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FEEDING RATES OF CETACEA

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INTRODUCTION

A variety of porpoises and dolphins of the superfamily Delphinoidea, ranging through three magnitudes of weight from the harbour porpoise *Phocoena* to the killer whale *Orcinus*, have now been kept in captivity. From aquarium records of body weights and weights of food ingested, daily food consumption can be determined. Following IVLEV (1961) I shall call this index the daily ration. There is no suitable term in the literature for the index daily ration expressed as percent of body weight which I shall therefore call the feeding rate. The purpose of this paper is to attempt to discover the feeding rates of whales which are too large to have yet been kept in oceanaria.

MATERIAL AND METHODS

Table 1 summarises the results of a literature search on feeding rates, supplemented by unpublished information obtained by correspondence with curators of various oceanaria. Least information was obtained for body weight, since curators are loath to weigh living animals, especially those of large size, and estimates of weight are usually too inaccurate to be useful. An independent search of literature and unpublished records on length and weights of whales, however, allowed construction of curves from which weight could be determined knowing body length; this information was useful for the killer whale *Orcinus*, for example. Data on body weight and daily ration, from which feeding rate could be calculated, were found for 8 genera of Delphinoidea maintained in captivity, ranging through 2 orders of magnitude of body size. Details are as follows:

Contribution given in honour of Gunnar Rollefsen at his 70th birthday.

Table 1. Summarised data on feeding rates of Delphinoidea in captivity.

Species	Number of animals	Location	Mean body length m	Mean body weight kg	Mean food weight per diem kg	Food as per-cent body weight	Num-ber of daily feeds
Phocoena phocoena	8	Strib, Denmark	1	40	4.3	10.8	3–4
Lagenorhynchus obliquidens	2	Vancouver, British Columbia	2	87	6.8	7.9	?
Phocoenoides dalli	1	Pt. Mugu, California	2	120	15	11.3	5
Tursiops truncatus	2	Pt. Mugu, California; Montreal, Quebec	2	168	7.0	4.2	2
Globicephala macrorhyncha juv.	1	Marineland, Florida	1	ca190	24.1	12.7	?
Delphinapterus leucas	2	Vancouver	2.8	238	23	5.5	2
Delphinapterus leucas	4	New York City	3.4	468	23	5.1	?
Pseudorca crassidens	1	Marineland of the Pacific, California	3.6	437	20.9	4.7	?
Globicephala scammoni	3	Marineland	5	842	33.2	4.0	?
Orcinus orca	4	Vancouver. Sea World, Calif.	4.75	1258	51	4.05	?

(Data on animals or groups of animals used in calculating feeding rates in Table 1 are shown by an asterisk in the text.)

Phocoena phocoena.

Harbour porpoise. ANDERSEN (1965, Tables 1 and 2) gave weights and daily rations of 7 porpoises held in captivity at Strib, Denmark. All but two of the animals were weighed at death, the other two at a point midway through experiments. Most of the animals presumably increased in weight during this period. The food was fish: herring, *Clupea harengus* and whiting, *Gadus merlangus*. From ANDERSEN's data I calculate that the mean weight at death was 51 kg, and the mean ration was 4.3 kg per diem. Hence the minimum estimate of feeding rate is 8.26%. ANDERSEN gives the mean body weight during captivity as

40 kg and the mean feeding rate about 10% (accurately 10.8%).* I have used this figure in calculating the feeding rate in Table 1, but necessarily weight at death in calculating its variability between animals in Table 2.

Table 2. Feeding rates of individual *Phocoena* (data from ANDERSEN 1965; Tables 1 and 2).

Animal number	Season (summer, winter)	Duration (months)	Food per diem (kg)	Animal weight (kg)	Feeding rate (Weight of food × 100 / Weight of animal)
1	W	5	3.0	—	—
2	S	1	2.0	38	5.26
3	S	2	4.1	32	12.81
4	W	3	5.4	63	8.57
5	W	3	4.8	55	8.73
6	S	2	4.1	30	13.67
7	W	5	4.1	68	6.03
7	S	5	4.8 (4.5)		7.06
8	S	5	4.2	71	5.92
8	W	5	5.1 (4.6)		7.18
Mean of animals 2 to 8			4.2	51	8.26
Range			2.0–5.4	32–71	5.26–13.67

Lagenorhynchus obliquidens.

Pacific white-sided porpoise. ANON (1968 a) gave the length of a male as 6 ft (183 cm) and weight 198 lb (90 kg); the weight of a companion female 185 lb (84 kg). Their food consumption was 15 lb (7 kg) of herring, *Clupea pallasii* and mackerel, *Pneumatophorus diego*, per diem (ANON. 1967 a).*

Phocoenoides dalli.

Dall porpoise. RIDGWAY (1966) gave the daily feeding rate of a specimen of weight 120 kg as 15 kg of mackerel, *Pneumatophorus diego*, in 4 feeds per diem.*

Tursiops truncatus.

Bottlenose porpoise. RIDGWAY (personal communication), gave the feeding rate of a female *T. truncatus* of weight 390 lb (177 kg) as 16 lb (7.3 kg) per diem of mixed fresh mackerel, *Pneumatophorus* and smelt, *Osmerus mordax*. Mr. BRIAN BECK (personal communication) from experience at the Montreal Aquarium gave the feeding rate of a female *T. truncatus* of weight 350 lb (159 kg), fed on herring and smelt, as 30 lb

(13.6 kg). However at this rate of feeding, the animal soon reached satiety and ceased to feed. With a free choice, the average daily intake levelled off to 15 lb (6.8 kg) per diem after 11 days. Feeding rate for both experiments agrees at 4.2% (Table 1).*

Delphinapterus leucas.

White whale. ANON. (1968 a) gave the current lengths of two white whales as 10.5 and 8 ft (320 cm, 244 cm) and the lengths at capture, on September 16 1967, as 10 ft 4 in and 7 ft 5 in (315 cm, 226 cm). ANON. (1967 b) gave the weight of the calf as 490 lb (223 kg) having increased from 238 lb (108 kg) at capture. ANON. (1967 a) gave the feeding rates as 50 lb (23 kg) of herring and salmon (*Onchorhynchus* sp.) for the adult and 25 lb (11.5 kg) for the young animal, but the calf was reported to be taking some food from the adult. I calculate the adult's weight to have been 300 kg, the weight of the young animal in November–December 165 kg, giving estimated feeding rates of 4.1 and 6.9%.*

Mr. R. MORRIS (personal communication) gave me details of two male and two female white whales held at the New York Aquarium. Lengths ranged from 10 to 13 ft with a mean of 11 ft 3 in (3.43 m). Weights were estimated at from 700 to 2000 lb with an average of 1250 lb (567 kg), and feeding rates from 40 to 60 lb per animal per diem with an average of 50 lb (23 kg) in two daily feeds, giving an estimate of feeding rate of 4.1%. These weights however, were estimates and may have been high. Known weights of the four animals were given to me by MORRIS and Mr. P. MONTREUIL as: two females at capture in August 1967—625 lb (284 kg) each; the larger male, on May 17, 1965—1181 lb (538 kg). Dr. J. R. GERACI (personal communication) estimated the weight of the two males in 1967 at 900 and 1100 lb. All these weights had presumably increased by February 1968 when the feeding rate was given by MORRIS. Using the known weights one obtains a mean weight of 369 kg and a mean feeding rate of 6.2%. The mean of the two estimates of feeding rate for the New York animals is 5.1%.*

Pseudorca crassidens.

False killer whale. BROWN, CALDWELL and CALDWELL (1966) gave the cumulative food consumption of a captive female false killer whale between November 4, 1963 and August 31, 1965 as 30,650 lb (13,903 kg) of fish and squid. I calculate a mean daily ration of 45.95 lb (20.84 kg). The animal weighed 825 lb at capture and 1100 lb at writing. Taking the mean weight at 962.5 lb (456.6 kg) I find a mean daily feeding rate of 4.7% of body weight.*

Globicephala macrorhyncha.

Southern Atlantic pilot whale. KRITZLER (1952) gave a total food consumption of a young captive pilot whale at Marineland, Florida, between October 6, 1948 and July 5, 1949 as about 7 tons of squid, plus small, unmeasured quantities of fish. Weight at capture was estimated at 300 lb and at death 505 lb. Daily food consumption was at least 53.03 lb (squid only) and mean weight during this period at least 400 lb, giving a daily feeding rate of 4.7% of body weight.*

Globicephala scammoni.

Pacific pilot whale. BROWN (1960, 1962) and GILMORE (1962) gave the weights and daily feeding rates of three Pacific pilot whales held at Marineland of the Pacific, California, in about September, 1959: the smallest weighed an estimated 1100 lb and ate 40–45 lb of food daily; the median animal weighed 1360 lb and ate 80 lb daily; the largest weighed an estimated 3000 lb and ate 100 lb of food daily. For the median animal, of known weight, the feeding rate was 5.9% of body weight per day. Taking the mean of the three weights, known and estimated, as 1850 lb, and the mean daily ration as 74 lb, the mean feeding rate is calculated at close to 4.0% of body weight per diem.*

Orcinus orca.

Killer whale. A female at the Vancouver Aquarium on January 16, 1968 measured 16 ft 2 in (4.9 m) along the curve of the back, or 15 ft 6 in (4.7 m) in a straight line (ANON. 1968 a). In November, 1967 this animal ate 110 lb (50 kg) of herring and ling cod, *Ophiodon elongatus*, daily (ANON. 1967 a). The weight of this animal was estimated at 2500 lb (1136 kg), giving an estimated feeding rate of 4.4% per diem.* A previously-captured male, length 15 ft 4 in (4.67 m), weighed 2300 lb (1040 kg) and ate a steady diet of 100 lb (45 kg) daily (NEWMAN and MCGEER 1966), giving a feeding rate of 4.3% of body weight per day.* A male killer whale of length 16 ft (49 m) held at Pender Harbour, British Columbia, ate 130 lb (59 kg) of herring daily before its escape (ANON. 1968 b). From a weight/length curve I calculate its weight to have been about 1500 kg, giving a feeding rate of 3.9%.* [Data for construction of the weight/length curve for *Orcinus orca* were obtained from the compendium of SCHEFFER (MS 1967), from SLEPTSOV (1961) and BURGESS (1968)]. BURGESS (1968) gave the daily food intake of a killer whale at Sea World, San Diego California, as between 36 and 63 kg, or a mean of 49.5 kg. The length at capture in October, 1965 was 4.1 m and the

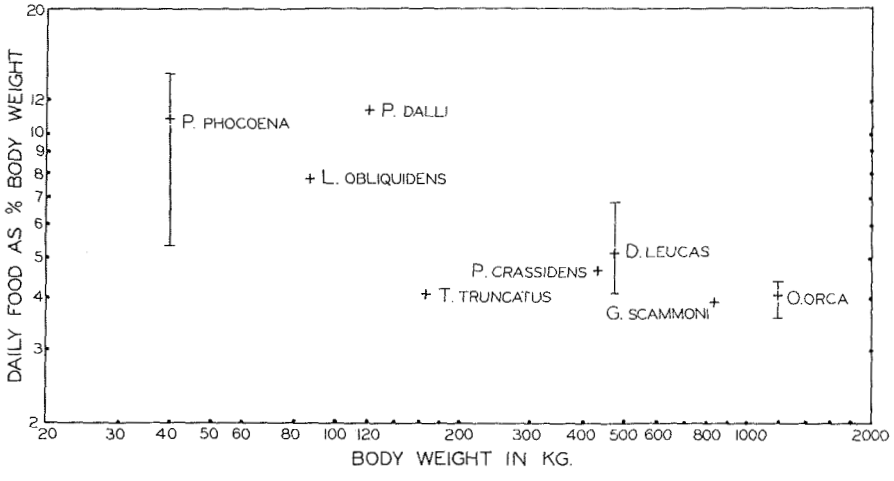

Fig. 1. Feeding rates of Delphinoidea.

weight 1088 kg. The length after 17 months was 4.5 m and the weight had increased about 270 kg, implying a weight at writing of about 138 kg. I calculate a daily feeding rate of 3.6% of body weight daily.*

RESULTS

Fig. 1 shows that the feeding rate decreases from the smaller genera of Delphinoidea to the larger, but levels off at about 4 to 5% of body weight for genera of length 2 m (weight 650 kg—adult *Tursiops*) or greater.

This pattern is complicated by several factors:

(*a*) Differences occur in feeding rates between young and adult animals.

Best data are those of ANDERSEN (1965) for *Phocoena* which show a variation in feeding rate of from 5.26 to 13.67% for 7 animals (Table 2). With the exception of one short-lived and probably sick animal (No. 2), which was small yet fed at a low level, feeding rate was inversely proportional to body weight. Only two animals, having weights of less than 30 kg, showed feeding rates in excess of 10% of body weight. MØHL-HANSEN (1954) gave birth weight of Danish porpoises as 6–8 kg, weight at full weaning as 25 kg, so that the animals below 30 kg in weight were young.

A young pilot whale, *Globicephala macrorhyncha*, showed a feeding rate of 13% (KRITZLER 1952). This is twice as high as the feeding rate of an adult *G. scammoni*, which was 6% of body weight (Table 1).

The young *Delphinapterus leucas* held in captivity consumed about 6.9% of body weight per diem compared to its mother's consumption of about 4.1%. However the account makes clear that the young animal

stole food given to the mother, which would increase further the disparity between the feeding rates.

(*b*) Species differences occur between genera of the same weight.

Phocoenoides dalli has a higher feeding rate than the slightly smaller *Lagenorhynchus obliquidens*, as well as the larger *Tursiops truncatus*. *Phocoenoides dalli* is exceptional also in having a high metabolic rate, large heart, thin fat layer and ability to dive very deep (RIDGWAY 1966). RIDGWAY and JOHNSTON (1966) gave the heart weights of these three species, which I have included in Table 3. Heart weights are exactly proportional to daily feeding rates, being close to 0.11 × feeding rate, as follows:

Species	Body weight kg	Feeding rate %	Heart weight	Heart weight / Feeding rate
L. obliquidens	87	7.8	8.5	0.109
P. dalli	120	11.3	13.1	0.116
T. truncatus	168	4.2	5.0	0.119

This result is not unexpected since both heart weight and feeding rate are expressions of metabolic rate. *P. dalli* appears to be exceptional also in the number of daily feeds necessary in captivity to maintain its high metabolism; 5 compared with 2 for *Tursiops truncatus* and *Delphinapterus leucas*; 3 or 4 for *Phocoena phocoena*. While the metabolic rate of many genera is not known, we now have three measures of it: proportional heart weight, feeding rate, and number of daily feeds.

DISCUSSION

The measures of the metabolic rate give us a key to discovering the feeding rate of large whales which cannot yet be kept in captivity. The assumption involved is that heart weight retains the same proportionality to feeding rate in large whales as in the Delphinoidea. I made a literature search on total weights and heart weights of whales starting from the paper of SLIPJER (1958). The main references were: BJARNASON and LINGAAS (1954); FUJINO (1955); KLEINENBERG (1956); KLEINENBERG *et al.* (1964); LAURIE (1933); NISHIWAKI (1950); OHNO and FUJINO (1952); OMURA (1950, 1957); QUIRING (1943); RIDGWAY and JOHNSTON (1966); SLEPTSOV (1961); SLIJPER (1958); and TOMILIN (1967), the last quoting several Soviet authors. Results are summarised in Table 3 and Fig. 2.

Adults of the large whalebone whales (Mysticeti) are seen to have heart weights of 3.5 to 6‰ of body weight. For good numbers of 4 species

Table 3. Body and heart weights of Cetacea.

Species in order of increasing size	No. of specimens	Body length cm	Mean body weight kg	Heart weight × 1000 Body weight	
				Range	Mean
Phocoena phocoena	27	67–171	35.9	6.5–12.2	8.4
Delphinus delphis	50	—	54.2	—	4.84
Phocoenoides dalli	3	—	97	12.5–13.4	13.1
Lagenorhynchus obliquidens	5	—	110	7.0– 9.2	8.5
Tursiops truncatus	50	—	133	—	5.00
Kogia breviceps	1	298	417	—	3.26
Delphinapterus leucas	20	327–425	821	3.7– 6.9	5.7
Globicephala melaena	1	—	1,230	—	4.4
Orcinus orca	3	495–650	2,288	5.0– 7.3	6.41
Balaenoptera acutorostrata	1	790	4,846	—	4.75
Berardius bairdi	1	—	8,560	—	6.30
Balaenoptera borealis	17	1160–1460	12,551	3.4– 4.9	4.04
B. brydei	20	1220–1380	13,077	2.3– 6.8	4.6
Eubalaena glacialis	2	1160–1250	22,556	6.9– 7.9	7.4
Eschrichtius glaucus	1	1335	31,466	—	5.47
Megaptera novaeangliae	4	1250–1390	31,913	3.6– 5.8	5.31
Physeter macrocephalus	30	1110–1800	31,525	2.4– 6.1	3.32
Balaenoptera physalus	29	1860–2320	51,632	2.3–11.0	3.96
B. musculus	32	2130–2710	85,520	3.7– 6.7	3.99

of rorqual (*Balaenoptera borealis, brydei, musculus* and *physalus*) the mean figure was close to 4‰; for smaller numbers of humpback, *Megaptera novaeangliae* and right whales, *Eubalaena glacialis*, the figure was about 5 to 6‰. It was significantly lower at 3.4‰ in a good series of sperm whales, *Physeter catodon* and, perhaps also significantly, in one specimen of the related pigmy sperm whale, *Kogia breviceps*. Data were scarce for medium-sized whales: a single specimen of lesser rorqual, *Balaenoptera acutorostrata*, gave 4.8‰ and SLIJPER without stating details of size gave a figure of 5.1‰ for a second specimen of this species. A heart weight/body weight ratio of 6.3‰ for one specimen of *Berardius bairdii* is too little to provide a reliable figure for the Ziphiidae. I have been able to find less data for the Delphinoidea than for large whales. Three adult specimens of adult killer whales, *Orcinus orca*, gave a proportional heart weight of 6.35‰; 20 white whales, *Delphinapterus leucas*, 5.7‰; 50 *Tursiops truncatus* 5.1‰; 50 *Delphinus delphis* 4.8‰; and 27 *Phocoena phocoena* 8.4‰. The data do not disagree with the previous conclusion that the heart weight/body weight ratio is equal to about one tenth of the feeding rate.

Heart weight is higher for young than for adult Cetacea of the same species. For *Delphinus delphis*, KLEINENBERG (1956) gave heart/body weight

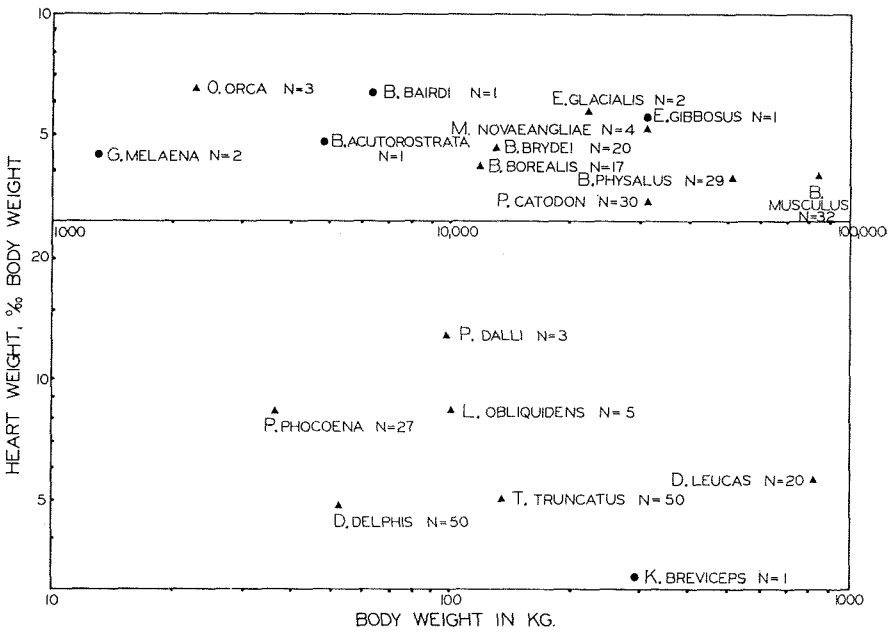

Fig. 2. Heart weight/body weight ratios of Cetacea. Solid circle—single animal; triangle—mean of more than one animal. N = number of animals from which data obtained.

ratios of 7.59‰ for late embryos, 6.93‰ for underyearlings and 4.84‰ for older animals. The data of SLIJPER (1958) suggest the same for *Tursiops truncatus*: 9.4‰ for a juvenile compared with 5.0‰ for KLEINENBERG's adult sample; and also for *Lagenorhynchus acutus*: 17.7‰ for a newborn animal compared with 8.5‰ for RIDGWAY and JOHNSTON's (1966) adult sample of the related *L. obliquidens*. However SLIJPER's (1958) data for 27 *Phocoena phocoena* show no decline in heart weight/body weight ratio with increase in body weight (age). This exception suggests that *Phocoena* (like *Phocoenoides dalli*) may retain a high metabolic rate throughout life. However, KLEINENBERG's data for Black Sea *Phocoena phocoena* gave a mean heart weight/body weight ratio of only 4.5‰ for 50 Black Sea *Phocoena*, indicating that the question must be re-examined.

Assuming that the ratio of heart weight to body weight equals approximately one tenth of the feeding rate in large whales, I conclude that the large rorquals eat some 4% of their body weight daily. A lower figure for *Physeter* seems quite reasonable since *Physeter* feeds through the eyar, but the large rorquals feed during the summer months only.

KLUMOV (1963) has deduced from data on maximal stomach con-

Table 4. Weights of full stomachs of some Mysticete whales.

Species	Region	Length (m)	Body weight (metric tons)	Weight of stomach contents (metric tons)	Ratio
Blue	Antarctic	24	65	1.10 *a*)	1.7
Fin	N. Pacific	22	57*f*	0.85 *b*)	1.5
Fin	N. Pacific	18.5	35	0.75 *c*)	2.0
Fin	N. Pacific	18.5	35	0.76 *d*)	2.2
Sei	N. Pacific	12	10*e*	0.60 *d*)	2.0

a) KLUMOV 1963 p. 141, *b*) KLUMOV 1963 p. 149, *c*) KLUMOV 1963 p. 154, *d*) NEMOTE 1959 pp. 218–220, *e*) OMURA 1950, *f*) NISHIWAKI 1950.

tents of Mysticeti and the biomass of planktonic food that " the whalebone whales require about 30–40 g per kg of live weight daily." This conclusion agrees well with my own. " Proceeding from the above indices " says KLUMOV " the 24-hour long requirement of food for the blue whale of average size and weight (23.5–24.5 m, 60–70 tons) is 2–2.5 tons." KLUMOV makes clear that this level of feeding is optimal, depending on an adequate biomass of plankton or pelagic fish. Table 4 shows data on maximum stomach volumes of large rorquals. With KLUMOV's suggested feeding rate, the ratio of stomach volume to body weight suggests a twice-daily feeding rate for blue, fin and sei whales. By contrast IVASHIN (1961) suggests that the daily food consumption of a humpback whale, *Megaptera novaeangliae*, in Antarctic seas in February is about 4 metric tons, with feeds every 3–4 hours. Assuming a body weight of about 25 tons the feeding rate would be 16%, which would demand a much higher metabolism of *Megatera* than of the genus *Balaenoptera*. Such a feeding rate would be comparable with that of *Phocoenoides dalli* among the Delphinoidea and would necessitate a large heart. The average heart weight for 4 large specimens of *Megaptera* is 5.3‰, which is higher than for the species of *Balaenoptera*, but not as high as IVASHIN's suggestion would require. I conclude that KLUMOV's assumptions on feeding rates are probably closer to reality than IVASHIN's.

The data of KLUMOV (1963) and NEMOTO (1959) on stomach contents suggest that baleen whales rarely find optimal quantities of food, at least in the North Atlantic and Pacific Oceans; this would imply that they must actively search out feeding concentrations. The sensory and navigational basis of this search has yet to be discovered.

SUMMARY

1. The feeding rate of a whale is defined as the weight of daily food ingested expressed as percentage of body weight. Records of daily rations of Delphinoidea (porpoises and dolphins) in captivity allow calculation of feeding rates for eight genera having adult body weights of 10^1 to 10^3 kg.

2. There is an inverse relation between feeding rate and body weight, both between species and between young and adult Delphinoidea. The range of feeding rates is from 12–13% to 4–6%. Above a body weight of 6×10^2 kg, represented by adult *Tursiops truncatus*, feeding rate remains constant at 4–6% up to the largest species in which it has been measured, the killer whale, *Orcinus*, of body weight 2×10^3 kg.

3. Heart weight expressed as proportion of body weight varies directly with feeding rate and is equal to about one tenth of it. Young animals of all species, as well as adults of *Phocoenoides dalli* and possibly *Phocoena phocoena* have high feeding rates and heart weights, showing that both indices measure metabolic rate. From their heart weight/body weight ratio an attempt has been made to calculate feeding rates of whales too large to be kept in aquaria.

4. Heart weight/body weight ratios of adults rorquals of the genus *Balaenoptera* are about 4‰; of sperm whales, *Physeter* and one example of the small, related *Kogia*, lowest of all at 3.5‰. These data suggest a feeding rate of 4% for adult rorquals, so that from curves relating body length and body weight, their daily food consumption may be calculated.

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