



DIET COMPOSITION AND TROPHIC LEVELS OF MARINE MAMMALS^a

by

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ABSTRACT

Standardized diet compositions for 108 species of marine mammals were derived from published accounts of stomach contents and morphological, behavioural and other information.

Based on the trophic levels (TL) of the eight types of food items used to describe the diet compositions (previously estimated using the ECOPATH II approach and software, applied to over 50 marine ecosystems) TLs were estimated for each marine mammal species, and compared with published estimates derived using stable isotope ratios. We anticipate that these TL estimates and ancillary statistics that may be derived from the data herein may be of use for ecosystem modelling and similar purposes.

Keywords: Marine mammals, diets, trophic levels.

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Introduction

Food and feeding habits determine the position of animals within food webs, and hence largely define their ecological role.

This is also true for marine mammals, whose food and feeding habits have been reported in numerous published accounts based on analyses of stomach contents, or scats, or from direct observations, or inferred by indirect methods such as isotope ratios (Orstrom et al. 1993).

The majority of the available quantitative studies pertain, however, to small numbers of individuals, and/or a small fraction of a species range, both of which usually cannot be used for direct inferences involving the entire (global or oceanwide) distribution areas of these species.

Some authors have attempted, on the other hand, to summarize scattered data on the food and feeding habits of mammals species (notably Evans 1987, and Klinowska 1991 for cetaceans, and King 1983 and Bonner 1990 for pinnipeds), but they have done so on a broad qualitative basis, precluding the direct use of their summaries for trophic modelling, or comparative studies.

This study is our attempt to combine the scattered quantitative studies with the broad qualitative summaries mentioned above, thus yielding standardized diet compositions for use in trophic modelling and related studies. These potential uses are here illustrated by our presentation of trophic levels for 108 species of marine mammals, derived from the diet composition, and contrasted with trophic level estimates obtained using different approaches.

Material and Methods

The 108 species of marine mammals (I) considered here are those listed in Jefferson et al. (1993), minus sirenians, which are herbivores; freshwater dolphins, which are not marine; and polar bear, which feed almost exclusively on seals.

Following trials with various other schemes, we settled on eight categories to describe diet compositions; these are defined further below; their own mean trophic levels (TL_j), mainly adapted from Table 1 in Pauly and Christensen (1995), are added [in square brackets].

BI - benthic invertebrates: mainly molluscs, notably bivalves and gastropods, but also including octopus, and echinoderms and crustaceans [2.2];

LZ - large zooplankton: mainly small crustaceans, especially euphausiaceans (krill) e.g., *Euphasia superba* in Antarctic waters [2.2];

SS - small squids: consisting of families with species with mantle lengths of up to 50 cm, e.g., Gonatidae [3.2];

LS - large squids: consisting of families with species reaching mantle lengths above 50 cm, e.g., Onychoteuthidae [3.7, i.e., assumed, based on food webs in Christensen and Pauly (1993) to be ½ a trophic level above small squids];

SP - small pelagic fishes: consisting of clupeoids, small scombroids and allied groups [2.7];

MP - mesopelagic fishes: consisting predominantly of fish of the family Myctophidae and of other groups occurring in the Deep Scattering Layer [3.2; from central south China Sea model in Pauly and Christensen 1993];

MF - miscellaneous fishes: probably a too diverse group, consisting mainly of demersal round fish (e.g., gadoids and perciforms), but also including anadromous fishes such as salmon [3.3];

HV - higher vertebrates, i.e., other marine mammals, seabirds, plus the occasional turtle [4.0; i.e., mean of all marine mammals not consuming higher vertebrates].

The diet compositions (DC_{ij}) themselves consist of fractions of items (j), always adding up to 1, for each species (i).

The definition of the diet compositions was performed in four steps, of which the first two were:

- a) ranking of food items by weight or volume, which is largely equivalent (see MacDonald and Green 1983) reported in published accounts, and assigning a fraction 0.5 of the total diet to the item reported as "most common", "major prey", or similarly identified as main food;
- b) assignment of decreasing diet fraction, generally in steps of 0.1, to successive items as a function of their rank in qualitative accounts.

Once (a) and (b) were completed (by DP), using the above-cited four major data compilation on marine mammals, the coauthors independently checked the assignments of diet fractions using mainly species- and locale-specific accounts, with emphasis on the North Pacific and Antarctica (AT), using e.g., Goodall and Galeazzi (1985 and Perez (1990), the tropical Indo-Pacific (EC), using e.g., Tan (1995) and the North Atlantic (VC), using e.g., González et al. (1994).

This was done in two further steps:

- c) identifying from additional references, food items not included in the above-cited sources, and incorporating them in the rankings used for steps (a) and (b);
- d) adjusting the initial diet compositions given (c) and checking that the final diet composition was compatible, overall, with all information otherwise available on a given species (items (e) and (f) below).

Information not emanating from explicit diet studies, but which were also used here to infer diet compositions, consisted of:

- e) dentition or lack thereof; e.g., absence of teeth, and presence of serrated palates in some *Mesoplodon* species, suggesting a diet consisting mainly of squids;
- f) feeding time; e.g., nocturnal feeding habits in oceanic *Stenella* species, indicating a tendency to feed on mesopelagic fishes;
- g) similarity of morphology and habits with species whose diet has been studied, used here to infer diet in a few recently described species e.g., *Mesoplodon peruanus*, for which species-specific studies are still lacking.

Reconciliation of the different diet compositions derived by the four authors was performed by averaging (using steps not smaller than 0.05), with emphasis being given to the diet compositions for which most data was available (see supplement to Table 1, which also lists our sources).

Once the consolidated DC_{ij} values were available, trophic levels (TL_i) were computed for each species (i) from

$$TL_i = 1 + \left(\sum_{j=1}^8 TL_j \cdot DC_{ij} / \sum_{j=1}^8 DC_{ij} \right) \quad \text{Equation 1}$$

whose terms were all defined above.

In principle, the variance of the TL_i values could have been estimated, by combining an equation for estimating the variance of specific TL_j values (see Table 1 in Pauly and Christensen 1995) with an equation accounting for the variance among TL_j values (see Christensen and Pauly 1992). However, this approach would still not account for the differences in estimated DC_{ij} values among the four coauthors [documented in our Supplement to Table 1 (see below, and more fully in a Microsoft Excel spreadsheet available from the first author)]. We believe that a resampling scheme would do better, therefore, in capturing the uncertainty inherent in our approach (see below).

Results and Discussion

Table 1 presents our key results - the diet composition of 108 species of marine mammals, and their trophic levels.

The diet compositions as such require little comment except perhaps to emphasize their tentative character: we do expect detailed, species-specific studies to invalidate them, at least in part,

and thus in the meantime that they should be used only in aggregate form, i.e., to express the food composition of *groups* of species. In such cases, some of our errors should cancel out each other. Another approach to deal with the imprecision and likely inaccuracy of our suggested diet compositions would be to use them only in the context of some resampling scheme (e.g., a Monte Carlo simulation), wherein say 10 variants of the diet composition of each species are generated, and these used to generate distributions of item-specific food consumption.

Using the diet composition as presented, and the preys' trophic levels (TL_j) allows estimation, for each of our 108 marine mammal species (*i*), of a mean trophic level (TL_i), presented in the last column of Table 1. As may be seen, the TL_i s range from 3.2 in baleen whales, and 3.4 in sea otter, to 3.8-4.4 in most species of cetaceans and pinnipeds, to 4.5-4.6 in killer whales. Minimum and maximum TL values would occur in groups not considered here, i.e., 2.0 in sirenians and about 5 in polar bears, which overwhelmingly feed on animals with a TL of about 4 (Table 1).

For any comparison to be possible, we must account for the fact that Ostrom et al. (1993) assigned an arbitrary trophic level of 1.0 to basking shark and based thereon, of 1.2 to fin whales, which both feed on large zooplankton. We have thus added 2 (two) to each of their TL values (Table 2).

This leads to trophic levels that are markedly lower than ours in three whale species (pygmy sperm whale, sperm whale and Sowerby's beaked whale), and in fact incompatible with their observed diet, consisting of a large fraction of squids (whose TL is probably overestimated by Ostrom et al., especially for large ones), and to trophic levels much higher than ours in the other 5 species (white-beaked dolphin to Minke whale, see Table 2). Thus, while we agree with Ostrom et al. (1993) that "isotope data are a valuable source of information in the absence of stomach contents and when feeding is difficult to observe", we would hesitate to endorse their calculation that " $\delta^{15}N$ values are excellent indicators of trophic position".

Indeed we suspect that while it may be true that "the $\delta^{15}N$ composition of an individual is typically 3‰ greater than that of its diet" (Harrigan et al. 1989; Wada et al. 1987), it may not be true that "this 3‰ increase occurs with each change in trophic position within the food web" (Ostrom et al. 1993), i.e., that this 3‰ rule can be turned into a linear relationship valid from the lowest to the highest trophic levels occurring in marine mammals.

The data in Table 1 also allow estimation of the calorific contents of the diet of marine mammals of which Evans (1987) gives approximate values. Computed values may differ by a factor of 2: beaked whales, feeding exclusively on squids will tend to have the diet with the lowest energy content, while polar bears, leopard seals, and (false) killer whales, which feed exclusively, or predominantly on higher vertebrates will tend to have the diet richest in energy.

This information may be used to estimate food consumption, given predictive models for energy requirements as presented by Innes et al. (1987), a topic to which we shall return elsewhere.

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Table 1. Tentative diet compositions and related statistics of marine mammals (BI = benthic invertebrates; LZ = large zooplankton; SS = small squids; LS = large squids; SP = small pelagics; MP = mesopelagics; MF = miscellaneous fishes; HV = higher invertebrates). [Species arranged as in Jefferson et al. 1993].

Common names	Diet Composition							Trophic level
	BI	LZ	SS	LS	SP	MP	MF	
Northern right whale		1						3.2
Southern right whale		1						3.2
Bowhead whale	0.2	0.8						3.2
Pygmy right whale		1						3.2
Blue whale		1						3.2
Fin whale		0.8	0.05		0.05	0.05	0.05	3.4
Sei whale		0.8	0.05		0.05	0.05	0.05	3.4
Bryde's whale		0.4			0.2	0.2	0.2	3.7
Minke whale		0.65			0.3		0.05	3.4
Humpback whale		0.55			0.15		0.3	3.6
Gray whale	0.9	0.05				0.05		3.3
Sperm whale	0.05		0.1	0.6	0.05	0.05	0.15	4.4
Pygmy sperm whale	0.05		0.35	0.4		0.1	0.1	4.4
Dwarf sperm whale	0.1		0.4	0.4		0.05	0.05	4.3
Narwhal	0.1	0.05	0.3	0.2	0.05		0.3	4.2
White whale	0.2		0.05	0.05	0.2	0.1	0.4	4.0
Baird's beaked whale	0.1		0.3	0.25	0.1	0.1	0.15	4.2
Arnoux's beaked whale	0.1		0.2	0.1	0.2	0.2	0.2	4.1
Cuvier's beaked whale	0.1		0.3	0.3		0.15	0.15	4.3
Northern bottlenose whale	0.15		0.35	0.35		0.05	0.1	4.2
Southern bottlenose whale		0.2	0.4	0.2			0.2	4.1
Shepherd's beaked whale	0.1	0.3	0.3		0.1	0.1	0.1	3.8
Blainville's beaked whale			0.2	0.3		0.3	0.2	4.4
Gray's beaked whale			0.4	0.4		0.2		4.4
Ginkgo-toothed beaked whale			0.4	0.4			0.2	4.4
Hector's beaked whale			0.4	0.4			0.2	4.4
Hubb's beaked whale			0.4	0.4		0.2		4.4
Pygmy beaked whale	0.05		0.4	0.35		0.2		4.3
Sowerby's beaked whale			0.25	0.3	0.05	0.2	0.2	4.3
Gervais' beaked whale			0.3	0.3	0.1	0.15	0.15	4.3
True's beaked whale			0.5	0.5				4.5
Strap-toothed whale			0.3	0.4			0.3	4.4
Andrews' beaked whale			0.4	0.4			0.2	4.4
Longman's beaked whale			0.4	0.4		0.2		4.4
Stejneger's beaked whale			0.5	0.45			0.05	4.4
Irrawaddy dolphin	0.2		0.1		0.2		0.5	4.0
Killer whale			0.05	0.05	0.1		0.4	4.5
Long-finned pilot whale			0.4	0.35			0.25	4.4
Short-finned pilot whale			0.3	0.3	0.1	0.1	0.2	4.3
False killer whale			0.2	0.3			0.3	4.5
Pygmy killer whale			0.3	0.2	0.1		0.2	4.4
Melon-headed whale			0.35	0.35	0.1	0.1	0.1	4.3
Tucuxi	0.2		0.1		0.2		0.5	4.0
Indo-Pac. hump-backed dolphin	0.05	0.05			0.4		0.5	4.0
Atlantic hump-backed dolphin					0.5		0.5	4.0
Rough-toothed dolphin	0.1		0.2	0.1	0.2		0.4	4.1
Pacific white-sided dolphin			0.3	0.05	0.3	0.2	0.15	4.1
Dusky dolphin			0.15	0.05	0.4	0.25	0.15	4.0
White-beaked dolphin	0.05		0.15	0.05	0.15		0.6	4.2
Atlantic white-sided dolphin	0.1		0.15	0.1	0.15	0.1	0.4	4.1
Hourglass dolphin			0.5		0.2	0.1	0.2	4.1
Peale's dolphin	0.1		0.3	0.1	0.1	0.1	0.3	4.1
Risso's dolphin	0.05		0.5	0.35	0.05		0.05	4.3
Bottlenose dolphin			0.2	0.05	0.15		0.6	4.2

Table 1 Cont'd.

Common names	Diet Composition							Trophic	
	BI	LZ	SS	LS	SP	MP	MF	HV	level
Pantropical spotted dolphin			0.3	0.2	0.1		0.4		4.3
Atlantic spotted dolphin			0.3	0.2	0.1		0.4		4.3
Spinner dolphin			0.2	0.2		0.4	0.2		4.3
Clymene dolphin			0.2	0.2	0.1		0.4	0.1	4.4
Striped dolphin	0.05		0.2	0.15	0.05	0.3	0.25		4.2
Common dolphin			0.15	0.15	0.1	0.4	0.2		4.2
Fraser's dolphin	0.05		0.3	0.05	0.05	0.35	0.2		4.2
Northern right whale dolphin			0.3	0.2		0.4	0.1		4.3
Southern right whale dolphin			0.2	0.3		0.4	0.1		4.4
Commerson's dolpin	0.1	0.1	0.2	0.1	0.35		0.15		3.9
Heaviside's dolphin			0.2	0.2	0.1	0.2	0.3		4.3
Hector's dolphin	0.05		0.25	0.2	0.2	0.1	0.2		4.2
Black dolphin			0.2	0.2	0.4		0.2		4.1
Dall's porpoise	0.05		0.3	0.1	0.2	0.2	0.15		4.1
Spectacled porpoise			0.2	0.1	0.3		0.4		4.1
Harbour porpoise	0.05		0.1	0.1	0.3		0.45		4.1
Burmeister's porpoise		0.1	0.2	0.1	0.35		0.25		4.0
Vaquita			0.3	0.2	0.2		0.3		4.2
Finless porpoise	0.1		0.4		0.2	0.1	0.2		4.0
Franciscana	0.1		0.2	0.2	0.2		0.3		4.1
Steller sea lion	0.15		0.2	0.15	0.05		0.4	0.05	4.2
California sea lion	0.1		0.2	0.15	0.25		0.3		4.1
South American sea lion	0.1	0.15	0.15	0.1	0.1		0.35	0.05	4.0
Australian sea lion	0.1		0.15	0.05	0.1		0.55	0.05	4.2
Hooker's sea lion	0.2	0.05	0.3	0.05	0.15		0.2	0.05	4.0
Northern fur seal			0.15	0.15	0.25	0.15	0.3		4.2
Guadalupe fur seal	0.2		0.3		0.3		0.2		3.9
Juan Fernandez fur seal	0.15		0.3	0.15	0.25		0.15		4.0
Galapagos fur seal			0.4		0.2	0.3	0.1		4.1
South American fur seal	0.2	0.05	0.1	0.05	0.35		0.25		3.8
New Zealand fur seal	0.2		0.2	0.1	0.1	0.1	0.25	0.05	4.1
Subantarctic fur seal		0.15	0.3	0.15	0.1		0.25	0.05	4.1
Antarctic fur seal		0.5	0.1	0.05	0.1	0.05	0.15	0.05	3.7
South African fur seal	0.15		0.15	0.05	0.3		0.35		4.0
Australian fur seal	0.1		0.3	0.15	0.2		0.25		4.1
Pacific walrus	0.85						0.05	0.1	3.4
Harbour seal	0.1		0.1	0.05	0.3		0.45		4.0
Largha seal	0.15		0.05	0.05	0.3		0.45		4.0
Ringed seal	0.2	0.2			0.15	0.05	0.4		3.8
Harp seal	0.05	0.2	0.05		0.3		0.4		3.8
Ribbon seal	0.35		0.1		0.25		0.3		3.8
Grey seal	0.15		0.05		0.3		0.45	0.05	4.0
Bearded seal	0.65	0.15			0.05		0.15		3.4
Hooded seal			0.2	0.2	0.2		0.4		4.2
Mediterranean monk seal	0.2				0.2		0.5	0.1	4.0
Hawaiian monk seal	0.2		0.1				0.7		4.1
Northern elephant seal	0.05		0.4	0.2		0.2	0.15		4.3
Southern elephant seal	0.05		0.4	0.35	0.05		0.15		4.3
Crabeater seal		0.9			0.1				3.3
Ross seal	0.05	0.15	0.5	0.15			0.15		4.1
Leopard seal		0.35	0.1		0.1		0.05	0.4	4.1
Weddell seal	0.2		0.15		0.15		0.5		4.0
Sea otter	0.8		0.05		0.05		0.1		3.4
Marine otter	0.65				0.1		0.25		3.5

Supplement to Table 1. Details on marine mammal diets, by species and author.

The following present, by family and species the notes of the authors (DP; AT; EC and VC), documenting the sources they used to derive the diet compositions that were averaged to obtain the diet compositions in Table 1. Species missing below have, in Table 1, a diet composition derived by the senior author only as described in the text; details are available from DP in form of a Microsoft Excel spreadsheet). The diet components (BI, LZ, SS, etc.) are defined in the text.

NORTHERN RIGHT WHALE: VC: Feed on patches dominated by *Calanus finmarchicus*, *Pseudocalanus minutus*, *Centropages* sp. and larval barnacles (Mayo and Marx 1990; Wishner et al. 1988); EC: primarily copepods, secondarily euphausiids (Leatherwood and Reeves 1983; Jefferson et al. 1993); *Calanus finmarchicus* (North Atlantic and Great South Channel off New England, North Pacific) (Northridge 1984; Wishner et al. 1988).

SOUTHERN RIGHT WHALE: VC: Hamner et al. (1988); EC: copepods and krill (Jefferson et al. 1993; Leatherwood and Reeves 1983).

BOWHEAD WHALE: AT: consume mostly LZ, maybe 5% small fish; Lowry and Frost (1984); Lowry (1993); EC: feed at or near the bottom of shallow waters; small to medium-sized zooplankton (euphausiids, amphipods, copepods *C. finmarchicus*, mysids, pteropods in all areas where it is found) (Jefferson et al. 1993; Leatherwood and Reeves 1983; Leatherwood et al. 1988; Northridge 1984).

PYGMY RIGHT WHALE: EC: copepods (Jefferson et al. 1993; Leatherwood and Reeves 1983; Northridge 1984).

BLUE WHALE: AT: Nemoto (1970); VC: diet from Sigurjónsson and Víkingsson (1992); EC: feed almost exclusively on krill (*E. superba*) (Gambell 1979; Jefferson et al. 1993; Leatherwood and Reeves 1983; Northridge 1984; Reilly and Thayer 1990).

FIN WHALE: AT: Bering Sea: fishes 16%, cephalopods 2%, euphausiids, copepods 82% (Kawamura 1980; Nemoto 1957, 1959, 1970); VC: "In all four seasons most of the stomachs examined contained only krill. However in 4 fin whales and 1 sei whale single specimens of fish also occurred. In addition in 3 fin whales in 1969 and 1 fin whale in 1973, fish only were present. The fishes were all sand eel, capelin and blue whiting (Lockyer and Brown 1978); MF 3%, LZ 97% (diet from Sigurjónsson and Víkingsson 1992). EC: versatile feeder; krill, small invert., schooling fish (capelin, sandlance, herring, pollack, and lanternfish), squid (Gambell 1985a; Jefferson et al. 1993; Leatherwood and Reeves 1983; Leatherwood et al. 1988); small pelagics (herring, smelt, capelin, Arctic cod, sand eels); pelagic crustacean; krill (*Euphausia superba*) in the summer; SS not mentioned (Northridge 1984).

SEI WHALE: AT: Nemoto (1970), Ostrom et al. (1993); VC: Lockyer and Brown (1978) or diet = LZ 0.9, MF 0.1; MF 2%, LZ 98% (diet from Sigurjónsson and Víkingsson 1992); EC: copepods (*Calanus* spp.) (northern part of its range); krill, amphipods, squid and varied schooling fish (rest of its range) (Gambell 1985b; Jefferson et al. 1993; Leatherwood and Reeves 1983; Leatherwood et al. 1988; Northridge 1984).

BRYDE'S WHALE: EC: euphausiids and fish (pilchards, anchovies, herring, mackerel, bonito) (Leatherwood and Reeves 1983); fish-eaters and invertebrates (agree with DP, very general) (Jefferson et al. 1993); agree with DP's diet estimates (Northridge 1984); Leatherwood et al. (1988) mentioned red crabs, a planktonic crustacean in Baja California; also krill (inshore) and epi- or mesopelagic fishes (offshore whales), off South Africa and Japan.

MINKE WHALE: AT: Ichii and Kato (1991); Jonsgaard (1982); Kasamatsu and Hata (1985); Kawamura (1980); VC: Bushuev (1986, 1991); Haug et al. (1993, 1994); Lydersen et al. (1991a); Nordoy and Blix (1992); SP 100% (from Santos et al. 1994, SP is ammodytidae, diet is coastal); MF 59, LZ 41 (diet from Sigurjónsson and Víkingsson 1992); EC: Agree with DP's diet estimates, general description of diet given, assuming true in all areas (Jefferson et al. 1993; Leatherwood and Reeves 1983; Leatherwood et al. 1988; Northridge 1984); mentioned feeding on older size-group of *Euphausia superba* only (Antarctic area) (Bushuev 1991).

HUMPBACK WHALE: AT: Bering Sea: fishes 29%, cephalopods 2%, euphausiids 69%, copepods 1%; eat sandlance, herring, krill (Hain et al. 1981; Kawamura 1980; Nemoto 1957, 1959, 1970); VC: "seemingly, euphausiid crustaceans were their main prey when they arrived in late spring, whereas capelin became more and more important throughout the season" but no value was entered (Christensen et al. 1990); MF 60%, LZ 40% (diet from Sigurjónsson and Víkingsson 1992). EC: agree with DP's diet estimates (general description of diet), krill and schooling fish, assuming true in all areas (Jefferson et al. 1993; Leatherwood and Reeves 1983; Leatherwood et al. 1988); fish classified (capelin, clupeids, osmerids, gadids, ammodytid, hexagrammid - SP and MF (Salmonidae)) (Northridge 1984).

GRAY WHALE: AT: Bogoslovskaya et al. (1981); Nerimi (1984); EC: agree with DP on diet (Leatherwood and Reeves 1983; Northridge 1984), but SP not mentioned in other references; feeds mainly on swarming mysids and tube-dwelling amphipods (Jefferson et al. 1993); tube-dwelling amphipods (Avery and Hawkinson 1992); and ghost shrimps (Weitkamp et al. 1992).

SPERM WHALE: AT: fish 18%, squid 82% (Clarke 1956; Kawakami 1980; Okutani and Nemoto 1964); VC: Roe (1968) reports more fish than found by many others, possibly because these were feeding east of Greenland and squids are more common when feeding by the Azores. The fish are larger species, not small mesopelagics. Nothing is stated about squid species, but it is probably larger squids as sperm whales feed at depth, and SP are not recorded in the stomachs; Gaskin and Cathorn (1967) found that fish species made up to 37% of the stomach contents by weight. The rest were squids; "The sperm whale... its diet being predominantly teuthoid cephalopods..." The stomach of the stranded sperm whale consisted solely of cephalopod beaks (Pascoe et al. 1990); SS 100% (González et al. 1994); SS 30%, LS 70% (from Santos et al. 1994, diet is coastal); MF 76%, SS 12%, LS 12% (diet from Sigurjónsson and Víkingsson 1992); EC: mainly squids (SS, LS), occasionally octopuses and a variety of fish (salmon, rockfish, lingcods and skates) (Leatherwood and Reeves 1983); squids and octopuses are major prey items, also a variety of fish, cephalopods and non-food items (Jefferson et al. 1993); feeds mainly on squids, also octopuses and a variety of fish (Leatherwood et al. 1988); deep-water and bottom dwelling species (Tan 1995).

PYGMY SPERM WHALE: VC: only contained beaks from 5 families of oceanic teuthoid cephalopods of which the family Histioteuthidae was the most numerous (Martins et al. 1985); EC: squids and octopuses, also stomatopods, crabs and fish (Leatherwood and Reeves 1983); deep-water cephalopods, less often on deep-sea fishes and shrimps (Jefferson et al. 1993); mainly on squid, also on pelagic crustaceans and some fishes (Leatherwood et al. 1988); deep-water and bottom dwelling species (Tan 1995).

DWARF SPERM WHALE: VC: The stomach contained shrimp remains and 78 cephalopod beaks...Of the identified cephalopod beaks, 55% belonged to Histioteuthidae, 14% to Chiroteuthidae (Pinedo 1987). EC: mainly squids, fish, crustaceans (Leatherwood and Reeves 1983); Jefferson et al. (1993) mentioned deep-water cephalopods only, main diet is squid supplemented by deep-water fish (Northridge 1984); mainly cephalopods, variety of deep-water fish and crustaceans are also eaten, agree with DP's diet estimates (Leatherwood et al. 1988).

NARWHAL: EC: squid, polar cod, demersal fish and crustaceans; shrimps mentioned but BI = 0 in the diet (Jefferson et al. 1993; Leatherwood and Reeves 1983); diet estimates agree with DP's, but no LZ mentioned (Northridge 1984).

WHITE WHALE (BELUGA WHALE): AT: fish 93%, squid 2%, euphausiids 3%, amphipods 1%, other 1% (Lowry et al. 1985, Seaman et al. 1982); EC: various spp. of fish; wide variety of molluscs and benthic invertebrates (Jefferson et al. 1993).

BAIRD'S BEAKED WHALE: AT: Rice (1986); EC: deep-sea fish (also mackerel, sardines, rockfish), octopus, squid, crustaceans, sea cucumber (Leatherwood and Reeves 1983); mainly deep water and bottom-dwelling fish, cephalopods, and crustaceans (Jefferson et al. 1993); squid only (Northridge 1984).

ARNOUX'S BEAKED WHALE: DP: Diet assumed similar to that of Baird's beaked whale (Klinowska 1991, p. 272); EC: deep-sea fish (also mackerel, sardines, rockfish), octopus, squid, crustaceans, sea cucumbers (Leatherwood and Reeves 1983); benthic and pelagic fishes and cephalopods (Jefferson et al. 1993); mentioned cephalopods only (Northridge 1984);

CUVIER'S BEAKED WHALE: EC: squid and deep-water fish, no BI mentioned (Leatherwood and Reeves 1983; Northridge 1984); mostly deep-sea squid, fish, and some crustaceans (Jefferson et al. 1993); primarily squid (in Japan consistent under 1000 m); fish in animals taken in deeper waters (Heyning 1989).

NORTHERN BOTTLENOSE WHALE: VC: diet from Sigurjónsson and Víkingsson 1992; EC: squid, fish, sea stars (starfish), sea cucumbers, prawns (Jefferson et al. 1993; Leatherwood and Reeves 1983; Mead 1989b; Northridge 1984).

SOUTHERN BOTTLENOSE WHALE: VC: Sekiguchi et al. (1993); EC: fish, squid (Jefferson et al. 1993; Leatherwood and Reeves 1983; Northridge 1984).

BLAINVILLE'S BEAKED WHALE: DP: adapted from Klinowska (1991, p.282); EC: squid probably the main food (SS and LS?), but fish is also taken (MP and MF?) (Jefferson et al. 1993); "trace quantities of squid beaks but no fish remains" (Mead 1989a); deep-water species (Tan 1995).

GRAY'S BEAKED WHALE: DP: "Mean", based on beaked whales for which some data are available.

GINKGO-TOOTHED BEAKED WHALE: DP: "Mean", based on beaked whales for which some data are available.

HECTOR'S BEAKED WHALE: DP: Adapted from Klinowska (1991, p. 292); EC: squid (Jefferson et al. 1993; Mead 1989a; Mead and Baker 1987).

HUBB'S BEAKED WHALE: DP: Adapted from Klinowska (1991, p. 312); EC: squid and mesopelagic fish (Leatherwood and Reeves 1983); squid and deep-water fish (Jefferson et al. 1993).

PYGMY BEAKED WHALE: DP: "Mean", based on beaked whales for which some data are available; EC: small mid-water fishes; oceanic squid and shrimps (Jefferson et al. 1993).

SOWERBY'S BEAKED WHALE: DP: "Mean", based on beaked whales for which some data are available; also compatible with data in Ostrom et al. (1993); VC: Diet is coastal, from Santos et al. (1994); EC: squid and small fish (Jefferson et al. 1993).

GERVAIS' BEAKED WHALE: DP: Assumed similar to diet of Blainville's beaked whale (see also Klinowska 1991, p. 285); EC: squid only, no fish mentioned (Jefferson et al. 1993); squid only, generally eat mesopelagics squid and fish (Mead 1989a).

TRUE'S BEAKED WHALE: DP: Adapted from Klinowska (1991, p. 305); EC: squids (Jefferson et al. 1993; Mead 1989a).

STRAP-TOOTHED WHALE: DP: Adapted from Klinowska (1991, p. 289), assuming that algae were ingested while feeding on epipelagic fishes; EC: squid, but no fish mentioned (Jefferson et al. 1993).

ANDREW'S BEAKED WHALE: DP: "Mean", based on beaked whales for which some data are available.

LONGMAN'S BEAKED WHALE: DP: Mean, based on beaked whales for which some data are available.

STEJNEGER'S BEAKED WHALE: DP: Based on Klinowska (1991, p. 300); EC: squid only, no fish mentioned (Jefferson et al. 1993; Mead 1989a).

IRRAWADDY DOLPHIN: EC: fish, cephalopods, crustacean (Jefferson et al. 1993; Leatherwood and Reeves 1983; Northridge 1984)

KILLER WHALE: AT: estimates chosen in consultation with John Ford (Vancouver Aquarium, pers. comm.); also: Hoyt 1990; Rice 1968; VC: diet from Sigurjónsson and Víkingsson (1992); EC: agree with DP's HV estimate, fish (herring, salmon), LS not mentioned (Leatherwood and Reeves 1983); agree with DP's HV estimate, various fish and cephalopods, occasionally on seabirds and marine turtles (Jefferson et al. 1991, 1993; Northridge 1984); agree with DP's HV estimate, squid and many types of fish (Tan 1995); all prey mentioned except squids (Crozet Island) (Guinet 1992).

LONG-FINNED PILOT WHALE: VC: SS 80%, MF 20%; Mainly a squid eater; detailed study of 720 stomachs year round, but all in numbers and occurrence (Desportes and Mouritsen 1988); SS 30%, MF 70% (Overholtz and Waring 1991); SS 100% (González et al. 1994); SS 50%, LS 50% (from Santos et al. 1994, diet is coastal); EC: diet estimates agree with DP's (Jefferson et al. 1993; Leatherwood and Reeves 1983; Northridge 1984; Sergeant 1962).

SHORT-FINNED PILOT WHALE: EC: Leatherwood and Reeves (1983) mentioned squids only; squids, also some fish (Jefferson et al. 1993; Northridge 1984); bottom-dwelling species (Tan 1995).

PYGMY KILLER WHALE: DP: Assuming a diet similar to that of the killer and false killer whales, and considering information in Klinowska (1991, p. 233). EC: mostly fish and squid, occasionally attack dolphins (Jefferson et al. 1993); main prey appears to be squid, but also pelagic crustacean and some fish (Leatherwood et al. 1988); surface-dwelling fish and marine mammals (Tan 1995).

MELON-HEADED WHALE: EC: squids (SS and LS?) and a variety of small fish (SP, MP, MF?), agree with DP's diet estimates (Leatherwood and Reeves 1983; Jefferson et al. 1993); Pitman and Ballance (1992) mentioned ommastrephid squids (mainly *Dosidicus gigas*) only (Eastern Pacific area).

TUCUXI: EC: fish and crustaceans (prawns and crabs) (Leatherwood and Reeves 1983); wide variety of fish (schooling pelagic, demersal) and cephalopods; no BI mentioned (Jefferson et al. 1993).

INDO-PACIFIC HUMP-BACKED DOLPHIN: VC: contained fish and cephalopod species (Barros and Cockcroft 1991); EC: fish (mullet; nearshore, estuarine and reef fish) (Jefferson et al. 1993; Leatherwood and Reeves 1983; Northridge 1984).

ATLANTIC HUMP-BACKED DOLPHIN: EC: fish (Jefferson et al. 1993; Leatherwood and Reeves 1983; Northridge 1984).

ROUGH-TOOTHED DOLPHIN: EC: pelagic octopus and squid and several species of fish, but no BI mentioned (Leatherwood and Reeves 1983); feed on cephalopods and fish (including large ones like mahi-mahi) (Jefferson et al. 1993); pelagic octopus (Florida), fish and molluscs (Pacific) (Northridge 1984).

PACIFIC WHITE-SIDED DOLPHIN: AT: percentages based on 23 individuals tabulated in Walker et al. (1986); suggest SP 80%, MF 10%, SS 10%; but Stroud et al. (1981) suggest diet from 33 stomachs is 60% squid, 30% SP and 10% MF. Squids consumed in highest frequencies are *Abraliopsis*, *Octopoteuthis*, *Gonatidae*, *Gonatus*, *Gonatopsis borealis*, *Onychoteuthis borealijaponicus* and small quantities of *Chiroteuthis* and *Cranchiidae*; VC: both dolphins (northern right

whale dolphin and Pacific white-sided dolphin) fed on over 30 species of mesopelagic fish and cephalopods (Walker and Jones 1993); EC: wide variety of fish and squid (Leatherwood and Reeves 1983; Leatherwood et al. 1988)

DUSKY DOLPHIN: VC: *Engraulis ringens* 75-87% (82%), *Trachurus symmetricus* 1-8% (5%), *Merluccius gayi* 0-8% (5%), *Sardinops sagax* 0-16% (3%), *Loligo gahi* 1-13% (4%), *Dosidicus gigas* 0-9% (1%). Figures are given averages over different female stages and then over females and males (McKinnon 1993); EC: fish (anchovy) and squid (Argentina) (Leatherwood and Reeves 1983); southern anchovy, mid-water and benthic prey (squid and lanternfish) (Jefferson et al. 1993).

WHITE-BEAKED DOLPHIN: VC: Diet is coastal, from Santos et al. (1994); MF 95%, SS 2.5%, LS 2.5% (diet from Sigurjónsson and Víkingsson 1992); EC: fish, some crustaceans, molluscs and cephalopods (Jefferson et al. 1993; Northridge 1984).

ATLANTIC WHITE-SIDED DOLPHIN: VC: diet from Sigurjónsson and Víkingsson (1992); EC: squid, herring, smelts, silverhakes and several kinds of shrimps (Leatherwood and Reeves 1983); no BI mentioned (Jefferson et al. 1993; Northridge 1984).

PEALE'S DOLPHIN: EC: octopus, fish (snooks, silversides) (Jefferson et al. 1993).

RISSO'S DOLPHIN: VC: González et al. (1994); Diet is coastal, 98% *Eledone cirrhosa* (Santos et al. 1994); SS 100%, "it is usually stated that this species eats little, if anything, other than cephalopods"; "the present collection upholds the more general belief that the species takes little or no fish" (Würtz et al. 1992); EC: mainly squid (SS, LS), rarely on fish, no BI (Leatherwood and Reeves 1983); squid, crustaceans and cephalopods, no fish (Jefferson et al. 1993); almost exclusively on cephalopods, less on fish, no BI (Leatherwood et al. 1988); bottom-dwelling species (Tan 1995).

BOTTLENOSE DOLPHIN: VC: primarily fish-eating (González et al. 1994); Diet is coastal, from Santos et al. (1994); "The diet of bottlenose dolphins is known to include salmonids, squid herring and sprat" (ICES 1991); EC: wide variety of fish and invertebrates (coastal kind), squids (offshore) (Leatherwood and Reeves 1983); schooling fish, feed behind shrimp trawlers (Jefferson et al. 1993); fish (mullet, gizzard shad, weakfish and sea trout, croaker, spot), squid (Central Atlantic coast) (Mead and Potter 1990); fish (mullet, gizzard shad, weakfish and sea trout, croaker, spot, hake, silver perch, mojarra), squid (*Loligo pealei*), mollusc shells, hermit crabs (probably ingested incidentally) (northeast US Coast) (Leatherwood et al. 1978); fish (mullet), feed at night (Florida) (Irvine et al. 1981); surface and mesopelagic species (Tan 1995).

PANTROPICAL SPOTTED DOLPHIN: EC: fish, cephalopods (Eastern Tropical Pacific), squid, carangid, small eels, herring, anchovies (Atlantic, coastal spotted) (Leatherwood and Reeves 1983); epipelagic fish, squid (Jefferson et al. 1993); epipelagic fish and squid, mesopelagic fish and squid (Perrin et al. 1973); meso- and epipelagic fish and squid (Leatherwood et al. 1988); surface-dwelling species (Tan 1995).

ATLANTIC SPOTTED DOLPHIN: EC: wide variety of fish and squid (Jefferson et al. 1993; Leatherwood et al. 1988).

SPINNER DOLPHIN: VC: see Karbhari et al. (1985); EC: mainly mesopelagic fish, epi- and mesopelagic squids (Leatherwood and Reeves 1983); midwater fish and squid (Jefferson et al. 1993); mesopelagic fish, squids and crustaceans (East Pacific, Hawaii, India, Atlantic), deep-living organisms (Hawaii), reef-living and benthic organisms (North Atlantic) (Perrin et al. 1989); mesopelagic fish, epi- and mesopelagic fish, squid (Perrin et al. 1973); surface and mesopelagic species (Tan 1995).

CLYMENE DOLPHIN: EC: small fish and squid (feeds mainly at night on midwater spp.) (Jefferson et al. 1993; Leatherwood and Reeves 1983; Perrin et al. 1981; Northridge 1984).

STRIPED DOLPHIN: VC: Diet is coastal, from Santos et al. (1994); SS 40%, LS 10%, MP 10%, MF 40% (Würtz and Marrale 1993); EC: variety of mesopelagic fish, shrimps and squids (Jefferson et al. 1993; Leatherwood and Reeves 1983).

COMMON DOLPHIN: VC: Overholtz and Waring (1991); primarily fish-eating (González et al. 1994); Diet is coastal, from Santos et al. (1994), SP is ammodytidae; EC: mesopelagic fish and squids (species in Deep Scattering Layer) (Jefferson et al. 1993; Leatherwood and Reeves 1983; Leatherwood et al. 1988; Northridge 1984).

FRASER'S DOLPHIN: VC: contained mesopelagics and nectobenthic species (*Trisopterus* sp., *Micromesistius poutassou*, *Merlangius merlangus* and *Sepia* sp.) (Van Bree et al. 1986); diet guessed; EC: squids, crustaceans, deep-sea fish (Leatherwood and Reeves 1983); mid-water fish, squid, crustaceans (Jefferson et al. 1993); mesopelagic fishes, shrimps, and squids (Robinson and Craddock 1983); mesopelagic species (Tan 1995); mesopelagic and nectobenthic species (Van Bree et al. 1986).

NORTHERN RIGHT WHALE DOLPHIN: VC: both dolphins (northern right whale dolphin and Pacific white-sided dolphin) feed on over 30 species of mesopelagic fish and cephalopods (Walker and Jones 1993); EC: squids, fish

(myctopids and bathylagids) (Leatherwood and Reeves 1983; Northridge 1984; Walker and Jones 1993); squid, lanternfish; also wide variety of surface and midwater spp. (Jefferson et al. 1993; Leatherwood et al. 1988).

SOUTHERN RIGHT WHALE DOLPHIN: EC: myctopids and squid (off Chile, New Zealand, off South Africa) (Jefferson et al. 1993; Leatherwood and Reeves 1983; Northridge 1984).

COMMERSON'S DOLPHIN: EC: opportunistic feeder, feeding mainly near the bottom; krill, squid, crabs, cuttlefish; fish (San Jorge Gulf) (Leatherwood and Reeves 1983); various fish, squid and shrimp (Jefferson et al. 1993).

HEAVISIDE'S DOLPHIN: EC: squid and bottom-dwelling fish (Jefferson et al. 1993; Leatherwood and Reeves 1983).

HECTOR'S DOLPHIN: EC: shellfish, crustaceans, small fish and squids (Leatherwood and Reeves 1983); small fish and squid (opportunistic feeder) (Jefferson et al. 1993).

DALL'S PORPOISE: DP: Adapted from diet of other phocoenids, but excluding krill and benthic invertebrates; AT: Crawford (1981); Kajimura et al. (1980); EC: opportunistic feeder; squids, crustaceans, fish (meso- and bathypelagic, deep-water benthic spp.) (Leatherwood and Reeves 1983; Leatherwood et al. 1988); surface and mid-water fish and squid especially lanternfish and gonatid squids (Jefferson et al. 1993); DP's diet OK (Northridge 1984).

HARBOUR PORPOISE: AT: Frost and Lowry (1981); Lowry et al. (1982); Prescott and Fiorelli (1980); Recchia and Read (1989); VC: primarily fish-eating (González et al. 1994); Diet is coastal, SP is ammodytidae (all from Santos et al. 1994); "co (Baltic Sea) and flatfish (North Sea) were important components of the diet, which included fish up to 62 m long" (Lick 1991); Porpoises are known to prey on a wide range of pelagic and demersal fish, and cephalopods. Recent studies (e.g. Martin et al. 1990) have indicated that demersal and deep-water fish may be more important than the published record suggests. (ICES 1991); MF 95%, SS 2.5%, LS 2.5% (diet from Sigurjónsson and Víkingsson 1992); EC: fish (school-ing, benthic, demersal), cephalopods (Leatherwood and Reeves 1983; Jefferson et al. 1993; Leatherwood et al. 1988); most important fish in the diet (capelin *Mallotus villosus*, Atlantic herring *Clupea harengus*, and redfish *Sebastes marinus*) (estuary and Gulf of St. Lawrence) (Fontaine et al. 1994).

BURMEISTER'S DOLPHIN: EC: fish (anchovies and hake), squids (Jefferson et al. 1993).

VAQUITA: EC: gulf croakers and squid (Leatherwood et al. 1988).

FINLESS PORPOISE: EC: small squid, shrimp and prawns, as well as fish eggs, rice and other grains (Leatherwood and Reeves 1983); small fishes, squids and shrimps, ingest some plant material (leaves and rice) (Jefferson et al. 1993); small squids and cuttlefish, crustaceans and some fish (sandlance) (Northridge 1984).

FRANCISCANA: EC: feeds near the bottom on fish, cephalopods and crustaceans (Jefferson et al. 1993).

STELLER SEA LION: AT: Calkins and Goodwin (1988); NMFS (1992); EC: variety of fish and squid; prefers bottom species (Jefferson et al. 1993); squids, fish, molluscs, others (crustaceans, isopods, segmented worms, sand dollars, coelenterates; kelp; rocks, sand, gravel) (Mathisen 1959; Mathisen et al. 1962).

CALIFORNIA SEA LION: AT: percentages were worked out from a table showing the number of samples containing different prey. Actual percentages were: SP 45.17%, MF 29.98%, SS+LS 16.34%, BI 8.52% (from Lowry et al. 1991); EC: squid, octopus, and many species of fish (Jefferson et al. 1993).

SOUTH AMERICAN SEA LION: DP: Muck and Fuentes (1987) assume fish (especially *Engraulis ringens*) to dominate diet off Peru; AT: a summary citing Aguayo and Maturana (1973) and Olivia (1984) states: they feed on rock fish, South Pacific hake and herring. Molluscs and crustaceans such as squid and sea snails are also part of their diet. Other species eaten include elephant fish (*Callorhynchus capensis*), Peruvian anchoveta, grenadier, South American pilchard, cusk eels, butter fish, squid and octopus; VC: "observed 33 seals being killed. Only a small proportion of adult sea lions hunted fur seals" (Harcourt 1993); conclusion: HV should be included in the diet of southern sea lion; EC: benthic and pelagic fish and invertebrates (lobster, krill, squid, octopus, jellyfish); occasionally on penguins and young South American fur seals (Jefferson et al. 1993).

AUSTRALIAN SEA LION: AT: "generally their diet is very broad, consisting of many species of fish, including salmon, whiting, and sharks, as well as cephalopods (especially *Sepia*) and some penguins (N. Gales, pers. comm.)" (Reijnders et al. 1993); EC: wide variety of fish (including rays and small sharks); squid, cuttlefish, penguins (Jefferson et al. 1993).

HOOKE'S SEA LION: AT: Reijnders et al. (1993) state: "the diet includes cephalopods, prawns, crayfish, crabs and small fish. Occasionally penguins are taken"; EC: wide variety of prey including squid and demersal fish, octopus, crustaceans, penguins; occasionally on fur seal and elephant seal pups (Jefferson et al. 1993).

NORTHERN FUR SEAL: AT: SP 50%, MF 30%, SS 10%, LS 10% (from Perez and Bigg 1986); Primary squids consumed were market squid *Loligo opalescens*, onychoteuthid squids and gonatid squids (Kajimura 1984); VC: (Sinclair

et al. 1994): diet based on % of number, not on weight [not good]; EC: epipelagic and vertically-migrating mesopelagic schooling and non-schooling fish and squid (Jefferson et al. 1993; Northridge 1984).

GUADALUPE FUR SEAL: DP: "Average" diet composition of *Arctocephalus* spp., but excluding krill; AT: "diet not well studied; have been observed to eat squid and lantern fish" (Reeves et al. 1992);

JUAN FERNANDEZ FUR SEAL: DP: Adapted from "average" diet composition of *Arctocephalus* spp, but excluding krill and emphasizing squids (Majluf and Reyes 1989); AT: diet consists of fish and cephalopods, *Dosidicus gigua*, *Octopoteuthis* sp., *Tremoctopus violaceus*, *Todarodes filippovae* and *Moroteuthis banksii* (Torres 1987a); According to fishers, this fur seal feeds on various species of fish, squid and lobsters. Squid beaks recovered include *Dosidicus gigas*, *Octopoteuthis* sp., *Tremoctopus violaceus*, *Todarodes filippovae* and *Moroteuthis banksii* (Torres 1987b); EC: squid, fish, lobsters (Jefferson et al 1993; Northridge 1984).

GALAPAGOS FUR SEAL: AT: "feed at night mostly at depths of between 10 and 50 m. Their main diet is myctophids, bathylagids and small cephalopods" (Reijnders et al. 1993); According to Trillmich (1987), very little information is available. One sample found 74% of biomass was *Onychoteuthis banksi*, while another had ommastrephids comprising 84% of all squid beaks found. A large number of otoliths have been recovered but not identified; Clarke and Trillmich (1980). EC: feeds mostly at night, possibly exploiting Deep Scattering Layer; small squids and several schooling fish (Jefferson et al. 1993).

SOUTH AMERICAN FUR SEAL: DP: Muck and Fuentes (1987) assume fish (especially *Engraulis ringens*) to dominate diet off Peru; AT: "in Peru, Majluf (1987) found that South African fur seal forage mainly on sardine *Sardinops sagax*, anchovy *Engraulis ringens*, and jack mackerel *Trachurus symmetricus*."; "in Uruguay, feeding probably occurs offshore (as much as 200 km). Stomachs sometimes contain fish otoliths, snails, prawns and cephalopod beaks. Thirteen drowned specimens contained anchovy *Engraulis anchoita*, mackerel *Trachurus lathami*, *Cynoscion striatus*, *Pneumatophorus* (=Scomber) *japonicus*, *Peprilus* sp. Nine others contained shrimps, *Paralichthys brasiliensis*, *Micropogonias furnieri* and *Sympterygia acuta*" (Vaz-Ferreira and Ponce de Leon 1987); EC: variety of small schooling fishes and invertebrates (cephalopods, crustaceans and gastropods) (Jefferson et al. 1993).

NEW ZEALAND FUR SEAL: AT: Estimates are from Reijnders et al. (1993). Note that no sources for the information are given. assumed that the 20% squid diet is split equally between SS and LS. Information given indicates 38% barracuda (*Sphyræna* sp.), 27% octopus, 24% squid and 9% small fish. Occasionally birds are eaten too; Mattlin (1987) states: feed mainly on cephalopods and fish, though they are known to take penguins, particularly at the Subantarctic islands. Stomach contents of 64 seals contained 28.8% octopus, 23.9% squid, 38.1% barracouta (*Thyrstites atun*), and 9.2% other fish by weight (Street 1964); EC: appear to feed mainly at night; wide variety of pelagic, near-surface fishes and squids and benthic prey, particularly octopus; occasionally on penguins and marine birds (Jefferson et al. 1993); barracouta (*Thyrstites atun*) 38%, octopus 25%, squid 24% are the main prey, also on penguins (Carey 1992).

SUBANTARCTIC FUR SEAL: AT: Diet consist of several fish species, cephalopods, euphausiids and penguins. Rand (1956) reports that the stomachs contained mostly fish (Notothentidae - inshore, benthic), cephalopods, and euphausiids.; Condry (1981) recorded cephalopod beaks, fish remains, penguin feathers, seaweed and stones and assumed diet was 50% cephalopods, 45% fish, and 5% euphausiids.; Of beaks identified by Bester (1987), 52.5% were Ommastrephidae, 25.2% Histiotethidae, 19.9% Onychoteuthidae, 2.1% Cranchiidae and 0.3% Octopoteuthidae; EC: diet varies on location and season; fish, squid, penguins and krill predominant (Jefferson et al. 1993); cephalopods most important., also euphausiids and some notothenid fish (Northridge 1984).

ANTARCTIC FUR SEAL: AT: 69% krill, 19% fish, mainly *Champsocephalus gunnari*, 12% squid, *Martialia hyadesi*, *Kondokovia longimana* and *Moroteuthis glacialis*; Doidge and Croxall (1985); Green et al (1989); Green et al. (1991); North et al. (1983); VC: see Boveng et al. (1991): should give diets, "the seals' primary prey species, antarctic krill..."; EC: nocturnal feeding in summer; adult females feed heavily on krill, also fish, birds, squids (Jefferson et al. 1993; Northridge 1984); fish predominated (mainly myctophids, *Gymnoscopelus nicholsi*); increase in squids from 3.4% in summer 87/88 to 49.3% at present (Heard Island) (Green et al. 1991).

SOUTH AFRICAN FUR SEAL: AT: Contents by volume of 245 stomachs showed 67% fish, 21% cephalopods, 10% miscellaneous, 2% crustaceans. Most important fish species were horse mackerel, *Trachurus capensis* (40%), and pilchard *Sardinops ocellatus* (13%), hake and anchovy comprised 1.4% (from Rand 1959); Pelagic samples showed 75% teleost fish, 17% cephalopods, 1.2% elasmobranch and 5% crustaceans. Fish consisted of 74% demersal and 26% pelagic fish. Two most important species were Cape hake (32%) and anchovy (15%) (from David 1987); "75% fish (massbankers *Trachurus*, pilchards *Sardina pilchardus*, anchovies *Engraulis capensis* and hake *Merluccius* sp.), 17% cephalopods (*Loligo* is the most common), 8% crustaceans" (from Reijnders et al. 1993); Lipinski and David (1990); EC: opportunistic feeder, thought to feed most often during the day; pelagic and mid-water and benthic animals such as schooling and solitary fish, cephalopods and crustaceans (Jefferson et al. 1993).

AUSTRALIAN FUR SEAL: AT: The Australia fur seal is a deep diver (down to 500 m) and probably obtains its food from deeper waters. Squid, octopus and a wide range of fish are taken, depending on seasonal availability and local opportunity. Most important prey are fish, cephalopods and crustaceans. Most important fish are snook (*Leionura atun*). Most frequent squid are *Nototodarus* and *Sepioteuthis*, cuttlefish (*Sepia*) and octopus. Of crustaceans, rock lobster are sometimes taken. (Shaughnessy and Warneke 1987); VC: "fish were the most prevalent prey with cephalopods occurring less frequently" (Gales and Pemberton 1994), also Gales et al. (1993); EC: opportunistic feeder, thought to feed most often during the day; pelagic and mid-water and benthic animals such as schooling and solitary fish, cephalopods and crustaceans (Jefferson et al. 1993); small schooling fish - 60% of volume consumed (Northridge 1984); largely squid (*Nototodarus*, *Sepioteuthis*) as well as a variety of fishes (*Thyrstites*, small fishes e.g., mullet, pilchards, parrotfish); no BI; fish prevalent (main prey: *Emmelichthys nitidus*, redbait, *Trachurus declivis*, jack mackerel, and leatherjackets); cephalopods less frequently; crustaceans and birds, negligible (Tasmanian waters); no BI (Gales and Pemberton 1994).

PACIFIC WALRUS: VC: predominant prey: *Mya truncata*. The hair in a single scat showed that the walrus had eaten part of a white coated ringed seal pup (Gjertz and Wiig 1992); Fay's (1982) review of walrus feeding concludes that they are highly selective, but tend to take a few of most of the macrofaunal invertebrates present; Timoshenko and Popov (1990) review walrus prey in Svalbard (8 refs). There are indications that walrus males can be predatory on seals; Fay et al. (1984); EC: chiefly benthic invertebrates (clams, worms, snails, slow-moving fish); some feed on seals and small whales (Jefferson et al. 1993); benthic invertebrates in shallow waters (molluscs, echinoderms, tunicates, crustaceans, priapulids) (Northridge 1984).

HARBOUR SEAL: AT: diet from Olesiuk et al. (1990); small amounts of mussels, crabs, squids, octopus and shrimp have also been recorded (<5%). Summaries of diet contained in IUCN report for 3 stocks of harbour seals (Atlantic and Pacific) are consistent with the above; VC: Härkönen 1987; Härkönen and Heide-Jørgensen (1991); it seems that harbour seals in the Skagerrak only eat fish, BI 10%, SP 20%, MF 70% (Behrends 1982); food: numerous common fish plus some brown shrimps. Difficult to assess diet in weight based on the number based on paper; EC: opportunistic feeder, diet varies with season and location; variety of fish, cephalopods and crustaceans of surface, mid-water and benthic habitats (Jefferson et al. 1993); wide range of pelagic and demersal fish (gadids, clupeids, pleuronectids, salmonids and other commercially important species) (Northridge 1984); pelagic, benthic, anadromous fishes, as well as molluscs and crustaceans (Haaker et al. 1984); American sand lance (*Ammodytes americanus*), the single dominant prey item (waters adjacent to Cape Cod) (Payne and Selzer 1989).

LARGHA SEAL: AT: Bukhtiyarov et al (1984); Lowry et al. (1982); EC: diet varies with age; pups on small crustaceans; adolescents on schooling fish; larger ones on crustaceans and octopi; and much older ones on bottom-dwelling fish and cephalopods (Jefferson et al. 1993).

RINGED SEAL: AT: Lowry et al. (1978, 1980b); VC: "...foraging on benthic crustaceans. Ringed seals are also known to feed on pelagic crustaceans, herring, bullhead and cod" (ICES 1991); EC: many fish species and planktonic crustaceans, taken throughout the water column (Jefferson et al. 1993); most important prey: arctic cod *Boreogadus saida*, shrimp *Pandalus borealis*, krill *Thysanoessa inermis* and amphipod *Themisto libellula*. In summer, they feed on krill. Mysids, amphipod crustaceans and small, coastal fishes taken secondarily (fjord of West Svalbard) (Weslawski et al. 1994).

HARP SEAL: AT: Lydersen et al. (1991b); Sergeant (1991); VC: "samples are from 3 locations. Averaging these 3 resulted in LZ 10, SP 60, MF 30" (Beck et al. 1993); "BI were mainly amphipods and *Pandalus*; there was 1% cephalopods (*Gonatus*). Ignoring the cephalopods the diet is BI 70, MF 30. Including them diet would be BI 60%, SS 10% MF 30%" (Lydersen et al. 1991b); "In winter some feeding on squids, SP is capelin (or are they MF?); LZ is *Euphausia* and pelagic amphipods: LZ 10%, SS 10%, SP 30%, MF 50%" (Kapel and Angantyr 1989); "Based on mean estimated weight averaging first within localities and then between localities, average is LZ 30%, SS 10%, SP 20%, MF 40%. Assuming the same distribution between SP and MF as in Kapel and Angantyr 1989 (same study) as fish, breakdown is not reported here." (Kapel 1994); "Fed exclusively on capelin during this time" (Nilssen et al. 1993), SP 100%; EC: diet varies with age; variety of crustaceans and oceanic fishes during migration and switch to several varieties of bottom-dwelling fishes in the summer (northern grounds) (Jefferson et al. 1993); large zooplankton, pelagic fish (capelin, herring, cod), benthic crustaceans e.g., shrimp *Pandalus borealis* and benthic fish (flatfish, redfish) (Sergeant 1976; Northridge 1984); pelagic amphipods *Parathemisto libellula* (Barent's sea) (Nilssen and Haug 1993); fish: cod *Boreogadus saida*, and capelin *Mallotus villosus* (Finmark); saithe *Pollachius virens* (Norwegian Sea); and herring (Lofoten fjords) (Ugland et al. 1993).

RIBBON SEAL: AT: Burns (1986); Frost and Lowry (1980); Shustov (1969); EC: prey vary by area; probably by season; several fish species and crustaceans (Jefferson et al. 1993); crustaceans (shrimps, crabs, mysids) followed by fish (*Boreogadus saida*, *Theragra chalogramma*, and *Gadus macrocephalus*); cephalopods in third place (Northridge 1984).

GREY SEAL: VC: Sand lance 81%, Atlantic cod 11%, silver hake 2.6%, American plaice 1.4%, redfish 1.3%, yellowtail flounder 1.1%, witch flounder 1.1%, capelin 0.4%, squid (beaks) 0.3%; thus: SP 80, MF 20, if sand lance is considered

small pelagic, otherwise all food is MF (Bowen and Harrison 1994); note offshore feeding; *Clupea harengus* 38.5%, *Merluccius bilinearis* 8.8%, white hake 2.4%, cod 19.2%, sand lance 12.8%, mackerel 2.7%, American plaice 0.3%, pollock 5.6%, winter flounder 0.3%, yellowtail flounder 1.9%, cusk 0.4%, sea raven 0.1%, squid 8.3%. Thus: SS 10. SP 50 MF 40. or if sand lance is not SP: SS 20%, SP 40%, MF 50% (Bowen et al. 1993); "cod herring and capelin contributed 72% of the wet mass...Invertebrates contributed negligible mass" (Murie and Lavigne 1992); EC: inshore benthic habitats; variety of fishes and invertebrates; also schooling fish in the water column, occasionally birds (Jefferson et al. 1993); DP's diet OK (Northridge 1984); fish: sand eels, gadids, flatfish, sculpins, ling (Hammond et al. 1994).

BEARDED SEAL: AT: feeds mainly on bottom invertebrates such as crustaceans, molluscs and polychaetes, and a few fish (sculpins, flounders and Arctic cod); Kosygin (1966); Lowry et al. (1980a); VC: "Most frequent prey were capelin, cods, snow crab, *Chinocoetes*, eelpouts, *Lycodes*, prickleback, *Lumpenella*, clams, *Nuculana*, moon snails..." (Antonelis et al. 1994b); EC: small invertebrates that live on and in the bottom; may supplement diet with fish (Jefferson et al. 1993); fish (polar cod, herring, flounder, sand eel), molluscs, crabs, shrimps and worms (Northridge 1984); 86% of 78 stomachs with fish (capelin *Mallotus villosus*, codfish and other gadids, eelpouts *Lycodes* spp., longsnout prickleback *Lumpenella longirostris*); others were crabs, clams, snails, amphipods, shrimp, mysids, marine worms, and cephalopods (Antonelis et al. 1994b).

HOODED SEAL: EC: dive deeper than harp seals; appears to be mainly squids and fishes, both coastal and benthic species (Jefferson et al. 1993); feed on larger prey, e.g., squid *Gonatus fabricius* and the redfish *Sebastes marinus* (Sergeant 1976).

MEDITERRANEAN MONK SEAL: EC: octopus, ray, a variety of fishes (Jefferson et al. 1993).

HAWAIIAN MONK SEAL: EC: reef fishes, eels, cephalopods, and lobsters (Jefferson et al. 1993).

NORTHERN ELEPHANT SEAL: AT: Antonelis et al. (1994a) tabulate 53 species found in the stomachs of 167 adults, and indicate % of the stomachs that contained each of the 53 prey items. I estimated the diet composition based on absence or presence of above values. Note that the authors give no indication of volume or frequency of occurrence, only presence or absence of prey type. There were 32 different species of squid, of which I assume 80% were <50 cm; EC: mainly squids, small sharks, and deep-water fishes (Jefferson et al. 1993).

SOUTHERN ELEPHANT SEAL: AT: major components in the diet are cephalopods. Of these, the *Kondakovia longimana* and *Moroteuthis knipovitchi* represent over 50% of the biomass. Of 31 stomachs with food, 24 contained squid and 9 fish. Laws (1977) suggested diet consisted of 75% squid and 25% fish by weight; Boyd et al. 1994; Green and Williams 1986; Rodhouse et al. 1992; VC: "51 stomachs were lavaged at Husvik, South Georgia; only cephalopod remains were retrieved. Most important species: *Moroteuthis knipovitchi* (31%), *Kondakovia longimana* (24%), *Psychroteuthis glacialis* (15%), *Martialia hyadesi* (11%), *Alluroteuthis antarcticus* (11%) and *Gonatus antarcticus* (4%) (Rodhouse et al. 1992); EC: 75% cephalopods, 25% fish (Jefferson et al. 1993); feed mostly on squid and fish (Green and Burton 1993).

CRABEATER SEAL: AT: main food taken is Antarctic krill (Laws 1977; Oristland 1977); 94% krill, 2% cephalopods, 1% invertebrates, 3% fish (Oristland 1977); EC: believed to feed mainly at night; mostly on krill (Jefferson et al. 1993).

ROSS SEAL: AT: squid form a major part (47%) of the diet, followed by fish (34%) and krill (19%) (from Laws 1977); 9% krill, 64% cephalopods, 5% other invertebrates, 22% fish (from Oristland 1977); EC: mainly cephalopods, includes fish and krill in some areas (Jefferson et al. 1993).

LEOPARD SEAL: AT: diet is composed of approximately 1/3 krill, 1/3 fish and squid, and 1/3 seabirds and seals (Laws 1977); 37% krill, 8% cephalopods, 3% other invertebrates, 13% fish, 26% birds, 13% seals (Oristland 1977); Lowry et al. (1988); EC: known to prey on penguins; consume krill, fish, squid, young seals; occasionally scavenge whale carcasses (Jefferson et al. 1993).

WEDDELL SEAL: AT: 1% krill, 11% cephalopods, 35% other invertebrates 53% fish (Oristland 1977); Only 13 stomachs showed 96.3% of prey were fish (cods) and 3.6% were cephalopods (Plotz et al. 1991); also Green and Burton (1987); EC: mostly fish, smaller amounts of squid and other invertebrates (Jefferson et al. 1993).

SEA OTTER: AT: Kenyon (1969); Lowry et al. (1982); EC: feed on or near the bottom in shallow waters; major prey are benthic invertebrates (abalones, sea urchins, and rock crabs); also cephalopods and sluggish, near-bottom fishes (Jefferson et al. 1993).

MARINE OTTER: DP: Adapted from information in Majluf and Reyes (1989); EC: crabs, shrimps, molluscs, and fish; in rivers, on freshwater prawns (Jefferson et al. 1993).

Table 2. Comparisons of trophic levels in Ostrom et al. (1993), based on isotope ratios and the food web approach implied in Table 1.

Species	Trophic levels	
	Isotope ratios ^{a)}	Table 1
Cetaceans		
White-beaked dolphin (<i>Lagenorhynchus albirostris</i>)	5.4	4.2
Common dolphin (<i>Delphinus delphis</i>)	5.0	4.2
Beluga whale (<i>Delphinapterus leucas</i>) ^{b)}	4.6	4.0
Humpback whale (<i>Megaptera novaeangliae</i>)	4.5	3.6
Minke whale (<i>Balaenoptera acutorostrata</i>)	4.1	3.4
Pygmy sperm whale (<i>Kogia breviceps</i>)	3.0	4.4
Sperm whale (<i>Physeter macrocephalus</i>)	3.7	4.4
Sowerby's beaked whale (<i>Mesoplodon bidens</i>)	3.7	4.3
Blue whale (<i>Balaenoptera musculus</i>)	3.2	3.2
Shark		
Basking shark (<i>Cetorhinus maximus</i>)	3.2	≈ 3.2 ^{c)}
Prey items		
Capelin (<i>Mallotus villosus</i>)	4.1	n.a.
Squid (<i>Illex illecebrosus</i>)		
Small, offshore, Grand Banks (14.5 ± 1 cm)	3.2	(3.7) ^{d)}
Large, nearshore (24.5 cm)	5.1	(3.2) ^{d)}

^{a)} original values +2 to account for different definition of lowest possible level (herbivores TL = 0 in Ostrom et al. (1993), but = 1 in Pauly and Christensen 1995);

^{b)} also known as "white" or "belukha" whale;

^{c)} assuming a diet consisting exclusively of large zooplankton, with TLj = 2.2 (see text);

^{d)} values for generic squids.