The daily food consumption of 26 California sea lions at the Harderwijk Marine Mammal Park was recorded. Average annual food consumption of males increased with age to stabilize at approximately 4,000 kg/year by the age of 10 years. Females showed a rapid increase in average annual food consumption until they were 3 years old. Thereafter, females housed outdoors averaged 1,800 kg/year, whereas those housed indoors ate approximately 1,400 kg/year. Between the ages of 4 and 7 years, the food intake of males began to fluctuate seasonally, decreasing between May and August. The low food intake in summer was associated with an increase in aggressive behavior. Seasonal fluctuation in the food intake of non-reproductive females was negligible. Between the ages of 6 and 8 years, many females began to reproduce successfully. Pups were born in May and June. The females’ food intake decreased approximately 3 days before birth and ceased the next day. Feeding resumed the day after birth, and by 2 days after birth, it had usually returned to normal. On average, female intake increased in the year of conception, the year of birth, during which the pup was suckled for 6 months, and the following calendar year, during which the pup was weaned. Pups began to eat fish at approximately 11 months of age. When forcefed, they were fully weaned within 2 to 23 days. Male weight and body length increased until approximately 20 years of age. Females increased in body length until 6 years and in weight until approximately 13 years of age. The relationship between standard body length and body weight is given. The heavier an animal is, the lower is its food intake as a percentage of body weight.
INTRODUCTION

The California sea lion (Zalophus californianus californianus; Lesson, 1828) is distributed along the west coast of North America, from Baja, California to British Columbia [Odell, 1981]. The stomach contents and fish otoliths in the feces of wild California sea lions have been widely studied, providing data on prey species and the proportions in which they are taken [Dyche, 1903; Scheffer and Neff, 1948; Daugherty, 1965; Fiscus and Baines, 1966; Keyes, 1968; Jameson and Kenyon, 1977; Bowlby, 1981; Everitt et al., 1981; Jones, 1981; Ainley et al., 1982; Bailey and Ainley, 1982; Antonelis et al., 1984, 1990; Aurioles et al., 1984; Roffe and Mate, 1984; Lowry et al., 1991]. Although regional, seasonal and annual changes were demonstrated in diet, very little is known about daily food intake or about variations in intake owing to time of year, reproductive status, age, gender, or ambient temperature [Bryden, 1972]. Because, at present, such information is impossible to collect in the field [Beddington et al., 1985], it must be obtained from animals kept in human care.

This paper, therefore, describes the food consumption of California sea lions at the Harderwijk Marine Mammal Park and may be relevant to other institutions that keep California sea lions and for the management of wild populations.

MATERIALS AND METHODS

Study Animals

Twelve male and 14 female California sea lions of diverse ages and origins were maintained in human care (Table 1). The number of animals varied during the study period as some died, and others were moved to other zoos to prevent overpopulation and inbreeding. Also, pups were born during the study period. Age 1 is defined as the first calendar year after the year of birth. Male 015 was castrated at the age of 6 years and male 050 at the age of 5 years.

Study Areas

The study was carried out at the Harderwijk Marine Mammal Park, which lies in the central Netherlands (5°37' E and 52°20' N). The animals were maintained either in an outdoor enclosure with a freshwater pool (21 x 4 m, 2 m deep) or in an indoor enclosure with a saltwater (2.5% NaCl) pool (17 x 8 m, 2.5 m deep). The pools had sand filters, and the water was disinfected with chlorine by means of dosage pumps. Many animals were housed in both pools at various times in their lives. The average monthly outdoor water temperature varied between 10°C in February and 20°C in July (annual average, 14°C), whereas the average monthly air temperature varied between -0.3°C in February and 16.8°C in July (annual average, 11°C). Indoors, the average monthly water temperature varied between 16°C in January and 21°C in August (annual average, 18°C), and the average monthly air temperature varied between 5°C and 25°C (annual average, 15°C). In both enclosures, the study animals were exposed to the natural light cycle as the indoor enclosure had many windows.

Feeding

The sea lions were fed three to six times per day on a diet of on average 40% mackerel (Scomber scombrus), 40% herring (Clupea harengus), 15% sprat (Sprattus sprattus), and 5% squid (Illex spp.), based on weight. Multivitamins (Seavit; 1 tablet...
per 2.5 kg of food) were added to this diet after it had been defrosted. During the last feed of the day, feeding continued until each animal began to play with its food instead of consuming it quickly. This was considered a sign of satiety. In February, however, the food intake of those animals used in shows was deliberately reduced by 10 to 20% to facilitate training. The daily food intake of each individual since 1967 was recorded. Only food records of healthy animals were used in this study.

### Body Measurements

The weight and standard body length (the straight line between nose and tail tip) were measured in a number of the study animals.

### Statistics

The significance of seasonal fluctuations in food intake between years were tested 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 the previous or next year. However, by ranking the food intakes per month within a year, annually returning seasonal patterns could be tested for.

---

**TABLE 1. The studied California sea lions and their affinity**

<table>
<thead>
<tr>
<th>Animal</th>
<th>Sex</th>
<th>Date of birth (day-mo-yr)</th>
<th>Origin</th>
<th>Arrival date at the park (day-mo-yr)</th>
<th>Code father</th>
<th>Code mother</th>
</tr>
</thead>
<tbody>
<tr>
<td>ZcZH001</td>
<td>F</td>
<td>ca. 1960</td>
<td>Channel Islands, CA</td>
<td>01-10-1963</td>
<td>Wild</td>
<td>Wild</td>
</tr>
<tr>
<td>ZcZH003</td>
<td>F</td>
<td>ca. 1970</td>
<td>Channel Islands, CA</td>
<td>24-06-1971</td>
<td>Wild</td>
<td>Wild</td>
</tr>
<tr>
<td>ZcZH004</td>
<td>F</td>
<td>ca. 1970</td>
<td>Channel Islands, CA</td>
<td>24-06-1971</td>
<td>Wild</td>
<td>Wild</td>
</tr>
<tr>
<td>ZcZH005</td>
<td>F</td>
<td>ca. 1970</td>
<td>Channel Islands, CA</td>
<td>24-06-1971</td>
<td>Wild</td>
<td>Wild</td>
</tr>
<tr>
<td>ZcZH007</td>
<td>F</td>
<td>09-06-1978</td>
<td>Harderwijk Park, NL</td>
<td>—</td>
<td>ZcZH024</td>
<td>ZcZH005</td>
</tr>
<tr>
<td>ZcZH008</td>
<td>F</td>
<td>22-06-1978</td>
<td>Harderwijk Park, NL</td>
<td>—</td>
<td>ZcZY023</td>
<td>ZcZH001</td>
</tr>
<tr>
<td>ZcZH009</td>
<td>M</td>
<td>ca. 1971</td>
<td>Mystic Aquarium, CT</td>
<td>17-11-1980</td>
<td>Unknown</td>
<td>Unknown</td>
</tr>
<tr>
<td>ZcZH010</td>
<td>F</td>
<td>10-06-1980</td>
<td>Delphin. Münster, Germany</td>
<td>15-04-1981</td>
<td>ZcZY023</td>
<td>ZcZY022</td>
</tr>
<tr>
<td>ZcZH011</td>
<td>M</td>
<td>13-06-1982</td>
<td>Delphin. Münster, Germany</td>
<td>10-12-1985</td>
<td>ZcZY023</td>
<td>ZcZY002</td>
</tr>
<tr>
<td>ZcZH012</td>
<td>F</td>
<td>26-05-1979</td>
<td>Delphin. Münster, Germany</td>
<td>24-03-1980</td>
<td>ZcZY023</td>
<td>ZcZY022</td>
</tr>
<tr>
<td>ZcZG013</td>
<td>F</td>
<td>31-05-1985</td>
<td>Harderwijk Park, NL</td>
<td>—</td>
<td>ZcZH009</td>
<td>ZcZH012</td>
</tr>
<tr>
<td>ZcZH014</td>
<td>F</td>
<td>30-05-1986</td>
<td>Harderwijk Park, NL</td>
<td>—</td>
<td>ZcZH009</td>
<td>ZcZH012</td>
</tr>
<tr>
<td>ZcZH015</td>
<td>M</td>
<td>06-06-1986</td>
<td>Harderwijk Park, NL</td>
<td>—</td>
<td>ZcZH006</td>
<td>ZcZH008</td>
</tr>
<tr>
<td>ZcZH024</td>
<td>M</td>
<td>ca. 1969</td>
<td>Santa Barbara, CA</td>
<td>27-02-1970</td>
<td>Wild</td>
<td>Wild</td>
</tr>
<tr>
<td>ZcZH025</td>
<td>M</td>
<td>ca. 1968</td>
<td>Wild</td>
<td>20-09-1969</td>
<td>Wild</td>
<td>Wild</td>
</tr>
<tr>
<td>ZcZH040</td>
<td>M</td>
<td>ca. 1969</td>
<td>Wild</td>
<td>08-10-1974</td>
<td>Wild</td>
<td>Wild</td>
</tr>
<tr>
<td>ZcZH050</td>
<td>M</td>
<td>30-05-1987</td>
<td>Harderwijk Park, NL</td>
<td>—</td>
<td>ZcZH009</td>
<td>ZcZH012</td>
</tr>
<tr>
<td>ZcZH051</td>
<td>F</td>
<td>01-06-1988</td>
<td>Harderwijk Park, NL</td>
<td>—</td>
<td>ZcZH009</td>
<td>ZcZH012</td>
</tr>
<tr>
<td>ZcZH052</td>
<td>M</td>
<td>31-05-1989</td>
<td>Harderwijk Park, NL</td>
<td>—</td>
<td>ZcZH009</td>
<td>ZcZH012</td>
</tr>
<tr>
<td>ZcZH053</td>
<td>M</td>
<td>03-06-1990</td>
<td>Harderwijk Park, NL</td>
<td>—</td>
<td>ZcZH009</td>
<td>ZcZH012</td>
</tr>
<tr>
<td>ZcZH054</td>
<td>F</td>
<td>22-06-1990</td>
<td>Harderwijk Park, NL</td>
<td>—</td>
<td>ZcZH015</td>
<td>ZcZH008</td>
</tr>
<tr>
<td>ZcZH055</td>
<td>F</td>
<td>13-06-1991</td>
<td>Harderwijk Park, NL</td>
<td>—</td>
<td>ZcZH006</td>
<td>ZcZH012</td>
</tr>
<tr>
<td>ZcZH056</td>
<td>F</td>
<td>09-06-1992</td>
<td>Harderwijk Park, NL</td>
<td>—</td>
<td>ZcZH006</td>
<td>ZcZH012</td>
</tr>
<tr>
<td>ZcZH058</td>
<td>M</td>
<td>01-06-1994</td>
<td>Harderwijk Park, NL</td>
<td>—</td>
<td>ZcZH006</td>
<td>ZcZH012</td>
</tr>
<tr>
<td>ZcZH060</td>
<td>M</td>
<td>12-06-1994</td>
<td>Antwerp Zoo, Belgium</td>
<td>01-06-1995</td>
<td>Unknown</td>
<td>Unknown</td>
</tr>
</tbody>
</table>
RESULTS

Annual Food Consumption

The annual food consumption of males increased until approximately 10 years of age, stabilizing at approximately 4,000 kg/year (11 kg/day; Fig. 1A). The food consumption of females showed a similar pattern, with a peak around 10 years of age and stabilization at approximately 2,000 kg/year (6 kg/day; Fig. 1B).

Fig. 1. The annual food consumption of male (A) and female (B) California sea lions housed indoors and outdoors at the Harderwijk Park. Age 1 represents the first calendar year after the year of birth. 1, Year in which the animal was castrated. *Year in which a pup was born and suckled. +Year in which a full-term dead pup was born.
consumption of males 015 and 050 remained low after castration. Intake of males housed indoors was similar to that of males housed outdoors. The annual food consumption of females increased until the age of approximately 3 years (Fig. 1B) and stabilized at approximately 1,800 kg/year (4.9 kg/day) for non-lactating females housed outdoors and at approximately 1,400 kg/year (3.8 kg/day) for those housed indoors. The influence of reproduction on the food consumption of females is described later.

**Maximum Consumption in 1 Day**

The total daily food consumption during a year varied more in males than in females. The maximum consumption by a male was 35.5 kg/day at 16 years of age. His average daily food intake that year was 9.5 kg. The most eaten by a female was 16 kg/day by an 8-year-old reproducing animal. Her average daily food intake that year was 6.9 kg (Fig. 2).

**Seasonal Changes**

Between the ages of 4 and 7 years, males began to show a seasonal fluctuation in food intake. Male 006, a representative example of an animal for which a long dataset was available, showed no significant systematic seasonal fluctuation between the age of 3 and 5 years (Fig. 3A; Kendall’s coefficient of concordance \( \chi^2 = 13.53, 0.25 < P < 0.50 \)). Between the age of 6 and 17 years, his food intake showed a significant seasonal fluctuation, falling generally below average between May and August and remaining high for the rest of the year, except in February, when his food ration was reduced for training purposes (Fig. 3B; Kendall’s coefficient of concordance \( \chi^2 = 67.58; P < 0.001 \)). The seasonal period of low food intake by adult males (older than 4 years) coincided with an increase in aggressive behavior.

![Graph showing maximum consumption in 1 day by male and female California sea lions of different ages.](image)
The food intake of non-reproductive adult females showed little but significant seasonal fluctuation. Female 001, a representative example of an animal for which a long dataset was available, ate on average slightly less during the first half of the year than during the second half between the ages of 7 and 31 years (Fig. 4A; Kendall’s coefficient of concordance $\chi^2_c = 57.55; P < 0.001$). Again, food intake in February was reduced for training purposes. Food intake of reproducing

![Bar chart showing food consumption deviation for male California sea lions.](image)
females, however, fluctuated more strongly. Between the age of 6 and 13 years, female 012, a representative example, delivered and suckled a pup every year, generally eating less than average between February and July, but more than average between August and January (Fig. 4B; Kendall’s coefficient of concordance $\chi^2_r = 52.8; P < 0.001$).
Perinatal Changes

Between the age of 6 and 8 years, many females began to reproduce successfully (Table 2). Pups were born in May and June (Table 1).

The daily food intake of five females was examined for 5 days before and 5 days after parturition (18 births). Food intake usually began to decrease 3 days before birth, ceasing entirely between 2 days before birth and the day of birth. Feeding generally resumed the day after birth, and by 2 days after birth the daily food intake had returned to normal.

The effects of pregnancy and lactation on food intake were investigated separately in three cases in which a pup was born and raised by a female that was not lactating at the time of conception and that did not become impregnated immediately after parturition. On average, these females ate 13% more during the calendar year of conception, 6% more during the calendar year of parturition (which included approximately 6 months of lactation), and 18% more during the next calendar year (during which the pup was suckled for some months, then weaned) than during previous years in which they were not pregnant or lactating.

Transfer to Solid Food

Pups began to eat fish spontaneously around the age of 11 months (Table 3) and, when force-fed, were eating independently within 2 to 23 days after force-feeding commenced. In one case, when a pup was abandoned by its mother at an early age, the transfer to solid food was expedited by force-feeding fish; this pup (ZcZH054) voluntarily began to eat fish at the age of 6 weeks.

Growth

Males increased in body length until approximately 20 years of age, whereas female body length stabilized at approximately 6 years of age (Fig. 5A). Body weight in males increased at least until 20 years of age and in females until 13 years of age, after which it decreased (Fig. 5B).

There is a significant positive relationship between standard body length and body weight in both male and female sea lions (Fig. 6).

<table>
<thead>
<tr>
<th>TABLE 2. Ages (in years) at which five female California sea lions at Harderwijk Marine Mammal Park gave birth</th>
</tr>
</thead>
<tbody>
<tr>
<td>Successive pup</td>
</tr>
<tr>
<td>First</td>
</tr>
<tr>
<td>Second</td>
</tr>
<tr>
<td>Third</td>
</tr>
<tr>
<td>Fourth</td>
</tr>
<tr>
<td>Fifth</td>
</tr>
<tr>
<td>Sixth</td>
</tr>
<tr>
<td>Seventh</td>
</tr>
<tr>
<td>Eighth</td>
</tr>
<tr>
<td>Ninth</td>
</tr>
</tbody>
</table>

<sup>a</sup>Pup born dead.
DISCUSSION AND CONCLUSIONS

Age-Related Changes and Sexual Differences

California sea lions are highly sexually dimorphic [Lluch-Belda, 1969a,b; Odell, 1972; McLaren, 1993]. Males are much larger than females by the time they become reproductively active (but not yet socially mature), which occurs at approximately 4 years of age in the wild [Odell, 1972]. The present study shows that until 3 to 4 years of age, males and females consume a similar amount of food; thereafter, male consumption is much higher (Fig. 1), unless males are castrated. Males in the present study continued to grow for much longer than females. Wild females have been shown to be socially mature at 6 to 8 years of age, whereas males do not mature socially until 9 years of age, although both sexes continue to grow somewhat [Spalding, 1964; Lluch-Belda, 1969a]. Although females in the present study were shorter than those of similar age reported by Spalding [1964], this may be owing to a different measuring technique (straight line or following the body contour). A linear relationship was demonstrated between body weight and standard body length for male California sea lions caught in Puget Sound, Washington, between November and June [Gosho et al., 1995]. During those months, however, males gain weight, so such a formula, lacking a girth measurement, may be of little significance. Males in Puget Sound weighed less than animals of similar length in the present study (Fig. 6), although this may be owing to the latter being measured at irregular intervals and not in a particular season such as often occurs in field studies (usually during the mating season when males may already have lost weight).

Food intake of females was lower among those housed indoors; male intake did not vary with housing (Fig. 1). As adult females have a larger surface area to

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**TABLE 3. Ages at which the California sea lion pups started to eat fish voluntarily (suckling sometimes continued for some time afterward)**

<table>
<thead>
<tr>
<th>Animal</th>
<th>Gender</th>
<th>Age at which first fish was eaten (mo)</th>
</tr>
</thead>
<tbody>
<tr>
<td>ZcZH007</td>
<td>F</td>
<td>15</td>
</tr>
<tr>
<td>ZcZH008</td>
<td>F</td>
<td>10.5</td>
</tr>
<tr>
<td>ZcZH013</td>
<td>F</td>
<td>13</td>
</tr>
<tr>
<td>ZcZH014</td>
<td>F</td>
<td>12</td>
</tr>
<tr>
<td>ZcZH015</td>
<td>M</td>
<td>11*</td>
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<td>M</td>
<td>11.5</td>
</tr>
<tr>
<td>ZcZH051</td>
<td>F</td>
<td>12.5</td>
</tr>
<tr>
<td>ZcZH052</td>
<td>M</td>
<td>13*</td>
</tr>
<tr>
<td>ZcZH053</td>
<td>M</td>
<td>11*</td>
</tr>
<tr>
<td>ZcZH054</td>
<td>F</td>
<td>1b</td>
</tr>
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<td>10</td>
</tr>
<tr>
<td>ZcZH058</td>
<td>M</td>
<td>6b</td>
</tr>
</tbody>
</table>

*Force-fed after the mother stopped suckling. Independent feeding occurred within 2 to 23 days.

bHand-raised on fish after being suckled for 1 month by its mother. Began to eat fish voluntarily after 14 days of force-feeding.

---

**Daily Food Intake as a Percentage of Body Weight**

Average daily food intake as a percentage of body weight shows a clear decrease with body weight increase (Fig. 7).
body ratio than males, they would be expected to lose more heat to convection and conduction than males and thus require more energy in the colder outdoor enclosure.

**Maximum Consumption in 1 Day**

The maximum daily food intake values (Fig. 2) indicate that the stomach capacity of a California sea lion is larger than necessary for the average daily intake calculated over 1 year, indicating that individuals can exploit temporarily high prey densities.
Seasonal Changes

Seasonal fluctuations in food intake are unlikely to have been caused by variations in the composition and caloric value of the diet, as food batches were bought at irregular intervals and stored, whereas seasonal fluctuation patterns in food intake showed little variations between years.

Fluctuations in food intake of males in the present study became pronounced at between 4 and 7 years of age, when sexual maturity was reached. Previous studies demonstrated seasonal weight fluctuations commencing at 4 to 5 years of age, when males become sexually mature and develop sagittal crests [Schusterman and Gentry, 1971; Odell, 1972].

Seasonal fluctuations in male food intake and weight have been documented in four other otariids and in one phocid. Two 7-year-old male Northern fur seals (*Callorhinus ursinus*) in human care showed reduced food intake in summer [Spotte and Adams, 1979], the breeding season of wild conspecifics. Body weight in South African fur seals (*Arctocephalus pusillus*) has been shown to increase before, and fall during, the breeding season [Rand, 1959]. Food consumption of a male of this species at Harderwijk Park also showed seasonal fluctuations after 6 years of age [Kastelein et al., 1990a]. Food consumption in male Steller sea lions (*Eumetopias jubatus*) in human care fluctuates seasonally after the age of 4 to 7 years [Kastelein et al., 1989], and in male South American sea lions (*Otaria flavescens*) after the age of 5 to 6 years [Kastelein et al., 1995]. One adult male gray seal (*Halichoerus grypus*) in human care reduced his food intake during the breeding season in winter [Kastelein et al., 1990b].
The seasonal reduction in food intake of adult male California sea lions in the present study coincided with the breeding season (May to August) at the Harderwijk Park and in the wild [Odell, 1972] and also with an increase in aggressive behavior. Territorial male California sea lions defend their territories in the breeding season, during which they do not feed [Peterson and Bartholomew, 1967]. They remain on their territory for an average of 27 days [Odell, 1972], and in captivity have been shown to lose as much as 90 kg during the breeding season [Schusterman and Gentry, 1971].

The ability to store fat and defend territories for long periods, therefore, has clear implications for male reproductive success. The lower food intake during the breeding season is independent of food availability (the animals are not interested in fish offered to them), suggesting the possibility of an endogenous rhythm, whereas the simultaneous increased aggressive behavior suggests testosterone involvement [Schusterman and Gentry, 1971]. Weight loss in California sea lion males during the breeding season has previously been attributed to hormone regulation [Schusterman and Gentry, 1971].

Reproductive adult females in the present study showed a less profound fluctuation in monthly food intake than adult males, possibly because females are non-territorial and do feed during the breeding season. Approximately 4 days after pupping in May or June [Peterson and Bartholomew, 1967; Odell, 1972, 1975], females begin periodically to leave the rookery to feed. Thereafter, pups are suckled only once every day or 2 days. Approximately 3 weeks after parturition the females come into estrus.

Seasonal food intake fluctuations in the present study appear to be influenced by hormone levels and by the energy requirements of reproduction, but seasonal
variation in temperature may also be important. Males in particular ate less when air and water temperatures were high (Fig. 8) and a thick fat layer was less important for maintenance of a constant core body temperature. In addition, conductive heat loss is lower during the breeding season than during other times of the year as males spend very little time in water (which conducts heat 25 times more efficiently than air) during the breeding season.

The primary breeding range of California sea lions is from the Gulf of California to the Channel Islands off the coast of southern California. After breeding, males migrate northward along the coasts of California, Oregon, Washington, and British Columbia [Mate, 1975]. It would be of interest to know whether they begin to feed during migration or only after arrival at their wintering areas. The migratory pattern of females and young is not clear. If migrating California sea lions do not eat because they travel through areas without suitable prey or because they prefer to spend time traveling than eating, this may have developed in an endogenously regulated seasonal decrease in appetite.

**Perinatal Changes**

The timing of reproduction in females in the present study did not differ from that in the wild, females maturing at 6 to 8 years of age and giving birth in May and June [Peterson and Bartholomew, 1967; Lluch-Belda, 1969a; Odell, 1972, 1975].

Female food intake in May and June can be used to predict the day of birth, as intake begins to drop 3 days before birth, only returning to normal 2 days after birth. The peak copulation period for California sea lions is July, and the total gestation period is thought to be approximately 11 months, although implantation may be delayed until mid-October [Odell, 1972]. In the present study, during the first 3 months of real fetal development (i.e., after implantation has occurred), the three non-lactating females that were studied ate 13% more than usual at that time of year. During the last 6 months of gestation and the first 6 months of suckling, their food intake was 6% higher than usual at that time of year. In the calendar year after the year of birth, when pups were suckled for approximately 6 months, females ate 18% more than usual. In theory, 3- to 5-week-old pups (weighing approximately 12 kg) require 2.4 times as much energy as adult terrestrial mammals of similar body mass [Thompson et al., 1987]. This is probably owing to the high energy requirements for both growth and thermoregulation, as pups are poorly insulated [Wartzok, 1991]. A large proportion of the energy obtained from milk is required for maintenance rather than growth, owing to the high energy demands of the aquatic environment [Oftedal et al., 1987]. Consequently, the fat content of California sea lion's milk is higher than that of terrestrial mammals (47% water, 37% fat, 14% protein in milk drained from mammary glands [Pilson and Kelly, 1962] and 65% water, 15% fat, and 19% protein in milk from a pup’s stomach [Schroeder and Wedgeforth, 1935]).

**Transfer to Solid Food**

Pups in the present study began to eat fish at approximately 1 year of age. This is a little later than in the wild, where pups begin to wean themselves at approximately 6 months of age [Peterson and Bartholomew, 1967; Odell, 1972]. Wild pups may be stimulated by encounters with live fish or may be hungrier than captive pups because their mothers leave them from time to time to forage [Bowen, 1991]. Pups
are capable of digesting fish at a much earlier age: one animal in the present study, which was force-fed fish at an early age, grew to be a similar size as suckled animals of the same age class. It is possible that, in the wild, California sea lions do not eat fish before the age of 6 months because they are not yet sufficiently skilled to catch fish. At the Harderwijk Park, the pups were not provided live fish. Dead fish was the first solid food they ate.

Fig. 8. A: The average monthly outdoor and indoor air temperatures at the Harderwijk Park. B: The average monthly outdoor and indoor water temperatures at the Harderwijk Park and the average minimum and maximum sea surface temperatures in the distribution area of California sea lions in the wild.
Food Consumption of California Sea Lions

Ecological Significance

To estimate the food requirements of wild California sea lions, it would be necessary to determine the temperatures that wild sea lions are exposed to, their activity levels, and the caloric value of the diet in both the present study and in the wild. The diet in the present study consisted mainly of herring and mackerel and may have varied in both composition and caloric value depending on the year, age class, and season in which the fish was caught [Geraci, 1975]. Wild California sea lions eat a variety of prey, including many species of teleost fish, squid, shellfish, and crustaceans, depending on geographic area and annual and seasonal availability [Dyche, 1903; Scheffer and Neff, 1948; Daugherty, 1965; Fiscus and Baines, 1966; Keyes, 1968; Jameson and Kenyon, 1977; Bowlby, 1981; Everitt et al., 1981; Jones, 1981; Bailey and Ainley, 1982; Antonelis et al., 1984, 1990; Aubin and Mate, 1984; Roffe and Mate, 1984; Lowry et al. [1991] conclude that California sea lions are flexible specialists. They exploit a few resources at a time, but the composition of their diet changes over time, as the sea lions capitalize on the accessible prey.

Food consumption in females in the present study was partly influenced by ambient temperature; this relationship has also been observed in Northern fur seals [Spotte and Adams, 1981]. Water temperatures in the present study (Fig. 8A) may reflect those experienced by wild conspecifics, as both indoor and outdoor temperatures lay between the extremes for the distribution area of California sea lions (Fig. 8B). Wild sea lions, however, experience colder water during dives, the majority of which are less than 80 m in depth [Feldkamp et al., 1989], although dives of up to 275 m have been recorded [Evans and Harmon, 1968; Ridgway, 1972]. Dive depth and duration appear to be strongly influenced by the rate of prey encounter [Feldkamp et al., 1989]. The haul-out pattern is also influenced by thermoregulation, as sea lions cannot sweat or pant to lose heat and thus have to enter the water to cool off [Whittow et al., 1972, 1975; Matsuura and Whittow, 1973; Odell, 1974; South et al., 1976].

At sea, California sea lions are active most of the time and rest for approximately 3% of the time at the surface [Feldkamp et al., 1989]. The animals in the present study were kept in social groups of at least four animals and were also active most of the day but could not make deep dives. In the present study, daily food intake ranged between 3 and 9% of body weight, depending on size. A non-lactating female of 76 kg had a daily intake of approximately 5.5% of her body weight when housed outdoors; during lactation, this increased to approximately 7%. The daily food intake of lactating wild females of similar size was estimated to be approximately 11% of their body weight [Costa et al., 1991]. The 4% difference in food intake may be owing to higher activity in the wild females or to the inaccuracy of the estimation. The food consumption data presented in the present study therefore should be used only as a conservative estimate of food intake in wild California sea lions, as wild individuals dive deeper and require more energy for locomotion and thermoregulation than those in oceanaria.

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