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Diet composition and trophic levels of marine mammals

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Standardized diet compositions were derived for 97 species of marine mammals from published accounts of stomach contents as well as from morphological, behavioural and other information. Diet was apportioned among eight categories of prey types (benthic invertebrates, large zooplankton, small squids, large squids, small pelagic fishes, mesopelagic fishes, miscellaneous fishes and higher invertebrates). Trophic levels were estimated for each species of marine mammals and compared with published estimates derived using stable isotope ratios. Trophic levels ranged from 3.2–3.4 in baleen whales and sea otters, to 3.8–4.4 in most pinnipeds and odontocete whales, to 4.5–4.6 in killer whales. Such information can be used for ecosystem modelling and related studies.

Key words: marine mammals, diets, trophic levels.

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Introduction

Food and feeding habits determine the position of animals within food webs, and define their ecological role. This is true for marine mammals, whose food and feeding habits have been reported from direct observations and analyses of scat and stomach contents, or inferred by indirect methods such as isotope ratios. Unfortunately, the majority of quantitative dietary studies of marine mammals pertain to small numbers of individuals and/or a small fraction of a species range, and may not apply to their entire, ocean-wide or global distribution. Some authors have attempted to summarize scattered data on the food and feeding habits of marine 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 that precludes the direct use of their summaries for trophic studies.

Our study apportioned marine mammals' diets among eight prey types. We combined the scattered quantitative studies of diet with the broad qualitative summaries mentioned above to obtain standardized diet compositions for use in trophic modelling and related food web studies. To illustrate the potential use of such data, we calculate the trophic levels for each of the 118 species of marine mammals, and compare them with trophic level estimates derived from stable isotope ratios.

Materials and methods

The 97 species of marine mammals considered here were those listed in Jefferson *et al*. (1993), minus the sirenians (which are herbivores), freshwater dolphins (which are not marine), polar bears (which feed almost exclusively on seals), and 11 cetacean species (mainly beaked whales, genus *Mesoplodon*) for which no diet information was found. Rather than compiling detailed lists of prey species, we apportioned the existing dietary information among eight prey categories, j: benthic invertebrates, large zooplankton, small squids, large squids, small pelagic fishes, mesopelagic fishes, miscellaneous fishes, and higher vertebrates (Table 1). The amount of prey j consumed by species i was estimated as a fraction (wet weight) of total diet. Diet compositions, DC_{ij} summed to unity for each species of marine mammal.

The first two steps in defining diet compositions were:

(a) to rank published accounts of food items by weight or volume, which are largely equivalent as shown by MacDonald and Green (1983), and assign a fraction of 0.5 of the total diet to the

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Table 1. Eight prey categories used to apportion dietary information for marine mammals. Mean trophic levels of each prey type are from Pauly and Christensen (1995).

	Group	Description	Trophic level
BI	Benthic invertebrates	Mainly molluscs (notably bivalves and gastropods, but also including octopus, echinoderms and crustaceans	2.2
LZ	Large zooplankton	Mainly small crustaceans, especially euphausiids (krill) such as *Euphausia superba* in Antarctic waters	2.2
SS	Small squids	Families with mantle lengths of up to 50 cm, such as Gonatidae, (see Roper *et al.*, 1984)	3.2
LS	Large squids	Families with mantle lengths above 50 cm, such as Onychoteuthidae	3.7†
SP	Small pelagic fishes	Consisting of clupeoids, small scombroids and allied groups	2.7
MP	Mesopelagic fishes	Predominantly fish of the family Myctophidae and other groups of the Deep Scattering Layer	3.2§
MF	Miscellanous fishes	A diverse group consisting mainly of demersal round fish such as gadoids and perciforms, but also including anadromous fishes such as salmon	3.3
HV	High vertebrates	Marine mammals, seabirds, plus the occasional turtle	4.0‡

†Trophic levels assumed to be $\frac{1}{2}$ higher than trophic level of small squids, based on food webs in Christensen and Pauly (1993).
§Trophic level calculated from Central South China Sea model in Pauly and Christensen (1993).
‡Mean of all marine mammals not consuming higher vertebrates.

item reported as ''most common'', ''major prey'', or similarly identified as main food; and

(b) to assign decreasing diet fraction (generally in steps of 0.1) to successive items as a function of their rank in qualitative accounts.

Steps a and b were completed using four major data compilations on marine mammals (Bonner, 1990; King, 1983; Evans, 1987; Klinowska, 1991). Assignments of diet fractions were then verified using predominantly species- and area-specific accounts, such as Perez (1990) and Goodal and Galeazii (1985) for the North Pacific and Antarctica, Tan (1995) for the tropical Indo-Pacific and González *et al*. (1994) for the North Atlantic. The steps taken included:

(c) identify food items not included in the above-cited sources from additional references and incorporate them in the rankings used for steps a and b; and

(d) adjust the initial diet compositions given c, and verify that the final diet composition was compatible with all information otherwise available on a given species (items (e) and (f) below).

Information related to diet composition, that did not emanate directly from diet studies, consisted of:

(e) dentition or lack thereof (e.g. absence of teeth, and presence of serrated palates in some *Mesoplodon* species suggests a diet consisting mainly of squids); and

(f) feeding time; e.g. nocturnal feeding habits in oceanic *Stenella* species suggest a tendency to feed on mesopelagic fishes.

Reconciliation of the different diet compositions derived by different approaches or from different sources was performed by averaging the percentages using steps not smaller than 0.05. Emphasis was placed on diet compositions derived from large samples and/or wide areas.

Once the consolidated DC_{ij} values were available, trophic levels (TL_i) were computed for each of the 97 species i feeding on 8 prey types j using:

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

In principle, the variance of the TL_i values could be estimated, by combining an equation that estimates 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). We abstained from this, as a resampling scheme would probably be better at capturing the uncertainty inherent in our approach (see below).

Results and discussion

Diet composition and estimated trophic levels of 97 species of marine mammals are contained in Table 2.

The diet compositions require little comment, except perhaps to emphasize their tentative character. Detailed species-specific studies will probably invalidate some of them with time. Thus they should probably be used only in aggregate form (i.e. to express the food composition of *groups* of species, occurring at specific locations) and in the context of resampling schemes (e.g. a Monte Carlo simulation), wherein, say, a random 1000 variants of the diet composition of each species are generated to produce distributions of item-specific food consumption. Ideally, such analyses would use the data presented here for little-studied species, complemented by recent,

Table 2. Diet compositions of 97 species of marine mammals feeding on 8 prey groups (BI = benthic invertebrates; LZ = large zooplanktons; 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). Dietary details (including independently-derived diet compositions, before averaging), are available as a Microsoft Excel spreadsheet and/or hard copy, deposited at the Depository of Unpublished Data, Document Delivery, CISTI, National Research Council of Canada, Ottawa ON K1A 0S2, Canada.

Species		Diet composition								Trophic level	Source
		BI	LZ	SS	LS	SP	MP	MF	HV		
Balaenidae											
Eubalaena glacialis	Northern right whale	—	1.00	—	—	—	—	—	—	3.2	Northridge (1984); Wishner *et al.* (1988); Mayo and Marx (1990); Klinowska (1991); Northridge (1984)
E. australis	Southern right whale	—	1.00	—	—	—	—	—	—	3.2	Leatherwood and Reeves (1983); Hamner *et al.* (1988)
Balaena mysticetus	Bowhead whale	0.20	0.80	—	—	—	—	—	—	3.2	Leatherwood and Reeves (1983); Lowry and Frost (1984); Leatherwood *et al.* (1988); Lowry (1993); Northridge (1984)
Neobalaenidae											
Caperea marginata	Pygmy right whale	—	1.00	—	—	—	—	—	—	3.2	Jefferson *et al.* (1993); Leatherwood and Reeves (1983); Northridge (1984)
Eschrichtiidae											
Eschrichtius robustus	Gray whale	0.90	0.05	—	—	—	0.05	—	—	3.3	Bogoslovskaya *et al.* (1981); Leatherwood and Reeves (1983); Nerimi (1984); Northridge (1984); Avery and Hawkinson (1992); Weitkamp *et al.* (1992)
Balaenopteridae											
Balaenoptera physalus	Fin whale	—	0.80	0.05	—	0.05	0.05	0.05	—	3.4	Nemoto (1957), (1959), (1970); Lockyer and Brown (1978); Kawamura (1980); Leatherwood and Reeves (1983); Gambell (1985a); Sigurjónsson and Vikingsson (1992)
B. musculus	Blue whale	—	1.00	—	—	—	—	—	—	3.2	Nemoto (1970); Leatherwood and Reeves (1983); Northridge (1984); Gambell (1985a); Reilly and Thayer (1990); Sigurjónsson and Vikingsson (1992); Gambell (1979)
B. acutorostrata	Minke whale	—	0.65	—	—	0.30	—	0.05	—	3.4	Sergeant (1975); Kawamura (1980); Jonsgaard (1982); Kasamatsu and Hata (1985); Bushuev (1986), (1991); Ichii and Kato (1991); Lydersen *et al.* (1991a); Nordoey and Blix (1992); Sigurjónsson and Vikingsson (1992); Haug *et al.* (1993), (1994); Santos *et al.* (1994); Bushuev (1991)
B. borealis	Sei whale	—	0.80	0.05	—	0.05	0.05	0.05	—	3.4	Lockyear and Brown (1978); Gambell (1985b); Nemoto (1970); Sigurjónsson and Vikingsson (1992)
B. edeni	Bryde's whale	—	0.40	—	—	0.20	0.20	0.20	—	3.7	Leatherwood and Reeves (1983); Northridge (1984); Leatherwood *et al.* (1988)
Megaptera novaeangliae	Humpback whale	—	0.55	—	—	0.15	—	0.30	—	3.6	Nemoto (1957), (1959), (1970); Sergeant (1975); Kawamura (1980); Hain *et al.* (1981); Christensen *et al.* (1990); Sigurjónsson and Vikingsson (1992)
Ziphiidae											
Berardius arnuxii	Arnoux's beaked whale	0.10	—	0.20	0.10	0.20	0.20	0.20	—	4.1	Leatherwood and Reeves (1983); Northridge (1984); Klinowska (1991); Jefferson *et al.* (1993)
B. bairdii	Baird's beaked whale	0.10	—	0.30	0.25	0.10	0.10	0.15	—	4.2	Leatherwood and Reeves (1983); Northridge (1984); Rice (1986); Jefferson *et al.* (1993)
Mesoyloden bidens	Sowerby's beaked whale	—	—	0.25	0.30	0.05	0.20	0.20	—	4.3	Jefferson *et al.* (1993); Ostrom *et al.* (1993); Santos *et al.* (1994)

Table 2. Continued.

Species		Diet composition BI	LZ	SS	LS	SP	MP	MF	HV	Trophic level	Source
Ziphiidae *continued*											
M. densirostris	Blainville's beaked whale	—	—	0.20	0.30	—	0.30	0.20	—	4.4	Mead (1989a); Klinowska (1991); Jefferson *et al.* (1993); Tan (1995)
M. layardii	Strap-toothed whale	—	—	0.30	0.40	—	—	0.30	—	4.4	Klinowska (1991); Jefferson *et al.* (1993); Rice (1986)
M. hectori	Hector's beaked whale	—	—	0.40	0.40	—	—	0.20	—	4.4	Mead and Baker (1987); Mead (1989a); Klinowska (1991); Jefferson *et al.* (1993)
M. stejnegeri	Stejneger's beaked whale	—	—	0.50	0.45	—	—	0.05	—	4.4	Mead (1989a); Klinowska (1991); Jefferson *et al.* (1993); Loughlin and Perez (1985)
M. mirus	True's beaked whale	—	—	0.50	0.50	—	—	—	—	4.5	Mead (1989a); Klinowska (1991); Jefferson *et al.* (1993)
M. carlhubbsi	Hubb's beaked whale	—	—	0.40	0.40	—	0.20	—	—	4.4	Leatherwood and Reeves (1983); Klinowska (1991); Jefferson *et al.* (1993)
Ziphius cavirostris	Cuvier's beaked whale	0.10	—	0.30	0.30	—	0.15	0.15	—	4.3	Leatherwood and Reeves (1983); Northridge (1984); Heyning (1989); Jefferson *et al.* (1993)
Hyperoodon ampullatus	Northern bottlenose whale	0.15	—	0.35	0.35	—	0.05	0.10	—	4.2	Leatherwood and Reeves (1983); Northridge (1984); Mead (1989b); Sigurjónsson and Vikingsson (1992); Jefferson *et al.* (1993)
H. planifrons	Southern bottlenose whale	—	0.20	0.40	0.20	—	—	0.20	—	4.1	Leatherwood and Reeves (1983); Northridge (1984); Jefferson *et al.* (1993); Sekiguchi *et al.* (1993)
Physeteridae											
Physeter catodon	Sperm whale	0.05	—	0.10	0.60	0.05	0.05	0.15	—	4.4	Clarke (1956); Okutani and Nemoto (1964); Gaskin and Cawthorn (1967); Roe (1968); Kawakami (1980); Pascoe *et al.* (1990); Sigurjónsson and Vikingsson (1992); Gonzalez *et al.* (1994); Santos *et al.* (1994); Tan (1995)
Kogiidae											
Kogia breviceps	Pygmy sperm whale	0.05	—	0.35	0.40	—	0.10	0.10	—	4.4	Leatherwood and Reeves (1983); Martins *et al.* (1985); Leatherwood *et al.* (1988); Jefferson *et al.* (1993); Tan (1995)
K. simus	Dwarf sperm whale	0.10	—	0.40	0.40	—	0.05	0.05	—	4.3	Leatherwood and Reeves (1983); Northridge (1984); Pinedo (1987); Leatherwood *et al.* (1988); Jefferson *et al.* (1993)
Monodontidae											
Monodon monoceros	Narwhal	0.10	0.05	0.30	0.20	0.05	—	0.30	—	4.2	Leatherwood and Reeves (1983); Northridge (1984); Jefferson *et al.* (1993)
Delphinapterus leucas	White whale (beluga)	0.20	—	0.05	0.05	0.20	0.10	0.40	—	4.0	Seaman *et al.* (1982); Lowry *et al.* (1985); Jefferson *et al.* (1993)
Delphinidae											
Steno bredanensis	Rough-toothed dolphin	0.10	—	0.20	0.10	0.20	—	0.40	—	4.1	Leatherwood and Reeves (1983); Northridge (1984); Jefferson *et al.* (1993)
Sotalia fluviatilis	Tucuxi	0.20	—	0.10	—	0.20	—	0.50	—	4.0	Leatherwood and Reeves (1983); Jefferson *et al.* (1993)
Sousa chinensis	Indo-Pac. hump-backed dolphin	0.05	0.05	—	—	0.40	—	0.50	—	4.0	Leatherwood and Reeves (1983); Northridge (1984); Barros and Cockcroft (1991); Jefferson *et al.* (1993); Parson, (1996)

Table 2. Continued.

Species		Diet composition BI	LZ	SS	LS	SP	MP	MF	HV	Trophic level	Source
Delphinidae *continued*											
S. teuszii	Atlantic hump-backed dolphin	—	—	—	—	0.50	—	0.50	—	4.0	Leatherwood and Reeves (1983); Northridge (1984); Jefferson *et al.* (1993)
Orcaella brevirostris	Irrawaddy dolphin	0.20	—	0.10	—	0.20	—	0.50	—	4.0	Leatherwood and Reeves (1983); Northridge (1984); Jefferson *et al.* (1993)
Peponocephala electra	Melon-headed whale	—	—	0.35	0.35	0.10	0.10	0.10	—	4.3	Leatherwood and Reeves (1983); Pitman and Ballance (1992); Jefferson *et al.* (1993)
Feresa attenuata	Pygmy killer whale	—	—	0.30	0.20	0.10	—	0.20	0.20	4.4	Klinowska (1991); Jefferson *et al.* (1993); Tan (1995)
Orcinus orca	Killer whale	—	—	0.05	0.05	0.10	—	0.40	0.40	4.5	Rice (1968); Hoyt (1990); Jefferson *et al.* (1991); Guinet (1992); Sigurjónsson and Vikingsson (1992); Jefferson *et al.* (1993); Tan (1995)
Globicephala melas	Long-finned pilot whale	—	—	0.40	0.35	—	—	0.25	—	4.4	Desportes and Mouritsen (1988); Overholtz and Waring (1991); Gonzalez *et al.* (1994); Santos *et al.* (1994)
G. macrorhynchus	Short-finned pilot whale	—	—	0.30	0.30	0.10	0.10	0.20	—	4.3	Leatherwood and Reeves (1983); Northridge (1984); Jefferson *et al.* (1993); Tan (1995)
Lagenorhynchus albirostris	White-beaked dolphin	0.05	—	0.15	0.05	0.15	—	0.60	—	4.2	Northridge (1984); Sigurjónsson and Vikingsson (1992); Jefferson *et al.* (1993); Santos *et al.* (1994)
L. acutus	Atlantic white-sided dolphin	0.10	—	0.15	0.10	0.15	0.10	0.40	—	4.1	Leatherwood and Reeves (1983); Northridge (1984); Sigurjónsson and Vikingsson (1992); Jefferson *et al.* (1993)
L. obscurus	Dusky dolphin	—	—	0.15	0.05	0.40	0.25	0.15	—	4.0	Leatherwood and Reeves (1983); Jefferson *et al.* (1993); McKinnon (1993)
L. australis	Peale's dolphin	0.10	—	0.30	0.10	0.10	0.10	0.30	—	4.1	Jefferson *et al.* (1993)
L. obliquidens	Pacific white-sided dolphin	—	—	0.30	0.05	0.30	0.20	0.15	—	4.1	Stroud *et al.* (1981); Leatherwood and Reeves (1983); Walker *et al.* (1986); Leatherwood *et al.* (1988); Walker and Jones (1993); Kajimura *et al.* (1980)
Lagenodelphis hosei	Fraser's dolphin	0.05	—	0.30	0.05	0.05	0.35	0.20	—	4.2	Leatherwood and Reeves (1983); Robinson and Craddock (1983); Van Bree *et al.* (1986); Jefferson *et al.* (1993); Tan (1995)
Tursiops truncatus	Bottlenose dolphin	—	—	0.20	0.05	0.15	—	0.60	—	4.2	Leatherwood *et al.* (1978); Irvine *et al.* (1981); Leatherwood and Reeves (1983); Mead and Potter (1990); ICES (1991); Jefferson *et al.* (1993); Gonzalez *et al.* (1994); Santos *et al.* (1994); Tan (1995)
Grampus griseus	Risso's dolphin	0.05	—	0.50	0.35	0.05	—	0.05	—	4.3	Leatherwood *et al.* (1978); Leatherwood and Reeves (1983); Wurtz *et al.* (1992); Jefferson *et al.* (1993); Santos *et al.* (1994); Tan (1995)
Stenella longirostris	Spinner dolphin	—	—	0.20	0.20	—	0.40	0.20	—	4.3	Perrin *et al.* (1973); Perrin *et al.* (1989); Leatherwood and Reeves (1983); Karbhari *et al.* (1985); Jefferson *et al.* (1993); Tan (1995)
S. coeruleoalba	Striped dolphin	0.05	—	0.20	0.15	0.05	0.30	0.25	—	4.2	Leatherwood and Reeves (1983); Jefferson *et al.* (1993); Wurtz and Marrale (1993); Santos *et al.* (1994)
S. attenuata	Pantropical spotted dolphin	—	—	0.30	0.20	0.10	—	0.40	—	4.3	Perrin *et al.* (1973); Leatherwood *et al.* (1978); Leatherwood and Reeves (1983); Jefferson *et al.* (1993); Tan (1995)

Table 2. Continued.

Species		Diet composition								Trophic level	Source
		BI	LZ	SS	LS	SP	MP	MF	HV		
Delphinidae *continued*											
S. frontalis	Atlantic spotted dolphin	—	—	0.30	0.20	0.10	—	0.40	—	4.3	Leatherwood *et al.* (1978); Jefferson *et al.* (1993)
S. clymene	Clymene dolphin	—	—	0.20	0.20	0.10	—	0.40	0.10	4.4	Perrin *et al.* (1981); Leatherwood and Reeves (1983); Northridge (1984); Jefferson *et al.* (1993)
Delphinus delphis	Common dolphin	—	—	0.15	0.15	0.10	0.40	0.20	—	4.2	Leatherwood *et al.* (1978); Leatherwood and Reeves (1983); Northridge (1984); Overholtz and Waring (1991); Jefferson *et al.* (1993); Gonzalez *et al.* (1994); Santos *et al.* (1994)
Lissodelphis peronii	Southern right whale dolphin	—	—	0.20	0.30	—	0.40	0.10	—	4.4	Leatherwood *et al.* (1978); Northridge (1984); Jefferson *et al.* (1993)
L. borealis	Northern right whale dolphin	—	—	0.30	0.20	—	0.40	0.10	—	4.3	Leatherwood *et al.* (1978); Leatherwood and Reeves (1983); Northridge (1984); Jefferson *et al.* (1993); Walker and Jones (1993)
Cephalorhynchus heavisidii	Heaviside's dolphin	—	—	0.20	0.20	0.10	0.20	0.30	—	4.3	Leatherwood and Reeves (1983); Jefferson *et al.* (1993)
C. hectori	Hector's dolphin	0.05	—	0.25	0.20	0.20	0.10	0.20	—	4.2	Leatherwood and Reeves (1983); Jefferson *et al.* (1993)
C. commersonii	Commerson's dolphin	0.10	0.10	0.20	0.10	0.35	—	0.15	—	3.9	Leatherwood and Reeves (1983); Jefferson *et al.* (1993)
Phocoenidae											
Phocoena phocoena	Harbour porpoise	0.05	—	0.10	0.10	0.30	—	0.45	—	4.1	Prescott and Fiorelli (1980); Frost and Lowry (1981); Recchia and Read (1989); Martin *et al.* (1990); Ichii and Kato (1991); Lick (1991); Sigurjónsson and Vikingsson (1992); Fontaine *et al.* (1994); Gonzalez *et al.* (1994); Santos *et al.* (1994)
P. sinus	Vaquita	—	—	0.30	0.20	0.20	—	0.30	—	4.2	Leatherwood *et al.* (1978)
P. spinipinnis	Burmeister's porpoise	—	0.10	0.20	0.10	0.35	—	0.25	—	4.0	Jefferson *et al.* (1993)
Phocoenoides dalli	Dall's porpoise	0.05	—	0.30	0.10	0.20	0.20	0.15	—	4.1	Leatherwood *et al.* (1978); Kajimura *et al.* (1980); Crawford (1981); Leatherwood and Reeves (1983); Northridge (1984); Jefferson *et al.* (1993); Loeb (1972)
Neophocoena phocaenoides	Finless porpoise	0.10	—	0.40	—	0.20	0.10	0.20	—	4.0	Leatherwood and Reeves (1983); Northridge (1984); Jefferson *et al.* (1993)
Pontoporiidae											
Pontoporia blainvillei	Franciscana	0.10	—	0.20	0.20	0.20	—	0.30	—	4.1	Jefferson *et al.* (1993)
Otariidae											
Eumatopias jubatus	Steller's sea lion	0.15	—	0.20	0.15	0.05	—	0.40	0.05	4.2	Mathisen (1959); Mathisen *et al.* (1962); Calkins and Goodwin (1988); NMFS (1992)
Zalophus californianus	California sea lion	0.10	—	0.20	0.15	0.25	—	0.30	—	4.1	Jefferson *et al.* (1993); Lowry *et al.* (1991)
Otaria byronia	South American sea lion	0.10	0.15	0.15	0.10	0.10	—	0.35	0.05	4.0	Aguayo and Maturana (1973); Olivia (1984); Muck and Fuentes (1987); Harcourt (1993)
Neophoca cinerea	Australian sea lion	0.10	—	0.15	0.05	0.10	—	0.55	0.05	4.2	Jefferson *et al.* (1993); Reijnders *et al.* (1993)

Table 2. Continued.

Species		Diet composition BI	LZ	SS	LS	SP	MP	MF	HV	Trophic level	Source
Otariidae *continued*											
Phocarctos hookeri	Hooker's sea lion	0.20	0.05	0.30	0.05	0.15	—	0.20	0.05	4.0	Jefferson *et al.* (1993); Reijnders *et al.* (1993)
Callorhinus ursinus	Northern fur seal	—	—	0.15	0.15	0.25	0.15	0.30	—	4.2	Kajimura (1984); Kajimura *et al.* (1980); Perez and Big (1986); Jefferson *et al.* (1993); Sinclair *et al.* (1994); Stroud *et al.* (1981)
Arctocephalus townsendi	Guadalupe fur seal	0.20	—	0.30	—	0.30	—	0.20	—	3.9	Reeves *et al.* (1992)
A. philippii	Juan Fernandez fur seal	0.15	—	0.30	0.15	0.25	—	0.15	—	4.0	Torres (1987a,b); Majluf and Reyes (1989)
A. galapagoensis	Galapagos fur seal	—	—	0.40	—	0.20	0.30	0.10	—	4.1	Clarke and Trillmich (1980); Trillmich (1987); Reijnders *et al.* (1993)
A. australis	South American fur seal	0.20	0.05	0.10	0.05	0.35	—	0.25	—	3.8	Majluf (1987); Muck and Fuentes (1987); Vaz-Ferreira and Ponce de Leon (1987)
A. pusillus pusillus	South African fur seal	0.15	—	0.15	0.05	0.30	—	0.35	—	4.0	Rand (1959); David (1987); Lipinski and David (1990); Reijnders *et al.* (1993)
A. p. doriferus	Australian fur seal	0.10	—	0.30	0.15	0.20	—	0.25	—	4.1	Shaughnessy and Warneke (1987); Gales *et al.* (1993); Gales and Pemberton (1994)
A. forsteri	New Zealand fur seal	0.20	—	0.20	0.10	0.10	0.10	0.25	0.05	4.1	Street (1964); Carey (1992); Reijnders *et al.* (1993); Mattlin (1987)
A. gazella	Antarctic fur seal	—	0.50	0.10	0.05	0.10	0.05	0.15	0.05	3.7	North *et al.* (1983); Doidge and Croxall (1985); Boveng *et al.* (1991); Green *et al.* (1989); Green *et al.* (1991)
A. tropicalis	Subantarctic fur seal	—	0.15	0.30	0.15	0.10	—	0.25	0.05	4.1	Rand (1956); Condy (1981); Bester (1987)
Odobenidae											
Odobenus rosmarus	Walrus	0.85	—	—	—	—	—	0.05	0.10	3.4	Fay (1982); Fay *et al.* (1982); Gjertz and Wiig (1992); Timoshenko and Popov (1990)
Phocidae											
Phoca vitulina	Harbour seal	0.10	—	0.10	0.05	0.30	—	0.45	—	4.0	Boulva and McLaren (1979); Behrends (1982); Haaker *et al.* (1984); Härkönen (1987); Payne and Selzer (1989); Olesiuk *et al.* (1990); Härkönen and Heide-Jorgensen (1991)
P. largha	Larga seal	0.15	—	0.05	0.05	0.30	—	0.45	—	4.0	Lowry *et al.* (1982); Bukhtiyarov *et al.* (1984)
P. hispida	Ringed seal	0.20	0.20	—	—	0.15	0.05	0.40	—	3.8	Lowry *et al.* (1978); Lowry *et al.* (1980b); ICES (1991); Weslawski *et al.* (1994)
P. groenlandica	Harp seal	0.05	0.20	0.05	—	0.30	—	0.40	—	3.8	Sergeant (1976); Sargeant (1991); Kapel and Angantyr (1989); Lydersen *et al.* (1991b); Beck *et al.* (1993); Nilssen and Haug (1993); Ugland *et al.* (1993); Kapel (1994); Nilson *et al.* (1993)
P. fasciata	Ribbon seal	0.35	—	0.10	—	0.25	—	0.30	—	3.8	Shustov (1969); Frost and Lowry (1980); Burns (1986)
Erignathus barbatus	Bearded seal	0.65	0.15	—	—	0.05	—	0.15	—	3.4	Lowry *et al.* (1980a); Antonelis *et al.* (1994b)

Table 2. Continued.

Species		Diet composition BI	LZ	SS	LS	SP	MP	MF	HV	Trophic level	Source
Phocidae *continued*											
Cystophora cristata	Hooded seal	—	–	0.20	0.20	0.20	—	0.40	—	4.2	Sergeant (1976)
Halichoerus grypus	Grey seal	0.15	—	0.05	—	0.30	—	0.45	0.05	4.0	Murie and Lavigne (1992); Bowen and Harrison (1994); Bowen *et al.* (1993); Hammond *et al.* (1994)
Monachus monachus	Mediterranean monk seal	0.20	—	—	—	0.20	—	0.50	0.10	4.0	Jefferson *et al.* (1993)
M. schauinslandi	Hawaiian monk seal	0.20	—	0.10	—	—	—	0.70	—	4.1	Polovina (1984)
Mirounga leonina	Southern elephant seal	0.05	—	0.40	0.35	0.05	—	0.15	—	4.3	Laws (1977); Green and Williams (1986); Rodhouse *et al.* (1992); Green and Burton (1993); Boyd *et al.* (1994)
M. angustirostris	Northern elephant seal	0.05	—	0.40	0.20	—	0.20	0.15	—	4.3	Antonelis *et al.* (1994a)
Lobodon carcinophagus	Crabeater seal	—	0.90	—	—	0.10	—	—	—	3.3	Laws (1977); Oritsland (1977); Lowry *et al.* (1988)
Ommatophoca rossii	Ross seal	0.05	0.15	0.50	0.15	—	—	0.15	–	4.1	Laws (1977); Oritsland (1977)
Hydrurga leptonyx	Leopard seal	—	0.35	0.10	—	0.10	—	0.05	0.40	4.1	Oritsland (1977); Lowry *et al.* (1988)
Leptonychotes weddellii	Weddell seal	0.20		0.15		0.15		0.50	—	4.0	Oritsland (1977); Green and Burton (1987); Plotz *et al.* (1991)
Mustelidae											
Enhydra lutris	Sea otter	0.80	—	0.05	—	0.05	—	0.10	—	3.4	Kenyon (1969); Lowry *et al.* (1982); Antonelis *et al.* (1994b)
Lutra felina	Marine otter	0.65	—	—	—	0.10	—	0.25	—	3.5	Majluf and Reyes (1989); Barros and Cockcroft (1991); Antonelis *et al.* (1994b)

Table 3. Comparisons of trophic levels in Ostrom *et al.* (1993), based on stable isotope ratios and the food web approach implied in Table 2.

Species	Trophic levels: Isotope ratios*	Trophic levels: from Table 2
Cetaceans		
White-beaked dolphin (*Lagenorhynchus albirostris*)	5.4	4.2
Common dolphin (*Delphinus delphis*)	5.0	4.2
Beluga whale (*Delphinapterus leucas*)†	4.6	4.0
Humpback whale (*Megaptera novaeangliae*)	4.5	3.6
Minke whale (*Balaenoptera acutorostrata*)	4.1	3.4
Pygmy sperm whale (*Kogia breviceps*)	3.0	4.4
Sperm whale (*Physeter macrocephalus*)	3.7	4.4
Sowerby's beaked whale (*Mesoplodon bidens*)	3.7	4.3
Blue whale (*Balaenoptera musculus*)	3.2	3.2
Shark		
Basking shark (*Cetorhinus maximus*)	3.2	≈3.2§
Prey items		
Capelin (*Mallotus villosus*)	4.1	n.a.
Squid (*Illex illecebrosus*)		
Small, offshore, Grand Banks (14.5 ± 1 cm)	3.2	(3.7)‡
Large, nearshore (24.5 cm)	5.1	(3.2)‡

*Original values +2 to account for different definition of lowest possible level, i.e., the herbivores have a $TL=0$ in Ostrom *et al.* (1993), but TL = 2 in Pauly and Christensen (1995), the latter following the standard set by the International Biological Programme.
†Also known as ''white whale''.
§Assuming a diet consisting exclusively of large zooplankton, with $TLj=2.2$ (see text).
‡Values for generic squids, from Pauly and Christensen (1995).

detailed, locale-specific analyses, such as that of Christensen *et al.* (1992).

Mean trophic levels were calculated for each of the 98 marine mammals using diet composition and prey trophic levels (Table 2). The trophic levels range from 3.2–3.4 in baleen whales and sea otters, 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 occur in groups not considered here, i.e. 2.0 in sirenians and 5.0 in polar bears (which overwhelmingly feed on animals with a TL near 4.0).

Published estimates of trophic levels with which these estimates could be compared are rare (see Hobson *et al.*, 1997). Ostrom *et al.* (1993) are the few that present TL values. In their study, they assigned an arbitrary trophic level of 1.0 to basking shark and 1.2 to fin whales, which both feed on large zooplankton. Given our definition of trophic levels, which put baleen whales at a trophic level of 3.2, we added 2.0 to each of their TL values to obtain comparable estimates (Table 3).

Ostrom *et al.*'s (1993) trophic levels are markedly lower than ours in three whale species (sperm whale, pygmy sperm whale and Sowerby's beaked whale). Moreover, their results appear incompatible with diets consisting of a substantial fraction of large squids, for which they reported an extremely high TL estimate – 5.1 (see Table 3). Conversely, Ostrom *et al.*'s (1993) trophic level estimates are much higher than ours in the other five species they considered (beluga whale, minke whale, humpback whale, common dolphin and white-beaked dolphin, see Table 3). Given such discrepancies, we are hesitant to endorse their suggestion that ''$\delta^{15}N$ values are excellent indicators of trophic position'', although we do agree that ''isotope data are a valuable source of information in the absence of stomach contents and when feeding is difficult to observe''.

Beyond their use in trophic modelling, the dietary data in Table 2 can be used in other ways, such as to estimate the calorific contents of marine mammals diets (see Evans, 1987). Note, however, that caloric food contents values for the marine mammals in Table 2 may differ by as much as a factor of 2, from beaked whales that feed exclusively on squids and tend to have a diet with the lowest energy content to polar bears, leopard seals, and kiler whales that feed exclusively or predominantly on higher vertebrates and tend to have the diet richest in energy.

The information in Table 2 can also be used, given a predictive model of energy requirements such as that of Innes *et al.* (1987), to estimate area-specific (Trites and Heise, 1996a,b; Wada, 1996), or global food consumption by marine mammals, an area of growing interest in view of increasing competition between this attractive megafauna, and often embattled industrial fisheries.

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