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Review of data on diets of beaked whales: evidence of niche separation and geographic segregation

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This study reviewed published data on dietary preferences of beaked whales (Ziphiidae) from stomach contents analysis. Detailed data were only available for three of the six beaked whale genera (*Hyperoodon*, *Mesoplodon* and *Ziphius*). Stomach samples of these three beaked whale genera primarily contained cephalopod and fish remains, although some also contained crustaceans. *Mesoplodon* spp. were found to contain the most fish, with some species containing nothing but fish remains, while the southern bottlenose whale (*Hyperoodon planifrons*) and Cuvier's beaked whale (*Ziphius cavirostris*) rarely, if ever, contained fish. Of cephalopods identified, Histioteuthid, Gonatid, Cranchiid and Onychoteuthid species usually contributed most to prey numbers and biomass for all beaked whale genera. There was a wide range of species and families of cephalopods recorded from stomach contents, with no obvious preference for bioluminescent prey species, vertical migrating prey species or prey species with specific body compositions. Whales of the genus *Mesoplodon* generally contained smaller prey, such as cephalopods under 500 g in weight, compared with other beaked whales. *Hyperoodon* and *Ziphius* frequently contained much larger cephalopods with many important prey species having a mean weight of over 1000 g. This suggests that *Mesoplodon* occupies a separate dietary niche from *Hyperoodon* and *Ziphius*, which may be an example of niche segregation. In contrast, *Hyperoodon* and *Ziphius* appear to occupy very similar dietary niches but have geographically segregated distributions, with *Hyperoodon* occupying cold-temperate to polar waters and *Ziphius* occupying warm-temperate to tropical waters.

INTRODUCTION

Diet is an important aspect of the ecology of any predator. The distribution of preferred prey items will relate to the distribution of the predator and will, in part, define the habitats in which a specific predator occurs, while the abundance of preferred prey may affect the abundance of the predator within a specific habitat (e.g. Mills & Knowlton, 1991; Pike et al., 1999; Elmhagen et al., 2000). In addition, the degree of similarity in diet between two or more predators which occur in the same habitat will affect the level of competition between these predators (Schoener, 1983). Competition between predators can result in the exclusion of one, or more, of them from a specific habitat (e.g. Thiollay, 1988; Kruuk et al., 1994; Ebensperger & Botto-Mahan, 1997).

In terrestrial predators, and marine predators that live in shallow waters or spend some time on land (such as seals), dietary preferences can be examined by direct observations of foraging and feeding behaviour, analysis of faecal samples or examination of stomach contents (by lavaging or pumping in live animals or removal of the stomach from carcases) (Pierce & Boyle, 1991). However, for many marine predators, particularly those which feed at great depth, direct observation or analysis of faecal samples is not usually viable, although occasionally possible. This has led to a reliance on stomach contents analysis (Pierce & Boyle, 1991; Harvey & Antonelis, 1994; Clarke, 1996).

This paper reviews the results of stomach contents analysis of beaked whales from around the world. The beaked whales, or family Ziphiidae, are the second largest family of cetaceans and with 21 currently recognized species they make up approximately one-quarter of all cetacean species. Most of the available data on diets refers to just three of the six genera. The genus *Hyperoodon* contains two species, *Mesoplodon* 14 and *Ziphius* one (Heyning, 1989; Mead, 1989a,b; Reyes et al., 1991, 1995). These species range in size from under four metres in the pygmy beaked whale, *Mesoplodon peruvianus* Reyes et al., 1991, to about ~10 m in the northern bottlenose whale, *Hyperoodon ampullatus* Forster 1770 (Mead, 1989a; Reyes et al., 1991). However, most species reach sizes of between five and seven metres in length (Mead, 1984, 1989a,b; Heyning, 1989). Less dietary information is available for the remaining genera (*Tasmacetus*, *Indopacetus* and *Berardius*) which together contain four species (one in each of the first two and two in the last).

The beaked whales are typified by a very reduced dentition, with almost all species having only one or two pairs of teeth, set in the lower jaw (Moore, 1968). These teeth either remain embedded in the gums or erupt to form tusks (usually in adult males), and do not function during feeding. Instead, prey capture is thought to occur by suction feeding and beaked whales have a greatly reduced gape in comparison to other toothed whales to aid in this method of feeding (Heyning & Mead, 1996).

In some parts of the world, beaked whales are amongst the most numerous cetaceans and as such are important apex predators for marine ecosystems (Sekiguchi et al., 1993; Kasamatsu & Joyce, 1995). However, little is currently known about the ecology of most beaked whale

Table 1. *Reports of stomach contents analysis with main items (greater than 5% of total) by number and mass for* Hyperoodon *species. By-caught animals are marked with an * before the species name, and animals caught during whaling by a* +. *Stranded animals are unmarked.*

Location	No. stomachs analysed	No. items	Main item by numbers (% of total)	Main item by mass (% of total, mean mass)	Reference
H. ampullatus, Hargen, The Netherlands	1 (female 7.8 m)	1641	*Gonatus* sp. (99.46%)	*Gonatus* sp. (100%, 166 g)	Santos et al., 2001a
H. ampullatus Texel, The Netherlands	1 (adult female)	539	*Gonatus* sp. (94.25%)	*Gonatus* sp. (98.84%, 148 g)	Santos et al., 2001a
H. ampullatus Tåsinge, Denmark	1 (immature male 5.9 m)	1120	Upper beaks (42.75%), *Gonatus* sp. (19.46%), *Teuthowenia megalops* (15.18%), *Taonius pavo* (14.37%)	*Gonatus* sp. (54.34%, 128 g), *Teuthowenia megalops* (17.29%, 60 g), *Taonius pavo* (15.29%, 49 g)	Santos et al., 2001a
H. ampullatus Dunbar, Scotland	1 (immature male)	198	*Gonatus* sp. (95.45%),	*Gonatus* sp. (99.85%, 107 g)	Santos et al., 2001a
H. ampullatus Faroe Islands	1	699	*Gonatus fabricii* (74.1%), *Taonius pavo* (19.3%)	*G. fabricii* (83.7%, 177 g), T. pavo (9.9%, 81 g)	Clarke & Kristensen, 1980
H. ampullatus Jutland, Denmark	1 (female 7.28 m)	2386	*Gonatus fabricii* (99.98%)		Clarke & Kristensen, 1980
H. ampullatus Baltic Sea	1 (female 7.8 m)	2531	*Gonatus fabricii* (100%)	*G. fabricii* (100%, 220.7 g)	Lick & Piatkowski 1998
+*H. ampullatus* Faroe Islands	8	–	Cranchiidae (found in 8 stomachs), Gonatidae (7), Octopoteuthidae (5), Brachioeuthidae (2), Histioteuthidae (2), and Vampyroteuthidae (2).	–	Bloch et al., 1996
+*H. ampullatus* Iceland	46	–	*Gonatus fabricii* (found in 44 stomachs), Fish (4)	–	Benjaminsen & Christensen, 1979
+*H. ampullatus* Labrador	108	–	*Gonatus fabricii* (found in 102 stomachs), Fish (54)	–	Benjaminsen & Christensen, 1979
H. planifrons, Tierra del Fuego	1 (whale a)	714	*Histioteuthis eltanine* (50%), *Taonius pavo* (29.4%) and *Gonatus antarcticus* (8.1%)	*Kondakovia longimana* (58.5%, 4071 g), *G. antarcticus* (11.0%, 215 g) *H. eltanine* (8.1%, 77 g), *Moroteuthis ingens* (6%, 2457 g)	Clarke & Goodall, 1994
H. planifrons, Tierra del Fuego	1 (whale b)	2424	*Taonius pavo* (59.9%), *Histioteuthis eltanine* (15.1%), *Gonatus antarcticus* (8.9%)		
H. planifrons, South Africa	1 (male, 6.43 m)	1974	*Histioteuthis meleagroteuthis* (20.11%), *Chiroteuthis* spp. (17.63%), *Taonius pavo* (14.29%), *Galiteuthis glacialis* (11.4%), *Gonatus antarcticus* (9.57%)	*Mesonychoteuthis hamiltoni* (22.5%, 4080.72 g), *Kondakovia longimata* (12.9%, 2568.7 g), *G. antarcticus* (6.61%, 256 g)	Sekiguchi et al., 1993
H.planifrons, South Africa	1 (female, 6.55 m)	1622	*Histioteuthis* spp. (23.68%), *Taonius pavo* (20.47%), *Galiteuthis glacialus* (10.85%), *Gonatus antarcticus* (7.09%)		
H. planifrons, Victoria, Austalia	1 (male, 3.67 m)	–	Tunicata	–	Dixon et al., 1994
H. planifrons, Heard Island	1 (female, 6.30 m)	3025	*Psychroteuthis glacialis* (50.0%), *Galiteuthis glacialis* (12.4%), *Liochranchia* sp. (11.0%), *Taonius pavo* (5.9%).	*Kondakovia longimana* (54.77%, 2664.6 g), *Psychroteuthis glacialis* (8.22%, 26.2 g), *Gonatus antarcticus* (7.38%, 186.1 g), *Liochranchia* sp. (6.01%, 86.6 g), *Tanous pavo* (5.89%, 159,5 g), *Galiteuthis glacialis* (5.47%, 70.3 g)	Slip et al., 1995

species and few studies (Whitehead et al., 1997; MacLeod, 1999; Williams et al., 1999) have been carried out on living animals in their natural environment. As a result, much of the current knowledge of beaked whale biology comes from dead animals, either killed in a small number of directed fisheries, by-caught or found stranded on beaches. Most publications on beaked whales describe information from a limited number of individuals (Heyning, 1989; Mead, 1989a,b; MacLeod, 2000b). This is particularly true of publications dealing with stomach contents analysis of stranded animals (e.g. Debrot & Barros, 1992; Lick & Piatkowski, 1998; Santos et al., 2001a,b). This paper collates and summarizes data on stomach contents from such publications, as well as available unpublished data, with the aim of examining the variation in diet both within and between species to see if any conclusions can be drawn regarding prey preferences and dietary niches of the different genera.

Limitations and biases of inferring dietary preferences from stomach contents analysis

Before examining dietary preferences of beaked whales based on stomach contents analysis, it is worth considering what biases and limitations are associated with this methodology (Pierce & Boyle, 1991; Harvey & Antonelis, 1994). Firstly, stomach contents are representative only of prey consumed shortly before the stomach contents were collected. Beaked whales are primarily deep water animals and if they remain in shallow waters for a period of time before stranding they may ingest prey items which are not normally part of their diet (as has been suggested to explain the presence of a number of shallow water species in various beaked whale stomach contents—Dixon et al., 1994; Sekiguchi, 1994). Stomach contents from animals which have been killed on or close to the feeding grounds (e.g. Nishiwaki & Oguro, 1972; Benjaminsen & Christensen, 1979; Sekiguchi, 1994) may be more representative of normal dietary preferences, but whether recent feeding is indicative of long-term dietary preferences will still not be known (Pierce & Boyle, 1991).

Secondly, different prey types may be digested at different rates (Bigg & Fawcett, 1985; Pierce & Boyle, 1991; Harvey & Antonelis, 1994; Santos et al., 2001c). This may be particularly true for cephalopods in comparison with fish. While the soft tissue of cephalopods may be digested faster than that of fish, cephalopod beaks are particularly resistant to digestion in comparison with fish bones and otoliths—and tend to accumulate in the folds of the stomach lining, in which the hooked upper beaks can become lodged. Thus, when no soft tissue is present fish may be under-represented in stomach samples in comparison with cephalopods (Harvey & Antonelis, 1994; Hilton et al., 1998; Santos et al., 2001c). This is a particular problem when using stomach contents from stranded animals which may not have fed for a long period of time before stranding (Pierce & Boyle, 1991).

Thirdly, in foraging an animal is aiming to meet daily metabolic requirements as well as any additional metabolic and nutrient requirements, such energy stores for growth, migration or reproduction. Therefore, it is important to consider the energy contribution represented by prey items. One larger individual may contribute an equal or greater amount of energy than a large number of small individuals. Therefore, biomass represented by each species is a better measure (than numbers) of contribution to the energy budget of the animal, but such data were not available in many reports of beaked whale stomach contents examined here and this may bias interpretations of the relative importance of each prey species contribution to the animal's energy budget. However, the use of biomass

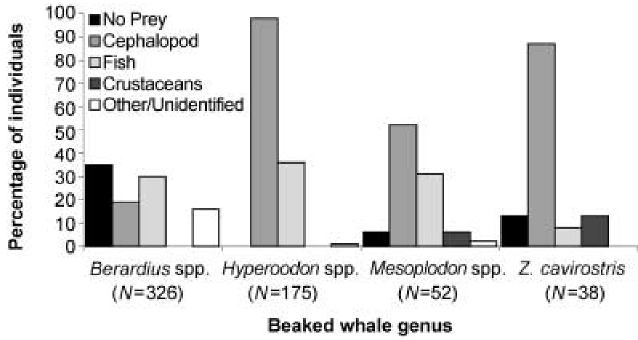

Figure 1. Occurrence of different prey types for different beaked whale genera.

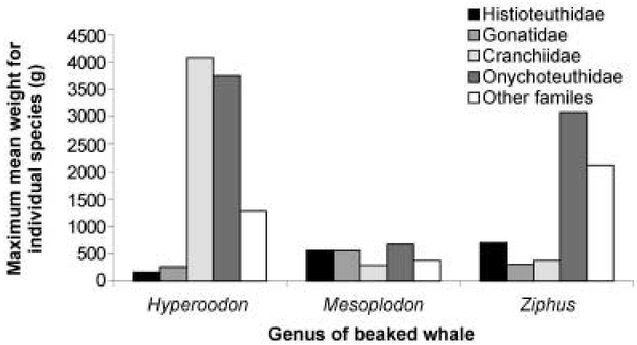

Figure 2. Largest mean body weight for individual species of various cephalopod families recorded from stomachs of each genus of beaked whales.

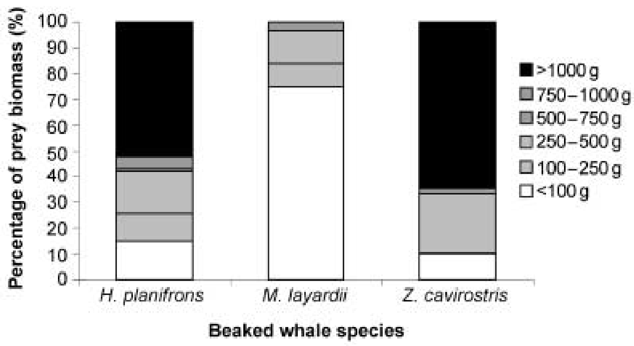

Figure 3. Average percentages of total prey biomass comprising cephalopod species of different mean weights in three species of beaked whale from South African waters. Data for *Hyperoodon planifrons* are the combined values for two animals from Sekiguchi et al., 1993, data for *Mesoplodon layardii* are the combined values of 13 animals from Sekiguchi et al., 1996 and data for *Ziphius cavirostris* are the combined values for four animals from Sekiguchi, 1994.

Table 2. *Reports of stomach contents analysis with main item by number and mass for* Mesoplodon *species. By-caught animals are marked with an * before the species name, and animals caught during whaling by a* $^{+}$. *Stranded animals are unmarked.*

Species and location	No. stomachs analysed	No. items	Main item by numbers (% of total)	Main item by mass (% of total, mean mass)	Reference
M. bidens, Scotland	3 (2 females, one male, 4.59–5.04 m	17	Merluccidae spp. (52.9%) and Gadidae spp. (41.3%)	–	Santos, unpubl. data
M. bidens, Newfoundland, Canada	1 (Male, 4.10 m)	1	Gadidae spp.	–	Dix et al., 1986
* *M. bidens*, NE US	6	4106	Bethopelagic fish (98.9%)	–	Gannon et al., 1998
M. carlhubbsi, W. Coast US	1 (HSUZ 1999)	9	*Octopoteuthis deletron* (44.4%), *Gonatus* spp. (33.3%), and *Onychoteuthis borealijaponica* (22.2%)	–	Mead et al., 1982
M. carlhubbsi, W. Coast US	1 (HSUZ 2680)	741	*Gonatus* spp. (86.1%), *Onychoteuthis borealijaponica* (5.7%), *Octopoteuthis deletron* (3.9%), and *Lampanictus regalis* (2.6%)	–	Mead et al., 1982
M. carlhubbsi, W. Coast US	1 (USNM 504128)	99	*Histioteuthis dofleini* (51.5%), *Gonatus* spp. (41.4%)	–	Mead et al., 1982
M. carlhubbsi, W. Coast US	1 (LACM 54327)	2	*Onychoteuthis borealijaponica* (100%)	*O. borealijaponica* (100%)	Mead et al., 1982
M. carlhubbsi, W. Coast US	1 (CAS 16596)	6	*Histioteuthis dofleini* (66.7%), *Onychoteuthis borealijaponica* (16.7%), *Octopoteuthis deletron* (16.7%)	–	Mead et al., 1982
M. densirostris, Brazil	1 (female, 4.19 m)	1	Plastic threads (100%)	–	Secchi & Zanzur, 1999
M. densirostris, South Africa	1 (Male)	16	Hake (36.75%), unidentified fish (31.25%), *Ptrygosquilla armata* (18.75%) and *Lepidopus caudatus* (12.5%)	*L. caudatus* (97.4%)	Sekiguchi, 1994
M. densirostris, Wales	1 (female, 4.11 m)	1	*Histioteuthis reversa*	–	Herman et al., 1994
M. europaeus, St Croix	1 (male, 4.57 m)	–	*Gnathophausia ingens*	–	Rossairo-Delestre et al., 1999

Table 2. *Continued.*

M. europaeus, Curaçao	1 (male)	35	*Chauliodus sloani* (37.1%), *Gnathophausia ingens* (34.3%), *Octopoteuthis* spp. (11.4%)	–	Debrot & Barros 1992
M. grayi, Brazil	1 (male 4.46 m)	0	–	–	Andre Barreto, Pers. Comm.
+*M. grayi*, South Africa	1 (male)	6	Unidentified fish (83.3%), Merluccidae spp. (16.7%)	–	Sekiguchi, 1994
M. grayi, Indian Ocean	1 (female)	2	*Phoyichthys argenteus* (50%) and *Lampadena* sp. (50%)	–	Sekiguchi, 1994
M. hectori, North Pacific	1 (female, 4.43 m)	3	*Octopoteuthis deletron* (66.7%) and unidentified invertebrate (33.3%)	–	Mead, 1981
M. hectori, New Zealand	1 (male, 2.9 m)	0	–	–	Baker et al., 2001
M. layardii, South Africa	13	223	*Histioteuthis* sp. (26.01%), *Taonius pavo* (17.49%), *Histioteuthis macrohista* (9.42%), *Teuthoweinia pellucida* (5.38%), *Taonius* sp. (4.48%) and *Chiroteuthis* spp. (4.04%)	*Histioteuthis* spp. (22.6%, 73.9 g), *T. pavo* (21.01%, 92.67 g), *H. macrohista* (9.84%, 88.86 g), *Gonatus antarcticus* (9.08%, 344.43 g) and *Mastigoteuthis* spp (7.62%, 65.64 g)	Sekiguchi et al., 1996
M. layardii, New Zealand	1	9	*Chiroteuthis* spp. (33.3%), *Teuthowenia pellucida* (22.2%), *Histioteuthis* spp. (22.2%) and *Taonius pavo* (11.1%)	*Histioteuthis miranda* (53.94%, 566.2 g), *T. pellucida* (18.30%, 96.05 g), *Histioteuthis meleagroteuthis* (12.21%, 128.2 g) and *Chiroteuthis* spp. (10.18%, 35.6 g)	Sekiguchi et al., 1996
M. mirus, South Africa	1	6	*Teuthowenia* sp. (50%), unidentified fish (50%)	–	Sekiguchi, 1994
M. peruvianus, Peru	1	70	? *Notoscopelus resplendens* (34.2%), Nemipteridae ? (34.3%), Ophidiiformes (25.7%)	–	Reyes et al., 1991
M. stejnegeri, Alaska	11	264	*Gonatus pyros* (28.8%), *Belonella borealis* (25.4%), *Gonatus berryi* (9.9%), *Gonatopsis–Berryteuthis* (8.3%) and *Ecogonatus tinro* (6.1%)	–	Walker & Hanson, 1999

Table 3. *Reports of stomach contents analysis with main item by number and mass for* Ziphius cavirostris. *By-caught animals are marked with an * before the location name, and animals caught during whaling by a* $^{+}$. *Stranded animals are unmarked.*

Location	No. stomachs analysed	No. items	Main item by numbers (% of total)	Main item by mass (% of total, mean mass)	Reference
Bay of Biscay, France	1	378	Plastic bags and sheets	–	Poncelet, et al., 2000
Galicia, Spain,	1 (male, 5.10 m)	694	*Teuthowenia megalops* (35.31%), *Taonius pavo* (17.15%), *Mastigoteuthis* sp. (17.15%) and *Chiroteuthis* spp. (6.05%)	*Teuthowenia pellucida* (25.3%, 194.05 g), *Pholidoteuthis boschmai* (20.09%, 2284.34 g), *Todarodes sagittatus* (14.31%, 2210.54 g), *Mastigoteuthis* sp. (11.01%, 92.13 g) and *T. pavo* (9.96%, 75.38 g)	Santos et al., 2001b
Galicia, Spain	1 (female, 5.10 m)	674	*Teuthowenia megalops* (43.32%), *Histioteuthis reversa* (27.6%) and *Mastigoteuthis* sp. (5.19%)	*Teuthowenia megalops* (41.26%, 109.07 g), *Histioteuthis reversa* (17.77%, 61.18 g) and *Todarodes sagittatus* (13.8%, 1262.39 g)	Santos et al., 2001b
Outer Hebrides, UK	1 (female, 5.86 m)	8430	*Teuthowenia megalops* (22.23%), unidentified oegopsid (12.06%), *Gonatus* spp. (11.18%), *Taonius pavo* (10.78%) and *Mastigoteuthis* sp. (6.32%)	*Gonatus* sp. (30.67%, 191.85 g), *Teuthowenia megalops* (16.23%, 50.16 g), *Taonius pavo* (10.99%, 78.70 g), *Histioteuthis arcturi* (7.85%, 46.21 g) and *Mastigoteuthis* sp. (7.63%, 307.65 g)	Santos et al., 2001b
Coasts of France	8	–	Cephalopods (5 animals), fish (1), empty (3)	–	Desportes, 1985
Mediterranean coast of Spain	1 (male, 5.10 m)	385	*Histioteuthis reversa* (63.1%), *Galiteuthis armata* (9.3%), *Histioteuthis bonnellii* (7.5%) and *Todarodes sagittatus* (6.2%)	*H. bonnellii* (35.0%) and *H. reversa* (24.7%)	Blanco et al., 1997
Mediterranean coast of Spain	1 (female, 3.85 m)	88	*Chiroteuthis veranyi* (26.1%), *Histioteuthis reversa* (20.4%), Cranchiidae sp. (12.5%), *Todarodes sagittatus* (9.9%) and *Histioteuthis bonnellii* (8.1%)	*H. bonnellii* (37.6%) and *T. sagittatus* (36.7%)	Blanco et al., 1997
Mediterranean	1 (female 5.05 m)	233	*Histioteuthis reversa* (86.7%) and *Histioteuthis bonnellii* (7.7%)	–	Carlini et al., 1992
Greece	7	38	*Octopoteuthis sicula* (47.4%), *Histioteuthis bonnellii* (39.5%)	–	Lefkaditou & Poulopoulos, 1998

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Table 3. *Continued.*

Mediterranean	1 (female, 3.3 m)	79	*Histioteuthis reversa* (65.8%), *Ancistroteuthis lichtensteinii* (22.7%)	–	Podesta & Meotti, 1991
Dutch Antilles	1 (female, 5.38 m)	–	Unidentified cephalopods and *Gnathophausia ingens*	Unidentified cephalopods (77%) and *G. ingens* (23%)	Debrot & Barros 1994
Texas, USA	1 (female, 5.70 m)	–	*Loligo peali*, unidentified cephalopods, Mango seed, Corncob and black coal-like material	–	Fertl et al., 1997
South Africa	4	69	*Octopoteuthis* sp. (15.94%), *Teuthowenia* sp. (15.94%), *Gnathophauisa ingens* (14.49%), *Chiroteuthis* sp. (10.14%), *Moroteuthis knipovitchi* (5.8%) and *Moroteuthis robsoni* (5.8%)	*M. knipovitchi* (24.89%, 2521.6 g), *M. robsoni* (14.35%, 1453.7 g), *Teuthowenia* sp. (7.95%, 292.96 g), *Octopoteuthis* sp. (6.87%, 253.19 g), *Taningia danae* (6.82%, 2763.7 g) and *Moroteuthis* sp. (6.8%, 62756.1 g)	Sekiguchi, 1994
Alaska, USA	1 (6.58 m)	433	*Taonius* sp. (36.7%), *Gonatus middendorffi* (14.8%) *Galiteuthis* sp. (10.4%), *Gonatus madakoi* (10.2%)	–	Fiscus, 1997
Alaska, USA	1 (female, 5.93 m)	458	*Taonius/Chiroteuthis* (67.9%), *Taonius* sp. (13.5%), *Chiroteuthis* sp. 8.7%) and *Gonatopsis/Berryteuthis* (7.0%)	–	Forster & Hare, 1990
Alaska, USA	2	1304	Unidentified cephalopods (99.1%)	–	Kenyon, 1961
California, USA	1 (male)	0	–	–	Houck, 1958
Taiwan	1 (female, 4.68 m)	1	One cephalopod beak and crustacean parts	–	Wang et al., 1995
Taiwan	1 (female, 5.60 m)	63	*Enoploteuthis chuni*, *Pholidoteuthis* sp., *Octopoteuthis* sp., *Histioteuthis* sp. Mastigoteuthidae/Chiroteuthidae and Ommatostrephidae. Also contained crustacean parts and a wooden stick	–	Wang et al., 1995
Taiwan	1 (female, 5.60 m)	580	575 cephalopod beaks, 5 fish otoliths, crustacean parts and five or six soft, flaky rocks	–	Wang et al., 1995
New Zealand	1 (male, 6.18 m)	94	*Teuthowenia megalops* (45.7%), *Taonius cymoctypus* (30.8%), *Histioteuthis atlantica* (5.3%), *Teuthowenia antarctica* (4.3%)	–	Fordyce et al., 1979

as an indicator of contributions of specific prey species to an animal's total energy budget also has limitations. For example, biomass is usually calculated from hard remains such as otoliths, bones or beaks using regression models (e.g. Clarke, 1986). Some of these models, particularly for less-well known species of cephalopods, are based on very small numbers of samples and their accuracy is unknown (Santos et al., 2001c). In addition, individual prey species can vary greatly in their weight and composition over time (e.g. Hislop et al., 1991), something not taken into account in most regression models. As a result, estimated biomass may be a poor indicator of actual biomass and particularly of the energy obtained from prey. In addition, the use of biomass will over-estimate the importance of prey of low calorific density (Pierce & Boyle, 1991; Santos et al., 2001c). For example, Clarke et al. (1985) found that although the calorific density of dry squid remained similar across various species of oceanic squid, the calorific density of wet weights varied considerably being almost twice as much in some species ('muscular' species) as others ('ammoniacal' species). This variation is thought to be primarily due to differences in water content of the squid. However, while the use of actual energy obtained from prey may be a better measure of dietary preferences, sufficient data on the energy values and how they vary within species may not be available for many of the species which are recorded from beaked whales.

Finally, stomach contents may be contaminated by animals which were consumed by the whale's prey before it was eaten (Pierce & Boyle, 1991). For example, smaller items in a predator's stomach may have come from the prey's stomach rather than having actually been directly consumed by the predator in question. Such items would, therefore, not reflect prey preferences of the predator (or contribute significantly to its energy budget). Secondary digestion can, as a result, lead to an over-estimate of the importance of smaller prey items with less easily digested body parts (such as small cephalopods) in the actual diet. The larger a prey item the less likely it is to have been indirectly consumed, so it is more certain that larger prey items actually represent dietary preferences than smaller ones (Mead et al., 1982). However, separating which prey remains represent direct consumption and which do not is not a simple matter and the results can vary between studies. For example, when examining diet in sperm whales (*Physeter macrocephalus* Linnaeus, 1758), some authors consider all sizes of cephalopods found in the stomach to have been directly consumed (e.g. M.R. Clarke et al., 1976, 1993) while others consider smaller squid in sperm whale stomachs to have been indirectly consumed (e.g. R.M. Clarke et al., 1988). These limitations and biases of stomach contents analysis need to be taken into account when considering dietary preferences of beaked whales based solely on such data.

METHODOLOGY

This study is based mainly on published literature and personal communications. In general, information on individual whales from known locations was used to allow intraspecific comparisons to be carried out. Where possible, exact numbers of each prey species identified from an individual beaked whale's stomach were noted along with estimated body size, estimated body weight, and proportion of stomach contents represented by that species, both in terms of total numbers and total estimated biomass. Interspecific comparisons of the importance of particular prey taxa in the diet used data on frequencies of occurrence, numbers of individual prey animals and prey biomass, as available. In some cases, the required data (e.g. biomass) were not presented in the original papers but could be derived from other data presented (e.g. cephalopod rostral lengths). Regressions relating cephalopod beak size to body weight were taken from Clarke (1986). Although species identified from beaked whale stomachs are reported here as 'prey' species, this does not necessarily imply direct consumption (see above).

Data on prey species which contributed substantially to the stomach contents of beaked whales, in terms of numbers or biomass, were analysed for a number of ecological characteristics. Body length and weight (whether reconstructed or measured directly) of individuals in stomach contents were noted. From the literature, data were acquired on the typical range of body length, vertical distribution, vertical migration pattern, habitat preference, use of bioluminescence and buoyancy strategy. This allowed the identification of aspects of prey ecology which may indicate dietary preferences in beaked whales.

RESULTS AND DISCUSSION

Available data on beaked whale stomach contents from different beaked whale genera

Sufficiently detailed data to allow investigation of dietary preferences were located for three genera, comprising data from 265 individual beaked whales representing 14 different species. Of this, 175 stomachs were obtained from *Hyperoodon* species, 52 from *Mesoplodon* species and 38 from the single *Ziphius* species. Limited information was also available on two species of the genus *Berardius* and one individual from the single species in the genus *Tasmacetus*. No information is avaliable on stomach contents of the final beaked whale genus *Indopacetus*.

The genus Hyperoodon

Data from stomach contents analysis were found for 169 specimens of *Hyperoodon ampullatus* (the northern bottlenose whale), contained in five separate reports (see Table 1). These whales came from Labrador and Iceland (108 and 46 animals respectively), the Faeroe Islands (one), the Netherlands (two), Scotland (one), Denmark (two) and Hiddensee Island in the Baltic (one). The whales from the first report (Benjaminsen & Christensen, 1979) were taken during commercial whaling activities, in the second (Bloch et al., 1996) the whales were taken during a traditional drive fishery, and in the last three reports (Clarke & Kristensen, 1980; Lick & Piatkowski, 1998; Santos et al., 2001a) the whales were found stranded.

Four reports of stomach content analysis of *Hyperoodon planifrons* Flower, 1882 (the southern bottlenose whale) were located, consisting of data on six separate animals; stranded in Australia (one animal), South Africa (two), Heard Island in the South Atlantic (one) and Tierra del Fuego at the southern tip of South America (two). The most important prey items in terms of numbers and biomass represented are shown in Table 1.

The two *Hyperoodon* species occupy temperate, sub-polar and polar regions. *Hyperoodon ampullatus* is restricted to such waters in the North Atlantic, while *H. planifrons* is found throughout such waters in the southern oceans (Mead, 1989a). In total, *Hyperoodon* species were reported to contain the remains of 45 species of cephalopods from 18 families, eight species of fish, two species of tunicates and one specie of crustacean. *Hyperoodon planifrons* were generally reported to contain a greater range of cephalopod species than *H. ampullatus* (41 species from 17 families in the former and 12 species from nine families in the latter). Where information on prey was available, *Gonatus* species, such as *Gonatus fabricii* Lichtenstein, 1818, were found to contribute the greatest biomass in *H. ampullatus*, while Onychoteuthid, Cranchiid, Gonatid and Histioteuthid species contributed almost all of the biomass in *H. planifrons*. The largest individual prey item reported in *H. ampullatus* was much smaller than that found in *H. planifrons* (1219 g and approximately 4080 g respectively, although the latter figure is the mean of several individual prey items). In general, *H. ampullatus* contained the remains of smaller squid than *H. planifrons*.

Fish were commonly recorded in *H. ampullatus* from some locations (Labrador and Iceland) but were reported only once, in small numbers, from *H. planifrons* (the Heard Island specimen—Slip et al., 1995). However, this may reflect the differential digestion rates of cephalopod and fish remains (see above) as almost all the *H. ampullatus* specimens containing fish were animals killed during commercial whaling operations (Benjaminsen & Christensen, 1979), while the *H. planifrons* stomachs examined came from stranded animals (e.g. Slip et al., 1995). Similar differences have been noted when comparing recent and historical records of sperm whale diet—the latter, based on animals caught during whaling, suggest that fish may form a substantial part of the diet while the former, based on strandings, report a diet consisting almost exclusively of cephalopods (Santos et al., 1999).

The genus Mesoplodon

The genus *Mesoplodon* contains 14 currently recognized species which are found in all the world's oceans and most of the adjacent seas that offer suitable deep water (>200 m) habitats, with the possible exception of the Mediterranean (Mead, 1989b). Although little is known about actual distributions of some species, it is almost certain that all species are, for at least part of their range, sympatric with one, or more, other *Mesoplodon* species (MacLeod, 2000a,b).

When comparing stomach contents of *Mesoplodon* species, two problems readily become apparent. Firstly, relatively few studies have been published for *Mesoplodon* species (52 stomachs from 11 species) and most of these were from *Mesoplodon layardii* Gray, 1865, the strap-toothed whale, and *Mesoplodon stejnegeri* True, 1885, Stejneger's beaked whale (Table 2). In particular, in relation to the number of strandings of *Mesoplodon* whales around the world, it is surprising that more stomach contents have not been reported and there is a need to ensure that in the future this information is reported whenever possible. Secondly, in the *Mesoplodon* stomachs which have been examined, relatively few prey remains have been recorded. Numbers of prey individuals are typically in double figures, but stomachs often contained few—or no—prey (the *Mesoplodon* stomachs discussed here averaged 34 prey individuals per stomach—Table 2). By comparison, individual *Hyperoodon* and *Ziphius* stomachs commonly contain hundreds and even thousands of prey (the former averaged 1452 prey per stomach for this study, while the latter averaged 454). Analysis of the dietary preferences of *Mesoplodon* species is thus somewhat limited by lack of data.

Some general points emerge however. In total, 32 species of cephalopods from 10 families, 14 species of fish and two species of crustaceans were recorded from the stomachs of *Mesoplodon* species. Cephalopoda were recorded in 77% of individuals, while fish were recorded in 20% and crustacea in 5% of individuals (Figure 1). Of cephalopods, the families Cranchiidae, Histioteuthidae, and Gonatidae were the most commonly recorded. Of the *Mesoplodon* species included in this study, *Mesoplodon carlhubbsi* Moore, 1963 (Hubbs' beaked whale), *M. layardii* and *M. stejnegeri* most frequently contained cephalopods and contained the greatest range of cephalopod species. No cephalopods were reported from *Mesoplodon mirus* True, 1913 (True's beaked whale) or *Mesoplodon grayi* van Haast, 1896 (Gray's beaked whale). With the exception of *M. stejnegeri*, fish were found in some individuals of all *Mesoplodon* species. Freshly killed *Mesoplodon bidens* Sowerby, 1904 (Sowerby's beaked whale) primarily contained bottom-dwelling deep-water (greater than 400 m) fish of between 100 and 200 mm (Gannon et al., 1998). In two cases, *Mesoplodon europaeus* Gervais, 1855 (Gervais' beaked whale) was reported to contain the crustacean *Gnathophausia*, and in one of these two cases the stomach was reported to contain nothing else.

Insufficient information was available to compare the importance of different prey in terms of biomass as such information was only available in sufficient quantities for *M. stejnegeri* and *M. layardii*. However, these two species, along with a lesser number of *M. carlhubbsi*, were found to contain squid of approximately similar sizes, usually of under 500 g in weight (Table 2).

On the basis of these scant data for *Mesoplodon* species, it seems that both cephalopods and fish are important components of diet, rather than cephalopods alone (Figure 1). Indeed, some species (*M. bidens*, *M. grayi* and *M. mirus*) may rely principally on fish rather than cephalopods as the main component of their diet. Only *M. carlhubbsi*, *M. layardii* and *M. stejnegeri* were recorded to primarily contain cephalopods in their stomach. Interestingly these are the species for which more data are available and the picture could change if more data were available for the other species. However, if the differential digestion rates of fish and cephalopod hard parts are taken into account (cephalopod remains, particularly beaks being more resistant to digestion), it is more likely that fish are under-represented in the stomachs analysed than cephalopods (see above).

The genus Ziphius

The genus *Ziphius* contains one species, *Ziphius cavirostris* G. Cuvier, 1823 (Cuvier's beaked whale). This is the most widely distributed species of beaked whale, found throughout all warm-temperate, sub-tropical and tropical waters of the world (Heyning, 1989). Dietary data were available for 38 specimens of *Z. cavirostris* from throughout the range of the species, including Alaska, California, the north-eastern Atlantic, the Mediterranean, the Gulf of Mexico, the Caribbean, Brazil, South Africa, Taiwan and New Zealand (Table 3). In total, 46 species of cephalopods from 15 families, and two species of crustaceans, were reported from the stomachs of *Z. cavirostris*. Eighty-seven per cent of the individuals contained the remains of cephalopods, while 13% contained crustacean remains and 8% contained the remains of fish (Figure 1).

Of the cephalopods, the families Histioteuthidae (65% of records), Gonatidae (59%), Chiroteuthidae (53%), Cranchiidae (53%), Octopoteuthidae (53%), Onychoteuthidae (47%), Ommastrephidae (41%), Pholidoteuthidae (24%) and Branchioteuthidae (18%) were the most frequently reported (Table 3). In terms of numbers and biomass, the families Histioteuthidae, Cranchiidae and/or Gonatidae were the most important in most cases (Table 3). In addition, in one specimen, the family Onychoteuthidae made up a significant proportion of the total biomass (46%). These four families of cephalopods together contributed between 44% and 99.5% of numbers, and between 49% and 76% of biomass, of prey in individual stomachs.

Only one report, summarizing stomach contents from four specimens from South Africa (Sekiguchi, 1994) provided mean weights for species consumed. However data were also available for three animals from the north-east Atlantic examined by Santos et al. (2001b). In the South African animals, the largest mean weight for a prey species was 3088 g for specimens of *Onychoteuthis banksi* Leach, 1817. Prey species with a mean individual weight of over 1 kg accounted for 64% of biomass represented in the stomach contents. In the animals from the north-east Atlantic, the largest mean weight for a squid species from any one whale was 2211 g for *Todarodes sagittatus* Lamarck, 1798, while the largest individual squid was a 4372 g specimen of the same species. Prey species with a mean weight over 1000 g accounted for between 11% and 34% of total biomass represented in these whales.

Crustaceans were recorded from three specimens. In two specimens the crustacean was *Gnathophausia ingens* Dohrn, 1870 and in one case it was *Pasiphaea tarda* Krøyer, 1845. Fish do not seem to be an important component of reported stomach contents of *Z. cavirostris*, with a small number being recorded in three animals (Desportes, 1985; Sekiguchi, 1994; Wang et al., 1995). However, Nishiwaki & Oguro (1972) found that although *Z. cavirostris* taken by whalers in waters less than 1000 m depth predominantly contained cephalopod remains, whales taken in deeper waters had eaten mainly fish. This is at odds with the information from stranded animals reviewed here, but could be the result of a bias due to differential digestion rates of the hard parts of cephalopod and fish, resulting in fish being under-represented in the stomachs of stranded animals vs those killed on feeding grounds (see below). In addition, animals in shallower waters may be more likely to strand, again resulting in an under-representation of fish species. Therefore, fish may be an important component of *Ziphius* diet in some areas, or water depths, but this does not show up in analysis of stomach contents of stranded animals.

The genus Berardius

For the two species in the genus *Berardius*, although a large number of animals have been examined for one species, only very limited information on stomach contents was available. Haast (1870) noted that a single Arnoux's beaked whale (*Berardius arnuxii* Duvernoy, 1851) stranded in New Zealand contained about 'half a bushel' of cephalopod beaks (approximately 18 litres). Nishiwaki & Oguro (1971) noted that of 383 Baird's beaked whales taken during a Japanese whale fishery off the coasts of Japan (*Berardius bairdii* Stegneger, 1883) 55% contained food and 30% were empty. The remainder were not examined. However no information is given as to the quantities of different prey types or details of what individual animals contained. Instead this information is summarized as the percentage of animals which contained certain categories of prey, therefore allowing no detailed comparisons to be made with other species or between individuals of the same species. In addition, no data are given on prey size. Of the approximately 200 animals with food remains in the stomachs, 40.7% contained deep-water fish, 28.9% squid, 3.9% mackerel, 1.3% sardines, and 24.3% contained unidentified food. It was also noted that squid were the predominant prey in areas III and IV (to the east of the island of Hokkaido in northern Japan between approximately 41°N and 46°N), a mix of prey types in area II (east of the Japanese mainland between approximately 36°N and 41°N) and predominantly deep-water fish in areas I (south of 36°N). Nishiwaki & Oguro (1971) attribute this to whales taking common prey types in each area without intentional choice and that whales primarily consume deep-water fish while migrating north in spring and squid while migrating south again as squid are most commonly recorded from whales in northern areas and from August to November. In addition, Baird's beaked whales have been recorded to contain saury (*Coloabis* sp.), rockfish (*Scorpaenidae*), skates (*Raja* sp.), rat-tails (*Coryphenoides* sp.) and squid of the genera *Gonatus*, *Onychoteuthis* and *Moroteuthis* (Balcolm, 1989).

The genus Tasmacetus

Stomach contents analysis has only been reported from one individual of Shephard's beaked whale (*Tasmacetus shepherdi* Oliver, 1937). This species differs from all other beaked whales in having functional teeth in the upper jaw and numerous teeth in the lower jaw (Oliver 1937). This individual from Punta Buenos Aires, Argentina contained *Merluccius hubbsi*, an unidentified serranid and an unidentified brotulid (all bottom living fish) as well as one small squid beak and remains of the crab *Peltarion spinulosum*. Mead (1989c) does not consider these latter two to be direct prey of this species.

Ecology of the prey species

With regards to the ecology of prey species, there was no apparent preference for prey with specific physiological or ecological characteristics (for example bioluminescence, vertical migration patterns, or, in the case of cephalopods, specific buoyancy control mechanisms) other than the depth at which they occur. All beaked whales apparently preferred prey which occur predominantly between 200 and 2000 m, i.e. species occurring off the Continental Shelf. Many of these prey species occur at or close to the bottom for at least part of their life cycle, although some are also found in mid-water. Coupled with the high number of different prey species and families (particularly cephalopods) recorded, this suggests that beaked whales are generalist feeders taking whatever suitable prey they come across or which are locally abundant in their preferred feeding habitat. In this respect, beaked whales may be considered generalist predators of deep-water squid, fish and crustaceans, with a possible preference for benthic or benthopelagic species.

Comparison between the genera

Due to the limited range of species from each genera (especially the genus *Mesoplodon*) for which stomach contents data were available, comparisons were limited to the generic level. This allowed the question of whether different genera occupied different dietary niches to be investigated and to look for potential competition between genera. Although stomach samples from all genera were found to contain primarily cephalopod remains, the importance of other types of prey varied between the genera (Figure 1). *Ziphius cavirostris* contained almost exclusively cephalopod remains, while *Mesoplodon* stomachs frequently contained a large proportion of fish. In fact, in three species of *Mesoplodon* (*M. bidens*, *M. grayi* and *M. mirus*) fish were the most important prey. In the genus *Hyperoodon*, one species, *H. ampullatus*, was frequently recorded as having eaten fish, while fish were rarely recorded in *H. planifrons*. There is a similar relationship in the genus *Beradius*, with the northern species, *B. bairdi*, being found to contain a mixture of fish and squid (although varying in proportion between locations) while the southern species, *B. arnuxii*, has only been found to contain cephalopod remains (although based on a single sample). Again based on a very limited sample size (one individual) *T. shepherdi* contained primarily fish. This in conjunction with its very different dentition suggests that it primarily consumes fish rather than cephalopods (Mead, 1989c). Crustaceans, particularly *G. ingens*, may be a minor, but important, component of the diet of *Ziphius* and in some cases *Mesoplodon* species (Figure 1).

Of the cephalopods, Cranchiid, Histioteuthid, Gonatid and Onychoteuthid species all contributed substantially to total numbers and biomass of prey recorded in *Hyperoodon*, *Ziphius* and *Mesoplodon* species (no such data were available for any other genera). Although based on the small number of reports, a general pattern can be seen. *Hyperoodon* (particularly *H. planifrons*) and *Ziphius* species had eaten much larger cephalopods than *Mesopolodon* species (Figure 2). *Mesoplodon* species generally contained cephalopods of under 500 g body weight and the largest recorded prey item was 672 g. By comparison, *Hyperoodon* and *Ziphius* species frequently contained cephalopods over 1 kg in weight, and in some cases over 4 kg.

This generalization is supported when stomach contents of beaked whale species from the same locations are compared. Stomach contents from all three genera have been examined from whales stranded in South Africa (Figure 3). *Hyperoodon planifrons* contained the remains of the largest squid (4081 g mean weight for *Mesonychoteuthis hamiltoni* Robson, 1925) and the majority of prey biomass was made up of cephalopod species with a mean mass of over 1000 g (Sekiguchi et al., 1993). *Ziphius cavirostris* contained slightly smaller squid (maximum mean weight 3088 g for *O. banksi*), but cephalopod species with a mean mass over 1000 g still made up the bulk of the diet (Sekiguchi, 1994). In contrast, *Mesoplodon layardii* from South Africa contained the remains of much smaller squid (Figure 3). The largest individual recorded squid was 672 g (*Moroteuthis robsoni* Adam, 1962) and the majority of biomass consisted of cephalopod species with a mean mass of less than 100 g (Sekiguchi et al., 1996).

In Alaska, strandings of two species of beaked whale have been recorded, *Z. cavirostris* and *M. stejnegeri*. When both beaked whale species were recorded to contain the same squid species, *Z. cavirostris* tended to take larger specimens. When all squid species were compared, *Z. cavirostris* contained larger individuals (up to 485 g for *Gonatus madakai* Kubodera & Okutani, 1977) than *M. stejnegeri* (up to 278 g for *Gonatus berryi* Naef, 1923—Fiscus, 1997; Walker & Hanson, 1999).

Finally, in the north-east Atlantic, when *H. ampullatus* and *Z. cavirostris* stomachs contained the same species they contained similar-sized individuals (e.g. mean weights: *Gonatus* species—110 g to 221 g in *H. ampullatus* and 174 g to 259 g in *Z. cavirostris*; *T. sagittatus*—1158 g in *H. ampullatus*, 1262 g to 2111 g in *Z. cavirostris*—Clarke & Kristensen, 1980; Lick & Piatkowski, 1998; Santos et al., 2001a,b).

It is possible that differences in prey sizes between different beaked whale genera relate to differences in body size. *Ziphius* and *Hyperoodon* species are consistently larger than *Mesoplodon* species (in the range of 12 to 100% larger than the *Mesoplodon* size depending on species). However, that beaked whales simply take prey in relation to body size does not fit the observed difference in prey sizes consumed. Firstly, both *Hyperoodon* and *Ziphius* species take smaller prey in the eastern North Atlantic than off South Africa, and in the latter area the largest prey is found in *Ziphius* rather than *Hyperoodon*, despite the *Hyperoodon* species being consistently larger than *Ziphius*. In South Africa, *Ziphius* and *Hyperoodon* take prey which are more than five times heavier than the largest prey consumed by *M. layardii* despite the fact that the *Hyperoodon* species is only approximately 20% longer than the *Mesoplodon* species and *Z. cavirostris* is only about 10% longer. Finally, in Alaska the size of prey consumed by *Ziphius* is similar to the size of prey consumed by a *Mesoplodon* species in South Africa, yet *M. stegnegeri* in Alaska still takes consistently smaller individuals of the same species. This suggests that differences in prey sizes between these three genera is not simply related to differences in body size.

Instead, *Mesoplodon* species appear to consistently consume smaller prey than sympatric *Hyperoodon* and *Ziphius* species. Such a difference in diet would limit direct competition between *Mesoplodon* species and *Ziphius* or *Hyperoodon* species and may represent segregation of the deep-diving cetacean niche to reduce competition. A lack of competition between *Mesoplodon* species and the other two genera is supported by the fact that *Mesoplodon* species are broadly sympatric with one or both of these genera (Heyning, 1989; Mead, 1989a,b; MacLeod, 2000b) and have been sighted at the same locations at the same time

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of year (e.g. *Mesoplodon densirostris* de Blainville, 1817 (Blainville's beaked whale) and *Z. cavirostris* in the north-east Bahamas—MacLeod, unpublished data; *M. bidens* and *H. ampullatus* in the Gully off Nova Scotia—Hooker & Baird, 1999b; *Mesoplodon* sp. and *H. ampullatus* off the coast of Scotland—Weir, 1999).

As well as reducing competition between *Mesoplodon* species and *Hyperoodon* and *Ziphius* species, preferences for different sizes of prey may be linked to small differences in the observed distributions of *M. densirostris* and *Z. cavirostris* in the Bahamas, where the former were most commonly observed in water depths of between 200 and 1000 m, while the latter were most frequently observed in waters greater than 1000 m (MacLeod, unpublished data).

Individual *Mesoplodon* species are frequently sympatric with one or more other *Mesoplodon* species (e.g. in the North Atlantic four species have overlapping distributions in warm temperate waters—MacLeod, 2000b). There was a great deal of variation in the types of prey items found in the stomachs of *Mesoplodon* species, with some containing exclusively fish, some a mixture of fish and cephalopods and some only cephalopods. While this may be an artefact of small sample sizes, it could also represent real differences between sympatric species that allow them to co-exist without undue levels of competition. There is currently not enough information available either on diet or distribution to make any concrete assertions regarding niche separation between *Mesoplodon* species.

The sizes of prey consumed by *Hyperoodon* and *Ziphius* appear to overlap quite considerably, with both commonly containing larger cephalopods of over 1000 g, suggesting that these two genera occupy a similar dietary niche. As a result, there may be competition between these two genera for the same prey items and, if this is the case, geographic segregation between *Hyperoodon* and *Ziphius* species may occur to reduce competition for food resources. The current distribution of *Hyperoodon* and *Ziphius* species supports this hypothesis. *Hyperoodon* species are limited to polar, sub-polar and cold-temperate waters of the North Atlantic and the southern oceans, although *H. ampullatus* is occasionally recorded in warm-temperate waters (Mead, 1989a). *Ziphius*, by contrast, is recorded from tropical, sub-tropical and warm-temperate waters of all the world's oceans as well as the Mediterranean and the Caribbean/Gulf of Mexico, with the exception of the North Pacific where it is recorded from colder temperate and sub-polar waters, an area where no *Hyperoodon* species occur (Heyning, 1989). There is some geographic overlap in warm-temperate waters in the North Atlantic and in the southern oceans. However, *Hyperoodon* species are thought to be at least partially migratory, moving to higher latitudes in summer (Sekiguchi, et al., 1993; Bloch et al., 1996). *Ziphius* may undertake similar movements so that, although there is a geographic overlap between the two genera, there is no temporal overlap. This is supported by observations in the Bay of Biscay where both *H. ampullatus* and *Z. cavirostris* are recorded, but sightings occur in different months of the year (*H. ampullatus*: May to August, *Z. cavirostris*: March to May—Williams et al., 1999). Reports of *Hyperoodon*-like species from the tropical Indo-Pacific (e.g. Urban et al., 1994), occurring sympatrically with *Ziphius cavirostris*, may at first seem to contradict the above hypothesis of geographic segregation between these two genera. However, it is now thought that these tropical '*Hyperoodon*' are actually *Indopacetus pacificus* (Pitman et al., 1999). Currently nothing is known about the diet of this species, but it would be predicted that its diet would differ in some way from sympatric species of other genera to reduce any potential competition. The same may be expected for other beaked whale genera. *Tasmacetus*, as suggested by its dentition and the single stomach contents, may specialize in feeding on deep-water fish, so limiting competition with other species of beaked whales in the southern oceans where it occurs (where few other beaked whale species have been found to contain large proportions of fish). How the genus *Berardius* fits into this hyopthesis of niche separation or geographic segregation is unclear. In the North Pacific, it may fill a niche somewhat similar to *Hyperoodon* in the North Atlantic, although it has a greater level of sympatry with *Ziphius* than would be expected if this were the case. In the southern oceans, *Berardius* is sympatric with *Hyperoodon*, again suggesting this genus occupies a niche which differs in some way from the proposed *Hyperoodon*/*Ziphius* niche. More data are required to clarify the dietary niche occupied by *Berardius* and allow a full comparison with the dietary niches occupied by other beaked whale genera.

Information on dietary preferences of beaked whales from other sources

There are other methods for acquiring information on diet such as stable isotope analysis and fatty acid analysis of predator body tissues. Stable isotope analysis is based on the ratios of naturally occurring isotopes of a number of elements (usually nitrogen and carbon). The ratios between the isotopes of each element alter in a predictable way depending on trophic position. For example, the ratio of ^{15}N to ^{14}N increases by approximately three parts per thousand for each increase in trophic level (Kelly, 2000). Stable isotope analysis can be used to examine longer-term dietary preferences than is possible using stomach contents analysis (Walker & Macko, 1999; Kelly, 2000) and will be unaffected by many of the biases associated with stomach contents analysis. Although it is difficult to extract detailed information on diet, stable isotope analysis can be used to assess the relative trophic positions of different species (Hobson et al., 1994; Kelly, 2000). For example, Ostrom et al. (1993) analysed the stable isotopes of *M. bidens* and concluded that it fills a trophic position somewhere between the pygmy sperm whale (*Kogia breviceps* de Blainville, 1838) and the sperm whale. In comparison, Hooker (1999) analysed stable isotopes from blubber samples of 17 *H. ampullatus* and the results suggest that this species occupies a higher tropic level than *M. bidens* from the same region (*M. bidens*: $\delta^{15}N=11.7‰\pm0.6$—Ostrom et al., 1993; *H. ampullatus*: $\delta^{15}N=15.3‰\pm0.1$—Hooker, 1999). These results are consistent with the idea that *Mesoplodon* species occupy a different feeding niche to *Hyperoodon*, preying on smaller animals.

Fatty acid signatures can also be used to analyse diet (e.g. Hooker, 1999). This type of analysis is based on the observation that many fatty acids are conserved between trophic levels and so can be used to indicate which species have been contributing to the diet of an animal (Iverson, 1993). Again, this can provide a longer-term record of dietary preferences and is free of many of the biases associated with stomach contents analysis. Hooker (1999) compared fatty acid signatures of blubber samples from *H. ampullatus* to potential prey items. In this case the fatty acid signature of the blubber samples matched that of *Gonatus fabricii*, which has commonly been found in the stomach of *H. ampullatus*. Such analysis may be important in confirming that items found in stomachs are representative of prey consumed over a longer length of time. However, for fatty acid analysis to be of use in identifying prey species, fatty acid signatures of all potential prey species need to be known and this can be a limitation. Fatty acid analysis may be of most use when samples from the whale can be screened against samples from the species which are identified from the stomach. This will highlight any inconsistencies which need further investigation.

To date, these alternative techniques for examining diet have not been applied to beaked whales in a sufficient number of cases to allow any meaningful comparison with stomach contents data. As a result data from stomach contents analysis provide the best available indication of dietary preferences in beaked whales and continue to do so until other techniques are more routinely applied to beaked whales. Given the shortcomings of the limited stomach contents data, the information on trends in diet outlined in this review should be considered preliminary, and be used as a basis for further research rather than acting as a definitive statement of dietary preferences in beaked whales.

The above results and discussion can be summarized by four main hypotheses:

1. All species of beaked whales are generalists and probably feed at or close to the bottom in deep oceanic waters, taking whatever suitable prey they encounter or feeding on whatever species are locally abundant.
2. *Mesoplodon* species occupy a separate ecological niche from both *Ziphius* and *Hyperoodon* species, which allows them to locally co-exist with species of these two genera. This separate niche is for smaller prey, for example cephalopods under 500 g.
3. *Hyperoodon* and *Ziphius* species occupy similar ecological niches, both consuming larger prey than *Mesoplodon* species, for example, cephalopods greater than 500 g and commonly over 1000 g. Competitive exclusion occurs between these two genera, and as a result the two genera are geographically and/or temporally segregated.
4. The remaining genera (*Indopacetus*, *Tasmacetus* and *Berardius*) are predicted to either occupy a different dietary niche from the three genera discussed above, or will segregate from these genera in some way. This may involve geographic segregation and/or habitat segregation. However, currently available data does not provide enough information to suggest which of these, if any, are correct.

Further research will be required to fully test the hypotheses suggested by the above review, particularly research which will examine diet in beaked whales where there are currently few or no suitable data (such as *Tasmacetus*, *Indopacetus* and *Berardius* species) or which uses other techniques to allow the accuracy of stomach contents data to be examined.

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