

Food consumption and suckling in Killer whales

Orcinus orca

at Marineland Antibes

R. A. KASTELEIN^{1,4}, J. KERSHAW², E. BERGHOUT¹ & P. R. WIEPKEMA³

¹Harderwijk Marine Mammal Park, Strandboulevard Oost 1, 3841 AB Harderwijk, The Netherlands (part of Grevin et Compagnie, France), ²Marineland, Avenue Mozart, 06600 Antibes, France, and ³Emeritus Professor of Ethology, Wageningen Agricultural University, Stationsweg 1, 6861 EA Oosterbeek, The Netherlands

Between 1976 and 1996 food consumption and suckling in Killer whales *Orcinus orca* maintained at Marineland Antibes, France, were studied. The food intake of the whales was still increasing at 20 years of age, when they were consuming c. 19 000 kg of fish per year. Wild Killer whales will expend more energy foraging than captive animals and probably eat more than 19 000 kg/year. A seasonal pattern of food consumption was observed in all the whales, although this may have been caused by seasonal changes in the feeding schedule. Data on the number of suckling bouts per 24 hours in the first 5–10 days after birth of 1.1 calves are presented, together with the body measurements of a 13 year-old ♂.

Key-words: energetics, food consumption, killer whale, lactation, odontocete, reproduction, suckling

Although the Killer whale *Orcinus orca* is the third most widely kept odontocete, or toothed whale, in the world after the Bottlenose dolphin *Tursiops truncatus* and the Beluga or White whale *Delphinapterus leucas*, few studies have been carried out on the food requirements of the species (Scheffer & Slipp, 1948; Nishiwaki & Handa, 1958; Norris & Prescott, 1961; Burgess, 1968; Griffin & Goldsberry, 1968; Hewlett & Newman, 1968; Rice, 1968; Caldwell & Caldwell, 1969; Martinez & Klinghammer, 1969; Sergeant, 1969; Yukhov *et al.*, 1975; Castello, 1977; Heyning, 1988; Kastelein & Vaughan, 1989; Hoyt, 1990; Kriete, 1995; Kastelein *et al.*, 2000). Information on food consumption, body measurements and changes in mass of toothed whales could

be useful for veterinary and husbandry purposes to permit staff to compare the data from their animals with other reference material. Data on food consumption are also needed for the management of odontocetes in the wild to evaluate the relationship between a species and its prey populations, and for the management of fish stocks to create a carrying capacity for a certain number of toothed whales in a particular geographical area. This paper describes food consumption and suckling in Killer whales at Marineland Antibes, France, between 1976 and 1996.

STUDY ANIMALS

The study animals were 4.4 Killer whales and included 3.3 individuals which originated from the waters around Iceland and 1.1 calves born at Marineland Antibes (Table 1). The older an animal was on arrival, the more difficult it was to estimate age. Age 1 is the first calendar year after birth. The standard body length, measured as a straight line between the tip of the rostrum and the notch in the tail-fluke, and body mass were recorded for ♂ 006 at 13 years of age and ♀ 002 at 4 years of age.

STUDY AREA

Between 1976 and 1986 the Killer whales were maintained in an outdoor pool system comprising a square main pool

⁴ Present address: Julianalaan 46, 3843 CC Harderwijk, The Netherlands.

ID CODE	SEX	ESTIMATED YEAR OR DATE OF BIRTH	ORIGIN	DATE OF ARRIVAL AT MARINELAND ANTIBES
OoMA001	♂	1967	Iceland	29 October 1976
OoMA002	♀	1974	Iceland	30 November 1978
OoMA003	♀	1975 (1973–1978)*	Iceland	6 March 1983
OoMA004	♂	1976 (1975–1980)*	Iceland	6 March 1983
OoMA005	♀	1982	Iceland	12 January 1990
OoMA006	♀	1982	Iceland	12 January 1990
OoMA007	♀	25 February 1993	Antibes‡	
OoMA008	♂	13 February 1996	Antibes§	

* Range of estimated birth year.

‡ Calf of ♂ 004 and ♀ 005.

§ Calf of ♂ 004 and ♀ 003.

Table 1. The eight Killer whales *Orcinus orca* maintained at Marineland Antibes and included in the study of food consumption and suckling.

measuring 25 m × 15 m × 3.5 m deep and an adjacent medical pool measuring 15 m × 8 m × 3.5 m deep. One to three Bottlenose dolphins were kept in the same pool. Between 1986 and 1996 the Killer whales were maintained as a single-species group in a larger outdoor pool system comprising an oval main pool, measuring 70 m × 30 m × 2.5–10 m deep with a volume of 8000 m³, and two circular side pools, each measuring 20 m diameter and 4.5 m deep.

The pools were filled with sea water from the Mediterranean. Marineland Antibes is located at 7° 3' E and 43° 30' N and the average monthly air temperature ranged between 8°C in January and 23°C in July and August. The average monthly water temperature ranged between 9°C in February and 24°C in August.

DIET

The whales were fed four or five times per day from December to June and six or seven times per day during the evening-show season, between July and November. The diet comprised c. 50% Herring *Clupea harengus* and 50% Mackerel *Scomber scombrus*, based on mass. The fish were frozen and stored for a maximum of 4 months. After defrosting,

Sea-tabs® or Aquavits® vitamins were added to the fish. The whales were offered as much fish as they could eat at the last feed of the day; feeding was stopped when the whales started to play with the fish instead of swallowing immediately. Females which were known to be pregnant, and their pool mates, were offered fish *ad libitum* at every feed.

Records were kept of the amount and type of food consumed at each feed and the daily food intake data formed the basis of the present study. Only data collected for complete calendar years were included.

SUCKLING

On 25 February 1993, after a gestation period of 15 months, ♀ 005 gave birth to calf ♀ 007. The calf had a standard body length of 2.1 m. Between 25 February and 7 March ♀ 005 and the calf were observed 24 hours a day and the duration of all suckling bouts was recorded.

On 13 February 1996 ♀ 003 gave birth to calf ♂ 008. Between 13 and 18 February ♀ 003 and the calf were observed 24 hours a day and the duration of all suckling bouts was recorded.

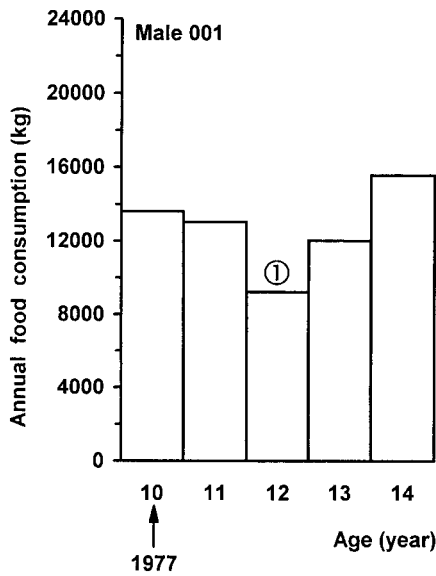


Fig. 1. The annual food consumption of Killer whale *Orcinus orca* ♂ 001. Age 1 is the first calendar year after birth: 1. a year when ♂ 001 was ill for several months.

STATISTICAL ANALYSIS

The statistical analysis was carried out using MINITAB release 10 for Windows with a significance level of 5% (Ryan *et al.*, 1985).

ANNUAL FOOD CONSUMPTION

All ages are estimates except for animals born at Marineland Antibes.

Males Between 10 and 14 years of age the annual food consumption of ♂ 001 was *c.* 13 500 kg, except at *c.* 12 years old when food intake decreased, probably as a result of illness and sexual activity with newly introduced ♀ 002 (Fig. 1).

The annual food intake of ♂ 004 gradually increased from 7000 kg at 8 years of age to *c.* 17 000 kg at 14 years of age, when it appeared to stabilize (Fig. 2). In 1993, however, ♀ 003 and ♀ 005 were pregnant, and ♂ 004 (17 years old) and ♂ 006 (11 years old) both ate more than usual. This increase in food intake in the ♂♂ was probably the result of fish being

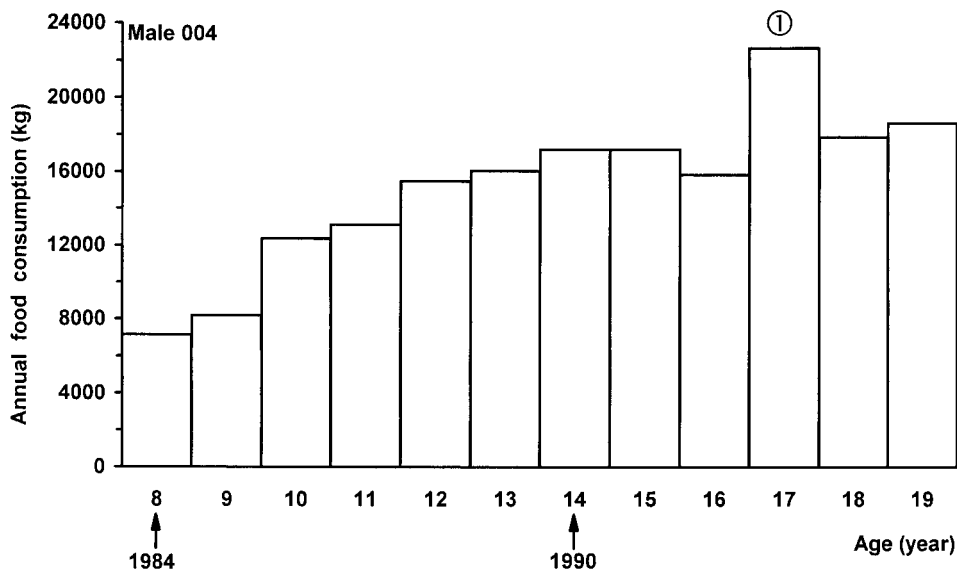


Fig. 2. The annual food consumption of Killer whale ♂ 004: 1. high level of food intake coincided with pregnancy in ♀ 003 and ♀ 005, and suckling of ♀ 007. Years 1984 and 1990 are indicated to allow comparison of the data for all animals in the present study.

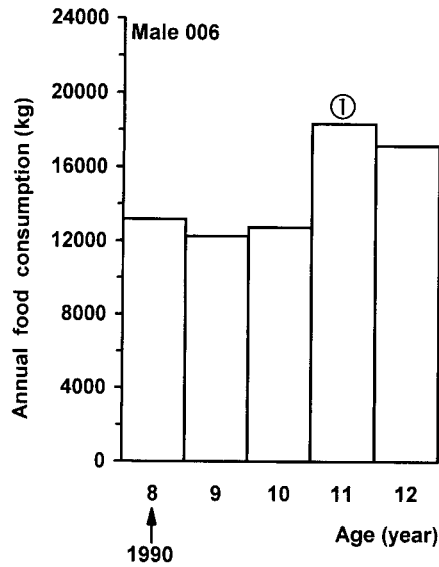


Fig. 3. The annual food consumption of Killer whale ♂ 006: 1. high level of food intake coincided with pregnancy of ♀ 003 and ♀ 005.

offered *ad libitum* at every feed to pregnant ♀♀ and their pool mates.

The annual food intake of ♂ 006 was *c.* 12 500 kg between 8 and 10 years of age

(Fig. 3). At 11 and 12 years of age 18 000 and 17 000 kg of fish were consumed annually, respectively. In November 1995 ♂ 006 was transferred to Sea Paradise, Japan.

Females Between 5 and 9 years of age the annual food intake of ♀ 002 increased gradually from 3600 kg to 14 000 kg and then fell to *c.* 12 000 kg (Fig. 4).

The annual food intake of ♀ 003 was *c.* 10 500 kg at 9 and 10 years of age and then increased to *c.* 14 500 kg (Fig. 5). Female 003 was pregnant for the first time at 15 years of age and annual food consumption rose to 18 000 kg. On 3 March 1991 a full-term stillborn calf was delivered. At 17 years of age ♀ 003 was pregnant again and annual food consumption was 22 000 kg. On 5 June 1993 another full-term stillborn calf was delivered. The last pregnancy for this ♀ during the present study was at 20 years of age when ♀ 003 consumed 20 500 kg of fish annually. On 13 February 1996 calf ♂ 008 was delivered alive and ♀ 003 increased her daily food consumption

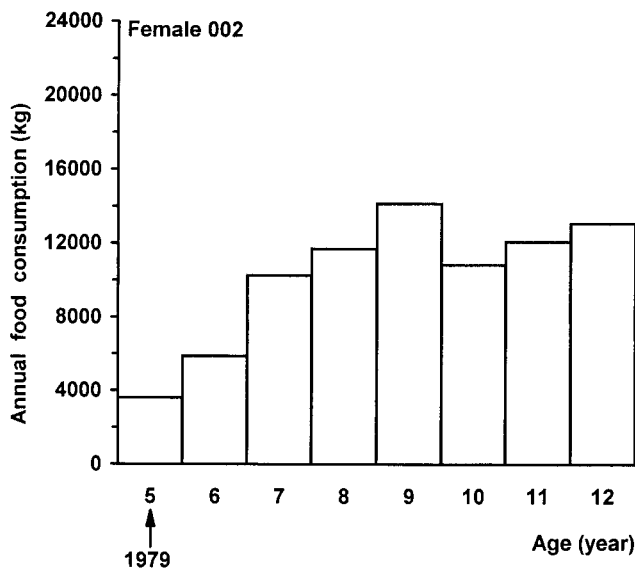


Fig. 4. The annual food consumption of Killer whale ♀ 002.

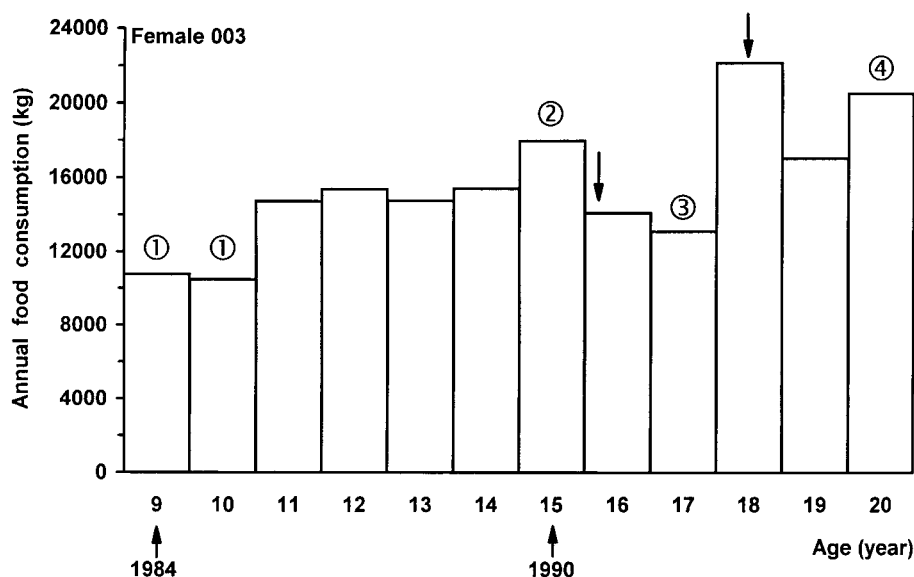


Fig. 5. The annual food consumption of Killer whale ♀ 003: 1. years in which ♀ 003 was ill for several months; 2. year when ♀ 003 was pregnant (arrow indicates 3 March the following year when a full-term calf was stillborn); 3. year when ♀ 003 was pregnant (arrow indicates 5 June the following year when a full-term calf was stillborn); 4. year when ♀ 003 was pregnant (♂ 008 was live-born on 13 February 1996). Years 1984 and 1990 are indicated to allow comparison of the data for all animals in the present study.

from *c.* 55 to 80 kg/day. Four months after giving birth her food intake had returned to the pre-birth level.

The annual food intake of ♀ 005 at 8–10 years of age was *c.* 12 000 kg (Fig. 6). This ♀ became pregnant for the first time at 9 years of age and 15 months later, at 11 years of age, delivered a live calf (♀ 007) and her food consumption increased to *c.* 18 000 kg/year. In early 1993 ♀ 005 was consuming 55 kg/day but, after delivering the calf on 25 February, she did not eat much for 3 weeks. In April her food intake increased to 65 kg/day and then to *c.* 80 kg/day in May. Four months after giving birth her food intake decreased to *c.* 50 kg/day, approximately 10 kg above pre-birth levels.

At 6 months of age ♀ 007 began to eat fish regularly and annual solid food intake increased from 575 kg in the first year to 4700 kg in the second year of age (Fig. 7). Calf ♀ 007 suckled, at least occasionally, until *c.* 2 years of age.

The annual food consumption data for the seven study animals which consumed solid food are shown in Fig. 8. Food consumption in *O. orca*, both ♂♂ and ♀♀, increased until 20 years of age; older animals were not available for this study.

SEASONAL FLUCTUATION IN FOOD CONSUMPTION

To determine whether seasonal fluctuations in food intake occurred, the average daily food intake was calculated for each month and, for each year, the average monthly food intakes were ranked from one to 12. The average rank per month was calculated for each animal, only including years in which no extreme growth, pregnancy, lactation or illness occurred.

Most of the whales consumed less than the annual average between February and June, and more than average between July and January (Fig. 9). The average sea-

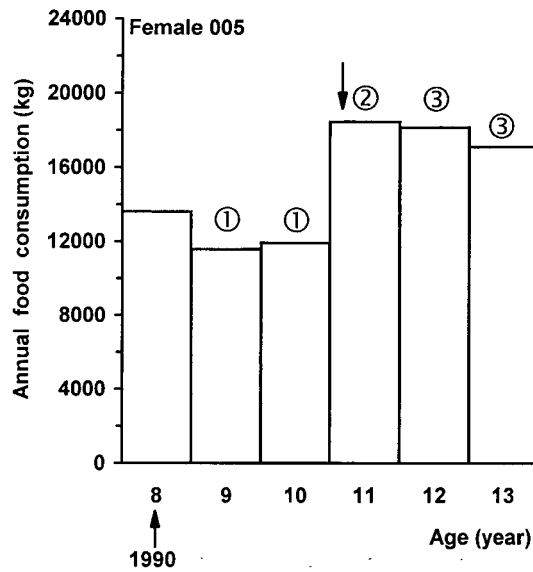


Fig. 6. The annual food consumption of Killer whale ♀ 005: 1. years when ♀ 005 was pregnant; 2. ♀ 007 was live-born on 25 February (arrow) and was suckled during the rest of the year; 3. years in which the calf was still suckling occasionally.

sonal air and water temperatures at the study area are shown in Fig. 10.

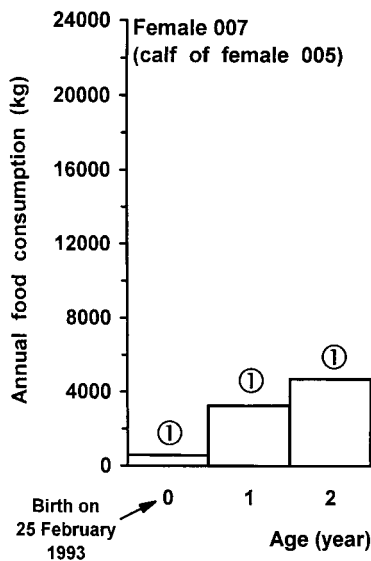


Fig. 7. The annual food consumption of Killer whale calf ♀ 007: 1. year in which the calf was still suckling in addition to eating fish.

SUCKLING

On 25 February 1993 at 2200 hours ♀ 007 was born and began to suckle 12 hours later (Plates 1 and 2). The number of suckling bouts per day and their mean duration for the first 10 days after birth are shown in Table 2. In April 1993, at the age of 2 months, ♀ 007 began to eat fish and from the end of August 1993 she consumed some fish every day (Fig. 8).

On 13 February 1996 at 1719 hours ♂ 008 was born and began to suckle 3 hours later. The number of suckling bouts per day and their mean duration for the first 5 days after birth are shown in Table 2. A Student's *t*-test showed no significant differences between the number of suckling bouts for the two calves ($t=0.39$; $df=5$; $P=0.71$). On 2 April 1996, at the age of 6 weeks, calf ♂ 008 began to eat fish and by mid-September was consuming fish every day. By February 1997 ♂ 008 was eating larger quantities of fish and no longer appeared to rely on his mother for food.

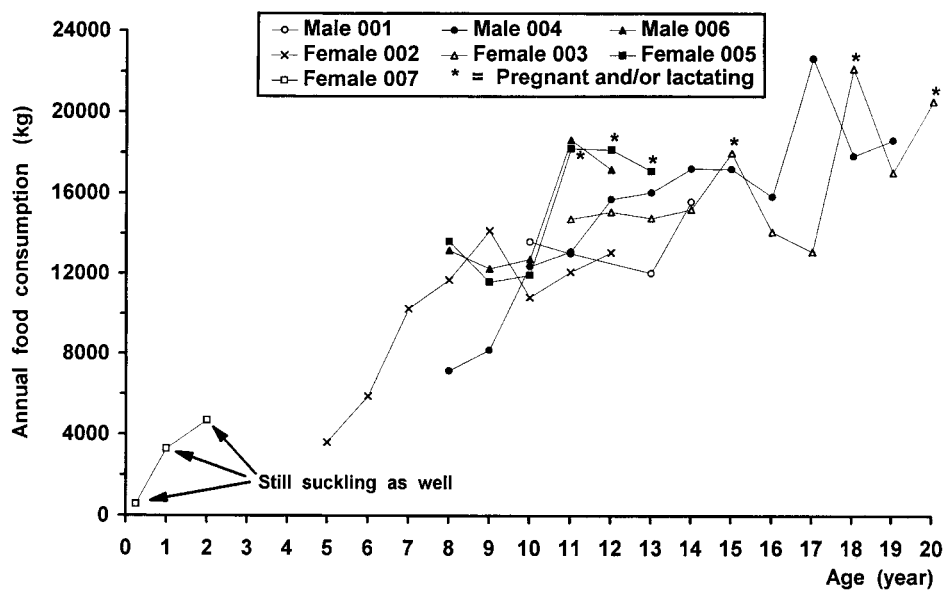


Fig. 8. The annual food consumption for all the study animals eating fish. Low annual food intakes as a result of illness are not included: * pregnant and/or lactating.

BODY MEASUREMENTS

The standard body length and mass of Killer whales in the literature, and ♂ 006

and ♀ 002 in the present study are shown in Table 3 and are plotted in Fig. 11. The relationship of standard body length to

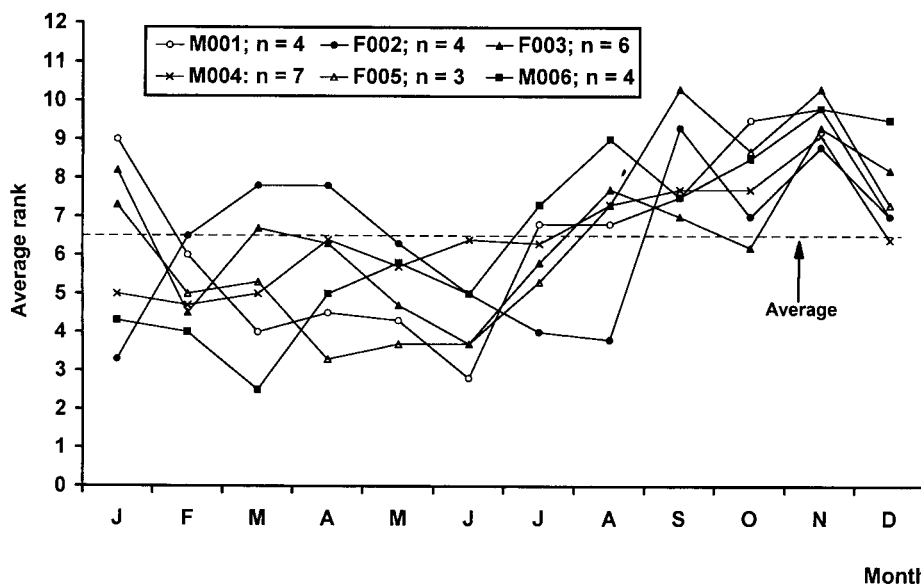


Fig. 9. The average monthly rank in food intake for six Killer whales. A high rank number indicates a high food intake: n = number of years of data.

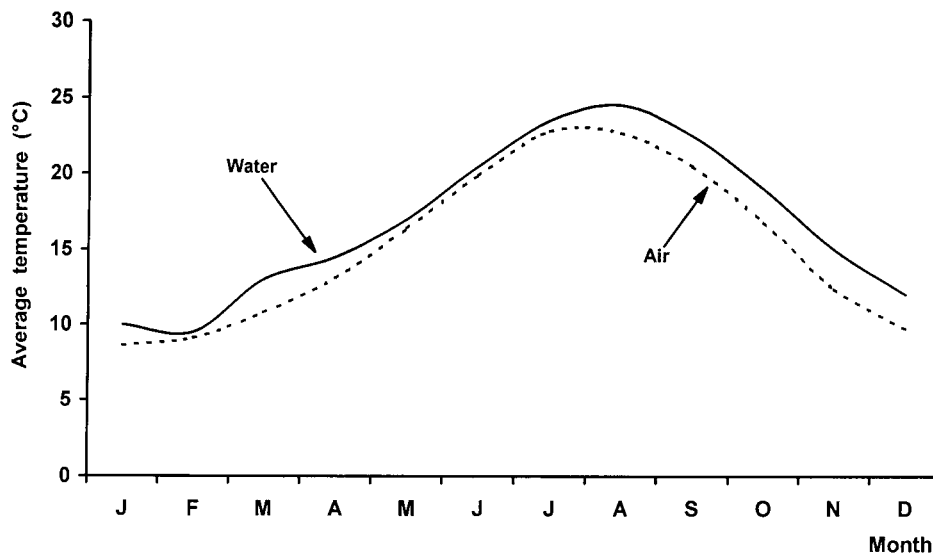


Fig. 10. The average monthly air and water temperatures in the study area at Marineland Antibes: $n = 10$ years.

body mass can be expressed as $W = 246.92e^{0.0063(L-200)}$, where L is standard body length (cm) and W is body mass (kg).

On 14 March 1995, when ♂ 006 was 13 years old and had a mass of 2900 kg, some of his body measurements were recorded (Table 4).

FOOD CONSUMPTION AS A PERCENTAGE OF BODY MASS

The average daily food consumption, calculated as a percentage of body mass, is shown in Table 3 and the data are plotted in Fig. 12. The relationship between body mass and average daily food consumption, calculated as a percentage of body mass, can be expressed as $F = 7.8325^{-0.0005W}$, where W is body mass (kg) and F is average daily food consumption (wet mass) as a percentage of body mass.

DISCUSSION AND CONCLUSIONS

Annual food consumption Food consumption in Killer whales in the present study continued to increase to the age of 20 years. In the wild, Killer whales reach

physical maturity at 20–25 years of age (Christensen, 1984). The average annual food consumption of the whales in the present study was similar to that of a non-pregnant, non-lactating ♀ Killer whale between 5 and 11 years of age at Harderwijk Marine Mammal Park (Kastelein & Vaughan, 1989) and to that of a non-pregnant, non-lactating ♀ Killer whale kept both at Windsor Safari Park and Sea World (Kastelein *et al.*, 2000). The small difference in food intake between the sexes, despite the difference in body mass after 10 years of age, is probably a result of the higher level of activity of ♀♀, which interacted with the calves more than ♂♂. The average food consumption of Killer whales at Vancouver Aquarium and Marine World Africa, Vallejo, CA, USA, was higher than in the present study for animals of similar mass and gender (Kriete, 1995). This may have been the result of a higher calorific content of the diet and/or a higher water temperature in the present study.

Seasonal fluctuation in food consumption The seasonal fluctuation in food

intake reported here does not seem to be related to the water temperature (see Figs 9 and 10) and may be related to seasonal changes in the feeding schedule. Between July and November additional shows take place in the evening, allowing the whales to eat over a longer period of the day and resulting in a higher daily food intake than in periods without evening shows. No regular seasonal pattern in food intake was observed in two Killer whales at other facilities (Kastelein & Vaughan, 1989; Kastelein *et al.*, 2000).

Influence of gestation and lactation When ♀ 005 was pregnant at 9–10 years of age,

her food intake remained within the normal range and only increased after giving birth. This phenomenon was also observed by Kriete (1995) in *O. orca* at two oceanaria in North America. The length of gestation can range between 15 and 18 months (Duffield *et al.*, 1995). Asper *et al.* (1988) described a pregnant ♀ Killer whale with an estimated mass of 2200 kg which ate 64–68 kg fish per day during the first few months of gestation but increased to 77 kg/day at 13 months. Towards the end of month 14 and throughout month 15, her food consumption varied between 64 and 82 kg/day, stabilizing at 82 kg/day for the rest of the



Plate 1. Killer whale *Orcinus orca* ♀ 005 and her calf ♀ 007 a few days after birth. Jacques Foudraz.



Plate 2. Killer whale ♀ 005 and her calf ♀ 007 on the left, and ♀ 003 on the right. Jacques Foudraz.

pregnancy. In the week before giving birth ♀ 005 consumed *c.* 91 kg/day but reduced her food intake 1 day before the birth.

After giving birth in 1996, ♀ 003's daily food consumption increased from *c.* 55 to

80 kg/day. Four months later food intake had returned to the pre-birth level. The food consumption of the Killer whale described by Asper *et al.* (1988) increased to 110–118 kg/day after giving birth and

DAYS AFTER BIRTH	♀ 007			♂ 008		
	NO. SUCKLING BOUNTS (per day)	MEAN BOUT DURATION (seconds)	TOTAL DAILY SUCKLING TIME (minutes)	NO. SUCKLING BOUNTS (per day)	MEAN BOUT DURATION (seconds)	TOTAL DAILY SUCKLING TIME (minutes)
0	0	0	0	10	84 ± 88	14
1	38	183 ± 303	116	55	282 ± 230	252
2	28	663 ± 313	287	33	473 ± 344	260
3	34	403 ± 218	215	27	469 ± 200	211
4	35	364 ± 164	188	26	443 ± 314	192
5	34	400 ± 180	194	20	486 ± 347	162
6	36	316 ± 151	187			
7	24	320 ± 172	122			
8	21	341 ± 141	113			
9	26	389 ± 173	149			
10	34	283 ± 131	146			

Table 2. The number of suckling bouts per day, mean bout duration (\pm standard deviation), and total daily suckling time for Killer whale calves ♀ 007 and ♂ 008 at Marineland Antibes. Day 0 is the day of birth.

INSTITUTION	STANDARD BODY LENGTH (cm)	BODY MASS (kg)	AVERAGE DAILY FOOD CONSUMPTION (kg)	AVERAGE DAILY FOOD CONSUMPTION AS % OF BODY MASS	SOURCE
♂♂					
Vancouver Aquarium	467	1040	45	4.3 ⁵	Hewlett & Newman (1968)
Marineland Antibes	560	2900	47	1.6 ⁶	Present study (♂ 006)
Seattle Aquarium	660	3600			Griffin & Goldsberry (1968)
Seattle Aquarium	430	1000			Griffin & Goldsberry (1968)
Seattle Aquarium	698	4554†			Griffin & Goldsberry (1968)
Seattle Aquarium	385	1031†			Griffin & Goldsberry (1968)
Windsor Safari Park	432	1200			Kastelein <i>et al.</i> (2000)
♀♀					
Vancouver Aquarium	470	1136	50	4.4 ¹	Sergeant (1969)
Sea World San Diego	411	1088			Burgess (1968)
Sea World San Diego	450	1358		3.6 ⁴	Burgess (1968)
Marineland Antibes	350	856			Present study (♀ 002)
Harderwijk Park	270	315	19	6.0 ²	Kastelein & Vaughan (1989)
Harderwijk Park	520	1900	41	2.1 ²	Kastelein & Vaughan (1989)
Sea World of Ohio	441	1530	56	3.6 ⁷	Kastelein <i>et al.</i> (2000)
Seattle Aquarium	430	1000*	54	5.4 ³	Griffin & Goldsberry (1968)
Seattle Aquarium	250	270			Griffin & Goldsberry (1968)
Seattle Aquarium	290	390			Griffin & Goldsberry (1968)
Seattle Aquarium	330	700			Griffin & Goldsberry (1968)
Seattle Aquarium	460	1360			Griffin & Goldsberry (1968)
Seattle Aquarium	579	2540†			Griffin & Goldsberry (1968)
Wild (California)	260	213†			Heyning (1988)

* Estimated mass.

† Post mortem.

Table 3. Body length and mass measurements, and food consumption of Killer whales in the literature and in the present study: ¹Herring *Clupea harengus* and Ling cod *Ophiodon elongatus*; ²35% Herring, 36% Mackerel *Scomber scombrus*, 6% Whiting *Merlangius merlangus*, 12% Sprat *Sprattus sprattus* and 11% Squid *Illex sp*; ³Salmon *Oncorhynchus spp*; ⁴Mackerel and Bonita *Sarda sarda*; ⁵Ling cod, Herring and Salmon; ⁶50% Herring and 50% Mackerel; ⁷46% Herring, 28% Capelin *Mallotus villosus*, 15% Surf smelt *Osmeridae*, 10% Mackerel and 1% Salmon *Salmo salar*.

remained stable until the calf was weaned and for 6 months after weaning. Lactating ♀♀ probably eat more than ♀♀ in late pregnancy because suckling calves require high energy levels, and therefore more milk, for thermoregulation.

Suckling and transfer to solid food For the first 10 days after birth ♀ 007 suckled, on average, 32 times per day for an average of 172 minutes/day. For the first 5 days after birth ♂ 008 suckled, on average, 32 times per day for an average of 215 minutes/day, excluding the day of birth. Asper *et al.* (1988) describe a ♀ calf

which suckled for 26 minutes on the day of birth and for 55–90 minutes/day over the next 5 days. Suckling bouts lasted for 4–26 seconds, with the mean duration of bouts decreasing over time to 8 seconds.

The calf described by Asper *et al.* (1988) first consumed fish at 3 months of age and was eating fish regularly at 5.5 months, although she continued to suckle until *c.* 18 months of age. Calves ♀ 007 and ♂ 008 began to eat fish at *c.* 2 months of age and ate fish regularly by *c.* 6 months. Calf ♀ 007 continued to suckle, at least occasionally, for 2 years. For wild and captive Killer whales the consumption of

solid food begins at an early age but weaning takes much longer (Heyning, 1988).

Body measurements The study animals were rarely weighed and measured, and were probably not fully grown at the end of the study. Males can reach a length of 9.5 m and a mass of 8000 kg while ♀♀ are smaller, rarely exceeding 7 m and 4000 kg (Matkin & Leatherwood, 1986). Christensen (1984) presented data on ♂ Killer whales from the Lofoten area showing that, on average, after *c.* 14 years of age, ♂♂ are longer than ♀♀. Physical maturity is reached at 20–25 years of age.

The body measurements of a ♂ Killer whale calf and an adult ♂ from South African waters (Ross, 1984), and a ♀ Killer whale (Kastelein & Vaughan, 1989) have been published. Bigg & Wolman (1975) present a length (*L*) to body mass (*W*) relationship based on data from 32 *O. orca* from the eastern Pacific ($W=0.00208L^{2.577}$), which is almost the same as that reported in the present study.

	LENGTH (cm)
Standard body length	560
Tip lower jaw to anterior insertion of flipper	95
Distance between insertion of flippers (chest)	64
Flipper length	65
Flipper width	50
Dorsal fin height	88
Tail fluke span	155
Tail fluke width	60

Table 4. Body measurements of 13 year-old ♂ 006 as measured on 14 March 1995. The ♂ had a mass of 2900 kg at this time.

Food consumption as a percentage of body mass The present study suggests that the larger the Killer whale, the smaller the average daily food consumption as a proportion of body mass. Data from *O. orca* with body masses ranging from 500 to 5500 kg at Vancouver Aquarium and Marine World Africa showed a similar relationship between body mass and food consumption (Kriete, 1995). A decrease in metabolic rate per kg of body mass with

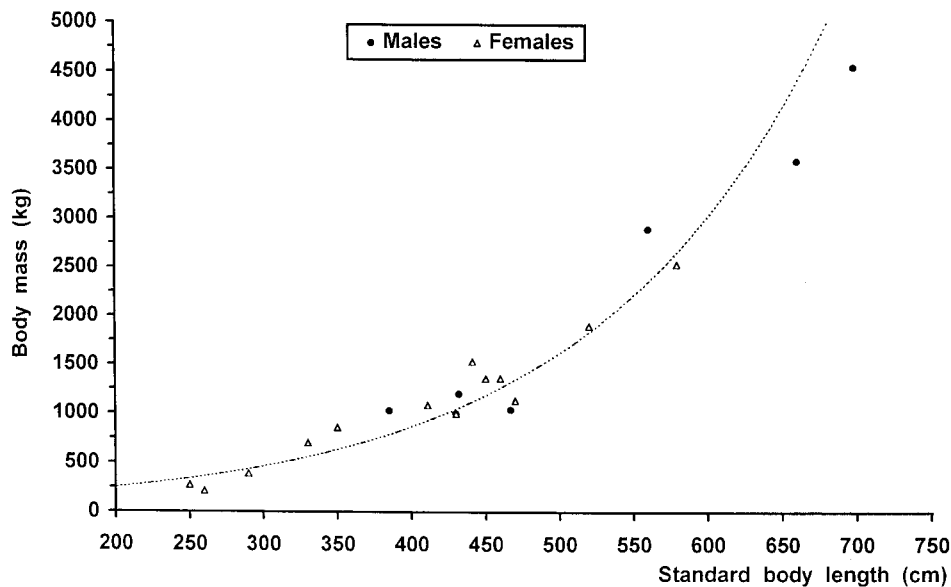


Fig. 11. The relationship between standard body length and body mass of the Killer whales in the present study and those available in the literature. Only independent data from Table 3 are used.

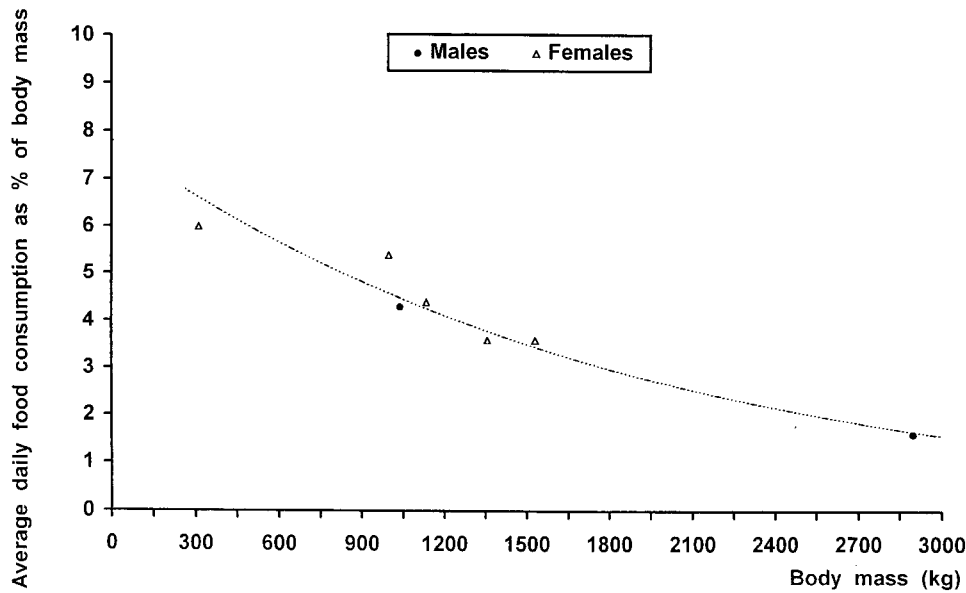


Fig. 12. The relationship between body mass and average daily food consumption as a percentage of body mass of Killer whales in the present study and those available in the literature. Only independent data from Table 3 are used.

increasing mass is also observed in terrestrial mammals (Kleiber, 1975).

Ecological significance The movements of Killer whales appear to be linked to changes in the distribution of fish stocks (Heimlich-Boran, 1986). If we wish to ensure that *O. orca* populations remain healthy, fish-catch quotas should be determined accordingly. How well the food consumption of the whales in the present study reflects that of wild Killer whales is not known. The food intake of odontocetes is probably influenced by individual variation in metabolic rate, activity level, water temperature, and the calorific content and digestibility of the diet.

The diet of the whales in the present study was not the same as that of wild conspecifics. Wild Killer whales hunt in groups and feed opportunistically on invertebrates, fish and marine mammals (Rice, 1968; Castello, 1977; Slijper, 1979; Gaskin, 1982; Hall, 1986; Heyning & Dahlheim, 1988; Thomas & Felleman,

1988; Wenzel & Sears, 1988; Hoyt, 1990; Silber *et al.*, 1990; Matkin & Dahlheim, 1995; Yano & Dahlheim, 1995). The effect of water temperature on food consumption is not clear. The body mass to surface ratio of Killer whales is higher than that of smaller odontocetes (Brody, 1945), therefore they lose comparatively less energy to the environment by convection than smaller odontocetes. In addition, the blubber layer has good insulating properties (Kasting *et al.*, 1989). Because Killer whales have a wide distribution, they probably have an adaptable thermoneutral zone, like Bottlenose dolphins (Williams *et al.*, 1992). No correlation was found between water temperature and food consumption in Killer whales maintained in water between 7 and 23°C, so these temperatures are probably within the thermoneutral range of the species (Kriete, 1995). Little is known about the activity level of wild Killer whales but it is probably much higher than that of the study animals which swam most of the

time but did not make deep dives or encounter ocean currents. Chasing and catching live fish or mammals requires more energy than taking defrosted fish from a trainer (Kastelein *et al.*, 1997). Therefore, wild Killer whales probably consume more than the captive animals in the present study, a conclusion also reached by Kriete (1995).

ACKNOWLEDGEMENTS

We thank all the trainers at Marineland Antibes, especially Bruce Walton and Jean Chaperon, for record-keeping. The air temperatures were provided by Météo-France. We thank Nicole Schooneman and Carolien Staal for carrying out part of the analysis, Rob Triesscheijn for preparing the graphs and Nancy Vaughan, University of Bristol, UK, for her comments on the manuscript.

PRODUCTS MENTIONED IN THE TEXT

Aquavits: marine mammal vitamins, manufactured by Taylor and Greenwood, International Zoo Veterinary Group, Keighley Business Centre, South Street, Keighley, West Yorkshire BD21 1AG, UK.

Sea-tabs: marine mammal vitamins, manufactured by Sea World, Inc., 7007 Sea World Drive, Orlando, FL 32821-8097, USA.

REFERENCES

- ASPER, E. D., YOUNG, W. G. & WALSH, M. T. (1988): Observations on the birth and development of a captive-born killer whale *Orcinus orca*. *International Zoo Yearbook* **27**: 295–304.
- BIGG, M. A. & WOLMAN, A. A. (1975): Live-capture killer whale (*Orcinus orca*) fishery, British Columbia and Washington 1962–73. *Journal of the Fisheries Research Board of Canada* **32**: 1213–1221.
- BRODY, S. (1945): *Bioenergetics and growth, with special reference to the efficiency complex in domestic animals*. New York: Reinhold.
- BURGESS, K. (1968): The behaviour and training of a killer whale *Orcinus orca* at San Diego Sea World. *International Zoo Yearbook* **8**: 202–205.
- CALDWELL, D. L. & CALDWELL, M. C. (1969): Addition of the leatherback sea turtle to the known prey of the killer whale, *Orcinus orca*. *Journal of Mammalogy* **50**: 636.
- CASTELLO, H. P. (1977): Food of a killer whale: eagle sting-ray, *Myliobatis* found in the stomach of a stranded *Orcinus orca*. *Scientific Reports of the Whales Research Institute* **29**: 107–111.
- CHRISTENSEN, I. (1984): Growth and reproduction of killer whales, *Orcinus orca*, in Norwegian coastal waters. In *Report of the international whaling commission special issue 6*: 253–258. Perrin, W. F., Brownell Jr, R. L. & Demaster, D. P. (Eds). Cambridge: Black Bear Press Ltd.
- DUFFIELD, D. A., ODELL, D. K., MCBAIN, J. F. & ANDREWS, B. (1995): Killer whale (*Orcinus orca*) reproduction at Sea World. *Zoo Biology* **14**: 417–430.
- GASKIN, D. E. (1982): *The ecology of whales and dolphins*. Exeter: Heinemann Educational Books.
- GRIFFIN, E. I. & GOLDSBERRY, D. G. (1968): Notes on the capture, care and feeding of the killer whale *Orcinus orca* at Seattle Aquarium. *International Zoo Yearbook* **8**: 206–208.
- HALL, J. D. (1986): Notes on the distribution and feeding behavior of killer whales in Prince William Sound, Alaska. In *Behavioral biology of killer whales*: 69–83. Kirkevold, B. C. & Lockard, J. S. (Eds). New York: Alan R. Liss, Inc.
- HEIMLICH-BORAN, J. R. (1986): Fishery correlations with the occurrence of killer whales in Greater Puget Sound. In *Behavioral biology of killer whales*: 113–131. Kirkevold, B. C. & Lockard, J. S. (Eds). New York: Alan R. Liss, Inc.
- HEWLETT, K. G. & NEWMAN, M. A. (1968): 'Skana', the killer whale *Orcinus orca* at Vancouver Public Aquarium. *International Zoo Yearbook* **8**: 209–211.
- HEYNING, J. E. (1988): Presence of solid food in a young calf killer whale (*Orcinus orca*). *Marine Mammal Science* **4**: 68–71.
- HEYNING, J. E. & DAHLHEIM, M. E. (1988): *Orcinus orca*. *Mammalian Species* **304**: 1–9.
- HOYT, E. (1990): *Orca, the whale called killer*. London: Robert Hale.
- KASTELEIN, R. A. & VAUGHAN, N. (1989): Food consumption, body measurements and weight changes of a female killer whale (*Orcinus orca*). *Aquatic Mammals* **15**: 18–21.
- KASTELEIN, R. A., HARDEMAN, J. & BOER, H. (1997): Food consumption and body weight of harbour porpoises (*Phocoena phocoena*). In *The biology of the harbour porpoise*: 217–233. Read, A. J., Wiepkema, P. R. & Nachtigall, P. E. (Eds). Woerden: De Spil Publishers.
- KASTELEIN, R. A., WALTON, S., ODELL, D., NIEUWSTRATEN, S. H. & WIEPKEMA, P. R. (2000): Food consumption of a captive female killer whale (*Orcinus orca*). *Aquatic Mammals* **26**: 127–131.
- KASTING, N. W., ADDERLEY, S. A., SAFFORD, T. & HEWLETT, K. G. (1989): Thermoregulation in beluga (*Delphinapterus leucas*) and killer (*Orcinus orca*) whales. *Physiological Zoology* **62**: 687–701.
- KLEIBER, M. (1975): *The fire of life: an introduction to animal energetics*. Huntington, NY: R. E. Kreiger Publishing Co. Ltd.
- KRIETE, B. (1995): *Bioenergetics in the killer whale, Orcinus orca*. PhD thesis, University of British Columbia, Canada.
- MARTINEZ, D. R. & KLINGHAMMER, E. (1969): The behavior of the whale, *Orcinus orca*: a review of the literature. *Zeitschrift für Tierpsychologie* **27**: 828–839.

- MATKIN, C. O. & LEATHERWOOD, S. (1986): General biology of the killer whale, *Orcinus orca*: a synopsis of knowledge. In *Behavioral biology of killer whales*: 35–68. Kirkevoold, B. C. & Lockard, J. C. (Eds). New York: Alan R. Liss, Inc.
- MATKIN, D. R. & DAHLHEIM, M. E. (1995): Feeding behaviors of killer whales in Northern Southeastern Alaska. In *Proceedings of the third Glacier Bay science symposium*: 246–253. Engstrom, D. R. (Ed.). Anchorage, Alaska: National Park Service.
- NISHIWAKI, M. & HANDA, C. (1958): Killer whales caught in the coastal waters off Japan for recent 10 years. *Scientific Reports of the Whales Research Institute* **13**: 85–96.
- NORRIS, K. S. & PRESCOTT, J. H. (1961): Observations on Pacific cetaceans of Californian and Mexican waters. *University of California Publications in Zoology* **63**: 291–402.
- RICE, D. W. (1968): Stomach contents and feeding behavior of killer whales in the eastern North Pacific. *Norsk Hvalfangst-Tidende* **57**: 35–38.
- ROSS, G. J. B. (1984): The smaller cetaceans of the south-east coast of southern Africa. *Annals of the Cape Provincial Museums of Natural History* **15**: 173–410.
- RYAN, B. F., JOINER, B. I. & RYAN, T. A. (1985): *Minitab handbook* (2nd edn). Boston: PWS-Kent.
- SCHEFFER, V. B. & SLIPP, J. W. (1948): The whales and dolphins of Washington State with a key to the cetaceans of the west coast of North America. *The American Midland Naturalist* **39**: 257–337.
- SERGEANT, D. E. (1969): Feeding rates of cetacea. *Fiskeridirektoratets Skrifter Serie Havundersokelser* **15**: 246–258.
- SILBER, G. K., NEWCOMER, M. W. & PÉREZ-CORTÉZ M. H. (1990): Killer whales (*Orcinus orca*) attack and kill a Bryde's whale (*Balaenoptera edeni*). *Canadian Journal of Zoology* **68**: 1603–1606.
- SLIPPER, E. J. (1979): *Whales*. Ithaca, NY: Cornell University Press.
- THOMAS, G. L. & FELLEMAN, F. L. (1988): Acoustic measurement of the fish assemblage beneath killer whale pods in the Pacific Northwest. *Rit Fiskideildar, Journal of the Marine Research Institute Reykjavik* **11**: 276–284.
- WENZEL, F. & SEARS, R. (1988): A note on killer whales in the Gulf of St. Lawrence, including an account of an attack on a minke whale. *Rit Fiskideildar, Journal of the Marine Research Institute Reykjavik* **11**: 202–204.
- WILLIAMS, T. M., HAUN, J. E., FRIEDL, W. A., HALL, R. W. & BIVENS, L. W. (1992): Assessing the thermal limits of bottlenose dolphins: a cooperative study by trainers, scientists, and animals. *IMATA Soundings Fall 1992*: 16–17.
- YANO, K. & DAHLHEIM, M. E. (1995): Killer whale, *Orcinus orca*, depredation on longline catches of bottomfish in the southeastern Bering Sea and adjacent waters. *Fishery Bulletin* **93**: 355–372.
- YUKHOV, V. L., VINOGRADOVA, E. K. & MEDVEDEV, L. P. (1975): The diet of killer whales (*Orcinus orca* L.) in the Antarctic and adjacent waters. In *Marine mammals* **2**: 183–185. Translated by the Canadian Department of Environment, Fisheries and Marine Services. Translation Series No. 3844 (1976).

Manuscript submitted 29 March 1999;
accepted 14 August 2000