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Cephalopods as Prey. III. Cetaceans

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Cephalopods as prey. III. Cetaceans

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SUMMARY

Over 80% of odontocete species and two balaen whale species include cephalopods in their diet regularly. In 28 odontocetes they comprise the main food. Predominently cephalopod-eating species are found in the Physeteridae, Ziphiidae, Phocaenidae and Delphinidae. By far the most important of the 28 families of cephalopods represented in the diet of cetaceans are the oceanic Ommastrephidae, Histioteuthidae and the Cranchiidae, with the neritic Loliginidae assuming most importance on the continental shelves. Onychoteuthidae and Gonatidae assume greater importance in polar regions and the North Pacific. The other 22 families form a reservoir from which various cetaceans eat opportunistically and as their sizes permit. There are probably less than 60 cephalopod species regularly in the diet of cetaceans.

Species composition of the food varies regionally, seasonally and annually. Locally, the greatest difference is found between cetaceans that live in oceanic water and continental shelf water. There is a positive correlation between the size of the prey and both the size of pelagic feeding cetacean species and the growth stage within a species. This leads to some partitioning of the food and less competition. Broad estimates show that the biomass of oceanic cephalopods consumed annually by the largest odontocete, *Physeter catodon*, may be over twice the biomass of fish caught by man. Regional estimates show that consumption by cetaceans of little known cephalopod species may greatly exceed the local catches of commercial fish.

1. INTRODUCTION

It has long been known that many odontocetes include cephalopods in their diets. An early awareness (Joubin 1895; Robson 1925) that much could be learnt about cephalopods by the study of their remains in sperm whale (*Physeter catodon* Linnaeus 1758) stomachs received a boost when means were found to identify cephalopod mandibles or 'beaks' (Akimushkin 1955; Clarke 1962) since as many as 28000 were reported from a single stomach. Refinement of the technique (Clarke 1980, 1986*b*) led to studies of sperm whale diet throughout the world (Clarke 1962; Clarke & McLeod 1974, 1976; Clarke *et al.* 1976; Clarke 1977; Clarke *et al.* 1979; Clarke 1980; Clarke & Kristensen 1980; Clarke & McLeod 1980; Clarke *et al.* 1980; Clarke & McLeod 1982; Clarke & Pascoe 1985; Clarke 1986*a*, *b*; Clarke 1987; Clarke *et al.* 1993; Clarke & Goodall 1994; Clarke 1996*a*, *b*; Clarke & Young 1996), and the more detailed study of cephalopods in the diets of many other cetaceans reported here (e.g. Ross 1984; Desportes, 1985).

2. MATERIAL & METHODS

Oportunities for studying cetacean diets are limited to species killed in direct commercial exploitation, such as the sperm whale (Clarke 1980), the pilot whale, *Globicephalus melas* Traill 1809; Desportes & Mouritsen 1993), the species killed unintentionally when fishing for fish (Perrin *et al.* 1973) and animals of all species which are stranded 'naturally'. Rather few workers have had the oportunity to obtain quantitative data from more than a few specimens of any species, particularly enough for obtaining meaningful % occurences.

More details of the methods and the use of cephalopod beaks in dietary studies are given on p. 1067 with an outline of problems (see also Clarke 1986*b* and Clarke *et al.* 1988). Cetacean taxonomy according to Mead & Brownell (1993) is used here.

Qualitative notes on the occurrence of cephalopods in cetaceans were listed previously (Clarke 1986*a*) and these, together with more quantitative studies published before and since 1986 are used here to obtain a general idea of the importance of cephalopods of the various families in the diets of cetaceans. Data for figures 2–7 were extracted from or calculated from the literature; some valuable publications were excluded because the presentation of results prevented such extraction.

For brevity, the termination 'teuthidae' is omitted from cephalopod family names in figures.

3. CETACEANS EATING CEPHALOPODS

Cetaceans in the family Balaenidae are not known to eat cephalopods, although one would assume that they might be taken accidentally with the whales' normal food of zooplankton. The grey whale (*Eschrichtius robustus* Lilljeborg 1861) has been kept healthy in captivity on dead squid and can suck these off the bottom by swimming on its side (Ray & Schevill 1974),

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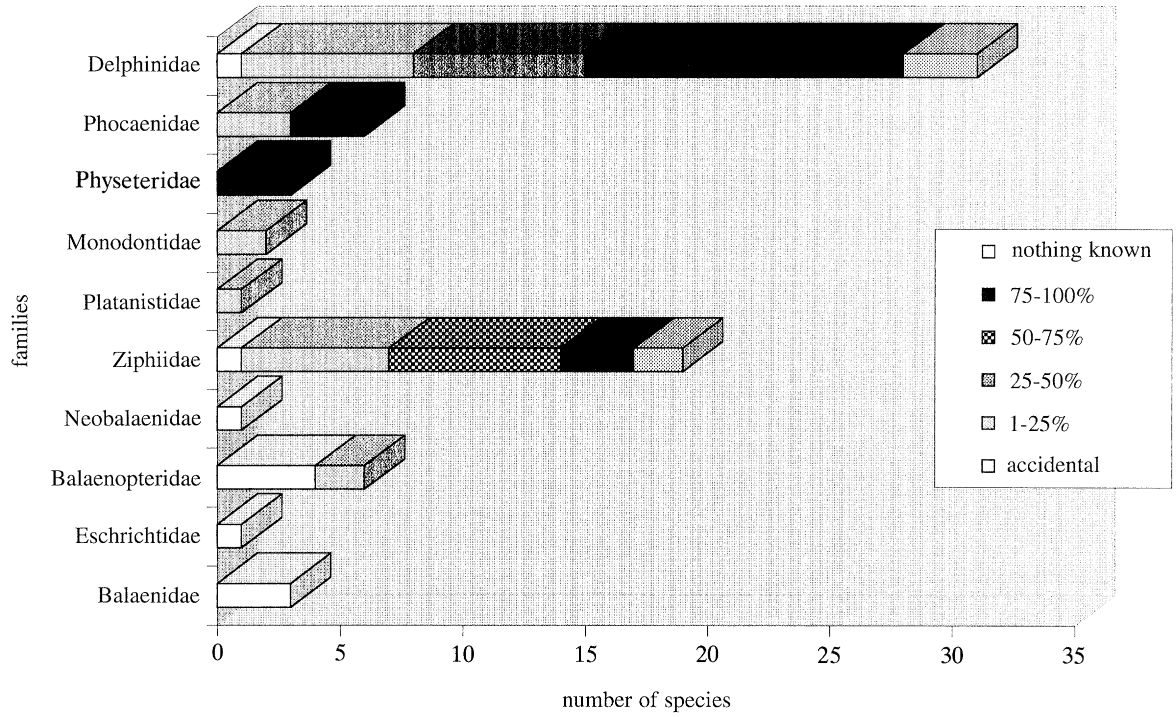

Figure 1. The number of species in each cetacean family having certain percentages of cephalopods in their diet. Based on % mass of stomach contents where possible but otherwise on % number or by subjective observations in the literature. 0–25% includes species known to include cephalopods in the diet but %s are not known.

Table 1. *The occurrence of the main cephalopod families by % of species in the cetacean families*

Family	Ziphiidae	Monodontidae	Physeteridae	Phocaenidae	Delphinidae	Stenidae[a]	Globiocephalidae[a]	Totals
No. of species	13	2	3	5	20	3	6	52
Ommastrephidae	23	50	100	20	45	0	17	18
Onychoteuthidae	46	50	100	20	20	0	0	15
Gonatidae	38	50	33	20	20	0	33	14
Enoploteuthidae	15	0	33	20	30	0	33	12
Octopoteuthidae	46	0	100	0	25	0	17	15
Histioteuthidae	23	0	66	20	30	0	66	16
Cranchiidae	23	0	66	0	15	33	100	12
Loliginidae	8	0	33	60	40	33	66	18
Sepiidae	8	50	0	0	20	0	17	7
Octopoda	15	100	0	0	40	0	50	15

[a] Included in Delphinidae by Meade & Brownell 1993.

but squid are not known to contribute to its normal diet. Of the rorquals (Balaenopteridae), two, Minke (*Balaenoptera acutorostrata* Lacepede 1804) and Sei (*B. borealis* Lesson 1828) whales, certainly eat squid intentionally as food at times, although they mainly take zooplankton (Kawamura 1980). Blue whales (*B. musculus* Linnaeus 1758) and fin whales (*B. physalus* Linnaeus 1758) probably only include squid accidentally with krill. *Caperea marginata* Gray 1846, the only member of the Neobalaenidae, eats copepods and is not known to eat cephalopods (Baker 1987).

While the Ziphiidae and Physeteridae are usually regarded as including the main odontocete cephalopod-eaters, it is clear from figure 1 that cephalopods form an appreciable part of the diet in all the families and in all marine odontocete genera which are sufficiently well known for there to be any certainty.

At least 60 of 67 odontocete species include cephalopods in their diet and, in at least 28 odontocetes, they form the main food (figure 1). Four platanistids living in fresh water, *Orcaella brevirostris* Gray 1866, *Mesoplodon peruvianus* Reyes, Mead & van Waerebeek 1991 and *M. grayi* von Haast 1876 are known to eat fish and are not known to eat cephalopods. We have no knowledge of the food of three species, *Indopacetus pacificus* Longman 1926, *M. ginkgodens* Nishiwaki & Kamiya 1958 and *M. bowdoini* Andrews 1908. Recently, cephalopods have been recorded from *Sousa chinensis* Osbeck 1757 by Barros (personal communication), and from *Phocoena sinus* Norris & McFarland 1968 by Findley *et al.* (1994). The report of their occurrence in *Stenella clymene* Gray 1850 by Perrin *et al.* (1981) has been confirmed by Barros & Odell (personal communication).

4. CEPHALOPODS IN THE DIET

In the Balaenopteridae, 13 families of cephalopod have been recorded (Clarke 1986*a*). Where the proportions of the various families have been found, the histioteuthids and the cranchiids were the most

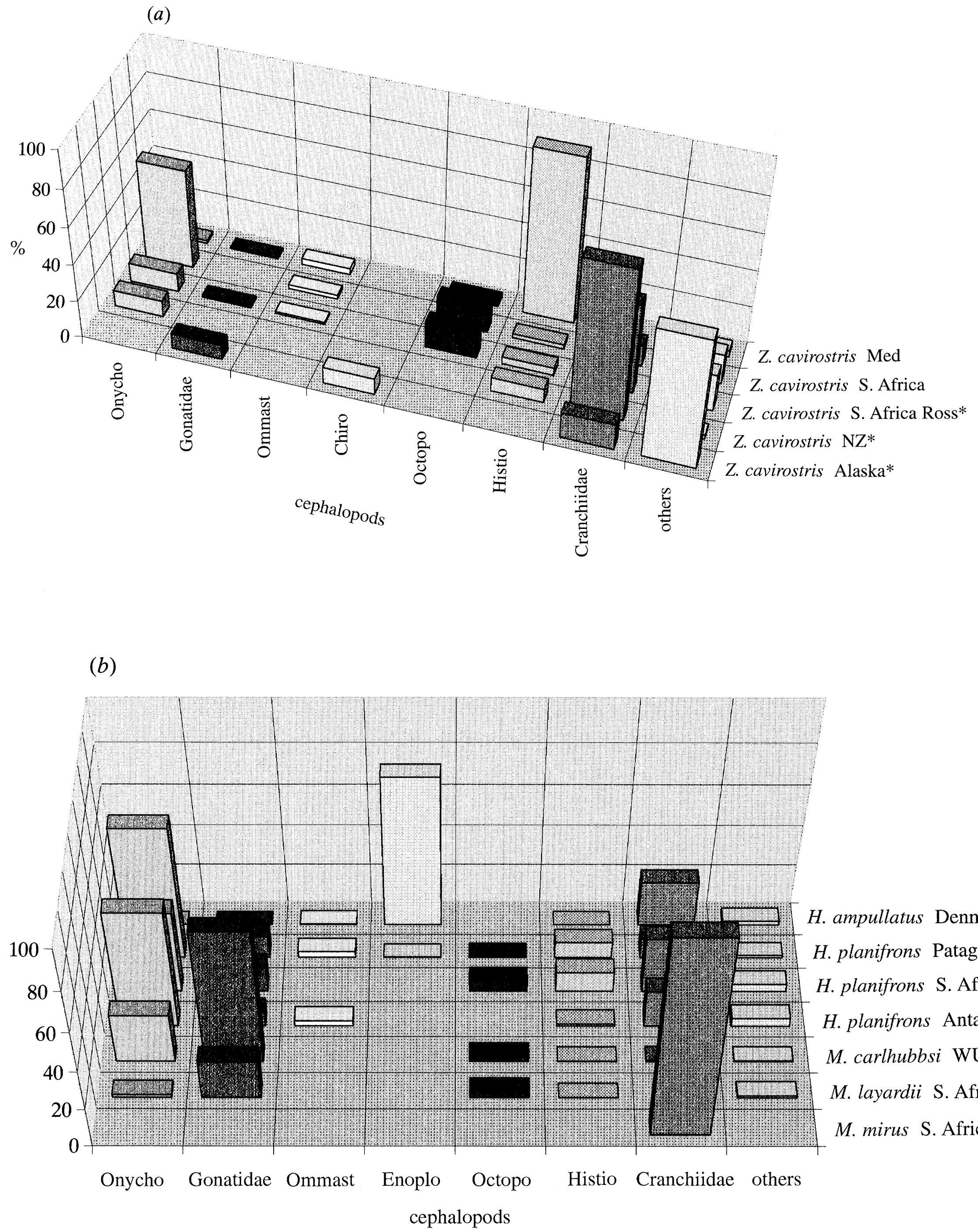

Figure 2. The Ziphiidae. (*a*) Percentages of cephalopod families in the diet of *Ziphius cavirostris* from the Mediterannean (Wurtz *et al*. 1993), South Africa (Ross, 1984; Sekiguchi *et al*. 1992) and New Zealand (Fordyce *et al*. 1979) and Alaska (Foster & Hare 1990, in which 'other' is a mixture of chiroteuthids and cranchiids). Percentages based on weight or volume or number* of cephalopods in the stomach contents. (*b*) Percentages of cephalopod families in the diet of *Hyperoodon ampullatus* from the Arctic but stranded in Denmark (Clarke & Kristensen 1980), *H. planifrons* from Patagonia (Clarke & Goodall 1994), South Africa (Sekiguchi *et al*. 1992, 1993) and Heard Island, Antarctica (Slip *et al*. 1995), *Mesoplodon carlhubbsi* (Mead *et al*. 1982), *M. layardii* (Sekiguchi *et al*. 1992) and *M. mirus* (Sekiguchi *et al*. 1992). Percentages based on weight or volume or number* of cephalopods in the stomach contents.

numerous. The occurrence of the inshore loliginids in *Balaenoptera physalis* and octopodids in *B. borealis* were probably due to their feeding unnaturally in shallow water prior to stranding.

The presence of the main cephalopod families in the diets of odontocete species of each family (table 1) show that the Ommastrephidae is the oceanic family and the Loliginidae is the neritic family eaten by most cetacean species. Each odontocete family favours different cephalopod families, e.g. the Ziphiidae favours the Onychoteuthidae and the Physeteridae favours the Ommastrephidae, Onychoteuthidae and Octopoteuthidae.

Figures 2–7 show the relative masses of the various cephalopod families in the diet of odontocete species, derived by estimates from beak sizes (Clarke 1980,

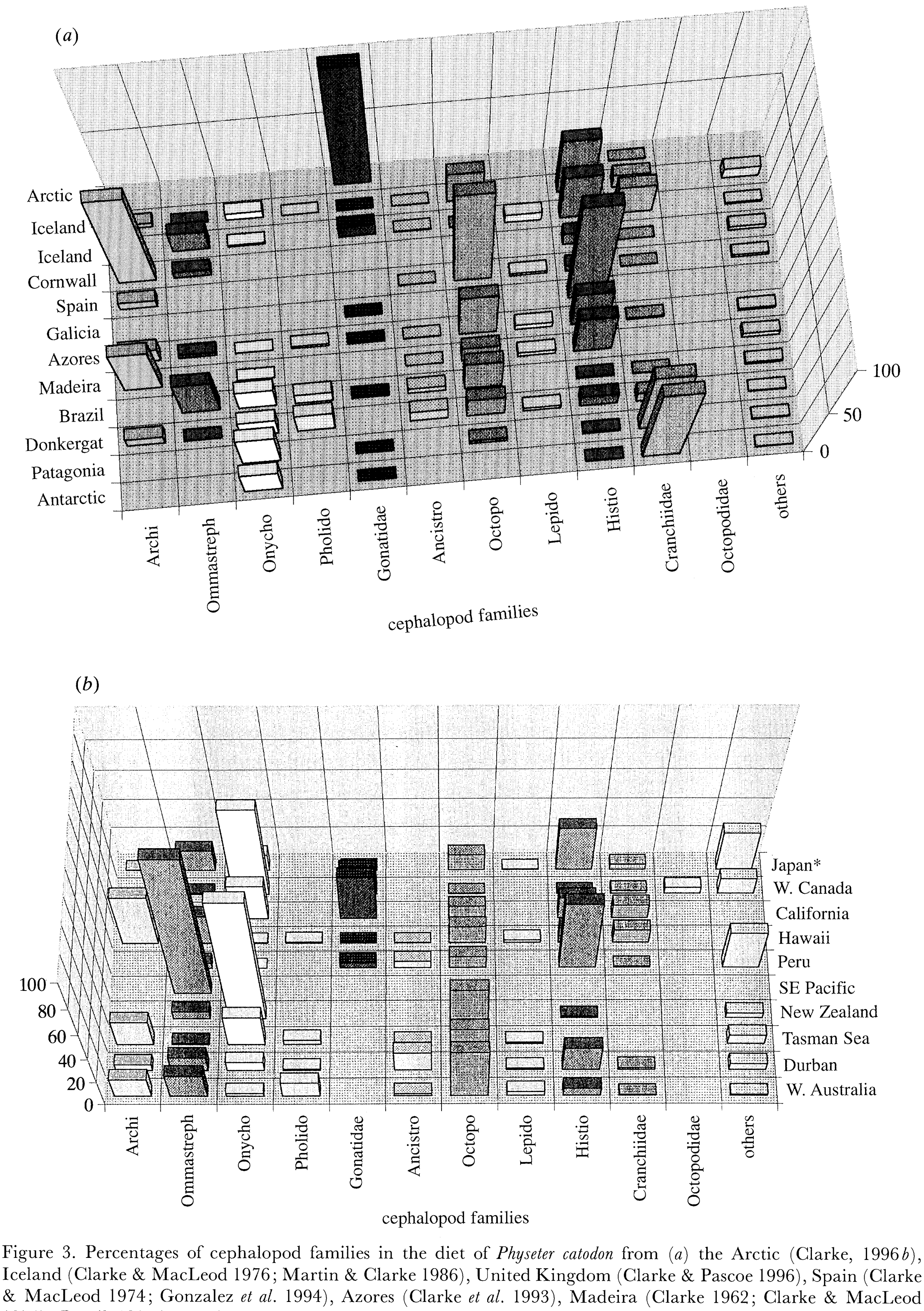

Figure 3. Percentages of cephalopod families in the diet of *Physeter catodon* from (*a*) the Arctic (Clarke, 1996*b*), Iceland (Clarke & MacLeod 1976; Martin & Clarke 1986), United Kingdom (Clarke & Pascoe 1996), Spain (Clarke & MacLeod 1974; Gonzalez *et al.* 1994), Azores (Clarke *et al.* 1993), Madeira (Clarke 1962; Clarke & MacLeod 1974), Brazil (Clarke *et al.* 1980), Donkergat, South Africa (Clarke 1980), Patagonia (Pascoe *et al.* 1990) and Antarctic (Clarke 1980); and (*b*) Japan (Okutani *et al.* 1976), W. Canada (Clarke & MacLeod 1980), California (Fiscus *et al.* 1989), Hawaii (Clarke & Young 1996), S. E. Pacific (Clarke *et al.* 1976; Clarke *et al.* 1988), New Zealand (Gaskin & Cawthorn 1967), Tasman Sea (Clarke & MacLeod 1982), Durban, South Africa (Clarke 1980) and West Australia (Clarke 1980). Percentages based on weight or volume or number* of cephalopods in the stomach contents.

1986*b*) or from prey volumes (Sekiguchi *et al.* 1992) or, when these are not available, the proportions by number of beaks or specimens. As many geographical areas as possible have been covered for each cetacean species.

In the Ziphiidae, 18 cephalopod families have been

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recorded. There is little evidence that members of this family feed regularly inshore, as they eat almost entirely oceanic squid, although *Sepia* is recorded from *Hyperoodon ampullatus* Forster 1770 and loliginids from *Mesoplodon layardi*. In the six species in which the proportions of the mass of families have been found (figure 2), the Onychoteuthidae and the Cranchiidae are most important in general, but the Gonatidae assume greater importance in the Arctic and north east Pacific and the Histioteuthidae in the Mediterannean. Little is known of *Tasmacetus shepherdi* Oliver 1937, but it may take some squid (Mead 1989).

Four of the five species in the Platanistidae live entirely in fresh water and therefore cannot eat cephalopods (which are limited to seawater), but loliginids are eaten by *Pontoporia blainvillei* Gervais & d'Orbigny 1844 which has a coastal distribution (Pinedo 1982).

Inshore and oceanic cephalopods, including five families, have been recorded from both members of the Monodontidae (see Clarke 1986*a* for references).

Of the Physeteridae, *Physeter catodon* shows considerable variation in its cephalopod diet throughout the world (figure 3). Only off Iceland and New Zealand do the fish contribute anything but a very minor part of its diet.

Members of 19 cephalopod families are eaten. The most important in the diet by mass in general are the Octopoteuthidae and Histioteuthidae, but others assume major importance in some regions: the Architeuthidae in the North Atlantic and Hawaii, Ommastrephidae in the south east Pacific, the Onychoteuthidae in New Zealand and north east Pacific, the Gonatidae in the Arctic (where one species may provide almost all food; Santos *et al.* 1995*a*) and North Pacific and the Cranchiidae in the Antarctic. Large species such as *Architeuthis* spp., the cosmopolitan octopoteuthid *Taningia danae* Joubin 1931 and the Antarctic cranchiid *Mesonychoteuthis hamiltonii* Robson 1925 greatly influence the importance of their families when they occur. The active, widespread ommastrephids are particularly important in the south east Pacific, where *Dosidicus gigas* provides an almost monospecific diet (Clarke *et al.* 1988), and off Brazil. Even though histioteuthids are relatively small, being less than 1 m long, they are so numerous as to provide a substantial proportion of the mass of the diet in most tropical and temporate regions. Poorly known families which almost always occur but contribute less than 10% of the weight to the diet are Pholidoteuthidae, Ancistrocheiridae, Lepidoteuthidae, Cycloteuthidae, Mastigoteuthidae, Chiroteuthidae and the Alloposidae.

Kogia species have 11 families of cephalopods represented in their diet, of which the histioteuthids are generally the most important with the inshore sepiids (in *Kogia simus* Owen 1866) and loliginids (in *Kogia breviceps* de Blainville 1838) assuming major importance in some samples off South Africa. Also, somewhat surprising for their size, the Lycoteuthidae off South Africa and Brazil and the Chiroteuthidae off the Azores are important. Ommastrephids are most important off Brazil.

Cephalopods have been recorded in the diets of *Sousa bredanensis* (by Nielson 1930; Layne 1965), *S. teuszii* Kukenthal 1892 (by Ross 1979*a*), *S. chinensis* (by Barros (personal communication) and *Sotalia fluviatilis* Gervais & Deville 1853 (by Barros & Teixeira 1994).

All the Phocoenidae are known to eat cephalopods (see Clarke 1986*a* for references; also Findley *et al.* 1994) and these include seven species including neritic Loliginidae and *Illex* (Recchia & Read 1988; Desportes 1985; Santos *et al.* 1994). *Phocoenoides dalli* True 1885 of the North Pacific eats some cephalopods including the oceanic *Abraliopsis*, *Gonatus* and *Onychoteuthis* off California (Loeb 1972) and *Ommastrephes sloani* and *Watasenia* off Japan (Wilke & Nicholson 1958), but also includes shelf species of *Loligo* and *Octopus* and concentrates on gonatids in some areas (figure 4*b*).

Of the Delphinidae, *Orcinus orca* eats neritic species (figure 4*b*) and sometimes oceanic species of the Gonatidae and Histioteuthidae (Santos *et al.* 1995*b*), while *Pseudorca crassidens* favours oceanic thysanoteuthids and ommastrephids and *Peponocephala electra* favours the small oceanic enoploteuthids in Hawaii, the neritic loliginids off South Africa, ommastrephids and onychoteuthids off Brazil (Barros *et al.* 1994) and the ommastrephid *Dosidicus gigas* in the east Pacific (Pitman & Ballance 1992).

The two pilot whales (*Globicephala*) eat 19 families of cephalopods including both oceanic and neritic species (figure 5). The ommastrephids are a main ingredient of the diet in most places (see also Martin & Clarke (1986), who found only ommastrephids off Britain and Gannon *et al.* (1995), who found the loliginids the dominant food in the north west Atlantic). In Patagonia the large onychoteuthid *Moroteuthis ingens* may take their place or rank second in importance (Crespo *et al.* 1994). The presence of all three neritic families may be, in part, a reflection of the source of some of the collections (stranded whales), but is also likely to indicate a regular feeding of the species on the continental shelves or upper slopes. One stranded example off California had eaten both oceanic histioteuthids and the onychoteuthid *Moroteuthis* and also shelf-living *Loligo* (Seagards & Henderson 1985).

All but two members of the Delphinidae are known to eat cephalopods (Clarke 1986*a*) and they include 19 families in their diet. *Orcaella brevirostris* is not thought to include cephalopods. Four *Lagenorhynchus* species eat neritic species, but at least two of these also eat oceanic species (figure 6*a*), particularly ommastrephids, which seasonally come on to the shelf (Sergeant *et al.* 1957; Santos *et al.* 1995*b*). Both *Lissodelphis* species eat oceanic squids (Robertson & Henshaw 1995) and *L borealis* Peale 1848 also includes neritic species in its diet. Two species of *Cephalorhynchus* are known to eat exclusively shelf species (figure 6*a*). Three *Stenella* species (figure 6*b*, *c*) favour ommastrephids of the oceanic squids and usually loliginids of the neritic species, although they may favour enoploteuthids (Hawaii) or lycoteuthids (South Africa) in some regions.

Grampus griseus Cuvier 1812 generally eats both oceanic and neritic cephalopods from 14 families, including sepiids and bottom-living octopods (figure 7*a*). Ommastrephiidae are the most favoured oceanic

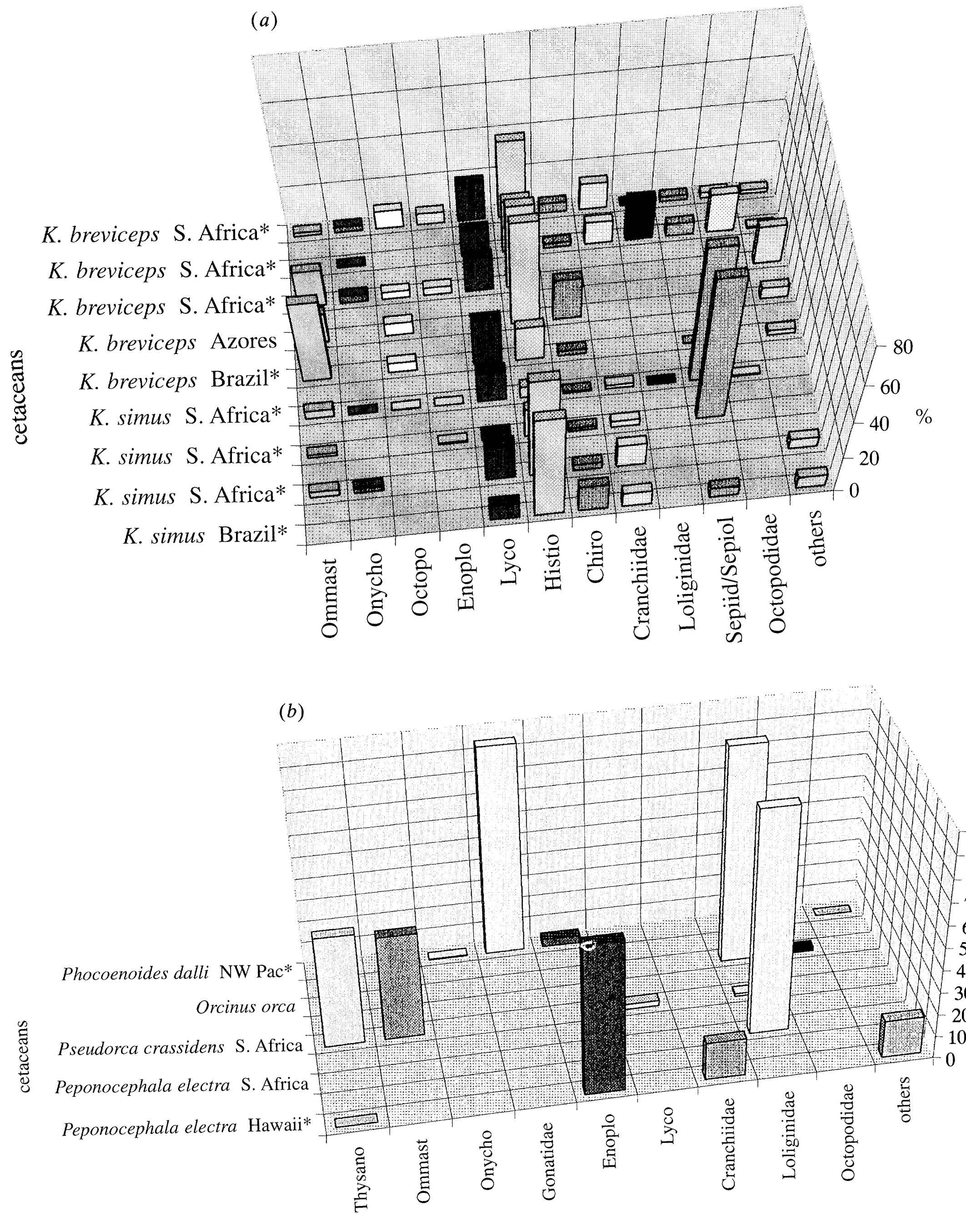

Figure 4. Percentages of cephalopod families in the diet of (*a*) *Kogia breviceps* from South Africa (Ross 1979*b*, 1984; Sekiguchi *et al*. 1992), the Azores (Martins *et al*. 1985) and Brazil (Secchi *et* al. 1994) and *K. simus* from South Africa (Ross 1979*b*, 1984; Sekiguchi *et al*. 1992) and Brazil (Pinedo 1987); and (*b*) four other odontocetes: *Phocoenoides dalli* (Kuramochi *et al*. 1993), *Orcinus orca* (Frost & Lowry 1981), *Pseudorca crassidens* (Sekiguchi *et al*. 1992) and *Peponocephala electra* from South Africa and Hawaii (Sekiguchi *et al*. 1992; Clarke & Young 1996). Percentages based on weight or volume or number* of cephalopods in the stomach contents.

family, although histioteuthids are important in the Mediterannean. *Delphinus delphis* Linnaeus 1758 also eats a mixture of oceanic and neritic species (figure 7*b*). Similarly *Tursiops truncatus* Montagu 1821 eats both oceanic and neritic squids (figure 6*c*; see also Waerebeek *et al*. 1990), favouring the ommastrephid *Illex* off eastern Canada but lycoteuthids off South Africa. The composition of the food organisms, including cephalopods, has been used to differentiate the *Tursiops* populations off Florida (Barros 1993).

From figures 2–7, it is evident that the diet varies considerably according to region and year (e.g. *Globicephalus* in northern Japan). However, by far the most important of the 28 families in the diets of oceanic cetaceans in general are the ommastrephids, the histioteuthids and the cranchiids, with the loliginids assuming most importance on the continental shelves. Onychoteuthids and gonatids assume greater importance in the polar regions and North Pacific. The other 22 families form a reservoir from which various cetaceans eat as they require or as their size permits.

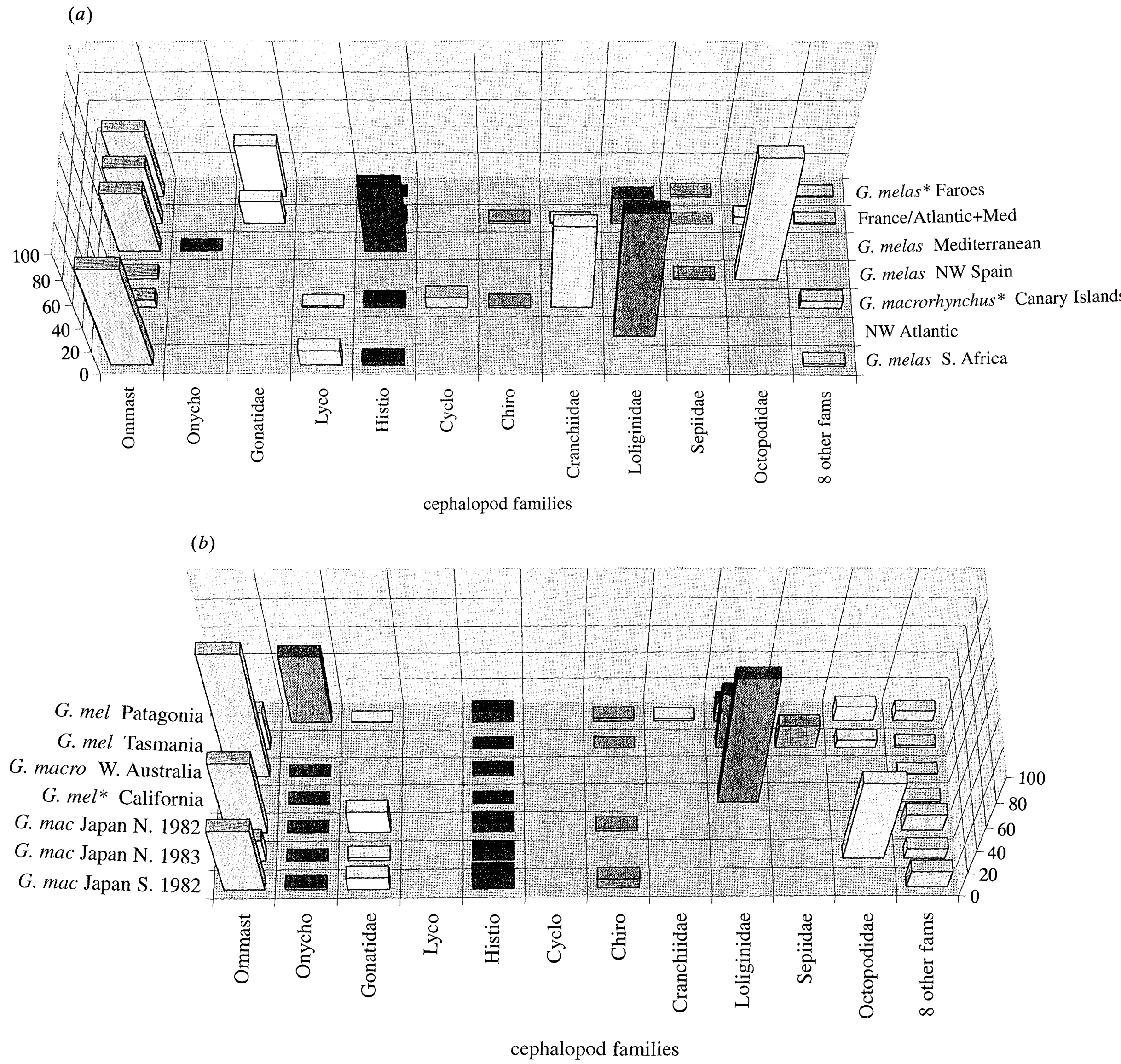

Figure 5. Percentages of cephalopod families in the diets of *Globicephalus melas* and *G. macrorhynchus* from (*a*) the Atlantic area, the Faroes (Desportes & Mouritsen 1988), France (Desportes 1985), Mediterannean (Orsi Relini & Garibaldi 1992), Spain (Gonzales *et al.* 1994), Canary Islands (Hernandez-Garcia & Martin 1994), N. W. Atlantic (Overholz & Waring 1991) and South Africa (Sekiguchi *et al.* 1992); and (*b*) the Indo-Pacific off Patagonia (Clarke & Goodall 1994), Tasmania (Gales *et al.* 1992), West Australia (Clarke, unpublished), California (Seagards & Henderson 1985) and Japan (Kubodera & Miyazaki 1993). Percentages based on weight or volume or number* of cephalopods in the stomach contents.

5. SIZE OF CEPHALOPODS IN THE DIET

The sizes of cephalopods consumed by cetaceans vary from 3–4 cm in length and just a few grams in weight to the largest known squids of over 20 m long and weight possibly exceeding 500 kg. The size may be dictated by the types of cephalopods prevalent in any particular region, as in the sperm whale, where the mean estimated weight of the cephalopods varies from 0.6 to 8.0 kg.

The mean weight of cephalopods consumed varies according to the region (Clarke 1986*a*). While sperm whales certainly take some large squid, the mean weight of 600 g in some regions is very small compared to the weight of the whale, representing a ratio similar to that of a copepod to a herring! The mean weights eaten are greatest in the Antarctic (7.2 kg). The size is not clearly correlated with latitude, as between 30° and 40° the mean weight varies from 0.6 to 3.6 kg for different regions. Although the body size of 17 cephalopod species eaten by sperm whales was the same from west to east in the southern hemisphere, the size for two genera (possibly species), *Architeuthis* and *Kondakovia*., increased steadily eastwards over the range from South Africa, via Australia, to Peru.

The average and maximum length and weight of each squid species eaten by sperm whales often differs to some extent by regions, e.g. off Western Australia *Taningia danae* had lengths of 87–120 cm and weights of 26–61 kg respectively. At Madeira these values were 102–140 cm and 35–86 kg.

Several cetacean species take larger prey as they grow bigger (Ross 1979*b*; Desportes 1985). In the smaller cetaceans this may well be a selection for size,

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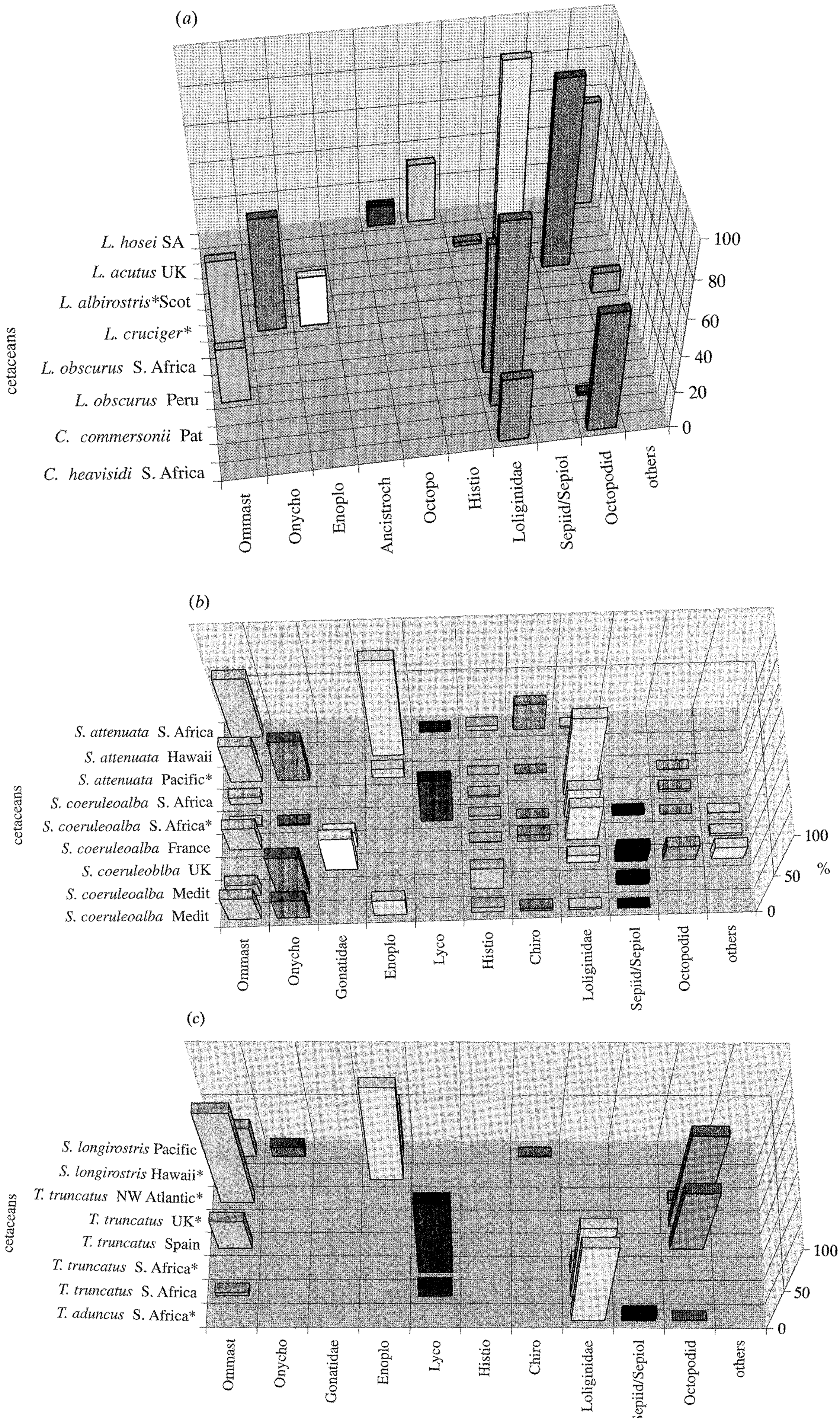

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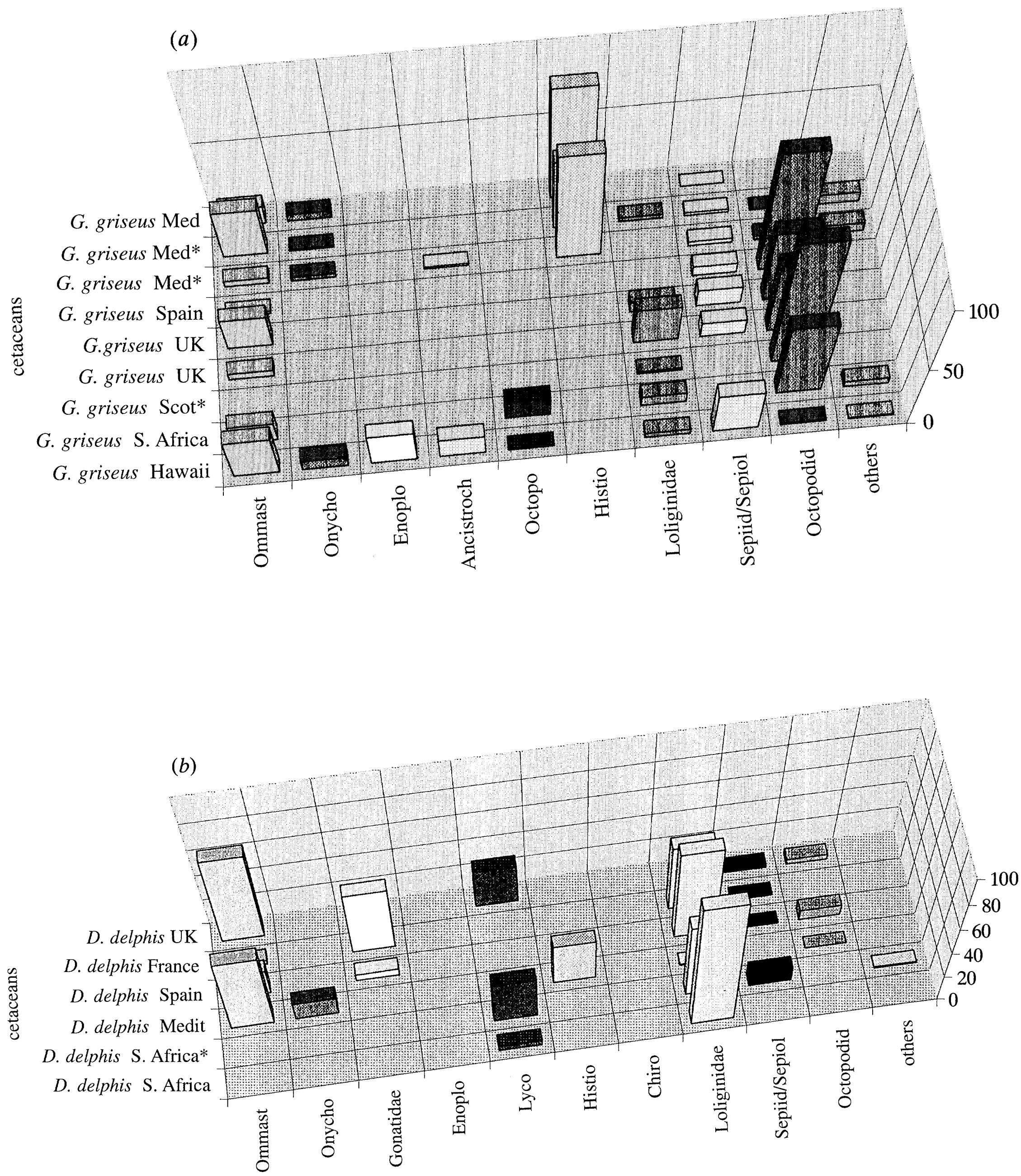

Figure 7. Percentages of cephalopod families in the diets of (*a*) *Grampus griseus* in the Mediterannean (Bello 1992; Carlini *et al.* 1992; Wurtz *et al.* 1992), off Spain (Gonzalez *et al.* 1994), Great Britain (Clarke & Pascoe 1985; Clarke 1996*a*), South Africa (Sekiguchi *et al.* 1992) and Hawaii (Clarke & Young 1996); and (*b*) *Delphinus delphis* off Great Britain (Clarke 1996*a*), France (Desportes 1985), Spain (Gonzales *et al.* 1994), in the Mediterannean (Wurtz *et al.* 1992) and South Africa (Ross, 1984; Sekiguchi *et al.* 1992; Young & Cockroft 1994). Percentages based on weight or volume or number* of cephalopods in the stomach contents.

but where the disparity in size between predator and prey is as great as in sperm whales and pilot whales, for instance, size may also be determined by the depth dived by the cetacean. Female and juvenile (< 11.9 m) sperm whales off Durban eat cephalopods with a mean weight of 0.5 kg, while adult males eat cephalopods with a mean weight of 1.0 kg (Clarke 1980) and, as some cephalopods are known to descend during

Figure 6. Percentages of cephalopod families in the diets of five genera of Delphinidae. (*a*) *Lagenorhynchus hosei* (Sekiguchi *et al.* 1992), *Lagenorhynchus acutus* (Clarke 1996*a*), *L. albirostris* (Santos *et al.* 1994), *L. cruciger* (Clarke 1986*a*), *L. obscurus* in South Africa (Sekiguchi *et al.* 1992) and in Peru (McKinnon 1994), *Cephalorhynchus commersoni* (Clarke & Goodall 1994) and *C. heavisidi* (Sekiguchi *et al.* 1992). (*b*) *Stenella attenuata* (Perrin *et al.* 1973; Sekiguchi *et al.* 1992; Clarke & Young 1996), *S. coeruleoalba* in South Africa (Ross 1984; Sekiguchi *et al.* 1992), France (Desportes 1985), the U.K. (Clarke 1996*a*) and the Mediterranean (Bello 1992; Pulcini *et al.* 1992; Wurtz & Marrale 1993; Blanco *et al.* 1995). (*c*) *S. longirostris* (Perrin *et al.* 1973; Clarke & Young 1996), *Tursiops truncatus* (Mercer 1973; Sekiguchi *et al.* 1992; Gonzalez *et al.* 1994; Clarke 1986*a*) and *T. aduncus* (Ross 1984). Percentages based on weight or volume or number* of cephalopods in the stomach contents.

growth, diving performance is the most likely reason for the difference.

Considering specific differences between cetaceans, Ross (1979*b*) found a positive correlation between the size of pelagic feeding cetaceans and the size of the prey. The relationship is $y = 13.06x^{1.872}$ ($r = 0.81$, $n = 11$), where y = mean prey item mass (g) and x = mean predator length (m). Some cetaceans seem restricted to families of cephalopods according to their size, e.g. *Physeter catodon* is the only one known to eat architeuthids and it does not take the small enoploteuthids.

Seasonal changes in the relative numbers of cephalopod species and adults, particularly in shorter-lived cephalopods, must influence the diet of the cetaceans. Annual fluctuations between fish and different cephalopod species are known to influence diet in *Globicephalus melas*, and possibly choice between species such as *Todarodes sagittatus* and *Gonatus fabricii* is exercised (Desportes, 1985).

Within particular regions differences in food by size and species causes a partitioning of the cephalopod food resource so that different cetaceans are not in direct competition, although the cause may not be preference in taste or intended selection.

6. ADVANTAGES OF CEPHALOPODS AS A FOOD SOURCE

Cephalopods provide a very broad size range of food organism which, in the oceanic midwater extends to a greater size than most midwater fish susceptible to cetaceans (see p. 1103). Muscular cephalopods are very high in proteins. Most cephalopods are made less difficult to catch by their quick exhaustion after fast swimming and many of the families favoured by cetaceans (e.g. histioteuthids and cranchiids) are neutrally buoyant and sluggish (Clarke *et al.* 1979). In sperm whales, for example, ammoniacal squids comprise 53 to 78% of the cephalopods consumed by sperm whales (Clarke 1980, 1986*a*). Although these provide lower energy content (Croxall & Prince 1982) they require less energy to catch than fast-swimming species. Many species school and congregate to spawn, presenting concentrated, productive targets for large predators. Because they grow fast to maturity and their lifespan is usually less than two years they react to good conditions quickly, reproduce rapidly and quickly compensate for population reduction by heavy predation.

Most are terminal spawners and some cetaceans (e.g. *Physeter catodon*, *Globicephalus melas*) feed on the spawning grounds. This may be an advantage to both predator and prey species. The predator takes the protein at its maximum production and concentration. Probably some prey are eaten after they have spawned and some, by the sperm whale, after they have died, so that the maximum protein is derived from growth of the cephalopod populations with minimum effect on their survival.

Many species consumed by cetaceans are luminous and this may have advantages for the predator at night or at the great depths at which some eat, particularly with gelatinous cephalopods which may present poor targets for sonar. For example, squids known to have luminous organs comprise 97%, 80%, 84% and 41% of the cephalopods consumed by sperm whales at Durban, Donkergat, Albany and in the Antarctic respectively. Luminous species comprise 70%, 85%, 80% and 60% of the species in the diet in the same regions (Clarke 1980).

Compared with fish, cephalopods are not a very specious group and the 28 families represented probably contain only 50–60 species regularly in the diet of cetaceans. However, these are enough to provide sufficient size range and diverse protein reservoir throughout the world to be resilient to short period fluctuations in fish populations which also contribute to the diets of cetaceans.

7. TOTAL WEIGHTS EATEN

Although estimates of population of marine mammals must be taken with considerable caution, some do afford reason-based figures for indicating the worldwide annual consumption of cephalopods. Sperm whales are of particular interest because they are by far the largest odontocetes with males reaching over 20 m and 60 t and females 12 m and 30 t. Because they were exploited commercially, we have estimates of their population and exploitable stock size and the 1973 report of the International Whaling Scientific Committee (IWC/24/4R) permitted a first estimate of the total weight of cephalopods eaten by sperm whales as at least 100–320 mt (Clarke 1977, 1987). This calculation can now take into account more recent work on stocks (IWC 1994) and energetic requirements (Lockyer 1981; Clarke *et al.* 1988), but we can still only make cautious guesses at the mean weights of whales. However, 213–320 mt (1950000 sperm whales × 15 t (mean mass) × 2–3 (daily feeding rate % mass) × 365) still seems a likely estimate of the mass of cephalopods (mainly oceanic squids) eaten by sperm whales each year.

Clarke *et al.* (1988) came to the conclusion that *Physeter catodon* of the south east Pacific were almost limiting their diet to *Dosidicus gigas* and, after a careful reappraisal of Lockyer's (1981) estimates of whale energy budgets, they calculated, from details of the stock of 1959–61 in the area 100°–60° W, that the exploitable stock of sperm whales then consumed 8.69 mt (confidence limits = 6.66–13.14 mt) to 13.67 mt (10.56–20.18 mt) of this ommastrephid.

Kasumatsu *et al.* (1995) calculate, on the basis of recent population estimates, that odontocetes (67% of them Ziphiidae) in the Antarctic Ocean probably consume annually 14 mt of cephalopods, mainly squids. Sekiguchi *et al.* (1993) point out that 93% of these ziphiids are bottlenose whales and that they are possibly as important predators of cephalopods as sperm whales in the region.

Considering just *Phocoena phocoena*, in the North Atlantic, Pierce & Santos (1996) have estimated that they eat over 11000 t of *Loligo* annually, representing over 50 million squids. Such estimates of the influence of cetaceans on target species of fisheries will certainly attract more attention as estimates of cetacean populations become more accurate and their food becomes better known.

If doubts are admissible about population estimates of cetaceans, hard data of catches cannot be doubted. To take an example, the Azores island region sustained an annual catch rate of over 400 whales from 1935 to 1949. If we assume the population necessary to sustain this yield was only the total taken in that time, i.e. $400 \times 14 = 5600+$, the whales averaged 40 t in weight (Clarke, 1956) and that they only spent 2 months of the year in azorean waters (probably an underestimate), the weight of cephalopods eaten in the region would be over 373 000 t per year. If one applies this to the proportion of the species eaten, the consumption in azorean waters by these whales was 148 000 t of octopoteuthids, mainly *Taningia danae*, 122 000 t of histioteuthids, mainly *Histioteuthis bonnellii*, 45 000 t of *Architeuthis* sp., 12 000 t of ommastrephids, mainly *Todarodes sagittatus* and 12 000 t of onychoteuthids, mainly *Onychoteuthis borealis-japonicus*. These compare with an annual catch of about 14 000 t of all species of fish in the Azores.

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REFERENCES

Akimushkin, I. I. 1955 Nature of the food of the cachelot. *Dokl. Akad. Nauk SSSR* **101**, 1139–40.

Baker, A. N. 1985 Pygmy right whale – *Caperea marginata*. In *Handbook of Marine Mammals*, vol. 3. *The Sirenians and Baleen Whales* (ed. S. H. Ridgway & R. Harrison), pp. 345–354. London: Academic Press.

Barros, N. 1993 Feeding ecology and foraging strategies of bottlenose dolphins on the central east coast of Florida. PhD dissertation. University of Miami.

Barros, N., Klages, N., Lodi, L. & Siciliano, S. 1994 O encalhe em de golfinhos cabeca-de-melao (*Peponocephala electra*) em Itacare, Bahia, Brazil; habitos alimentares. In *Anales de la IV Reunion de trabajo de Especialistas en mamiferos Aquaticos de America del sur* 12–15 *Nov.* 1990, *Chile* (ed. J. A. Oporto), p. 5.

Barros, N. & Teixeira, R. L. 1994 Incidental catch of marine Tucuxi, *Sotalia fluviatilis*, in Alagoas, northeastern Brazil. *Rep. Int. Whal. Commn* (Special issue 15), 265–268.

Bello, B. 1992 Stomach contents of a Risso's dolphin, *Grampus griseus*. Do dolphins compete with fishermen and swordfish, *Xiphius gladius? Eur. Res. Cetaceans* **6**, 199–202.

Blanco, C., Aznar, J. & Raga, J. A. 1995 Cephalopods in the diet of the striped dolphin *Stenella coeruleoalba* from the western Mediterranean during an epizootic in 1990. *J. Zool. Lond.* **237**, 151–158.

Carlini, R., Pulcini, M. & Wurtz, M. 1992 Cephalopods from the stomachs of Risso's dolphins, *Grampus griseus* (Cuvier, 1812), stranded along the central Tyrrhenian coast. *Eur. Res. Cetaceans* **6**, 196–198.

Clarke, M. R. 1962 Stomach contents of a sperm whale caught off Madeira in 1959. *Norsk HvalFangstidende* **51**, 173–191.

Clarke, M. R. 1977 Beaks, nets and numbers. *Symp. zool. Soc. Lond* **38**, 89–126.

Clarke, M. R. 1980 Cephalopoda in the diet of sperm whales of the southern hemisphere and their bearing on sperm whale biology. '*Discovery*' *Rep.* **37**, 1–324.

Clarke, M. R. 1986*a* Cephalopods in the diet of odontocetes. In *Research on Dolphins* (ed. M. M. Bryden & R. Harrison), pp. 281–321. Oxford: Clarendon Press.

Clarke, M. R. (ed.) 1986*b* *A Handbook for the Identification of Cephalopod Beaks*. Oxford: Clarendon Press.

Clarke, M. R. 1987 Cephalopod biomass estimation from predation. In *Cephalopod Life Cycles*, vol. 2. *Comparative Reviews* (ed. P. R. Boyle), pp. 221–237. London: Academic Press.

Clarke, M. R. 1996*a* Report on the cephalopod remains from stomachs of cetaceans stranded in England and Wales 1990–94. In Stomach Contents of Stranded Cetacea. A report for the Welsh Office by the Natural History Museum 1995, 31–36.

Clarke, M. R. 1996*b* Cephalopods in the stomach of a sperm whale stranded between the islands of Tersshelling and Ameland, southern North Sea. *Lutra*. (In the press.)

Clarke, M. R., Denton, E. J. & Gilpin-Brown, J. B. 1979 On the use of ammonium for buoyancy in squids. *J. mar. biol. Ass. U.K.* **59**, 259–276.

Clarke, M. R. & Goodall, N. 1994 Cephalopods in the diets of three odontocete cetacean species stranded at Tierra del Fuego, *Globicephala melaena* (Traill, 1809), *Hyperoodon planifrons* (Flower, 1882) and *Cephalorhynchus commersonii* (Lacepede, 1804). *Antarctic Science* **6**, 149–154.

Clarke, M. R. & Kristensen, T. K. 1980 Cephalopod beaks from the stomachs of two northern bottlenosed whales (*Hyperoodon ampullatus*). *J. mar. biol. Ass. U.K* **60**, 151–156.

Clarke, M. R. & MacLeod, N. 1974 Cephalopod remains from a sperm whale caught off Vigo, Spain. *J. mar. biol. Ass. U.K.* **54**, 959–968.

Clarke, M. R. & MacLeod, N. 1976 Cephalopod remains from sperm whales caught off Iceland. *J. mar. biol. Ass. U.K.* **56**, 733–750.

Clarke, M. R & MacLeod, N. 1980 Cephalopod remains from sperm whales caught off western Canada. *Mar. Biol.* **59**, 241–246.

Clarke, M. R & MacLeod, N. 1982 Cephalopod remains from the stomachs of sperm whales caught in the Tasman Sea. *Memoirs Victoria Mus.* **43**, 25–42.

Clarke, M. R., MacLeod, N., Castello, H. P. & Pinedo, M. C. 1980 Cephalopod remains from the stomach of a sperm whale stranded at Rio Grande do Sul in Brazil. *Mar. Biol.* **59**, 235–239.

Clarke, M. R., MacLeod, N. & Paliza, O. 1976 Cephalopod remains from the stomachs of sperm whales caught off Peru and Chile. *J. Zool.* **180**, 477–493.

Clarke, M. R., Martins, H. R. & Pascoe, P. L. 1993 The diet of sperm whales (*Physeter macrocephalus* Linnaeus 1758) off the Azores. *Phil. Trans .R. Soc. Lond.* B **339**, 67–82.

Clarke, M. R. & Pascoe, P. L. 1985 The stomach contents of a Risso's dolphin (*Grampus griseus*) stranded at Thurlestone, South Devon. *J. mar. biol. Ass. U.K.* **65**, 603–605.

Clarke, M. R. and Pascoe, P. L. 1996 Cephalopod species in the diet of a sperm whale *Physeter catodon* L. stranded at Penzance, Cornwall. *J. mar. biol. Ass. U.K.* (In the press.)

Clarke, M. R. and Young, R. E. 1996 Cephalopod species in the diet of six species of cetaceans, *Physeter catodon* L., *Grampus griseus*, *Peponocephala electra*, a beaked whale, *Stenella attenuata* and *S. longirostris* from the Hawaiian islands. *J. mar. biol. Ass. U.K.* (In the press.)

Clarke, R. 1956 Sperm whales of the Azores. '*Discovery*' *Rep.* **28**, 237–298.

Clarke, R., Paliza, O. & Aguayo, L. 1988 Sperm whales of the southeast Pacific. Part IV: Fatness, food and feeding. *Investigations on Cetacea* (ed. G. Pilleri) **21**, 153–185.

Crespo, E. A., Nepomnaschy, P., Alonso, M. K. & Garcia, N. 1994 Analisis preliminar de la dieta de maniferos marinos sobre la base de contenidos estomacales y heces. In *Anales de la IV Reunion de trabajo de Especialistas en mamiferos Aquaticos de America del sur* 12–15 *Nov*. 1990, *Chile* (ed. J. A. Oporto), pp. 75–87.

Croxall, J. P. and Prince, P. A. 1982 Calorific content of squid (Mollusca: Cephalopoda). *Br. Ant. Survey Bull.* No. 55, 27–31.

Desportes, G. 1985 La nutrition des odontocetes an Atlantique Nord-est (Cotes francaises-Iles Faroe). PhD thesis, University of Poitiers.

Desportes, G. & Mouritsen, R. 1993 Preliminary results on the diet of the long-finned pilot whales off the Faroe Islands. *Rep. Int. Whal Commn* (Special issue 14), 305–321.

Findley, L. T. Nava, J. M. & Torre, J. 1994 Food habits of the Vaquita, *Phocoena sinus*. *Conservation International*, 1–6.

Fiscus, C. H., Rice, D. W. & Wolman, A. A. 1989 Cephalopods from the stomachs of sperm whales taken off California. *NOAA Technical Report NMFS* **83**, 1–12.

Fordyce, R. E., Mattlin, R. H. & Wilson, G. J. 1979 Stranding of a Cuvier's beaked whale *Ziphius cavirostris* Cuvier, 1823, at New Brighton, New Zealand. *Mauri ora* **7**, 73–82.

Foster, N. R. & Hare, M. P. 1990 Cephalopod remains from a Cuvier's beaked whale (*Ziphius cavirostris*) stranded in Kodiak, Alaska. *Northwestern Naturalist* **71**, 49–51.

Frost, K. J. and Lowry, L. F. 1981 Foods and trophic relationships of cetaceans in the Bering Sea. In *The eastern Bering Sea Shelf oceanography and resources*, vol. 2 (ed. D. W. Hood & J. A. Calder), pp. 825–836. US National Oceanic and Atmospheric Administration, Office of Marine Pollution Assessment.

Gales, R., Pemberton, D. & Clarke, M. R. 1992 Stomach contents of long-finned pilot whale (*Globicephalus melas*) and bottlenose dolphins (*Tursiops truncatus*) in Tasmania. *Mar. Mamm. Sci.* **8**, 405–413.

Gannon, D. P., Read, A. J., Craddock, J. E., Fristup, K. M. & Mead, J. G. 1995 Foraging ecology of N. W. Atlantic long-finned pilot whales. Eleventh Biennial Conference on the Biology of Marine Mammals, Orlando, Florida, U.S.A., Dec. 14–18, 1995.

Gaskin, D. E. and Cawthorn, M. W. 1967 Squid mandibles from the stomachs of sperm whales (*Physeter catodon* L.) captured in the Cook Strait region of New Zealand. *N.Z. J. mar. freshwater Res.* **1**, 59–70.

Gonzalez, A. F., Lopez, A., Guerra, A & Barreiro, A. 1994 Diets of marine mammals stranded on the northwest spanish Atlantic coast with special reference to cephalopoda. *Fisheries Res.* **21**, 179–191.

Hernandez-Garcia, V. & Martin, V. 1994 Stomach contents of two short-finned pilot whale (*Globicephala macrorhynchus* Gray, 1846) (Cetacea, Delphinidae) off the Canary Islands: a preliminary note. *I.C.E.S. C.M.1994/N*: **16**, 1–9.

Joubin, L. 1895 Cephalopodes recueillis dans l'estomac d'un cachelot capture aux iles Acores. *C. R. Seanc. Acad. Sci. Paris* **121**, 1172.

Kasamatsu, F. & Joyce, G. G. 1995 Current status of odontocetes in the Antarctic. *Antarctic Science* **7**, 365–379.

Kawamura, A. 1980 A review of food of balaenopterid whales. *Sci Rep. Whales Res. Inst., Tokyo* **32**, 155–197.

Kubodera, T. & Miyazaki, N. 1993 Cephalopods eaten by short-finned pilot whales, *Globicephalus macrorhynchus*, caught off Ayukawa, Ojika peninsula, in Japan, in 1982 and 1983. In *Recent Advances in Fisheries Biology* (ed. T. Okutani, R. K. O'Dor & T. Kubodera), pp. 215–227. Tokyo: Tokai University Press.

Kuramochi, T., Kubodera, T. & Miyazaki, N. 1993 Squids eaten by Dall's porpoises, *Phocoenoides dalli* in the Northwestern North Pacific and in the Bering Sea. In *Recent Advances in Fisheries Biology* (ed. T. Okutani, R. K. O'Dor & T. Kubodera), pp. 229–240. Tokyo: Tokai University Press.

Layne, J. N. 1965 Observations on marine animals in Florida waters. *Bull.Fla Stata Mus.* (*Biol.Sci.*) **9**, 131–181.

Lockyer, C. 1981 Estimates of growth and energy budget for the sperm whale, *Physeter catodon*. *FAO Fish. Ser.* **3**, 489–504.

Loeb, V. J. 1972 A study on the distribution and feeding habits of the Dall porpoise in Monterey Bay, California. M.S. Thesis, San Jose State College, San Jose, California.

McKinnon, J. 1994 Feeding habits of the dusky dolphin, *Lagenorhynchus obscurus*, in the coastal waters of central Peru. *Fishery Bulletin* **92**, 569–578.

Martin, A. R. & Clarke, M. R. 1986 The diet of sperm whales (*Physeter macrocephalus*) captured between Iceland and Greenland. *J. mar. biol. Ass. U.K.* **66**, 779–790.

Martins, H. R., Clarke, M. R., Reiner, F. & Santos, R. S. 1985 A pygmy sperm whale, *Kogia breviceps* (Blainville, 1838) (Cetacea: Odontoceti) stranded on Faial Island, Azores, with notes on cephalopod beaks in stomach. *Arquipelago* **6**, 63–70.

Mead, J. G. 1989 Beaked whales of the genus *Mesoplodon*. In *Handbook of Marine Mammals* vol. 4, chap. 14 (*River dolphins and the large toothed whales*) (ed. S. H. Ridgway & R. G. Harrison). San Diego: Academic Press.

Mead, J. G. & Brownell, R. L. 1993 Order Cetacea. In *Mammal Species of the World*, 2nd edn (ed. D. E. Wilson & D. M. Reeder), pp. 349–364. Washington, D.C.: Smithsonian Institute Press.

Mead, J. G., Walker, W. A. & Houck, W. J. 1982 Biological observations on *Mesoplodon carlhubbsi* (Cetacea: Ziphiidae). *Smithsonian Contrib. Zool.* **344**, 1–25.

Mercer, M. C. 1975 Modified Leslie-DeLury population models of the long-finned pilot whale (*Globicephala melas*) and the short-finned squid (*Illex illecebrosus*) based upon their interaction at Newfoundland. *J. Fis. Res. Bd Can.* **32**, 1145–1154.

Nielsen, E. 1930 Cephalopoda. *Zool. Faroes* **56**, 1–9.

Okutani, T., Sataki, Y., Ohsumi, S. & Kawakami, T. 1976 Squids eaten by sperm whales caught off Joban district, Japan, during January–February, 1976. *Bull. Tokai Reg. Fish. Res. Lab.* **87**, 67–113.

Orsi Relini, L. & Garibaldi, F. 1992 Feeding of the pilot whale, *Globicephala melas*, in the Ligurian Sea: a preliminary note. *Eur. Res. Cetaceans*, 142–145.

Overholtz, W. J. & Waring, G. T. 1991 Diet composition of pilot whale, *Globicephala* sp. and common dolphins *Delphinus delphis* in the Mid-Atlantic Bight during Spring 1989. *Fishery Bulletin*, **89**, 723–728.

Pascoe, P. L., Mickiewicz, M. C. & Castello, H. P. 1990 Cephalopod remians from the stomach of a sperm whale stranded off Patagonia. *Mar. Biol.* **104**, 1–4.

Perrin, W. F., Warner, R. R., Fiscus, C. H. & Holts, D. B. 1973 Stomach contents of porpoise, *Stenella* spp., and yellowfin tuna, *Thunnus albacares in* mixed species aggregations. *Fish. Bull. Nat. Oceanic Atmos. Admin. U.S.* **71**, 1077–1092.

Perrin, W. F., Mitchell, E. D., Mead, J. G., Caldwell, D. K. & van Bree, P. J. H. 1981 *Stenella clymene*, a rediscovered tropical dolphin of the Atlantic. *J. Mamm.* **62**, 583–598.

Pierce, G. J. & Santos, M. B. 1996 Trophic interactions of squid in Scottish waters. *Proc. R. Soc. Edinb.* (Symp.), 58–64.

Pinedo, M. C. 1982 Analise dos conteudos estomacais de *Pontoporia blainvillei* (Gervais e d'Orbigny, 1844) e *Tursiops gephyreus* (Lahille, 1908) (Cetacea, Platanistidae e Delphinidae) na zona esturial e costeira de Rio Grande, RS, Brasil. *Rio Grande Fund. Univ. de R. Grande.*

Pinedo, M. C. 1987 First record of a dwarf sperm whale from southwest Atlantic with reference to osteology, food habits and reproduction. *Sci. Rep. Whales Res. Inst.* **38**, 171–186.

Pitman, R. L. & Ballance, L. T. 1992 Parkinson's petrel distribution and foraging ecology in the Eastern Pacific: aspects of an exclusive feeding relationship with dolphins. *Condor* **94**, 825–835.

Pulcini, M., Carlini, R. & Wurtz, M. 1992 Stomach contents of striped dolphins, *Stenella coeruleoalba* (Meyen, 1933) from the south-central Tyrrhenian coast. *Eur. Res. Cetaceans*, 194–195.

Ray, G. C. & Schevill, W. E. 1974 Feeding of a captive gray whale *Eschrichtius robustus*. *Mar. Fish. Rev.* **36**, 31–38.

Recchia, C. A. & Read, A. J. 1989 Stomach contents of harbour porpoises, *Phocoena phocoena* (L), from the Bay of Fundy. *Can J. Zool.* **67**, 2140–2146.

Robertson, K. M. & Henshaw, A. 1995 Prey of the Northern right whale dolphin in Californian coastal waters. Eleventh Biennial Conference of Marine Mammals, Orlando, Florida, U.S.A., Dec. 14–18.

Robson, G. C. 1925 On *Mesonychoteuthis*, a new genus of oegopsid. Cephalopoda. *Ann. Mag. nat. Hist.* **16**, 272–277.

Ross, G. J. B. 1979*a* Records of pigmy and dwarf sperm whales, genus *Kogia*, from southern Africa, with biological notes and some comparisons. *Ann. Cape Province Mus.* (*Nat. Hist.*) II, 259–327.

Ross, G. J. B. 1979*b* The smaller cetaceans of the South East coast of Southern Africa. Ph.D. thesis, University of Port Elizabeth.

Ross, G. J. B. 1984 The smaller cetaceans of the south east coast of southern Africa. *Ann. Cape Province Mus. nat. Hist.* **15**, 173–411.

Santos, M. B., Boyle, P. R., Pierce, G. J., Wijnsma, G., Ross, H. M., Reid, R. J. & Clarke, M. R. 1995*a* Diets of sperm whales stranded in Scotland. *Int. Counc. Explor. Sea* C.M. 1995/N; 5.

Santos, M. B., Pierce, G. J., Gonzalez, A., Lopez, A. & Guerra, A. 1995*b* Diets of small cetaceans stranded on the Galician coast. *Int. Counc. Explor. Sea* C.M. 1995/N; 11.

Santos, M. B., Pierce, G. J., Ross, H. M., Reid, R. J. & Wilson, B. 1994 Diets of small cetaceans from the Scottish coast. *Int. Counc. Explor. Sea* C.M. 1994/N; 11.

Seagards, D. A. & Henderson, J. R. 1985 Cephalopod remains from the stomach of a short-finned pilot whale collected near Santa Catalina island, California. *J. Mamm.* **66**, 777–779.

Secchi, E. R., Campolom, M. B. & Moller, L. 1994 Notas sobre o encalhe de dois cachalotes pigmeus *Kogia breviceps* NA costa sul do Rio Grande do Sul – Brasil. In *Anales de la IV Reunion de trabajo de Especialistas en mamiferos Aquaticos de America del sur* 12–15 *Nov.* 1990, *Chile* (ed. J. A. Oporto), pp. 244–262.

Sekiguchi, K., Klages, N. & Best, P. B. 1992 Comparative analysis of the diets of the smaller odontocete cetaceans along the southern african coast. *South African Journal of Marine Science* **12**, 843–864.

Sekiguchi, K., Klages, N., Findlay, K. & Best, P. B. 1993 Feeding habits and possible movements of southern bottlenose whales (*Hyperodon planifrons*). *Proc. Nipr. Symp. polar Biol.* **6**, 84–97.

Sergeant, D. E. & Fisher, H. D. 1957 The smaller Cetacea of eastern Canadian waters. *J. Fish. Res. Bd Can.* **14**, 83–115.

Slip, D. J., Moore, G. J. & Green, K. Stomach contents of a southern bottlenose whale, *Hyperodon planifrons*, stranded at Heard Island. *Mar. Mamm. Sci.* **11**, 575–584.

Wilke, F. & Nicholson, A. J. 1958 Food of porpoises in waters off Japan. *J. Mammal.* **39**, 441–443.

Wurtz, M. & Marrale, D. 1993 Food of striped dolphin, *Stenella coeruleoalba*, in the Ligurian Sea. *J. mar. biol. Ass. U.K.* **73**, 571–578.

Wurtz, M., Podesta, M. & Pulcini, M. 1993 The food of the Cuvier's beaked whale (*Ziphius cavirostris* Cuvier, 1823) in the Mediterranean sea. *Eur. Res. Cetaceans* **7**, 1–13.

Wurtz, M., Poggi, R. & Clarke M. R. 1992 Cephalopods from the stomachs of a Risso's dolphin (*Grampus griseus*) from the Mediterranean. *J. mar. biol. Ass. U.K.* **72**, 861–867.

Young, D. D. & Cockcroft, V. G. 1994 Diet of common dolphins (*Delphinus delphis*) off the south-east coast of southern Africa: opportunism or specialisation? *J. Zool., Lond.* **243**, 41–53.