balcomb, K., Barlow, J., Caldwell, J., Cranford, T., Crum, L., D'Amico, A., D'Spain, G., Fernández, A., Finneran, J., Gentry, R., Gerth, W.,

- Gulland, F., Hildebrand, J., Houser, D., Hullar, T., Jepson, P.D., Ketten, D., MacLeod, C.D., Miller, P., Moore, S., Mountain, D., Palka, D., Ponganis, P., Rommel, S., Rowles, T., Taylor, B., Tyack, P., Wartzok, D., Gisiner, R., Mead, J. and Benner, L. 2006. Understanding the impacts of anthropogenic sound on beaked whales. *J. Cetacean Res. Manage.* 7(3):This volume.
- Cranford, T.W. 1999. The sperm whale's nose: sexual selection on a grand scale? *Mar. Mammal Sci.* 15(4):1133-57.
- Dalebout, M.L., Mead, J.G., Baker, C.S., Baker, A.N. and Van Helden, A.L. 2002. A new species of beaked whale *Mesoplodon perrini* sp. N. (Cetacea: Ziphiidae) discovered through phylogenetic analyses of mitochondrial DNA sequences. *Mar. Mammal Sci.* 18(3):577-608.
- Dalebout, M.L., Ross, G.J.B., Scott Baker, C., Anderson, R.C., Best, P.B., Cockcroft, V.G., Hinsz, H.L., Peddemors, V. and Pitman, R.L. 2003. Appearance, distribution and genetic distinctiveness of Longman's beaked whale, *Indopacetus pacificus*. *Mar. Mammal Sci.* 19(3):421-61.
- D'Amico, A., Mineur, F., Alvarez, A., Mori, C., Podesta, M., Fortunato, N., Ballardini, M. and Nani, B. 2001. Oceanographic correlation with the distribution of Cuvier's beaked whales (*Ziphius cavirostris*) in the Ligurian Sea. Abstracts of the 14th Biennial Conference on the Biology of Marine Mammals, Vancouver, 28 November – 3 December 2001. [Available from: www.marinemammalogy.org].
- D'Amico, A., Bergamasco, A., Zanasca, P., Carniel, S., Nancini, E., Fortunato, N., Teloni, V., Mori, C. and Barbanti, R. 2003. Qualitative correlation of marine mammals with physical and biological parameters in the Ligurian Sea. *IEEE J. Ocean. Engr.* 28(1):29-43.
- Dawson, S., Barlow, J. and Ljungblad, D. 1998. Sounds recorded from Baird's beaked whale, *Berardius bairdii*. *Mar. Mammal Sci.* 14(2):335-44.
- Ford, J.K.B. 1989. Acoustic behaviour of resident killer whales (*Orcinus orca*) off Vancouver Island, British Columbia. *Can. J. Zool.* 67(3):727-45.
- Frantzis, A. 1998. Does acoustic testing strand whales? *Nature* 392(6671):29.
- Frantzis, A. and Cebrian, D. 1998. A rare, atypical mass stranding of Cuvier's beaked whales: cause and implications for the species' biology. *Eur. Res. Cetaceans [Abstracts]* 12:332-5.
- Frantzis, A., Goold, J.C., Skarsoulis, E.K., Taroudakis, M.I. and Kandia, V. 2002. Clicks from Cuvier's beaked whales, *Ziphius cavirostris* (L.). *J. Acoust. Soc. Am.* 112(1):34-7.
- Gowans, S. 1999. Social organization and population structure of northern bottlenose whales in the Gully. Ph.D. Thesis, Dalhousie University, Halifax, Nova Scotia, Canada. 222pp.
- Gowans, S., Whitehead, H., Arch, J.K. and Hooker, S.K. 2000. Population size and residency patterns of northern bottlenose whales (*Hyperoodon ampullatus*) using the Gully, Nova Scotia. *J. Cetacean Res. Manage.* 2(3):201-10.
- Gowans, S., Whitehead, H. and Hooker, S.K. 2001. Social organisation in northern bottlenose whales (*Hyperoodon ampullatus*): not driven by deep water foraging? *Anim. Behav.* 62:369-77.
- Gray, J.E. 1850. *Cetacea*. Part I. *Catalogue of the Specimens of Mammalia in the Collection of the British Museum*. British Museum, London. 153pp + plates.
- Heyning, J.E. and Mead, J.G. 1996. Suction feeding in beaked whales: morphological and observational evidence. *Smithson. Contrib. Sci.* 464:1-12.
- Hinde, R.A. 1976. Interactions, relationships and social structure. *Man* 11:1-17.
- Hooker, S.K. and Baird, R.W. 1999a. Deep-diving behaviour of the northern bottlenose whale, *Hyperoodon ampullatus* (Cetacea: Ziphiidae). *Proc. R. Soc. Lond. Ser. B.* 266:671-6.
- Hooker, S.K. and Baird, R.W. 1999b. Observations of Sowerby's beaked whales, *Mesoplodon bidens*, in the Gully, Nova Scotia. *Can. Field-Nat.* 113(2):273-7.
- Hooker, S.K. and Whitehead, H. 2002. Click characteristics of northern bottlenose whales (*Hyperoodon ampullatus*). *Mar. Mammal Sci.* 18(1):69-80.
- Hooker, S.K., Iverson, S.J., Ostrom, P. and Smith, S.C. 2001. Diet of northern bottlenose whales inferred from fatty-acid and stable-isotope analyses of biopsy samples. *Can. J. Zool.* 79:1,442-54.
- Hooker, S.K., Whitehead, H., Gowans, S. and Baird, R.W. 2002. Fluctuations in distribution and patterns of individual range use of northern bottlenose whales. *Mar. Ecol. Prog. Ser.* 225:287-97.
- International Whaling Commission. 2006. Report of the IWC Scientific Committee Workshop on Habitat Degradation, 12-15 November 2004, Siena, Italy. *J. Cetacean Res. Manage. (Suppl.)* 8:313-334.
- Jepson, P.D., Arbelo, M., Deaville, R., Patterson, I.A.P., Castro, P., Baker, J.R., Degollada, E., Ross, H.M., Herraes, P., Pocknell, A.M., Rodriguez, F., Howiell, F.E., Espinosa, A., Reid, R.J., Jaber, J.R., Martin, V., Cunningham, A.A. and Fernández, A. 2003. Gas-bubble lesions in stranded animals: Was sonar responsible for a spate of whale deaths after an Atlantic military exercise? *Nature* 425(6958):575-76.
- Johnson, M. and Tyack, P.L. 2003. A digital acoustic recording tag for measuring the response of wild marine mammals to sound. *IEEE J. Ocean. Engr.* 28:3-12.
- Kasuya, T. 1986. Distribution and behaviour of Baird's beaked whales off the Pacific coast of Japan. *Sci. Rep. Whales Res. Inst., Tokyo* 37:61-83.
- Kasuya, T., Brownell, R.L. and Balcomb, K.C. 1997. Life history of Baird's beaked whales off the Pacific coast of Japan. *Rep. int. Whal. Commn* 47:969-79.
- Leaper, R. and Scheidat, M. 1998. An acoustic survey for cetaceans in the Southern Ocean Sanctuary conducted from the German Government research vessel *Polarstern*. *Rep. int. Whal. Commn* 48:431-7.
- Leaper, R., Gillespie, D. and Papastavrou, V. 2000. Results of passive acoustic surveys for odontocetes in the Southern Ocean. *J. Cetacean Res. Manage.* 2(3):187-96.
- Lynn, S.K. and Reiss, D.L. 1992. Pulse sequence and whistle production by two captive beaked whales, *Mesoplodon species*. *Mar. Mammal Sci.* 8(3):299-305.
- MacLeod, C.D. 2005. Niche partitioning, distribution and competition in North Atlantic beaked whales. Thesis, University of Aberdeen, Aberdeen, UK.
- MacLeod, C.D. 2006. How big is a beaked whale? A review of body size and sexual dimorphism in the family Ziphiidae. *J. Cetacean Res. Manage.* 7(3):This volume.
- Macleod, C.D. and Mitchell, G. 2006. Key areas for beaked whales worldwide. *J. Cetacean Res. Manage.* 7(3):This volume.
- MacLeod, C.D. and Zuur, A.F. 2005. Habitat utilisation by Blainville's beaked whales off Great Abaco, Northern Bahamas, in relation to seabed topography. *Mar. Biol.* 174:1-11.
- MacLeod, C.D., Santos, M.B. and Pierce, G.J. 2003. A review of data on diets of beaked whales: Evidence of niche separation and geographic segregation between three genera. *J. Mar. Biol. Assoc. UK* 83:651-5.
- Manghi, M., Montesi, G., Fossati, C., Pavan, G., Priano, M. and Teloni, V. 1999. Cuvier's beaked whales in the Ionian Sea: first recordings of their sounds. *Eur. Res. Cetaceans [Abstracts]* 13:39-42.
- Marten, K. 2000. Ultrasonic analysis of pygmy sperm whale (*Kogia breviceps*) and Hubb's beaked whales (*Mesoplodon carlhubbsi*) clicks. *Aquat. Mamm.* 26(1):45-8.
- Martin-Martel, V. 2002. Resumen del informe sobre los varamientos en masa atípicos de zifios en Canarias en Septiembre de 2002 durante la celebración de ejercicios navales. [Available from www.gobiernodecanarias.org/medioambiente/varamientos/Informe_Biologico.pdf]. [In Spanish].
- Mead, J.G. 1984. Survey of reproductive data for the beaked whales (Ziphiidae). *Rep. int. Whal. Commn* (special issue) 6:91-6.
- Mead, J.G. 1989. Shepherd's beaked whale *Tasmacetus shepherdi* Oliver, 1937. pp. 309-20. In: S.H. Ridgway and R. Harrison (eds.) *Handbook of Marine Mammals*. Vol. 4. *River Dolphins and the Larger Toothed Whales*. Academic Press Inc, London and San Diego. i-xix+442pp.
- Mead, J.G. and Payne, R.S. 1975. A specimen of the Tasman beaked whale, *Tasmacetus shepherdi*, from Argentina. *J. Mammal.* 56(1):213-8.
- Moore, P.W.B. 1980. Cetacean obstacle avoidance. pp. 97-108. In: R.G. Busnel and J.F. Fish (eds.) *Animal Sonar Systems*. Plenum Press, New York. 1,135pp.
- Norris, K.S. and Mohl, B. 1983. Can odontocetes debilitate prey with sound? *Am. Nat.* 122:85-104.
- Ostrom, P.H., Lien, J. and Macko, S.A. 1993. Evaluation of the diet of Sowerby's beaked whale, *Mesoplodon bidens*, based on isotopic comparisons among northwestern Atlantic cetaceans. *Can. J. Zool.* 71(4):858-61.
- Pitman, R.L. and Lynn, M.S. 2001. Biological observations of an unidentified mesoplodont whale in the eastern tropical Pacific and probable identity: *Mesoplodon peruvianus*. *Mar. Mammal Sci.* 17:648-57.
- Pitman, R.L., Palacios, D.M., Brennan, P.L.R., Brennan, B.J., Balcomb III, K.C. and Miyashita, T. 1999. Sightings and possible identity of a bottlenose whale in the tropical Indo-Pacific: *Indopacetus pacificus*. *Mar. Mammal Sci.* 15(2):531-49.
- Ritter, F. and Brederlau, B. 1999. Behavioural observations of dense beaked whales (*Mesoplodon densirostris*) off La Gomera, Canary Islands (1995-1997). *Aquat. Mamm.* 25(2):55-61.
- Rogers, T.L. and Brown, S.M. 1999. Acoustic observations of Arnoux's beaked whale (*Berardius arnuxii*) off Kemp Land, Antarctica. *Mar. Mammal Sci.* 15:192-8.
- Simmonds, M.P. and Lopez-Jurado, L.F. 1991. Whales and the military. *Nature* 351(6326):448.

- Smolker, R.A., Mann, J. and Smuts, B.B. 1993. Use of signature whistles during separations and reunions by wild bottlenose dolphin mothers and infants. *Behav. Ecol. Sociobiol.* 33(6):393-402.
- Thompson, D.H. and Richardson, W.J. 1995. Marine mammal sounds. pp. 205-40. In: C.R. Richardson, C.I. Greene, D.H. Malme and D.H. Thompson (eds.) *Marine Mammals and Noise*. Academic Press, San Diego. 576pp.
- Waring, G.T., Hamazaki, T., Sheenan, D., Wood, G. and Baker, S. 2001. Characterization of beaked whale (Ziphiidae) and sperm whale (*Physeter macrocephalus*) summer habitat in shelf-edge and deeper waters off the northeast US. *Mar. Mammal Sci.* 17(4):703-17.
- Watkins, W.A. and Schevill, W.E. 1977. Sperm whale codas. *J. Acoust. Soc. Am.* 62:1,485-90. [+ phono. record].
- Weilgart, L.S. and Whitehead, H. 1988. Distinctive vocalisations from mature male sperm whales (*Physeter macrocephalus*). *Can. J. Zool.* 66(9):1931-7.
- Weilgart, L. and Whitehead, H. 1993. Coda communication by sperm whales (*Physeter macrocephalus*) off the Galapagos Islands. *Can. J. Zool.* 71(4):744-52.
- Weilgart, L. and Whitehead, H. 1997. Group-specific dialects and geographical variation in coda repertoire in South Pacific sperm whales. *Behav. Ecol. Sociobiol.* 40:277-85.
- Whitehead, H. 1996. Babysitting, dive synchrony, and indications of alloparental care in sperm whales. *Behav. Ecol. Sociobiol.* 38:237-44.
- Whitehead, H. and Weilgart, L. 1990. Click rates from sperm whales. *J. Acoust. Soc. Am.* 87(4):1798-806.
- Whitehead, H., Gowans, S., Faucher, A. and McCarrey, S. 1997. Population analysis of northern bottlenose whales in the Gully, Nova Scotia. *Mar. Mammal Sci.* 13(2):173-85.
- Williams, A.D., Brereton, T.M. and Williams, R. 1999. Seasonal variation in the occurrence of beaked whales in the southern Bay of Biscay. *Eur. Res. Cetaceans* [Abstracts] 13:275-80.
- Winn, H.E., Perkins, P.J. and Winn, L. 1970. Sounds and behaviour of the northern bottlenose whale. 7th Annual Conference on Biological Sonar and Diving Mammals, Stanford Research Institute, Menlo Park, California, pp.53-59.

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