

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.

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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

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 <i>Euphausia superba</i> in Antarctic waters	2.2
SS	Small squids	Families with mantle lengths of up to 50 cm, such as Gonatidae, (see Roper <i>et al.</i> , 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	Miscellaneous 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 Galeazzi (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:

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

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=mesocarnivorous 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	—	1.00	—	—	—	—	—	—	—	3.2	Northridge (1984); Wishner et al. (1988); Mayo and Marx (1990); Klinowska (1991); Northridge (1984)
E. australis	—	1.00	—	—	—	—	—	—	—	3.2	Leatherwood and Reeves (1983); Hamner et al. (1988)
Balaena mysticetus	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	—	1.00	—	—	—	—	—	—	—	3.2	Jefferson et al. (1993); Leatherwood and Reeves (1983); Northridge (1984)
Eschrichtiidae											
Eschrichtius robustus	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	—	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 Víkingsson (1992)
B. musculus	—	1.00	—	—	—	—	—	—	—	3.2	Nemoto (1970); Leatherwood and Reeves (1983); Northridge (1984); Gambell (1985a); Reilly and Thayer (1990); Sigurjónsson and Víkingsson (1992); Gambell (1979)
B. acutorostrata	—	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); Nordoy and Blix (1992); Sigurjónsson and Víkingsson (1992); Haug et al. (1993), (1994); Santos et al. (1994); Bushuev (1991)
B. borealis	—	0.80	0.05	—	0.05	0.05	0.05	—	—	3.4	Lockyer and Brown (1978); Gambell (1985b); Nemoto (1970); Sigurjónsson and Víkingsson (1992)
B. edeni	—	0.40	—	—	0.20	0.20	0.20	—	—	3.7	Leatherwood and Reeves (1983); Northridge (1984); Leatherwood et al. (1988)
Megaptera novaeangliae	—	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 Víkingsson (1992)
Ziphiidae											
Berardius arnuxii	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	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)
Mesoplodon bidens	—	—	0.25	0.30	0.05	0.20	0.20	—	—	4.3	Jefferson et al. (1993); Ostrom et al. (1993); Santos et al. (1994)
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										Trophic level	Source	
	BI	LZ	SS	LS	SP	MP	MF	HV					
Ziphiidae													
<i>M. densirostris</i>	—	—	0.20	0.30	—	0.30	0.20	—	—	—	—	—	Mead (1989a); Klinowska (1991); Jefferson et al. (1993); Tan (1995)
Blainville's beaked whale	—	—	0.30	0.40	—	—	0.30	—	—	—	—	—	Klinowska (1991); Jefferson et al. (1993); Rice (1986)
<i>M. layardii</i>	—	—	0.40	0.40	—	—	0.20	—	—	—	—	—	Mead and Baker (1987); Mead (1989a); Klinowska (1991); Jefferson et al. (1993)
Hector's beaked whale	—	—	0.50	0.45	—	—	0.05	—	—	—	—	—	Mead (1989a); Klinowska (1991); Jefferson et al. (1993); Loughlin and Perez (1985)
<i>M. stejnegeri</i>	—	—	0.50	0.50	—	—	—	—	—	—	—	—	Mead (1989a); Klinowska (1991); Jefferson et al. (1993)
True's beaked whale	—	—	0.40	0.40	—	0.20	—	—	—	—	—	—	Leatherwood and Reeves (1983); Klinowska (1991); Jefferson et al. (1993)
<i>M. mirus</i>	—	—	0.30	0.30	—	0.15	0.15	—	—	—	—	—	Leatherwood and Reeves (1983); Northridge (1984); Heyning (1989); Jefferson et al. (1993)
<i>M. carlhubbsi</i>	0.10	—	0.35	0.35	—	0.05	0.10	—	—	—	—	—	Leatherwood and Reeves (1983); Northridge (1984); Mead (1989b); Sigurjónsson and Vikingsson (1992); Jefferson et al. (1993)
<i>Ziphius cavirostris</i>	—	0.20	0.40	0.20	—	—	0.20	—	—	—	—	—	Leatherwood and Reeves (1983); Northridge (1984); Jefferson et al. (1993); Sekiguchi et al. (1993)
Hubb's beaked whale	—	—	0.10	0.60	0.05	0.05	0.15	—	—	—	—	—	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)
<i>Physeter catodon</i>	0.05	—	0.30	0.30	—	0.15	0.15	—	—	—	—	—	Leatherwood and Reeves (1983); Martins et al. (1985); Leatherwood et al. (1988); Jefferson et al. (1993); Tan (1995)
Sperm whale	0.05	—	0.35	0.40	—	0.10	0.10	—	—	—	—	—	Leatherwood and Reeves (1983); Northridge (1984); Pinedo (1987); Leatherwood et al. (1988); Jefferson et al. (1993)
Kogiidae													
<i>Kogia breviceps</i>	0.05	—	0.40	0.40	—	0.05	0.05	—	—	—	—	—	Leatherwood and Reeves (1983); Northridge (1984); Pinedo (1987); Leatherwood et al. (1988); Jefferson et al. (1993)
Pygmy sperm whale	0.10	—	0.40	0.40	—	0.05	0.05	—	—	—	—	—	Leatherwood and Reeves (1983); Northridge (1984); Pinedo (1987); Leatherwood et al. (1988); Jefferson et al. (1993)
<i>K. simus</i>	0.10	—	0.30	0.20	0.05	—	0.30	—	—	—	—	—	Leatherwood and Reeves (1983); Northridge (1984); Jefferson et al. (1993)
Narwhal	0.10	0.05	0.05	0.05	0.20	0.10	0.40	—	—	—	—	—	Seaman et al. (1982); Lowry et al. (1985); Jefferson et al. (1993)
Monodontidae													
<i>Monodon monoceros</i>	0.20	—	0.05	0.05	0.20	0.10	0.40	—	—	—	—	—	Seaman et al. (1982); Lowry et al. (1985); Jefferson et al. (1993)
White whale (beluga)	0.10	—	0.20	0.10	0.20	—	0.40	—	—	—	—	—	Leatherwood and Reeves (1983); Northridge (1984); Jefferson et al. (1993)
Delphinidae													
<i>Steno bredanensis</i>	0.10	—	0.10	0.20	0.20	—	0.40	—	—	—	—	—	Leatherwood and Reeves (1983); Jefferson et al. (1993)
Rough-toothed dolphin	0.20	—	0.10	—	0.20	—	0.50	—	—	—	—	—	Leatherwood and Reeves (1983); Jefferson et al. (1993)
<i>Sotalia fluviatilis</i>	0.05	0.05	—	—	0.40	—	0.50	—	—	—	—	—	Leatherwood and Reeves (1983); Northridge (1984); Barros and Cockcroft (1991); Jefferson et al. (1993); Parson, (1996)
Tucuxi	0.05	0.05	—	—	0.40	—	0.50	—	—	—	—	—	Leatherwood and Reeves (1983); Northridge (1984); Barros and Cockcroft (1991); Jefferson et al. (1993); Parson, (1996)
<i>Sousa chinensis</i>	0.05	0.05	—	—	0.40	—	0.50	—	—	—	—	—	Leatherwood and Reeves (1983); Northridge (1984); Barros and Cockcroft (1991); Jefferson et al. (1993); Parson, (1996)
Indo-Pac. hump-backed dolphin	0.05	0.05	—	—	0.40	—	0.50	—	—	—	—	—	Leatherwood and Reeves (1983); Northridge (1984); Barros and Cockcroft (1991); Jefferson et al. (1993); Parson, (1996)

Table 2. Continued.

Species	Diet composition										Trophic level	Source	
	BI	LZ	SS	LS	SP	MP	MF	HV	FV				
Delphinidae continued													
<i>S. teuszii</i>	—	—	—	—	0.50	—	0.50	—	0.50	—	—	4.0	Leatherwood and Reeves (1983); Northridge (1984); Jefferson et al. (1993)
<i>Orcaella brevirostris</i>	0.20	—	0.10	—	0.20	—	0.50	—	0.50	—	—	4.0	Leatherwood and Reeves (1983); Northridge (1984); Jefferson et al. (1993)
<i>Peponocephala electra</i>	—	—	0.35	0.35	0.10	0.10	0.10	—	0.10	—	—	4.3	Leatherwood and Reeves (1983); Pitman and Ballance (1992); Jefferson et al. (1993)
<i>Feresa attenuata</i>	—	—	0.30	0.20	0.10	—	0.20	0.20	0.20	—	—	4.4	Klinowska (1991); Jefferson et al. (1993); Tan (1995)
<i>Orcinus orca</i>	—	—	0.05	0.05	0.10	—	0.40	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)
<i>Globicephala melas</i>	—	—	0.40	0.35	—	—	0.25	—	0.25	—	—	4.4	Desportes and Mouritsen (1988); Overholtz and Waring (1991); Gonzalez et al. (1994); Santos et al. (1994)
<i>G. macrorhynchus</i>	—	—	0.30	0.30	0.10	0.10	0.20	—	0.20	—	—	4.3	Leatherwood and Reeves (1983); Northridge (1984); Jefferson et al. (1993); Tan (1995)
<i>Lagenorhynchus albirostris</i>	0.05	—	0.15	0.05	0.15	—	0.60	—	0.60	—	—	4.2	Northridge (1984); Sigurjónsson and Vikingsson (1992); Jefferson et al. (1993); Santos et al. (1994)
<i>L. acutus</i>	0.10	—	0.15	0.10	0.15	0.10	0.40	—	0.40	—	—	4.1	Leatherwood and Reeves (1983); Northridge (1984); Sigurjónsson and Vikingsson (1992); Jefferson et al. (1993)
<i>L. obscurus</i>	—	—	0.15	0.05	0.40	0.25	0.15	—	0.15	—	—	4.0	Leatherwood and Reeves (1983); Jefferson et al. (1993); McKinnon (1993)
<i>L. australis</i>	0.10	—	0.30	0.10	0.10	0.10	0.30	—	0.30	—	—	4.1	Jefferson et al. (1993)
<i>L. obliquidens</i>	—	—	0.30	0.05	0.30	0.20	0.15	—	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)
<i>Lagenodelphis hosei</i>	0.05	—	0.30	0.05	0.05	0.35	0.20	—	0.20	—	—	4.2	Leatherwood and Reeves (1983); Robinson and Craddock (1983); Van Bree et al. (1986); Jefferson et al. (1993); Tan (1995)
<i>Tursiops truncatus</i>	—	—	0.20	0.05	0.15	—	0.60	—	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)
<i>Grampus griseus</i>	0.05	—	0.50	0.35	0.05	—	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)
<i>Stenella longirostris</i>	—	—	0.20	0.20	—	0.40	0.20	—	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)
<i>S. coeruleoalba</i>	0.05	—	0.20	0.15	0.05	0.30	0.25	—	0.25	—	—	4.2	Leatherwood and Reeves (1983); Jefferson et al. (1993); Wurtz and Marralle (1993); Santos et al. (1994)
<i>S. attenuata</i>	—	—	0.30	0.20	0.10	—	0.40	—	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													
<i>S. frontalis</i>	—	—	0.30	0.20	0.10	—	0.40	—	—	—	—	4.3	Leatherwood et al. (1978); Jefferson et al. (1993)
Atlantic spotted 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)
<i>S. clymene</i>	—	—	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)
Clymene dolphin	—	—	0.20	0.30	—	0.40	0.10	—	—	—	—	4.4	Leatherwood et al. (1978); Northridge (1984); Jefferson et al. (1993)
Common 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)
<i>Lissodelphis peronii</i>	—	—	0.20	0.20	0.10	0.20	0.30	—	—	—	—	4.3	Leatherwood and Reeves (1983); Jefferson et al. (1993)
<i>L. borealis</i>	—	—	0.25	0.20	0.20	0.10	0.20	—	—	—	—	4.2	Leatherwood and Reeves (1983); Jefferson et al. (1993)
Cephalorhynchus heavisidii	0.05	—	0.10	0.20	0.10	0.35	—	0.15	—	—	—	3.9	Leatherwood and Reeves (1983); Jefferson et al. (1993)
<i>C. hectori</i>	0.10	0.10	0.20	0.10	0.35	—	0.15	—	—	—	—	4.2	Leatherwood and Reeves (1983); Jefferson et al. (1993)
<i>C. commersonii</i>	0.10	0.10	0.20	0.10	0.35	—	0.15	—	—	—	—	3.9	Leatherwood and Reeves (1983); Jefferson et al. (1993)
Phocoenidae													
<i>Phocoena phocoena</i>	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); Sigurjonsson and Vikingsson (1992); Fontaine et al. (1994); Gonzalez et al. (1994); Santos et al. (1994)
Harbour porpoise	—	—	0.30	0.20	0.20	—	0.30	—	—	—	—	4.2	Leatherwood et al. (1978)
<i>P. sinus</i>	—	—	0.10	0.20	0.10	0.35	—	0.25	—	—	—	4.0	Jefferson et al. (1993)
<i>P. spinipinnis</i>	—	—	0.30	0.20	0.20	—	0.30	—	—	—	—	4.2	Leatherwood et al. (1978)
Burmeister's porpoise	—	—	0.10	0.20	0.10	0.35	—	0.25	—	—	—	4.0	Jefferson et al. (1993)
<i>Phocoenoides dalli</i>	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)
Dall's porpoise	0.10	—	0.40	—	0.20	0.10	0.20	—	—	—	—	4.0	Leatherwood and Reeves (1983); Northridge (1984); Jefferson et al. (1993)
Finless porpoise	0.10	—	0.40	—	0.20	0.10	0.20	—	—	—	—	4.0	Leatherwood and Reeves (1983); Northridge (1984); Jefferson et al. (1993)
<i>Franciscana</i>	0.10	—	0.20	0.20	0.20	—	0.30	—	—	—	—	4.1	Jefferson et al. (1993)
Neophocoena phocaenoides													
<i>Steller's sea lion</i>	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)
<i>California sea lion</i>	0.10	—	0.20	0.15	0.25	—	0.30	—	—	—	—	4.1	Jefferson et al. (1993); Lowry et al. (1991)
<i>South American sea lion</i>	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)
<i>Australian sea lion</i>	0.10	—	0.15	0.05	0.10	—	0.55	0.05	—	—	—	4.2	Jefferson et al. (1993); Reijnders et al. (1993)
Otaridae													
<i>Eumatopias jubatus</i>	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)
<i>Zalophus californianus</i>	0.10	—	0.20	0.15	0.25	—	0.30	—	—	—	—	4.1	Jefferson et al. (1993); Lowry et al. (1991)
<i>Otaria byronia</i>	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)
<i>Neophoca cinerea</i>	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										Trophic level	Source	
	BI	LZ	SS	LS	SP	MP	MF	HV					
Otariidae continued													
Phocarcotus hookeri	0.20	0.05	0.30	0.05	0.15	—	0.20	0.05	—	—	—	—	Jefferson et al. (1993); Reijnders et al. (1993)
Callorhinus ursinus	—	—	0.15	0.15	0.25	0.15	0.30	—	—	—	—	—	Kajimura (1984); Kajimura et al. (1980); Perez and Big (1986); Jefferson et al. (1993); Sinclair et al. (1994); Stroud et al. (1981)
Arctocephalus townsendi	0.20	—	0.30	—	0.30	—	0.20	—	—	—	—	—	Reeves et al. (1992)
A. philippii	0.15	—	0.30	0.15	0.25	—	0.15	—	—	—	—	—	Torres (1987a,b); Majluf and Reyes (1989)
A. galapagoensis	—	—	0.40	—	0.20	0.30	0.10	—	—	—	—	—	Clarke and Trillmich (1980); Trillmich (1987); Reijnders et al. (1993)
A. australis	0.20	0.05	0.10	0.05	0.35	—	0.25	—	—	—	—	—	Majluf (1987); Muck and Fuentes (1987); Vaz-Ferreira and Ponce de Leon (1987)
A. pusillus pusillus	0.15	—	0.15	0.05	0.30	—	0.35	—	—	—	—	—	Rand (1959); David (1987); Lipinski and David (1990); Reijnders et al. (1993)
A. p. doriferus	0.10	—	0.30	0.15	0.20	—	0.25	—	—	—	—	—	Shaughnessy and Warneke (1987); Gales et al. (1993); Gales and Pemberton (1994)
A. forsteri	0.20	—	0.20	0.10	0.10	0.10	0.25	0.05	—	—	—	—	Street (1964); Carey (1992); Reijnders et al. (1993); Mattlin (1987)
A. gazella	—	0.50	0.10	0.05	0.10	0.05	0.15	0.05	—	—	—	—	North et al. (1983); Doidge and Croxall (1985); Boveng et al. (1991); Green et al. (1989); Green et al. (1991)
A. tropicalis	—	0.15	0.30	0.15	0.10	—	0.25	0.05	—	—	—	—	Rand (1956); Condy (1981); Bester (1987)
Odobenidae													
Odobenus rosmarus	0.85	—	—	—	—	—	0.05	0.10	—	—	—	—	Fay (1982); Fay et al. (1982); Gjertz and Wiig (1992); Timoshenko and Popov (1990)
Phocidae													
Phoca vitulina	0.10	—	0.10	0.05	0.30	—	0.45	—	—	—	—	—	Boulva and McLaren (1979); Behreids (1982); Haaker et al. (1984); Härkönen (1987); Payne and Selzer (1989); Olesiuk et al. (1990); Härkönen and Heide-Jørgensen (1991)
P. largha	0.15	—	0.05	0.05	0.30	—	0.45	—	—	—	—	—	Lowry et al. (1982); Bukhtiyarov et al. (1984)
P. hispida	0.20	0.20	—	—	0.15	0.05	0.40	—	—	—	—	—	Lowry et al. (1978); Lowry et al. (1980b); ICES (1991); Westlawski et al. (1994)
P. groenlandica	0.05	0.20	0.05	—	0.30	—	0.40	—	—	—	—	—	Sergeant (1976); Sergeant (1991); Kapel and Angantyr (1989); Lydersen et al. (1991b); Beck et al. (1993); Nilssen and Haug (1993); Uglund et al. (1993); Kapel (1994); Nilson et al. (1993)
P. fasciata	0.35	—	0.10	—	0.25	—	0.30	—	—	—	—	—	Shustov (1969); Frost and Lowry (1980); Burns (1986)
Erignathus barbatus	0.65	0.15	—	—	0.05	—	0.15	—	—	—	—	—	Lowry et al. (1980a); Antonelis et al. (1994b)

Table 2. Continued.

Species	Diet composition										Trophic level	Source	
	BI	LZ	SS	LS	SP	MP	MF	HV					
Phocidae continued													
<i>Cystophora cristata</i>	—	—	0.20	0.20	0.20	—	0.40	—	—	—	4.2	Sergeant (1976)	
<i>Haliocoerus grypus</i>	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)	
<i>Monachus monachus</i>	0.20	—	—	—	0.20	—	0.50	0.10	—	—	4.0	Jefferson et al. (1993)	
<i>M. schauinslandi</i>	0.20	—	0.10	—	—	—	0.70	—	—	—	4.1	Polovina (1984)	
<i>Mirounga leonina</i>	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)	
<i>M. angustirostris</i>	0.05	—	0.40	0.20	—	0.20	0.15	—	—	—	4.3	Antonelis et al. (1994a)	
<i>Lobodon carcinophagus</i>	—	0.90	—	—	0.10	—	—	—	—	—	3.3	Laws (1977); Oritsland (1977); Lowry et al. (1988)	
<i>Ommatophoca rossii</i>	0.05	0.15	0.50	0.15	—	—	0.15	—	—	—	4.1	Laws (1977); Oritsland (1977)	
<i>Hydrurga leptonyx</i>	—	0.35	0.10	—	0.10	—	0.05	0.40	—	—	4.1	Oritsland (1977); Lowry et al. (1988)	
<i>Leptonychotes weddelli</i>	0.20	—	0.15	—	0.15	—	0.50	—	—	—	4.0	Oritsland (1977); Green and Burton (1987); Plotz et al. (1991)	
Mustelidae													
<i>Enhydra lutris</i>	0.80	—	0.05	—	0.05	—	0.10	—	—	—	3.4	Kenyon (1969); Lowry et al. (1982); Antonelis et al. (1994b)	
<i>Lutra felina</i>	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*	from Table 2
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>)†	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§
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)‡
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 $TL_j=2.2$ (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 killer 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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References

- Aguayo, A. and Maturana, R. 1973. Presencia del lobo marino comun *Otaria flavescens* en el litoral chileno. I. Arica (18°20'S) a Punta Maiquillahue (39°27'S). *Biología Pesquera*, Chile, 6: 45–75.
- Antonelis, G. A., Lowry, M. S., Fiscus, C. H., Stewart, B. S., and DeLong, R. L. 1994a. Diet of the northern elephant seal. *In* *Elephant Seals*, pp. 211–223. Ed. by B. J. Le Boeuf and R. M. Laws. University of California Press, Los Angeles.
- Antonelis, G. A., Melin, S. R., and Bukhtiyarov, Y. A. 1994b. Early spring feeding habits of bearded seals (*Erignathus barbatus*) in the central Bering Sea, 1981. *Arctic*, 47: 74–79.
- Avery, W. E. and Hawkinson, C. 1992. Gray whale feeding in a northern California estuary. *Northwest Science*, 66: 199–205.
- Barros, N. B., and Cockcroft, V. G. 1991. Prey of humpback dolphins (*Sousa plumbea*) stranded in eastern Cape Province, South Africa. *Aquatic Mammals*, 17: 134–136.
- Beck, G. G., Hammill, M. O., and Smith, T. G. 1993. Seasonal variation in the diet of harp seals (*Phoca groenlandica*) from the Gulf of St Lawrence and Western Hudson Strait. *Canadian Journal of Fisheries and Aquatic Sciences*, 50: 1363–1371.
- Behrends, G. 1982. Analysis of stomach and colon contents of 185 common seals from the Waddensea of Schleswig-Holstein. *ICES CM 1982/N:11*.
- Bester, P. N. 1987. Subantarctic fur seal, *Arctocephalus tropicalis*, at Gough Island (Tristan da Cunha group). *In* *Status, biology, and ecology of fur seals*, pp. 57–60. Ed. by J. P. Croxall and R. L. Gentry. NOAA Technical Report NMFS 51.
- Bogoslovskaya, L. S., Votrogov, L. M., and Semenova, T. N. 1981. Feeding habits of the gray whale off Chukotka. Report of the International Whaling Commission, 31: 507–510.
- Bonner, W. N. 1990. The natural history of seals. *Fact of File Publications*, New York. 196 pp.
- Boulva, J. and McLaren, I. A. 1979. Biology of the Harbor Sea, *Phoca vitulina*, in Eastern Canada. *Fisheries Research Board of Canada Bulletin* 200, 24 pp.
- Boveng, P. L., Bengtson, J. L., and Goebel, M. E. 1991. AMLR program: Antarctic fur seal foraging patterns at Seal Island, South Shetland Islands, Antarctica during austral summer 1990–1991. *Antarctic Journal of the U.S.*, 26: 215–216.
- Bowen, W. D. and Harrison, G. D. 1994. Offshore diet of grey seals *Halichoerus grypus* near Sable Island, Canada. *Marine Ecology – Progress Series*, 112: 1–11.
- Bowen, W. D., Lawson, J. W., and Beck, B. 1993. Seasonal and geographic variation in the species composition and size of prey consumed by grey seals (*Halichoerus grypus*) on the Scotian Shelf. *Canadian Journal of Fisheries and Aquatic Sciences*, 50: 1768–1778.
- Boyd, I. L., Arborm, T. A., and Fedak, M. A. 1994. Biomass, diet and energy consumption of the South Georgia stock of southern elephant seals. *In* *Elephant Seals*, pp. 98–117. Ed. by B. J. Le Boeuf and R. M. Laws. University of California Press, Los Angeles.
- Bukhtiyarov, Y. A., Frost, K. J., and Lowry, L. F. 1984. New information on foods of the spotted seal, *Phoca largha*, in the Bering Sea in spring. *In* *Soviet-American cooperative research on marine mammals. Vol. 1: Pinnipeds*, pp. 55–59. Ed. by F. H. Fay and G. A. Fedoseev. U.S. Dep. Commer., NOAA Technical Report NMFS 12.
- Burns, J. J. 1986. Ice seals. *In* *Marine mammals of eastern North Pacific and arctic waters*, 2nd Ed., rev., pp. 216–229. Ed. by D. Haley. Pacific Search Press, Seattle.
- Bushuev, S. G. 1986. Feeding of minke whales, *Balaenoptera acutorostrata* in the Antarctic. Report of the International Whaling Commission, 36: 241–245.
- Bushuev, S. G. 1991. Distribution and feeding of minke whales in Antarctic Area I. Report of the International Whaling Commission, 41: 303–312.
- Calkins, D. G. and Goodwin, E. 1988. Investigation of the declining sea lion population in the Gulf of Alaska. Unpublished Report, Alaska Department of Fish and Game, Anchorage. 76 pp.
- Carey, P. 1992. Fish prey species of the New Zealand fur seal (*Arctocephalus forsteri*, Lesson). *New Zealand Journal of Ecology*, 16: 41–46.
- Christensen, I., Haug, T., and Øien, N. 1990. A review of the distribution, migrations, food, reproduction, exploitation and present abundance of humpback whales (*Megaptera novaeangliae*) in the Northeast Atlantic. *ICES CM 1990/N:10*.
- Christensen, I., Haug, T., and Øien, N. 1992. A review of feeding and reproduction in large baleen whales and sperm whales in Norwegian and adjacent waters. *Fauna Norvegica, Series A*, 13: 39–48.
- Christensen, V. and Pauly, D. 1992. The ECOPATH II – a software for balancing steady-state models and calculating network characteristics. *Ecological Modelling*, 61: 169–185.
- Christensen, V. and Pauly, D. (Eds) 1993. *Trophic models of aquatic ecosystem*. ICLARM Conference Proceedings 26, 390 pp. ICLARM, Manila, Philippines.
- Clarke, M. R. 1956. Sperm whales of the Azores. *Discovery Reports*, 28: 237–298.
- Clarke, M. R. and Trillmich, F. 1980. Cephalopods in the diet of fur seals of the Galapagos Islands. *Journal of Zoology (London)*, 190: 211–215.
- Condy, P. R. 1981. Annual food consumption, and seasonal fluctuations in biomass of seals at Marion Island. *Mammalia*, 45: 21–30.
- Crawford, T. W. 1981. Vertebrate prey of *Phocoenoides dalli* (Dall's porpoise), associated with the Japanese high seas salmon fishery in the North Pacific Ocean. M.S. Thesis, University of Washington, Seattle. 72 pp.
- David J. H. M. 1987. Diet of the South African fur seal (1974–1985) and an assessment of competition with fisheries in southern Africa. *In* *South African Journal of Marine Science* 5: The Benguela and comparable ecosystems, pp. 693–713. Ed. by A. I. L. Payne, J. A. Gulland and K. H. Brink.
- Desportes, G. and Mouritsen, R. 1988. Diet of the pilot whale, *Globicephala melas*, around the Faroe Islands. *ICES CM 1988/N:12*.
- Doidge, D. W. and Croxall, J. P. 1985. Diet and energy budget of the Antarctic fur seal, *Arctocephalus gazella*, at South Georgia. *In* *Antarctic nutrient cycles and food webs*, pp. 543–550. Ed. by W. R. Siegfried, P. R. Condy and R. M. Laws. Springer-Verlag, Berlin.

- Evans, P. G. H. 1987. The natural history of whales and dolphins. Fact of File Publications, New York. 343 pp.
- Fay, F. H. 1982. Ecology and biology of the Pacific walrus, *Odobenus rosmarus divergens* Illiger. United States Department of Interior Fish and Wildlife Service, North American Fauna 74.
- Fay, F. H., Bukhitiyarov, Yu. A., Stoker, S. W., and Shults, L. M. 1984. Foods of the Pacific walrus in winter and spring in the Bering Sea. In Soviet-American cooperative research on marine mammals, Vol. 1. Pinnipeds, pp. 81–88. Ed. by F. H. Fay and G. A. Fedoseev. NOAA Technical Report NMFS 12.
- Fontaine, P. M., Hammill, M. O., Barrette, C., and Kingsley, M. C. 1994. Summer diet of the harbour porpoise (*Phocoena phocoena*) in the estuary and the northern Gulf of St Lawrence. Canadian Journal of Fisheries and Aquatic Sciences, 51: 172–178.
- Frost, K. J. and Lowry, L. F. 1980. Feeding of ribbon seals (*Phoca fasciata*) in the Bering Sea in spring. Canadian Journal of Zoology, 58: 1601–1607.
- 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, pp. 825–836. Ed. by D. W. Wood and J. A. Calder. University of Washington Press, Seattle.
- Gales, R. and Pemberton, D. 1994. Diet of the Australian fur seal in Tasmania. Australian Journal of Marine and Freshwater Research, 45: 653–664.
- Gales, R., Pemberton, D., Lu, C. C., and Clarke, M. R. 1993. Cephalopod diet of the Australian fur seal: variation due to location, season and sampling type. Australian Journal of Marine Freshwater Research, 44: 657–671.
- Gambell, R. 1979. The blue whale. Biologist, 26: 209–215.
- Gambell, R. 1985a. Fin whale *Balaenoptera physalus* (Linnaeus 1758), Chapter 7. In Handbook of marine mammals. Volume 3: The sirenians and baleen whales, pp. 171–192. Ed. by S. H. Ridgway and R. J. Harrison. Academic Press, San Diego. 362 pp.
- Gambell, R. 1985b. Sei whale *Balaenoptera borealis* Lesson 1828, Chapter 6. In Handbook of marine mammals. Volume 3: The sirenians and baleen whales, pp. 155–170. Ed. by S. H. Ridgway and R. J. Harrison. Academic Press, San Diego. 362 pp.
- Gaskin, D. E. and Cawthorn, M. W. 1967. Diet and feeding habits of the sperm whale (*Physeter catodon* L) in the Cook Strait region of New Zealand. New Zealand Journal of Marine and Freshwater Research, 1: 156–179.
- Gjertz, I. and Wiig, O. 1992. Feeding of walrus *Odobenus rosmarus* in Svalbard. Polar Record 28: 57–59.
- González, A. F., López, A., Guerra, A., and Barreiro, A. 1994. Diets of marine mammals stranded on the northwestern Spanish Atlantic coast with special reference to Cephalopoda. Fisheries Research, 21: 179–191.
- Goodall, R. N. P. and Galeazzi, A. R. 1985. A review of the food habits of the small cetaceans of the Antarctic and Sub-Antarctic. In Antarctic nutrient cycles and food webs, pp. 566–572. Ed. by W. R. Siegfried, P. R. Condy, and R. M. Laws. Springer-Verlag, Berlin and Heidelberg.
- Green, K. and Williams, R. 1986. Observations of the food remains in faeces of elephant, leopard and Crabeater seals. Polar Biology, 6: 43–45.
- Green, K. and Burton, H. R. 1987. Seasonal and geographical variation in the food of Weddell seals, *Leptonychotes weddellii*, in Antarctica. Australian Wildlife Research, 14: 475–489.
- Green, K. and Burton, H. R. 1993. Comparison of the stomach contents of southern elephant seals, *Mirounga leonina*, at Macquarie and Heard Islands. Marine Mammal Science, 9: 10–22.
- Green, K., Burton, H. R., and Williams, R. 1989. The diet of Antarctic fur seals, *Arctocephalus gazella* (Peters) during the breeding season at Heard Island. Antarctic Science, 1: 317–324.
- Green, K., Williams, R., and Burton, H. R. 1991. The diet of Antarctic fur seals during the late autumn and early winter around Heard Island. Antarctic Science, 3: 359–362.
- Guinet, C. 1992. Hunting behavior in killer whales (*Orcinus orca*) around Crozet Islands. Canadian Journal of Zoology, 70: 1656–1667.
- Haaker, P. L., Parker, D. O., and Henderson, K. C. 1984. Observations of harbor seal, *Phoca vitulina richardsi* feeding in southern California waters. Bulletin of South California Academy of Sciences, 83: 152–153.
- Hain, J. H., Carter, G. R., Kraus, S. D., Mayo, C. A., and Winn, H. E. 1981. Feeding behavior of the humpback whale, *Megaptera novaeangliae*, in the western North Atlantic. Fishery Bulletin, 80: 259–268.
- Hammond, P. S., Hall, A. J., and Prime, J. H. 1994. The diet of grey seals around Orkney and other island and mainland sites in northeastern Scotland. Journal of Applied Ecology, 31: 340–350.
- Hammer, W. M., Stone, G. S., and Obst, B. S. 1988. Behavior of southern right whales, *Eubalaena australis*, feeding on the Antarctic krill, *Euphausia superba*. Fishery Bulletin U.S., 86: 143–150.
- Harcourt, R. 1993. Individual variation in predation on fur seals by southern sea lions (*Otaria byronia*) in Peru. Canadian Journal of Zoology, 71: 1908–1911.
- Härkönen, T. 1987. Seasonal and regional variations in the feeding habits of the harbour seal, *Phoca vitulina*, in the Skagerrak and the Kattegat. Journal of Zoology (London), 213: 535–543.
- Härkönen, T. and Heide-Jørgensen, M.-P. 1991. The harbour seal *Phoca vitulina* as a predator in the Skagerrak. Ophelia, 34: 191–207.
- Haug, T., Gjøsaeter, H., Lindstrøm, U., and Nilssen, K. T. 1993. Studies of minke whale *Balaenoptera acutorostrata* ecology in the northeast Atlantic: Preliminary results from studies of diet and food availability during summer 1992. ICES CM 1993/N:7.
- Haug, T., Lindstrøm, U., Nilssen, K. T., and Røttingen, I. 1994. Studies of minke whale (*Balaenoptera acutorostrata*) ecology in the northeast Atlantic: description of the 1993 scientific catch operations and preliminary results from stomach analyses and resource surveys. ICES CM 1994/N:14.
- Heyning, J. E. 1989. Cuvier's beaked whale *Ziphius cavirostris* Cuvier 1823. In Handbook of marine mammals. Volume 4: River dolphins and the large toothed whales. Ed. by S. H. Ridgway and R. J. Harrison. Academic Press, San Diego. 442 pp.
- Hobson, K. A., Sease, J. L., Merrick, R. L., and Platt, J. F. 1997. Investigating trophic relationships of pinnipeds in Alaska and Washington using stable isotope ratios of nitrogen and carbon. Marine Mammal Science, 13: 114–132.
- Hoyt, E. 1990. Orca: the whale called killer. E. P. Dutton, New York. 291 pp.
- ICES. 1991. Report of the study group on seals and small cetaceans in northern European seas. ICES CM 1991/N:19.
- Ichii, T. and Kato, H. 1991. Food and daily food consumption of southern minke whales in the Antarctic. Polar Biology, 11: 479–487.
- Innes, S., Lavigne, D. M., Earle, W. M., and Kovacs, K. M. 1987. Feeding rates of seals and whales. Journal of Animal Ecology, 56: 115–130.
- Irvine, A. B., Scott, M. D., Wells, R. C., and Kaufmann, J. H. 1981. Movements and activities of the Atlantic bottlenose

- dolphin, *Tursiops truncatus*, near Sarasota, Florida. Fishery Bulletin U.S., 79: 671–688.
- Jefferson, T. A., Stacey, P. J., and Baird, R. W. 1991. A review of killer whale interactions with other marine mammals: predation to co-existence. Mammalogy Reviews, 21: 151–180.
- Jefferson, T. A., Leatherwood, S., and Webber, M. A. 1993. Marine mammals of the world. FAO Species Identification Guide. Food and Agriculture Organization, Rome. 320 pp.
- Jongsgaard, A. 1982. The food of minke whales (*Balaenoptera acutorostrata*) in northern North Atlantic waters. Report of the International Whaling Commission, 32: 259–262.
- Kajimura, H. 1984. Opportunistic feeding of the northern fur seal, *Callorhinus ursinus*, in the eastern North Pacific Ocean and eastern Bering Sea. NOAA Technical Report NMFS SSRF-779, 49 pp.
- Kajimura, H., Fiscus, C. H., and Stroud, R. K. 1980. Food of the Pacific white-sided dolphin, *Lagenorhynchus obliquidens*, Dall's porpoise, *Phocoenoides dalli*, and northern fur seal, *Callorhinus ursinus*, off California and Washington; with appendices on size and food of Dall's porpoise from Alaskan waters. U.S. Dep. Commer., NOAA Technical Memorandum NMFS F/NWC-2, 30 pp.
- Kapel, F. O. 1994. Variation in the feeding of harp seals (*Phoca groenlandica*) in Southwest Greenland waters. ICES CM 1994/N:4.
- Kapel, F. O. and Angantyr, L. A. 1989. Feeding patterns of harp seals (*Phoca groenlandica*) in coastal waters of west Greenland, with a note on offshore feeding. ICES CM 1989/N:6.
- Karbhari, J. P., Aravindakshan, M., Wagmare, K. B., and Gandhi, R. 1985. Note on the food of the spinner dolphin *Stenella longirostris* Gray, caught off Maharashtra coast. Journal of Marine Biological Association (India), 27: 193–195.
- Kasamatsu, F. and Hata, T. 1985. Notes on minke whales in the Okhotsk Sea-West Pacific area. Report of the International Whaling Commission, 35: 299–304.
- Kawakami, T. 1980. A review of sperm whale food. Scientific Report of the Whales Research Institute (Tokyo), 32: 199–218.
- Kawamura, A. 1980. A review of food of balaenopterid whales. Scientific Report of the Whales Research Institute (Tokyo), 32: 155–197.
- Kenyon, K. W. 1969. The sea otter in the eastern Pacific Ocean. North American Fauna 68, 352 pp.
- King, J. E. 1983. Seals of the world (2nd Edition). Cornell University Press, Ithaca, New York. 240 pp.
- Klinowska, M. 1991. Dolphins, porpoises and whales of the world: the IUCN Red Data Book. IUCN – the World Conservation Union, Gland, Switzerland. 429 pp.
- Laws, R. M. 1977. Seals and whales of the Southern Ocean. Philosophical Transactions of the Royal Society of London, 279: 81–96.
- Leatherwood, S. and Reeves, R. R. 1983. The Sierra Club handbook of whales and dolphins. Dai Nippon Printing, Tokyo. 302 pp.
- Leatherwood, S., Deerman, M. W., and Potter, C. W. 1978. Food and reproductive status of nine *Tursiops truncatus* from the Northeastern United States coast. Cetology, (28): 1–6.
- Leatherwood, S., Reeves, R. R., Perrin, W. F., and Evans, W. E. 1988. Whales, dolphins, and porpoises of the Eastern North Pacific and adjacent Arctic waters: a guide to the identification. Dover Publishing, New York. 245 pp.
- Lick, R. 1991. Parasites from the digestive tract and food analysis of harbour porpoise *Phocoena phocoena* from German coastal waters. In European Research on Cetaceans, pp. 13–19. Ed. by P. G. H. Evans. Proceedings of the Fifth Annual Conference of the European Cetacean Society, Sandefjord, Norway, 21–23 February 1991.
- Lipinski, M. R. and David, J. H. M. 1990. Cephalopods in the diet of the South African fur seal (*Arctocephalus pusillus pusillus*). Journal of Zoology (London), 221: 359–374.
- Lockyer, C. and Brown, S. G. 1978. Biology of fin and sei whales off Iceland. ICES CM 1978/N:6.
- Loeb, V. J. 1972. A study of the distribution and feeding habits of the Dall porpoise in Monterey Bay, California. M.S. Thesis, San Jose State College, San Jose, California. 62 pp.
- Loughlin, T. R. and Perez, M. A. 1985. *Mesoplodon stejnegeri*. American Society of Mammalogists, Mammalian Species, No. 250: 1–6.
- Lowry, L. F. 1993. Foods and feeding ecology. In The Bowhead Whale, pp. 201–238. Ed. by J. J. Burns, J. J. Montague and C. J. Cowles. The Society for Marine Mammalogy, Special Publication Number 2.
- Lowry, L. F. and Frost, K. J. 1984. Foods and feeding of Bowhead whales in western and northern Alaska. Scientific Report of the Whales Research Institute (Tokyo), 35: 1–16.
- Lowry, L. F., Frost, K. J., and Burns, J. J. 1978. Food of ringed seals and Bowhead whales near Point Barrow, Alaska. Canadian Field-Naturalist, 92: 67–70.
- Lowry, L. F., Frost, K. J., and Burns, J. J. 1980a. Feeding of bearded seals in the Bering and Chukchi seas and trophic interactions with Pacific walrus. Arctic, 33: 330–342.
- Lowry, L. F., Frost, K. J., and Burns, J. J. 1980b. Variability in the diet of ringed seals, *Phoca hispida*, in Alaska. Canadian Journal of Fisheries and Aquatic Sciences, 37: 2254–2261.
- Lowry, L. F., Frost, K. J., and Seaman, G. A. 1985. Investigations of beluga whales in coastal waters. III. Food habits. Final rep., OCSEAP Res. Unit 512, 24 pp. Alaska Department of Fish and Game, Fairbanks.
- Lowry, L., Testa, J. W., and Calert, W. 1988. Winter feeding of crabeater and leopard seals near the Antarctic Peninsula. Polar Biology, 8: 475–478.
- Lowry, L. F., Frost, K. J., Calkins, D. G., Swartzman, G. L., and Hills, S. 1982. Feeding habits, food requirements, and status of Bering Sea marine mammals. Council. Doc. Nos 19 and 19A (annotated bibliography), 574 p. North Pacific Fisheries Management Council, Anchorage.
- Lowry, M. S., Stewart, B. S., Heath, C. B., Yochem, P. K., and Francis, J. M. 1991. Seasonal and annual variability in the diet of California sea lions *Zalophus californianus* at San Nicolas Island, California, 1981–1986. Fishery Bulletin, 89: 331–336.
- Lydersen, C., Weslawski, J. M., and Oristland, N. A. 1991a. Stomach content analysis of minke whales *Balaenoptera acutorostrata* from the Lofoten and Vesteraalen areas, Norway. Holarctic Ecology, 14: 219–222.
- Lydersen, C., Angantry, L. A., Wigg, O., and Oristland, T. 1991b. Feeding habits of Northeast Atlantic harp seals (*Phoca groenlandica*) along the summer ice edge of the Barents Sea. Canadian Journal of Fisheries and Aquatic Sciences, 48: 2180–2183.
- MacDonald, J. S. and Green, R. H. 1983. Redundancy of variables used to describe importance of prey species in fish diet. Canadian Journal of Fisheries and Aquatic Sciences, 40: 635–637.
- Majluf, P. 1987. South American fur seal, *Arctocephalus australis*, in Peru. In Status, biology, and ecology and fur seals, pp. 33–35. Ed. by J. P. Croxall and R. L. Gentry. NOAA Technical Report NMFS 51.
- Majluf, P. and Reyes, J. C. 1989. The marine mammals of Peru: a review. In The Peruvian upwelling ecosystem: dynamics and interactions, pp. 344–363. Ed. by D. Pauly, P. Muck,

- J. Mendo and I. Tsukayama. ICLARM Conference Proceedings 18, 438 pp.
- Martin, A. R., Lockyer, C. H., Northridge, S., Hammond, S., and Law, R. J. 1990. Aspects of the population biology of the harbour porpoise, *Phocoena phocoena*, in British waters: A preliminary analysis of recent by-caught and stranded animals. Paper SC/42/SM53 submitted to the Scientific Committee of the International Whaling Commission.
- Martins, H. R., Clarke, M. R., Reiner, F., and 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 Ciencias Natural*, 6: 63–70.
- Mathisen, O. A. 1959. Studies on Stellar sea lion (*Eumetopias jubata*) in Alaska. Transactions of the 24th North American Wildlife Conference, 2–4 March 1959, Wildlife Management Institute, Washington.
- Mathisen, O. A., Boade, R. T., and Lapp, R. J. 1962. Breeding habits, growth, and stomach contents of the Stellar sea lion in Alaska. *Journal of Mammalogy*, 43: 469–477.
- Mattlin, R. H. 1987. New Zealand fur seal, *Arctocephalus forsteri*, within the New Zealand region. In Status, biology, and ecology of fur seals, pp. 49–51. Ed. by J. P. Croxall and R. L. Gentry. NOAA Technical Report NMFS 51.
- Mayo, C. A. and Marx, M. K. 1990. Surface foraging behaviour of the North Atlantic right whale, *Eubalaena glacialis*, and associated zooplankton characteristics. *Canadian Journal of Zoology*, 68: 2214–2220.
- McKinnon, J. 1993. Feeding habits of the dusky dolphin, *Lagenorhynchus obscurus*, in the coastal waters of Central Peru. *Fishery Bulletin*, 92: 569–578.
- Mead, J. G. 1989a. Beaked whales of the genus *Mesoplodon*, Chapter 14. In Handbook of marine mammals. Volume 4: River dolphins and the large toothed whales. Ed. by S. H. Ridgway and R. J. Harrison. Academic Press, San Diego. 442 pp.
- Mead, J. G. 1989b. Bottlenose whales *Hyperoodon ampullatus* (Forster 1770) and *Hyperoodon planifrons* Flower 1882, Chapter 13. In Handbook of marine mammals. Volume 4: River dolphins and the large toothed whales. Ed. by S. H. Ridgway and R. J. Harrison. Academic Press, San Diego. 442 pp.
- Mead, J. G. and Baker, A. N. 1987. Notes on the rare beaked whale, *Mesoplodon hectori* (Gray). *Journal of the Royal Society of New Zealand*, 17: 303–312.
- Mead, J. G. and Potter, C. W. 1990. Natural history of bottlenose dolphins along the Central Atlantic coast of the United States. In The bottlenose dolphins, pp. 165–195. Ed. by S. Leatherwood and R. R. Reeves. Academic Press, San Diego.
- Muck, P. and Fuentes, H. 1987. Sea lion and fur seal predation on the Peruvian anchoveta, 1953 to 1982. In The Peruvian anchoveta and its upwelling ecosystem: three decades of change, pp. 234–247. Ed. by D. Pauly and I. Tsukayama. ICLARM Studies and Reviews 15, 351 pp.
- Murie, D. J. and Lavigne, D. M. 1992. Growth and feeding habits of grey seals (*Halichoerus grypus*) in the northwestern Gulf of St Lawrence, Canada. *Canadian Journal of Zoology*, 70: 1604–1613.
- Nemoto, T. 1957. Foods of baleen whales in the northern Pacific. Scientific Report of the Whales Research Institute (Tokyo), 12: 33–89.
- Nemoto, T. 1959. Food of baleen whales with reference to whale movements. Scientific Report of the Whales Research Institute (Tokyo), 14: 144–290.
- Nemoto, T. 1970. Feeding pattern of baleen whales in the ocean. In Marine food chains, pp. 241–252. D.M. Ed. by J. H. Steele. Oliver and Boyd, Edinburgh.
- Nerimi, M. 1984. A review of gray whale feeding ecology. In The Gray Whale: *Eschrichtius robustus*, pp. 423–450. Ed. by M. L. Jones, S. L. Swartz and S. Leatherwood.
- Nilssen, K. T. and Haug, T. 1993. Studies on feeding and condition of Barents Sea harp seals *Phoca groenlandica* throughout the year. In Nordic Workshop on Predation processes and predation Models, pp. 13–105. Seminar at Stykkishomur, 7–11 September. Fisheries Research Institute, Reykjavik, Iceland and Copenhagen, Denmark Nordisk-Ministerraad. No. 572.
- Nilssen, K. T., Haug, T., Potelov, V., and Stasenkov, V. 1993. Diets of harp seals *Phoca groenlandica* feeding between the breeding and moulting seasons in the southern Barents and White Seas. ICES CM 1993/N:8.
- NMFS [National Marine Fisheries Service]. 1992. Recovery Plan for the Steller sea lion (*Eumetopias jubatus*). Prepared by the Steller sea lion Recovery Team for the National Marine Fisheries Service. Silver Spring, Maryland. 92 pp.
- Nordoy, E. S. and Blix, A. S. 1992. Diet of minke whales in the northeastern Atlantic. Report of the International Whaling Commission, 42: 393–398.
- North, A. W., Croxall, J. P., and Doidge, D. W. 1983. Fish prey of the Antarctic fur seal *Arctocephalus gazella* at South Georgia. *British Antarctic Survey Bulletin*, 61: 27–38.
- Northridge, S. P. 1984. World review of interactions between marine mammals and fisheries. FAO Fisheries Paper 251, 190 pp.
- Okutani, T. and Nemoto, T. 1964. Squids as the food of sperm whales in the Bering Sea and Alaskan Gulf. Scientific Report of the Whales Research Institute (Tokyo), 18: 111–122.
- Olesiuk, P. F., Bigg, M. A., Ellis, G. M., Crockford, S. J., and Wigen, R. J. 1990. An assessment of the feeding habits of harbour seals (*Phoca vitulina*) in the Strait of Georgia, British Columbia, based on scat analysis. *Canadian Technical Report in Fisheries and Aquatic Sciences* 1730, 135 pp.
- Olivia, D. 1984. Espectro trófico y circarmitos de actividad alimentaria en loberias permanentes y temporarias de *Otaria byronia*. Tesis de Licenciado en Biología, Facultad de Medicina, Universidad de Valparaíso. 115 pp.
- Oritsland, T. 1977. Food consumption of seals in the Antarctic pack ice. In Adaptations within Antarctic ecosystems, pp. 749–768. Ed. by G. A. Llano. Third Symposium on Antarctic Biology. Scientific Committee for Antarctic Research. Smithsonian Institution/Gulf Publishing Co., Washington.
- Ostrom, P. H., Lien, J., and Macko, S. A. 1993. Evaluation of the diet of Sowerby's beaked whale, *Mesoplodon bidens*, based on isotopic comparisons among northwestern Atlantic cetaceans. *Canadian Journal of Zoology*, 71: 858–861.
- Overholtz, W. J. and Waring, G. T. 1991. Diet composition of pilot whales *Globicephalus* sp. and common dolphins *Delphinus delphis* in the mid-Atlantic bight during spring 1989. *Fishery Bulletin U.S.*, 89: 723–728.
- Parson, E. C. M. 1996. Trace metal levels in North Lantau fishes: implication of the health of Hong Kong's Indo-Pacific Hump-backed dolphin (*Sausa chinensis*) population. Unpublished manuscript, available from The Swire Institute of Marine Sciences, The University of Hong Kong, Cape d'Aguiar, Hong Kong, 12 p.
- Pascoe, P. L., Mickiewicz, M. C., and Castello, H. P. 1990. Cephalopod remains from the stomach of a sperm whale stranded off Patagonia. *Marine Biology*, 104: 1–4.
- Pauly, D. and Christensen, V. 1993. Stratified models of large marine ecosystems: a general approach and an application to the South China Sea. In Large marine ecosystems: stress, mitigation and sustainability, pp. 148–174. Ed. by K. Sherman, L. M. Alexander and B. D. Gold. AAAS Press, Washington.

- Pauly, D. and Christensen, V. 1995. Primary production required to sustain global fisheries. *Nature*, 374: 255–257.
- Payne, P. M. and Selzer, L. A. 1989. The distribution, abundance, and selected prey of the harbor seal, *Phoca vitulina concolor*, in southern New England. *Marine Mammal Science*, 5: 173–192.
- Perez, M. A. 1990. Review of marine mammal population and prey information for Bering Sea ecosystem studies. NOAA Technical Memorandum NMFS F/NWC-186, 81 pp.
- Perez, M. A. and Bigg, M. A. 1986. Diet of northern fur seals, *Callorhinus ursinus*, off western North America. *Fishery Bulletin*, 84: 957–971.
- Perrin, W., Miyazaki, N., and Kasuya, T. 1989. A dwarf form of the spinner dolphin (*Stenella longirostris*) from Thailand. *Marine Mammal Science*, 5: 213–227.
- Perrin, W. F., Mitchell, E. D., Mead, J. G., Caldwell, D. K., and van Bree, P. J. H. 1981. *Stenella clymene*, a rediscovered tropical dolphin of the Atlantic. *Journal of Mammalogy*, 62: 583–598.
- Perrin, W. F., Warner, R. R., Fiscus, C. H., and Holts, D. B. 1973. Stomach contents of porpoise, *Stenella* spp. and yellowfin tuna, *Thunnus albacares*, in mixed species aggregations. *Fishery Bulletin*, 71: 1077–1092.
- Pinedo, M. C. 1987. First record of a dwarf sperm whale from southern Atlantic, with reference to osteology, food habits and reproduction. Scientific Report of the Whales Research Institute (Tokyo), 38: 171–186.
- Pitman, R. L. and Ballance, L. T. 1992. Parkinson's petrel distribution and foraging ecology in the Eastern Pacific: aspects of an exclusive feeding relationship with dolphins. *The Condor*, 94: 825–835.
- Plotz, J., Werner, E., and Reijnders, P. J. H. 1991. Diet of Weddell seals *Leptonychotes weddellii* at Vestkapp, eastern Weddell Sea (Antarctica), in relation to local food supply. *Marine Mammal Science*, 7: 136–144.
- Polovina, J. J. 1984. Model of a coral reef ecosystem. I. The ECOPATH model and its application to French Frigate Shoals. *Coral Reefs*, 3: 1–11.
- Prescott, J. H. and Fiorelli, P. M. 1980. Review of the harbour porpoise (*Phocoena phocoena*) in the U.S. Northwest Atlantic. U.S. Marine Mammal Commission Report MMC-78/08, 64 pp. (Available from Natl. Tech. Inf. Serv., Springfield, VA, as PB80-176928.)
- Rand, R. W. 1956. Notes on the Marion Island fur seal. *Proceedings of the Zoological Society of London*, 12: 65–82.
- Rand, R. W. 1959. The Cape fur seal (*Arctocephalus pusillus*). Distribution, abundance and feeding habits off the south western coast of the Cape Province. South Africa Sea Fisheries Branch Investigational Report 34, 75 pp.
- Recchia, C. A. and Read, A. J. 1989. Stomach contents of harbour porpoises, *Phocoena phocoena* (L.), from the Bay of Fundy. *Canadian Journal of Zoology*, 67: 2140–2146.
- Reeves, R. R., Stewart, B. S., and Leatherwood, S. 1992. The Sierra Club handbook of Seals and Sirenians. Sierra Club Books, San Francisco.
- Reijnders, P., Brasseur, S., van der Toorn, J., van der Wolf, P., Body, I., Harwood, J., Lavigne, D., and Lowry, L. 1993. Seals, fur seals, sea lions, and walrus. Status survey and conservation action plan. International Union for Conservation of Nature and Natural Resources, Gland Switzerland. 88 pp.
- Reilly, S. B. and Thayer, V. G. 1990. Blue whale (*Balaenoptera musculus*) distribution in the Eastern tropical Pacific. *Marine Mammal Science*, 6: 265–277.
- Rice, D. W. 1968. Stomach contents and feeding behavior of killer whales in the eastern North Pacific. *Norsk Hvalfangst-Tidende*, 1968: 35–38.
- Rice, D. W. 1986. Beaked whales. In *Marine mammals of eastern North Pacific and arctic waters*, 2nd Ed., rev., pp. 102–109. Ed. by D. Hale. Pacific Search Press, Seattle.
- Robinson, B. H. and Craddock, J. E. 1983. Mesopelagic fishes eaten by Fraser's dolphin, *Lagenodelphis hosei*. *Fishery Bulletin U.S.*, 81: 283–289.
- Rodhouse, P. G., Arnobom, T. R., Fedak, M. A., Yeatman, J., and Murray, A. W. A. 1992. Cephalopod prey of the southern elephant seal, *Morounga leonina* L. *Canadian Journal of Zoology*, 70: 1007–1015.
- Roe, H. S. J. 1968. The food and feeding habits of the sperm whales taken off the west coast of Iceland. *ICES CM* 1968/N:5.
- Roper, C. F. E., Sweeny, M. J., and Nauen, C. E. 1984. Cephalopods of the world: an annotated and illustrated catalogue of species of interest to fisheries. *FAO Species Catalogue Vol. 3, FAO Species Synopses* (125), 277 pp.
- Santos, M. B., Pierce, G. J., Ross, H. M., Reid, R. J., and Wilson, B. 1994. Diets of small cetaceans from the Scottish coast. *ICES CM* 1994/N:11.
- Seaman, G. A., Lowry, L. F., and Frost, K. J. 1982. Foods of beluga whales (*Delphinapterus leucas*) in western Alaska. *Cetology*, 44: 1–19.
- Sekiguchi, K., Klages, N., Findlay, K., and Best, P. B. 1993. Feeding habits and possible movements of southern bottlenose whales (*Hyperoodon planifrons*). *Proceedings of the NIPR Symposium on Polar Biology*. National Institute of Polar Research, Tokyo. No. 6, 84–97.
- Sergeant, D. E. 1962. The biology of the pilot or pothead whale *Globicephala melaena* (Traill) in Newfoundland waters. *Fisheries Research Board of Canada Bulletin No. 132*, 84 pp.
- Sergeant, D. E. 1975. An additional food supply for humpback (*Megaptera novae-angliae*) and minke whales (*Balaenoptera acutorostrata*). *ICES CM* 1975/N:13. 6 pp. +3 figures.
- Sergeant, D. E. 1976. History and present status of populations of harp and hooded seals. *Biological Conservation*, (10): 95–118.
- Sergeant, D. E. 1991. Harp seals, man and ice. *Canadian Special Publications in Fisheries and Aquatic Sciences* 114, 153 pp.
- Shaughnessy, P. S. and Warneke, R. M. 1987. Australian fur seal, *Arctocephalus pusillus doriferus*. In *Status, biology, and ecology of fur seals*, pp. 73–77. Ed. by J. P. Croxall and R. L. Gentry. NOAA Technical Report NMFS 51.
- Shustov, A. P. 1969. [The food of ribbon seal in Bering Sea.] [In Russ.]. *Izv Tikhookean. Nauchno-issled. Inst. Rybn. Khoz. Okeanogr. (TINRO)*, 59: 178–183. [Transl. by U.S. Bur. Commer. Fish., Seattle, WA, 1968, 10 p.]
- Sigurjónsson, J. and Vikingsson, G. A. 1992. Investigations on the ecological role of cetaceans in Icelandic and adjacent waters. *ICES CM* 1992/N:24.
- Sinclair, E., Loughlin, T., and Pearcy, W. 1994. Prey selection by northern fur seals (*Callorhinus ursinus*) in the eastern Bering Sea. *Fishery Bulletin U.S.*, 92: 144–156.
- Street, R. J. 1964. Feeding habits of the New Zealand fur seal. *New Zealand Marine Department of Fisheries Technical Report 9*, 20 pp.
- Stroud, R. K., Fiscus, C. H., and Kajimura, H. 1981. Food of the Pacific white-sided dolphin, *Lagenorhynchus obliquidens*, Dall's porpoise, *Phocoenoides dalli*, and northern fur seal, *Callorhinus ursinus*, off California and Washington. *Fishery Bulletin U.S.*, 78: 951–959.
- Tan, J. L. 1995. A field guide to whales and dolphins in the Philippines. *Bookmark, Makati, Metro Manila*. 125 pp.
- Timoshenko, Yu. and Popov, L. A. 1990. On predatory habits of Atlantic walrus. In *The ecology and management of walrus populations*. Ed. by F. H. Fay, B. P. Kelly and B. A.

- Fay. Washington, Marine Mammal Commission Report PB91-100479.
- Torres, D. N. 1987a. Antecedentes sobre el lobo fino de Juan Fernandez *Arctocephalus philippii* y proyecciones para su estudio. *En* Islas Oceanicas Chilenas: Conocimiento científico y necesidades de investigaciones, pp. 287–317. Ed. by J. C. Castilla. Ediciones Universidad Católica de Chile.
- Torres, D. N. 1987b. Juan Fernandez fur seal, *Arctocephalus philippii*. *In* Status, biology, and ecology of fur seals, pp. 37–41. Ed. by J. P. Croxall and R. L. Gentry. NOAA Technical Report NMFS 51.
- Trillmich, F. 1987. Galapagos fur seal, *Arctocephalus galapagoensis*. *In* Status, biology, and ecology of fur seals, pp. 23–27. Ed. by J. P. Croxall and R. L. Gentry. NOAA Technical Report NMFS 51.
- Trites, A. and Heise, K. 1996a. Marine Mammals of the Alaska Gyre. *In* Mass-balance models of North-eastern Pacific Ecosystems, pp. 25–30. Ed. by D. Pauly and V. Christensen. University of British Columbia, Fisheries Centre Research Reports 4(1).
- Trites, A. and Heise, K. 1996b. Marine Mammals of the Southern Coast of British Columbia. *In* Mass-balance models of North-eastern Pacific Ecosystems, pp. 51–55. Ed. by D. Pauly and V. Christensen. University of British Columbia, Fisheries Centre Research Reports 4(1).
- Ugland, K. I., Joedestael, K. A., Aspholm, P. E., Kroeyer, A. B., and Jakobsen, T. 1993. Fish consumption by invading harp seals off the Norwegian coast in 1987 and 1988. *ICES Journal of Marine Science*, 50: 27–38.
- Van Bree, P. J. H., Collet, A., Desportes, G., Hussenot, E., and Raga, J. A. 1986. Fraser's dolphin, *Lagenodelphis hosei* (Cetacea, Odontoceti), a new species for the fauna of Europe. *Mammalia*, 50: 57–86.
- Vaz-Ferreira, R. and Ponce de Leon, A. 1987. South American fur seal, *Arctocephalus australis*, in Uruguay. *In* Status, biology, and ecology of fur seals, pp. 29–32. Ed. by J. P. Croxall and R. L. Gentry. NOAA Technical Report NMFS 51.
- Wada, Y. 1996. Marine mammals and birds of the Strait of Georgia. *In* Mass-balance models of North-eastern Pacific Ecosystems, pp. 69–73. Ed. by D. Pauly and V. Christensen. University of British Columbia, Fisheries Centre Research Reports 4(1).
- Walker, W. A. and Jones, L. L. 1993. Food habits of northern right whale dolphin, Pacific white-sided dolphin, and northern fur seal caught in the high seas driftnet fisheries of the North Pacific Ocean, 1990. *In* Biology, distribution and stock assessment of species caught in the high seas driftnet fisheries in the North Pacific Ocean, pp. 285–295. Ed. by J. Ito, W. Shaw and R. L. Burgner. INPFC Bulletin 53.
- Walker, W. A., Leatherwood, S., Goodrick, K. R., Perrin, W. F., and Stroud, R. K. 1986. Geographic variation and biology of the Pacific white-sided dolphin, *Lagenorhynchus obliquidens*, in the north-eastern Pacific. *In* Research on Dolphins, pp. 441–465. Ed. by M. M. Bryden and R. Harrison. Clarendon Press, Oxford.
- Weitkamp, L. A., Wissmar, R. C., Simestad, C. A., Fresh, K. L., and Odell, J. G. 1992. Gray whale foraging on ghost shrimp (*Callinassa californiensis*) in littoral sand flats of Puget Sound, USA. *Canadian Journal of Zoology*, 70: 2275–2280.
- Weslawski, J. M., Ryg, M., Smith, T. G., and Oritsland, N. A. 1994. Diet of ringed seals (*Phoca hispida*) in a fjord of West Svalbard. *Arctic*, 47: 109–114.
- Wishner, K., Durbin, E., Durbin, A., Macaulay, M., Winn, H., and Kenney, R. 1988. Copepod patches and right whales in the Great South Channel off New England. *Bulletin of Marine Science*, 43: 825–844.
- Würtz, M. and Marrale, D. 1993. Food of striped dolphin, *Stenella coeruleoalba*, in the Ligurian Sea. *Journal of the Marine Biological Association of the U.K.*, 73: 571–578.
- Würtz, M., Poggi, R., and Clarke, M. R. 1992. Cephalopods from the stomachs of a Risso's dolphin (*Grampus griseus*) from the Mediterranean. *Journal of the Marine Biological Association of the U.K.*, 72: 851–867.