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Estimating mean body masses of marine mammals from maximum body lengths

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Abstract: Generalized survival models were applied to growth curves published for 17 species of cetaceans (5 mysticetes, 12 odontocetes) and 13 species of pinnipeds (1 odobenid, 4 otariids, 8 phocids). The mean mass of all individuals in the population was calculated and plotted against the maximum body length reported for each species. The data showed strong linearity (on logarithmic scales), with three distinct clusters of points corresponding to the mysticetes (baleen whales), odontocetes (toothed whales), and pinnipeds (seals, sea lions, and walruses). Exceptions to this pattern were the sperm whales, which appeared to be more closely related to the mysticetes than to the odontocetes. Regression equations were applied to the maximum lengths reported for 76 species of marine mammals without published growth curves. Estimates of mean body mass were thus derived for 106 living species of marine mammals.

Résumé : Des modèles généralisés de survie ont été appliqués aux courbes de croissance publiées de 17 espèces de cétacés (5 mysticètes, 12 odontocètes) et 13 espèces de pinnipèdes (1 odobénidé, 4 otariidés, 8 phocidés). La masse moyenne de tous les individus de la population a été calculée et confrontée, dans un diagramme, à la longueur corporelle maximale de chaque espèce. Les diagrammes ont mis en lumière une forte linéarité (sur des échelles logarithmiques) et regroupé trois nuages distincts de points correspondant aux mysticètes (baleines à fanons), aux odontocètes (baleines à dents) et aux pinnipèdes (phoques, otaries et morses). Les cachalots font exception dans cette classification, puisqu'ils se rapprochent plus des mysticètes que des odontocètes. Des équations de régression ont permis de déterminer la masse moyenne de 76 espèces de mammifères marins à longueur maximale connue, mais dont les courbes de croissance n'ont jamais été publiées. Nous avons donc pu obtenir l'estimation de la masse moyenne chez 106 espèces vivantes de mammifères marins.
[Traduit par la Rédaction]

Introduction

Knowing the amount of living matter is fundamental to assessing energy fluxes within ecosystems. One of the key parameters required for estimating the amount of food eaten by marine mammals occupying the top trophic layers of the world's oceans is biomass. The simplest way to estimate the total food consumption of a population is to multiply the mean individual body mass by the total population size and relative ration (e.g., Trites et al. 1997). Mean body masses can, in turn, be calculated from life tables and growth curves.

Unfortunately, mean masses cannot be directly calculated for many marine mammals because growth curves have only been constructed for about 30 of the living species, and life tables are available for even fewer. In a number of species, little more is known about their morphology than a few measurements of body length.

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The following outlines a method for estimating the mean masses of marine mammal populations from measurements of maximum body length, and is based upon the strong correlations that exist among growth rate, survival, longevity, and maximum length. We regress maximum length against mean mass for 30 species with known growth curves (13 pinnipeds and 17 cetaceans), then apply these equations to the longest body lengths reported for an additional 76 species. Estimates of mean mass are thus derived for 106 living species of marine mammals, and the relationships between growth rate, survival, longevity, and maximum length are briefly explored in terms of the energy needs and functional evolution of marine mammals.

Methods

The functional relationship between the maximum body length of a given species, L_{max}, and the mean mass of all individuals in the population, $\overline{M}$, is expressed as

$$[1] \qquad \overline{M} = a\,L_{max}^{b}$$

Maximum body lengths were assumed to be the longest recorded from a given population with known growth curves (Appendix). Maximum lengths of species without growth curves were taken primarily from Klinowska (1991), McLaren (1993), and Jefferson et al. (1993).

Mean mass equalled the total biomass of all age-classes divided by the total population size:

$$[2] \qquad \overline{M} = \frac{\sum_{x=0}^{n} N_x M_x}{\sum_{x=0}^{n} N_x}$$

Table 1. Parameters for the general survival models (eq. 3) of male and female pinnipeds (P_1 and P_2) and cetaceans (C_1 and C_2). Model P_1 describes the survival of male pinnipeds with strong sexual dimorphism (elephant seals, sea lions, and fur seals); model P_2 was applied to all female pinnipeds and all non-dimorphic male pinnipeds.

Model variable	Northern fur seals		Humans/cetaceans	
	F	M	F	M
a_1	14.343	8.857	21.274	23.969
a_2	0.171	2.419	0.420	0.383
a_3	0.012	0.044	0.011	0.016
b_1	10.259	11.821	78.936	73.142
b_2	6.688	4.398	6.766	6.252
Ω	19	13	81	78
Model	P_2	P_1	C_2	C_1

where M_x is the mean mass of an individual aged x years, N_x is the number of individuals of age x alive, and n is the maximum age attained. N_x can be replaced in eq. 2 with life-table values of l_x (the probability of an individual surviving to age x), given that these two variables are proportional to each other.

The functional relationship between maximum length and mean mass of all individuals in a population (eq. 1) was thus derived from the known growth curves of 30 species, then used to predict the mean masses of an additional 76 species of marine mammals from their maximum recorded body lengths.

Life tables

Age-specific survival rates were calculated using Siler's (1979) model as described by Barlow and Boveng (1991). The probability of surviving to a given age (l_x) is expressed as a function of three components: an exponentially decreasing risk with age of dying from sources of juvenile mortality ($l_{j,x}$); an exponentially increasing risk due to mortality factors associated with senescence ($l_{s,x}$); and an age-independent base mortality ($l_{c,x}$). Thus,

$$[3] \qquad l_x = l_{j,x}\, l_{s,x}\, l_{c,x}$$

where

$$[4] \qquad l_{j,x} = \exp\{(-a_1/b_1)[1 - \exp(-b_1 x/\Omega)]\}$$

$$[5] \qquad l_{s,x} = \exp\{(-a_3/b_3)[1 - \exp(-b_3 x/\Omega)]\}$$

and

$$[6] \qquad l_{c,x} = \exp[(-a_2 x/\Omega)]$$

Age is expressed as a fraction of longevity (Ω) to produce a general model that can be applied over a wide range of life-spans. Longevity is here defined as the 99th percentile of the age distribution of a sample (i.e., only 1% of the sample is older than Ω; Barlow and Boveng 1991).

We derived separate, sex-specific general models of survivorship for pinnipeds and cetaceans as per Barlow and Boveng (1991). The pinniped survival curves were calculated from the sampled age distribution of northern fur seals tabulated by Lander (1981) for males and by Smith and Polacheck (1981) for females. Longevity was estimated to be 13 and 19 years for males and females, respectively. As per Barlow and Boveng (1991), an alternative-model life table was calculated for cetaceans, using age-structure data from humans (circa 1900; Merriam 1902) because insufficient data were available for cetaceans and because humans share life-history traits with cetaceans. Human longevity was estimated at 78 years for males and 81 years for females.

We calculated the probability of surviving to a given age for male fur seals and for male and female humans/cetaceans by fitting eq. 3 to their respective age distributions, using the Nonlin Simplex Algorithm (SYSTAT 1988). Survival parameters for female fur seals were taken from Barlow and Boveng (1991).

Growth curves and longevity

Growth curves showing changes in body mass of 30 species of marine mammals were compiled from published sources (see the Appendix for details). In a few cases, body mass was estimated from length curves, using $M_x = a\, L_x^b$. A potential confounding factor, at least among some male pinnipeds, was seasonal fattening associated with breeding. We therefore tried to establish the mean mass of an age-class over the course of a year, or failing this, we used conservative estimates (i.e., postbreeding masses).

Longevity was calculated for most species from the age structure of the samples used to construct their growth curves, using the 99th percentile rule. For some species of cetaceans, however, estimates of longevity were taken from Ohsumi (1979) and were based on earplug growth layers or on maximum number of corpora, ovulation rate, and age at sexual maturity.

Results

Parameter estimates for the general models of pinniped and cetacean survivorship are given in Table 1. Estimates of mean mass for the 30 species of marine mammals with known growth curves are contained in Table 2, along with estimates of their longevity and maximum recorded body lengths. These 30 pairs of points (masses and lengths) were plotted on logarithmic scales (Fig. 1). The data show strong linearity, with three distinct clusterings of points corresponding to the mysticetes (baleen whales), odontocetes (toothed whales), and pinnipeds (seals, sea lions, and walruses). Within male pinnipeds, however, there were two distinct groupings related to the presence or absence of strong sexual dimorphism in body size (Fig. 1). Only one species, the sperm whale (No. 6 in Fig. 1), did not fit within its family grouping. Sperm whales appear to be more closely related to the mysticetes than to the odontocetes (see below), and were thus pooled with the former for regression analysis.

The linear regressions fitted to each of the grouped data were all highly significant (Table 3). Figure 2 shows the slope of the regressions plotted against their intercept. Estimates of mean population body mass were derived for the 76 species of marine mammals without growth curves by applying the regression equations to maximum recorded body lengths (Table 4).

Discussion

The 30 estimates of mean body mass (Table 2) were based on growth and survival curves constructed from relatively large samples, and should be reliable. However, the reliability of the mean masses estimated for the 76 species without growth curves, such as the beaked whales, depends upon the single measurements of body length reported as their maximum length. Such estimates will undoubtedly be refined as more data are collected from stranded and incidentally caught marine mammals.

We were not able to substantiate the maximum lengths reported in the species compilations by Klinowska (1991) and Jefferson et al. (1993). Original data sources should be con-

Table 2. Estimates of longevity, maximum length, and mean body mass for 30 species of marine mammals with known growth curves (for details see the Appendix).

No.	Species	Longevity[a] (years) F	Longevity[a] (years) M	Max. length (cm) F	Max. length (cm) M	Mean mass (kg) F	Mean mass (kg) M	Group F	Group M
	Balaenopteridae								
1	Blue whale	100	100	3358	3190	110 126	95 347	A	A
2	Fin whale	98	98	2700	2500	59 819	51 361	A	A
3	Sei whale	69	69	1800	1710	17 387	16 235	A	A
4	Humpback whale	75	75	1860	1768	32 493	28 323	A	A
5	Minke whale	47	47	1070	980	7 011	6 121	A	A
	Physeteridae								
6	Sperm whale	69	69	1200	1800	10 098	26 939	A	A
	Monodontidae								
7	White whale	32	36	420	460	289	337	B	B
	Delphinidae								
8	Killer whale	50	50	850	980	1 974	2 587	B	B
9	Long-finned pilot whale	45	38	570	762	672	1 029	B	B
10	Short-finned pilot whale	45	45	550	610	467	819	B	B
11	Bottlenose dolphin	47	47	367	381	172	203	B	B
12	Striped dolphin	30	32	253	260	115	117	B	B
13	Spotted dolphin	35	42	218	223	59.1	71.7	B	B
14	Spinner dolphin	17	18	196	197	39.5	43.1	B	B
15	Hector's dolphin	19	20	153	138	36.7	29.8	B	B
	Phocoenidae								
16	Harbour porpoise	13	13	189	178	32.6	29.5	B	B
	Platanistidae								
17	Franciscana dolphin	12	9	171	152	31.3	22.3	B	B
	Odobenidae								
18	Walrus	29	36	312	356	530	643	C	C
	Phocidae								
19	Bearded seal	30	30	265	250	200	200	C	C
20	Weddell seal	14	13	265	262	162	154	C	C
21	Grey seal	39	27	235	265	152	168	C	C
22	Harp seal	26	26	192	192	92.2	92.2	C	C
23	Harbour seal	31	28	170	190	58.4	68.8	C	C
24	Ringed seal	28	27	158	165	40.7	44.3	C	C
25	Southern elephant seal	17	12	304	490	327	543	C	D
26	Northern elephant seal	17	13	282	415	330	412	C	D
	Otariidae								
27	Steller sea lion	22	14	247	330	186	214	C	D
28	Northern fur seal	19	13	147	208	25.3	30.2	C	D
29	Subantarctic fur seal	23	18	143	181	24.6	30.1	C	D
30	Antarctic fur seal	16	11	141	198	22.7	30.7	C	D

Note: Mean masses were determined by applying the survival models (Table 1) to the growth data (Appendix). Species groupings (A–D) were assigned according to the grouped relationships between mean mass and maximum length shown in Fig. 1.
[a]Given as the 99th percentile.

sulted wherever possible, given the wide range of unsubstantiated maximum lengths reported for many marine mammals on the World Wide Web and in the published literature. Humpback whales, for example, have been reported to have a wide range of maximum lengths. Unfortunately, a number of the cited lengths are incorrect, such as the 75-ft (1 ft = 0.305 m) humpback whale that was actually a fin whale (data suggest that the maximum length of a humpback whale is 61 ft; Clapham et al. 1997).

The maximum length used should be the length of a member of the general population and not that of a giant or freak of nature. One approach to safeguarding against choosing an

Fig. 1. Relationship between mean body mass and maximum body length for 30 species of mysticetes (Nos. 1–5) (A), odontocetes (Nos. 7–17) (B), and pinnipeds (Nos. 18–30) (C). Male pinnipeds (C and D) include those with and without sexual dimorphism (lower and upper line, respectively). Species numbers and group letters correspond to those in Table 2 and the Appendix. Circled data points denote male and female sperm whales (No. 6) among the baleen whales.

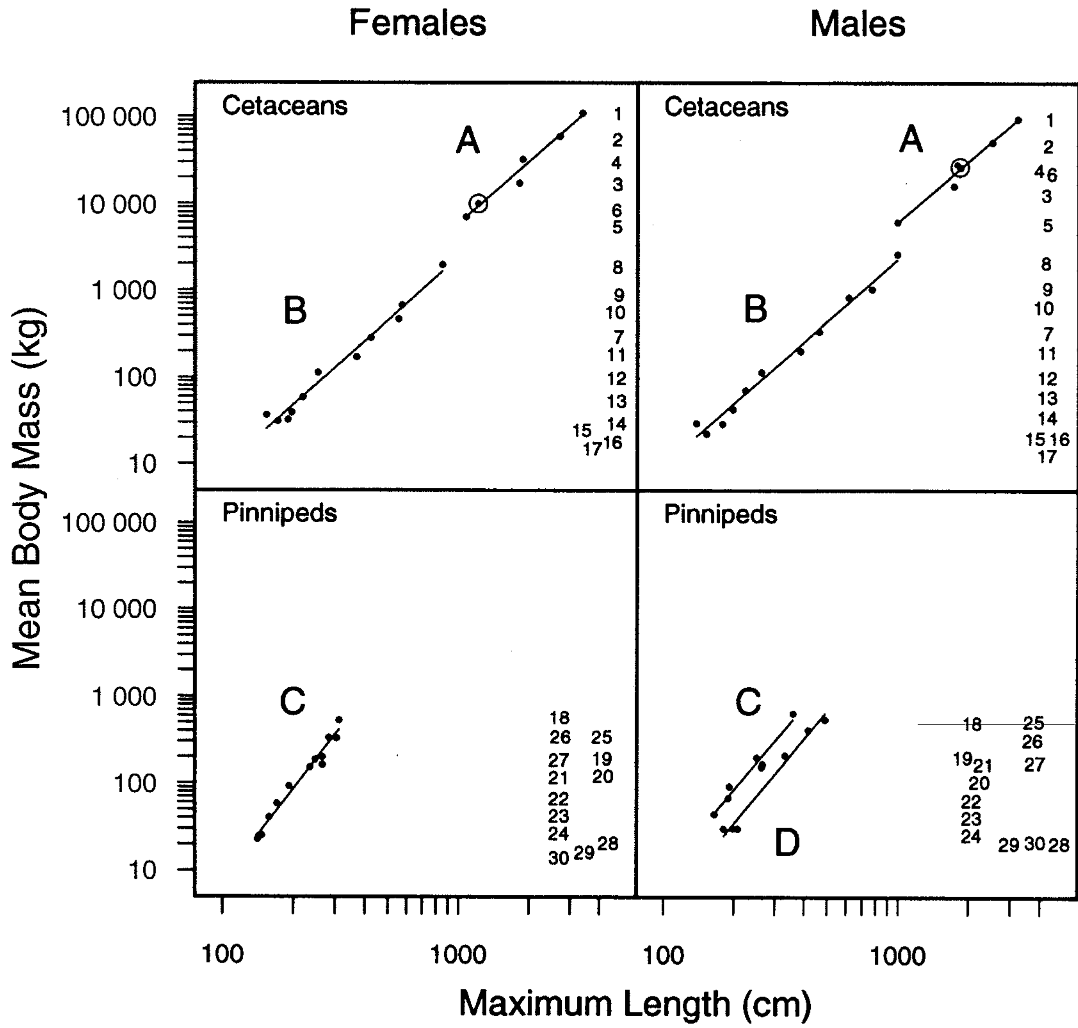


Table 3. Linear regression coefficients describing the relationship $\log_e M_{mean} = a + b \log_e L_{max}$, where mass is measured in kilograms and length in centimetres.

Group	Species	Sex	a	b	SE_b	r^2	n
A	Mysticetes	M	−7.347	2.329	0.450	0.971	6
A	Mysticetes	F	−7.503	2.347	0.454	0.985	6
B	Odontocetes	M	−8.702	2.382	0.310	0.978	11
B	Odontocetes	F	−9.003	2.432	0.349	0.970	11
C	Pinnipeds (monomorphic)	M	−12.609	3.217	0.571	0.982	7
C	Pinnipeds (all)	F	−14.265	3.532	0.420	0.974	13
D	Pinnipeds (dimorphic)	M	−13.732	3.259	0.473	0.982	6

Note: Regressions were run on the data groupings shown in Fig. 1. They correspond to baleen whales (mysticates), toothed whales (odontocetes), and pinnipeds (otariids, phocids, and odobenids). Male pinnipeds were split between dimorphic and non-dimorphic species. Note the low standard errors of the estimated slopes (SE_b).

unrepresentative individual may be to apply the 99th percentile rule to length distributions (such as to those plotted in McLaren 1993). Maximum lengths may also vary among stocks and subspecies with known size differences and could be used with our regressions (Table 3) to predict corresponding mean masses.

The biomass of an entire population equals the mean body mass (Tables 2 and 4) multiplied by the total population num-

Table 4. Maximum body lengths (from Klinowska 1991; Mclaren 1993; Jefferson et al. 1993) and estimated mean body masses for 76 species of marine mammals calculated using one of the sex-specific regression equations shown in Table 3 (groups A–D).

	Max. length (cm)		Group		Mean mass (kg)	
Species	F	M	F	M	F	M
Balaenidae						
Northern right whale	1830	1710	A	A	24 960	21 805
Southern right whale	1650	1520	A	A	19 576	16 574
Bowhead whale	2000	2000	A	A	30 745	31 406
Eschrichtidae						
Gray whale	1500	1460	A	A	15 653	15 090
Balaenopteridae						
Bryde's whale	1550	1472	A	A	16 905	15 381
Ziphiidae						
Tasman beaked whale	660	700	B	B	886	789
Arnoux's beaked whale	885	960	B	B	1 809	1 656
Baird's beaked whale	1200	1140	B	B	3 794	2 479
Longman's beaked whale	750	750	B	B	1 210	928
Sowerby's beaked whale	505	550	B	B	462	448
Blainville's beaked whale	471	580	B	B	390	508
Gervais's beaked whale	520	456	B	B	496	289
Strap-toothed whale	615	584	B	B	746	516
Hector's beaked whale	443	430	B	B	336	252
Gray's beaked whale	533	564	B	B	527	475
Stejneger's beaked whale	525	525	B	B	508	402
Andrews' beaked whale	457	467	B	B	363	305
True's beaked whale	510	533	B	B	473	416
Ginkgo-toothed beaked whale	490	477	B	B	430	321
Hubb's beaked whale	532	532	B	B	525	414
Pygmy beaked whale	352	370	B	B	192	177
Cuvier's beaked whale	660	693	B	B	886	771
Northern bottlenose whale	850	980	B	B	1 640	1 738
Southern bottlenose whale	780	714	B	B	1 331	827
Physeteridae						
Pygmy sperm whale	340	340	B	B	177	177
Dwarf sperm whale	270	270	B	B	101	101
Monodontidae						
Narwhal	400	470	B	B	262	388
Delphinidae						
Rough-toothed dolphin	255	265	B	B	87.7	96.3
Tucuxi	182	182	B	B	38.6	38.6
Indo-Pacific hump-backed dolphin	244	320	B	B	78.8	152
Atlantic hump-backed dolphin	235	248	B	B	71.9	82.0
Irrawaddy dolphin	232	275	B	B	69.7	105
Melon-headed whale	275	273	B	B	105	104
Pygmy killer whale	243	287	B	B	78.0	117
False killer whale	506	596	B	B	464	692
White-beaked dolphin	305	315	B	B	136	147
Atlantic white-sided dolphin	243	275	B	B	78.0	105
Dusky dolphin	193	211	B	B	44.6	55.3
Hourglass dolphin	183	163	B	B	39.2	29.5
Peale's dolphin	216	216	B	B	58.6	58.6
Pacific white-sided dolphin	236	250	B	B	72.7	83.6
Fraser's dolphin	264	264	B	B	95.4	95.4

Table 4 (*concluded*).

Species	Max. length (cm)		Group		Mean mass (kg)	
	F	M	F	M	F	M
Risso's dolphin	366	383	B	B	211	236
Atlantic spotted dolphin	229	226	B	B	67.5	65.4
Clymene dolphin	197	197	B	B	46.8	46.8
Common dolphin	230	260	B	B	68.3	92.0
Southern right whale dolphin	230	210	B	B	68.3	54.7
Northern right whale dolphin	230	310	B	B	68.3	141
Heaviside's dolphin	170	170	B	B	32.7	32.7
Black dolphin	165	167	B	B	30.4	31.3
Commerson's dolphin	163	158	B	B	29.5	27.3
Phocoenidae						
Vaquita	150	140	B	B	24.1	20.4
Burmeister's porpoise	189	189	B	B	42.3	42.3
Spectacled porpoise	204	224	B	B	51.0	64.0
Dall's porpoise	220	220	B	B	61.3	61.3
Finless porpoise	181	190	B	B	38.1	42.9
Phocidae						
Larga seal	160	170	C	C	38.9	50.0
Ribbon seal	190	190	C	C	71.4	71.5
Hooded seal	230	285	C	D	140	109
Mediterranean monk seal	280	280	C	C	281	249
Hawaiian monk seal	240	210	C	C	163	98.6
Crabeater seal	260	260	C	C	216	196
Ross seal	240	228	C	C	163	128
Leopard seal	338	320	C	C	546	382
Otariidae						
California sea lion	200	240	C	D	85.6	62.1
South American sea lion	220	280	C	D	120	103
Australian sea lion	180	250	C	D	59.0	70.9
Hooker's sea lion	200	330	C	D	85.6	175
Guadalupe fur seal	140	190	C	D	24.3	29.0
Juan Fernandez fur seal	150	210	C	D	31.0	40.2
Galapagos fur seal	130	160	C	D	18.7	16.6
South American fur seal	150	190	C	D	31.0	29.0
South African fur seal	180	230	C	D	59.0	54.0
Australian fur seal	180	230	C	D	59.0	54.0
New Zealand fur seal	150	200	C	D	31.0	34.3

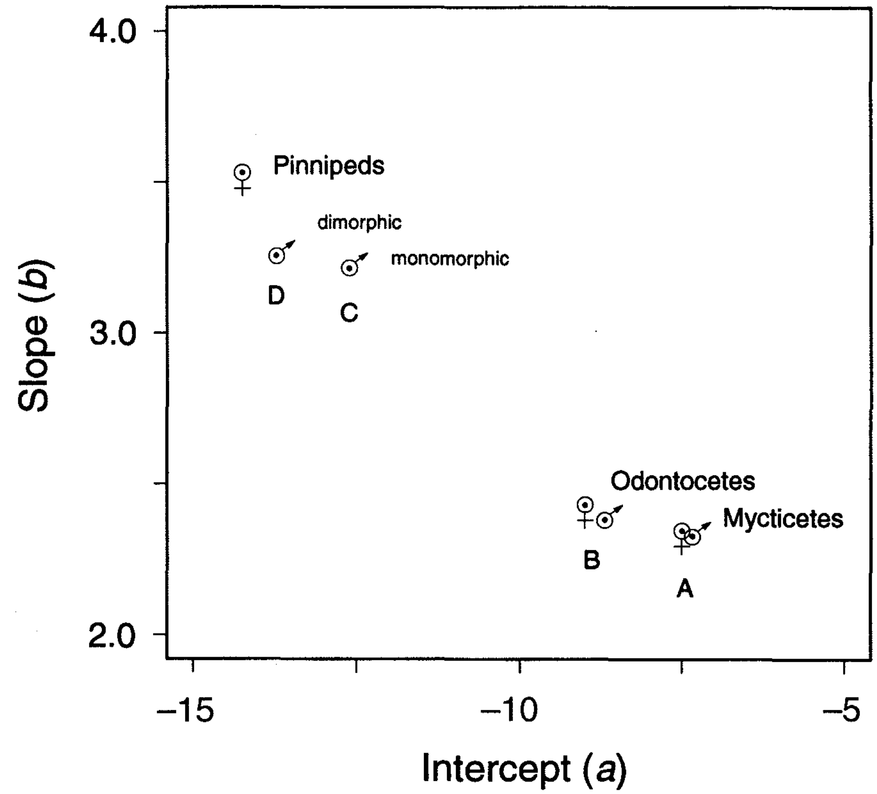
Note: The species names and their sequence follow those in Jefferson et al. (1993).

ber, and includes all age categories (from the newborn to the senescent). Estimating the mean mass of one component of a population, such as adult males in a population of California sea lions, would thus require a new set of calculations using eq. 2. Sex ratios of the entire population, as determined from the survival models (Table 1), were approximately 50% for all species except the sexually dimorphic species, which had a population sex ratio of 40% males and 60% females. This means, for example, that the biomass of 1 million northern fur seals with 60% females would be 27 000 t (i.e., $0.6 \times 1\,000\,000 \times 25.3 + 0.4 \times 1\,000\,000 \times 30.2$).

The relationship we established between mean body mass and maximum length (Fig. 1) supports the traditional separation of whales into two suborders (Barnes et al. 1985; Novachek 1992, 1993), with one exception. Our data suggest that sperm whales are more closely related to the baleen whales than to other toothed whales, and are in agreement with recent molecular phylogeny (Milinkovitch et al. 1993, 1994, 1995; Arnason and Gullberg 1994; Adachi and Hasegawa 1995). The exponents of our maximum length – mean mass relationship for each of the taxonomic orders (Table 3, Fig. 2) ranged from 2.3 to 3.5 and imply sex and taxonomic differences in the balance between growth and survival among different groups of marine mammals (as expressed by eq. 1). These exponents should not be confused with those of traditional length–mass relationships, which often have a value near 2.8.

Size is an important attribute of individual animals, provid-

Fig. 2. Relationship between the exponents (b) and the intercepts (a) of the empirical relationship (Table 3) of mean mass to maximum length in mysticetes (A), odontocetes (B), and pinnipeds (C and D).



ing a scale for all their living processes (Peters 1983; Calder 1984; Schmidt-Nielsen 1984). It should therefore not be too surprising that maximum body length is so closely related to mean body mass in marine mammal populations.

Managing marine mammal populations requires estimates of vital statistics (growth, mortality, fertility, etc.) that are either hard or impossible to obtain by direct sampling. Greater consideration should therefore be given to deriving empirical models for estimating hard-to-estimate parameters (such as the mean mass of an individual in an age-structured population) from an easy-to-estimate parameter (maximum length). This approach has proved useful in the study of fish (e.g., Pauly 1980). Plotting other attributes of marine mammals (related to their morphology, population dynamics, or physiology) against maximum length should generally lead to plots as tight as those we found. Such plots and the various interrelationships they imply should lead to a deeper understanding of the adaptations and evolution of marine mammals, as illustrated in Figs. 1 and 2.

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Appendix

The following identifies all data sources and outlines the major assumptions that were made for each species considered.

1. **Blue whale**: Growth curves were obtained from Lockyer (1981*a*). The longest reported female measured was 33.58 m (Klinowska 1991). The maximum length of a male was assumed to be 5% less, at 31.90 m. The maximum age was estimated to be 100 years for both sexes (Ohsumi 1979).

2. **Fin whale**: Mass growth curves were drawn from equations in Lockyer (1981*a*). Maximum lengths of 27.00 m (females) and 25.00 m (males) were taken from Klinowska (1991). The maximum age for males and females was assumed to be 98 years (Ohsumi 1979).

3. **Sei whale**: Growth curves were established by Lockyer (1981*a*). Data presented in Horwood (1987) suggest maximum lengths of 17.10 m (males) and 18.0 m (females). Lengths up to 19.50 m for females and 18.60 m for males have been reported but may not be representative of the population. The maximum age as determined by Ohsumi (1979) was 69 years.

4. **Humpback whale**: Growth curves for body lengths were drawn by Brown and Lockyer (1984). Maximum lengths were 17.68 m for males and 18.60 m for females, based on 1593 whales taken at Moss Landing and Trinidad (Clapham et al. 1997). Masses were derived from the length–mass relation (LMR; all in centimetres and kilograms) calculated by Lockyer (1976). The maximum age was set at 75 years, based on the analysis by Ohsumi (1979).

5. **Minke whale**: Estimates of mean body length were digitized from growth curves in Evans (1987) that originated from Brown and Lockyer (1984). Body masses were derived from the LMR calculated by Lockyer (1976). Maximum lengths were 9.80 m for males and 10.70 m for females (Klinowska 1991). The average maximum age estimated by Ohsumi (1979) for three stocks was 47 years for both sexes.

6. **Sperm whale**: Body mass growth curves were derived by applying the LMR of Lockyer (1981*b*) to length curves digitized from Evans (1987). Maximum lengths were 18.00 and 12.00 m for males and females, respectively (Klinowska 1991), with a maximum age of 69 years (Ohsumi 1979).

7. **White whale**: The LMR used was from Sergeant and Brodie (1969) and Brodie (1971), and was similar to that of Doidge (1990). This was applied to the length growth curves taken from Braham (1984) to estimate body mass. Maximum ages noted by Burns and Seaman (1985) were 35+ years for females (99th percentile age = 32 years) and 38+ years for males (99th percentile age = 36 years) (cf. Hazard 1988). Maximum lengths were 4.60 m for males and 4.20 m for females (Doidge 1990).

8. **Killer whale**: Length–age data were digitized from growth curves presented in Christensen (1984). Masses were derived using the LMR calculated by Bigg and Wolman (1975). Ohsumi (1979) estimated a maximum age of 50 years. Maximum lengths reported in Klinowska (1991) were 9.80 m for males and 8.50 m for females.

9. **Long-finned pilot whale**: Length–age data were digitized from Sergeant (1962). Masses were produced from the LMR in Bloch et al. (1993). Maximum ages were 46 years for males (99th percentile age = 38 years) and 59 years for females (99th percentile age = 45 years). The longest reported male was 7.62 m, while the largest female was 5.70 m long (Klinowska 1991).

10. **Short-finned pilot whale**: Body lengths by age were digitized from the growth curves drawn by Kasuya and Matsui (1984) and converted to masss using the LMR derived by Kasuya and Matsui (1984). The longest recorded lengths were 6.10 m for males and 5.50 m for females (Klinowska 1991). The maximum age estimated by Ohsumi (1979) was 45 years for both sexes.

11. **Bottlenose dolphin**: Age–mass equations calculated by Read et al. (1993) suggest a maximum age of 47 years for males and females. Corresponding maximum lengths were 3.81 m for males and 3.67 m for females (Klinowska 1991).

12. **Striped dolphin**: Growth curves were digitized from Miyazaki et al. (1981) and Miyazaki (1984). The longest males and females reported by Miyazaki (1984) were 2.60 and 2.53 m, respectively. The oldest animals were 45 years of age (99th percentile age = 32 years) for males and 38 years (99th percentile age = 30 years) for females.

13. **Spotted dolphin**: Length curves were drawn by Kasuya et al. (1974), Kasyua (1976), and Perrin et al. (1976). Body masses were estimated using the LMR from Bryden (1986). Maximum lengths were 2.23 m for males and 2.18 m for females (Perrin et al. 1976; Kasuya 1976). Maximum ages from Kasyua (1976) were 45 years for males (99th percentile age = 42 years) and 39 years for females (99th percentile age = 35 years).

14. **Spinner dolphin**: Growth curves for body length were taken from Perrin and Henderson (1984). Body masses were calculated using the LMR for spotted dolphins reported by Bryden (1986). Maximum ages were 20 and 19 years for males and females, respectively (Perrin and Henderson 1984); corresponding 99th percentile ages were 18 years for males and 17 years for females. Maximum lengths were 1.97 m for males and 1.96 m for females.

15. **Hector's dolphin**: Growth curves describing body length were estimated for males ($L = 125.359\{1 - \exp[-0.146\ (t + 0.05)]\}^{0.064}$) and females ($L = 144.137\{1 - \exp[-0.079\ (t + 0.05)]\}^{0.095}$), using data tabulated in Slooten (1991). The LMR for both sexes combined was $M = 1.689 \times 10^{-4}\ L^{2.53}$. Maximum lengths were 1.38 m for males and 1.53 m for females (Klinowska 1991), with maximum ages of 19 and 20 years for males and females, respectively (Slooten 1991).

16. **Harbour porpoise**: Mean body lengths by age were digitized from growth curves drawn by Gaskin et al. (1984). Body masses were estimated using the LMR from Bryden (1986). The maximum reported age was 15 years (99th percentile age = 13 years) for both sexes. Maximum lengths were 1.78 m for males and 1.89 m for females (Klinowska 1991).

17. **Franciscana dolphin**: A LMR was applied to length at age curves drawn by Kasuya and Brownell (1979) to construct the body mass growth curve. The longest recorded lengths were 1.52 m for males and 1.71 m for females. Maximum ages were 16 and 13 years for males and females, with corresponding 99th percentile ages of 9 and 12 years, respectively (Kasuya and Brownell 1979).

18. **Walrus**: Masses were digitized from smoothed growth curves drawn by Fay (1982). Maximum ages of males and females were 38 and 29 years, respectively (from data plotted in McLaren (1993) for animals sampled in Alaska and Russia). The 99th percentile ages were 36 and 29 years, respectively. Maximum lengths were 3.56 m for males and 3.12 m for females (from McLaren 1993).

19. **Bearded seal**: Body mass growth curves were obtained from Table 6 of Burns and Frost (1983). Data plotted in McLaren (from Benjaminsen 1973; Sager and Sammler 1986) suggest that females are about 5% longer than males. Thus, the maximum length of males was taken to be 2.50 m (Jefferson et al. 1993), while females were assumed to be 2.65 m long. Maximum ages were 31 years, with a 99th percentile age of 30 years for both sexes.

20. **Weddell seal**: Growth curves for body length were fit by Mclaren (1993) to data from Stirling (1971). Maximum lengths were 2.62 m for males and 2.65 m for females. Body mass growth was derived using $M = 2.023 \times 10^{-4}\ L^{2.53}$ calculated from data tabulated in Bryden et al. (1984). Maximum and 99th percentile ages for males and females were 13 and 14 years, respectively (from Mansfield 1958).

21. **Grey seal**: The functional relationship $M = 5.217 \times 10^{-5} L^{2.86}$ was calculated from digitized mean lengths and masses plotted in Platt et al. (1975). This was applied to the length growth curves fit by McLaren (1993) to data from Mansfield (1977) to obtain the mass. Maximum recorded lengths were 2.35 m for females and 2.65 m for males. The oldest reported female was 45 years (99th percentile age = 39 years), while the oldest male was 30 years of age (99th percentile age = 27 years).

22. **Harp seal**: Body masses were calculated by Innes et al. (1981). Pups were assumed to weigh 10.5 kg. Males and females were assumed to be of equal size and to have a maximum length of 1.92 m (McLaren 1993). The oldest reported animal was 29 years of age, with a 99th percentile age of 26 years (from Innes et al. 1981).

23. **Harbour seal**: Body mass was estimated by applying the LMR calculated by Markussen et al. (1989; $M = 4.04 \times 10^{-5} L^{2.89}$) to the sex-specific length at age curves drawn by McLaren (1993) using data from Bishop (1967), Pitcher (1977), and Pitcher and Calkins (1983). Maximum lengths appear to be 1.80 m for females and 1.90 m for males (Fig. 41 in McLaren 1993; cf. Naito and Nishiwaki 1972; Hayama 1985). Maximum ages were 31 and 36 years for males and females, with 99th percentile ages of 28 and 31 years, respectively (Fig. 36 in McLaren 1993; cf. Harkonen and Heide-Jorgensen 1990).

24. **Ringed seal**: Length measurements were obtained from Smith (1987) and converted to mass using the LWR derived by Ryg et al. (1990). Jefferson et al. (1993) suggest that males and females have a maximum length of 1.65 m. However, six sets of growth data plotted by McLaren (1993) suggest that males are about 5% longer than females. Thus, maximum lengths were assumed to be 1.65 m for males and 1.58 m for females. The oldest animals aged were 37 years for females and 31 years for males (Helle 1979); 99th percentile ages were 29 and 27 years, respectively.

25. **Southern elephant seal**: Mean body masses were obtained from Boyd et al. (1994). Maximum reported ages were 12 and 17 years for males and females, respectively (Boyd et al. 1994). Maximum curvilinear body lengths appear to be 3.20 m for females and 5.20 m for males (Laws 1953). The maximum length of males may be as high as 5.50 m, based on data collected by Laws (1953) and plotted by McClaren (1993), but this value does not appear to be representative of the population, given its large departure from all other measurements. Maximum body lengths were converted from curvilinear to standard measures by reducing the curvilinear lengths by 5% (i.e., 3.04 m for females and 4.90 m for males) as suggested by McClaren (1993).

26. **Northern elephant seal**: Length growth curves were obtained from Clinton (1994) for males and from Reiter (1981) and McLaren (1993) for females. Maximum lengths, based on presented data, appear to be 2.82 m for females and 4.15 m for males, although general species summaries suggest that females could be as long as 3.00 or 3.60 m and males 4.50 or 5.00 m (Jefferson et al. 1993; Reijnders et al. 1993). Body mass was estimated using the mean of the LMR calculated for males and females at the beginning and end of the breeding season (from Deutsch et al. 1994). The oldest known-aged males and females were 13 and 11 years, respectively. However, the 99th percentile age for females was assumed to be 17 years, based on the larger aged sample of southern elephant seals.

27. **Steller sea lion**: McLaren (1993) constructed growth curves for changes in body length of animals measured in the Gulf of Alaska by Calkins and Pitcher (1982) and Calkins and Goodwin (1988). Estimates of body mass were derived using $M = 3.328 \times 10^{-5} L^{2.92}$ for females and $M = 4.350 \times 10^{-5} L^{2.87}$ for males <262 cm and $M = 2.585 \times 10^{-5} L^{2.99}$ for larger males (calculated using unpublished data from D. Calkins, Alaska Department of Fish and Game, Anchorage, Alaska, personal communication). Maximum recorded ages were 18 and 25 years for males and females, with 99th percentile ages of 14 and 22 years, respectively. Maximum recorded lengths recorded by D. Calkins (upublished data) were 3.30 m for males and 2.47 m for females (cf. Calkins et al. 1998).

28. **Northern fur seal**: Estimates of body mass were taken from Table 1 of Trites and Bigg (1996). Maximum recorded lengths were 2.08 m for males and 1.47 m for females (Trites and Bigg 1996). The oldest reported animals were 17 (male) and 26 (female) years of age, with 99th percentile ages of 13 and 19 years, respectively.

29. **Subantarctic fur seal**: Body mass growth curves for males and females were constructed by Bester and Van Jaarsveld (1994). However, the parameter $b = 2.03$ in the Gompertz equation for female body mass was misprinted and was replaced with the correct value of 0.131 (M. Bester, personal communication). The oldest animals measured were 18 (males) and 23 (females) years of age. Maximum lengths were 1.81 and 1.43 m, respectively.

30. **Antarctic fur seal**: Body masses were digitized from smoothed growth curves drawn by Payne (1979). These data indicate maximum and 99th percentile ages of 11 and 16 years for males and females, respectively. Maximum recorded body lengths were 1.41 m for females and 1.98 m for males, as shown in McLaren (1993).