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Estimated Feeding Rate Relationship for Marine Mammals Based on Captive Animal Data

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ESTIMATED FEEDING RATE RELATIONSHIP
FOR MARINE MAMMALS
BASED ON CAPTIVE ANIMAL DATA

by

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ABSTRACT

A feeding rate relationship for active energy expenditure by marine mammals was estimated from data obtained from aquariums and the literature for 115 active, captive pinnipeds and cetaceans (age \geq years). The calculated geometric mean regression line ($r^2 = 86.2\%$) obtained from fitting the food consumption data (expressed as energy consumption) of the captive animals to body mass data was presented

$$\log_{10}E = 2.520 + 0.747(\log_{10}M), \text{ which may also be written as } \mathbf{E} = 331M^{0.75}$$

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INTRODUCTION

For most marine ecosystems, data on feeding rates of marine mammals based on direct observation are not available. There are at least two alternative measurements of food consumption for study of free-ranging animals. Feeding rates may either be estimated from the food consumption rates of captive animals maintained at activity levels and under environmental conditions approximating those of free-ranging animals, or from food consumption rates calculated as a function of a known and measurable biological parameter.

Kleiber and others have described energy use as a power function of body mass for terrestrial mammals over a wide range of body sizes (e.g., Kleiber 1961; Platt and Silvert 1981; Peters 1983; Calder 1984; Schmidt-Nielsen 1984). Most metabolic studies on marine mammals have measured only resting or basal metabolic rates, and few studies have provided data on the energetic costs of the different components of activity in a marine mammal species. If basal metabolism of marine mammals is approximated by use of an allometric relationship (e.g., Kleiber's equation -- Kleiber 1961) which describes energy use as a function of body mass, then food consumption can be estimated when the energy requirements of active, free-ranging marine mammals can be determined in terms of their resting metabolism.

Since data on food consumption by captive animals under active conditions are not available for all marine mammal species of interest, an allometric relationship similar to Kleiber's power function has been assumed (as suggested by Lavigne et al. 1986a). The equation parameters have been determined using data on the diet and the average amount of food fed to active pinnipeds and cetaceans held in zoos and aquariums. The database we

gathered was analyzed both by species groups and pooled to provide a single allometric equation applicable over the entire range of marine mammals.

METHODS

Captive Animal Feeding Rate Database

We have not made use of data in the literature intended for use in basal metabolic studies since these databases are limited to fully adult, resting animals. The database selected for use here consists of active, nonresting animals over a range of ages and activity levels. Information on the feeding rates of captive marine mammals were requested from zoos and aquariums worldwide during 1980 for this study. A preliminary presentation of the data in this study was reported by McAlister (1981). Responses from 11 of these zoos and aquariums provided data on the average daily feeding rate, diet, and environmental water temperature of 82 active, nonreproducing animals, age 4 years or greater, of five pinniped and nine cetacean species. Data were also compiled from Sergeant (1969), Bigg et al (1978), Ashwell-Erickson et al. (1979), Hinga (1979), Ashwell-Erickson (1981), Ashwell-Erickson and Elsner (1981), Spotte and Adams (1981), and Fay (1982) on 33 nonreproducing marine mammals in aquariums and research centers where there were active animals, and information was provided on the feeding rate, diet, and age of the animals.

Table 1 summarizes the data on species, location, sex, age, body mass, average quantity of food consumed daily, and diet for the 115 captive marine mammals in our feeding-rate database. The estimated energy values of their diets, based on the comparative energy equivalents listed in Table 2, are given in Table 1 (however, energy data for food fed

to the captive animals cited in the original reference were used directly and not based on Table 2). The 115 animals ranged in body mass from 29 kg to 4,300 kg. Water temperatures of the pools in which they were maintained ranged from 10°C to 25°C, with most held at or near 20°C.

Daily energy consumption (kcal/d) was calculated from the reported average quantity (kg) of food fed to each animal based on the estimated energy value (kcal/g) of the edible portion of whole specimens (raw, wet mass) for each prey species in its diet. These energy values (Table 2) were either estimated from proximate composition data on the percentages of fat, protein and carbohydrate in the prey species samples using the energy factors for these components cited by Watt and Merrill (1963), or based on published data from heats of combustion of whole specimens. For some prey species, composition data on the energy value of whole, raw specimens were unavailable, and it was necessary to estimate comparative energy values based on caloric data for muscle tissue. These energy values were scaled to the estimated value for whole specimens by multiplying the estimated muscle tissue value by a factor of 1.1. This factor was based on the average ratio of caloric data (Sidwell 1981) for whole fish (capelin, *Mullotus villosus*; herring, *Clupea harengus*; walleye pollock, *Theragra chalcogramma*; and rainbow smelt, *Osmerus mordax*) to that of only muscle tissue of the same fish species. Caloric values from taxonomically related species (genus or family) were used as an approximation for prey species for which energy data were unavailable.

Rates of Food Consumption

Food consumption data from the 115 captive pinnipeds and cetaceans referenced in Table 1 have been used to simulate a feeding rate relationship for free-ranging animals.

Logarithmic (base 10) transformed data on food energy consumption (kcal/d) and body mass (kg) from these captive animals were fitted to a series of equations (sorted by related species groups) similar to the Kleiber relation of the form, $E = aM^b$, where E is energy use in kilocalories per day, M is body mass in kilograms, a is a constant (coefficient) to be determined, and b is the scaling factor (slope) of the fitted line of the relationship. The geometric mean regression line (GMR; Ricker 1984), which accounts for variance in both the independent and dependent variables, was used to fit the data to these allometric relationships. Data for otariids and odontocetes were fitted separately. The pooled database (all pinniped and cetacean species) has been fitted to a single allometric relationship of the same form. The coefficient of determination (r^2) and 95% confidence limits for a and b of each GMR were also calculated.

RESULTS

The GMR ($r^2 = 65.8\%$) obtained from fitting the food consumption data (expressed as energy consumption) of the 39 captive otariids in Table 1 to body mass data was $\log_{10}E = 2.571 + 0.733(\log_{10}M)$. This relationship may also be written as

$$E = 372M^{0.73} \quad (1)$$

The 95% confidence interval for the coefficient of this relationship for otariids was $\log_{10}2.308$ to $\log_{10}833$ (203 to 681). For the slope of the regression equation it was **0.604** to 0.890.

The GMR ($r^2 = 84.5\%$) for the 69 captive odontocetes in Table 1 was $\log_{10}E = 2.502 + 0.751(\log_{10}M)$. This relationship may also be written as

$$E = 317M^{0.75} \quad (2)$$

The 95% confidence interval for the coefficient of the relationship for odontocetes was $\log_{10}2.326$ to $\log_{10}2.677$ (212 to 475). For the slope of the regression equation it was 0.682 to 0.826.

In addition, the entire database was regressed to find a relationship over all marine mammal groups. The GMR ($r^2 = 86.2\%$) obtained from fitting the food consumption data of the 115 captive animals in Table 1 to body mass data was $\log_{10}E = 2.520 + 0.747(\log_{10}M)$ (Figure 1). This relationship may also be written as

$$E = 331M^{0.75} \quad (3)$$

The 95% confidence interval for the coefficient of this relationship was $\log_{10}2.403$ to $\log_{10}2.638$ (253 to 434). For the slope of the regression equation it was 0.697 to 0.801.

DISCUSSION

Captive Animal Feeding Rates

Kleiber (1961) found a relationship between body mass and basal metabolism for terrestrial mammals:

$$E = 7OM^{0.75} \quad (4)$$

Lavigne et al. (1986a) suggest that a similar power relationship is true for marine mammals. They argue that energy use in marine mammals follows that of terrestrial mammals and scales as a 0.75 power.

Our estimates of food consumption by captive marine mammals demonstrated a similar equation form relating food consumption to body mass of marine mammals. The rate at which an animal expends energy in a free-ranging state will depend on many factors besides basal metabolism. These factors may include age, activity levels, reproductive state, and environmental conditions.

Reliable feeding or energy data for large active cetaceans are very limited. The best estimates of energy use for baleen whales are probably those estimated for gray whales, *Eschrichtius robustus*, by Sumich (1983) (on the basis of observed respiration) and Wahrenbrock et al. (-1974) (feeding studies and observed respiration in one gray whale, Gigi II). Because of reduced activity levels for larger animals due to limited aquarium size and differences in food composition between aquarium feeding and wild feeding, the feeding rates of captive animals may not correctly estimate feeding rates of free-ranging animals (Innes et al. 1987). However, even captive cetaceans (e.g., killer whales, *Orcinus orca*) may

be very active when performing in public aquariums. While limitations on activity may generally reduce food requirements, there is a balancing tendency to overfeed captive marine mammals (Innes et al. 1987). Although some uncertainty remains, the limited data on free-ranging energetics for marine mammals (Nagy 1987) suggest that captive animal feeding rates are a good approximation to actual wild food consumption rates.

Estimated Feeding Rates

The calculated values for the slope of the geometric mean regression line for otariids (Equation 1; slope = 0.73) and odontocetes (Equation 2; slope = 0.75) were close to the theoretical value of 0.75 suggested by Lavigne et al. (1986a, 1986b). Therefore, the calculated coefficient values of the fitted equations for otariids (Equation 1; coefficient = 372) and odontocetes (Equation 2; coefficient = 317) should be close to the expected values for relationships with a 0.75 slope.

Feeding rate data are limited for marine mammal groups other than otariids and odontocetes. The data for the three phocid seals in Table 1 in terms of kilocalories per day were approximated as body mass (kg) to the 0.75 power in order to estimate the coefficient of the relationship. These estimated coefficient values for phocid seals (mean = 216) were averaged with values from other phocid seals reported by Innes et al. (1987) to yield an estimated feeding rate coefficient value of 200 (Table 3). Values for the walrus (*Odobenus rosmarus*), baleen whales (order Mysticeti), and the sea otter (*Enhydra lutris*) were based on data in the literature (Wahrenbrock et al. 1974; Costa 1978, 1982; Fay 1982; Sumich 1983). The set of feeding rate relationships and the subset of the database used for each taxonomic group are shown in Table 3.

Use of Mean Body Mass and Pooled Ages

Juvenile marine mammals consume at a higher rate per body mass than do adult marine mammals. Innes et al. (1987) have reported juvenile consumption rates for otariid and phocid seals of from 1.4 to 1.8 greater than those of adult seals. Many marine mammals continue to grow through much of their life span, although more slowly after reaching maturity.

Since the feeding rates of Table 3 (and also Equation 4) are nonlinear, use of a mean value for the biomass of a given species will slightly overestimate energy consumption. The inclusion in the biomass, without correction, of juveniles (which consume at a higher rate than adults) will result in an energy consumption value determined from the feeding rates in Table 3 that slightly underestimate the actual energy consumption. Since these two errors are largely compensating (the net result is small in comparison with uncertainties in both the population size and diet data), no correction has been made.

Effects of Energy Value of Diet

The calculated values of the coefficients in Table 3 depend directly on the estimated energy content of the food fed to the captive animals used in the analyses to estimate the feeding rate coefficients. The estimated energy value of the average diet in the captive animal database (Table 1) for otariids and odontocetes was 2.0 kcal/g. The content of fat in the flesh and other parts of the body of some fish species (e.g., Pacific herring, *Clupea harengus pallasii*; capelin; Atka mackerel, *Pleurogrammus monopterygius*, rockfishes, Scorpaenidae; and flatfishes, Pleuronectiformes) changes significantly during the year between spawning (summer) and foraging (winter) periods (Kizevetter 1971; Jangaard 1974; Bigg et

al. 1978). Fat content also varies by age, body mass, or stage of migration of the fish (e.g., salmon, *Oncorhynchus* spp.; sablefish, *Anoplqpomu fimbria*) (Kizevetter 1971). For many other fishes (e.g., walleye pollock; other gadids; sculpins, Cottidae) the fat content of the body does not vary appreciably during the year (Kizevetter 1971).

The data in Table 1 represent average annual food consumption data provided by the zoos and aquaria maintaining the animals. Energy consumption calculated 'directly from daily food consumption data, accounting for seasonal differences in the energy value of prey species (ideally measured by calorimetry studies on representative samples of the food fed each day), would presumably affect the value of the estimates of energy consumption for the captive animals referenced in Table 1. Since both the food consumption and energy content data used here are annual averages, the level of error in calculations of energy consumption is, most likely, minimal

Temperature Acclimatization

The amount of food eaten by captive dolphins '(e.g., the bottlenose dolphin, *Tursiops truncatus*) has been observed to vary with the water temperature of the tank in which the animals were kept and with the activity of each individual (Manton 1976; Abel 1986). Studies of northern fur seals, *Callorhinus ursinus*, kept on the Pribilof Islands and in San Diego (Kooyman et al. 1976) indicated that metabolic rates of acclimated animals may vary depending on tank temperatures. Change in metabolic rates appeared to be independent of the thermoneutral zone. Gunther (1975) and Economos (1979) have discussed acclimatization (change in the value of the exponent of metabolic rates with environmental temperature) in dogs and humans. If the metabolic rates of captive animals change as a result of a sustained

ambient temperature change, then the difference between the water temperature of the aquariums and the ambient sea surface temperature should be considered when determining how the energy assimilation measured at the aquariums differs from natural conditions.

Although acclimatization and metabolic adjustment may occur (at least under some conditions for some marine mammals), the data were inadequate to support a temperature correction for all species and temperature ranges, and no acclimatization factor has been developed in this study. If acclimatization effects should be found to hold generally for marine mammals kept at temperatures higher than natural, the result of using feeding data from acclimated marine-mammals could result in an underestimation of total annual food consumption by free-ranging marine mammals.

Metabolic Rates Related to Activity

Several authors have compared the energy use of active animals to the basal metabolism of marine mammals. Lavigne (1982) quotes estimates by Farlow (1976) that give ratios of actual energy use to resting metabolism for marine mammals ranging from 2.1 to 2.7. In a study of the California sea lion, *Zalophur californianus*, Feldkamp (1985) reported the energy required for extended swimming effort to be 2.5 times the resting metabolic rate. Innes et al. (1987) reported values for active metabolic rates based on captive feeding rates of marine mammals ranging from about twice the value calculated with Kleiber's basal metabolic relationship (Equation 4) for phocid seals to over four times the value from Equation 4 for otariid seals. Innes suggests that one reason for the difference in metabolic rates between phocid and otariid seals may be higher activity in the otariid seals.

Nagy (1987) quoted data from Costa et al. (1985) on direct measurements of “field metabolic rates” (total energy expended by a wild animal during the course of a day; similar to “active metabolism,” as defined here) for four individuals of three pinniped species (the northern fur seal; the Antarctic fur seal, *Arctocephalus* gazelle; and the California sea lion) using doubly-labeled isotopic water experiments. Although data of this type reported by Costa et al. (1985) and Nagy (1987) and in Gentry and Kooyman (1986) are still too few to be definitive, they suggest that free-ranging active pinnipeds may have active metabolic rates about three times their resting metabolic rates as determined using the Kleiber equation. Eventually, doubly-labeled isotopic water experiments should provide enough data from free-ranging animals to replace the present reliance on captive animals. The activity values derived here agree with previous published estimates, although our values for otariids and odontocetes are somewhat higher.

On the assumption that the standard mammalian equation for resting metabolism (Equation 4) also represents basal maintenance metabolism for marine mammals (at least within species groupings (Lavigne et al. 1986a)), the results derived from Equations 1-3 and the feeding rates in Table 3 can be interpreted as providing an estimate of active energy use compared to basal metabolism. The ratio of the coefficients of the feeding rates based on a 0.75 exponent (Table 3) to the resting metabolic level then provides an estimate of activity for each group. These estimated activity ratios (basal metabolism = 1.0) are 5.3 for otariid seals, 2.9 for phocid seals, 4.5 for toothed whales, and 2.7 for baleen whales; Fay (1982) and Costa (1982) have previously reported values for the walrus (5.4) and sea otter (8.0), respectively.

The ratio of energy use observed for active marine mammals to that expected for resting animals of equivalent size provided estimates of average metabolism ranging from approximately five times that of resting animals for smaller pinnipeds (50 kg) to approximately twice the resting rate for larger cetaceans (10,000 kg).

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Table I.--Species, location, sex, age, body mass, daily food intake, diet type, and estimated energy value of the diet of the captive marine mammals referenced in this study.

Species	Sex	Age (yr)	Body mass (kg)	Daily food intake (kg)	Diet type ^a	Estimated energy value of diet (kcal/g) ^b	Site ^c
Pinnipeds							
<i>Otaria flavescens</i>	Male	8	80	8.0	1	1.61	1
<i>Otaria fravescens</i>	Female	8	60	8.0	1	1.61	1
<i>Otaria flavescens</i>	Female	8	60	8.0	1	1.61	1
<i>Zalophus californianus</i>	Male	18	113	5.4	2	1.55	2
<i>Zalophus californianus</i>	Female	4	79	4.5	2	1.55	2
<i>Zalophus californianus</i>	Female	4	79	4.5	2	1.55	2
<i>Zalophus californianus</i>	Female	6	68	3.6	2	1.55	2
<i>Zalophus californianus</i>	Female	6	79	4.5	2	1.55	2
<i>Zalophus californianus</i>	Female	15	68	3.6	2	1.55	2
<i>Zalophus californianus</i>	Female	18	91	5.0	2	1.55	2
<i>Zalophus californianus</i>	Female	4	54	3.2	3	2.11	3
<i>Zalophus californianus</i>	Female	11	77	3.2	3	2.11	3
<i>Zalophus californianus</i>	Female	17	64	3.2	3	2.11	3
<i>Zalophus californianus</i>	Female	22	68	3.2	3	2.11	3
<i>Zalophus californianus</i>	Female	10	118	4.5	4	1.85	4
<i>Zalophus californianus</i>	Female	>3	91	4.6	4	1.85	4
<i>Zalophus californianus</i>	Female	>3	91	4.6	4	1.85	4
<i>Eumetopias jubatus</i>		17	750	22.5	5	2.13	5
<i>Eumetopias jubatus</i>	Male	>10	1,000	25.0	6	2.64	6
<i>Callorhinus ursinus</i>	Female	>5	37	2.8	7	2.56	7
<i>Callorhinus ursinus</i>	Female	>5	38	3.2	7	2.56	7
<i>Callorhinus ursinus</i>	Female	>5	41	2.9	7	2.56	7
<i>Callorhinus ursinus</i>	Female	>5	46	3.0	7	2.56	7
<i>Callorhinus ursinus</i>	Female	>5	47	2.5	7	2.56	7
<i>Callorhinus ursinus</i>	Female	>5	47	3.1	7	2.56	7
<i>Callorhinus ursinus</i>	Female	>5	48	2.7	7	2.56	7
<i>Callorhinus ursinus</i>	Female	>5	45	3.0	8	2.00	8
<i>Callorhinus ursinus</i>	Female	>5	41	3.1	8	2.00	8
<i>Callorhinus ursinus</i>	Female	>5	29	2.5	8	2.00	8
<i>Arctocephalus pusillus</i>	Male	4	60	3.5	9	1.70	9

Table 1 --Continued.

Species	Sex	Age (yr)	Body mass (kg)	Daily food intake (kg)	Diet type ^a	Estimated energy value of diet (kcal/g) ^b	Site ^c
<i>Arctocephalus pusillus</i>	Female	4	45	3.5	9	1.70	9
<i>Arctocephalus pusillus</i>	Male	7	165	5.0	10	1.95	10
<i>Arctocephalus pusillus</i>	Male	>3	115	5.0	10	1.95	10
<i>Arctocephalus pusillus</i>	Female	6	55	6.0	11	2.60	10
<i>Arctocephalus pusillus</i>	Female	>10	90	4.0	10	1.95	10
<i>Arctocephalus pusillus</i>	Female	>10	90	4.0	10	1.95	10
<i>Arctocephalus pusillus</i>	Male	4	60	5.7	1	1.61	1
<i>Arctocephalus pusillus</i>	Female	4	45	5.7	1	1.61	1
<i>Arctocephalus pusillus</i>	Female	4	50	5.7	1	1.61	11
<i>Phoca vitulina</i>	Female	4	50	2.4	8	1.91	11
<i>Phoca largha</i>	Male	5-9	74	2.3	12	2.35 ^d	12
<i>Phoca largha</i>	Female	5-9	82	2.2	12	2.35 ^d	12
<i>Odobenus rosmarus</i> ^e	Male	4	750	36.2	13	1.36	13
<i>Odobenus rosmarus</i> ^e	Male	7	700	38.5	13	1.36	
<i>Odobenus rosmarus</i> ^e	Female	4	430	22.6	13	1.36	13
<i>Odobenus rosmarus</i> ^e	Female	4-5	400	25.0	8	1.90	14
Cetaceans							
<i>Steno bredanensis</i>	Male	7-10	104	5.0	14	1.65	15
<i>Tursiops truncatus</i>	Male	15	170	7.9	15	1.66	2
<i>Tursiops truncatus</i>	Male	15	181	7.9	15	1.66	2
<i>Tursiops truncatus</i>	Female	4	147	6.8	15	1.66	2
<i>Tursiops truncatus</i>	Female	8	159	6.8	15	1.66	2
<i>Tursiops truncatus</i>	Female	9	159	6.8	15	1.66	2
<i>Tursiops truncatus</i>	Female	19	170	7.9	15	1.66	2
<i>Tursiops truncatus</i>	Female	19	181	7.9	15	1.66	2
<i>Tursiops truncatus</i>	Female	26	181	7.9	15	1.66	2
<i>Tursiops truncatus</i>	Female	31	181	7.9	15	1.66	2
<i>Tursiops truncatus</i>	Female	34	204	9.1	15	1.66	2
<i>Tursiops truncatus</i>	Female	36	170	7.9	15	1.66	2
<i>Tursiops truncatus</i>		15	213	9.1	16	1.20	15

Table 1 --Continued.

Species	Sex	Age (yr)	Body mass (kg)	Daily food intake (kg)	Diet type ^a	Estimated energy value of diet (kcal/g) ^b	Site ^c
<i>Tursiops truncatus</i>		20	272	11.3	16	1.20	15
<i>Tursiops truncatus</i>	Male	17	160	7.0	9	1.70	9
<i>Tursiops truncatus</i>	Male	25	200	7.0	9	1.70	9
<i>Tursiops truncatus</i>	Female	20	230	7.0	9	1.70	9
<i>Tursiops truncatus</i>	Male	>5	181	7.3	17	1.98	3
<i>Tursiops truncatus</i>	Male	>8	204	7.3	17	1.98	3
<i>Tursiops truncatus</i>	Female	5	136	7.3	17	1.98	3
<i>Tursiops truncatus</i>	Female	>5	170	7.3	17	1.98	3
<i>Tursiops truncatus</i>	Female	>5	170	7.3	17	1.98	3
<i>Tursiops truncatus</i>	Male	-	164	10.0	18	2.31	7
<i>Tursiops truncatus</i>	Female		168	9.2	18	2.31	7
<i>Tursiops truncatus</i>			177	7.3	19	1.92	16
<i>Tursiops truncatus</i>	Male	9	136	9.1	20	1.97	17
<i>Tursiops truncatus</i>	Male	9	142	6.4	20	1.97	17
<i>Tursiops truncatus</i>	Male	9	142	6.8	20	1.97	17
<i>Tursiops truncatus</i>	Male	9	159	6.8	20	1.97	17
<i>Tursiops truncatus</i>	Male	9	159	6.8	20	1.97	17
<i>Tursiops truncatus</i>	Male	10	147	6.4	20	1.97	17
<i>Tursiops truncatus</i>	Male	10	147	8.2	20	1.97	17
<i>Tursiops truncatus</i>	Male	13	147	6.4	20	1.97	17
<i>Tursiops truncatus</i>	Male	13	147	7.7	20	1.97	17
<i>Tursiops truncatus</i>	Male	15	210	9.1	20	1.97	17
<i>Tursiops truncatus</i>	Female	9	136	7.3	20	1.97	17
<i>Tursiops truncatus</i>	Female	9	136	9.1	20	1.97	17
<i>Tursiops truncatus</i>	Female	10	142	6.4	20	1.97	17
<i>Tursiops truncatus</i>	Female	11	181	8.2	20	1.97	17
<i>Tursiops truncatus</i>	Female	11	181	8.2	20	1.97	17
<i>Tursiops truncatus</i>	Female	15	193	8.2	20	1.97	17
<i>Tursiops truncatus</i>	Female	27	204	10.0	20	1.97	17
<i>Stenella longirostris</i>		>10	61	5.0	16	1.20	15
<i>Lagenorhynchus obliquidens</i>	Female	13	147	7.3	3	2.11	3
<i>Lagenorhynchus obliquidens</i>	Female	16	147	7.3	3	2.11	3
<i>Lagenorhynchus obliquidens</i> ^f	Male		90	6.8	21	2.41	18

Table 1 --Continued.

Species	Sex	Age (yr)	Body mass (kg)	Daily food intake (kg)	Diet type ^a	Estimated energy value of diet (kcal/g) ^b	Site ^c
<i>Lagenorhynchus obliquidens</i>	Female	>9	93	6.8	22	2.07	18
<i>Lagenorhynchus obliquidens</i> ^f	Female		84	6.8	21	2.41	18
<i>Grampus griseus</i>		>5	300	13.5	23	1.55	5
<i>Peponocephala electra</i>	Female	8-10	154	5.4	24	2.10	15
<i>Pseudorca crassidens</i>	Female	>10	400	16.0	5	2.13	5
<i>Pseudorca crassidens</i>	Male	13	531	22.6	25	1.38	15
<i>Pseudorca crassidens</i>	Female	20	499	22.6	25	1.38	15
<i>Orcinus orca</i>	Male		4,300	66.0	26	2.05	3
<i>Orcinus orca</i>	Female	14	4,193	63.5	3	2.11	3
<i>Orcinus orca</i>	Male	4	1,820	52.5	27	2.53	19
<i>Orcinus orca</i>	Female	13	3,640	51.0	S 28	2.35	19
				91.0	w 29	2.37	
<i>Orcinus orca</i>	Male	11	2,950	57.0	s 30	2.39	19
				91.0	w 29	2.37	
<i>Orcinus orca</i> ^h	Male	13	3,630	63.5	31	1.87	18
<i>Orcinus orca</i> ^h	Female	18	3,630	63.5	31	1.87	18
<i>Orcinus orca</i>	Male	12	4,250	74.0	32	2.07	20
<i>Phocoenoides dalli</i>			120	15.0	6	2.64	16
<i>Delphinapterus leucas</i>	Male	-	955	18.2	33	2.56	7
<i>Delphinapterus leucas</i>	Female		480	11.4	34	2.59	7
<i>Delphinapterus leucas</i> ^g	Male	12	1,136	16.0	35	2.18	18
<i>Delphinapterus leucas</i>	Female,	5	227	18.1	8	2.17	18
<i>Delphinapterus leucas</i>	Female	8	454	18.1	8	2.17	18
<i>Delphinapterus leucas</i> ^g	Female	8	682	10.0	35	2.18	18
<i>Delphinapterus leucas</i> ^f	-		300	23.0	36	2.13	18

S = summer

w = winter

Table 1.--Continued.

Average types of diet (1) 100% blue mackerel scad; (2) 20% blue fish, 20% smelt, 20% mackerel (Scombridae), 20% blue runner, and 20% squid; (3) 33% Atlantic herring, 33% capelin, and 33% Spanish mackerel; (4) 33% Atlantic herring, 33% capelin, and 33% smelt; (5) 50% chub mackerel and 50% blue mackerel scad; (6) 100% chub mackerel; (7) 50% Atlantic herring and 50% Atlantic mackerel; (8) 100% Pacific herring; (9) 50% whiting, 25% Atlantic herring, and 25% sprat; (10) 100% mullet; (11) 100% yellowtail amberjack; (12) 100% Atlantic mackerel; (13) 50% clams (without shells) and 50% bonito; (14) 50% smelt and 50% herring (Clupeidae); (15) 25% blue fish, 25% smelt, 25% mackerel (Scombridae), and 25% blue runner; (16) 100% smelt; (17) 25% Atlantic herring, 25% capelin, 25% Spanish mackerel, and 25% blue runner; (18) 33% Atlantic herring, 33% capelin, and 33% Atlantic mackerel; (19) 50% smelt and 50% chub mackerel; (20) 33% Atlantic herring, 33% capelin, and 33% blue runner; (21) 50% Pacific herring and 50% chub mackerel; (22) 90% Pacific herring and 10% squid; (23) 50% squid, 25% mackerel (Scombridae), and 25% scad (Carangidae); (24) 100% herring (Clupeidae); (25) 80% smelt and 20% herring (Clupeidae); (26) 60% mackerel (Scombridae), 10% Atlantic herring, 10% smelt, 10% capelin, and 10% blue runner; (27) 100% Atlantic herring; (28) 75% Atlantic herring and 25% capelin; (29) 50% Atlantic herring, 25% capelin, and 25% Atlantic mackerel; (30) 75% Atlantic herring, 20% capelin, and 5% Atlantic mackerel; (31) 70% Pacific herring, 10% walleye pollock, 10% sole, and 10% squid; (32) 90% Pacific herring, 3% smelt, 3% cod, and 4% squid; (33) 55% Atlantic mackerel and 45% Atlantic herring; (34) 95% Atlantic mackerel and 5% Atlantic herring; (35) 90% Pacific herring and 10% mackerel (Scombridae); (36) 50% Pacific herring and 50% salmon.

^b Calculated using the estimated comparative energy values for whole specimens in Table 2 weighted by the percentage composition of the diet. However, energy values of Pacific herring and other food given to the captive animals cited in the literature were used directly without consideration of values in Table 2.

^c Data were obtained from the site of captivity during 1980 for use in this study, unless otherwise indicated. The locations of captivity were: (1) Toba Aquarium, Toba 3-3-6. Toba City, Mie Prefecture, Japan; (2) Ocean World, Inc., 1701 Southeast 17th St, Fort Lauderdale, FL 33316; (3) Miami Seaquarium, 4400 Rickenbacker Causeway, Miami, FL 33149; (4) Oklahoma City Zoo, 2101 N.E. 50th St, Oklahoma City, OK 73111; (5) Enoshima Aquarium, 17-25, Katasekaigan 2 chome, Fujisawa City, Kanagawa Prefecture, 251 Japan; (6) Shimonoseki Municipal Aquarium, Sotoura Chofucho Shimonoseki City, Yamaguchi Prefecture, Japan; (7) Mystic Marinelife Aquarium, Mystic, CN [data from Hinga (1979) and Spotte and Adams (1981)]; (8) Dep. of Fisheries and Oceans, Pacific Biological Station, Nanaimo, B.C. V9R 5K6 [data from Bigg et al. (1978)]; (9) Kolmardens Djurpark, 618 00 Kolmarden, Sweden; (10) Taronga Zoo, Sydney, Australia; (11) Institute of Arctic Biology Animal Facility, University of Alaska, Fairbanks, AK 99701 [data from Ashwell-Erickson (1981) and Ashwell-Erickson and Elsner (1981)]; (12) School of Hygiene and Public Health Animal Facility, John Hopkins University, Baltimore, MD [data from Ashwell-Erickson et al. (1979)]; (13) Marineland of the Pacific, Palos Verdes, CA [data from Brown and Asper (1966) and Fay (1982)]; (14) Zoologisk Have, Copenhagen, Denmark [data from Reventlow (1951) and Fay (1982)]; (15) Sea Life Park, Makapuu Point, Waimanalo, HI 96795; (16) Marine Sciences Division, U.S. Naval Missile Center, Pt. Mugu, California [data from Ridgway (1966) and Sergeant (1969)]; (17) Marineland Research Laboratory, Route 1, Box 122, St. Augustine, FL 32084; (18) Vancouver Public Aquarium, P.O. Box 3232, Vancouver, B.C. V6B 3X8; (19) Marineland and Game Farm, Niagara Falls, Ontario [data from Hinga (1979)]; (20) Sealand, Victoria, B.C. [data from Hinga (1979)].

^d The energy value for muscle tissue was used because the seal was fed gutted fish.

^e Data from Fay (1982).

Table 1--Continued.

^f Data from Sergeant (1969).

^g Data from Hinga (1979).

^h Hinga (1979) also presents data from an earlier year, presumably for the same animal, which was not used.

Table 2.--Estimated comparative energy values (wet mass) for raw, whole prey species fed to the captive animals referenced in this study.

Prey species	Energy value (kcal/g) ^a	Analysis and tissue ^b	Data sources ^c	Estimated comparative energy value (Kcal/g) ^d
Fishes				
Yellowtail amberjack (<i>Seriola quinqueradiata</i>)	2.36	P, muscle	1, 2	2.60
Bluefish (<i>Pomatomus saltatrix</i>)	1.47	P, muscle	2, 3	1.62
Capelin (<i>Mallotus villosus</i>)	1.81	P, whole	2, 4, 5	1.81
Cod (<i>Gadus</i> spp.)	1.10	P, muscle	1, 2	1.21
Atlantic herring (<i>Clupea harengus harengus</i>)	2.53	P, whole	2	2.53
Pacific herring (<i>Clupea harengus pallasii</i>)	2.17	P, whole	2, 5, 6, 7	2.17
Herring (Clupeidae) ^e	2.10	P, whole	2	2.10
Atlantic mackerel (<i>Scomber scombrus</i>)	2.35	P, muscle	2, 8	2.59
Chub mackerel (<i>Scomber japonicus</i>)	2.40	P, muscle	1	2.64
Spanish mackerel (<i>Scomberomorus maculatus</i>)	1.82	P, muscle	2, 3, 5	2.00
Mackerel (Scombridae)	2.04	P, muscle	2	2.24
Mullet (Mugilidae) ^f	1.95	P, whole	9	1.95
Walleye pollock (<i>Theragra chalcogramma</i>)	1.25	C, P, R, whole	1, 2, 10, 11, 12	1.25
Blue runner (<i>Caranx crysos</i>)	1.42	P, muscle	2	1.56
Salmon (Salmonidae) ^g	1.90	P, muscle	1, 2	2.09
Blue mackerel scad (<i>Decapterus maruadsi</i>) ^h	1.46	P, muscle	1	1.61
Scad (Carangidae) ⁱ	1.52	P, muscle	1, 2	1.67
Smelt (Osmeridae) ^j	1.20	P, whole	2, 13	1.20
Sole (Pleuronectidae) ^k	1.14	P, whole	2	1.14
Sprat (<i>Sprattus sprattus</i>)	1.81	P, whole	2	1.81
Whiting (Gadidae) ^l	1.12	P, muscle	2	1.23

Table 2.--Continued.

Prey species	Energy value (kcal/g) ^a	Analysis and tissue ^b	Data sources ^c	Estimated comparative energy value (kcal/g) ^d
Invertebrates				
Squid	1.14	C, P, whole	2, 9, 14, 15, 16	1.14

The values given in column 1 represent the average of range values obtained from the data in the cited references. Values based on proximate-composition data, including estimates calculated from relative proportions of total body mass represented by different body parts, were calculated with the following energy factors (representing heats of combustion) derived from Watt and Merrill (1963): 9.50, 5.65, and 4.20 kcal/g respectively for fat, protein, and carbohydrate.

^b Analysis: C = bomb calorimetry combustion value; P = proximate composition data averaged (to the extent possible) over the seasonal range of values for the percentage of protein, fat and carbohydrate in the tissue sample; R = value estimated from data on the relative proportions of body parts and their respective energy value based on proximate composition data Tissue: muscle = raw flesh material only; whole = raw material from entire specimen.

^c Data sources: (1) Kizevetter 1971; (2) Sidwell 1981; (3) Gooch et al. 1987; (4) Jangaard 1974; (5) Krxynowek and Murphy 1987; (6) McBride et al. 1959; (7) Bigg et al. 1978; (8) Leu et al. 1981; (9) Vlieg 1984a; (10) Kizevetter et al. 1965; (11) Miller 1978; (12) Ashwell-Erickson and Elsner 1981; (13) Geraci 1975; (14) Croxall and Prince 1982; (15) Vlieg 1984b; (16) Perez and Bigg 1986.

^d Where data were not available for whole fish, the comparative energy value of edible whole specimens was estimated at 1.1 times the muscle tissue value. This factor was estimated based on data for capelin, herring, walleye pollock, and smelt in Sidwell (1981).

^e Includes round herring species.

^f Based on data for striped mullet, *Mugil cephalus*, and yellow-eyed mullet, *Aldrichetta forsteri*.

^g Average of values for chinook salmon, *Oncorhynchus tshawytscha*, chum salmon, *O. keta*, coho salmon, *O. kisutch*, pink salmon, *O. gorbuscha*, and sockeye salmon, *O. nerka*.

^h Based on *data* for *Decapterus* spp.

ⁱ Average of *values* for species of four genera: *Caranx*, *Decapterus*, *Selar*, and *Trachurus*.

Table 2.--Continued.

^j Based on the energy value for rainbow smelt, *Osmerus mordax*.

^k Average of **values** for Dover sole, *Microstomus pacificus*, *petrale* sole, *Eopsetta jordani*, and rex sole, *Glyptocephalus zachirus*.

^l Energy value data were unavailable for European whiting, *Merlangius merlangus*, which may have been fed to some of the seals and dolphins listed in Table 1. The value given above represents the average of energy values for the following gadoid species found in the North Sea: cusk, *Brosme brosme*; Atlantic cod, *Gadus morhua*; haddock, *Melanogrammus aeglefinus*; European hake, *Merluccius merluccius*; European *ling*, *Molva molva*; pollack, *Pollachius pollachius*, Atlantic pollock (saithe), *Pollachius virens*; and blue whiting, *Micromesistius poutassou*.

Table 3.--Estimated coefficients (*a*) for the feeding rates of marine mammals approximated to the allometric relationship, $E=aM^{0.75}$, where E is energy consumption (kcal/d) and M is body mass (kg).

Taxonomic group	Estimated coefficient <i>a</i>	Estimation method and references
Otariid seals	372	Geometric mean regression line fit of logarithmic (base 10) transformed values derived from data in Table 1
Phocid seals	200	Average of values from: 1) the feeding rate equation coefficients (weighted by sample size) in Innes et al. (1987) using average body mass of the species in this study, and 2) data in Table 1
walrus	380	Reported by Fay (1982)
Baleen Whales	192	Average of oxygen consumption data from Wahrenbrock et al. (1974) and Sumich (1983)
Toothed Whales	317	Geometric mean regression line fit of logarithmic (base 10) transformed values derived from data in Table 1
Sea Otter	520	Based on data in Costa (1978, 1982)

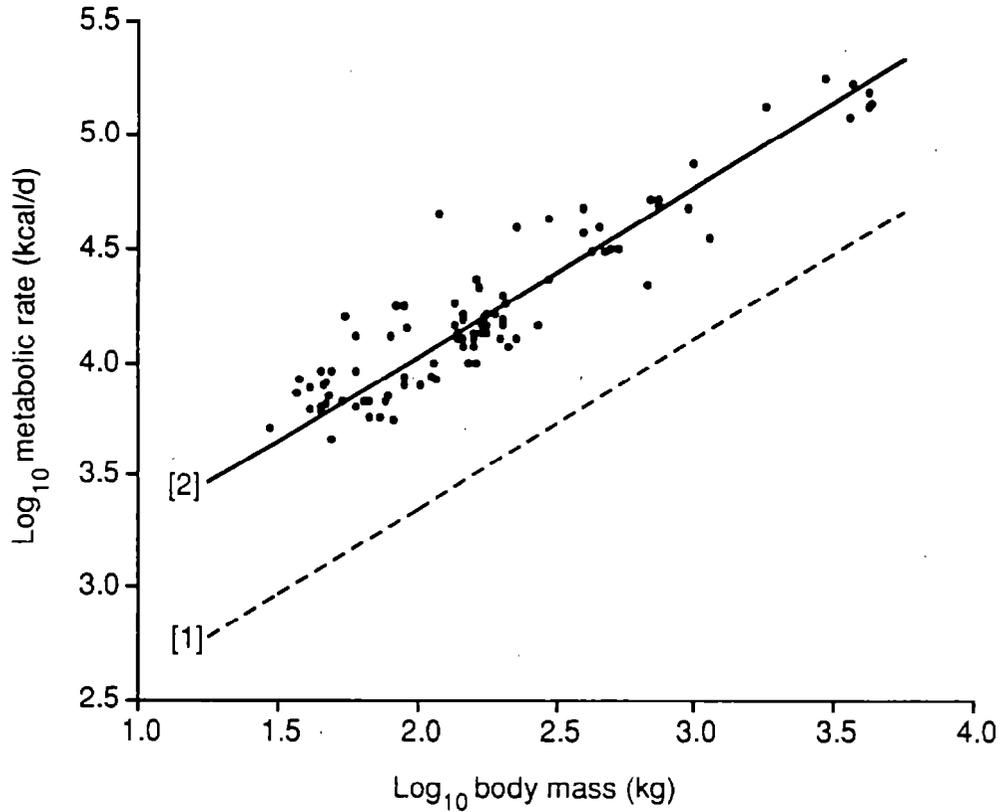


Figure 1.--Energy consumption (E; kcal/d) of marine mammals as a function of body mass (M, kg): 1) The resting metabolic rate predicted by the equation, $\log_{10}E = 1.85 + 0.75(\log_{10}M)$, derived by Kleiber (1961) for terrestrial mammals is indicated by the dashed line; and 2) Energy consumption by active marine mammals calculated with the equation, $\log_{10}E = 2.52 + 0.75(\log_{10}M)$, derived by geometric mean regression on the data in Table 1 is indicated by the solid line. The closed circles indicate the estimated energy consumption of the 115 captive pinnipeds and cetaceans listed in Table 1.