Food consumption and body weight of captive Pacific walruses (*Odobenus rosmarus divergens*)

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Abstract

Food consumption and body weight were recorded for 6 male and 3 female captive Pacific walruses. The study is based on historical data that were recorded for short-term husbandry purposes. Most animals came as calves from the wild and received formula during their first year at the park, although one male calf was born at the park, and was suckled. He began to eat fish at the age of 7 months and was fully weaned at the age of 19 months. During the calendar year of birth and the following year, all but one of the walruses were raised on formula. Thereafter the walruses consumed solid food, and the annual food intakes varied strongly between individuals of the same sex and age. In one female, a pronounced increase occurred in the year during which she was pregnant, gave birth, and suckled the calf for the rest of that year and the following calendar year. During gestation, her body weight increased from 750 kg to 1100 kg. The calendar year after delivery her food intake remained above normal. For the entire lactation period, the mother consumed 91% more food than during similar periods in non-reproductive years. The year after weaning, food intake of the mother decreased below the pre-reproductive level. In one male a rapid increase in food intake occurred after the age of 12 years. This coincided with a strong secondary growth spurt, following sexual maturity. During the first 4 years of life, the period of rapid growth, food consumption generally increased each month. Thereafter, there were seasonal fluctuations in food intake. These fluctuations appeared to be related to reproduction (February–April in males, and February in females) and molt (June–August). The body weight of one female stabilized at around 1200 kg, that of another at 750 kg. The body weight of the 2 males stabilized around 1400 kg. Between weaning and attaining a body weight of approximately 800 kg, individuals showed a negative relationship between body weight and food intake as a percent-age of body weight. Adult walruses consumed be-tween 2 and 3% of body weight per day in fish.

Key words: body weight, calf, energetics, food consumption, *Odobenus*, pinniped, reproduction, suckling, walrus.

Introduction

The relationship between the Pacific walrus (*Odobenus rosmarus divergens*) and its prey populations was estimated within the species range (Fay *et al*., 1977). However, the study was based largely on benthic fauna, and little is known about the food requirements of walruses. Feeding by wild Pacific walruses has previously been investigated only by examination of the stomach contents of dead animals (Nikulin, 1941; Brooks, 1954; Fay *et al*., 1977, 1984a; Lowry *et al*., 1980; Fay & Lowry, 1981; Fay, 1982; Fay & Stoker, 1982; Fay & Burns, 1988; Sheffield & Fay, 1995). Prey consists principally of bivalve mollusks, buried in the mud in water depths of up to 100 m, although walruses also some-times feed (or possibly only scavenge) on cetaceans and pinnipeds (Brown, 1868; Mansfield, 1958; Loughrey, 1959; Fay, 1982; Lowry & Fay, 1984; Fay *et al*., 1990). Pits and furrows observed in the ocean floor, along with discarded shells nearby, indicated foraging by walruses (Ray, 1973; Oliver *et al*., 1983, 1985; Nelson & Johnson, 1987). Examination of tracks left in the sediment after foraging suggested an excavation technique consisting of detection, excavation by nose or water jetting by the mouth, positioning the clam between the lips, and sucking the soft parts from the shells. This technique was later confirmed in experiments with walruses in a pool (Kastelein & Mosterd, 1989).

Because specific data, such as total food con-sumption per day, fluctuations in food intake dur-ing the year, and changes in intake due to age, sex or individual differences, are difficult to obtain in the wild, food records of captive animals provide

Table 1. Gender, birth date, place of origin and study period of the Pacific walruses used in the present study. *Offspring of male 003 and female 004. **North-east of Siberia.

Animal	Gender	Birth date	Origin	Study period
OrZH001	M	May 1974	Wrangel Island**	1975–1988
OrZH002	F	May 1974	Wrangel Island**	1975–1999
OrZH003	M	1982	Alaska, USA	1986–1999
OrZH004	F	1982	Alaska, USA	1986–1999
OrZH005	M	June 1978	Wrangel Island**	1980–1983
OrZH006	F	June 1978	Wrangel Island**	1980–1982
OrZH007	F	July 1974	Wrangel Island**	1975–1977
OrZH008	M	April 1974	Wrangel Island**	1975
OrZH009	M	June 1992	East Siberian Sea	1993–1995
OrZH010	M	June 1992	East Siberian Sea	1993–1994
OrZH011*	M	June 1995	Harderwijk Park NL	1995–1999

the only available information. Even though walruses in zoological parks are usually fed fish, not their natural invertebrate prey (Fay, 1982), changes in food intake relative to age, sex, time of year and physiological status can be studied. Available information on food intake and growth of hand-raised walrus calves and one suckled animal was summarized by Kastelein *et al.* (2001). Some food intake records of captive walruses are published (Reventlow, 1951; Bridges, 1953; Hagenbeck, 1962; Brown & Asper, 1966; Gehnrich, 1984; Dittrich, 1987; Fisher *et al.*, 1992), but the information is either anecdotal, or is based on only a few animals. The Harderwijk Marine Mammal Park has housed relatively many Pacific walruses and recorded their food intake over a relatively long period, thus creating a unique data base. The aim of this study was to describe the food intake and growth of 9 walruses kept at the park.

Materials and Methods

Study animals
The gender, birth date, origin, and study period of the male and female Pacific walruses used in this study are shown in Table 1. The age estimates are accurate, because all animals arrived at an early age at the Harderwijk park or (like animals 003 and 004) at a previous park. Age 1 is defined as the first calendar year after the year of birth. The animals usually arrived in groups of 2, which were housed together, and are referred to as couples (animals 001 and 002, 003 and 004, 005 and 006, and 009 and 010), regardless of their sexual composition. Animal 009 died of an intestine torsion, 010 died of a tooth infection shortly after his transition from formula to a fish diet, and 001, 005 and 006 died from upper canine infections during the year after the end of their study periods (Table 1). The study period for each animal includes only those years in which the

individual was healthy. The walruses were cared for in accordance with the principles and guidelines of the Canadian Council on Animal Care. Frequent weight measurements of older, heavier, animals are only available for the last 12 years of the study period. Of male 003 and females 002 and 004 monthly weight measurements were taken when they were adult.

Study area
The walruses were kept in an outdoor freshwater pool complex consisting of a main pool (20 m × 12 m) and a side pool (12 m × 9 m), both 4 m deep, and each with an adjacent, partially roofed land area (Kastelein & Wiepkema, 1989). The free chlorine level was maintained between 0.4 and 0.5 ppm and the combined chlorine level at 0.3 ppm. The average monthly water temperature varied between 9 and 19°C, while average monthly air temperature varied between − 0.3°C in February and 17.5°C in July (Fig. 1). The Harderwijk Marine Mammal Park is located at 52°20′N and 5°37′E. All the walruses were kept in the same facility with the same water treatment equipment during the study period. The only changing environmental conditions were the increasing experience of the trainers with walrus husbandry over time, and small climatic changes. The climate and level of experience of the trainers were exactly the same for animals within couples.

Diet and feeding
The animals were fed 3 to 6 times per day on an average diet of 35% herring (*Clupea harengus*; approx. 8880 kJ/kg), 26% mackerel (*Scomber scombrus*; approx. 9550 kJ/kg), 9% sprat (*Sprattus sprattus*; approx. 10.400 kJ/kg), 2% whiting (*Merlangius merlangus*; approx. 4750 kJ/kg), and 28% squid (*Illex* spp.; approx. 1000 kJ/kg) by weight. Vitamins (Seavit®, 1 tablet per 2.5 kg of food) were added to
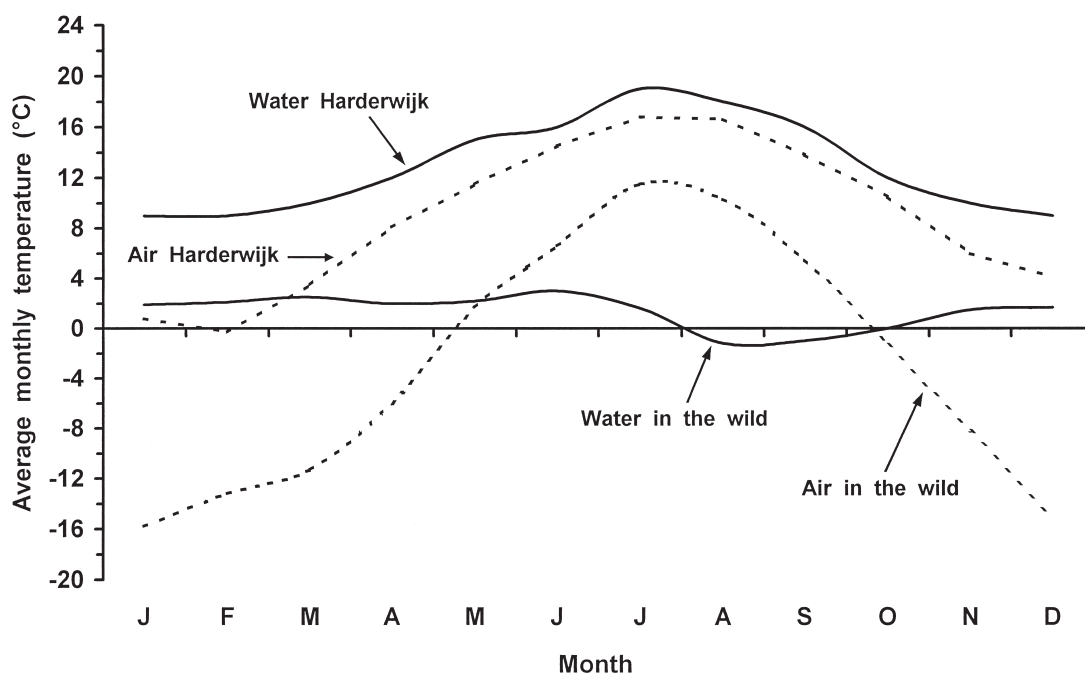
Figure 1. Average monthly water and air temperatures at the Harderwijk Marine Mammal Park (1980–1990) and average monthly air and sea surface temperatures experienced by wild Pacific walruses (this may vary per animal depending on migration).

this thawed diet. During the last meal of the day, the animals were fed *ad libitum*. Feeding was terminated as soon as the animals began to play with the food, instead of consuming it immediately. This was considered a sign of satiety. The daily amount (kg) and type of food consumed by each animal was recorded. For the analysis the total amounts per month and per year were used. These historical daily food records, originally collected for short-term husbandry purposes, form the basis of the present study. The composition and caloric content of the fish and squid species were not measured, but probably varied per year class of fish, seasonally and depending on the location where the fish was caught. To roughly estimate the energy used by the walruses, the food intake was calculated in kJ using average values for the fish species supplied by The Netherlands Commodity Board for Fish and Fishery Products. This yielded an average caloric value for this diet of 6900 kJ/kg.

Statistics
Similarities in seasonal fluctuations in food intake between years were tested for by means of Kendall's coefficient of concordance test (Kendall, 1962). The average daily food intake of each month of a year was given a rank number from 1 to 12. By comparing the rank numbers of the 12 months between years a potential seasonal pattern could be detected. This test was chosen because the food intake of most animals increased over time, so the total monthly food intake for a particular month in a year often differed from a previous or next year. However, by ranking the food intakes per month within a year, annually returning seasonal patterns could be tested for.

Results

Annual food consumption
All but one calf were obtained from the wild and received a formula during the calendar year of birth and the following year (Kastelein *et al.*, 2001). Food consumption during that period, therefore, is not shown. Only male 011 was born at the park in June 1995 and was suckled. He began to eat fish at the age of 7 months, consuming around 1000 kg of fish, in addition to milk in his first full calendar year. During his second year he no longer suckled and consumed around 3700 kg of fish. His food consumption increased to around 6300 kg during his fourth year (Fig. 2). Annual food intakes varied strongly between individuals of the same sex and age. The differences were smaller between animals that arrived as a couple than between animals from different couples (Fig. 2).
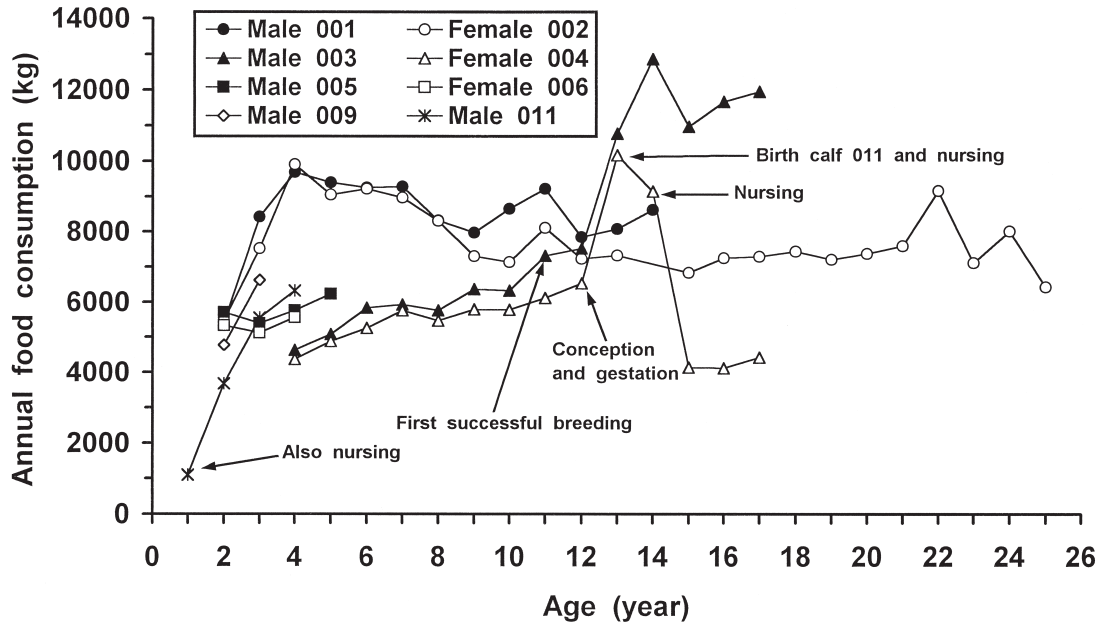
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Figure 2. Annual food intake of male and female Pacific walruses at Harderwijk Marine Mammal Park. Age one represents the first calendar year after the year of birth.

Annual food consumption of males

Male 001 was 5 months of age when he arrived, and was fed formula until the second month of his first year. He was on a complete fish diet by the following month. Annual food consumption increased rapidly from around 5500 kg in his second year to 10 000 kg by his fourth year (Fig. 2). Thereafter, food consumption decreased to around 8500 kg (estimated at 586.5×10^5 kJ) at the age of 14 years. He never bred or showed any sexual behaviour.

Male 003 was transferred from another facility to Harderwijk at the age of 4 years. His annual food consumption rose gradually from 4500 kg at the age of 4 years to around 7500 kg at the age of 12 years, after which it increased rapidly. Between his 12th and 14th year, he showed a rapid increase in annual food consumption, from 7500 kg to 13 000 kg, although it decreased to around 11 000 kg (estimated at 759×10^5 kJ) in his 15th year, after which it increased slightly again. His first successful breeding attempt occurred during his 11th year.

Male 005 was 2 months of age on arrival, and was fed formula during most of his first full calendar year at the park. He was fed exclusively on fish by July. His annual food intake increased from 5500 kg at the age of 2 years to around 6000 kg at the age of 4 years.

Male 009 arrived at the 5 months of age, was fed formula until September of his first complete calendar year at the park. His annual food consumption

was recorded for only 2 years. Between his second and third year, he showed an increase in annual food consumption similar to that of animals 001 and 002 at the same age, from around 4800 to 6700 kg.

Annual food consumption of females

Female 002 was 5 months of age when she arrived, and was fed formula until the second month of her first year. She was on a complete fish diet by the following month. Annual food consumption increased rapidly from around 5500 kg in her second year to 10 000 kg by her fourth year (Fig. 2). Thereafter, food consumption decreased to around 7500 kg at the age of 13 years. Her food intake remained stable until her 21st year, after which it fluctuated around 7500 kg/year.

Female 004 was transferred from another facility to Harderwijk at the age of 4 years. Her annual food consumption rose gradually from 4500 kg at the age of 4 years to around 7000 kg at the age of 12 years (Fig. 2). The next year, during which she was pregnant for 5.5 months, gave birth to calf 011 in June and nursed it for the rest of that year and the following calendar year, food intake increased strongly. In the calendar year of conception, she ate 7% more than in the previous year. During the 15-month gestation, food consumption was 30% higher than in a similar period shortly before she became pregnant. In the 5 months before
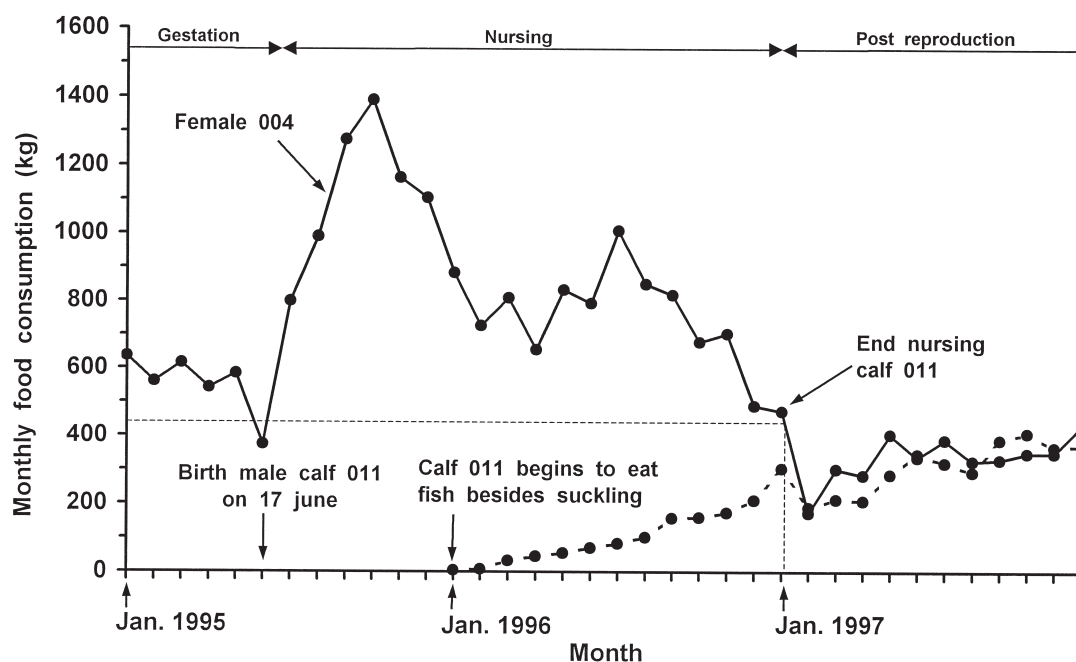
Figure 3. Monthly food consumption of female 004 before and after giving birth to calf 011 which suckled, and the monthly fish consumption of calf 011. The horizontal dashed line indicates the average monthly food consumption of the female during non-reproductive periods shortly before gestation. This level is used to determine the approximate date of weaning. Jan. signifies January.

parturition, her monthly food intake was fairly stable (Fig. 3). Food intake was 50% less than in previous weeks, on the day before and the day of parturition. No food was consumed for 5 days after the birth. Eleven days after birth, her food intake had returned to the pre-pregnancy level. Three weeks after giving birth, her food intake increased rapidly. Her food intake increased for the first 4 months of lactation, after which it decreased (Fig. 3). During the entire nursing period (estimated to be 19 months, based on the moment that the food intake of the mother returned to a pre-reproductive level and the cessation of occasionally witnessed suckling bouts by the trainers), the mother consumed 7800 kg more (91%) than in similar, non-reproductive periods. The calf consumed 1400 kg of fish during the last 13 months of the suckling period, in addition to milk (Fig. 3). By January of the mother's 15th year, the calf was weaned, and that year and the following 2 years, her annual intake was below the pre-reproductive level (Fig. 2).

Female 006 was 2 months old on arrival, and was fed formula during most of her first full calendar year at the park; she was fed exclusively on fish by November. She showed an increase in annual food consumption from 5500 kg at the age of 2 years to around 6000 kg at the age of 4 years (Fig. 2).

Seasonal changes

The food intake of male 001 gradually increased between the ages of 2 and 4 years (Fig. 4a). The monthly pattern of food intake was similar in all 3 years (Kendall's coefficient of concordance test: $\chi_r^2=20.68$; $P<0.05$). Molt occurred between June and July. After the age of 4 years, food intake showed seasonal fluctuations, with a similar pattern of monthly food intake in each of the following 9 years (Kendall's coefficient of concordance test: $\chi_r^2=50.42$; $P<0.001$). He ate more than average between September and February and less than average during spring and summer (Fig. 4b). During the study he did not breed or show any sexual behaviour. Molt occurred between June and August.

Female 002 showed a similar pattern, with the monthly food intake patterns of all available years falling into two distinct periods. Food intake gradually increased over each subsequent year during the first period (Fig. 5a). The monthly pattern of food intake was similar in all 3 years (Kendall's coefficient of concordance test: $\chi_r^2=26.88$; $P<0.005$). Molt occurred between June and July. After the age of 4 years, food intake fluctuated seasonally, with a similar pattern of monthly food intake in each of the subsequent 16 years (Kendall's
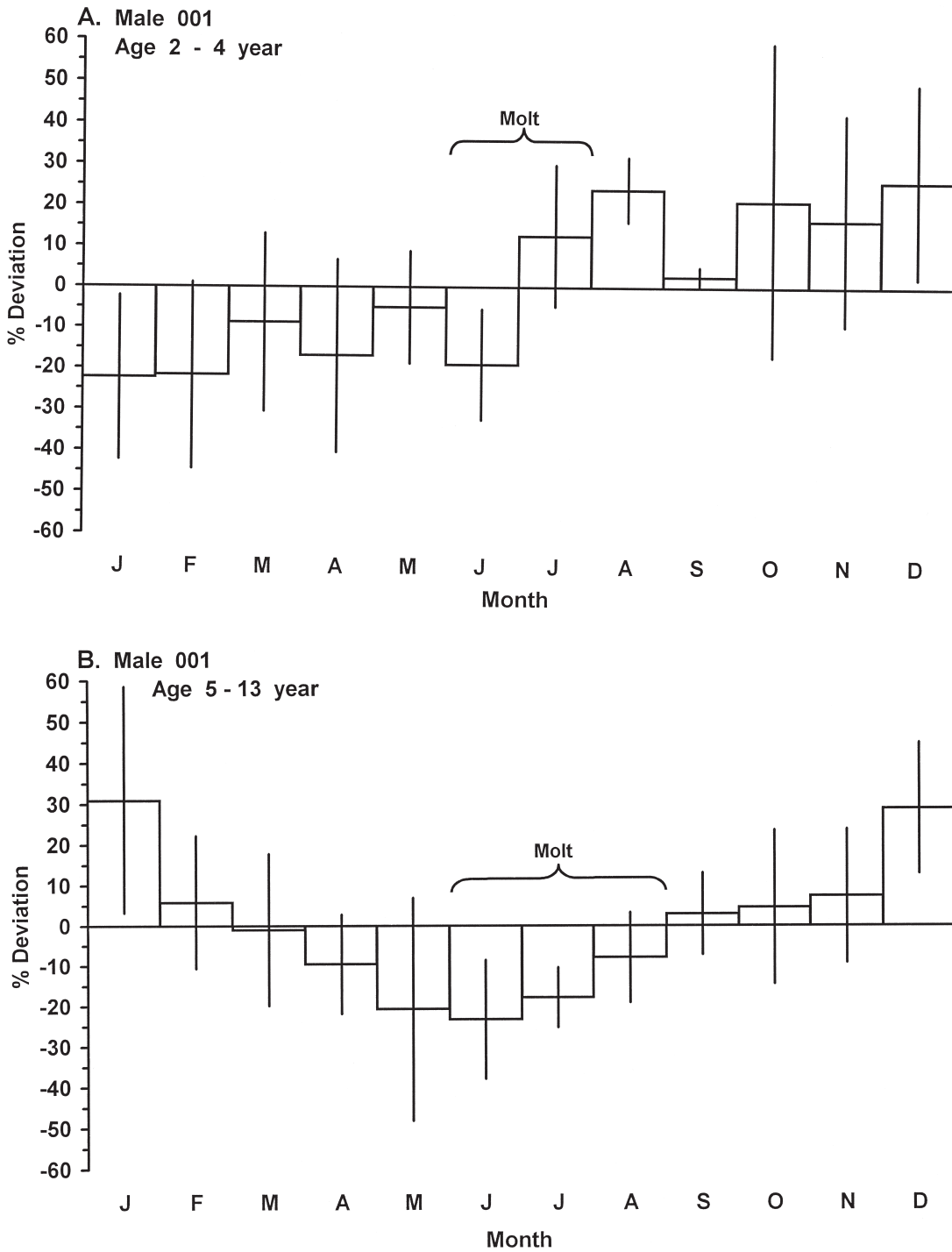
Figure 4. Mean percentage deviation in the mean monthly food consumption of male walrus 001 A. aged 2 to 4 years and B. aged 5 to 13 years. Bars indicate the standard deviations.
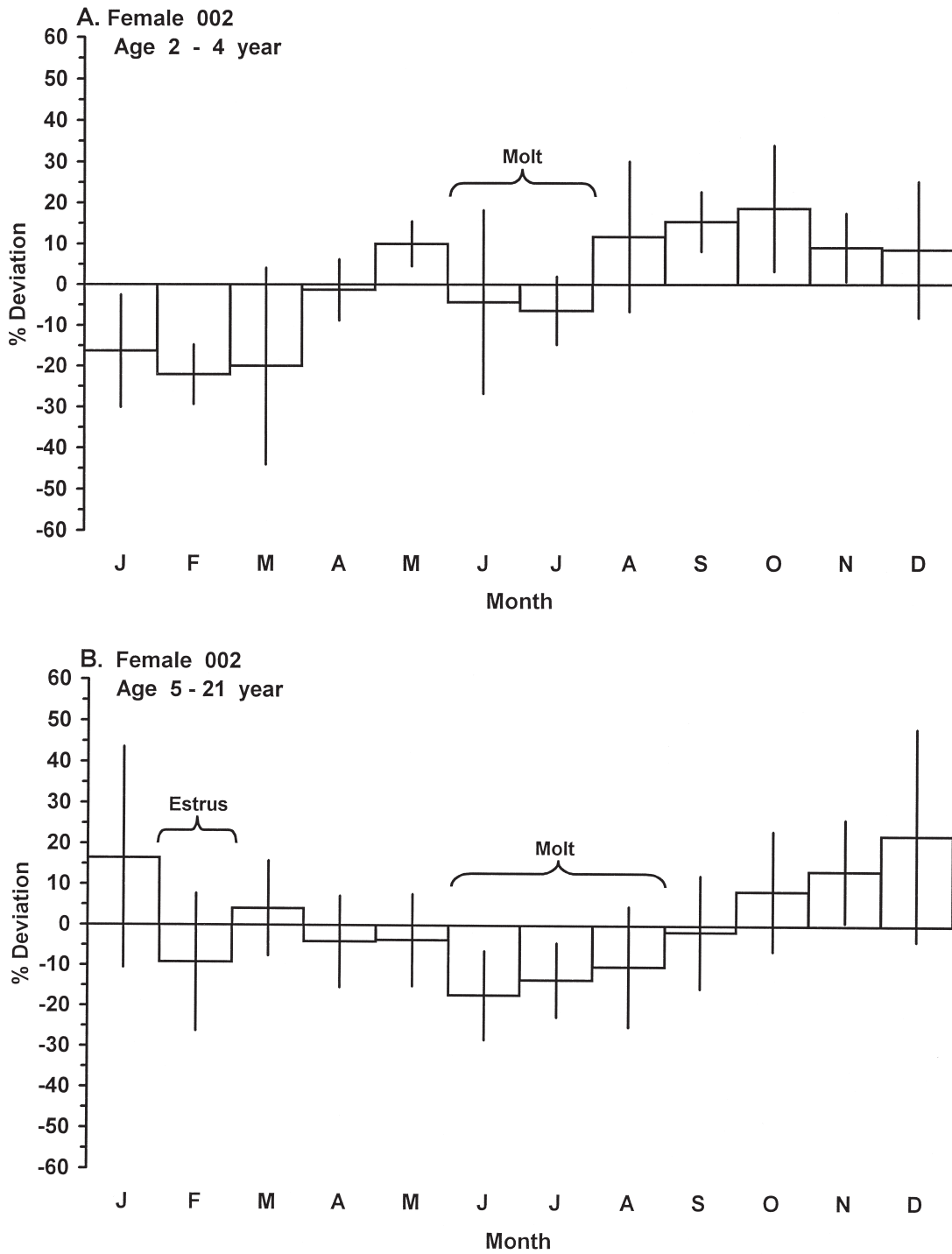
Figure 5. Mean percentage deviation in the mean monthly food consumption of female walrus 002 A. aged 2 to 4 years and B. aged 5 to 21 years. Bars indicate the standard deviations.

coefficient of concordance: $\chi_r^2=72.68$; $P<0.001$). Food intake was above average between October and January and less than average in spring and summer (Fig. 5b). The reduction in food intake in February coincided with estrus and first occurred when she was 6 years of age. Molt took place between June and August.

The monthly food intake patterns of male 003 for all available years can be divided into 2 periods. During his fourth year, food intake increased as he grew rapidly, but a slight seasonal pattern appeared (Fig. 6a). Molt occurred in July. After the age of 4 years, food intake showed more pronounced seasonal fluctuations, with a similar pattern of monthly food intake in each of the 10 years (Kendall's coefficient of concordance test: $\chi_r^2=75.52$; $P<0.001$). Consumption was above average between August and January and less than average from February to June (Fig. 6b). The mating season usually occurred between February and April, while molt took place between June and August.

Female 004 showed a similar seasonal food intake pattern, already apparent when she was 4 years of age. Between age of 4 and 11 years, when she was not pregnant or lactating, food intake fluctuated seasonally. The pattern of monthly food intake was similar in each of the 8 years (Kendall's coefficient of concordance test: $\chi_r^2=44.45$; $P<0.001$): above average between August and January, and below average from February to July (Fig. 7). The low food intake in February coincided with estrus, and first occurred when she was 5 years of age. The same pattern returned after nursing had stopped (between the age of 15 and 17). Molt took place between June and August. The reduction in food intake fell a little earlier in the year in animals 003 and 004 than in animals 001 and 002.

Body weight
Males 003 and 005 grew from around 60 kg at birth to approximately 750 kg at the age of 6 years (Fig. 8a), while male 003 and male 001 increased in weight to around 1400 kg at the age of 14 years. Between the ages of 13 and 18, the body weight of male 003 fluctuated seasonally; he weighed about 300 kg more in January and February than during the summer.

Females 004 and 006 increased from around 60 kg at birth to about 500 kg by 5 years of age (Fig. 8b). The body weight of female 002 stabilized at around 1200 kg. Female 004 appeared to have reached her maximum body weight (750 kg) by the age of 9 years, although during gestation, in her 12th year, weight increased by another 350 kg. After giving birth to a 60 kg calf, her weight decreased by 250 kg, owing to the weight of the calf, the placenta, amniotic fluid, and the demands of

lactation until September, after which it rose again. After peaking again at around 1100 kg, her weight gradually returned to around 750 kg. Adult females were about 100 kg heavier in winter than in summer.

Length measurements
Standard body length was measured only once in 3 animals. Male 001 was 350 cm long at a weight of 1300 kg when he was 15 years old, male 010 was 224 cm long at 323 kg when he was 2.5 years old, and female 004 was 259 cm at 550 kg, at the age of 6 years.

Food intake as percentage of body weight
There appears to be a negative relationship between body weight and daily food intake as a percentage of body weight up to around 800 kg. The database is too small to test this phenomenon statistically. In heavier animals, there was no further percentage decline (Fig. 9).

Discussion

Age and sex-related differences in food intake and body weight
Large differences in annual food intake between individual walruses of the same age were apparent until the age of 12 years. Until that age, there was little difference in food intake within couples, although in the 3 couples which consisted of a male and a female, the male tended to eat more than the female. This was probably because the male in each couple was heavier than the female. The large differences in annual food intake between couples 001 and 002, and 003 and 004 before the age of 12 years could have been due to the small size of female 004 (Fig. 8b), and the particularly pronounced decrease in the food intake of male 003 during the breeding season (Fig. 6). To some extent the difference may also have been caused by differences in the level of husbandry experience of the staff (and different staff members) over the years.

After the age of 10 years, male 003 rapidly increased his food intake. This coincided with a secondary growth spurt, related to sexual maturity. Wild males mature around the age of 10 years (Fay, 1982). A similarly increased food intake at around 11 years of age was observed in male Pacific walruses at Marineland, Los Angeles, which first bred successfully at the age of 10 years (Gehnrich, 1984). At Hannover Zoo, the food intake of a male and female Pacific walrus increased at the age of 9 years; that of the male more strongly (Dittrich, 1987). Sexual dimorphism in Pacific walruses becomes pronounced later in life than it does in other pinnipeds; males begin their secondary growth
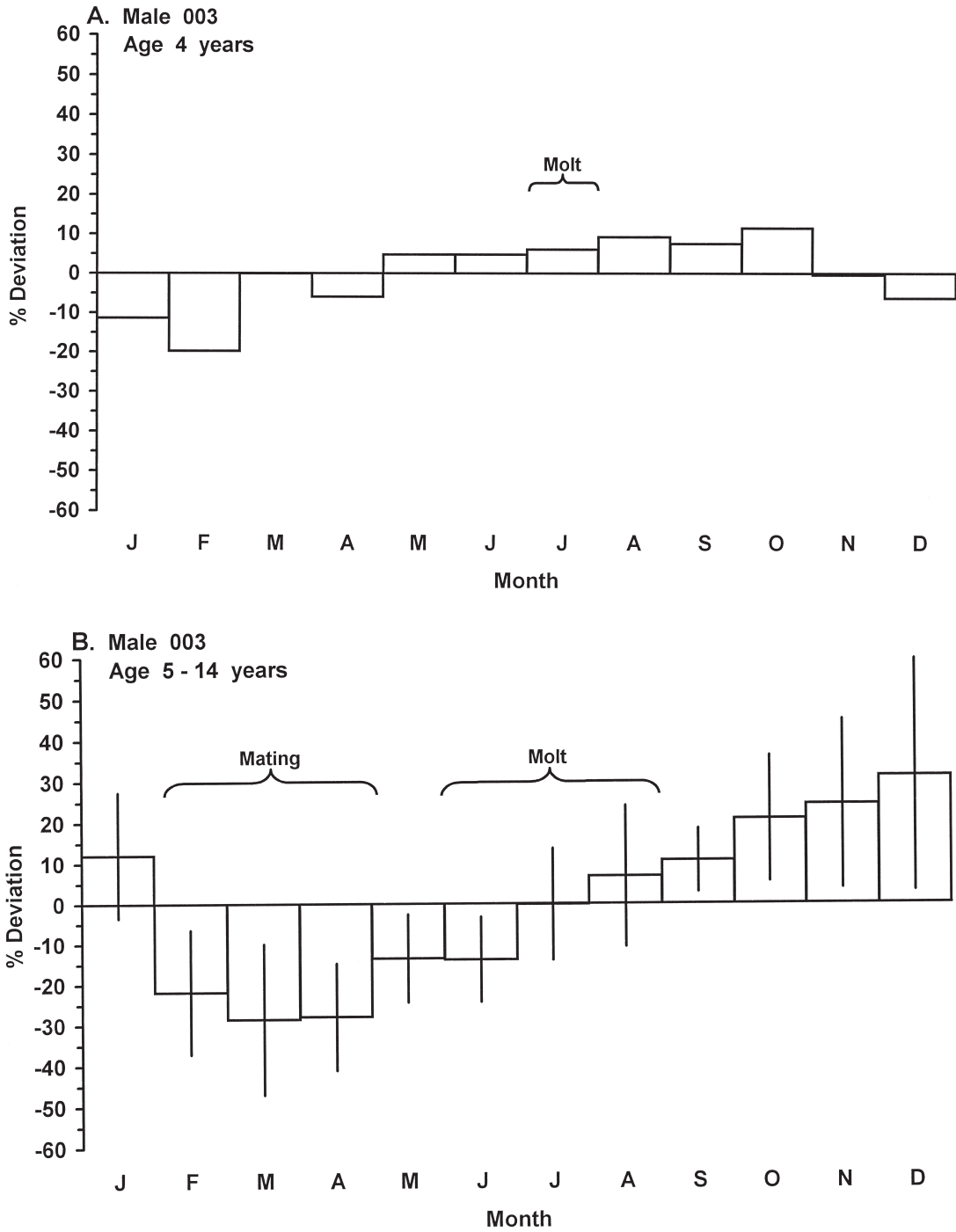
Figure 6. Mean percentage deviation in the mean monthly food consumption of male walrus 003 A. aged 4 years and B. aged 5 to 14 years. Bars indicate the standard deviations.
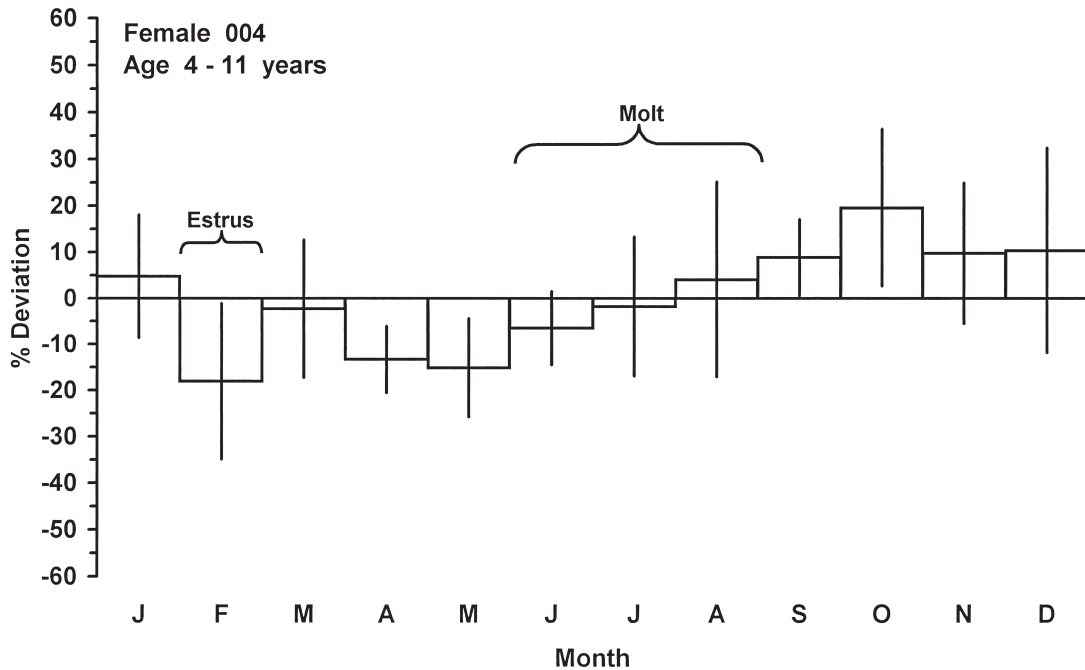
Figure 7. Mean percentage deviation in the mean monthly food consumption of non-pregnant, non-lactating female walrus 004 aged 4 to 11 years. Bars indicate the standard deviations.

spurt around puberty (at 10 to 15 years of age), and reach full physical maturity at about 16 years of age, at an average weight of 1200 kg. Adult males are about 18% longer than adult females (McLaren, 1993). The average annual food intake of a male and female Pacific walrus at Hannover Zoo (coming from the same stock as animals 001 and 002), up to the age of 12 years, was between that of the couples 001 and 002, and 003 and 004 in the present study (Dittrich, 1987). At the age of 12 years, the annual food consumption of the walruses in the present study and those at Hannover Zoo was similar (around 7500 kg).

The food intake of non-reproducing female 002 remained fairly constant after the age of 8 years. After the age of 12 years, the food intake of female 004, now breeding, increased rapidly. Females in the wild mature at 4 to 8 years of age (Fay, 1982) and attain full physical maturity at 12 to 14 years of age, at an average weight of 830 kg (Fay, 1982). In the present study, the 2 adult females had relatively constant levels of food intake when non-pregnant and non-lactating. A similar pattern was observed in non-reproductive adult females at Marineland, Los Angeles (Gehnrich, 1984). In wild non-reproducing females, the thickness of the blubber layer varies slightly during the year, but increases strongly during pregnancy (Fay and Kelly, 1980; Fay, 1982; Quakenbush et al., 1999).

In the present study, first estrus occurred at ages 5 and 6 years, within the range of wild Pacific walruses (4 to 8 years of age), which breed at 2-year intervals or less, and are most fecund between the ages of 8 and 15 years. Pregnancy lasts around 15 months (Fay, 1982).

The calf in the present study was born in mid-June and weighed 60 kg. This agrees with the calving season and weights of calves in the wild where births occur mainly between mid-April and mid-June (mean birth date around mid-May) and the average birth weight is 63 kg (Fay, 1982).

Female 004 consumed 30% more during gestation than when she was not pregnant. At Marineland, Los Angeles, females ate around 40% more than average during pregnancy (Gehnrich, 1984). The increase not only provides energy for the metabolism and growth of the fetus (Kleiber, 1961), but also increases the blubber thickness of the female (Fay and Kelly, 1980; Fay, 1982; Quakenbush, et al., 1999) to meet energetic requirements of future lactation and/or fasting immediately after birth (Fig. 8b). To some extent, the thicker blubber could have counterbalanced the energy required for the growth and metabolism of the fetus by reducing heat loss to the environment. For several days up to, and on the day of birth, the food intake of female walruses at Marineland, Los Angeles, decreased (Gehnrich, 1984). After they
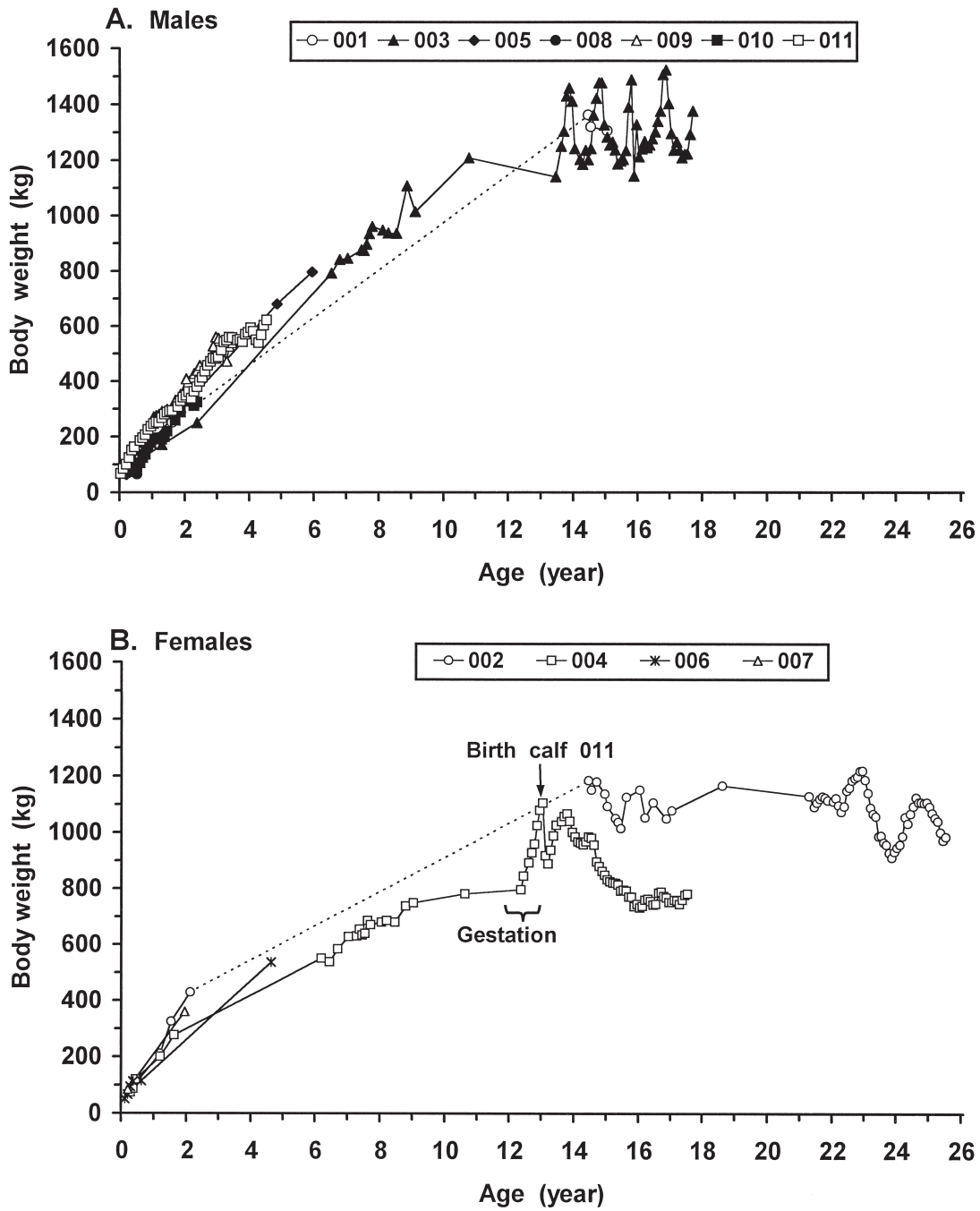
Figure 8. Weight changes of A. male and B. female Pacific walruses at Harderwijk Marine Mammal Park. Data points of the same animal are connected with dashed lines, which do not indicate the animals' body weight in the intervening period.
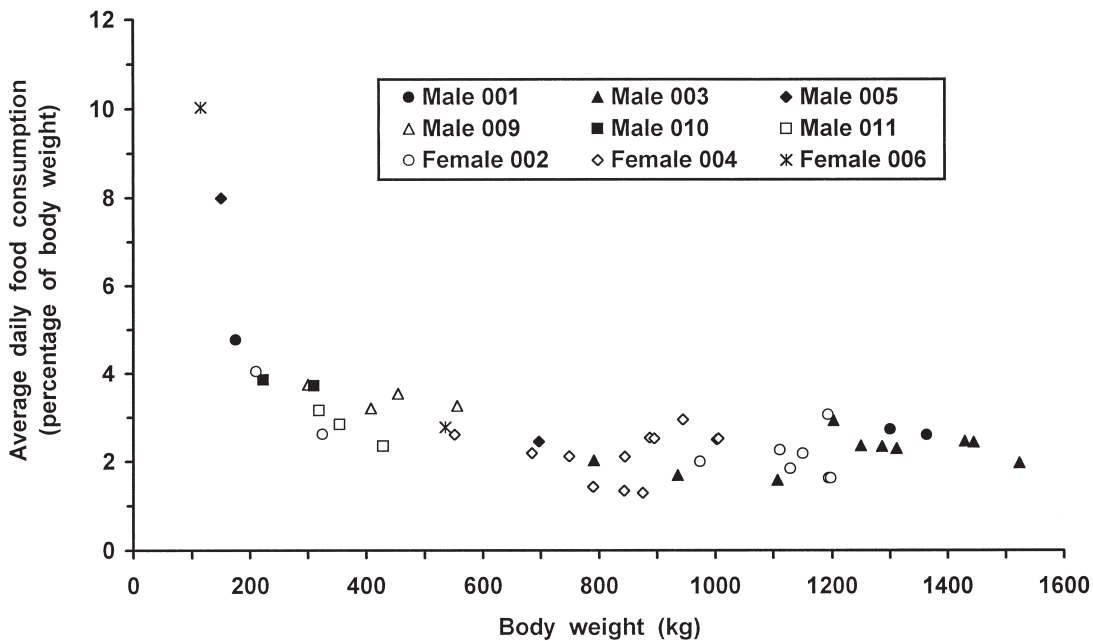
Figure 9. Relationship between body weight and average daily food consumption as a percentage of body weight of Pacific walruses of both sexes at Harderwijk Marine Mammal Park.

gave birth, intake increased slowly, but did not return to a normal level for several weeks. This agrees with the findings in the present study. Wild female walruses also eat very little when they have new-born calves (Fay, 1982). The decrease in food intake immediately after parturition could result from the need to stay near and tend the calf. Also, calves may not be capable of deep or prolonged feeding dives until they are a few weeks old, thus restricting the mother's feeding activities.

Three weeks after giving birth, the food intake of female 004 increased rapidly, possibly owing to the demands of lactation. The combined energetic needs of the mother and calf rose after delivery, with the calf's energy requirements for thermoregulation, locomotion and growth. The decrease in the mother's intake five months after the birth was probably caused by an increase in the blubber thickness of the calf, reducing heat loss to the environment. Even during the calendar year after giving birth, the mother's food intake was relatively high, because the calf remained partly dependent on milk during that entire year. Lactating females at Marineland, Los Angeles, consumed around 50% more during the first year of lactation (May–April) than during non-reproductive years (Gehnrich, 1984). This is less than the value obtained in the present study (101% from June–May); annual food

consumption increased by 66% during the calendar year of birth (January–December, including gestation between January and June). Walruses nurse their young for a relatively long period. In the wild, a pregnant female with a 2-year-old calf had milk in her glands (Belopolski, 1939), while 16-month-old walruses only had milk in their stomachs (Perry, 1967). On the basis of the examination of the contents of 11 stomachs, 3-year-old Atlantic walruses (*Odobenus rosmarus rosmarus*) consumed mostly milk, although some benthic invertebrates also were eaten (Fisher & Stewart, 1997).

In some terrestrial mammals, lactating females increase food intake by 100 to 200% relative to non-lactating females of similar body weight (Kleiber, 1961). On that basis, Fay (1982) estimated that pregnant and simultaneously lactating females might consume 100 to 200% more than non-pregnant, non-lactating females. Gehnrich (1984) suggests a 90% increase, while the results from the present study suggest a 130% increase in food intake for females simultaneously pregnant and lactating.

Comparison of body weight
When adult, the 2 males in present study were heavier than the 2 females. Although the body weights of most of the adult study animals

fluctuated seasonally, the weights of both sexes were within the range for wild Pacific walruses at similar ages (adult males: 900–1600 kg; adult non-pregnant females: 550–950 kg; Fay, 1982). Only adult female 002 (around 1100 kg) was heavier than most wild females of similar age.

At Hannover Zoo the pair of Pacific walruses, from the same stock as animals 001 and 002, were weighed up to the age of 4.5 years. Their weights were similar to the males and females in the present study at similar ages (Dittrich, 1987).

Seasonal changes
Seasonal fluctuations in food intake of the animals in the present study resemble those of wild Pacific walruses. After the age of 4 years, the food consumption of male 003 fell during the mating season. At that time, he whistled frequently (Verboom & Kastelein, 1995), a behaviour also observed in wild males during the mating season (Fay *et al.*, 1984b). At Marineland, Los Angeles, subadult and adult male Pacific walruses also had the lowest food intake during the breeding season (February–April; Gehnrich, 1984), as did males at Hannover Zoo (Dittrich, 1987). Wild male walruses need to fast for long periods to maintain mobile territories near females in estrus in the breeding season (January–March; Fay, 1982; Fay *et al.*, 1984b; Fay, 1985). Captive animals, with no such need, decrease their intake dramatically for several months during the breeding season, suggesting an underlying endogenous factor. Following the period of reduced intake in spring and early summer, consumption increased steadily until winter. Wild male Pacific walruses also feed intensively throughout the summer and autumn and tend to be fattest in early winter (Fay, 1982).

In the wild, little food is taken by Pacific walruses on the northward spring migration (April–June; Fay, 1982). During summer (July–September), however, when females and calves are in the Chukchi Sea and males are in the Bering Sea, walruses spend much of their time foraging. Consumption is also high during the autumn migration (October–December; Fay, 1985).

As adults, the females in the present study consumed less than average in February, while they were in estrus. Female Pacific walruses in the wild ovulate in January or February (Fay, 1982). The influence of estrus and mating on food consumption in wild females is unknown. At Marineland, Los Angeles, however, non-pregnant reproductively mature females stopped eating for about a week in January or February. This was thought to relate to ovulation, because all females mated and some became pregnant during these fasts; the males also fasted during this period (Gehnrich, 1984).

Molt in both Pacific and Atlantic walruses may occur between March and October (Fay, 1982; Born & Knutsen, 1990). However, most wild walruses molt during the summer. Moulting takes about 14 days, during which time an animal hauls out and does not feed (Pederson, 1962). In the present study, molt usually occurred between June and August, and coincided with a low food intake. The Pacific walruses at Marineland, Los Angeles, also often consumed less during the molt (June–August) than at other times, although a consistent pattern was not evident (Gehnrich, 1984). Both male and female Pacific walruses at Hannover Zoo also reduced their food intake during the molt (Dittrich, 1987).

The air and water temperatures at Harderwijk were higher than those in the foraging areas of wild Pacific walruses (Fig. 1). In addition, during the educational shows, most frequent in summer, the animals performed on land. During shows on warm days, the animals were very slow. Both the high water temperature and the time spent on land decreased the thermoregulatory demands of the walruses, possibly causing a reduction in appetite. In addition, the animals often slept in a sheltered area, and thus may not have needed to replenish their blubber layer to the extent of wild walruses after the breeding and molting seasons. Captive and wild walruses spend most of their time in the water and refrain from hauling out at high temperatures (Fay & Ray, 1968). It is possible that the metabolic rate of the captive males in their study decreased because they were unable to retreat from the heat to the cooler water. A decreased metabolic rate correlates with high environmental temperatures in many mammals (Kleiber, 1961).

As a result of seasonal food intake fluctuations, the alimentary tract is probably adapted to periods of high food intake. The present study shows that the stomach of a walrus can process, in one day, at least twice as much as the average daily food intake (taken over a year). This could allow the walrus to eat more during the autumn and early winter. Wet weights of the stomach contents (mainly bivalves) of Pacific walruses between 3.6 and 9.3 kg have been reported by Fay *et al.* (1977). The largest reported stomach content (bivalve feet and siphons), of around 43 kg in an adult male Pacific walrus (Brooks, 1954), agrees well with the linear relationship between lean body weight (total body weight–blubber weight) and stomach volume in Atlantic walruses (Knutsen & Born, 1991). The stomach volume of one-year-old animals was about 10 litres, and that of 10-year-old animals, about 40 litres. This suggests that a walrus can obtain its daily energy requirement in one meal if necessary.

Food consumption as a percentage of body weight
It has been suggested (based on a small sample size and a short time period) that the food intake of Pacific walruses, expressed as a percentage of body weight, is similar at all ages (Fedoseev, 1976). However, subsequent work (Gehnrich, 1984) and the present study, based on more individuals, over many years, and during various seasons (=varying body weight), showed a range of intakes. The lowest values per unit body weight were the maintenance levels for adults, while the highest were for growing juveniles. Above 800 kg, daily food intake as percentage of body weight varied between 2 and 3% for non-reproducing animals. Based on food consumption from captive animals, daily food consumption of adult Pacific walruses in the wild was estimated to be 4 to 8% of body weight (Fay, 1982). These high estimates could be due to lack of data for adults, or inaccurately based on the total weight of bivalve mollusks, including shells.

A 4-year-old captive Atlantic walrus consumed around 10% of its body weight (182 kg) in clams and fish each day (Ditmars, 1914). Although the animal was extremely underweight (a 4-year-old walrus should weigh around 450 kg), this value agrees with those for animals of that weight in the present study.

Ecological significance
The present study may also provide insight into the seasonal changes seen in blubber thickness of Pacific walruses in the wild (Quakenbush *et al.*, 1999). Blubber thickness is used as an indicator of body condition. An increased understanding of normal fluctuations may lead to a higher probability of detecting problems related to the prey resource or disease in the wild population.

To estimate food requirements of wild Pacific walruses, information on the relationship between food consumption of animals in the present study and that of wild animals of similar gender, age, and reproductive status is necessary. For such a comparison, data are required on the following parameters for both wild and captive walruses: caloric content of food, the water and air temperature, and the animals' activity level.

The animals in the present study were fed fish, whereas wild walruses eat mainly bivalve mollusks (Fay, 1982). Fish and the siphons and feet of the clam *Mya truncata*, a major constituent of the diet of wild walruses, have approximately the same caloric density (Fisher & Stewart, 1997). This suggests that the weight of food intake of the study animals can roughly be compared to the weight of the mollusk prey wild walruses consume (shells excluded).

The walruses in the present study were kept much further south than wild Pacific walruses, and encountered much higher water and air temperatures (Fig. 1). Adult walruses appear to be thermo-neutral in air at temperatures between about − 20 and +15°C (Fay & Ray, 1968). The study animals would be expected to spend less energy than wild conspecifics on thermoregulation during autumn, winter and spring. However, they may have been heat-stressed (increasing metabolism) on warm days in summer. Therefore it is difficult to compare the thermoregulatory energy requirements of the animals in the present study with those of wild conspecifics.

The present study reports food consumption of walruses in a limited artificial environment. Activity levels, however, may not have been lower than those of wild conspecifics, because the study animals were involved in shows, and had free access to water, spending a large amount of time swimming (Kastelein & Wiepkema, 1989). Mean swimming speed for Atlantic walruses around Greenland is 4.2 km/h, with a maximum swimming speed of 16.7 km/h (Born & Knutsen, 1990). General swimming speeds of the walruses in the present study are estimated to be between 4 and 8 km/h.

Energy expenditure during feeding is likely to be lower for captive animals because they are hand-fed on land, while animals in the wild must dive, search for, excavate, identify and process small prey (Fay, 1982; Kastelein & van Gaalen, 1988; Kastelein & Mosterd, 1989; Kastelein *et al.*, 1994). Walruses can take more than 6000 prey items in a single meal (Fay, 1981), at a rate of more than 6 clams per minute (Oliver *et al.*, 1983). The aerobic dive limit of walruses is around 10 minutes (Wiig *et al.*, 1993; Nowicki *et al.*, 1997), although dives usually last between 6 and 9 minutes with 1 minute surface intervals. This would allow 40–60 clams to be consumed per dive. This means that on days with such large meals (6000 prey items) a walrus has to dive almost for 17 hours per 24-hour period. Walruses are known to feed for several days after which they return to land and rest for several days.

Considerations of differences in diet, temperature and activity suggest that food intake values presented in the present study serve only as minimum estimates of food requirements of wild Pacific walruses of similar age, gender and reproductive status.

The most critical food shortages for wild Pacific walruses are thought to occur in winter, when males and females are in the same geographical area (Fay, 1982). In contrast, data from walruses in the present study and those at Marineland, Los Angeles, (Gehnrich, 1984), suggest that the highest intakes for both adult males and pregnant, lactating females occur during autumn (September–December).

Vibe (1950) reports that in Greenland waters, at a depth of 40 m, the total weight of shellfish prey,

including shells, was at least 138 g/m^2 (about 36 mollusks). The shells of mollusks are not consumed by walruses (Allan, 1880; Fay, 1982). A small study at Harderwijk showed that 50% of the total wet weight of a 50 g clam (*Mya arenaria*) consists of shell, while Steimle & Terranova (1985) report shell weights of 9 bivalve mollusk species between 30 and 80% of total body weight. This suggests an edible mollusk density of about 69 g/m^2 in Greenland waters. Adult male walruses in the present study consumed 12000 kg of fish annually. Assuming a similar caloric content for fish and the soft parts of bivalve mollusks (Steimle & Terranova, 1985; Fisher & Stewart, 1997), one adult male Pacific walrus may consume all the shellfish in 174 000 m^2 of sea bed each year. The impact, therefore, of the walrus on benthic fauna in areas with a high walrus density is probably profound (Oliver *et al*., 1985).

Acknowledgments

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