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Seasonal and Developmental Patterns of Energy Intake and Growth in Alaskan Ice Seals

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Abstract

Quantifying the energy needs of individual animals and understanding the relationship between food intake and physical growth are necessary to determine species-level food requirements and to model potential responses to changing environmental conditions. To provide fine-scale information about developmental and seasonal patterns in the energetic requirements of Arctic phocid seals, we documented longitudinal changes in food intake, body mass, and standard length in four spotted seals (*Phoca largha*), three ringed seals (*Pusa hispida*), and two bearded seals (*Erignathus barbatus*). The seals were studied for up to 9 years in subarctic and/or temperate climates while living under human care. Seals were fed using behavioral criteria that allowed their food intake and body mass to vary naturally. Gross energy intake (GEI) increased with age in all species, reaching a plateau as seals matured. GEI was greatest for the largest species (bearded seals) and lowest for the smallest (ringed seals). Mass-specific GEI declined with age and was similar between spotted and ringed seals, with bearded seals consuming about half as much as the smaller species. Overlaid upon long-term developmental changes were predictable seasonal cycles in food intake and body mass which became more pronounced as seals matured. Seasonal cycles in food intake and body mass did not always reflect simple cause-and-effect relationships. For example, seasonal peaks in food intake were regularly associated with simultaneous declines in body mass. The consistency of energy intake patterns, despite seals being maintained in semi-artificial conditions in different local climates, supports the hypothesis that seasonal oscillations are guided by underlying hormonal changes linked to key life history events and mediated by the physical environment. The described physiological patterns serve to highlight times of year when free-ranging Arctic seals may be more sensitive to environmental perturbations.

Key Words: food intake, caloric intake, body mass, growth, development, environmental conditions, nutrition, *Phoca largha*, *Pusa hispida*, *Erignathus barbatus*

Introduction

Quantifying the energy needs of individual animals and understanding the relationship between food intake and physical growth are both necessary to determine species-level food requirements and to model potential responses to changing environmental conditions. As with most vertebrates, pinnipeds consume progressively less energy (on a mass-specific basis) as they mature in tandem with declining growth rates (e.g., Kastelein et al., 1990a, 1990b; Noren et al., 2014). However, the detailed pattern and extent of developmental changes in energy intake and growth vary considerably between species (see Figure 29.6 in Rosen & Worthy, 2018), making extrapolations to data-deficient species problematic and introducing sources of error to predictive models.

Overlaid upon developmental trends are seasonal cycles in energy intake requirements of temperate and polar pinnipeds, which are associated with differential costs of key life history events (e.g., mating, lactation, molt), recurrent variation in local environmental conditions, and predictable changes in prey availability or foraging opportunities (Perez & Mooney, 1986; Boily, 1996; Coltman et al., 1998; Bowen et al., 2001; Winship et al., 2002). As a result, pinnipeds display seasonal variation in body mass and condition, although seasonal cycles in energy intake and body mass do not always vary in a parallel fashion (Ashwell-Erickson & Elsner, 1981; Renouf & Noseworthy, 1990, 1991; Renouf et al., 1993; Lager et al., 1994; Renouf & Gales, 1994; Hedd et al., 1997; Rosen & Renouf, 1998; Williams et al., 2007).

Understanding normal developmental and seasonal patterns in energy intake and growth—and the complex relationship between these two bioenergetic parameters—allows scientists to evaluate the prey requirements of wild individuals and better predict the potential effect of ecosystem perturbations on populations. Arctic and subarctic ecosystems are undergoing rapid and unprecedented changes in physical and biological characteristics due to human-induced climate change. Specific challenges for Arctic marine mammals, particularly phocid seals, include loss of available sea ice habitat, altered distribution and abundance of prey, and increasing anthropogenic disturbance (Laidre et al., 2008; Moore & Huntington, 2008). We are lacking information to predict the consequences of these disturbances for ice-dependent and ice-associated seals, particularly in terms of seasonal and developmental prey intake requirements and their relationship to typical growth rates (Lettrich et al., 2019).

Several studies have examined aspects of prey intake in free-ranging Arctic seals, with most focusing on describing commonly consumed prey species (e.g., Dehn et al., 2007; Boveng et al., 2009; Cameron et al., 2010; Kelly et al., 2010) or identifying trophic levels and geographic locations important for foraging (e.g., Ferreira et al., 2011; Crawford et al., 2012; Carroll et al., 2013; Gryba et al., 2019). While data for some aspects of seasonal bioenergetic cycles (mainly body mass and condition) have been obtained for a few Arctic phocids (Ryg et al., 1990; Chabot & Stenson, 2002; Ferguson et al., 2020), these efforts have almost exclusively been cross-sectional in nature. The cryptic behavior and remote habitats of ice-associated seals mean that many types of longitudinal data remain difficult or impossible to collect from free-ranging individuals, particularly given the seasonal and age-specific constraints of most field sampling efforts.

Like their wild counterparts, phocid seals living in human care display pronounced seasonal patterns of food intake, energy expenditure, and body mass that presumably reflect entrained physiological processes (Kastelein et al., 1990b; Renouf & Noseworthy, 1990; Renouf et al., 1993; Rosen & Renouf, 1998). Seals under human care may have lower levels of energy intake relative to free-ranging conspecifics. However, documenting their intrinsic seasonal and developmental changes in energy intake, and how these variations are related to body size and mass, can provide valuable information for bioenergetic and predictive population models.

To obtain direct information about the developmental and seasonal energetic requirements of Arctic seals, we quantified and compared patterns of energy intake, body mass, and standard length in three species. Study animals included four spotted seals (*Phoca largha*), three ringed seals (*Pusa hispida*), and two bearded seals (*Erignathus barbatus*) maintained in captivity as part of a long-term research program. Data collection involved repeated fine-scale measurements of individuals for up to 9 y, spanning distinct developmental stages. Our objectives were to use these long-term data (1) to quantify species-specific developmental changes and seasonal cycles in energy intake, body mass, and body length; (2) to investigate the seasonal relationship between energy intake and growth to identify potential critical physiological periods; and (3) to consider environmental and physiological factors that may drive these patterns and, thus, bioenergetic priorities for these species.

Methods

Study Animals

Data were collected from nine Alaskan ice seals under managed care: four spotted seals, three ringed seals, and two bearded seals. These seals were born in the wild and transferred into the research program following non-releasable designation after stranding and subsequent rehabilitation (spotted and ringed seals) or transferred from other research projects (bearded seals). Not all seals began the study at the same age, were born in the same calendar year, or had the same period of data collection (see Table 1 for details).

Research was authorized by the U.S. National Marine Fisheries Service under Marine Mammal Research Permits 14535 and 18902 with expressed support from the Ice Seal Committee, a tribally authorized Alaska Native co-management organization. Institutional Animal Care and Use Committees at the University of California Santa Cruz and Alaska SeaLife Center reviewed and approved study protocols and provided oversight of animal welfare. Seals were trained to participate in data collection and routine husbandry care using operant conditioning and positive reinforcement methods.

The study animals were housed in one of two research facilities (Table 1). Seals at Long Marine Laboratory (LML; Santa Cruz, CA, USA) lived in temperate environmental conditions (37.0° N latitude) in outdoor saltwater pools with access to surrounding haul-out areas. Ocean water was pumped from Monterey Bay, filtered, and directed to marine mammal pools. Due to proximity to deep-water canyons, water temperatures in the

Table 1. Seals used in study—data were collected at different laboratories (LML = Long Marine Lab; ASLC = Alaska SeaLife Center) and over different ages (in years) for each individual.

Species	Sex	Name (identifier)	Birth year	Location, seal ages (y)
Spotted	M	Amak (NOA0006675)	2010	LML, 0.5-5.5 ASLC, 5.5-9.0
	M	Tunu (NOA0006674)	2010	LML, 0.5-5.5 ASLC, 5.5-9.0
	F	Sura (NOA0010309)	2014	ASLC, 0.25-6.0
	M	Kunik (NOA0010310)	2015	ASLC, 0.5-5.0
Ringed	F	Nayak (NOA0006783)	2011	LML, 1.0-9.0
	M	Pimniq (NOA0010311)	2014	ASLC, 1.5-6.0
	F	Dutch (NOA0010460)	2016	ASLC, 1.0-4.0
Bearded	M	Noatak (NOA0010270)	2015	ASLC, 0.5-0.6 LML, 0.6-5.0
	M	Siku (NOA0010177)	2014	ASLC, 0.5-0.8 LML, 0.8-1.8

pools ranged seasonally from 9° to 19°C. Seals at the Alaska SeaLife Center (ASLC; Seward, AK, USA) lived in subarctic environmental conditions (60.1° N latitude) in outdoor saltwater pools with access to haul-out areas. Water for the pools at ASLC was pumped from Resurrection Bay and then filtered; water temperatures in the pools ranged seasonally from 4° to 11°C.

Of the four spotted seals, two males entered the study following their transfer to LML from the ASLC rehabilitation program (Table 1). Data collection began at LML when the seals were 6 mo old and continued after they were transferred back to ASLC during their fifth year of life where they remained through adulthood. A third male and a female spotted seal entered the study as pups, and data were collected solely at ASLC through to ages 5 and 6, respectively—a period that spanned early development through sexual maturity.

The ringed seals in the study included two females and one male from the ASLC rehabilitation program (Table 1). Data collection for one female ringed seal began after she was transferred to LML as a yearling, continuing until she was 9 y old. Data collection for a second female ringed seal began when she was transferred to the research program at ASLC as a yearling and continued until she was 4 y old. The male ringed seal stranded as a yearling and was placed in the research program at ASLC at 1½ y of age, where data were collected until he was 6 y old.

Data were also collected from a single male bearded seal for 2 mo at ASLC before he was transferred to LML at 8 mo old, where data collection continued until he was 5 y old. A smaller set of measurements was obtained from another male bearded seal that similarly spent 3 mo at ASLC and was then held at LML from when he was 10 to 22 mo old.

Seals were offered a daily diet composed of freshly thawed fish and seafood. This included a mixture of relatively high-fat clupeid fish species (e.g., herring) and relatively low-fat osmerid fish (e.g., capelin), supplemented periodically with cephalopods or bivalve mollusks. Seals also received daily marine mammal vitamin supplements (Mazuri Vita-Zu marine mammal tablets 5TLA or similar; PMI Nutrition International LLC, St. Louis, MO, USA). A subsample of each prey batch was analyzed for proximate and energetic composition in a commercial laboratory (Michelson Labs Inc., Commerce, CA, USA).

Daily levels of food offered to the seals were based on evaluation of behavior and motivation (i.e., perceived hunger levels). Food was presented throughout daytime hours during training and enrichment sessions, and individual diets were not constrained for research purposes. Behavioral metrics of food motivation and appetite were scored daily by experienced staff and used to determine optimal diet. While differing from true *ad libitum* intake, this approach permitted developmental and seasonal changes in food intake and allowed body mass to vary in a naturalistic manner. Daily food consumption was recorded both in units of mass (kg) and in energy (kcal), and the latter was used as our measure of gross energy intake (GEI).

Seals were weighed once a week—in the morning after an overnight fast—to the nearest 0.1 kg by voluntarily positioning on a platform scale. We obtained a weekly length measurement from a calibrated image of each seal positioned in sternal recumbency with a 0.5 or 1 m scale bar aligned above and along the dorsal midline. This image of a seal's lateral profile, obtained in a fixed orientation with a Canon Powershot G12 digital camera, was used to determine standard (linear) length (±1 cm) from the tip of the nose to the tip of the tail using *ImageJ*, Version 1.52a (Schneider et al., 2012).

Data Handling

While the majority of seals were born in April, a few were born in May, and for some seals the month of birth had to be estimated. We chose to "adjust" all birth months to 01 April so that all datasets were aligned by calendar month rather than age as we felt this would allow us to best describe seasonal trends with only minor distortions to developmental changes.

Monthly body mass for each seal was calculated as the mean of four to five weekly measurements for each seal within a calendar month. Monthly mean masses for individuals were also combined into monthly species mean values. While multiple individual ringed and spotted seals contributed to monthly species means over the majority of the study, there are some instances early or late in the dataset where a species mean may reflect a single individual. To provide a reliable metric of annual growth (given natural variation due to positional changes), body length was averaged from weekly measurements obtained for each individual during each developmental year (April to March).

Mean GEI (kcal d^{-1}) for each individual was calculated for each calendar month from daily values. Monthly mean mass-specific GEI (kcal kg^{-1} d^{-1}) was calculated by dividing monthly average GEI per individual by their mean body mass over the same period. GEI and mass-specific GEI from each individual for each month were used to calculate summary statistics (mean, median, standard deviation, and upper and lower quartile) for each developmental year (April through March) for each of the study species.

Monthly species means were calculated for both GEI and mass-specific GEI in the same manner as for body mass. This allowed us to identify a maximum and minimum monthly species mean GEI and mass-specific GEI for each developmental year (starting at 12 mo).

Data for individuals were not included in this study until seals had left the rehabilitation program and were deemed to be "in good health" by an attending veterinarian. Given the nature of these datasets (including uneven and limited sample sizes, lack of temporal overlap, cyclical nature of data, ontogenetic changes), only basic descriptive statistics were calculated. Apparent seasonal and ontogenetic patterns were primarily described rather than quantified as such fluctuations tend not to conform to simple mathematical functions. Data are summarized and reported by species. Data for individual seals can be found in Supplementary Table 1 (the supplementary table and figure for this article are available in the "Supplemental Material" section of the *Aquatic Mammals* website: https://www.aquaticmammalsjournal.org/index.php?option=com_content&view=article&id=10&Itemid=147).

Results

Spotted Seals

The size of the spotted seals fell within the observed range of body mass and length for wild conspecifics of similar ages (Quakenbush et al., 2009). Although there were differences in body mass between individuals, there were consistent trends with respect to developmental and seasonal growth. Mean annual mass increased over the entire study period but, as with most mammals, growth rate declined as seals matured (Supplementary Table 1). For example, between 6 and 18 mo of age, mass increased by 65%, but from years 2 to 5 (24 to 60 mo), mass increased by 20% each year (Figure 1A). Body length increased during the first 6 y of life and then largely plateaued (Figure 1A). This tracked the same general pattern reported for wild-caught seals (Quakenbush et al., 2009).

Long-term developmental changes in growth rates were punctuated by seasonal oscillations in body mass that were similar between individuals. The initial period of rapid increase in body mass (< 18 mo old) was followed by a plateau at the end of the seals' second summer (Figure 1A); this pattern of winter/spring growth and summer stability was repeated the following year. Seasonal cycles in body mass became increasingly apparent as the seals matured. They were characterized by sudden declines in body mass during the spring and early summer months (~April to July, prior to and during the annual molt) followed by periods of significant mass gain generally occurring from July to March of each year.

Absolute GEI increased during the first 4 y and then remained relatively stable (Figure 2A; Table 2). Considered with respect to body mass, GEI was highest in the first year and decreased throughout development (Figure 2B; Table 2). Interestingly, there was no difference in mass-specific GEI between individuals held in California or Alaska during their first 6 y of life, nor was there any apparent shift in average energy intake following the move from California to Alaska for the mature spotted seals.

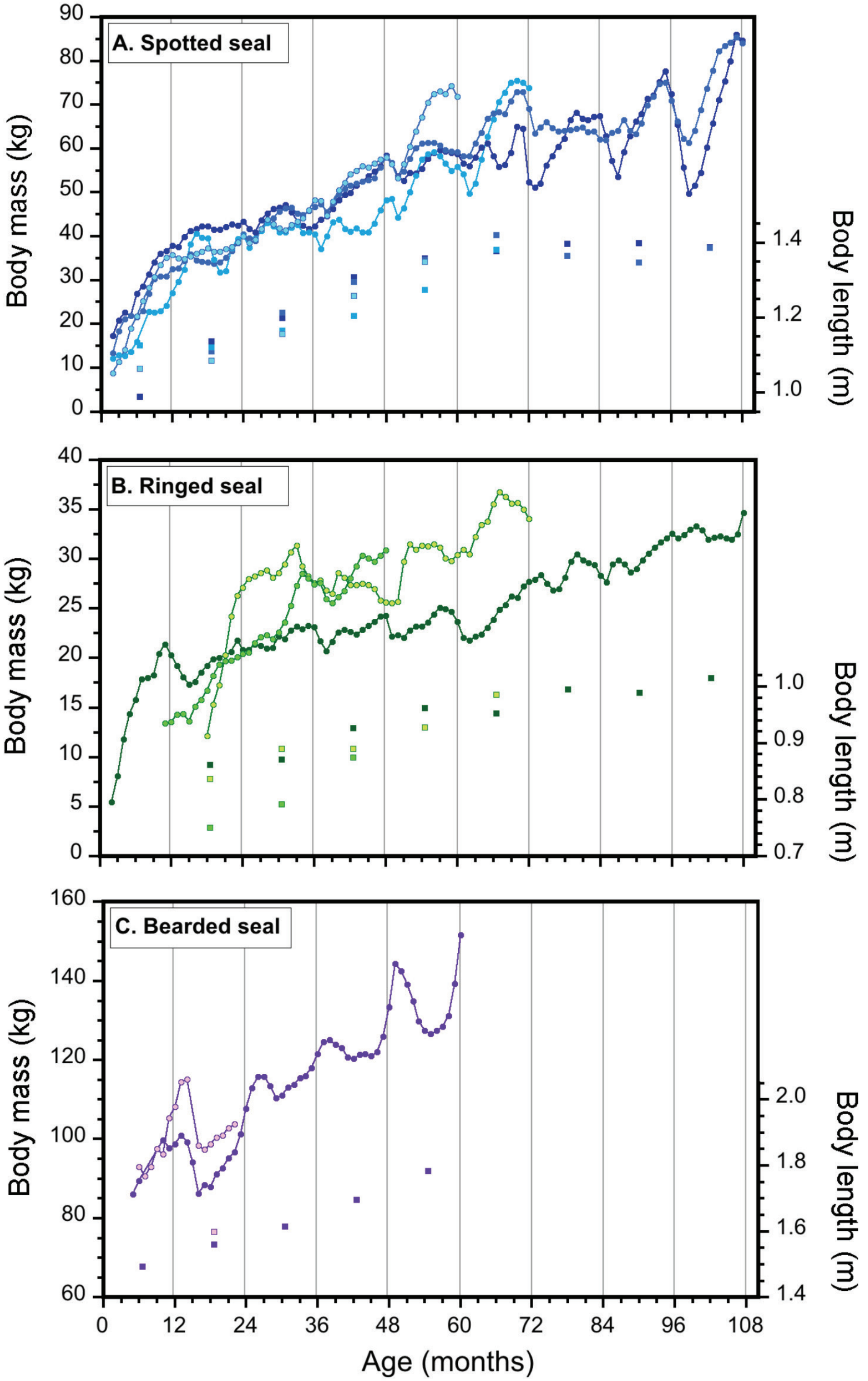

Figure 1. Developmental changes in body mass and length. Monthly average body mass (circles) and annual standard length (squares) for (A) spotted seals, (B) ringed seals, and (C) bearded seals. Data are aligned to reflect a similar imposed birth month (April) for all animals. Vertical lines indicate developmental years (01 April). Average standard length for a year is plotted in the middle of the 12-mo interval. Data from individual seals matched by color.

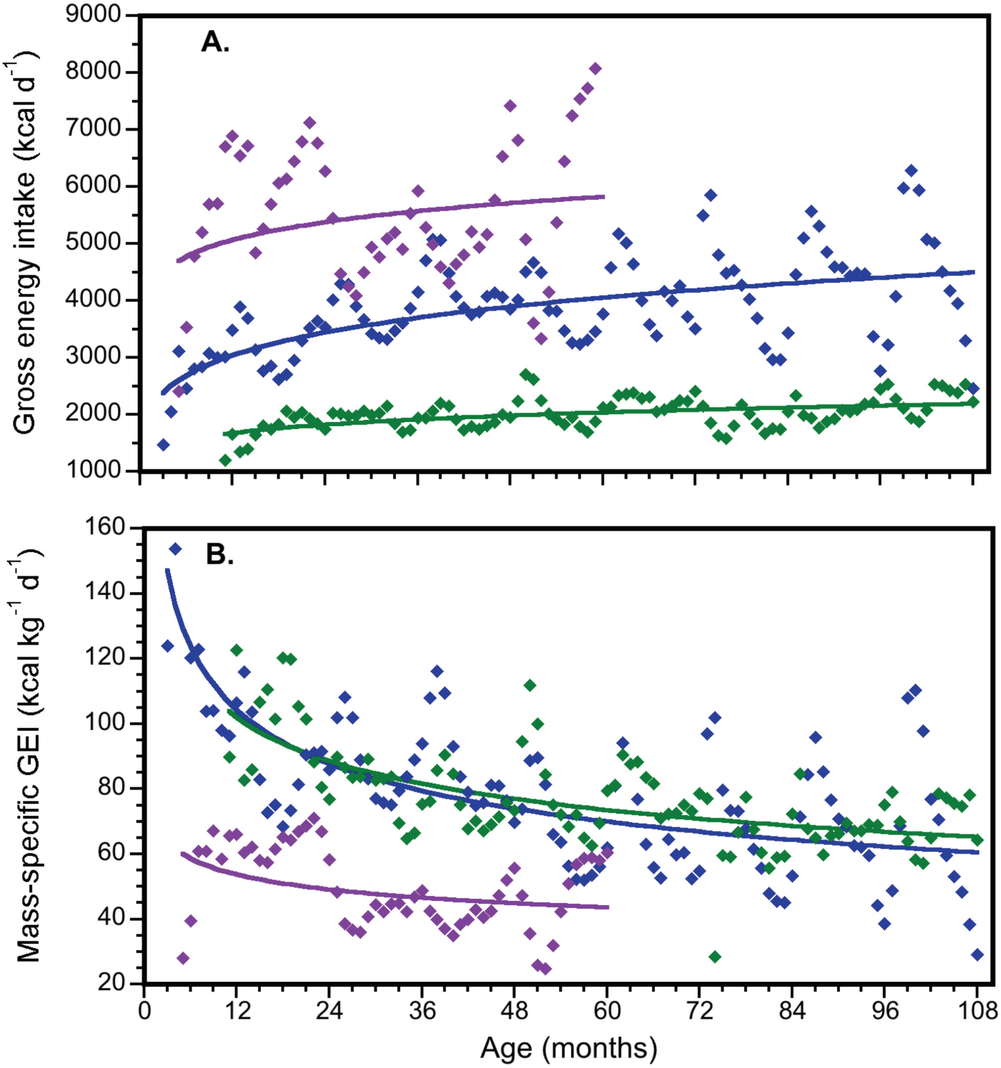

Figure 2. Developmental changes in food energy intake. Monthly averages of daily energy intake of spotted seals (blue diamonds), ringed seals (green diamonds), and bearded seals (purple diamonds) with age. Intake is presented (A) as absolute daily gross energy intake (kcal d^{-1}) and (B) as body mass-specific intake (kcal kg^{-1} d^{-1}). Each month is represented as the grand mean from the monthly averages of each individual seal. A power function is fit to each species for illustrative purposes.

Most of the variation around annual mean GEI for individual seals was associated with seasonal intervals of hyperphagia and hypophagia. Distinct maximums and minimums in monthly mean GEI were apparent in the spotted seals by their second year (Figure 3A). Periods of hyperphagia shifted from late spring (May/June) to early summer (July) as individuals matured. Periods of minimal food intake showed a similar developmental shift from early (October) to late (November to January) fall. These intervals of hyper- and hypophagia were similar across individuals up to 6 y of age, regardless of geographic location. At 5.5 y, the two older seals were transferred from California to Alaska, and the period of minimal food intake shifted progressively later over the remaining 3.5 y (to April in the final 2 y), although there was no apparent impact on the timing of the summer hyperphagia periods.

Intra-annual extremes in GEI became more pronounced as animals got older, similar to the

Table 2. Food energy intake—statistical descriptions of gross energy intake (kcal d^{-1}) and mass-specific gross energy intake (GEI; kcal kg^{-1} d^{-1}) for each species for each developmental year. Data are presented as median with lower (25%) and upper (75%) quartile below in parentheses, calculated from all monthly intake averages for that developmental year (April through March). Sample sizes that have an asterisk signify maximum sample size within a year that incorporates incomplete datasets from at least one animal.

GEI (kcal^{d-1})	Yr 1	Yr 2	Yr 3	Yr 4	Yr 5	Yr 6	Yr 7	Yr 8	Yr 9
Spotted	2,792 (2,270, 3,402) *n* = 4*	3,255 (2,551, 3,847) *n* = 4	3,859 (3,273, 4,252) *n* = 4	4,395 (3,652, 4,860) *n* = 4	3,759 (3,495, 4,216) *n* = 4	4,138 (3,465, 4,573) *n* = 3	4,002 (3,180, 4,869) *n* = 2	4,509 (4,137, 5,032) *n* = 2	4,693 (3,565, 5,413) *n* = 2
Ringed	1,433 (1,319, 1,547) *n* = 1*	1,733 (1,611, 1,887) *n* = 3*	1,979 (1,749, 2,130) *n* = 3	1,896 (1,598, 2,255) *n* = 3	2,016 (1,855, 2,181) *n* = 2	2,323 (2,133, 2,414) *n* = 1	1,821 (1,725, 2,019) *n* = 1	2,064 (1,938, 2,193) *n* = 1	2,328 (2,102, 2,510) *n* = 1
Bearded	5,541 (4,848, 6,547) *n* = 2*	6,257 (5,658, 6,768) *n* = 2*	4,923 (4,493, 5,259) *n* = 1	5,072 (4,763, 5,411) *n* = 1	6,632 (4,844, 7,594) *n* = 1	--	--	--	--
Mass-specific GEI (kcal kg^{-1} d^{-1})									
Spotted	109.6 (92, 135) *n* = 4*	89.2 (69, 99) *n* = 4	89.8 (76, 99) *n* = 4	87.2 (72, 102) *n* = 4	62.7 (53, 76) *n* = 4	61.9 (56, 79) *n* = 3	62.1 (49, 81) *n* = 2	64.6 (61, 82) *n* = 2	62.2 (43, 86) *n* = 2
Ringed	106.2 (98, 114) *n* = 1*	91.3 (83, 106) *n* = 3*	75.9 (68, 93) *n* = 3	68.0 (57, 92) *n* = 3	80.6 (67, 90) *n* = 2	83.6 (65, 93) *n* = 1	60.0 (59, 69) *n* = 1	67.5 (66, 69) *n* = 1	72.3 (64, 78) *n* = 1
Bearded	60.9 (56, 68) *n* = 2*	65.6 (58, 69) *n* = 2*	43.4 (40, 45) *n* = 1	41.6 (40, 44) *n* = 1	49.1 (35, 58) *n* = 1	--	--	--	--

developmental pattern seen in seasonal changes in body mass. In the fifth year, maximum species monthly food intake was 45% higher than the following period of hypophagia; while by the ninth year, maximum food intake was 155% (2.5 times) higher than during the subsequent minimum value. Although maximum GEI increased slightly in later years, the growing scope of the intra-annual differences in GEI was primarily the result of decreases in minimum intake during periods of hypophagia (Figure 3A); this is reflected in the overall increase in average annual GEI in this species with age (Table 2). The opposite pattern was seen on a mass-specific basis. Maximum mass-specific GEI remained relatively constant across development, whereas decreases in minimum intake contributed to the observed increase in intra-annual differences in mass-specific GEI as seals got older. Further, seasonal differences between maximum and minimum mass-specific GEI were even greater than for absolute GEI, with the maximum reaching 380% of the minimum in the ninth year.

Ringed Seals

Among the ringed seals, the female that entered the study at the youngest age and for whom there is the longest overall record displayed rapid growth over the first year of life, and then exhibited a 19% decline in body mass from the spring through mid-summer (March to July) of her second year (Figure 1B). Although the timing was similar to that seen in the spotted seals, this period also coincided with her move from Alaska to California. She then continued to gain body mass at a relatively constant rate as she matured through to 9 y old, although at a slower rate than when younger. While her body mass increased by 21% from 6 to 18 mo, it increased only 2 to 4% annually between 2 and 9 y of age. The male and female ringed seals housed in Alaska exhibited a period of more rapid growth between months 18 to 24 (likely related to their initial rehabilitation status) but subsequently displayed a growth rate of 2 to 4% per year (similar to the ringed seal in California).

For the female ringed seal with the longest record, initial growth in body length was relatively steady, and it slowed substantially after her

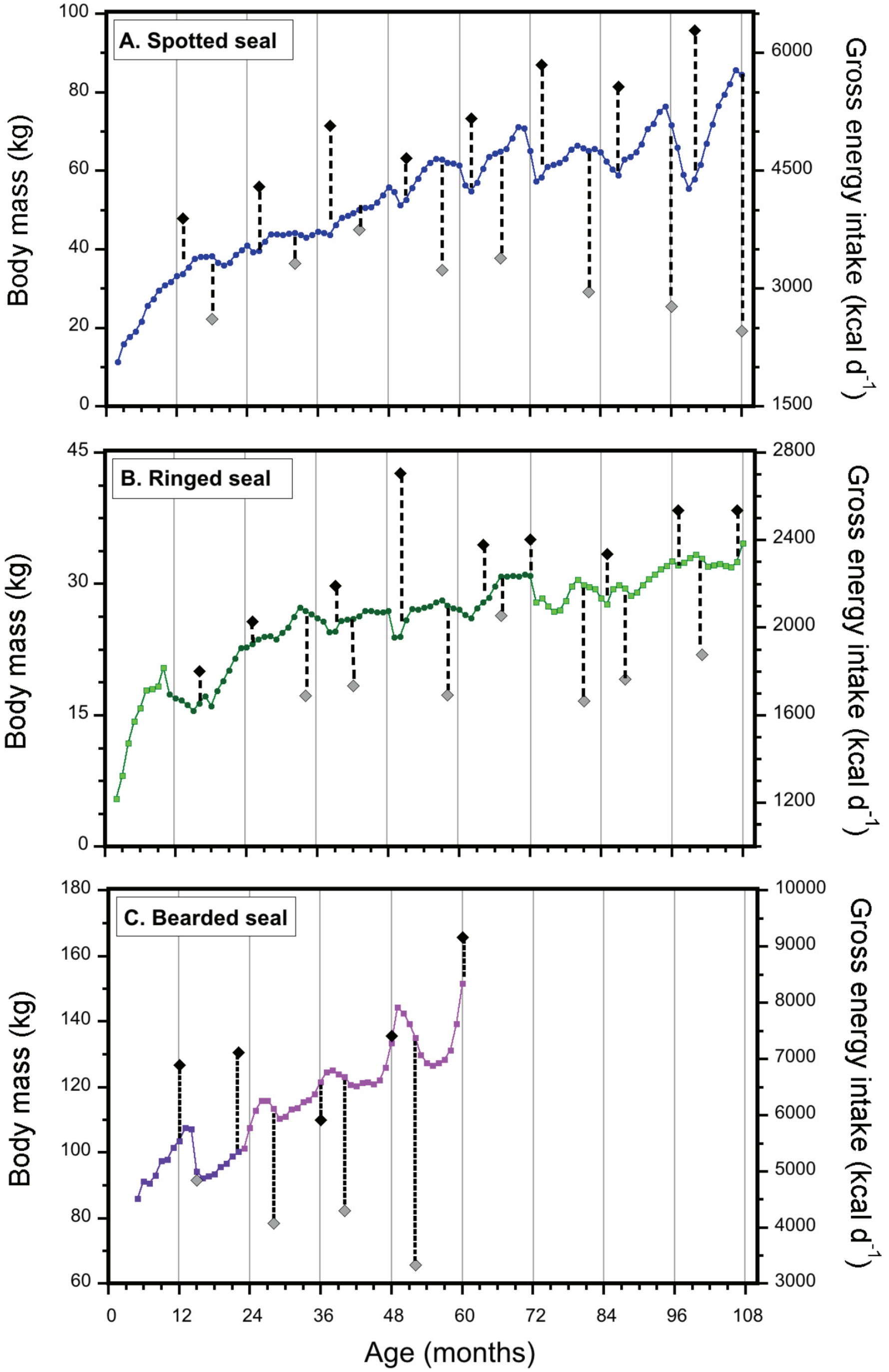

Figure 3. Changes in body mass relative to monthly maximum and minimum food energy intake. Body mass calculated as the grand species' mean from mean mass for each animal within a calendar month. Species' monthly grand means are represented by darker circles, while data from a single animal are represented by a lighter hued circle. Species' grand means of monthly gross food energy intake (kcal d^{-1}) were similarly calculated, and maximum (solid diamonds) and minimum (grey diamonds) grand means within each calendar year are identified. Maximum and minimum intakes are linked to body mass by dashed vertical lines. Vertical lines indicate developmental years (01 April).

fifth year (Figure 1B). The two ringed seals which were in rehabilitation as juveniles had shorter body lengths over the initial study period but grew quickly thereafter. In general, the body mass and length-at-age for the ringed seals in the study were at the lower end of that reported for wild seals (although a similar mass:length ratio; Krafft et al., 2006; Quakenbush et al., 2011b; Von Duyke et al., 2020), although it should be noted this species exhibits significant regional variation in body size (Ferguson et al., 2018).

As with the spotted seals, the ringed seals developed a characteristic seasonal pattern of mass loss and gain by their fourth year that repeated over the duration of the study. This was exemplified by a notable decline in body mass over several months in the late spring/early summer period (generally April to June, during and after molt) followed by a longer period of gradually increasing mass that resulted in a greater peak body mass than during the previous year.

Average annual GEI increased among the ringed seals between their first and second years, but then largely stabilized at levels that were lowest among the three species studied (Figure 2A; Table 2). On a mass-specific basis, GEI showed the expected characteristic decline with age and was similar in magnitude and pattern to that observed for spotted seals (Figure 2B; Table 2).

Like the spotted seals, the ringed seals showed significant seasonal fluctuations in food intake. Although the differences in intake between periods of hyper- and hypophagia were less dramatic than for the spotted seals, maximum monthly GEI was consistently about 50% greater than minimum values over the last several years of the study, whether considered on an absolute or mass-specific basis (Figure 3B). In contrast to the spotted seals, the relative differences between hyper- and hypophagia remained relatively constant over the years. These regular seasonal patterns in food intake emerged around year 3, with maximum food intake generally occurring in the summer (June to August) in years 3 to 5. The timing of episodes of minimum food intake were more variable between these years but generally occurred in late winter (January/February). Data past year 5 are only available from the single female housed in California, who demonstrated a shift during years 6 to 9 such that energy intake cycles occurred several months earlier, with maximum intake in May immediately following molt and minimum intake usually in August/September.

Bearded Seals

Annual changes in mean body length and body mass of the bearded seals were relatively linear over the 5-y data collection period (Figure 1C). The body mass and length-at-age measurements of the bearded seals in the study were on the lower end of the range reported for wild seals in Alaska, although their corresponding mass:length ratios were more representative (Burns, 1967; Burns & Frost, 1979; Quakenbush et al., 2011a).

The bearded seals also demonstrated distinct seasonal cycles in body mass, despite the more limited dataset compared to the other study species. For both of the bearded seals, an initial 14-mo period of rapid growth was disrupted by a period of abrupt weight loss during their second summer (May to September; Figure 1C), followed by another period of rapid growth through the subsequent fall and winter. This pattern was repeated for the one bearded seal monitored for the following three summers as well, indicating these changes were part of a regular annual seasonal pattern.

Absolute GEI remained relatively constant for the bearded seals over the initial 4 y (Table 2) and was greater than that for the other species over the same period (Figure 2A), likely due in part to their much larger body size. Mass-specific GEI was substantially lower than for the other species and showed the expected decline with age, with a significant drop between years 2 and 3 (Figure 2B). The limited data available from the single bearded seal housed over 5 y indicated that intra-annual variation in food intake was greater than for the other study species, increased in seasonal scope with age, and was relatively constant in its timing (Figure 3C). Between years 3 and 5, minimum intake in both absolute and mass-specific maximum GEI occurred in April immediately following molt, with a rapid increase until maximum intake was reached in August. Over these years, maximum intake progressed from being 40 to 125% higher than minimum due to an increasing extent of both hyper- and hypophagia as the seal got older.

Discussion

Quantifying the energy intake requirements of predators and the relationship between food consumption and physical growth is important for understanding the ecological impact of predators on prey populations, as well as for predicting the potential effect of environmental changes on the health, reproductive success, and survival of individuals within predator populations (Villegas-Amtmann et al., 2015; McHuron et al., 2018; Pirotta et al., 2018). Identifying seasonal changes in growth and energy intake further serves to highlight potential critical periods when disturbances can have an amplified effect on the energetic and health status of individuals. While studies with animals under managed care face inherent limitations primarily linked to sample size (e.g., effects of sex and reproductive state) and differences in total energy expenditure, they provide a valuable window into wild populations by providing detailed year-round, longitudinal measurements. Our study profiles developmental and seasonal changes in food intake and body mass for three ice-dependent Alaskan seal species, providing data that are foundational to understanding the effects of environmental changes.

Species Differences in Developmental Patterns

It is difficult to acquire detailed species-specific, longitudinal bioenergetic data from phocid seals. Often, "general mammalian values" or "data from other closely related species" are substituted when untangling ecological questions or constructing bioenergetic models. While the three phocid species in our study conformed to general mammalian patterns in growth and energy intake throughout development, there were also important species-specific characteristics. For example, while both spotted and ringed seal pups had rapid early body growth followed by a significant pause at 18 mo of age, subsequent growth rates were ~10 times higher for the spotted seals than the ringed seals.

There were also important differences in energy intake between species. At any given age, intake was highest for the bearded seals, intermediate for spotted seals, and lowest for ringed seals. This pattern might be predicted solely from differences in species' body size given that larger animals generally have greater absolute food requirements (Peters, 1983). Similarly, the declining trend in mass-specific GEI observed for all three species is consistent with the general mammalian pattern and previous studies of marine mammals (see Figure 29.6 in Rosen & Worthy, 2018). However, despite a minimum twofold difference in body mass, mass-specific GEI was almost identical for spotted and ringed seals each year, over the entire data collection period. In contrast, mass-specific GEI of bearded seals was 40 to 60% lower than the other species each year, which may be attributable to their overall lower resting metabolic rate (Thometz et al., 2021). Further, while spotted and ringed seals had almost identical mass-specific GEI to each other between the ages of 2 to 5 y, spotted seal body mass increased ~20% per year while the two ringed seals with complete records increased less than 3% per year over the same period. Such interspecific differences in broad developmental patterns highlight the importance of obtaining species-specific data to accurately quantify and model bioenergetic scenarios.

Seasonal Changes in Mass and Energy Intake

Overlaid onto overarching developmental patterns were regular seasonal changes in food intake and body mass. Much of the variation seen around annual mean GEI was associated with regular seasonal cycles of hyper- and hypophagia. These cycles differed between species both in their extent and emergence during development. For both spotted and ringed seals, these seasonal cycles in food intake were evident around the fourth year. For spotted seals, absolute GEI during seasonal periods of hyperphagia was 45 to 155% greater than during preceding periods of hypophagia, and 75 to 380% greater when calculated on a mass-specific basis. In contrast, for ringed seals, both absolute and mass-specific maximum GEI were lower—only ~50% above minimum GEI. These seasonal differences became more pronounced with maturation in spotted seals, while the extent of hyper- and hypophagia remained relatively constant in ringed seals. The bearded seal displayed pronounced seasonal shifts in both absolute and mass-specific GEI (40 to 125%), despite only being studied until early adulthood (5 y old). It will be interesting to determine how this pattern manifests through adulthood.

As with GEI, marked seasonal cycles in body mass emerged in the spotted and ringed seals as they reached maturity, with distinct 3- to 4-mo periods of mass loss becoming evident by the fourth year of life. Bearded seals again represent an interesting contrast in that in this species significant seasonal decreases in body mass were observed starting in their second summer. As is typical for temperate and polar mammals, seasonal mass fluctuations in all three study species reflected measured changes in subcutaneous lipid reserves, particularly in older, larger animals that have more extensive lipid stores and less somatic growth (Hartwick, 2020). The timing of these changes in body mass and lipid stores also corresponded to those reported for these species in the wild (Ryg et al., 1990; Quakenbush et al., 2009, 2011a).

Relationship Between Body Mass and Energy Intake

If all other bioenergetic demands are held constant, different levels of food intake will result in predictable changes in body mass. However, the simultaneous seasonal cycles in food intake and body mass observed in this study did not always follow simple cause-and-effect relationships. As predicted, minimum absolute GEI was observed as the spotted seals approached peak seasonal body mass—that is, at a time of minimal growth. However, maximum GEI was observed at the end of the period of seasonal mass loss. In other words, GEI actually increased over the period of seasonal mass loss, suggesting a simultaneous significant increase in some alternate cost(s) within the bioenergetic budget. Conversely, the rate of body mass growth was relatively constant during the seasonal "mass-recovery" period, despite a steady reduction in energy intake from peak GEI over this same period. The same disconnect between seasonal changes in GEI and body mass patterns was seen in the ringed seals, even though their seasonal cycles in food intake were less extreme. In contrast to both the spotted and ringed seals, there appeared to be a close relationship between seasonal changes in food intake and growth rates in the bearded seal with the longest record. For example, bearded seal food intake decreased from a maximum in April to a minimum in August, resulting in parallel decreases in body mass.

Quantifying seasonal changes in body mass and food intake provides a more complete understanding of the complex relationship between these two variables. It also suggests concurrent changes in other aspects of the animals' energy budgets and helps identify potential periods when the seals are particularly sensitive to environmental disturbances.

Environmental Cues for Bioenergetic Cycles

It is generally agreed that seasonal physiological cycles are innately controlled by hormones (Mrosovsky, 1990; Stanley et al., 2005; Ebling & Barrett, 2008). It is well documented that seals—even when maintained in semi-artificial environments with prey continuously available—display seasonal bioenergetic cycles that include changes in voluntary food intake and body mass (Riviere et al., 1977; Kastelein et al., 1990b, 1995, 2000; Renouf & Noseworthy, 1990; Renouf et al., 1993; Rosen & Renouf, 1998). Several studies have examined the roles that different agents (thyroid hormones, growth hormones, leptin, ghrelin, cortisol, etc.) play in regulating these seasonal energetic cycles in pinnipeds (Ashwell-Erickson et al., 1986; Renouf & Noseworthy, 1991; Boily, 1996; Myers et al., 2006; Rosen & Kumagai, 2008).

While these hormonal controls are thought to be triggered by changes in the abiotic environment (such as photoperiod, water or air temperatures, etc.), the role of specific environmental cues as *zeitgebers* is still unclear. Part of the difficulty lies in the fact that potential environmental cues are often synchronized with each other. For example, an inverse relationship between water temperature and food intake was observed in captive harbor seals (*Phoca vitulina*; Renouf & Noseworthy, 1990), but seasonal changes in water temperature are normally tied to changes in photoperiod. Our study provided several unique environmental comparisons to clarify potential hormonal triggers. For example, the spotted seals in our study held at lower latitudes in California experienced a slightly broader scope in water temperatures (9 to 19°C) than those held in Alaska (4 to 11°C) as well as less drastic changes in light cycles (see Supplementary Figure 1). These factors may partly explain why animals in California exhibited more dramatic seasonal changes in GEI. When two of the spotted seals were transferred from California to Alaska, the timing of their hypophagic period shifted several months earlier, although the timing of hyperphagia remained unaltered. Curiously, the oldest ringed seal, who was consistently housed in California, also displayed a gradual shift of several months in the timing of both hyper- and hypophagia when mature (6 to 9 y old).

Another natural experiment was due to a disruption in the normal cycle of water temperatures in Monterey Bay, California, resulting in abnormally warm ambient seawater temperature in winter 2014 (Peterson et al., 2015; Supplementary Figure 1). The effect of this anomalous period of warm water on the two spotted seals in California was evident in their GEI data. Rather than observing a normal period of hypophagia in winter 2014 (~43 mo of age), these two seals continued to consume quantities of food just slightly lower than during their spring hyperphagia period (subsequently followed by a small increase in food intake), while the spotted seal in Alaska displayed a normal hypophagia interval at this age. The potential effect of abnormal temperatures on energy intake is nontrivial given predicted climate change scenarios wherein changes in environmental temperatures could dampen or enhance natural fluctuations in energy requirements.

Timing of Seasonal Bioenergetic Cycles

The observed timing of seasonal cycles in energy intake was markedly consistent between individuals of a species, even when these cycles shifted during development. Although physiologically regulated, periods of hyper- and hypophagia are assumed to correspond to specific annual events associated with predictable changes in energy expenditure and/or food resources. The annual molt has long been associated with changes in the energy budget of pinnipeds, with periods of mass loss often occurring early in the process (Slip et al., 1992; Lager et al., 1994; Chabot & Stenson, 2002). It is unclear the degree to which this pattern is due to the costs associated with replacing the pelage, a decrease in food intake due to increased time spent hauled out, or some other bioenergetic realignment (Slip et al., 1992; Boily, 1996; Paterson et al., 2012). Increased metabolic rates have been identified during the molt in spotted, ringed, and bearded seals (Thometz et al., 2021); however, these costs alone do not account for the observed patterns of mass loss.

In this study, minimum food intake for each species typically occurred prior to the visible start of the molt. The ringed seals typically exhibited minimal GEI in February/March, about a month before the start of the spring molt (Thometz et al., 2021). For the spotted seals, minimal food intake shifted from early (October) to late (November to January) fall during development, several months preceding the spring molt. For the older bearded seal, minimum intake occurred at the end of the summer (August), while its extended molt occurred from December to April.

In many phocid species, the period of seasonal mass loss is typically followed by an interval of hyperphagia during the later portion of the molt period that serves to replenish energy reserves. For the oldest bearded seal, maximum GEI occurred in the spring (March/April) immediately following completion of the annual molt. In our spotted and ringed seals, hyperphagia occurred just prior to molt completion as has been similarly demonstrated in harbor seals (Renouf & Noseworthy, 1990), harp seals (*Phoca groenlandica*; Renouf et al., 1993; Hedd et al., 1997), and adult grey seals (*Halichoerus grypus*; Sparling et al., 2006). In our spotted seals, periods of hyperphagia shifted from late spring (May/June) to early summer (July) as individuals matured and as their molt also shifted later with development (also reported for their wild counterparts; Boveng et al., 2009). Curiously, the molting period in the oldest ringed seal (6 to 9 y old) was highly consistent (within a 2-wk period in April each year) despite the gradual shift of several months in the timing of both hyper- and hypophagia. These results suggest that, for all three of these species, this postmolt period of hyperphagia is an important physiological period required to restore critical energy reserves, as well as a time period in which any impact to foraging ability or success could be particularly detrimental to an individual.

Conclusions

The results of this study inform our understanding of overall seasonal and developmental energy intake requirements for three Alaskan ice seal species. Further, they can be used to improve predictions as to how seals may respond to environmental perturbations, including changes in climate and food supply, and will help to identify potential critical periods when environmental changes may have disproportionate effects. For example, the pattern of continued mass loss during the late spring and early summer for spotted and ringed seals, despite a marked increase in GEI, suggests this is a critical period for prey availability. Indeed, it has been shown that wild ringed seals exhibit more drastic seasonal changes in body condition and altered timing of these cycles in marginal habitats (Ferguson et al., 2020).

Although studied in a managed physical environment with year-round food availability, consistent temporal patterns in weight gain/loss and prey consumption oscillations observed in the seals in our study across temperate and subarctic environments are relevant to wild individuals. The consistency of seasonal patterns in energy intake and body mass, despite seals being maintained in semiartificial conditions in different climates, supports the hypothesis that these oscillations are guided by underlying hormonal changes linked to key life history events and mediated by the physical environment. Thus, environmental changes in the Arctic as a result of climate change may dampen and/or enhance the physiologically driven patterns of energy intake described herein. Longitudinal bioenergetic studies that detail developmental and seasonal trends in energy intake and body mass are fundamental to increasing our understanding of both short- and long-term energetic requirements of free-ranging seals and are urgently needed to parameterize robust bioenergetics and predictive population models in the face of climate uncertainty.

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Seasonal and Developmental Patterns of Energy Intake and Growth in Alaskan Ice Seals

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Supplementary Materials

Supplementary Table 1. Mean energy intake and body mass of individual seals. Annual data are presented as mean ± SD for gross energy intake (kcal d^{-1}), mass-specific gross energy intake (kcal kg^{-1} d^{-1}), and body mass (kg). Annual means calculated from the 12 monthly averages for each individual seal.

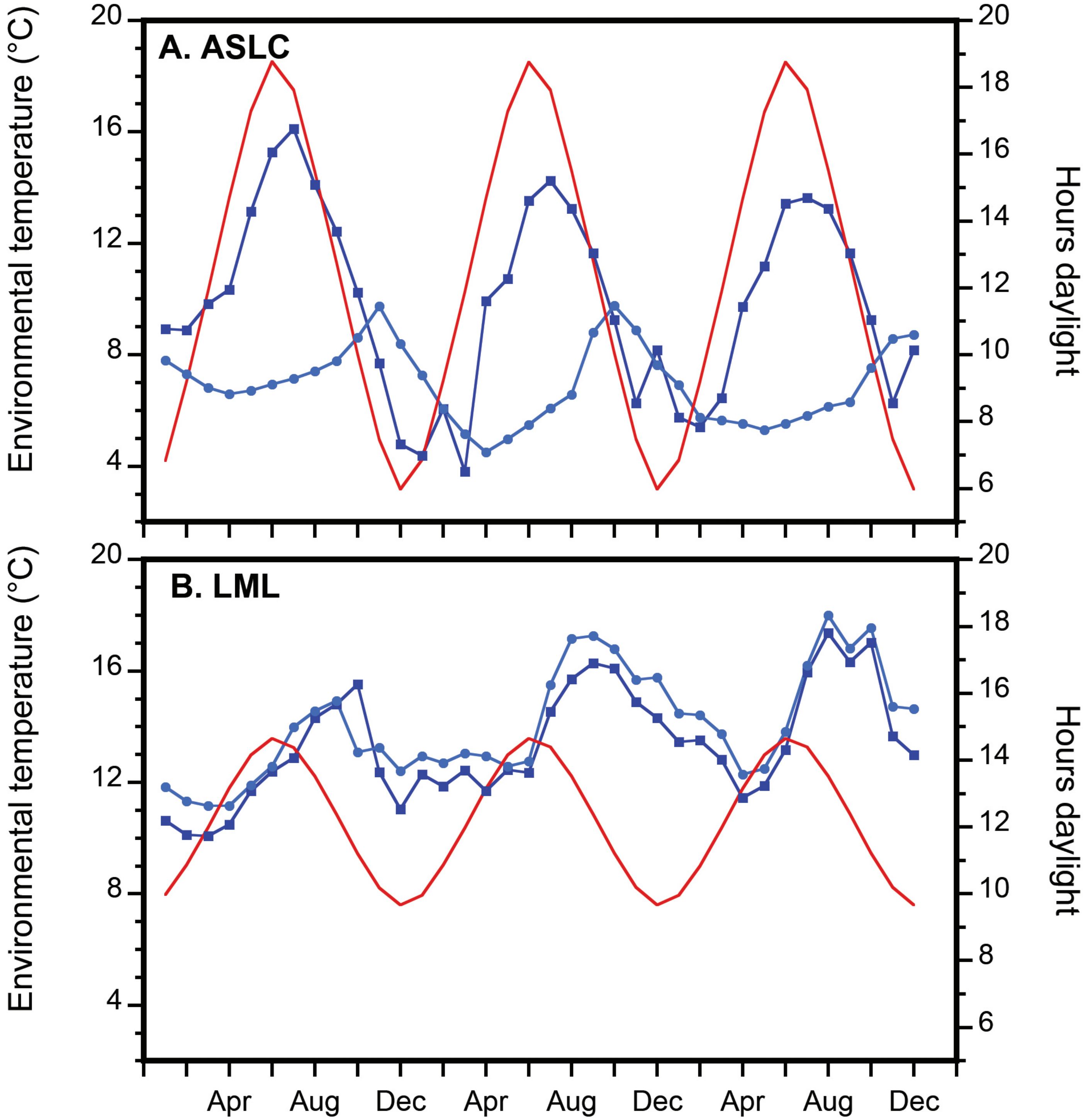
Gross energy intake (kcal d^{-1})

Species, sex	Individual	Yr 1	Yr 2	Yr 3	Yr 4	Yr 5	Yr 6	Yr 7	Yr 8	Yr 9
Spotted, M	Amak (NOA0006675)	3,327 ± 654	4,060 ± 446	4,479 ± 459	5,227 ± 367	4,102 ± 454	4,388 ± 865	4,290 ± 1,091	4,672 ± 939	4,602 ± 1,283
Spotted, M	Tunu (NOA0006674)	3,106 ± 610	3,551 ± 479	4,025 ± 278	4,648 ± 345	3,896 ± 546	4,450 ± 636	4,029 ± 851	4,436 ± 563	4,449 ± 1,204
Spotted, F	Sura (NOA0010309)	2,332 ± 673	2,771 ± 869	3,351 ± 436	3,728 ± 672	3,639 ± 801	3,753 ± 413	--	--	--
Spotted, M	Kunik (NOA0010310)	2,500 ± 434	2,474 ± 165	3,062 ± 502	3,487 ± 677	3,667 ± 408	--	--	--	--
Ringed, F	Nayak (NOA0006783)	--	1,702 ± 162	2,224 ± 211	2,247 ± 191	2,045 ± 156	2,254 ± 188	1,885 ± 250	2,042 ± 156	2,304 ± 242
Ringed, M	Pimniq (NOA0010311)	--	2,473 ± 216	1,898 ± 181	1,870 ± 436	2,085 ± 572	2,198 ± 293	--	--	--
Ringed, F	Dutch (NOA0010460)	--	1,577 ± 191	1,684 ± 212	1,668 ± 171	--	--	--	--	--
Bearded, M	Noatak (NOA0010270)	4,225 ± 978	6,119 ± 606	4,953 ± 611	5,179 ± 631	6,069 ± 1,694	--	--	--	--
Bearded, M	Siku (NOA0010177)	6,501 ± 1,075	6,395 ± 1,257	--	--	--	--	--	--	--

Mass-specific GEI (kcal kg^{-1} d^{-1})

Species, sex	Individual	Yr 1	Yr 2	Yr 3	Yr 4	Yr 5	Yr 6	Yr 7	Yr 8	Yr 9
Spotted, M	Amak (NOA0006675)	102 ± 13	99 ± 14	102 ± 13	107 ± 17	73 ± 11	75 ± 16	73 ± 25	72 ± 21	74 ± 30
Spotted, M	Tunu (NOA0006674)	115 ± 21	103 ± 15	93 ± 9	93 ± 12	67 ± 12	69 ± 14	62 ± 13	67 ± 11	63 ± 23
Spotted, F	Sura (NOA0010309)	138 ± 61	81 ± 32	82 ± 13	90 ± 18	70 ± 23	60 ± 14	--	--	--
Spotted, M	Kunik (NOA0010310)	112 ± 33	68 ± 5	73 ± 14	68 ± 19	58 ± 12	--	--	--	--
Ringed, F	Nayak (NOA0006783)	--	89 ± 11	102 ± 11	99 ± 8	87 ± 10	94 ± 7	63 ± 15	69 ± 6	71 ± 8
Ringed, M	Pimniq (NOA0010311)	--	136 ± 35	66 ± 7	68 ± 16	72 ± 23	66 ± 12	--	--	--
Ringed, F	Dutch (NOA0010460)	--	96 ± 16	72 ± 14	60 ± 7	--	--	--	--	--
Bearded, M	Noatak (NOA0010270)	42 ± 11	65 ± 7	44 ± 6	42 ± 5	46 ± 13	--	--	--	--
Bearded, M	Siku (NOA0010177)	67 ± 7	63 ± 7	--	--	--	--	--	--	--

		Body mass (kg)								
Species, sex	Individual	Yr 1	Yr 2	Yr 3	Yr 4	Yr 5	Yr 6	Yr 7	Yr 8	Yr 9
Spotted, M	Amak (NOA0006675)	27.6 ± 6.8	41.1 ± 1.7	44.0 ± 2.1	49.5 ± 4.5	56.7 ± 2.5	59.2 ± 3.1	60.7 ± 6.6	66.2 ± 7.3	65.7 ± 11.6
Spotted, M	Tunu (NOA0006674)	23.8 ± 5.8	34.7 ± 1.7	43.5 ± 2.8	50.5 ± 3.1	58.7 ± 2.6	65.7 ± 5.4	64.8 ± 1.5	67.0 ± 4.7	73.4 ± 9.0
Spotted, F	Sura (NOA0010309)	17.8 ± 5.2	35.2 ± 4.5	41.0 ± 1.5	41.7 ± 2.2	53.1 ± 5.3	64.0 ± 9.8	--	--	--
Spotted, M	Kunik (NOA0010310)	22.8 ± 9.3	36.5 ± 1.1	42.1 ± 2.1	52.3 ± 4.2	64.9 ± 7.7	--	--	--	--
Ringed, F	Nayak (NOA0006783)	15.2 ± 5.2	19.4 ± 1.3	21.9 ± 1.0	22.6 ± 0.9	23.6 ± 1.1	24.1 ± 1.9	28.6 ± 1.2	29.8 ± 1.3	32.5 ± 0.4
Ringed, M	Pimniq (NOA0010311)	--	19.3 ± 5.4	28.9 ± 1.2	27.3 ± 0.7	29.5 ± 2.4	33.9 ± 2.3	--	--	--
Ringed, F	Dutch (NOA0010460)	--	16.7 ± 2.6	23.7 ± 2.9	28.1 ± 1.8	--	--	--	--	--
Bearded, M	Noatak (NOA0010270)	93.2 ± 6.5	94.4 ± 5.3	113.6 ± 2.9	122.6 ± 1.9	133.7 ± 6.3	--	--	--	--
Bearded, M	Siku (NOA0010177)	95.9 ± 5.2	104.1 ± 6.5	--	--	--	--	--	--	--



Supplementary Figure 1. Environmental conditions at the two study sites: (A) the Alaska SeaLife Center (Seward, Alaska) and (B) Long Marine Laboratory (Santa Cruz, CA). Monthly data over 3 y are presented for ambient air temperature (dark blue squares), water temperature (light blue circles), and hours daylight (red lines). Data for ASLC are from January 2016 to December 2018, while data for LML are from January 2013 to December 2016. Note the abnormally warm ambient seawater temperature at LML in winter 2014 associated with the "blob" (Peterson et al., 2015).