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Food consumption, growth, body dimensions, and respiration rates of captive false killer whales (*Pseudorca crassidens*)

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Abstract

Food consumption, growth, body measurements, initial food passage times, and respiration rates of one male and 2 female false killer whales housed at the Harderwijk Marine Mammal Park are described. When between 5 and 10 years old, the two females ate between 5000 and 6000 kg annually. The annual food consumption of the male increased from 5500 kg during his fourth and fifth year to 6400 kg during his sixth year. No pattern of seasonal variation in food intake was observed. One female's body length increased at least until she was 10 years old. At the age of 5 years (350 kg) she consumed on average 4.1% of her body weight daily and at the age of 8 years (450 kg) she ate 3.4%. The other female's body length increased at least until she was 11 years old. At the age of 6 years (380 kg), she ate on average 4.1% of her body weight per day. The male grew from 310 kg at the age of 3 years to 425 kg at the age of 6 years. His body length increased steadily during the 5-year study. After the age of 5 years the male became more robust than the females. At the age of 4 years (350 kg), he consumed on average 4.3% of his body weight daily. Food consumption and body measurements from this study are compared to those reported in the literature and to unpublished data from Sea Life Park, Hawaii. The mean initial passage times of carmine red dye through the gastrointestinal tract of the two females were 218 and 236 min. The mean respiration rate of the animals varied during the day between 10 and 20 breaths per 5 min. In all 3 animals, the respiration rate was highest between 1200 and 1800 h.

Key words: odontocete, energetics, growth rate, initial passage time, carmine red.

Introduction

False killer whales (*Pseudorca crassidens*) are social pelagic odontocetes, which generally rarely approach land, except in some areas such as Hawaii, British Columbia and Washington state. They are found in temperate to tropical seas worldwide (Mörzer Bruyns, 1969; Odell and McClune, 1999). Large groups of false killer whales sometimes strand, most frequently in Australia (Mell, 1988; Phillips, 1988). The diet of false killer whales in the wild consists mainly of squid, and their large teeth allow them to feed on sizeable fish (Fraser, 1936; Tomilin, 1957; Ross, 1984; Stacey and Baird, 1991; Stacey *et al.*, 1994) and sometimes on other odontocetes (Perryman and Foster, 1980). Little is known about the energetic requirements of odontocetes in the wild, because it is not yet feasible to measure their energetic requirements in their natural environment. Some basic information on food intake can be derived from captive animals. Only anecdotal information exists on the energetic requirements of captive false killer whales because this species is rarely kept in oceanaria (Sergeant, 1969; Odell *et al.*, 1980; Thomas *et al.*, 1988). Therefore more structurally collected food intake data of false killer whales, together with information on diet and water temperature, is a valuable contribution to the scarce information presently existing on this topic, despite a small number of animals involved in a study. The present study describes food consumption, growth, detailed body measurements, initial food passage times and respiration rates of three false killer whales during their stay at the Harderwijk Marine Mammal Park, The Netherlands.

Materials and Methods

Study animals

The three false killer whales arrived at the Harderwijk Park in November 1987 from Kamogawa, Japan, and originated in waters around Japan. On arrival, the male (003) had a standard body length (*i.e.* a straight line from the tip of the rostrum to the notch of the tailfluke) of

312 cm and was estimated as 3 years old, one female (001) was 318 cm long and was estimated as 4 years old, and the other female (002) was 330 cm long and was estimated as 5 years old. Age estimates were based on the body length versus age curves reported by Kasuya (1986). Eventually all animals died of pneumonia and during their illness lost weight. Food intake, body weight, and girths during the year before their deaths are not included herein, as they are not considered to be representative of healthy individuals of this species.

Study area
At the Harderwijk Park the animals were kept in a facility consisting of 2 large pools and several small pools. One large oval pool (30 m (L) × 15 m (W) × 4 m (D)) has 2 adjacent holding pools (both 9 m in diameter; one 2.9 m deep and the other 4 m deep) and is connected by a channel to another large rectangular pool (21 m (L) × 7.5 m (W) × 3 m (D)) with 4 holding pools. A plan of this indoor pool system was given by Dudok van Heel (1970). In the pool system, a group of up to 8 bottlenose dolphins (*Tursiops truncatus*) was kept with the false killer whales. During the year the average monthly water temperature varied between 17°C in February and 22°C in August. The average annual water temperature between 1987 and 1993 gradually increased from 18 to 20°C. The salinity varied between 2.0 and 2.5% NaCl. The air temperature varied between approximately 0°C and 30°C. Through windows in the roof, the animals were exposed to the natural daily light cycle. The Harderwijk Park is at 5°37′E and 52°20′N.

Food
The animals were fed 3 to 10 times per day on an average diet of 45% herring (*Clupea harengus*), 45% mackerel (*Scomber scombrus*), 5% sprat (*Sprattus sprattus*), and 5% squid (*Illex* spp.). The percentages were based on total food weight. Dietary composition varied slightly according to each animal's preference. The composition and caloric content of the fish was not measured. Vitamins (Seavits®) were added to the fish, after it had been defrosted. Fish was stored for a maximum of 4 months at −20°C. Records were kept of the amounts and types of food consumed during each feeding session.

Body measurements
The animals were weighed on arrival and once during their time at the park on a digital weighing platform (0.5 kg accuracy). The standard body length and girths in front of the pectoral fins and at the axilla were frequently measured with a tape measure while the animals were in the water. Detailed morphological measurements were taken shortly after the animals died.

Food passage time
To estimate the passage time of food through the gastro-intestinal tract, 10 gelatin capsules each containing 100 mg carmine red dye, were fed to the whales in fish (herring or mackerel). The capsules were offered between 0800 and 1600h. The animals were watched constantly and the time at which red feces appeared was recorded. This is called the initial passage time (IPT). The IPTs of the 2 females (at the ages of 10 and 11 years) were measured between 22 July and 26 August 1993.

Respiration rate
Because the respiration rate in odontocetes varies greatly (Ridgway *et al*., 1969; Dral and Verwey, 1977; Kastelein and Gerrits, 1991; Kastelein *et al*., 1997a and b), the number of respirations were recorded in 5 min periods. To investigate diurnal changes, the animals' respiration rates were recorded during 4 six-hour-long periods throughout the day and night on various days over 2 months (November 1987–January 1988), when the 3 animals were kept together in the rectangular pool. Within each 6-h period, the respirations of each animal were counted for 4 to 6 five-min periods each hour. The animals were not fed nor did they interact with humans or other odontocete species during the respiration rate recordings.

Sea Life Park
Some information on food consumption and body weights of false killer whales was made available for this study from animals at Sea Life Park, Hawaii, USA (Marlee Breese, pers. comm., unpublished data). Their animals were fed herring, mackerel, smelt, and some squid and kept in water with average monthly temperatures between 24.6°C in January and 27.2°C in August (annual average: 25.9°C).

Results

Annual food consumption
The total annual food consumption of female 001 was on average approximately 5600 kg, while that of female 002 was on average approximately 5300 kg. The annual food consumption of male 003 increased from 5500 kg during his fourth and fifth year to 6400 kg during his sixth year (Fig. 1).

Seasonal food intake
Based on the monthly food consumption, no systematic seasonal variation could be detected in the food intake of any of the three study animals.

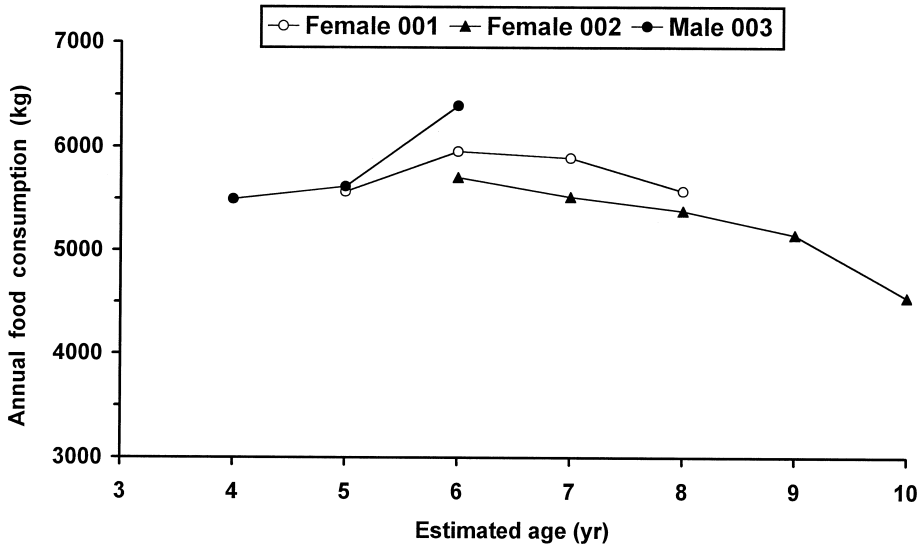

Figure 1. Annual food consumption of the 3 false killer whales.

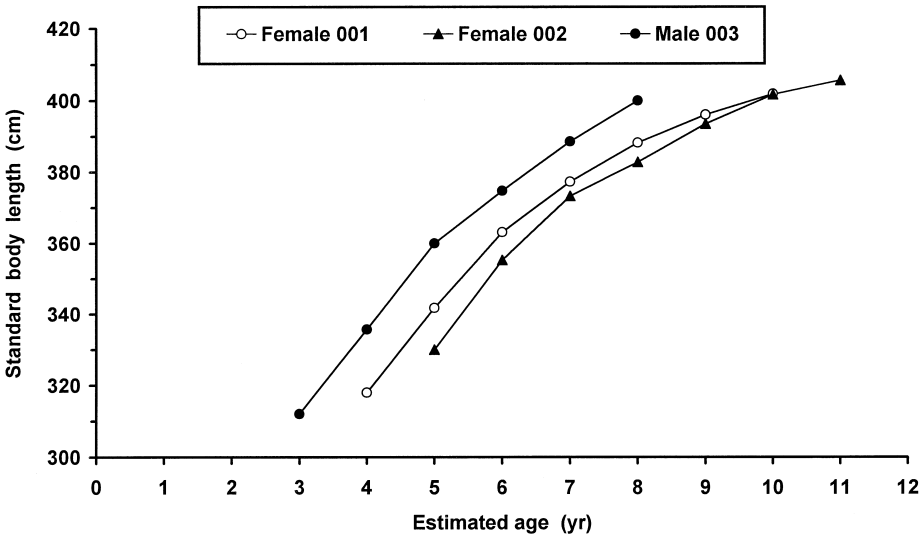

Figure 2. Standard body length of the 3 false killer whales.

Weight and size

Female 001 increased in weight from 340 kg when she was 4 years old to 450 kg when she was 8 years old. Her body length increased until the end of the study when she was 10 years old (Fig. 2). Between the ages of 4 and 6 years she grew about 20 cm per year, thereafter her growth rate decreased. Her girths in front of the pectoral fins and at the axilla increased at least until she was 8 years old (Fig. 3).

Female 002 increased in weight from 360 kg when she was 5 years old to 500 kg when she was 10 years old. Her body length increased until the end of the study when she was 11 years old (Fig. 2). Between the ages of 5 and 6 years she grew about 20 cm per year, thereafter her growth rate decreased. Her girth the axilla increased until she was 10 years old (Fig. 3).

Male 003 increased in weight from 310 kg when he was 3 years old to 425 kg when he was 6 years old. His body length increased until the end of the study when he was 8 years old (Fig. 2). Between the ages of 3 and 5 years he grew about 20 cm per year, thereafter his growth rate decreased, but less than those of the females. His girth in front of the

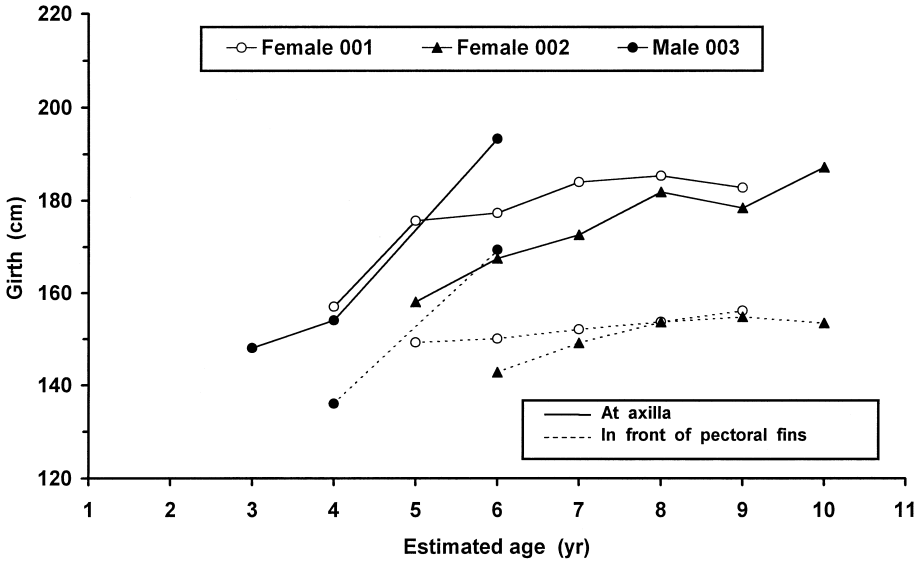

Figure 3. Girths in front of the pectoral fins and at axilla of the 3 false killer whales (note that after the age of 5 years, the male became more robust than the females).

pectoral fins and at the axilla increased at least until he was 6 years old (Fig. 3). After the age of 5 years the male became more robust than the females.

Detailed external body measurements of the three animals after death are shown in Table 1. The body of false killer whales is long and slender. The pectoral fins are long and have a distinct hump at the midpoint. The rostrum is broad with a bulging melon.

Food consumption relative to body weight
Daily food consumption, expressed as a percentage of the body weight, of the three animals is shown in Table 2. The heavier the animal, the lower the daily food intake as a percentage of body weight.

Food passage time through the digestive tract
The normal colour of the feces of the animals was green so the red dye was clearly visible. The initial passage times (IPTs) are shown in Table 3. The mean IPTs of carmine red dye through the gastrointestinal tract of the two females were 218 min (SD 9 min, $n=3$) and 236 min (SD 29 min, $n=4$).

Respiration rate
The animals' average respiration rates varied during the day between about 10 and 20 respirations per 5 min. Their respiration rate was highest between 1200 and 1800 h (Fig. 4).

Discussion

Seasonal food intake
No seasonal pattern of food intake was observed in any of the study animals, although a 5°C difference in average monthly water temperature occurred between summer and winter. Because the food was bought in different months of the year, and was stored in different quantities over many months, it is highly unlikely that any seasonal fluctuations in energy content of the fish did exactly counterbalance potential seasonal fluctuation in energy demands of the study animals. The lack of seasonal fluctuations could be due to the masking effect of growth; the animals grew during the entire study period. In contrast to the females, the male probably had not reached sexual maturity during the study and may not have experienced potential seasonal reproductive hormone fluctuations. Both male and female false killer whales reach sexual maturity between the age of 8 and 14 years (Purves and Pilleri, 1978). In males this occurs at a body length of between 4.0 to 4.5 m (Purves and Pilleri, 1978), and in females at a body length of around 3.6 to 4.0 m (Purves and Pilleri, 1968; Scott and Green, 1975; Kasuya, 1986). The lack of a seasonal food intake fluctuation despite seasonal water temperature fluctuations, also may be due to whales' ability to adapt their blubber layer thickness to the water temperature.

Table 1. Body measurements (cm) of three false killer whales at Harderwijk Marine Mammal Park. (S.l.=straight line parallel to the body axis; P.p=point to point).

Animal	001		002		003	
Gender	female		female		male	
Estimated age (yrs)	10		12		8	
Date (d/m/yr)	9-9-93		1-1-94		8-4-92	
Method of measurement	S.l.	P.p	S.l.	P.p	S.l.	P.p
Tip upper jaw to deepest part of fluke notch	399	—	406	—	410	—
Tip of upper jaw to centre of anus	277	—	272	—	255	—
Tip of upper jaw to centre of genital slit	253	—	249	—	220	—
Tip of upper jaw to centre of umbilicus	177	—	174	—	180	—
Tip of upper jaw to top of dorsal fin	212	—	208	—	230	—
Tip of upper jaw to leading edge of dorsal fin	167	—	161	—	180	—
Tip of upper jaw to anterior insertion of flipper (right)	66	—	67	—	70	—
Tip of upper jaw to anterior insertion of flipper (left)	—	—	—	—	70	—
Tip of upper jaw to anterior edge of blowhole	45	—	50	—	45	—
Tip of upper jaw to centre of blowhole	48	—	52	—	50	—
Tip of upper jaw to external auditory meatus (right)	58	—	57	—	60	—
Tip of upper jaw to external auditory meatus (left)	—	—	—	—	60	—
Tip of upper jaw to centre of eye (right)	44	—	45	—	48	—
Tip of upper jaw to centre of eye (left)	—	—	—	—	48	—
Tip of upper jaw to angle of gape	38	—	42	—	48	—
Tip of upper jaw to apex of melon	—	—	—	—	60	—
Maximum width rostrum	—	—	—	—	40	—
Projection of upper jaw beyond lower jaw	5	—	5	—	3	—
Length of eye (right)	—	4.5	—	5	—	6
Length of eye (left)	—	—	—	—	—	6
Centre of eye to angle of gape (right)	—	6	—	6	—	6
Centre of eye to angle of gape (left)	—	—	—	—	—	6
Centre of eye to external auditory meatus (right)	—	14	—	15	—	14
Centre of eye to external auditory meatus (left)	—	—	—	—	—	14
Centre of eye to centre of blowhole (right)	—	28	—	28.5	—	28
Centre of eye to centre of blowhole (left)	—	—	—	—	—	28
Blowhole length	—	—	—	—	—	5
Blowhole width	—	6	—	5	—	8
Flipper width (right)	—	20	—	21.5	—	20
Flipper width (left)	—	—	—	—	—	20
Flipper length: tip to anterior insertion (right)	—	55	—	55	—	53
Flipper length: tip to anterior insertion (left)	—	—	—	—	—	53
Flipper length: tip to axilla (right)	—	41	—	42	—	40
Flipper length: tip to axilla (left)	—	—	—	—	—	40
Dorsal fin height	—	31	—	28	—	30
Dorsal fin base	—	68	—	62	—	—
Fluke span	—	75	—	85	—	—
Fluke width	—	26	—	27.5	—	—
Fluke depth of notch	—	6	—	5.5	—	4
Notch of fluke to centre of anus	130	—	140	—	128	—
Notch of fluke to centre of genital aperture	150	—	163	—	168	—
Notch of fluke to umbilicus	226	—	242	—	252	—
Notch of fluke to nearest point on leading edge of flukes	23	—	25	—	—	—
Girth at anus	—	108	—	106	—	—
Girth at axilla*	—	162	—	140	—	—
Girth at eye	—	124	—	—	—	—
Girth right in front of flippers*	—	144	—	124	—	—
Genital slit length	42	—	40	—	52	—

*Unrepresentative measurements due to weight loss of the animals before death.

Table 2. Standard body lengths and weights of false killer whales from Sea Life Park, on a diet of herring, mackerel and smelt (Marlee Breese, pers. comm), from Marineland of the Pacific (Brown *et al*., 1966), from Sea World (Odell *et al*., 1980) which were fed mackerel and herring (2:1), and from the 3 animals in the present study at the Harderwijk Marine Mammal Park.

Date/location	Animal	Gender	Body length (cm)	Body weight (kg)		Food intake (kg/day)	Food intake/day as a percentage of body weight
				Measured	Estimated		
Sea Life Park							
May 1965	Makapu'u	Female	313	—	540	—	—
September 1967	Makapu'u	Female	335	—	—	9–16	—
March 1976	Makapu'u	Female	368	—	—	—	—
March 1979	Makapu'u	Female	393	—	—	14–20	—
August 1991	Makapu'u	Female	410	—	720	—	—
March 1972	I'anui	Male	305	—	—	—	—
—1979	I'anui	Male	368	456	—	16–20	3.9
September 1976	Ahinalu	Male	—	365	—	—	—
January 1977	Ahinalu	Male	—	369	—	11	—
February 1978	Ahinalu	Male	—	419	—	16–20	4.3
August 1967	Ola	Male	238	—	135	—	—
March 1972	Ola	Male	325	284	—	11–16	4.9
July 1965	Olelo	Female	340	—	570	—	—
March 1970	Olelo	Female	355	—	—	16–20	—
July 1992	Pono	Male	—	367	—	11–14	3.5
October 1992	Pono	Male	—	399	—	14–16	3.8
August 1993	Pono	Male	352	394	—	14–16	3.8
October 1995	Pono	Male	382	518	—	11–16	2.9
October 1992	Maluhia	Female	—	280	—	14–16	5.4
August 1993	Maluhia	Female	310	330	—	15	4.5
February 1995	Maluhia	Female	318	412	—	14–20	4.1
Marineland of the Pacific							
November 1963	X	Female	324	374	—	—	—
August 1965	X	Female	390	499	—	—	4.7*
Sea World							
—	A	Female	297	250	—	15	6.0
—	B	Female	338	327	—	20	6.1
—	C	Female	358	359	—	15	4.2
—	D	Female	475	773	—	20	2.6
Present study							
November 1987	001	Female	318	340	—	—	—
— 1988	001	Female	—	350	—	13.9	4.1
September 1993	001	Female	390	450	—	15.3	3.4
November 1987	002	Female	330	360	—	—	—
— 1988	002	Female	—	380	—	14.8	4.1
November 1987	003	Male	312	310	—	—	—
— 1988	003	Male	—	350	—	13.3	4.3

*Calculated from the animal's average weight between November 1963 and August 1965 during which 13000 kg of fish and squid were consumed (Sergeant, 1969).

Weight and size

False killer whales are about 1.6–1.9 m long at birth (Smithers, 1938; Cowley, 1944; Ross, 1984; Kasuya, 1986; Slijper, 1949; Purves and Pillery, 1978). The male in the present study was about 20 cm longer than the females at the same age, and after the age of 5 years, his growth rate became higher than that of the females (Fig. 2). The latter phenomenon was also observed by Kasuya (1986) in wild false killer whales inhabiting Japanese waters. The growth rate observed in the present study is similar to one reported by Brown *et al*. (1966); a captive female

Table 3. Initial passage times (IPTs) of carmine red dye through the digestive tract of two female false killer whales at Harderwijk Marine Mammal Park.

Animal	Age (yrs)	Date (d/m/yr)	Time of day the dye was fed (h)	IPT (min)
Female 001	10	22-07-1993	15:04	229
Female 001	10	18-08-1993	15:10	214
Female 001	10	26-08-1993	15:08	212
Female 002	11	22-07-1993	14:56	271
Female 002	11	18-08-1993	15:10	221
Female 002	11	23-08-1993	08:28	247
Female 002	11	26-08-1993	15:05	205

grew 35 cm (between 343 and 378 cm) in less than 2 years. Purves and Pilleri (1978) report of an average annual growth rate of 10.4 cm after the first few years, with males reaching lengths about 30 cm longer than females. All North Pacific animals in the present study were longer than the false killer whales of corresponding ages from the North Atlantic described by Purves and Pilleri (1978). The age versus body length relationship given by Purves and Pilleri suggests a length growth until at least the age of 22 years in both sexes. The age versus body length relationship given by Kasuya (1986) suggests a length growth until about the age of 20 years in females and around 25–30 years in males. The maximum recorded length in males is 610 cm (Leatherwood and Reeves, 1983) and in females 506 cm (Perrin and Reilly, 1984).

Odell *et al*. (1980) provided the following formula based on four captive false killer whales which allows the calculation of body weight from body length:

$$W = 2.16 \times 10^{-4}\ L2.437$$

in which W is the body weight in kg and L is the standard body length in cm. Applying their formula to the body length and weight data in the present study shows that it underestimates the whales' weight by about 60 kg when they were between 3.1 and 3.3 m long. When the whales were around 3.9 m long, the formula fitted the animals of the present study better. The standard body length and weight ratios of the animals in the present study are similar to those of animals kept at Marineland of the Pacific (Brown *et al*., 1966), Sea World (Odell *et al*., 1980) and at Sea Life Park (Marlee Breese, pers. comm. of unpublished data; Table 2). When data from all 4 parks are included (one data point per animal), the relationship between standard body length (L in cm) and body weight (W in kg) can be expressed as (Fig. 5):

$$W = 260.33e^{0.0061(L - 290)}$$

Ross (1984) reports an intact carcass of a 358-cm, 372-kg, male false killer whale from South African waters. The length/weight ratio of this wild animal agrees with the values in Figure 5. Scheffer and Slipp (1948) report a 523-cm-long animal of 902 kg. The length/weight ratio of this wild animal agrees with the values in Figure 5 when extrapolating the line. Comparisons of the real weights and estimated weights in Table 2 show a tendency to over-estimate the weights of false killer whales. This may be due to the long slender body shape of this species.

Because the detailed morphological measurements of the study animals were taken after a period of illness, which caused weight loss, some of the girth measurements deviate from those of healthy animals of the same length. External measurements of false killer whales have been published only in a few cases; a calf from waters around South Africa (Ross, 1984), from stranded animals on the British Isles (Fraser, 1936), an animal from the eastern North Atlantic (Purves and Pilleri, 1978) and animals from the western North Pacific (Mizue and Yoshida, 1961).

Food consumption relative to body weight

Only little information has been published on the body weights and food intake of false killer whales (Brown *et al*., 1966; Odell *et al*., 1980). The food intake, as a proportion of body weight, of the animals at Sea Life Park was in the same range as that of the animals in the present study which were kept in water with a lower annual average temperature (Table 2, Fig. 6). This intake similarity, despite a large water temperature difference, could be because the caloric content of the food at Sea Life Park was lower than in the present study (which is unlikely because the diets were similar), or because the animals were less active at Sea Life Park than in Harderwijk (this seems also unlikely after observing the animals at both parks). Maybe the animals adapted the thickness of their blubber layer (Williams and Friedl, 1990) or its composition (= insulating properties; Worthy and Edwards, 1990) to the water temperature. One of the two young animals at Sea World ate a relatively large amount. This and the relatively high food intake record reported for an animal at Marineland of the Pacific can not be explained with the available information (Brown *et al*., 1966).

Food passage time

Although this study is based on a small sample size, the passage time of carmine red through the digestive tract of the false killer whale was short for its body size, compared to other odontocetes (Kastelein *et al*., 1993, 1994, 1997c, 1999, 2000 a

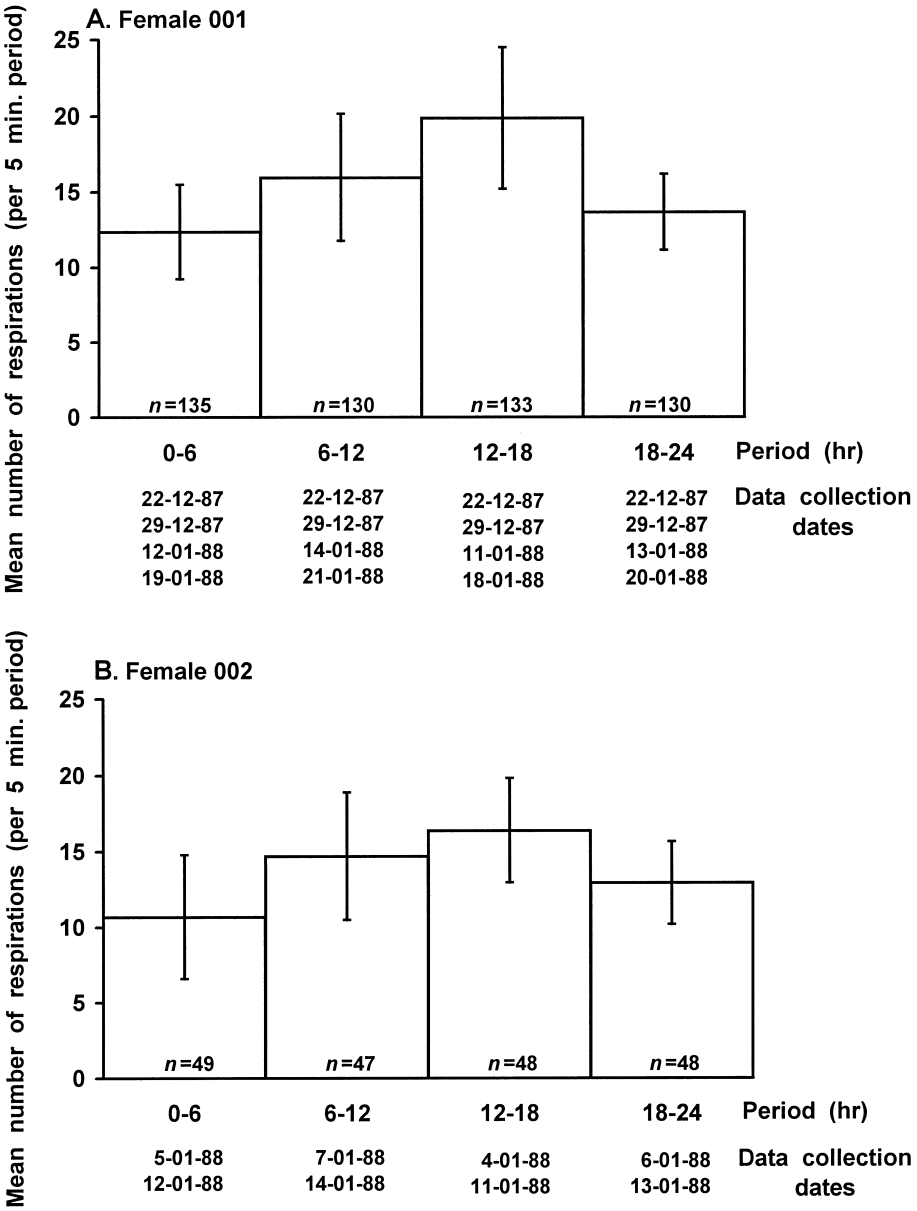

Figure 4 A and B

and b). This suggests that the species has a relatively short digestive tract or a high metabolic rate for its body weight and size. The latter seems to be the case, as the animals in the present study had a high daily food intake as a percentage of body weight, compared to the smaller bottlenose dolphins kept in the same pool system (Kastelein *et al.*, 2000b). This high metabolic rate may be due to the elongated body shape of the false killer whale, making the body surface to body volume ratio relatively large.

Respiration rate

Adult false killer whales in the wild breathe 20–25 times per 5 min when swimming at a speed of 11–22 km/h (Mörzer Bruyns, 1971). This rate is slightly higher than in the present study. However,

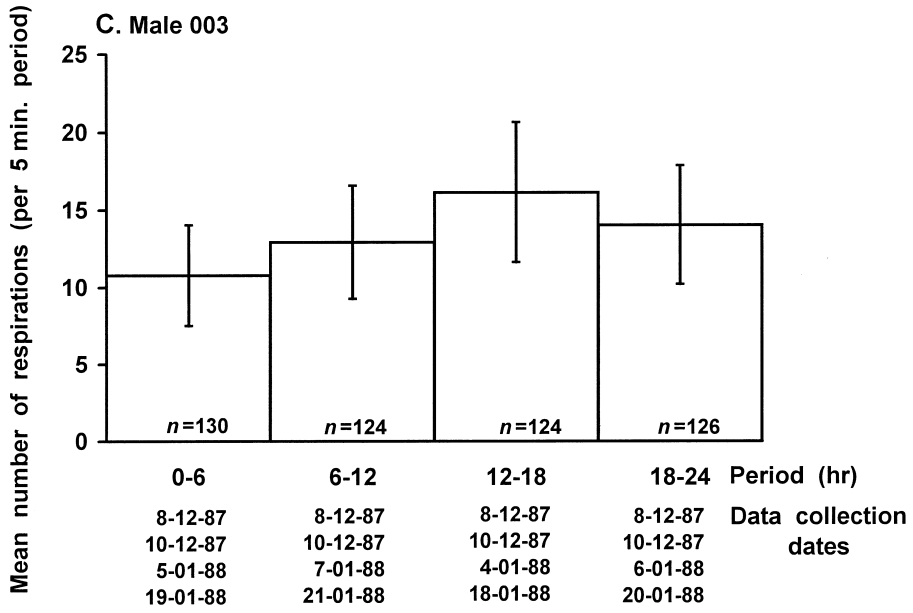

Figure 4 C

Figure 4. Average number of respirations during 5-min periods by three false killer whales during six-hour periods. *n*=the number of 5 min periods during which respirations were counted (these samples are not independent as they are taken on only 2 or 4 days per 6 h period). (A) female 001, (B) female 002, and (C) male 003. The date is shown in day-month-year.

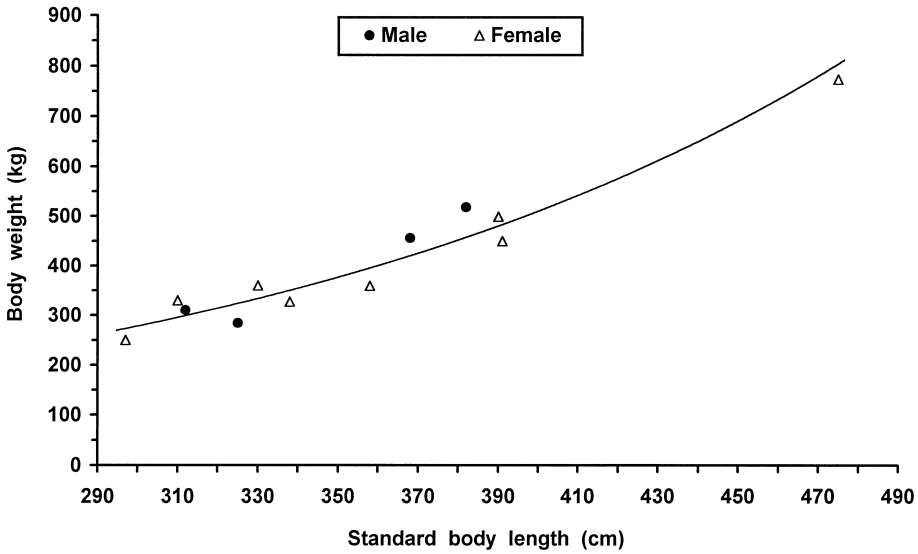

Figure 5. Relationship between standard body length and body weight of false killer whales (one data point per animal) at Harderwijk Marine Mammal Park (present study), Sea Life Park, Marineland of the Pacific, and Sea World.

because respiration rates depend on many parameters, such as age of an animal, activity level, physiological and psychological state, comparison of rates reported in the literature is of little value unless all relevant parameters are reported. Respiration rates in odontocetes are, for instance, related to diving patterns (Kastelein and Gerrits, 1991).

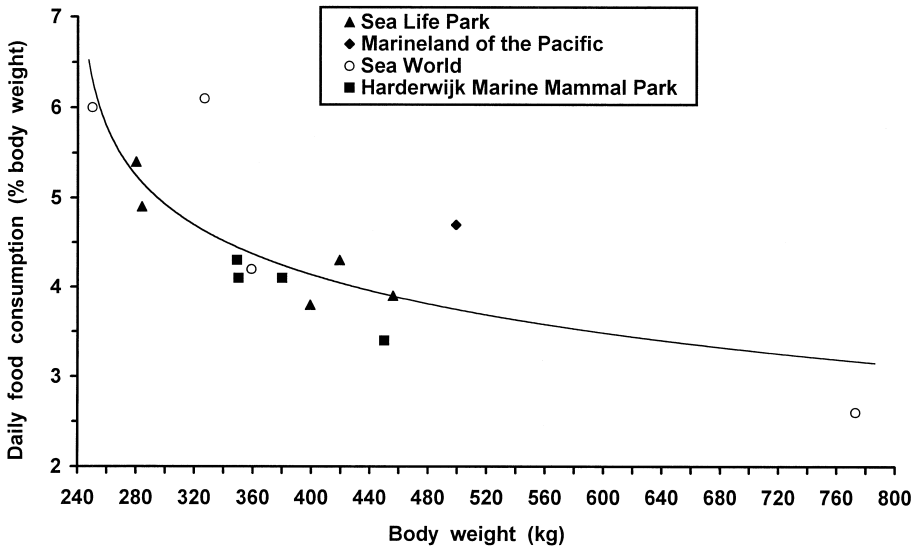

Figure 6. Relationship between body weight and daily food intake (as a percentage of body weight) of false killer whales of both sexes (one data point per animal) at 4 oceanaria. The line is described by the following formula: daily food intake (as % of body weight)=8.25 − 0.81 Ln (body weight (in kg) − 240).

Ecological significance

Potential differences between the food intakes reported in the present study and those of false killer whales of similar size and gender in the wild may be due to differences in the water temperature, the caloric content and composition of the food or the animals' activity levels.

The annual average water temperature in the present study was 19°C. False killer whales usually inhabit seas with surface temperatures of above 20°C (Mörzer Bruyns, 1971), although they are sometimes seen in waters as cool as 9°C (Stacey and Baird, 1991). When they dive, they encounter lower temperatures. Because the natural diet of false killer whales varies greatly geographically and probably seasonally (see summary in Odell and McClune, 1999), it is not useful to speculate about possible calorific differences between the diets of the animals in the present study and their wild conspecifics. Little is known about the diving behaviour of false killer whales, and thus about the energy used for locomotion, but wild false killer whales obviously dive deeper than the captive animals in the present study. Therefore, false killer whales in the wild probably consume more food than the animals in the present study.

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