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Food Consumption and Body Mass of Captive Harbor Seals (*Phoca vitulina*)

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Abstract

The food consumption (recorded as kg of individual fish species) of nine male and six female captive harbor seals is described. This longitudinal study is based on data originally archived for short-term husbandry purposes. The chemical composition and caloric value of the diet were not measured. Because caloric content of fish varies seasonally and annually, and depends on the geographical region where it was caught, the average food intake variations seen in this study may reflect the caloric content of the diet. However, because the effects of season, age, gender, and reproductive state are consistent in various seals, and all seals entered the study at different times, and food was caught in different seasons and stored for different lengths of time before being fed, the general patterns described are believed to be independent of variation in caloric content of the diet. There was a great deal of individual variation in the annual food consumption of male harbor seals, but generally it increased from around 950 kg at the age of one year to around 1,200 kg (estimated at 98 x10^5 kJ/year) at the age of 13 years. The annual food consumption of the nonreproductive female harbor seals also varied much among individuals, but generally fluctuated around 1,000 kg (estimated at 82 x 10^5 kJ/year). Adult male and female harbor seals had slightly different seasonal cycles in food consumption. Reproduction (producing a pup and suckling it) increased the degree of seasonal fluctuation in consumption by females. Immature animals did not experience seasonal changes in food intake. During molting, the seals usually lost weight. In males, molt occurred in August; and in females, usually in July. Males and females grew rapidly between birth and the age of 4 to 5 years. Thereafter, the growth rate decreased. Males reached a maximum body mass of around 100 kg and females around 90 kg. A negative relationship occurred between body mass and food intake when expressed as a percentage of body mass.

Key Words: body mass, energetics, feeding, nutrition, phocid, pinniped, reproduction, weaning, harbor seals, *Phoca vitulina*

Introduction

The harbor seal (*Phoca vitulina*) has the widest distribution of all phocids and inhabits both the North Atlantic and the North Pacific Oceans (Bonner, 1972). In many areas, harbor seals are thought to compete with the commercial fisheries for fish (Ashwell-Erickson & Elsner, 1981; Bonner, 1972; Fisher, 1952; Havinga, 1933; Makhnyr & Perlov, 1988; Payne & Selzer, 1989; Scheffer & Sperry, 1931; Spalding, 1964). To assess the level of competition involved, information is needed about the diet and daily energy requirements of harbor seals.

Information about the prey species and the proportions in which they are eaten has become available by examination of the stomach contents of harbor seals and the fish otoliths in seal feces (Härkönen, 1987; Havinga, 1933; Payne & Selzer, 1989; Rae, 1968, 1973; Scheffer & Sperry, 1931; Sergeant, 1951; Spalding, 1964). Compared to this knowledge on diet composition, relatively little is known about the amount of food consumed, or about fluctuations in food intake (Ashwell-Erickson & Elsner, 1981; Havinga, 1933; Olesiuk, 1993; Renouf & Noseworthy, 1990; Renouf et al., 1988; Rosen & Renouf, 1998; Scheffer, 1950). These kind of data can be derived partly from the food records of animals kept in zoos. Dolfinarium Harderwijk has housed harbor seals and recorded their daily food consumption and occasional body mass since 1977. The aim of this study, therefore, is to describe the food consumption and body mass changes of these seals between 1977 and 1999.

Materials and Methods

Study Animals

The study animals were nine male and six female harbor seals housed at Dolfinarium Harderwijk

Table 1. The characteristics of the harbor seals used in the present study; birth dates of animals in parks are known precisely; those of animals originating from the wild were estimated from body size on arrival. All animals but one (animal 003 died on 26/6/88) were at the park until the end of the study period (1999).

Animal	Sex	Date of birth (d-m-yr)	Arrival date at Harderwijk (d/m/yr)
PvZH001	F	1973*	24/5/77
PvZH002	M	1973*	24/5/77
PvZH003	F	1973*	24/5/77
PvZH004	F	1984*	6/9/84
PvZH009	M	2/7/81	27/10/86
PvZH013	M	11/6/92	1/12/93
PvZH014	M	7/82	3/3/94
PvZH015	F	7/87	3/3/94
PvZH016	M	6/94	12/9/94
PvZH017	F	26/5/94	6/10/94
PvZH018	F	1987*	11/10/94
PvZH019	M	1987*	11/10/94
PvZH020	M	1987*	11/10/94
PvZH023	M	6/5/96	Pup of 018 & 019
PvZH025	M	22/6/97	Pup of 018 & ?

* = Estimated birth date
? = Father unknown

between 1977 and 1999 (Table 1). Except for two animals born at the park, they originated from the east Atlantic Ocean, and came to Harderwijk either directly from the wild or from other parks. Most of the reported ages are accurate because the animals either arrived as abandoned pups or were born at Dolfinarium Harderwijk or a park where they were previously kept. Until 1995, no pups (neither fetuses or full-term stillbirths) were born at the park. This was probably due to behavioral reproductive malfunctioning of the males because reproduction started the first breeding season after new males were introduced in 1994. The animals were weighed irregularly, usually when arriving at the park or when they had to be moved due to pool maintenance.

Study Area

The animals were kept in an outdoor freshwater pool (40 m x 14 m, 1.2 m deep) with a surrounding artificial beach. The average monthly water temperature varied between 4° C in winter and 18° C in summer, while the average monthly air temperature varied between -0.3° C in February and 17.5° C in July (Figure 1). The park is located at 52° 20' N and 5° 37' E.

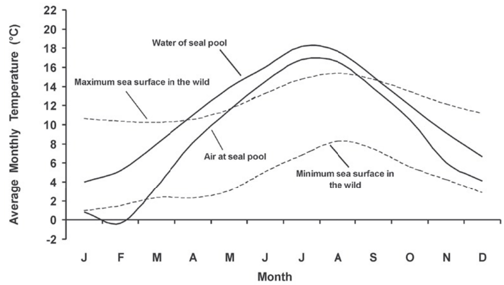

Figure 1. Average monthly air and water temperatures at the study area and the minimum and maximum average monthly sea surface temperatures (Bottomley et al., 1990) which wild harbor seals may encounter in their distribution area (depending on their geographical location; Bonner, 1972)

Food

Multivitamins (Seavit®, one tablet per 2.5 kg of food) were added to the fish after it had been defrosted in running tap water. The frozen fish was stored for different lengths of time before being fed to the seals, but for a maximum of four months. The animals were usually fed four times per day (six times per day in July and August). During the last feed of the day, the animals were allowed to eat as much as they wanted. Feeding was stopped as soon as the animal began to play with the food instead of consuming it immediately. After each meal, the amount of each fish species eaten per seal was recorded in kg. This resulted in a mixed diet of on average 45% mackerel (*Scomber scombrus*), 40% herring (*Clupea harengus*), 5% whiting (*Merlangius merlangus*), and 10% squid (*Illex* spp.), based on wet weight of the fish and squid species. Records were only used of animals in good health and from full calendar years.

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 by age class of fish, seasonal changes, and location where the fish was caught. For the analysis, the total amounts consumed by a seal per month (as the number of days in each month varies, the average food consumption within each month was adjusted to 30 days) and per year were used. Due to large changes between days, an average daily food intake quantity of a harbor seal seems of little value. To roughly estimate the energy used by the harbor seals, the food intake was calculated in kJ using average values for the fish species (van der Heijden et al., 1998; mackerel, approx. 9,550 kJ/kg wet weight; herring, approx. 8,880 kJ/kg wet weight; whiting, approx. 4,750 kJ/kg wet weight; squid, approx. 1,000 kJ/kg wet weight). This yielded an average energetic value for their diet of 8,200 kJ/kg (average taken over all fish/squid species consumed by the seals).

Statistical Analyses

The significance of seasonal fluctuations in food intake among years were tested by means of Kendall's (1962) coefficient of concordance test. 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 among 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 later year; however, by ranking the food intakes per month within a year, seasonal patterns could be examined.

Results

Age-Related Changes and Sexual Differences in Food Consumption

The two male pups began eating during their year of birth (intakes during calendar year of birth: 480 and 680 kg). The annual food consumption of the males varied among individuals, but generally increased from around 950 kg at the age of one year to around 1,200 kg (estimated at 98 x 10^5 kJ) at the age of 13 years (Figure 2A). The annual food consumption of the nonreproductive females varied also among individuals, but generally fluctuated around 1,000 kg (estimated at 82 x 10^5 kJ; Figure 2B). The annual food intake of the reproductive female was around 1,500 and 1,350 kg in the years she reproduced (at the ages of 9 and 10 years), and around 1,100 kg in the previous years, and around 1,000 kg in the following years (Figure 2B).

Seasonal Changes in Food Consumption

All adult (i.e., being of reproductive age: > 4 years) males showed a similar seasonal fluctuation in their food intake. Because the food intake fluctuations of male 002 were representative of the fluctuations in the food intakes of the other adult males, and because for this animal the data set spanned 18 years, his average seasonal fluctuations are shown. The fluctuations returned almost every year (Kendall's coefficient of concordance test: $\chi^2_r = 73.85$; $p < 0.001$). Between the ages of 5 and 22 years, male 002 generally ate less than the annual average between January and April, more than average in May, around average between June and August, and more than average between September and December (Figure 3A).

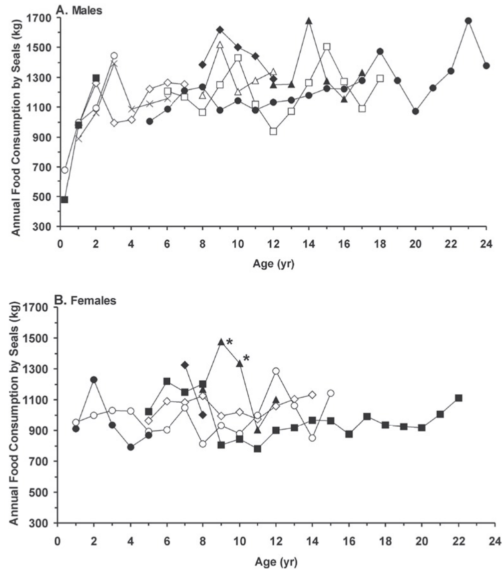

Figure 2. The annual food consumption (based on calendar years) of nine male (A) and six female (B) captive harbor seals by age in years; data points of the same individual are connected by lines. *Year in which a pup was born and suckled. Note that the food intake of the pups (age 0) do not encompass an entire calendar year as they were born in May.

Mating occurred in June and July. The males usually molted in August. They visibly lost weight during the mating and molting periods.

The seasonal fluctuations in the food intake of the adult nonreproductive females differed slightly from those of the males. Because the seasonal food intake fluctuations of female 001 were representative of the fluctuations in the other adult nonreproductive females, and because for this animal the data set spanned 18 years, her average seasonal fluctuations are shown. The fluctuations returned almost every year (Kendall's coefficient of concordance test: $\chi^2_r = 80.78$; $p < 0.001$). Between the ages of 5 and 22 years, nonreproductive female 001 generally ate less than the annual average between January and March, around average in April and May, and less than average in June and July. Between August and December, she consumed more than average (Figure 3B). The females usually molted in July.

Female 018 reproduced and nursed her pups in two successive years. During those two years, her seasonal fluctuation in food intake were similar but differed from those of nonreproductive adult females. She consumed less than average between November and May. After delivery of the pups in May and June, her food intake increased to above average, despite the molt period (Figure 3C).

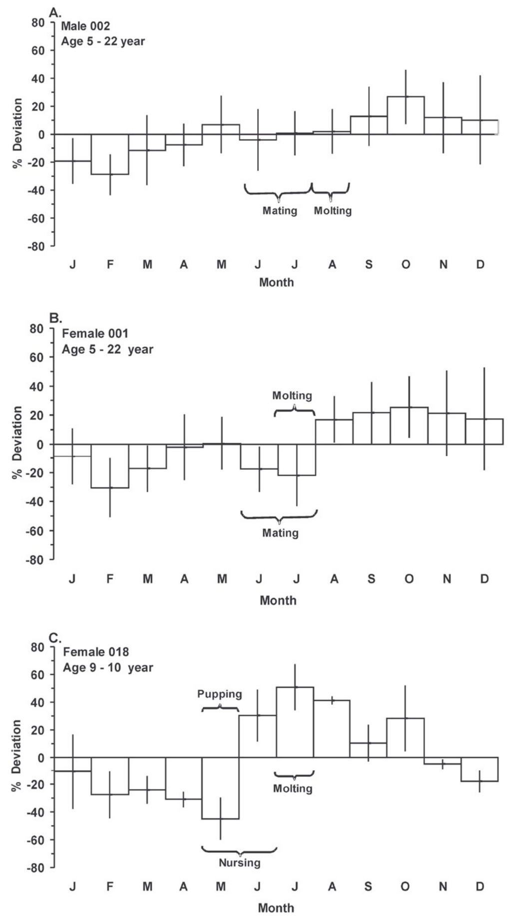

Figure 3. Deviation from the average monthly food intake of (A) adult male 002 between the age of 5 and 22 years (*n* = 18 years), (B) of adult female 001 between the age of 5 and 22 years (*n* = 18 years; she did not reproduce in those years), and (C) of female 018 at the ages of 9 and 10 years (*n* = 2 years; in both years she gave birth to a pup and nursed it); the bars indicate one standard deviation. Because the number of days in each month varies, the average food consumption within each month was adjusted to 30 days.

Body Mass

The animals were weighed relatively infrequently (Figure 4). Males grew rapidly between birth and the age of 4 years. Thereafter, the growth rate decreased. They reached a maximum body mass of around 100 kg. Females also grew quickly between birth and the age of 4 to 5 years. Thereafter, their growth rate decreased. They reached a maximum body mass of around 90 kg. Because the animals were measured at various moments in the year, some of the weight changes of an animal over time shown in Figure 4 may be due to seasonal fluctuations in body weight.

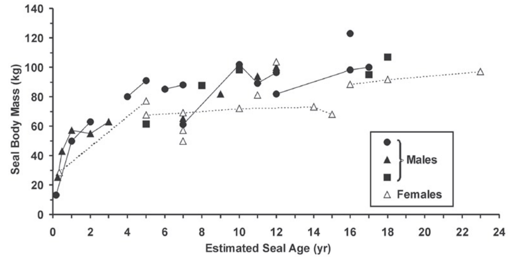

Figure 4. The relationship between estimated age and measured body mass of the nine male and six nonpregnant female captive harbor seals; measurements of the same animal are connected by lines but do not indicate the animal's body mass in the intervening period. Because the animals were measured at various moments in the year, some of the weight changes of an animal over time may be due to seasonal fluctuations in body weight.

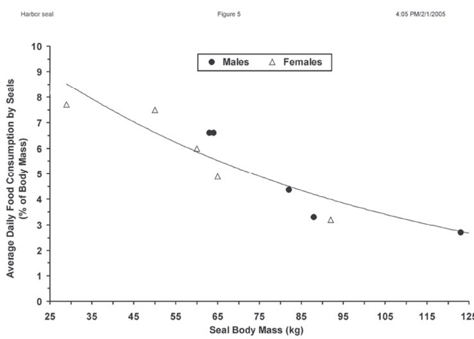

Figure 5. The relationship between body mass and average daily food consumption expressed as a percentage of body mass of five male and five nonreproducing captive female harbor seals (one data point per animal); best fit curve: Average daily food consumption (% of body mass) = $9.0535e^{-0.012\text{ (body mass in kg-25)}}$.

Daily Food Consumption as a Percentage of Body Mass

The average daily food consumption over the calendar month in which harbor seals were weighed was compared to their weights. A negative relationship occurred between body mass and average daily food consumption expressed as a percentage of body mass, both for males and females (Figure 5). Average daily food consumption (% of body mass) = $9.0535e^{-0.012\text{ (body mass in kg-25)}}$.

Discussion and Conclusions

This longitudinal study is based on data originally archived for short-term husbandry purposes. The chemical composition and caloric value of the diet were not measured. Because caloric content of fish varies seasonally and annually, and depends on the geographical region where it was caught, the food intake variations seen in this study may reflect the caloric content of the diet; however, because the effects of season, age, gender, and reproductive state are consistent in various seals, and all animals entered the study at different times, and the fish was bought at various seasons of the year and stored over various periods, the general patterns observed in the present study are believed to be independent of variation in caloric content of the diet.

The number of feeding bouts varied seasonally (normally four times per day and six times per day in July and August). In terrestrial mammals, the amount of food consumed in a day has been found to depend on the number of feeding bouts during the day; however, the four feeding bouts per day in the present study was already a large number of bouts (in some zoos, harbor seals are only fed two times per day and appear in good condition). Therefore, probably no, or only a small, difference in daily food intake is expected between days with four and days with six feeding bouts.

Sexual Differences in Annual Food Consumption

The observed general differences in annual food consumption between males and females of similar ages was probably related to the sexual dimorphism in body weight. Sexual dimorphism in body weight also occurs in harbor seals in the wild. Ashwell-Erickson & Elsner (1981) found that the weight difference between male and female Pacific harbor seals increased until they were 10 years old, after which the difference stabilized at around 20 kg (males reached their maximum weight at 130 kg and females at 110 kg). Atlantic harbor seals (the species in the present study) are smaller than Pacific harbor seals of the same age, and show about a 10 kg difference in body weight between adult males and adult females (Härkönen & Heide-Jørgensen, 1990; McLaren, 1993).

Influence of Reproduction on Food Consumption of Females

Although only one female reproduced (twice) during the study period, it is clear that reproduction requires extra food. The annual food intake of the reproducing female in the present study was 36% (400 kg = approx. 33 x 10^5 kJ) above her average annual intake (around 1,100 kg) in one case and 23% (250 kg = 21 x 10^5 kJ) in the other. An increase in food intake in years in which reproduction occurs also has been observed in captive grey seals (*Halichoerus grypus*; Kastelein & Wiepkema, 1988, 1990; Kastelein et al., 1990, 1991, 1994). The increase in food intake mainly occurs during the nursing period, during which food has to be converted into milk for the growing pup. Based on a model, Ashwell-Erickson & Elsner (1981) estimated the reproductive energy cost (gestation and lactation) of female harbor seals at 10 x 10^5 kJ/yr. This estimate is only half to one third of the observed extra energy consumed by the female in the present study in years that she reproduced. The large difference suggests that the model needs to be improved.

Seasonal Changes in Food Consumption

Captive feeding records do not suffer from effects of changes in seasonal foraging costs and food availability and, thus, may be useful in revealing natural bioenergetic/physiological rhythms.

Males

Adult males in the present study ate around average between June and August (during the breeding and molting seasons). In spite of this, they visibly lost weight. A weight loss during the breeding season has also been observed in other captive harbor seals (Rosen & Renouf, 1997) and in wild harbor seals (Härkönen & Heide-Jørgensen, 1990; Pitcher, 1986). In the wild, males spend much of their time ashore during the breeding season, and probably do not feed as often as they do in other seasons. The fact that the captive animals of the present study showed seasonal fluctuations in their food intake even though they were fed *ad lib.* suggests that these fluctuations are regulated by an internal endocrine rhythm. This idea is supported by the fact that the testes of wild male harbor seals are larger in the breeding season than in the rest of the year (Härkönen & Heide-Jørgensen, 1990). The animals in the present study showed natural cycles similar to those seen in the wild. Because these food intake cycles were not the result of dramatic changes in activity levels (no additional predation or large increases in swimming costs); they point to an inherent physiological rhythm. This rhythm may be seen in seasonal changes in metabolism (Rosen & Renouf, 1998). Obviously, phocids have to alter their energy intake to replenish or prepare energy stores for times when energy expenditures outstrip energy intake. In harbor seals, this is usually because of reduced foraging opportunities as well as increased seasonal costs.

Most of the animals in the present study were mature during part of the study period as east Atlantic males harbor seals reach maturity at 4 to 5 years of age (Härkönen & Heide-Jørgensen, 1990). Markussen et al. (1990) found no difference in maintenance requirements among individuals or age classes, or among seasons in harbor seals; however, this was probably because their four study animals were immature and, therefore, did not yet experience seasonal fluctuations in sex hormones. Walker & Bowen (1993) described wild adult male harbor seals that lost up to 24%

of their body mass during the breeding season, while subadult animals in the same area remained at the same weight. Adult males in the wild reduce feeding during the mating season, although they do enter the water (Thompson et al., 1989). Adult males also may lose weight through increased activity during aquatic mating (Reilly & Fedak, 1991). In zoos, adult male harbor seals are also very active during the breeding and molting seasons (Renouf, 1993).

Adult males in the present study increased their food intake between September and December probably to restore their fat reserves and insulation. A similar food intake fluctuation also was reported by Ashwell-Erickson & Elsner (1981). The low food intake of the males and females in the present study between January and April coincided with time of year at which they had a relatively thick insulating blubber layer and were not very active.

Females

Harbor seal pups in the east Atlantic are generally born in June, and suckling lasts for four to six weeks until the end of July when ovulation occurs (Bigg, 1981; Bonner, 1972; Härkönen & Heide-Jørgensen, 1990; Reijnders, 1990). The adult, nonreproducing females in the present study ate less than usual during the breeding and molting seasons; like in the males, their increased food intake between August and December probably served to restore their fat reserves.

Despite the fact that, unlike most larger phocid species, female east Atlantic harbor seals do feed during lactation, they lose on average 26 kg (35% of body mass) during the lactation period (Härkönen & Heide-Jørgensen, 1990); this is 79% of their stored fat and 20% of their stored protein (Bowen et al., 1992). Most females in the present study were mature but did not reproduce, except for one animal when she was 9 and 10 years old. In the east Atlantic, females become sexually mature at the age of 3 to 4 years (Härkönen & Heide-Jørgensen, 1990). The adult females in the present study that did not reproduce, still showed some seasonal fluctuations in food consumption (but clearly less fluctuation than the female during the two years she reproduced). This may be the result of natural changes in hormones such as those related to estrus. In female harbor seals of the east Pacific, estrus occurs only once a year, and pseudopregnancy lasts for about three months (Bigg, 1973; Bigg & Fisher, 1974).

The seasonal fluctuations in the food intake of the reproducing female in the present study coincided with those described by Renouf & Noseworthy (1990). Renouf et al. (1988) found seasonal variations in food consumption of captive west Atlantic harbor seals which were fed *ad lib.*, but unfortunately the food intakes of animals of various sexes and ages were combined to calculate the seasonal changes.

The above-mentioned studies suggest that adult male and female harbor seals have slightly different seasonal cycles in food consumption, that reproduction increases the degree of fluctuation in the females, and that immature animals may not experience seasonal food intake changes.

Influence of Molt on Food Consumption

In the present study, molting occurred in both sexes after the mating season. Food intake was low during molting, except when a female had nursed her pup in the previous two months.

The molt cycle of harbor seals is influenced by the photoperiod (Mo et al., 2000). Because the animals in the present study were housed outdoors, at the same latitude as wild harbor seals, the timing of the molt and its seasonal effect on the food intake of the study animals will probably reflect what occurs with harbor seals in the wild.

In the wild, molt of the adult pelage of harbor seals usually occurs soon after the breeding season, but there is individual variation in the date and pattern of molt (Bonner, 1972; Ling, 1972; Stutz, 1967). The blubber thickness of wild adult male harbor seals decreases during the molt (Pitcher, 1986). Serum cortisol levels reach a maximum just before or during the main period of shedding of hair, and decrease abruptly during the main period of rapid growth of hair. Cortisol favors fat catabolism. Serum thyroxin levels increase in the period of maximum hair growth (Ashwell-Erickson et al., 1986; Riviere et al., 1977). Harbor seal males around Orkney, UK, hauled out every day during molt (Thompson et al., 1989). In contrast, females spent more time than usual at sea during molt (probably feeding to restore their blubber layer). This sexual difference in behavior during the molt may explain why the nonreproducing females in the present study began to eat more than average in August, while the males did so in September. High skin temperatures may increase the speed of molt (Feltz & Fay, 1966; Ling & Bryden, 1981). In the present study, females molted in July, and males in August. Also, in the wild, female harbor seals complete their molt about three weeks earlier than males (Thompson & Rothery, 1987). Molt may be influenced by changes in the hormone levels involved in reproduction in both sexes. It is possible that in females ovulation triggers the onset of molt, while in males a drop in the testosterone level after the breeding season may be the triggering mechanism for molt. Ashwell-Erickson & Elsner (1981) and Rosen & Renouf (1998) found that metabolism in harbor seals during molt was reduced to 40-83% of pre-molt levels. This would allow the animals to stay on land without food for longer than usual.

Daily Food Consumption Expressed as Percentage of Body Mass

In general, the larger an animal, the lower the average daily food consumption as % of body mass under similar environmental conditions and with a similar diet. The smaller the animal, the higher the body surface to volume ratio, and, thus, the more thermal energy the animal loses to its environment. Ashwell-Erickson & Elsner (1981) found that absolute basal metabolism in harbor seals declined with increasing age, and that smaller animals, which were usually still growing, required extra food.

Havinga (1933) described a food consumption of 5% of body mass for a 30 kg harbor seal, and Scheffer (1950) noted 6% for a 32 kg harbor seal. These values are low compared to those of animals in the present study of similar size, perhaps because of short sampling periods in the other studies (coinciding with days in which the food intake is below the annual average). To determine the average daily food intake of adult harbor seals, sampling should continue for at least one year due to the seasonal variations in food intake. Ashwell-Erickson & Elsner (1981) described the food consumption of a male Pacific harbor seal. Food intake declined from a mean value of 13% of body mass during the first year to 3% at the age of 9 years. These values agree with those in the present study. Based on the food quantity found in the stomachs of wild harbor seals, Havinga (1933) estimated that the seals required on average 1,800 kg of fish per year per animal. This is much more than the animals in the present study consumed. Perhaps wild harbor seals do not feed every day, and, thus, they eat varying amounts of food per day (and Havinga sampled on days animals ate above average to compensate for previous day[s] in which they ate less than average), or the study of Havinga was conducted in a period in which seals were eating above the annual average. Maybe in the wild harbor seals sometimes have a diet of a lower caloric content than the animals in the present study, or maybe they need more food because of energy costs for foraging.

The average daily gross energy intake of six captive Atlantic harbor seals (average: 25.4 MJ/d; SD: 4.1 MJ/d) reported by Rosen & Renouf (1998) was similar to the estimated average gross energy consumption found in the present study (26.9 MJ/d), which was based on the average caloric density of the fish/squid species fed.

Ecological Significance

Can information from the present study be used to determine the energetic requirement of harbor seals in the wild? Differences in food consumption between the animals in the present study and conspecifics in the wild are probably mainly determined by differences in activity level, the energy content and digestibility of their diet, and food availability.

Temperatures experienced by wild harbor seals are probably within their thermoneutral zone, as they are probably well-adapted to their natural environment; however, by haul-out behavior harbor seals have some control over the temperature and heat conductance of their environment (Watts, 1992). Because the study area in the present study is close to the distribution area of a wild harbor seal population, the animals in the present study probably did not have different energy requirements than wild harbor seals due to air and water temperature differences. Only between June and August were the water temperatures in the present study slightly higher than the maximum sea surface temperatures experienced by many wild harbor seals in their distribution area (Figure 1).

Harbor seals are opportunistic feeders in choice of prey species (Härkönen, 1987), and their diet varies seasonally and geographically (Payne & Selzer, 1989; Spalding, 1964). Therefore, the composition and energy content of the diet in the present study is difficult to compare to that of wild harbor seals, but may have resembled that of some wild conspecifics.

The energy requirements of harbor seals also depend on the activity level of the seals. Davis et al. (1985) showed that metabolism increased curvilinearly with swimming speed. The study animals were kept in a large, shallow pool. They swam most of the time, but could not dive deep. Radio telemetry studies give insight into the activity levels of wild harbor seals, including their haul-out pattern, swimming speed, and diving depth (Thompson et al., 1989). Large differences in activity levels have been observed between individual seals of the same population (Mackay et al., 1995).

Based on the information and assumptions mentioned above, the food consumption of the harbor seals in the present study was probably less than that of wild conspecifics of similar age and gender, mainly due to a difference in energy expenditure for swimming and diving. The food consumption data of the present study thus can serve only to make a conservative estimate of the amount of fish wild harbor seals consume.

Acknowledgments

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