SEASONAL OSCILLATIONS IN THE MASS AND FOOD INTAKE OF STELLER SEA LIONS

by

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Abstract

Morphometric measurements and daily feeding records of 62 captive Steller sea lions (*Eumetopias jubatus*) were analyzed to provide information about seasonal growth and food consumption that has been impossible to collect from wild animals. Data from nursing pups, intact and castrated males, and pregnant, lactating and non-reproductive females were also used to determine differences in rates of maturity between males and females, and the effects that climate, sexual maturity, castration and pregnancy and lactation have on growth and food intake. Data were fit with seasonal (sine function) and annual (von Bertalanffy, logistic, Gompertz, Richard's and maturity) growth models, and showed that males achieved larger body sizes than females by undergoing a growth spurt during puberty and by extending their growth throughout adulthood. Annual increases in the length and mass of females slowed significantly following sexual maturity. Males and females both experienced seasonal oscillations in body mass, but the seasonal fluctuation in male mass peaked later (April) and was far more dramatic than that of females. The mass of lactating and non-reproductive females peaked in early spring (March), while increases in the mass of pregnant females paralleled fetal growth, reaching a maximum before parturition. Changes in mass did not parallel changes in consumption. Fish intake by males and females peaked during winter and bottomed during late spring, while seasonal changes in body mass reached their high and low 3 to 4 months later than food intake. Pregnant and non-reproductive females differed little in the amount of prey they consumed, unlike lactating females that significantly increased their consumption during summer and winter. The differences between females highlight the relatively low additional energetic requirements of pregnancy and the high costs of lactation. Differences between neutered and intact males further suggest that testosterone affected overall male growth, but had smaller effects on seasonal oscillations in mass and did not affect food intake. The reproductive cycle and thermoregulatory requirements appeared to drive seasonal changes in body mass and food intake of male and female Steller sea lions but at different time scales. Our findings also indicate that mass is not a simple reflection of food intake, which has important implications for future nutritional research and bioenergetic modeling of wild pinnipeds.

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Co-authorship statement

I, Pamela Allen, am the main contributor to this thesis in all of the required areas:

- Identification and design of research program: My supervisor, Andrew Trites, and I are the main identifiers of this research project. I am the main designer of this research program.
- Performing the research: I performed all of the research in this thesis. Data was provided from the directors of aquariums housing Steller sea lions (D. Rosen, R. van Schie, L. Mazzaro, H. Katsumata, T. Yamamoto, T. Izumito). Suggestions were given by my supervisor Andrew Trites, my committee member David Rosen and our lab biostatistician, Ruth Joy.
- Data analyses: I performed all of the data analyses in this thesis. Suggestions were given by Andrew Trites and Ruth Joy.
- Manuscript preparation: I prepared the whole manuscript. Editing was performed by myself, Andrew Trites and David Rosen.

Chapter 1: Introduction

Steller sea lion (*Eumetopias jubatus*) populations have declined in Alaska by 85% between 1980 and 2008 in the Gulf of Alaska and the Aleutian Islands, but the cause of this decline is unknown (Trites & Larkin 1996, National Research Council 2003, NMFS 2008). A leading hypothesis to explain this population drop is nutritional stress caused by reduced fish quality and availability. Considerable research has thus gone into assessing the nutritional status of Steller sea lions, ranging from physiological experiments on sea lions in captivity (e.g., Rosen & Trites 2005, Jeanniard du Dot et al. 2008), to monitoring diet in the wild (e.g., Sinclair & Zeppelin 2002, Trites et al. 2007). Recent research has focused on how responses of Steller sea lions to reduced energy intake may change seasonally (Rea et al. 1999, Kumagai et al. 2006, Rea et al. 2007, Jeanniard du Dot et al. 2008, Rosen & Kumagai 2008). However, relatively little is known about how growth and food intake vary seasonally because of the difficulties of studying Steller sea lions year-round in the wild. Having such data would be useful to quantify potential patterns in growth and food intake, and could be applied to future research to understand the factors that drive the intake and use of energy by Steller sea lions.

Steller sea lion growth and food intake

Patterns of growth in length and mass of wild Steller sea lions have been described by various researchers based on two sets of cross-sectional data collected from shot animals in Alaska in the 1970's and 1980's (McLaren 1993, Calkins et al. 1998, Winship et al. 2001). These sea lions were collected mainly from February to May and from October to November, and showed that growth in length was asymptotic, with a sharp decline in growth rate at age ~6 y in females and ~7 y in males (McLaren 1993, Calkins et al. 1998, Winship et al. 2001). Researchers also found that adult males experienced temporary increases in length between November and March, which were attributed to changes in body water content and the influences of mass gain on length measurements (Winship et al. 2001). In contrast to length, growth in mass occurred in females until age 13 y, and in males until age 9 y, suggesting that increases in mass continued long after asymptotic length. Males also experienced a growth spurt between the ages of 5 and 7 y coinciding with the timing of puberty. Seasonal changes in mass were not readily apparent in wild adult non-reproductive females, unlike males that exhibited large seasonal changes in mass after age 6, with a peak in March and a low in September (although a lack of springtime data precluded an understanding of breeding mass; Winship et al. 2001). A similar pattern in seasonal mass was reported for one captive male, and was also found for two female Steller sea lions that increased in mass during summer (Nitto et al. 1998). However, these small captive samples coupled with incomplete seasonal sampling of wild sea lions have prevented drawing more detailed conclusions about seasonal patterns of growth in Steller sea lions.

Food intake in Steller sea lions has been studied less than growth because it has not yet been possible to determine the energetic intake of Steller sea lions in the wild. Thus, estimates of food consumption have been obtained from captive studies and bioenergetic modeling. One small-scale captive study of one male and two female Steller sea lions and their eight offspring concluded that fluctuations in food intake began after sexual maturity for both sexes, with especially large fluctuations in consumption by pregnant and lactating females (Kastelein et al. 1990). Males and females both decreased their intake during the spring breeding period (Kastelein et al. 1990).

Steller sea lion energy intake has also been estimated through using bioenergetic models. Winship et al. (2002) used such parameters as body size collected from wild animals and metabolic scaling factors based on the time spent in the water and on land to develop a model of the energetic requirements of pups, immature animals and adults of both sexes. This bioenergetics model suggested that activity was the largest portion of the energy budget for all Steller sea lions, while the energetic cost of growth was relatively inexpensive in comparison. Reproduction also influenced energy intake in both sexes. Among females, energy demands rose only slightly towards the end of gestation, but increased steadily during lactation to their highest level in spring (almost double that of non-reproductive females; Winship et al. 2002). Not surprisingly, adult male food intake was predicted to drop sharply during the breeding season due to the time spent on land. This model provided the first approximation of the seasonal energy requirements of wild Steller sea lions, and gave insight into differences in food intake based on sex, season and reproductive state. The model also suggested that winter is a critical time period in which all animals, especially juveniles and lactating females, could be most affected by reductions in energy intake (Winship et al. 2002).

Potential effects on growth and feeding

Because Steller sea lions live in a highly seasonal environment, there is potential for food intake to change throughout the year, possibly affecting growth rates. Many land mammals living in seasonal environments gain fat mass in autumn and winter for insulation during colder months, and increase tissue mass in the spring during warmer food-plentiful periods (Prestrud & Nilssen 1992, Poulle et al. 1995, Hilderbrand et al. 1999). Aquatic species such as phocid seals retain blubber during colder times (Renouf & Noseworthy 1990, Ryg & Øritsland 1991, Renouf et al. 1993), while otariids that have less blubber must consume more during colder months to offset thermoregulatory costs (Winship et al. 2002). Changing temperatures can cause both mass and food intake of sea lions to vary throughout the year because of the demands of thermoregulation.

Food availability and quality affect the growth and food intake of land mammals (Lessage et al. 2001) as it does in aquatic mammals. For example, Northwest Atlantic harp seals (*Phoca groenlandica*) migrate to the Arctic in the summer to feed on rich food sources, which allows them to store mass and blubber (Chabot & Stenson 2002). Steller sea lions do not migrate, but encounter seasonal shifts in quantity and quality of prey from species that are more dispersed and lower in fat content during the winter months, to species that are higher in fat and more prevalent and grouped during the spring and summer

(Anthony et al. 2000, Kitts et al. 2004, Sigler et al. 2004, Womble et al. 2005). Such seasonal changes of prey availability and quality affect mass growth and energy requirements of Steller sea lions as shown by the response of captive animals to nutritional challenges during summer and winter (Rea et al. 1999, Kumagai et al. 2006, Rea et al. 2007, Jeanniard du Dot et al. 2008, Rosen & Kumagai 2008).

Reproduction is another influence on the growth and food intake of Steller sea lions. Mature males come on land prior to the breeding season to secure territory, and remain on land to defend a harem of females in order to maximize breeding success. During the breeding season, mature males forage infrequently (Mathisen et al. 1962, Pitcher & Calkins 1981) and rapidly lose mass. Territoriality and harem maintenance requires males to be large enough to fight off competitors (Winship et al. 2001). Such effects of breeding on body mass is well-documented in polygynous mammals (Deputte 1992, Kastelein et al. 1995, Hewison et al. 1996, Trites & Bigg 1996, Weckerly 1998, Zuercher et al. 1999, Kastelein et al. 2000, Mahoney et al. 2001, Setchell et al. 2001).

Females give birth to a single pup during May and June, and copulation follows closely afterwards (Pitcher & Calkins 1981, Milette & Trites 2003). Fetal growth is approximately 9 months but does not begin until three months after mating when the blastula implants in the uterine wall of females in late September or October (Pitcher & Calkins 1981). Pregnancy has little impact on energy needs until close to parturition (Winship et al. 2002). Following parturition, females remain on land for about 1 week to nurse their pups before making short foraging trips (Milette & Trites 2003). Pups normally wean at age 1 y, but many may stay with their mothers for an extra one or two years (Pitcher & Calkins 1981, Trites et al. 2006). Lactation is extremely costly and requires high food intakes (Kastelein et al. 1995, Kastelein et al. 2000, Winship et al. 2002, Williams et al. 2007). Reproduction is thus believed to be a major influence on seasonal changes in mass and food intake.

Objectives

Previous research has highlighted seasonal differences in how Steller sea lions respond to increases and decreases in food intake, and have identified temperature, food availability and quality, and reproduction as the main forces that drive yearly changes in physiological parameters and growth (Rosen & Renouf 1998, Rea et al. 1999, Sigler et al. 2004, Kumagai et al. 2006, Womble & Sigler 2006, Jeanniard du Dot et al. 2008). However, the seasonal relationship between growth and food intake has not been examined fully in Steller sea lions. Our study is comprised of two chapters. In Chapter 2 we use length, mass and food intake recorded from captive raised Steller sea lions of all ages (pups to adults) and reproductive statuses (non-reproductive, pregnant and lactating) to quantify growth and consumption on a finer scale than ever done before. We also compare our models of growth and consumption between the different groups of sea lions to better understand such life history stages as sexual maturity, pregnancy, and lactation. We examine male sexual maturity in Chapter

3 through comparison of mass and food intake data from intact and neutered males, and the role that testosterone plays in affecting these variables.

We expected growth of captive Steller sea lions to be similar to known patterns of wild sea lions, but that captive sea lions would consume less food than their wild counterparts due to diet and activity differences between these two groups. We also anticipated that male mass and food intake would oscillate as observed in wild males, and that these measurements would be highly influenced by changing hormone levels during puberty and seasonal reproduction (Winship et al. 2001, Winship et al. 2002). We further expected that we would be able to estimate the energetic cost of pregnancy and lactation, as well as determine whether non-pregnant females also experience seasonal changes in growth and food intake. As a whole, the research presented in this thesis was designed to provide a better understanding of seasonality in Steller sea lions and the relationship between food intake and body size.

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Chapter 2: Seasonal oscillations in the mass and food intake of Steller sea lions are influenced by thermoregulatory and reproductive needs[1]

Introduction

Growth models are useful tools to summarize increases in size measurements of animals with simple equations, and are often used to draw conclusions about similarities and differences between individuals, populations and species. They have been used to describe increases in weight and length over the lifespan of many species, and have provided insight into such things as reproduction, the attainment of sexual maturity and differences in growth patterns between the sexes (e.g., McLaren 1993, Trites & Bigg 1996, McKenzie et al. 2007). Growth models are also used to estimate the energetic needs of animals, and are central to bioenergetic models that assess food requirements (e.g., Markussen et al. 1992, Olesiuk 1993, Hammill & Stenson 2000, Winship et al. 2002). However, most growth models have tended to ignore seasonal patterns of growth that are common among sexually dimorphic species and those that live in seasonal environments. This is particularly true for otariid pinnipeds that undergo large yearly fluctuations in mass and possibly food intake in

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association with breeding (McLaren 1993, Trites & Bigg 1996, Williams et al. 2007).

Steller sea lions (*Eumetopias jubatus*) are the largest species of otariids with mature males weighing 2.5 times more than mature females (McLaren 1993, Calkins et al. 1998, Winship et al. 2001, Winship et al. 2002). However, the seasonal timing of fattening in preparation for the breeding season and its relationship with seasonal patterns in food intake are poorly understood. Nor is it clear to what extent females might incur seasonal changes in food intake and growth. Models that currently describe the growth of Steller sea lions have been based on a single set of morphometric measurements from two random samples of animals that were shot in Alaska mainly during the summers and falls of the 1970's and 1980's (McLaren 1993, Calkins et al. 1998, Winship et al. 2001). These data revealed increases in lengths and mass of males prior to the summer breeding season and decreases in mass and length post-breeding, but failed to show similar changes in the body size of non-pregnant females, due possibly to small numbers of measurements taken during spring and fall (Winship et al. 2001). These data were also to predict the annual food requirements of Steller sea lions, but failed to show significant seasonal difference in amounts consumed (Winship et al. 2002).

The existing morphometric data taken from Steller sea lions in the wild (1970s and 1980s) contain no winter measurements and do not fully represent animals from spring or fall. They also suffer from a cohort effect that resulted in a measurable size difference between animals from the 1970's versus the 1980's

(Calkins et al. 1998). Better estimates of growth and consumption for Steller sea lions thus require a more complete set of morphometric measurements from known aged individuals than can currently be obtained from the wild. One means for obtaining such data from all months of the year without having to capture wild individuals is to document the growth of captive animals. Not only can lengths and weights be recorded daily from captive sea lions to construct detailed growth models, but feeding records can also be analyzed to assess the relationship between growth and consumption.

Captive Steller sea lions appear to exhibit similar growth patterns to their wild counterparts (Nitto et al. 1998). One small-scale captive study of Steller sea lions (n_{male}=1, n_{female}=2) concluded that fluctuations in food intake began after sexual maturity for both sexes with especially large fluctuations in pregnant and lactating females (Kastelein et al. 1990). It also found decreased intake during the spring breeding period for adult males and females (Kastelein et al. 1990). While these data were not used to model food intake, a similar study on captive female California sea lions (*Zalophus californianus*) provided seasonal information on the energetic intakes of reproductive and non-reproductive animals and was used to estimate the amount of fish required by the corresponding wild population (Williams et al. 2007). Captive animal data are generally collected repeatedly from the same animals over time (longitudinal data), but must be analyzed with appropriate statistical techniques to address for potential biases that are inherent with these types of data.

The goal of our study was to quantify seasonal increases and decreases in body size and food intake using an extensive set of observations from captive Steller sea lions. We also sought to determine differences in rates of maturity between the sexes, and the effects that sexual maturity, pregnancy and lactation have on Steller sea lion growth and food intake. Using data from captive Steller sea lions to answer these questions provides an interesting counterpoint to the data collected from wild animals. They also fill in gaps in knowledge by providing seasonal information about growth and actual food intake that have been impossible to collect from wild animals.

Materials and methods

Data collection

Data were collected from captive Steller sea lions housed at the Vancouver Aquarium ("VA", Canada), Mystic Aquarium ("MA", USA), Dolfinarium Harderwijk ("DH", the Netherlands), Futami Sea Paradise ("FSP", Japan), Izu-Mito Sea Paradise ("ISP", Japan) and Kamogawa Sea World ("KSW", Japan). In total, lifetime records of 20 male and 42 female sea lions were obtained. The age distribution, location, breeding status, recruitment (captive versus wild-born) and types of data collected from these animals are summarized in Appendix 1. All of the animals were housed in outdoor enclosures with pools, and were exposed to ambient temperatures. The five facilities were located at comparable northern latitudes (VA=49°, MA=41°, DH=52°, FSP=34°, ISP=35°, KSW=35°), so photoperiod and seasons were similar between the facilities. The animals at VA and MA participated in research studies, so their food intake was influenced by both hunger, and by training and research needs, as well as by occasional feeding experiments. Preliminary graphical analysis showed these feeding experiments to be short, infrequent, and undetectable relative to the large size of the full data set. The Steller sea lions at DH, FSP, ISP and KSW were for display purposes, which meant that feeding reflected training and not research needs. The animals at these facilities were feed freely within daily training sessions and aquarium shows.

Data collection varied between the aquariums. Only VA collected length (to the nearest centimeter), measured in a straight line from the nose to the end of the tip of the tail as the animals were lying still on their ventral side (dorsal standard length or DSL). We converted DSL to SL using $SL = 0.98734 * DSL + 5.758$ ($p<0.001$; calculated by Winship et al. (2001) from measurements of wild Steller sea lions) to ensure comparability of length measurements between studies. This did not change the general shape of the resulting growth curves, but added between 2 and 4 cm to each measurement. VA, MA, DH, ISP and KSW collected mass data to the nearest kilogram by training the animals to voluntarily position themselves on a platform scale. DH, FSP and KSW had breeding programs, and also neutered some of their males. Males housed at ISP were all neutered.

Food intake (kg d^{-1}), measured to the nearest kilogram (or pound, converted into kilograms) was recorded for all animals at all facilities. Animals were usually fed on a daily basis at all aquariums. Primary foods were herring (*Clupea palasii & Clupea harengus*) and mackerel (*Pleurogrammus monopterygius, Trachurus trachurus* and *Scomber japonicus*), but other species were consumed depending upon availability and ongoing research projects. VA and MA determined the energy density of the fish fed to their animals using proximate chemical analysis (e.g. Rosen & Trites 1999). The energy content of fish from the other facilities was estimated from literature values as summarized in Appendix 2. Total energy intake (MJ d^{-1}) equaled the sum of each prey type consumed (mass) multiplied by the energy density of that particular species.

Data from each of the aquariums was compiled and examined to check for possible errors in data entry. A few obvious outliers were removed from the data sets, but no major aberrations were noted. Animals that were wild-born were assigned a birth date of June 15th, which is the average birth date in the wild Steller sea lion population (Mathisen et al. 1962, Pitcher et al. 2001). Animals that had an unknown year of birth were removed from the study (*n*=2). Females were classified according to their breeding status, and only data from non-pregnant, non-lactating females were incorporated into the main growth and feeding curve analyses. Males were classified as intact or neutered, but only data from intact males were analyzed. Data from neutered males are compared with intact males in Chapter 3.

Data analysis

Data were first examined graphically with LOESS smoothing functions to determine underlying patterns that might be present. Four models were considered to describe changes with age in body length, body mass and food intake:

1. von Bertalanffy (von Bertalanffy 1938, Ricker 1979):

$$S_t = A\ (1 - e^{-e^{[\ln(k)]}(t-t_0)})^3$$

2. Logistic (Ricker 1979):

$$S_t = \frac{A}{1 + e^{-k(t-t_0)}}$$

3. Gompertz (Ricker 1979):

$$S_t = Ae^{-e^{-k(t-t_0)}}$$

4. 3-parameter Richard's (Richards 1959, Leberg et al. 1989):

$$S_t = A^{1-m} - e^{\ [-2t(1+m)/T]1/(1-m)}$$

where S_t is the size at age t, A is the asymptotic size, k is the growth rate constant, t_0 is the age at which size is 0, m is the Richard's shape parameter, and T is the Richard's growth rate constant. The parameters do not necessarily represent the same property among growth models, but are comparable within an individual model used with different data sets.

In addition to using the four established growth models, a "maturity" function (Day & Taylor 1997) was fit to the intake and body size data to reflect pre- and post-maturity changes, herein called the maturity equation:

5. $$S_t = [\frac{1}{3}k(\frac{1-e^{-h(t-a)}}{h} + a) + {w_0}^{1/3}]^3$$

where *α* is the age at sexual maturity, *h* is a value that scales the rate of exponential decline in growth following sexual maturity, and w_0 is the size at age zero. This function can be used in determinant and indeterminate growth modeling, and is based on the principle that following sexual maturity animals decrease the amount of energy used for growth and invest this into reproduction, so growth has to be separated pre- and post-sexual maturity. This is in contrast to the four other growth models, which assume one relationship can describe lifetime growth (Day & Taylor 1997).

Mass and length were compared using a power equation: $mass = a \times length^b$. The allometric relationship between the mass and length of males was first examined using a LOESS smoothing function to determine whether it could be described using a single power function, since a previously analysis of data from wild male Steller sea lions found that two power equations rather than one fit the data more closely (Winship et al. 2001). The size (length) at which the mass-length pattern differed was used as the dividing point to fit two separate power equation models.

Seasonality in growth and food intake was examined using LOESS fits on individual animal and pooled data sets, and was found to have a sinusoidal pattern: $\mathrm{A}_{mp} \times \sin[2 \times pi \times \Omega(t-H)] + v$, where A_{mp} is the amplitude of the wave, *H* is the horizontal shift and *v* is the vertical shift in the position of the wave. One wavelength is equal to 2*pi*Ω, and the Ω parameter was set to 1 y because seasonal wave patterns in the data occurred on a yearly basis.

The nature of the data called for a careful approach to data analysis to address three primary biases: 1) the data were longitudinal such that the daily measurements for each animal were not independent of each other; 2) multiple explanatory variables could influence the shape of the models and their variance structures; and 3) the data set was unbalanced because some animals contributed more data that others. A mixed-effect modeling approach was used to address these three factors because mixed-effect models account for serial correlation in the data by specifying a correlation structure, and allowing assignment of fixed effects (the parameters which are to be estimated from the data) and random effects (aspects of the data that may influence the variation, and thus the estimation of fixed parameters). Mixed-effect models also give equal weight to each animal in the final model to eliminate the biases introduced by unbalanced data. Because mixed-effect models account for variation within individuals in the data, they can also be used to extrapolate to a population level rather than being restricted to purely describing a particular data set.

The fixed effects in our study were the growth model parameters being estimated from the length, mass or food intake data. The random effects identified as having a possible influence on variation in the data were the individual animals ("*Animal*"), the aquariums that housed these animals ("*Aquarium*"), and whether the animals were born in captivity or in the wild ("*Birthplace*"). *Animal* was always included as the main grouping factor, since most of the variation in the data was due to inter-animal variability, as determined by preliminary graphical analysis. The remaining random effects were tested for inclusion in the models, first individually with *Animal* and, if found to be significant, by interactions between multiple effects.

Preliminary analyses using nonlinear mixed-effect models (NLME's, R 2.8.0; Pinheiro et al. 2008, R Development Core Team 2008) revealed three shortcomings to our methods. The first was a lack of convergence in models that contained 4 or more parameters, such as the original maturity function, 4-parameter Richards function and the 5-parameter seasonal von Bertalanffy equation. Thus, only models with 3 or fewer parameters could be applied. The α (age at sexual maturity) term of the maturity function was therefore fixed by assuming it to be the first occurrence of pregnancy for females and the age of first successful insemination of a female for males among our animals. We tested multiple ages to determine the sensitivity of the model to this assumption.

The second limitation of using NLME modeling was the tendency of the software to reach maximum iterative size during model estimation because we had too much data. Data were recorded daily for many animals, resulting in a data set of up to 150,000 data points per category. We therefore reduced the number of data points by using a weekly average of length, mass and food intake because daily variation limited the analysis and was of little interest.

A third shortcoming of applying NLME to the sea lion data was associated with the fact that growth models cannot accurately describe the growth of both young and older animals (McLaren 1993, Winship et al. 2001). To resolve this, we divided the lifetime length and mass data into two age classes for model fitting: 0 to 1.5 years of age (the “juvenile” model) and age 1.5 y to adulthood (the “main” model). We determined this range by applying the same models to multiple age ranges, as well as by fitting this model to the entire age range, and examining the residual variance of each for the best fit. Splitting the data into these two age classes more accurately represented both young and asymptotic growth for all models, whereas one growth model fit to all of the data overestimated juvenile size and underestimated adult asymptotic size. Despite the fact that the maturity function was in part developed to address this problem (Day & Taylor 1997), we found it necessary to fit this equation to the two age classes to best reflect the rapid growth rate of young animals. We also removed animals from the “main” models that only contributed data in late adulthood or from age 1.5 to ~2 y as they did not provide any information on curve shape and severely restricted model convergence (Appendix 1).

We chose the most appropriate model to fit the data by constructing the simplest model structure possible, with the random effect *Animal* set on the fixed effect with the most within-animal residual variation, thus capturing the most variation possible within the least complex model framework. This method allowed for the simple and equal comparison of all growth models. Models were compared with a likelihood-ratio test of significance to determine which model fit best (Pinheiro & Bates 2002). In the case where there was no significant difference between two models, residual variance was graphically examined to determine best fit, and the model selected was one that had the best fit for both sexes. All growth equations were compared separately for length, mass and food intake versus age for males and females, and were graphically examined for their individual as well as their overall fit to the data.

A sine function was applied to the data overlapped by year to examine possible seasonal variation in length, mass and food intake. Overlapping the data was the best way to fit the sine equation because it was not possible to use seasonal equations with moving average components. It was also deemed appropriate because animals approached their asymptotic length, mass and food intake late in life. We conducted this procedure only for adult animals above the ages of sexual maturity to better approximate adult size and food intake. The individual and overall model fits were examined graphically to ensure the proper match of the sine function to the data.

Each of the models was refined to account for additional residual variance after first choosing appropriate models based on the simplest model structure. The remaining random effects *Aquarium* and *Birthplace* were added to the model with *Animal* grouped within *Aquarium* or *Birthplace*. The likelihood-ratio test statistics of the resulting models were compared to determine the proper grouping structure of the random effects.

Because of difficulty with convergence, it was not always possible to include random effects for all fixed parameters (although for most models the fixed terms were variable enough to warrant this procedure as determined during preliminary graphical analyses). In these cases, the random effects structure first included the most variable of the three fixed effects, and then incorporated the second and third-most variable fixed effects when analysis allowed. The likelihood-ratio statistics of all model fits were compared to choose the best fit for the data set.

Mixed-effect model assumptions associated with random effects and within-group error were tested when the models were properly refined. The within-group errors must be independent with a mean centered at zero, a constant variance and must be normally distributed, while the random effects must be independent and normally distributed. All of these assumptions were tested using graphical applications from the package nlme in R 2.8.0 (Pinheiro & Bates 2002, Pinheiro et al. 2008, R Development Core Team 2008), and showed that the assumption of independence of within-group error was violated in every model because of the nature of the data. A first-order autocorrelation function (corAR1) was therefore added to correct for this serial correlation in the individual animal data. While higher order autocorrelation functions may have been theoretically more suited to these data because growth and food intake data are often correlated over a long period of time, they proved impossible to use because of their extremely iterative nature. Upon comparison of likelihood-ratio test statistics, we decided to include the first-order autocorrelation function because every model that included the first-order autocorrelation function always fit significantly better than the corresponding model without the function ($p<0.001$ for all comparisons).

The assumption of heterogeneity of within-group residual variance was also violated in every model because the variance of all growth data increases with age. This can be corrected for in NLME modeling, but this process (in combination with the correction for autocorrelation) exceeded the maximum iteration limit of the software and was not as critical a procedure as the specification of correlation between animals. Model significance was determined for the individual model parameters as well as their interaction using Wald F-tests (α=0.05) after properly refining each model with the correct fixed and random effects and correlation structure.

While the NLME function provides confidence intervals for the individual fixed effects, these are not the intervals for the fitted model as a whole. The model 95% confidence intervals were determined by hierarchical bootstrapping on each data set replicated 1000 times. The NLME model originally applied to the data set with the same random effects and correlation structure was applied to each sampled data set to produce 1000 model estimates, from which the confidence intervals could be determined. Because of the general high variance in the data set within and among animals, NLME model convergence was not possible for every replicate. Thus, model starting values for the fixed and random parameters were optimized within each iteration, and the bootstrap was repeated until 1000 successful iterations were reached.

Non-linear mixed-effect models were also used when examining differences in length, mass and food and energy intake over time between the sexes, as well as determining differences between non-reproductive, pregnant and lactating females. The main model structure matched that of the original model describing the data. For example, when comparing male and female mass, the maturity model structure fit to mass growth of each sex was also used to compare between the sexes. However, instead of a single parameter determined for each fixed effect, parameters were allowed to vary with sex (when comparing males and females) or with reproduction (when comparing females of different reproductive status). The random effect was set as *Animal* on the simplest fixed-effects structure, and a first-order correlation function was used. A significant difference between groups was determined if the Wald F-test of interaction between the fixed effects and the covariate was below the significance level (α=0.05). When determining the age at which two groups were different, data were divided into yearly age groups to identify the first year in which there was a significant difference.

Results

Length-at-age models

The von Bertalanffy, Richard's and maturity growth models all fit the standard length-at-age data equally well for male and female Steller sea lions (likelihood-ratio test, $p>0.05$). However, the von Bertalanffy model was selected as the best fit for both the male and non-reproductive female length data upon examination of the residual variance (juvenile and main models Fig. 2.1; Table 2.1). The only possible random effect for both the juvenile and main models was *Animal* because all length measurements were from VA animals and all were born in the wild. For both sexes, *Animal* was significant in the juvenile and main

Table 2.1. Parameter estimates (±CI) of all models describing the growth and feeding of Steller sea lions. The “juvenile” models are all from ages 0 to 1.5y, and the “main” models are from age 1.5y onwards.

Measurement	Sex	*n*	Model	Parameters with random effect “Animal”	Parameters ±CI *
Standard Length (cm)	Male (juvenile)	5	von Bertalanffy	A, t_0	$A = 185.4262 \pm 10.9066$; $k = 1.1827 \pm 0.1379$; $t_0 = -1.4557 \pm 0.1683$
	Male (main)	5		A, t_0	$A = 297.6965 \pm 22.1789$; $k = 0.2305 \pm 0.0227$; $t_0 = -6.4231 \pm 0.8356$
	Female (non-reproductive, juvenile)	15		A, t_0	$A = 187.7325 \pm 6.8600$; $k =1.0162 \pm 0.0841$; $t_0 = -1.6744 \pm 0.1496$
	Female (non-reproductive, main)	15		A, t_0	$A = 227.5393 \pm 5.4562$; $k = 0.3278 \pm 0.0126$; $t_0 = -5.5228 \pm 0.2845$
Mass (kg)	Male (intact, juvenile)	6	maturity	h, w_0	$h = 0.7683 \pm 0.2426$; $k = 0.1373 \pm 0.1395$; $w_0 = 156.7223 \pm 13.1259$; ($a = 5$)
	Male (intact, main)**	5		k, w_0	$h = 0.1321 \pm 0.0115$; $k = 1.4835 \pm 0.2561$; $w_0 = 75.2630 \pm 21.5184$; ($a = 5$)
	Female (non-reproductive, juvenile)	20		h, w_0	$h = 1.8548 \pm 0.2060$; $k = 0.0064 \pm 0.0044$; $w_0 = 98.4936 \pm 7.5221$; ($a = 4$)
	Female (non-reproductive, main)	21		k, w_0	$h = 0.2654 \pm 0.0292$; $k = 0.6302 \pm 0.0650$; $w_0 = 84.0833 \pm 8.2014$; ($a = 4$)
Mass/Length (kg cm^{-1})	Male (up to 225 cm)	5	Power	a, b	$a = 2.4705e-05 \pm 1.0389e-05$; $b = 2.9585 \pm 0.0795$
	Male (225 onward)	4		a, b	$a = 1.7162e-09 \pm 5.4656e-09$; $b = 4.7488 \pm 0.5667$
	Female (non-reproductive)	15		a, b	$a = 1.3547e-04 \pm 2.0790e-05$; $b = 2.6120 \pm 0.0296$
Food Intake (kg d^{-1})	Male (main)	12	maturity	k	$h = 0.3882 \pm 0.1427$; $k = 0.2328 \pm 0.0406$; $w_0 = 7.3827 \pm 1.1330$; ($a = 5$)
	Female (non-reproductive, main)	31		k	$h = 0.5264 \pm 0.1128$; $k = 0.1718 \pm 0.0549$; $w_0 = 5.5708 \pm 0.2652$; ($a = 4$)
	Female (pregnant, main)	11		k	$h = 0.6474 \pm 0.2587$; $k = 0.1143 \pm 0.0555$; $w_0 = 6.3016 \pm 0.5514$; ($a = 4$)
	Female (lactating, main)	9		k	$h = 0.6240 \pm 0.2226$; $k = 0.2666 \pm 0.0912$; $w_0 = 5.9589 \pm 0.7889$; ($a = 4$)
Energy Intake (MJ d^{-1})	Male (main)	12		k	$h = 0.3877 \pm 0.1233$; $k = 0.4843 \pm 0.0730$; $w_0 = 55.6953 \pm 7.7901$; ($a = 5$)
	Female (non-reproductive, main)	31		k	$h = 0.6737 \pm 0.1269$; $k = 0.2738 \pm 0.0822$; $w_0 = 42.8252 \pm 2.1026$; ($a = 4$)
	Female (pregnant, main)	11		k	$h = 0.7193 \pm 0.2583$; $k = 0.2675 \pm 0.1090$; $w_0 = 49.9117 \pm 4.9607$; ($a = 4$)
	Female (lactating, main)	9		k	$h = 0.6261 \pm 0.2065$; $k = 0.5990 \pm 0.1857$; $w_0 = 45.0538 \pm 6.2439$; ($a = 4$)
Seasonal Mass (kg)	Male (intact, 5y onward)	5	sine	A_{mp}, H, v	$A_{mp} = -100.2413 \pm 45.2916$; $H = 7.6734 \pm 4.2556$; $v = 574.9260 \pm 74.1087$
	Female (non-reproductive, 4y onward)	21		A_{mp}, H, v	$A_{mp} = -8.6774 \pm 2.3889$; $H = 1.2913 \pm 1.3668$; $v = 170.4795 \pm 15.9148$
	Female (pregnant)	3		A_{mp}, H, v	$A_{mp} = -46.9813 \pm 14.7733$; $H = 6.3561 \pm 4.5318$; $v = 227.8539 \pm 9.9918$
	Female (lactating)	3		A_{mp}, H, v	$A_{mp} = -12.9238 \pm 4.8156$; $H = -1.6092 \pm 4.5764$; $v = 264.9344 \pm 13.1928$
Seasonal Food Intake (kg d^{-1})	Male (intact, 5y onward)	10	sine	A_{mp}, H, v	$A_{mp} = -3.9700 \pm 1.1712$; $H = -7.4330 \pm 2.0440$; $v = 17.6210 \pm 2.7302$
	Female (non-reproductive, 4y onward)	34		A_{mp}, H, v	$A_{mp} = 1.3760 \pm 0.3007$; $H = 13.1756 \pm 1.4156$; $v = 9.2908 \pm 1.0759$
	Female (pregnant)	9		A_{mp}, H, v	$A_{mp} = 1.4704 \pm 0.9711$; $H = 13.2617 \pm 4.2390$; $v = 8.5296 \pm 1.2436$
	Female (lactating)	9		A_{mp67}, H, v	$A_{mp} = 3.4230 \pm 1.9862$; $H = 9.7608 \pm 3.4237$; $v = 12.0959 \pm 3.4340$
Seasonal Energy Intake (MJ d^{-1})	Male (intact, 5y onward)	10	sine	A_{mp67}, H, v	$A_{mp} = 29.1716 \pm 9.6975$; $H = 125.4703 \pm 2.2070$; $v = 125.6197 \pm 12.1794$
	Female (non-reproductive, 4y onward)	34		A_{mp}, H, v	$A_{mp} = 7.5084 \pm 2.3317$; $H = 12.2982 \pm 1.8398$; $v = 61.2522 \pm 5.9807$
	Female (pregnant)	9		A_{mp}, H, v	$A_{mp} = 11.2984 \pm 6.3851$; $H = 12.7459 \pm 4.1779$; $v = 68.3823 \pm 7.1366$
	Female (lactating)	9			$A_{mp} = \pm$; $H = \pm$; $v = \pm$

*For every model, each parameter was highly significant ($p<0.001$), and the interaction between the parameters was highly significant ($p<0.001$).

**This model did not incorporate an autocorrelation function, which may inflate the asymptote

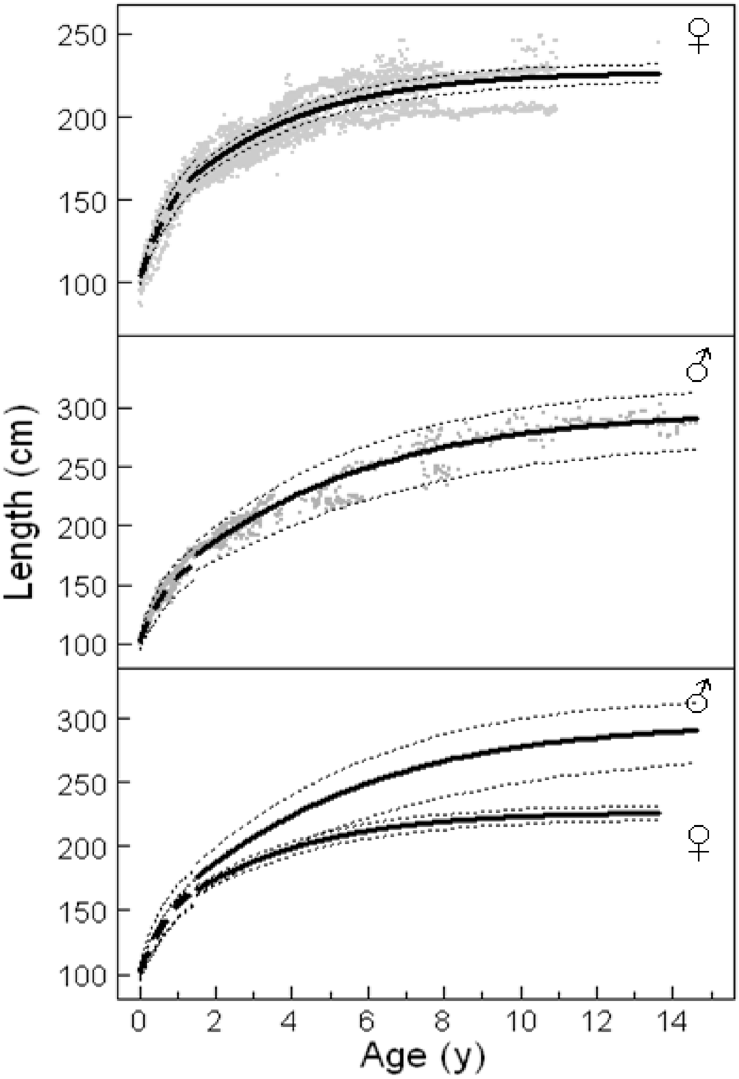

Fig. 2.1: Growth (standard length) of non-reproductive female (top; $n_{juvenile}$ =15, n_{main} =15) and male (middle; $n_{juvenile}$=5, n_{main}=5) Steller sea lions as described by the von Bertalanffy equation (Table 2.1) from age 0 to 1.5 y (dashed lines) and age >1.5 y (solid lines). Lengths of males and females differed significantly beginning their third year of life (p<0.001). Thin lines indicate 95% confidence intervals.

models on the fixed effects A and t_o (p<0.001; Table 2.1). Growth in length was asymptotic for males and females (Fig. 2.1). Growth rate of females was highest in the first year of life, and length reached 90% of their maximum at age 5.5 y (205 cm). Male growth rate also decreased with increasing age, with males achieving 90% of their asymptotic length later in life compared to females at age 8.2 y (268 cm). There was a significant difference in body lengths between males and females during their third year of life ($p<0.001$). Residual variance was similar between the sexes, and increased slightly with age.

Mass-at-age models

The maturity and von Bertalanffy growth equations fit to the mass data did not differ significantly from each other ($p>0.05$) and were found to fit better than all other functions (likelihood-ratio test, $p<0.05$). Inspection of the residuals showed that the maturity function best described the males and non-reproductive females because it predicted adult asymptotic mass better than the von Bertalanffy model. (Fig 2.2; Table 2.1). Despite this, the male mass model did not include an autocorrelation function because of problems with convergence due most likely to the large variance in these data. The α parameter was set at age 4 y for females and at age 5 y for males, since the youngest age at pregnancy in the data set for a female was 4 y, and the youngest age of fertilization by a male was 5 y. A range of ages was tested to ensure the validity of this method, and the maturity function tolerated a range of α values from 0 to 12 y in females while retaining the exact same curve shapes with no significant differences in the models ($p>0.9$). Among males, statistical significances and curve shapes of the maturity function were the same for α values ranging from ages 5 to 7 y. Out of the three possible random effects, only *Animal* was significant on the fixed parameters h and w_0 in the juvenile model for both sexes.

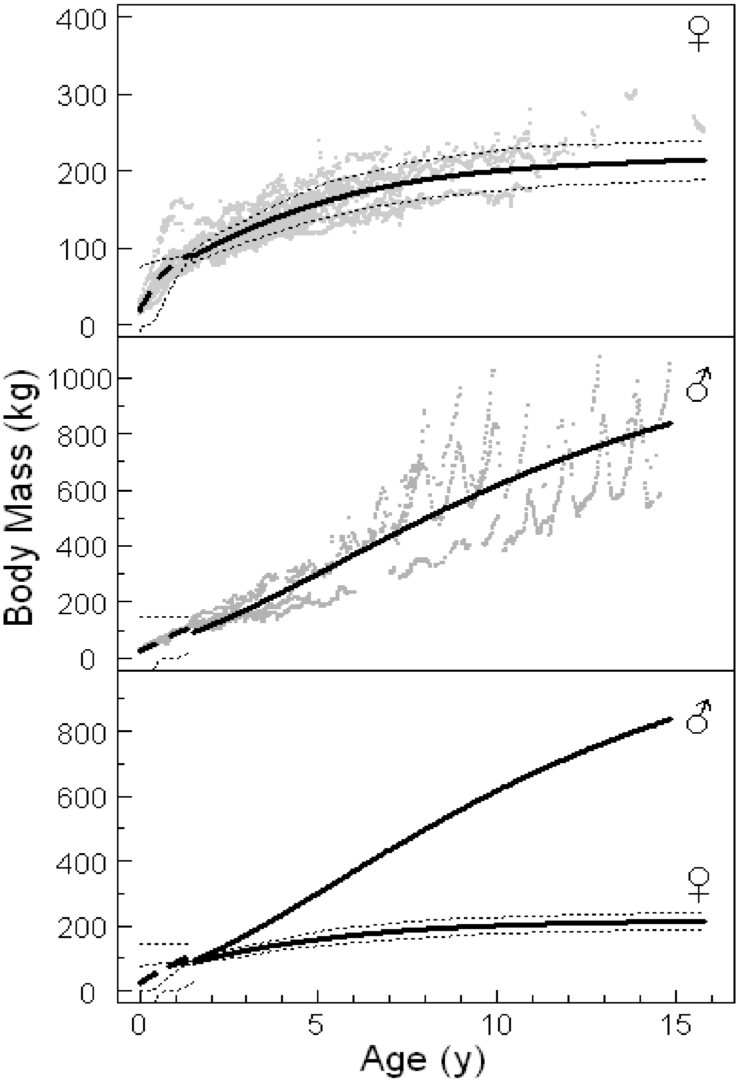

Fig. 2.2: Growth (body mass) of non-reproductive female (top; $n_{juvenile}$=20, n_{main}=21) and male (middle; $n_{juvenile}$=6, n_{main}=5) Steller sea lions as described by the maturity function (Table 2.1) from age 0 to 1.5 y (dashed lines) and >1.5 y (solid lines). The mass of males and females differed significantly beginning their second year of life ($p<0.001$). Thin lines indicate 95% confidence intervals. Confidence intervals are not included in the male mass model because it did not include an autocorrelation function.

In the main model for males and females, *Animal* was the only significant random effect on the fixed effects k and w_0 ($p<0.001$; Table 2.1).

Female mass growth rate decreased with age, with 90% of the asymptotic mass reached at age 9 y (195 kg; Fig. 2.2). For males, the overall mass growth rate reached a maximum at 7 y of age, after which it declined. The mass of male animals reached 90% of the asymptotic value at age 22.7 y (1023 kg), approximately 14 years later than females. A significant difference in mass between the sexes occurred during the first year of life ($p<0.001$). As well, males had a much larger residual variance than females, with the largest difference occurring in the ages following sexual maturity.

Length-to-mass models

A power function fit the relationship between length and mass well (Fig. 2.3; Table 2.1). *Animal* was the only possible random effect since all animals were from VA and were born in the wild, and this effect was significant on both of the fixed terms (*a* and *b*) in the models for both sexes (Table 2.1). A single equation was sufficient for the non-reproductive female data, although it underestimated mass at the longest lengths. This was due to females reaching their 90% asymptotic value in mass ~3.5 years after reaching this growth point in length. This discrepancy was noted in males as well, with 90% of asymptotic mass also reached ~14.5 years after that of length. Thus, a single power function did not fit the male data well because the greatest mass was severely underestimated. The male data was therefore divided into two length groups: 0 to 225 cm and 225 to 300 cm in length as determined from preliminary LOESS smoothing curves fit to different divisions of the length data. A length of 225 cm corresponds to an age of 4 y. These two groups were fit with separate power

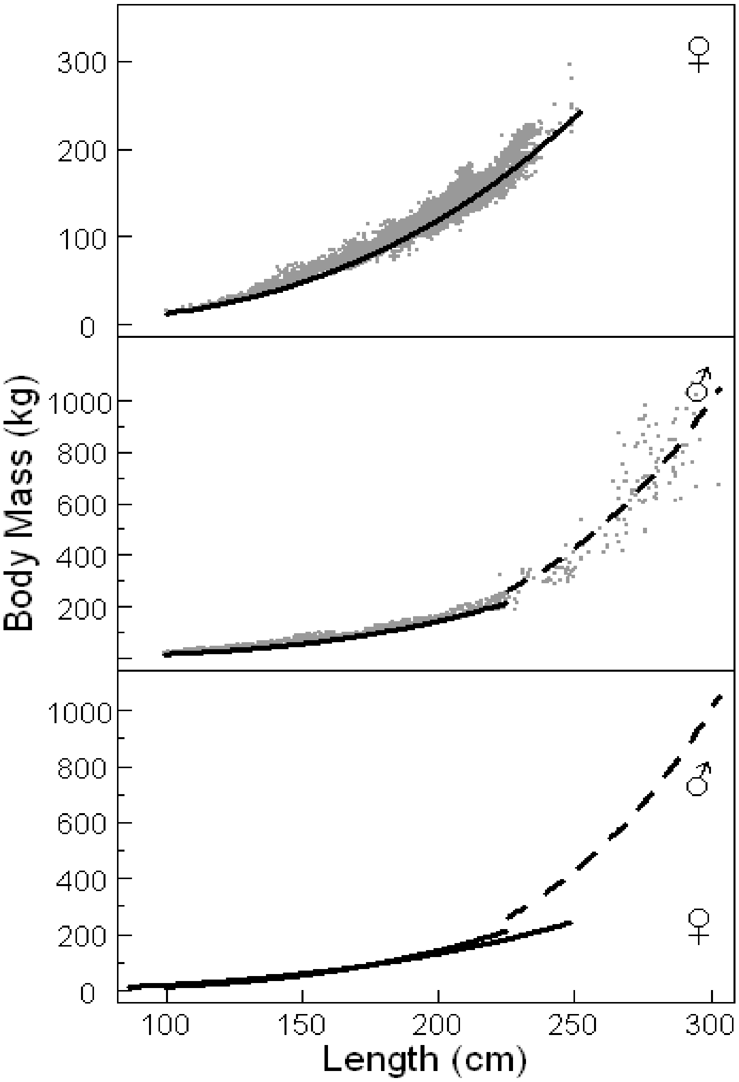

Fig. 2.3: Allometric relationship between mass and length of non-reproductive female (top; *n*=15) and male (middle; $n_{0\ to\ 225cm}$=5, $n_{225\ to\ 300\ cm}$=4) Steller sea lions fit by a power relationship (Table 2.1). The length to mass ratio of males was predicted by two equations representing immature and mature animals (0 to 225 cm and 225 to 300 cm in length). The statistical significance of the difference in the mass-length relationship of males and females and the confidence intervals of the models could not be determined due to problems with model convergence.

functions, which better reflected the relationship between length and mass at large size (Fig. 2.3).

A significant difference in the length-to-mass relationship between the sexes could not be found using NLME because of problems with model convergence. However, visual examination of the data showed males became heavier per unit length than females after approximately 200 cm, which corresponded to age 4 y in females and age 2.6 y in males. In addition, the residual variance became more variable as the animals grew, with males showing a sharp increase in variability at approximately 6 y of age.

Food and energy intake models

There was no statistical difference between any of the models fit to the food or energy intake data ($p>0.05$). However, we chose to retain the maturity function to describe the two data sets after examining the residuals of each of the models (Table 2.1). The food intake (Fig. 2.4) and energy intake (not shown) models were similar in shape, due to the obvious link between the two data sets. *Animal* was the only significant random effect on the fixed term *k* for both males and non-reproductive females in both models (Table 2.1).

Food intake reached an asymptote for both males and females (Fig. 2.4). Females reached 90% of their asymptotic food intake at age 4.8 y (8.5 kg d^{-1}). This point of intake was reached later for males, at age 7.1 y (14.7 kg d^{-1}). Male food intake appeared to increase more gradually, while female intake reached a steady yearly average at an early age. Both models had high variance due to the large fluctuations in intake, and the residual variance of the male food intake model was approximately double that of females. A significant difference in food intake between males and females occurred during the second year of life

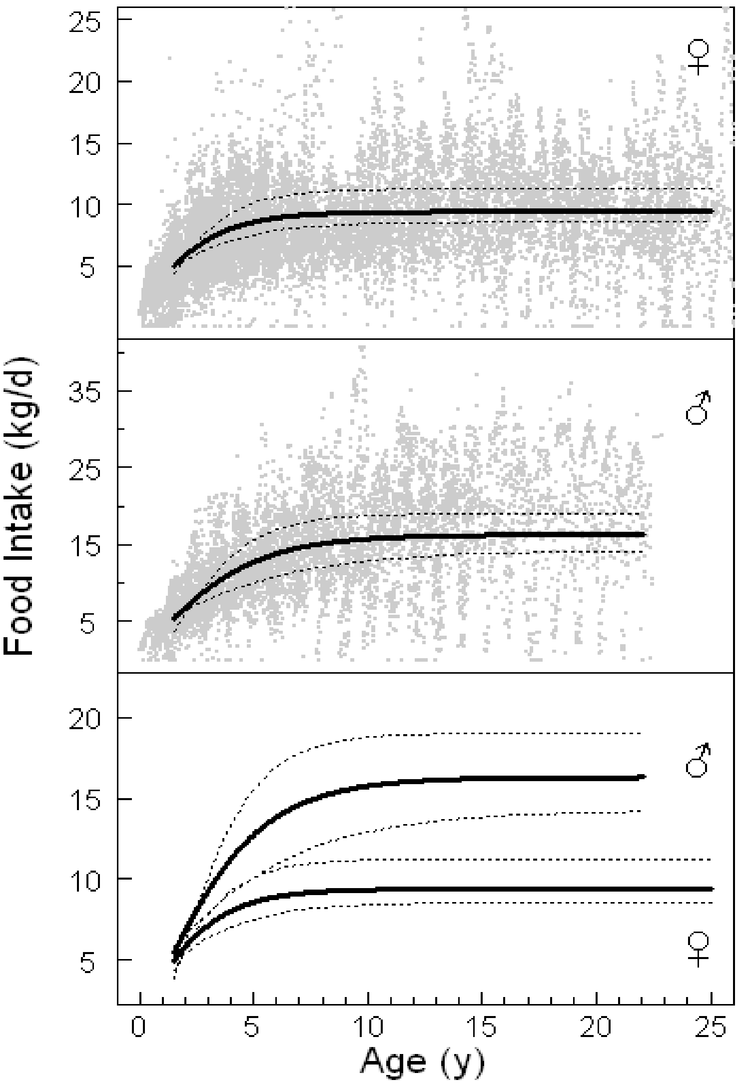

Fig. 2.4: Food intake (kg d^{-1}) of non-reproductive female (top; *n*=31) and male (middle; *n*=12) Steller sea lions as described by the maturity function (Table 2.1) from age 1.5 y onward (solid lines). Data from animals < 1.5 y is shown but was excluded from statistical analysis. Food intake differed significantly between males and females during their second year of life (p<0.001). Thin lines indicate 95% confidence intervals.

(p<0.001).

Energy intake had a slightly different pattern than that of food intake because the energy of fish fed to sea lions at VA and MA was determined with every batch of fish fed to the animals, and differed between batches. Fish

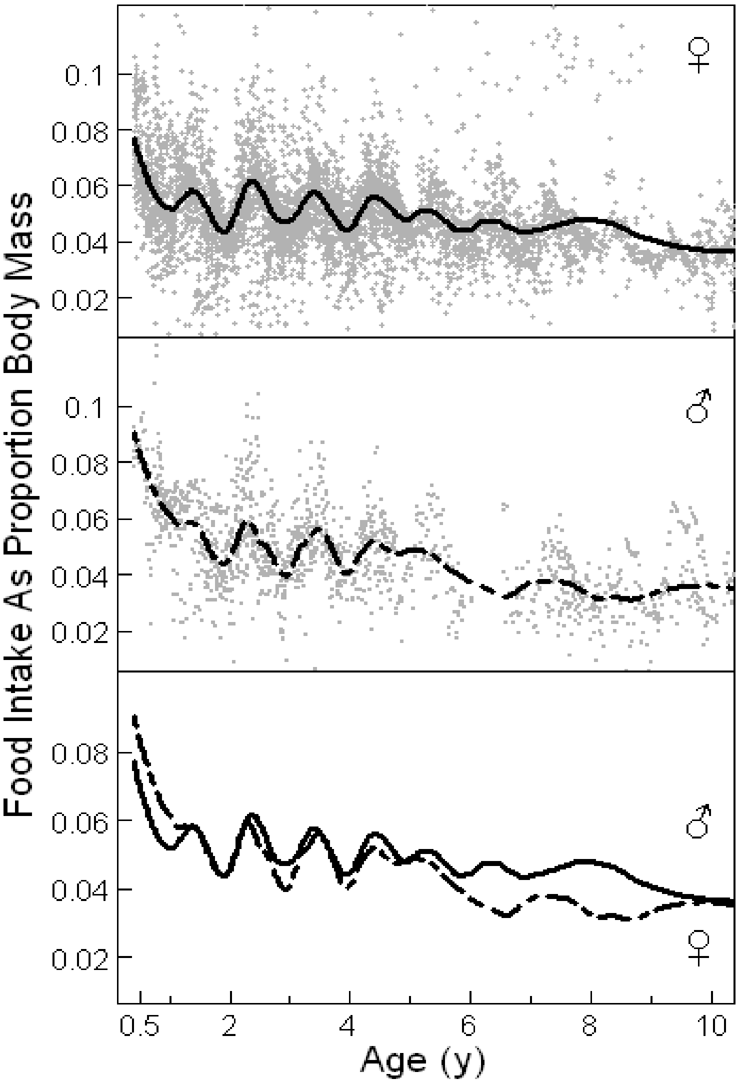

Fig. 2.5. Food intake as a proportion of body mass for non-reproductive female (top; bottom, solid line; *n*=21) and male (middle; bottom dashed line; *n*=9) Steller sea lions from age 0.5 to 10 y described by a LOESS smoothing function. Food intake until ~1 y reflects that of wild-born pups. Captive born animals tended to nurse until age 1 y and consumed little fish during that period.

energy content undoubtedly changed over time at the other facilities as well, but could not be included into our analysis because it was not measured. Females reached 90% of their asymptotic energy intake at age 4.0 y, while males reached this point at age 7.2 y (model parameters: Table 2.1). Energy intake was significantly different between the sexes during their second year of life ($p<0.001$).

Daily food intake expressed as a proportion of body mass decreased with age (Fig. 2.5). Food intake before 1 y of age reflected wild-caught pups that were fed fish, as captive-born animals did not consume significant amounts of fish until weaned at approximately 1 y of age. While the food intake per unit body mass decreased with age, there was considerable variation in this ratio that highlighted a seasonal effect. Seasonal food intake as a proportion of body mass increased in the early winter months and decreased into the spring, and was strongest from age 0.5 to 5 y for both sexes. After this point the pattern dampened, showing yearly oscillations in the food intake at young ages, with higher consumption in the colder months, during which mass steadily increased. Food intake and mass both oscillated seasonally after the animals reach sexual maturity between the ages of 4 - 5 y, thus steadying the consumption per unit body mass relationship of older animals.

Seasonality

Seasonal models fit to pooled yearly length, mass and food intake data for adult animals above the ages of sexual maturity (age 4 y for females and age 5 y for males) showed no significant differences in seasonal length models for males and non-reproductive females ($p>0.05$); nor did inspection of the data reveal any seasonal patterns. However, there were significant seasonal patterns in mass which were captured by the sine equation for males and non-reproductive

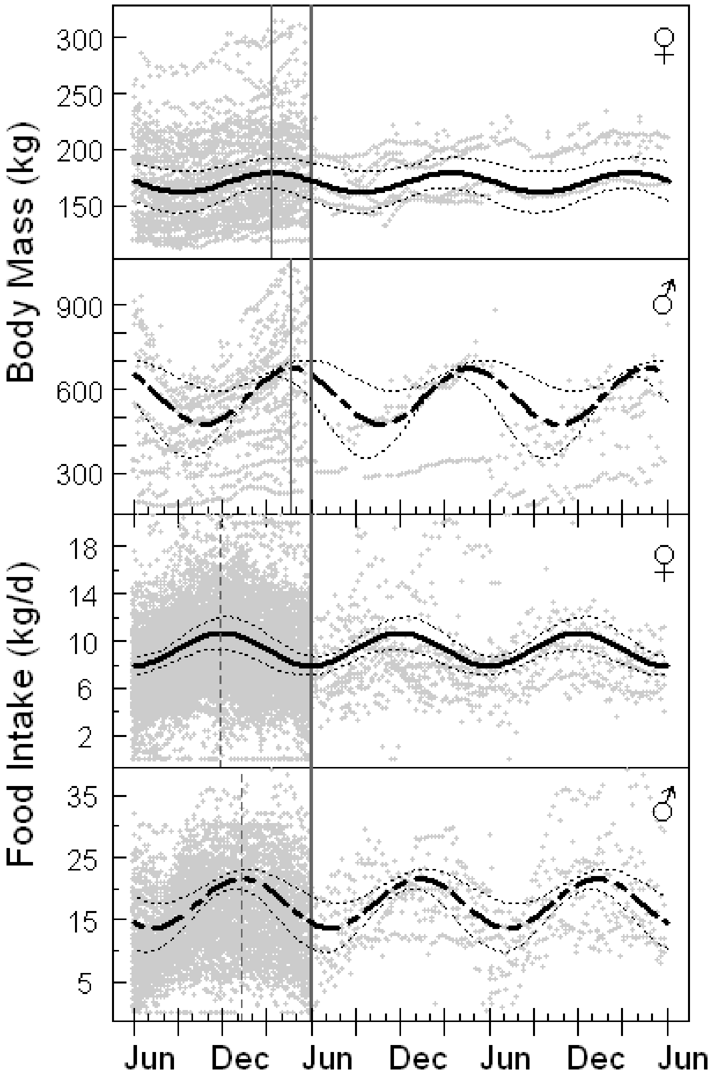

Fig. 2.6: Seasonal body mass (top) and food intake (bottom) of non-reproductive female (solid lines; n_{mass}=21; n_{food}=34) and male (dashed lines; n_{mass}=5; n_{food}=10) Steller sea lions as described by the sine equation fit to data pooled over one year for females ages ≥ 4 y and males ages ≥ 5 y (left-hand panels; Table 2.1). The right-hand portion of each panel shows data from animals ages 7 to 9 y (females: n_{mass}=11, n_{food}=16; males: n_{mass}=4; n_{food}=13) overlaid with the sine equation, demonstrating the sine wave pattern present in the raw data. A small amount of random noise was added to the left-hand panels to reduce data point overlap (random noise was excluded from data analysis). Male mass was highest in late April while females had the greatest mass in early March (vertical solid lines). Peak food intake occurred in late December for males and at the end of November for females (vertical dotted lines). Thin lines indicate 95% confidence intervals.

Table 2.2: Mean, standard deviation and high and low range of body mass (kg) and daily food intake (kg) of female (n_{mass}=21, n_{food}=34) and male (n_{mass}=5, n_{food}=10) Steller sea lions. The range is the mean of the highest 5% and lowest 5% of the values of each age class with data from two or more animals.

	Mass (kg)				Food Intake (kg)			
	Males		Females		Males		Females	
Age (years)	Mean ±SD	Range	Mean ±SD	Range	Mean ±SD	Range	Mean ±SD	Range
0-1	53 ± 17	24-89	51 ± 21	19-122	3.7 ± 1.4	0.1-6.0	3.0 ± 1.3	0.1-6.0
1-2	115 ± 21	85-163	88 ± 19	64-145	5.8 ± 2.2	0.6-11.4	4.6 ± 1.9	0.3-10.8
2-3	151 ± 25	102-209	108 ± 17	79-149	7.9 ± 3.0	2.1-16.6	6.4 ± 2.2	2.0-12.3
3-4	179 ± 40	133-289	128 ± 18	101-178	10.3 ± 4.2	3.4-20.0	7.2 ± 2.3	2.7-13.8
4-5	233 ± 53	157-333	142 ± 17	115-183	11.7 ± 3.8	4.4-21.9	8.0 ± 2.8	2.7-15.2
5-6	278 ± 84	185-463	162 ± 24	121-214	13.0 ± 4.6	4.0-24.9	8.4 ± 2.6	3.1-14.4
6-7	453 ± 77	300-587	171 ± 26	128-221	14.1 ± 4.4	5.3-23.7	7.9 ± 3.0	1.6-14.5
7-8	488 ± 146	289-742	175 ± 22	137-216	16.9 ± 5.7	5.3-26.4	8.7 ± 3.7	2.8-19.8
8-9	567 ± 175	328-909	192 ± 21	158-223	16.7 ± 6.0	5.1-29.5	8.4 ± 2.9	3.2-14.9
9-10	619 ± 162	390-955	197 ± 22	160-229	17.5 ± 8.8	4.0-37.7	8.2 ± 2.5	3.3-14.4
10-11	575 ± 142	394-854	206 ± 26	160-260	16.8 ± 5.7	4.5-26.6	9.2 ± 3.5	2.8-17.3
11-12	677 ± 153	465-1012	215 ± 12	194-237	19.1 ± 7.0	4.2-31.0	9.7 ± 3.6	3.4-17.9
12-13	707 ± 119	526-938	228 ± 20	202-268	16.9 ± 7.4	0.9-29.1	10.0 ± 3.4	3.8-17.9
13-14	759 ± 171	535-1027	257 ± 29	202-301	18.0 ± 6.6	2.6-29.6	10.5 ± 3.5	3.6-17.1
14-15			288 ± 15	267-310	18.7 ± 7.3	4.8-31.3	11.0 ± 4.6	3.3-22.6
15-16			275 ± 20	251-313	19.8 ± 7.8	4.6-33.4	10.9 ± 5.0	2.1-22.2
16-17			266 ± 21	234-304	20.9 ± 7.8	3.7-31.0	10.7 ± 3.5	3.6-18.4
17-18			253 ± 18	229-286	16.7 ± 9.1	0.5-29.3	9.8 ± 3.3	2.3-16.1
18-19			243 ± 8	227-255	20.7 ± 9.0	2.8-33.2	9.9 ± 3.1	3.1-16.1
19-20			249 ± 28	215-302	20.0 ± 8.2	2.9-30.5	9.2 ± 3.9	2.9-15.8
20-21			251 ± 11	238-274	19.0 ± 7.8	2.3-29.8	10.0 ± 3.0	2.2-15.3
21-22			276 ± 35	216-315	19.8 ± 6.8	1.6-29.1	9.7 ± 3.4	3.5-16.7
22-23			267 ± 19	227-287	17.8 ± 6.7	2.2-29.0	10.0 ± 3.9	2.5-19.3
23-24			237 ± 9	229-261			9.3 ± 4.3	0.5-18.5
24-25							9.9 ± 4.3	0.6-17.0
25-26							11.1 ± 6.5	1.0-24.9
26-27							12.5 ± 7.3	0.5-25.5
27-28							11.6 ± 5.9	2.1-19.3
28-29							8.7 ± 4.2	2.6-15.2

females, as shown with the overlapped mass data of animals aged 7 - 8 y (Fig. 2.6). *Animal* was the only significant random effect on all of three fixed effects: A_{mp}, H, and v for both sexes (Table 2.1).

Males were at their peak annual mass at the end of April (Fig. 2.6). The male sine equation predicted a drop of 200 kg from this point until the low at the

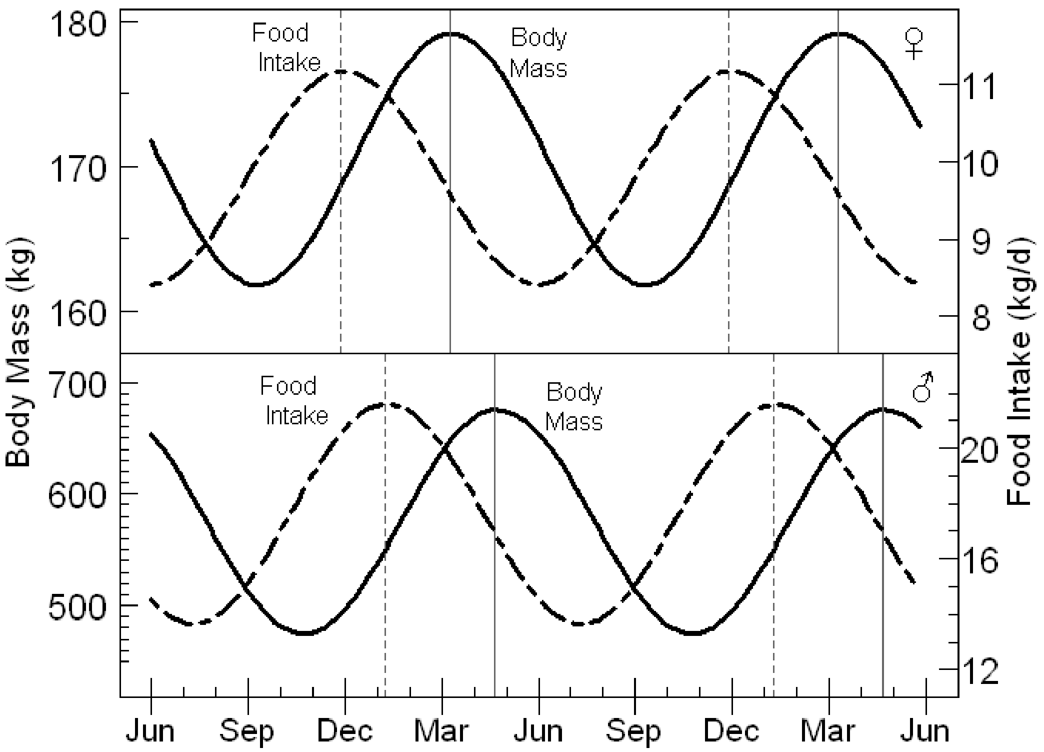

Fig. 2.7: Seasonal body mass (solid line) and food intake (dashed line) of non-reproductive female (top; n_{mass}=21; n_{food}=34) and male (bottom; n_{mass}=5; n_{food}=10) Steller sea lions as described by the sine equation (Table 2.1) over two years. Body mass and food intake highs and lows were offset by ~3 months. Female mass and food intake reached a peak ~1 mo before that of males (mass=vertical solid lines; food intake=vertical dotted lines).

end of October. However, since this reflects an average of all ages, true oscillations were smaller at younger ages, and increased as the animals aged. The top and bottom 5% of asymptotic (lifetime) mass for males and females was averaged and summarized in Table 2.2 to show the true changes in mass throughout each year. Males continued to grow after sexual maturity, gaining approximately 50 kg per year. In addition to this total yearly gain, males oscillated ~225 kg after sexual maturity, and ~450 kg later in life.

Females gained ~10 kg per year in body mass during sexual maturity up to age 14 y, after which there was no absolute mass increase (Table 2.2).

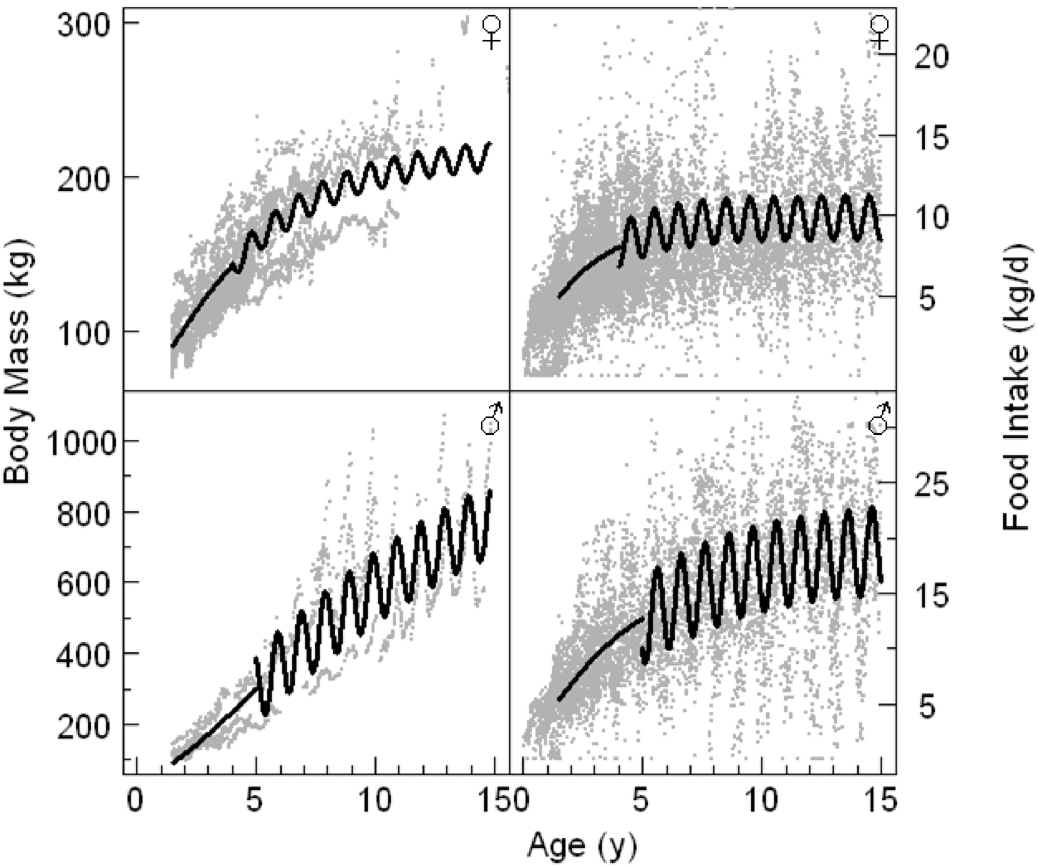

Fig. 2.8: Lifetime body mass (left) and food intake (right) of non-reproductive female (top; n_{mass}=21, n_{food}=31) and male (bottom; n_{mass}=5, n_{food}=12) Steller sea lions as described by the maturity function from age 1.5 to sexual maturity (females=age 4; males=age 5) and a combination of the maturity and sine equations ((maturity+sine)-mean(sine)) after the age of sexual maturity. The combination of these two equations created a model that captured both the moving average and seasonal oscillations present in the data within the limitations of the analysis.

Female mass peaked annually in early March (Fig. 2.6). The sine function predicted mass of females to decrease 16 kg from this point until the beginning of September. But some animals oscillated to a greater degree than predicted by the model because of variation in female mass data. The maximum seasonal oscillation in female mass was ~60 kg per year (Table 2.2).

The pattern in yearly food intake was also well described by the sine function (Fig. 2.6). The random effect of *Animal* was significant on the fixed effects A_{mp}, H and v for males and non-reproductive females (Table 2.1). Male food intake was predicted from the sine function to oscillate ~8 kg per year from the highest point in late December to a low in the end of June. However, fluctuations in yearly intake were larger than predicted by the model, with adult male food intake ranging from 20 to 30 kg (Table 2.2). For females, the sine function predicted a yearly change in food intake of 2.6 kg d^{-1} from their peak in the end of November to a low in late May, which was much lower than the observed range of approximately 15 kg per year after sexual maturity (Table 2.2). These discrepancies reflect the difficulty of the sine function to accurately predict the amplitude of the yearly oscillation in food consumption when data from young and old animals is overlapped.

The timing of peaks in mass and food intake was offset within and among male and female Steller sea lions (Fig. 2.7). Food intake of males peaked almost 4 months before body mass peaked. This lag was slightly shorter among females, whose peak mass occurred 3.5 months after maximum food intake. Steller sea lions of both sexes consumed the most during winter months but were at their maximum weights in early to late spring. Timing of these peaks did differ, however, between the sexes with females reaching their peak mass and food intake ~0.5 months prior to males reaching their peak levels (Fig. 2.7).

The sine functions for mass and food intake data were combined with the maturity models to better predict lifetime mass and fish consumption (Fig. 2.8).

Subtracting the mean of the sine model from the sum of the sine and maturity models for sexually mature animals allowed the sine wave to increase over time. While the amplitude of the sine oscillation for both males and females was smaller than the true yearly change in mass and food intake, the combination of the maturity and sine models better reflected the overall increase in consumption combined with seasonal oscillations in the mass and food intake of Steller sea lions.

Reproduction: weaning

Pups born in captivity were observed to wean at age ~1 y regardless of whether or not their mothers had new pups the following year. Mothers were never observed nursing their one-year-old pup if they had a new pup, although this could have occurred because the animals were not physically separated. The sample size of pups was too low to test whether there was a difference in the mass of pups with and without subsequent siblings, or in the amount of fish consumed by the two groups. Mass was collected from 2 male pups that did not have subsequent siblings, and food intake was collected from 6 male pups of which only one had a sibling the following year. In terms of female pups, only 3 that were weighed had siblings the following year, and only 2 of 12 female pups with fish intake data were followed by a sibling. Significant differences between the two groups could not be detected due to a lack of NLME model convergence.

There was a significant difference in the growth of male and female pups (NLME modeling, $p<0.001$). Pups weighed an average of 20 kg right after birth,

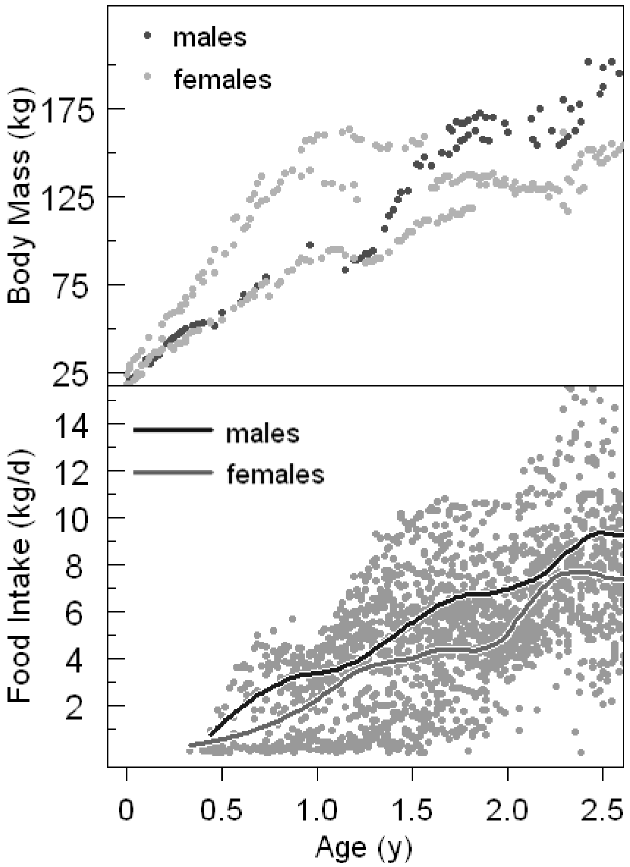

Fig. 2.9: Body mass (top; n=5) and food intake (bottom; n_{female}=12; n_{male}=6) of captive-born Steller sea lion pups. There was a significant difference in mass between male and female pups (p<0.001). Males ate significantly more than females during their second year of life (p=0.004). Food intake only represents the fish consumed by the pups and does not account for milk intake. Male and female food intakes are summarized by LOESS smoothing functions. Most animals were observed to wean at around age 1 y.

with mass increasing rapidly from age 0 to 1 y, and remaining at a plateau until1.5 y before increasing again (Fig. 2.9). Pups were offered fish at a young age, and ate solid food as early as age 0.3 y. The pattern in fish intake was hard to discern for pups, but appeared to increase rapidly after 0.5 y (Fig. 2.9). Food intake differed significantly between male and female pups during their second year of life (p=0.004).

Reproduction: pregnancy and lactation

The pattern in mass and food intake was similar between pregnant and lactating females (Fig. 2.10). Pregnant females were pooled based on stages of pregnancy rather than age because of the asynchrony in the timing of births (pups were born between June and July). They steadily gained approximately 50 kg following implantation of the blastocyst, which occurs approximately three months after fertilization (Pitcher & Calkins 1981), of which the pups accounted for approximately 20 kg (reflected by the sharp drop in mass following parturition; Fig. 2.10). Female mass remained high during lactation, and did not begin decreasing until one year after parturition.

Food consumption by reproductive females was independent of body mass, and showed no large change during pregnancy (Fig. 2.10). In fact, pregnant females decreased their intake leading up to parturition in the spring, and sharply increased their consumption of fish following birth to produce milk needed by their pups. Food intake of nursing females plateaued as the pups began supplemental feeding on fish, and declined to a low the following spring.

Pregnant and lactating female food intake was compared with the data from non-reproductive animals to determine changes in consumption during these periods (Fig. 2.11). Data of food intake ages 1.5 to 4 y from the lactating and pregnant females was incorporated into their respective models to properly anchor starting values. Due to model convergence errors, we were unable to determine if there was a significant difference between non-reproductive and pregnant female consumption. However, their model fits were indistinguishable

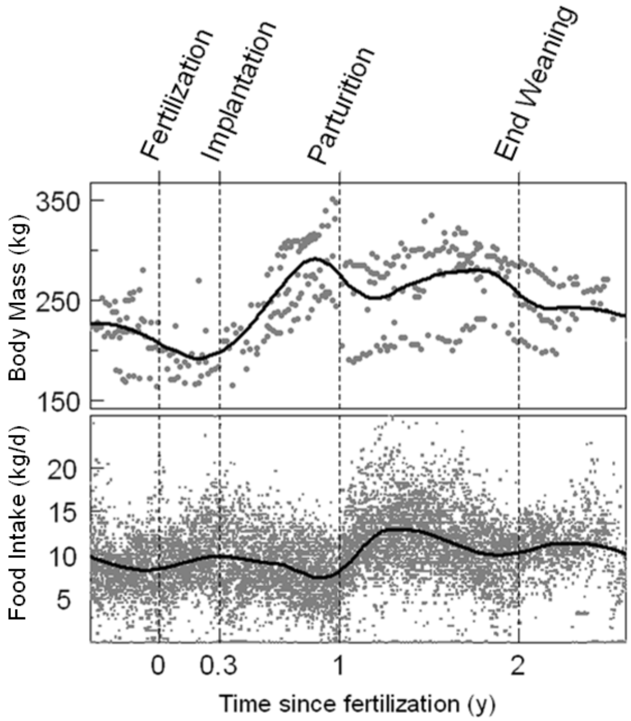

Fig. 2.10: Body mass (top) and food intake (bottom) of three animals (2 animals with two breeding events, 1 with one) with LOESS smoothing functions. The panels are divided into the different stages of pregnancy and lactation. The end of lactation (one year after parturition) is approximate and was based on animal observation.

from each other, and their consumption was similar. Models did show, however, that lactating females significantly increased their food and energy intake by 22% over their non-reproductive and pregnant counterparts ($p<0.001$; Fig. 2.11). Comparing seasonal changes in body mass of females revealed that lactating animals experienced similar seasonal changes as non-reproductive females, with both groups achieving peak mass in the beginning of March (Fig. 2.12). However, lactating animals were approximately 50 kg larger than females without pups. The larger size of lactating females was partly due to weight gained during pregnancy, as well as the fact that the three reproductive animals with mass

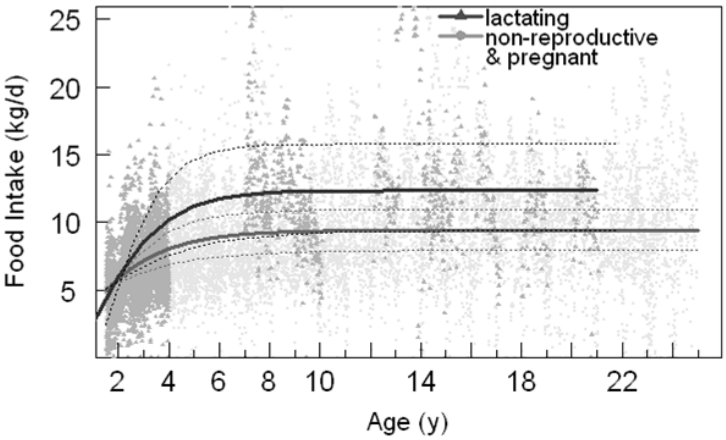

Fig. 2.11: Food intake of lactating (dark points and lines; n_{food}=8) and non-reproductive (gray points and lines; n_{food}=31) female Steller sea lions as described by the maturity equation (Table 2.1). Food intake of pregnant females (Fig. 4) was indistinguishable from non-reproductive animals. Lactating animals, consumed 22% more than pregnant and non-reproductive animals. The lactating model was anchored by including data from the lactating animals while they were juveniles (ages 1.5 to 4 y)

measurements were larger on average as adults than females that never had pups. As expected, pregnant females had a different seasonal mass pattern than lactating and non-pregnant animals, with the peak occurring at the end of April before the spring pupping period.

Only the food intake model for non-reproductive animals was compared with that of lactating animals because non-reproductive and pregnant food intake seasonal models were indistinguishable from one another (Fig 2.12). The minimum food intake for lactating females was similar to that of non-reproductive females at ~9 kg d^{-1}, and reached peak levels in the end of November when lactating females consumed ~15.5 kg d^{-1}. However, peak intake by lactating females was 40% greater than that of non-reproductive and pregnant females

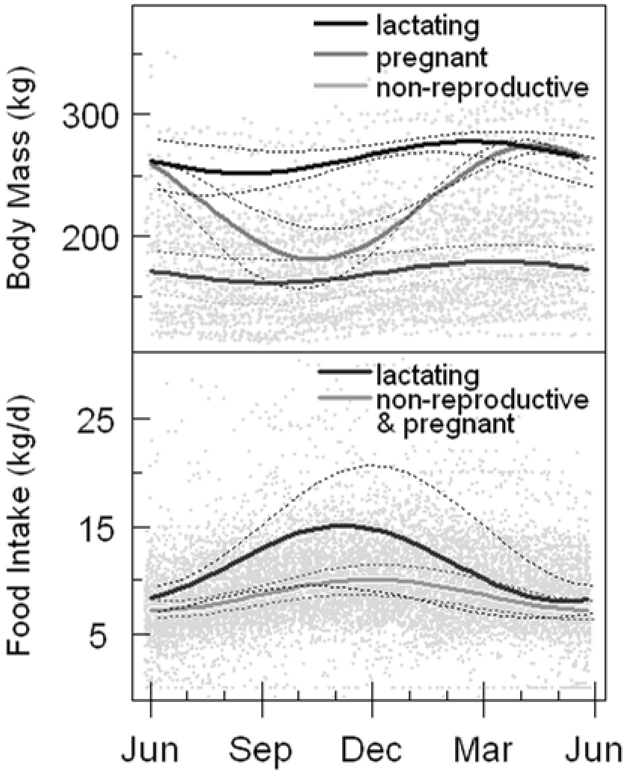

Fig. 2.12: Seasonal changes in body mass (top) and food intake (bottom) of female Steller sea lions during the time they are reproductive and non-reproductive as described by the sine equation (Table 2.1). The top panel shows the different seasonal patterns in body mass of lactating (*n*=3), pregnant (*n*=3) and non-reproductive (*n*=21) animals. The sine function for non-reproductive animals (Fig. 2.6; *n*=34) was compared with lactating animals (*n*=8) because the food intake and models of pregnant and non-reproductive animals overlapped.

during the winter (and averaged ~20% more on average than non-lactating females over the course of a year – Fig. 2.11).

Discussion

In the past, small sample sizes and incomplete seasonal sampling of wild and captive animals provided an incomplete understanding of seasonal growth of Steller sea lions and its relationship with seasonal patterns of food intake

(Kastelein et al. 1990, Nitto et al. 1998, Winship et al. 2001, Winship et al. 2002). Redressing these shortcomings using a large data set of weights, lengths and feeding records from all times of the year for captive Steller sea lions of all ages and reproductive statuses revealed strong seasonal increases and decreases in the mass of males and non-reproductive, pregnant and lactating females, as well as significant oscillations in their respective food intakes. The available data from captive Steller sea lions also showed that patterns of growth and food intake were out of sync with each other, with mass peaking prior to the spring breeding season, and food intake reaching a maximum during winter approximately three months prior to that of mass. Such seasonal increases and losses of mass were apparent for reproductive and non-reproductive individuals, and appear to have been driven by the timing of the breeding season. However, the processes that induced the seasonal increases and decreases in food intake patterns are likely complex.

Our findings provide a better understanding of the life history of Steller sea lions, particularly about the effects of reproduction and seasonality on body size and food intake. They help, for example, to show the varied influences of sexual maturity and potential environmental conditions on the large seasonal oscillations in growth and food consumption, and highlight an apparent discord between seasonal food intake and seasonal growth. They are, however, the findings from captive raised animals and must accordingly be scrutinized to ensure that their applicability to wild sea lions is not affected by potential biases associated with captivity and longitudinal data.

Captive-animal data analysis

We used non-linear mixed-effect (NLME) models to account for autocorrelation and some of the biases that are inherent in all longitudinal data. For example, we included the random effect "*Animal*" into all models to weight the models by the number of animals rather than by the number of data points. We initially suspected research animals at the Mystic Aquarium (MA) and Vancouver Aquarium (VA), as well as wild-born animals fed formula and fish from a young age, to have a reduced body size and a lower food intake compared to display animals and those that suckled from their mothers. However, adding random effects "*Aquarium*" or "*Birthplace*" to the models showed these factors to be insignificant. While there was evidence that the display-only animals at Dolfinarium Harderwijk (DH), Futami Sea Paradise (FSP) and Kamogawa Sea World (KSW) were larger and consumed more fish and energy than research animals at VA and MA, the amount of within-animal variation accounted for by "*Animal*" negated the effects of "*Aquarium*" and "*Birthplace*". Incorporating such random within-animal variation within the NLME models strengthened their applicability to other populations of Steller sea lions.

Two sources of biases could not be accounted for using NLME modeling: the relatedness of animals and the effect of captivity on food intake (Appendix 1). Growth of all animals is affected by both genetic and environmental influences (Lindström 1999), which means that it is possible for the growth of related sea lions (i.e., adults and their offspring) to be more similar than that of unrelated individuals. In our case, we suspect that homogeneity in growth and food intake of related animals would have been negated by the high amount of variation attributable to differences in weather, food supply and training protocols that occurred with time at each aquarium. This would have reduced any potential effect of relatedness on model predictions, as would our large sample sizes (which would carry greater weight in model predictions than the small similarities that might have been present between related animals). Thus environmental influences and large sample sizes lead us to believe that relatedness of individual sea lions did not have a measurable influence on the results of the growth and food intake models.

The other major potential bias we could not control for concerns the reduced food intake of sea lions in captivity relative to sea lions in the wild. Bioenergetic models predict that wild male Steller sea lions on a mixed diet require approximately 20 kg of fish per day as juveniles and 30 kg d^{-1} as adults. In contrast, pregnant females require 6 kg d^{-1} (during the breeding season) to 17 kg d^{-1} of fish (during winter), while lactating females require an additional 5 to 25 kg d^{-1} from parturition to the next breeding season (Winship et al. 2002). Models parameterized from studies of captive, non-reproductive females trained to dive repeatedly up to 30 m resulted in similar predictions in daily food requirements to those of wild, pregnant females (Hastie et al. 2006). However, these estimates of energy requirements for wild sea lions and those trained to swim freely are 50% higher than our modeled asymptotic food consumption for captive males, and are 64% higher for lactating females, and 47% higher for pregnant and non-reproductive females.

Differences in energy content of the diets can explain much of the difference between mass of food consumed by captive sea lions and that predicted by models for wild sea lions: captive animals consumed fish that had an average energetic density of 7.7 kJ g^{-1}, while the bioenergetic model assumed an average energy density of 5.1 kJ g^{-1} — 33% lower (Winship et al. 2002). The bioenergetic model and our estimates of energy density of prey for animals housed at DH, FSP and KSW assumed the dietary energy density remained constant, and were found to change only slightly over time in fish consumed by animals housed at VA and MA. Thus, approximately one-half to one-third of the difference between captive Steller sea lion consumption and predicted wild animal intake can be explained by differences in fish energy density, depending on the sex and breeding status of the animals.

The remaining 15 – 30% difference in food intake between captive and wild animals may be accounted for by differences in activity between the two groups and/or by error in the estimate of the activity costs for wild animals. Captive Steller sea lions likely had lower activity levels than their wild counterparts because they did not have access to deep water for diving and did not have to forage for food. Activity costs for wild Steller sea lions are assumed in bioenergetic models to be 1.2 times higher than basal metabolic rate while sea lions are on land (although this tripled in breeding males), and 4 times higher while in the water, resulting in a 70% increase in metabolism while swimming (Winship et al. 2002). Combining information on activity costs and time spent at sea (~77% of the year for females and 71% for males) results in a 50% increased energy need over animals that theoretically remained on land year-round. This estimate is higher than the 15 – 30% difference in food requirements of wild and intake of captive Steller sea lions, and suggests that captive sea lions probably had activity levels between that of on-land and at-sea animals.

Another explanation for the apparent discrepancy in food intake between captive and wild Steller sea lions is the possibility that the assumed activity levels of wild animals are incorrect. Activity is the most difficult parameter to measure in wild animals, and has the largest effect on uncertainty in model estimates of food consumption (Winship et al. 2002). Captive studies have shown that seals and sea lions can evoke energy saving mechanisms while foraging. For example, captive gray seals diving in a shallow pool have lower diving metabolic rates (DMRs) than predicted by activity multipliers, suggesting that wild animals may expend less energy and require less food than predicted by bioenergetic models (Sparling & Fedak 2004). Similarly, captive Steller sea lions trained to dive up to 50 m are less active during deep dives because they passively glide below depths of 5 m (Fahlman et al. 2008a). Gliding offsets the cost of having to actively swim to return to the surface (Fahlman et al. 2008a), and metabolic depression further reduces the cost of foraging during repeated diving bouts (Hastie et al. 2007, Fahlman et al. 2008b). This suggests that the simple multipliers used in models to estimate the energetic cost of foraging activity may be higher than necessary.

These studies of captive seals and sea lions demonstrate the difficulty of measuring activity costs, and show how Steller sea lions and other pinnipeds can reduce their expenditures through behavioral and metabolic adjustments. In our case, it appears that the decreased activity of captive animals and overestimated cost of activity of wild Steller sea lions can account for a significant portion of the difference we noted between the food intake of our captive animals and the predicted requirements of the wild sea lions. Further study into activity costs through captive animal diving experiments or through the use of biotelemetry (e.g., Cooke et al. 2004) may help to determine the metabolic effects of activity, and provide insight into its effects on food consumption.

Our food intake models express the actual amounts of prey consumed by the sea lions we studied as opposed to the generalized bioenergetic models that predict how much sea lions might eat in the wild. Our equations cannot therefore be used as a measure of the absolute amounts of prey consumed in the wild due to differences in activity levels and average energy densities of prey consumed by wild and captive animals. It should also be noted that we depicted seasonal changes in mass and food intake using a sine equation that inherently assumed that growth and consumption increased for 6 months of the year and decreased in the same time increment. We tested the validity of this assumption by visually inspecting the seasonal models fit to individual animal data (not shown) and the pooled data (Figs. 2.6, 2.8 and 2.12) and concluded that the symmetrical periodicity we imposed on the data was reasonable. As such, we feel our equations are useful to describe seasonal patterns in fish consumption (timings and relative amounts), and that these seasonal oscillations may be representative of patterns that occur in the wild.

Seasonal and reproductive effects on size

Previous studies that have modeled pinniped growth have tended to exclude data from young animals because growth functions cannot properly fit both pup and adult growth (e.g., McLaren 1993). In our case, we used two equations (one for pups younger than age 1.5 y and the second for juveniles and adults above age 1.5 y) that resulted in smaller residuals, thus better model fits compared to fitting a single model to all age groups. Juvenile growth in length and mass of Steller sea lions (Figs. 2.1 and 2.2) was rapid and almost linear, with males being significantly heavier starting in their first year, and significantly longer starting in their second year compared to females (Figs. 2.1 and 2.2). Field measurements indicate that male pups are heavier and longer on average than females at birth (Merrick et al. 1995, Ono & Boness 1996, Brandon et al. 2005). Our models showed greater growth rates among male pups, but failed to detect a difference in size at birth due to low statistical power associated with our relatively small sample sizes of captive-born pups.

Steller sea lions and otariids in general are among the most sexually dimorphic species (Weckerly 1998, Cassini 1999). The significant difference in growth between males and females presumably reflects the advantage that larger males have when competing with other males and defending large harems while fasting. Large size in females may provide a similar selective advantage if it confers greater ability to provide for young through enhanced foraging ability and higher body stores (Beauplet & Guinet 2007). Female growth in body length slowed after age 5.5 y, with females attaining 90% of their asymptotic length by age 5.4 y (Fig. 2.1). The first successful pregnancy in a captive female Steller sea lion occurred at age 4 y in our data set. Primiparity has been recorded as young as 3 y among wild Steller sea lions with an average age at first birth of 5 y (Pitcher & Calkins 1981). Increases in body mass of females continued until age 9 y (Fig. 2.2). These patterns of length and mass growth of captive female sea lions were similar to those reported for wild Steller sea lions (McLaren 1993, Calkins et al. 1998, Winship et al. 2001).

Male Steller sea lions took significantly longer to reach their adult size than did females, resulting in sexual size dimorphism. Males reached 90% of their asymptotic length at age 8.2 y (Fig. 2.1) with mass continuing to increase until ~22.7 y (Fig. 2.2). Males also experienced an increase in mass growth between the ages of 5 and 7 which further widened the gap in size between the sexes (Fig. 2.2) as also noted in studies of wild sea lions (Fig. 2.2, McLaren 1993, Calkins et al. 1998, Winship et al. 2001). This growth spurt was reflected in two distinct phases in the length-mass relationship of males that diverged at approximately age 5.5 y (225 cm; Fig. 2.3). Male sexual maturity is thought to be achieved between the ages of 5 to 7 y and bacular size and density increases rapidly during these years (Pitcher & Calkins 1981, Miller et al. 2000). Successful mating occurred among our study animals in a male aged 5 y, which likely occurred as a result of captive conditions and the absence of male-male competition since wild males are believed to reach socially mature size at age 9 y and older (Pitcher & Calkins 1981, Gisiner 1985). Overall, the growth equations describing changes in body length of captive male Steller sea lions were similar to those for wild animals, but the equation describing annual increases in mass had a much higher asymptote than that of wild males (McLaren 1993, Calkins et al. 1998, Winship et al. 2001) due to the inability of our model to accommodate an autocorrelation function (which could have inflated the asymptote).

Diverse groups of sexually dimorphic mammals exhibit similar patterns of mass gain and loss to those we found for male and female Steller sea lions, including the ungulates (e.g. roe deer, *Capreolus capreolus*; Hewison et al. 1996), rodents (e.g. voles, *Myodes rutilus*; Zuercher et al. 1999), primates (e.g. female gray-cheeked mangabeys; *Lophocebus albigena*; Deputte 1992 & mandrills, *Mandrillus sphinx*; Setchel et al. 2001) and ursids (e.g. black bears, *Ursus americanus*; Mahoney et al. 2001). In sexually dimorphic groups, females tend to slow growth following sexual maturity and possibly direct this energy to cover their high reproductive costs, while males have no parental care costs and can devote this energy to continued growth to achieve a large size for successful breeding (Weckerly 1998, Cassini 1999, Isaac 2005). Females may maximize fitness by switching resource allocation from growth to reproduction following sexual maturity, although large size in females has been correlated with higher pup survival in pinnipeds (Gaillard et al. 2000, Beauplet & Guinet 2007). Large size in males is likely a consequence of the increased reproductive benefits it confers during male-male competition. However this is not the only influence on large male size since the most polygynous species are not necessarily the most sexually dimorphic, possibly because achievement of large size may be constrained by additional maintenance costs (Cassini 1999, Lindenfors et al.

2002, Isaac 2005, McKenzie et al. 2007). Thus, the driving forces of sexual dimorphism are varied, but likely include the need for large size in competitive encounters in males, and an interaction between energy devoted to reproduction and to growth in females.

The seasonal changes in mass (Fig. 2.6) meant that the calculated degree of sexual dimorphism was not constant through the year. Sexual dimorphism was highest in the breeding season (males were ~3.8 times the mass of females) when the mass of males and females were at their maximum, and was lowest in late fall when both sexes were at their seasonally lowest masses (~2.9 times). These differences make them one of the most sexually dimorphic otariids, eclipsed only by northern fur seals in which males are 3.4 times heavier prior to mating and 5.4 times bigger during the breeding season (Trites & Bigg 1996). While elephant seals (*Mirounga angustirostris* and *M. leonina*) are the most sexually dimorphic of all pinnipeds, most phocids have low or no sexual dimorphism (Cassini 1999, Lindenfors et al. 2002).

The extent of sexual dimorphism among primates and ruminants has been linked with the degree of polygny and the amount of male-male competition (Plavcan & Van Shaik 1997, Weckerly 1998, Setchell et al. 2001, Isaac 2005). This likely holds true for pinnipeds given that higher degrees of sexual dimorphism appear to occur among species such as elephant seals, fur seals and sea lions that aggregate on land (Cassini 1999, Lindenfors et al. 2002). Aggregation can maximize the availability of resources to breeding females and newborn pups while producing male-male competition and increased polygny.

The males in our study and in other data sets also had larger changes in mass on a seasonal basis than females, providing further support that selection pressure on male size produces sexually dimorphic patterns in pinnipeds (Cassini 1999, Lindenfors et al. 2002).

Seasonal changes in length and mass is another element of growth related to reproduction. Seasonal fluctuations in body length have been observed in measurements taken from shot pinnipeds (Trites & Bigg 1996, Winship et al. 2001, Chabot & Stenson 2002). Seasonal peaks in body length appeared to occur prior to the breeding period but were attributed to increases in body water content and seasonal increases in body mass (such as pregnancy and fattening over the winter) that displaced and stretched the spines of the animals measured (animals were measured belly up on measuring boards; Trites & Bigg 1996, Winship et al. 2001, Chabot & Stenson 2002). We did not detect similar oscillations in our length measurements because of our small number of measurements and our method of measuring length of animals belly down. We did, however, find significant seasonal patterns in the mass growth of both sexes (Fig. 2.6).

Males gained mass as expected from the end of October to late April prior to the breeding season, and lost mass during the other six months of the year (Fig. 2.6; Nitto et al. 1998, Winship et al. 2001). These fluctuations likely reflected gains and losses of blubber that male pinnipeds stored prior to breeding and used while fasting during the breeding season (Chabot & Stenson 2002, Beck et al. 2003). However, our models failed to adequately describe the rapid loss of mass of wild sea lions following breeding because the sine equation we used assumed symmetrical seasonality (Nitto et al. 1998, Winship et al. 2001). Our males may have buffered their mass loss by consuming small amounts of fish during the breeding period (Fig. 2.6) compared with wild males that likely lost mass more rapidly during breeding because they likely fed more infrequently (Mathisen et al. 1962, Pitcher et al. 2000, Winship et al. 2002). Our models also predicted lower magnitudes of seasonal oscillations in mass of mature bulls than likely occur in the wild due to pooling data from younger, smaller animals with older, heavier males (Table 2.2).

Large body size is a determinant of reproductive success in pinnipeds and other polygynous mammals, and large males are most often noted as harem-masters (Haley et al. 1994, Modig 1996, McElligott et al. 2001, Setchell et al. 2001, Isaac 2005, Carlini et al. 2006). The seasonal patterns in body size noted in our study occurred even in males with no direct access to females, although the scent or sound of females in the vicinity may have been detected by the males. While it is possible that these patterns arose from female cues, evidence from other seasonally breeding mammals highlight the importance of photoperiodic control or endogenous rhythms on the timing and magnitude of mass changes in males (Dark & Zucker 1985, Loudon 1994, Mercer 1998).

Seasonal and reproductive effects on food intake

Captive animals and bioenergetic models have been the only means to estimate the amount of food consumed by wild marine mammals (Kastelein et al.

1990, Winship et al. 2002). However differences between the activity levels of captive and wild animals (as well as differences in the environmental conditions they experience) preclude using the amounts of food consumed by captive animals as absolute values for their wild counterparts (see above discussion). Instead, the food intake of captive animals is more useful to understand seasonal patterns in food consumption and its relationship with growth and reproduction given that food was offered to the captive Steller sea lions relative to their levels of hunger and interest in eating (except for infrequent, short-term feeding experiments conducted at VA and MA) (Renouf & Noseworthy 1990, Renouf et al. 1993, Rosen & Renouf 1998, Williams et al. 2007). In our study, food intake was directly proportional to energy intake because the latter was determined as a function of the former. The two terms can thus be used interchangeably in terms of our treatment of ingestion.

Most of the pups in our study began supplementing their milk intake with fish at age 0.5 y, and weaned at 1 y (Fig. 2.9). In the wild, most pups are believed to wean at 1 y, with some pups remaining with their mothers until 3 y of age (Raum-Suryan et al. 2004, Trites et al. 2006). Differences in the age at weaning in the wild is believed to reflect the quality of prey available to young sea lions given that pups eating fish can become satiated before consuming enough energy to meet their daily needs (Winship et al. 2002, Rosen & Trites 2004, Trites et al. 2006). The early age of weaning found in our study likely reflects the high quality of prey offered to the captive born sea lion lions and the lack of foraging required to obtain and consume this prey. Weaning among the captive animals appeared to be associated with growth plateauing at age 1 to 1.5 y (Fig. 2.9). This may reflect energy intake or it may be a natural phenomena similar to the decreases in pup weight of weaned Subantarctic (*Arctocephalus tropicalis*) and Antarctic fur seals (*Arctocephalus gazelle*) (Kerley 1985). Unfortunately, the small sample size in captive pup masses precluded us from further exploration of this pattern.

Juvenile sea lions of both sexes had a higher food intake as a proportion of body mass compared to adults, and decreased their proportional food intake from age 0.5 y to ~5 y (Fig. 2.5). This decrease in food intake corresponded to growth slowing with age, which constitutes the largest portion of their energy requirements of immature animals in captivity and in the wild (Winship et al. 2002). Males reached 90% of their asymptotic food consumption at age 7.1 y, at approximately the same age that they reached 90% of their asymptotic length but about 15.5 years before they reached 90% of their asymptotic mass (Fig. 2.4) Similarly, non-reproductive females reached 90% of their asymptotic food intake at age 4.8 y, one year before reaching 90% of their length, and 5 years before reaching 90% of their mass.

Food intake was not constant throughout the year but showed large seasonal patterns in males and non-reproductive females. Juvenile animals aged 1 to 5 y increased their energy intake in the winter (Fig. 2.5), possibly due to higher thermoregulatory costs incurred by smaller animals with greater surface area to volume ratios (Kleiber 1975, Donohue et al. 2000). Juvenile males tended to consume more than females, with adult males consuming over 40%

more fish than adult females. The sexually mature males increased their consumption from a low of 14 kg d^{-1} in late June to a peak of 22 kg d^{-1} at the end of December, while non-reproductive females increased their intake from an estimated 8 kg d^{-1} at the end of November to 11.6 kg d^{-1} in late May (Fig. 2.6), although actual changes in intake were higher than predicted because consumption by mature and immature animals were combined (Table 2.2). Reduced consumption is common among pinnipeds while breeding on land or ice because males spend time defending territory while females in the first few weeks following parturition spend time attending to their pups (Kastelein et al. 1990, Renouf & Noseworthy 1990, Renouf et al. 1993, Rosen & Renouf 1998, Winship et al. 2002). Seasonal food intake patterns in males and non-reproductive females are likely driven by the combined influence of reproductive behavior and decreased thermoregulatory costs in spring and increased thermoregulatory costs in winter.

Food intake patterns may be partly explained by endogenous processes that prepare pinnipeds for reproduction, given that our captive males and females experienced reduced food intake despite being offered fish during the breeding period (Miquelle 1990, Ryg & Øritsland 1991). This pattern of reduced food intake during the reproductive period is common in seasonal breeders, especially male rodents, ruminants and pinnipeds who decrease food intake during the breeding season regardless of the presence of food that is either offered by researchers in captive conditions or supplemented in wild populations (Dark & Zucker 1985, Miquelle 1990, Renouf & Noseworthy 1990, 1991, Loudon 1994, Kastelein et al. 1995, Mercer 1998, Nitto et al. 1998, Kastelein et al. 2000a, Kastelein et al. 2000b, Kastelein et al. 2005). While the control of appetite suppression is poorly understood, the voluntary reduction in consumption demonstrated by male animals in our study was likely controlled by physiological processes that decreased the urge to forage and feed in order to provide time for mating behaviours (Miquelle 1990). Similar controls are likely in place for females in order to prepare for the breeding season, as the small drop in female food intake during spring noted in our study has been found in other captive pinnipeds and is timed with ovulation in captive Pacific walruses (Renouf & Noseworthy 1990, 1991, Kastelein et al. 1995, Kastelein et al. 2000b, Kastelein et al. 2005, Williams et al. 2007).

Non-reproductive female Steller sea lions whose food intake was greatly reduced lost less mass during summer than winter demonstrating a physiological adaptation to severe restrictions in energy consumption during the summer breeding season (Rea et al. 1999, Kumagai et al. 2006, Rea et al. 2007). Reduced food intake during the breeding season may be cued by photoperiod, as seen in other mammals in seasonal environments (Dark & Zucker 1985, Loudon 1994, Mercer 1998). Captive South American fur seals (*Otaria flavescens*) housed in the northern hemisphere experienced reductions in food intake during breeding that were offset 6 months from the breeding season of wild animals in the southern hemisphere (Kastelein et al. 1995). Steller sea lions likely compensate for reduced food intake during the breeding season by increasing consumption following this period (Winship et al. 2002).

Reasons for the pattern in food increases following the breeding season are less understood, but are similar to those noted for many other pinnipeds and may include growth, thermoregulation and activity (Renouf & Noseworthy 1990, 1991, Kastelein et al. 1995, Kastelein et al. 2000a, Kastelein et al. 2000b, Kastelein et al. 2005, Williams et al. 2007). Some of the energy ingested by our study animals was likely incorporated into increased mass growth during late winter (Fig. 2.7), specifically gains in fat since this is commonly stored by pinnipeds, especially phocids, and used as insulation for thermoregulation in the colder winter months and as metabolic fuel during periods of low energy intake in the spring and summer (Renouf & Noseworthy 1991, Renouf et al. 1993, Beck et al. 2003, Jeanniard du Dot et al. 2008). Steller sea lions have a smaller blubber layer than phocids but they do increase fat stores from winter to spring, especially in males, and conserve their blubber layer preferentially in the winter (Pitcher et al. 2000, Kumagai et al. 2006, Rosen & Kumagai 2008).

The rise in food intake found in our study could also result from increased activity levels in winter, which occur in captive non-reproductive female California sea lions (*Zalophus californianus*) from November to March (although lactating females reduced activity during this period) (Williams et al. 2007). Increased activity levels are found in Steller sea lions exhibiting a “hunger response” during energy reduction experiments, presumably a behaviour that would increase foraging and thus energy intake in wild animals (Jeanniard du Dot et al. 2008 2002). Wild lactating Steller sea lions forage for longer periods of time and over a larger range in the winter, likely due to both the greater dispersion and lower energetic content of fish in the winter and higher energetic intake requirements (Merrick & Loughlin 1996, Anthony et al. 2000, Trites & Porter 2002, Trites et al. 2006). While it is curious that Steller sea lions would increase food intake during a time when most fish are more dispersed, recent diet information suggests that high-fat sand lance and herring may be important components of wild Steller sea lion diet during the non-breeding season (McKenzie & Wynne 2008). Thus, it is possible that we see longer foraging periods in winter in wild females because they are consuming a large amount of higher-fat fish, as opposed to the original hypothesis that females spend a longer time foraging in winter because prey is more difficult to capture (Merrick & Loughlin 1996, Anthony et al. 2000, Trites & Porter 2002, Trites et al. 2006).

There is always the possibility that the increase in fish intake we recorded during winter is unique to captive Steller sea lions and does not occur among wild animals. However, the prevalence of wintertime increases in fish consumption has been documented in other captive species of marine mammals (Renouf & Noseworthy 1990, 1991, Kastelein et al. 1995, Kastelein et al. 2000a, Kastelein et al. 2000b, Kastelein et al. 2005, Williams et al. 2007). Food restriction studies of Steller sea lions further indicate that winter is a time of greater fish intake needs (Rea et al. 1999, Kumagai et al. 2006, Rea et al. 2007, Jeanniard du Dot et al. 2008). Such findings support our conclusion that winter is a time when this species is likely to naturally increase their food intake. Unfortunately, it has not been possible to collect similar data from the wild to independently validate our conclusion. Such findings highlight the importance of conducting further captive and wild-animal research on the driving forces of fish consumption so that the basis for these patterns can be better understood.

Pregnancy does not seem to be energetically costly in Steller sea lions. Food intakes of pregnant and non-reproductive females were similar in terms of annual and seasonal consumption (Figs. 2.11 and 2.12). This was consistent with predictions from bioenergetic modeling that show little additional energetic cost for a female Steller sea lion to carry a fetus to term (Winship et al. 2002). While the cost of gestation is not well understood in other pinnipeds, it is estimated to be quite low with respect to overall reproductive expenditure (Winship et al. 2002, Williams et al. 2007). Captive California sea lions (*Zalophus californianus*) in the final stages of pregnancy remained more sedentary than non-reproductive females as a possible mechanism to reduce food intake needs during this likely energetically costly time (Williams et al. 2007). Our data showed that pregnant sea lions reduced their food intake in the weeks prior to birth (Figs. 2.10 and 2.12) as has been demonstrated for other species of captive pregnant otariids (Kastelein et al. 1990, Williams et al. 2007), but activity levels were not measured in our study.

Pinniped lactation is broadly recognized to be the most energetically expensive portion of female life history (Boness & Bowen 1996, Boyd 1998, Winship et al. 2002, Williams et al. 2007). Overall, lactating females in our study consumed 20% more fish on average than pregnant and non-reproductive animals (Fig. 2.11), similar to that noted in captive lactating California sea lions (*Zalophus californianus*; Kastelein et al. 2000a, Williams et al. 2007). However, lactating animals were also ~50 kg heavier than non-reproductive animals, which could increase their consumption. When expressed as a mass-corrected value, non-reproductive females consumed 0.041 kg of fish per kg body mass, while lactating females consumed 0.047 kg per kg mass, resulting in a 13% increase that was significantly different between the two groups ($p<0.001$). Mass-specific percentage increases were 16–17% depending on scaling mass$^{-0.67}$ or mass$^{-0.75}$. Thus the increase in lactating female food intake was in addition to larger body mass, but was not distributed uniformly over the year. The difference in food intake began in late summer after the pups were born and increased to a peak of 40% greater intake than non-lactating individuals in late November before falling in the spring to approximately the same level as pregnant and non-reproductive animals (Fig. 2.12). A bioenergetic model of wild Steller sea lions estimated that lactating females require 70% more fish during lactation than females of a similar age, with lactation costs continuously increasing throughout the whole lactation period (Winship et al. 2002).

The observed change in calculated costs of lactation was likely the result of seasonal and developmental variation in costs of maintaining a growing pup. As pinniped pups age, their milk consumption increases to meet the rising energy demands from growth, thermoregulation and activity (Bowen et al. 2001, Donohue et al. 2002, Winship et al. 2002). This can explain the increase in lactating female fish intake in late summer and early winter. The captive pups began supplementing their milk intake with fish as early as age ~0.5 y (Fig. 2.9) which may have reduced their milk consumption, resulting in the decreased intake of their mothers in late winter and spring (Fig. 2.12), despite the potential for continuing high costs of thermoregulation. Wild Steller sea lions pups are known to be able to capture prey but it is not clear what extent these fish contribute to their energy requirements (Raum-Suryan et al. 2004, Trites et al. 2006). In all likelihood, the supplemental fish intake noted in our study may reflect the fact that pups were being offered fish as opposed to wild pups that would have to capture and handle prey items.

One benefit of using captive data from lactating animals is that the increase in food (and thus energy) consumption above that of non-reproductive females reflected the true energy intake required to produce enough milk to raise a weaned pup in captivity in the span of one year (the weaning period noted in our study), since these females did not incur the cost of foraging. Averaged across a year, lactating females consumed 1,058 kg more fish during the year-long lactation period than non-reproductive females (Fig. 2.11). Using our fish energy density estimate of 7.7 kJ g^{-1} and a lactation period of 365 days, lactating females consumed an additional 22.3 MJ d^{-1} or 8,150 MJ to support their pup, a daily mass-specific rate of 0.08 MJ kg $^{-1}$ (divided by average lactating female mass from Fig. 2.12). Because lactation is estimated to increase fish consumption by 70% in wild Steller sea lions (based on a bioenergetics model; Winship et al. 2002), and the captive sea lions increased their consumption by 20%, the total energy invested by a wild female into her pup would appear to be 3.5 times our calculations.

In general, otariids and phocid seals employ different lactation strategies, due in part to differences in size and food availability (Boness & Bowen 1996, Boyd 1998). Most phocids are capital breeders that store energy in internal reserves that are depleted during the relatively short lactation period. Conversely, otariids are income breeders, and forage to meet lactation demands in an extended lactation period (Boyd 1991, Boness & Bowen 1996). In theory, females that forage during lactation have low daily expenditures but incur lactation costs over a longer period of time, while capital breeders that remain on land or ice during lactation incur high daily costs but over a shorter length of time. For example, in the Antarctic fur seal (*Arctocephalus gazella*, an income breeder) total food energy required to produce a pup during their 4 month lactation period is estimated to be 3,710 MJ, corresponding to 30.4 MJ d^{-1} or 0.79 – 0.80 MJ $kg^{-1}d^{-1}$ (Arnould 1997). In contrast, hooded seals (*Cystophora cristata*) are capital breeders, and lose 216.3 MJ d^{-1} of body energy during their 4 day lactation period, corresponding to ~0.9 MJ $kg^{-1}d^{-1}$ (Mellish et al. 1999). Steller sea lions have one of the longest lactation periods, which is reflected in low daily maternal input values but high overall energy expenditure (this study, Boness & Bowen 1996). This pattern is fairly universal over all pinniped species, and thus it appears that females that forage during lactation have low daily expenditures but incur lactation costs over a longer period of time, while pinnipeds such as the hooded seal that remain on land or ice during lactation incur high daily costs but over a shorter length of time (Boness & Bowen 1996).

Large body size, and thus capacity to store energy in preparation for periods of low food availability or reduced ability to forage, generally produce a capital breeding pattern like that of hooded seals since prey resources are not predictable and thus may not be exploitable during lactation but may be available intermittently and stored as blubber in preparation for breeding (Boness & Bowen 1996, Boyd 1998, Mellish et al. 1999). Small body size and greater predictability and availability of fish are generally found in income breeders, patterns which fit Antarctic fur seals well (Boness & Bowen 1996, Arnould 1997, Boyd 1998). Under these conditions, Steller sea lions match a capital breeding model better as they are both large and are in close proximity to prey resources during the spring and summer months. However since they are income breeders these criteria must not fully account for all factors influencing the evolution of reproductive behavior (Boness & Bowen 1996, Trillmich & Weissing 2006).

Steller sea lion prey resources are believed to be more aggregated, available and contain higher energy in the summer but are more dispersed and of lower energy density over winter (Anthony et al. 2000, Kitts et al. 2004, Sigler et al. 2004, Womble et al. 2005). Pups wean at age 1, 2 or 3 y prior to the breeding season (Raum-Suryan et al. 2004, Trites et al. 2006) which may allow them to maximize foraging success on more available, higher energy prey since they would wean in late summer or fall in a capital breeding system, and would have to learn to forage on more dispersed prey resources. Thus, the reproductive strategy of Steller sea lions maximizes pup survival (Boness & Bowen 1996, Trillmich & Weissing 2006).

Timing of seasonality in mass and food intake

Food consumption peaked ~4 months before seasonal body mass peaked in all the captive Steller sea lions (males and non-reproductive, pregnant and lactating females; Fig. 2.7). Similar asynchrony between mass and food intake has been reported for other captive otariids (Kastelein et al. 1990, Kastelein et al. 2000a, Williams et al. 2007), as well as for captive phocids (Renouf & Noseworthy 1990, 1991, Renouf et al. 1993, Rosen & Renouf 1998). Food intake and mass gains of harbor seals (*Phoca vitulina*) appear to be negatively correlated or uncoupled throughout the year, resulting in seasonal patterns in mass that are shifted 5 to 6 months ahead of food cycles (Renouf & Noseworthy 1990, 1991). The offset between mass and food intake may be shorter for otariids compared to phocids because otariids store less blubber and may have to consume more food (i.e., energy) to offset thermoregulatory costs during the winter, whereas phocid seals can rely on their internal reserves during periods of low energy (Costa & Williams 1991, Rosen & Renouf 1997). Thus, this offset pattern in mass and food intake is not unique to phocids, but appears to be also present in otariids such as the Steller sea lion.

This uncoupling of the mass and food intake cycles could occur through behavioural changes or by a shift in energetic priorities that allow mass gain during periods of reduced food intake. Pinnipeds may depress their resting metabolic rate (RMR) during periods of low energy intake, but because RMR does not incorporate a large portion of their energy output this is not likely to result in large savings (Renouf & Gales 1994, Rosen & Renouf 1998, Rosen &

Trites 1999, Winship et al. 2002). They are also able to adjust digestive efficiency in order to increase protein and lipid assimilation when consuming lower energy prey items. However, this result may be confounded by the amount of energy ingested, as digestive efficiency also increases when animals are maintained on below-maintenance energy diets (Lawson et al. 1998, Rosen et al. 2000, Trumble et al. 2003). Pinnipeds faced with increased energy demands or expenditures may reduce their activity levels, which comprises the largest portion of Steller sea lion energy usage (Winship et al. 2002, Beauplet et al. 2003, Williams et al. 2007). In addition, changes in thermoregulatory capacity are a possible mechanism to shift energy needs. Mass was likely stored as blubber, thus reducing their thermoregulatory costs. This has been demonstrated in harbour seals, although this effect may occur to a lesser extent in otariids because of their thinner blubber layer (Renouf & Noseworthy 1990, 1991, Rosen & Renouf 1997). While neither thermoregulatory ability nor activity level was measured in our study, these are two methods the animals could use to save energy for growth and could explain the asynchronicity in mass increasing in the face of decreased energy intake.

Many mammals living in seasonal environments have entrained seasonal patterns in both mass and food intake that are based around reproductive needs and food availability (Loudon 1994, Mercer 1998). Photoperiod appears to be the mechanism driving these cycles in many animals, as shown for rodents and ruminants that undergo mass changes as a result of light cycle manipulation (they modify intake to return to seasonally appropriate mass levels following a return to natural light levels; Dark & Zucker 1985, Loudon 1994, Mercer 1998). The limited number of photoperiodic manipulation experiments in pinnipeds have focused mainly on female reproductive timing, and indicate that while light levels may partially drive reproductive cycles, the controlling mechanism appears to be endogenous and likely hereditary (Spotte & Adams 1981, Temte 1991). Endogenous mass and food intake responses are found in many other seasonal mammals with predictable food resources (Dark & Zucker 1985, Loudon 1994, Mercer 1998), and may be present in Steller sea lions. Photoperiod manipulation experiments focusing on mass and food intake of Steller sea lions are needed to determine the source of seasonal patterns.

The offset between mass gain and food intake has important implications for bioenergetic models that often predict food consumption as a function of body mass. Our findings indicate that food intake should not be estimated as a simple scalar of body mass, but that bioenergetic models should include an offset between the two measurements. One means of doing so is to apply the mass and food intake equations we derived using the maturity and sine functions to quantify the average annual increases and seasonal oscillations (Fig. 2.8). These combined models should be used in future modeling to predict the food intake of wild Steller sea lions. A scaling factor that accounts for activity and diet differences between captive and wild Steller sea lions may be applied to the equations in our study to quantify wild animal food intake.

Knowing what time of the year is nutritionally critical for Steller sea lions has implications for fisheries management and may provide insights into the reason for their population decline in western Alaska (NMFS 2008). The current bioenergetic model for Steller sea lions (Winship et al. 2002) suggests that early spring is the time of highest energy needs for females that are pregnant or are nursing 1 or 2 year-old offspring. However, our data indicate that intake is lower during spring despite the costs of lactation and pregnancy, and that consumption is higher during winter (Fig. 2.12). Manipulative feeding experiments have shown that Steller sea lions lose more mass when fasted in winter than in summer, but are better able to recover from food deprivation in winter than in summer (Rea et al. 1999, Kumagai et al. 2006, Rea et al. 2007, Jeanniard du Dot et al. 2008, Rosen & Kumagai 2008), suggesting that females are better adapted to deal with nutritional deficits in winter than in summer when prey are generally considered to be predictably abundant (Anthony et al. 2000, Kitts et al. 2004, Sigler et al. 2004, Womble et al. 2005). Thus, energy intake and the physiological ability to deal with nutritional stress must be given equal consideration when determining what season is most critical to Steller sea lions.

The results of our analysis of feeding records of captive Steller sea lions and the findings of manipulative feeding experiments are consistent in concluding that adequate nutritional intake is critical to male and female Steller sea lions from late summer to early winter (Rea et al. 1999, Kumagai et al. 2006, Rea et al. 2007, Jeanniard du Dot et al. 2008, Rosen & Kumagai 2008). This reflects an increase in consumption from summer to early winter (Fig. 2.6) when sea lions are likely replenishing internal stores following breeding and incur increased thermoregulatory costs. It is also the time of year when lactating females likely face increased energy demands to meet the increased energetic needs of their growing pups (Figs. 2.9 and 2.12). Weaned pups are also likely to be energetically challenged during summer, fall and the winter months due to their small body size and high growth rates (Merrick et al. 1994, Merrick et al. 1995, Trites & Donnelly 2003).

Conclusions

Analyzing the detailed feeding and growth records of reproductive and non-reproductive male and female Steller sea lions from birth to adulthood revealed information that has not been available from wild-animal data (McLaren 1993, Calkins et al. 1998, Winship et al. 2001, Winship et al. 2002). Our study showed a seasonal increase in food intake that preceded a seasonal increase in body mass by about 4 months, with mass peaking before the spring breeding season in males and females of all ages and reproductive condition (Figs. 2.6 and 2.7). It further suggested that late summer through early winter are periods when food intake was increasing to its peak, and possibly when adequate nutrition is critical to the health of all animals, especially juveniles and lactating females. Our estimates of food intake of captive animals are lower than predicted requirements of wild animals due to reduced activity levels and higher caloric diets fed captive animals. However, the seasonal pattern of food intake is consistent among captive and wild sea lions and can be combined with the growth models to predict the food intake of wild Steller sea lions using a bioenergetic model (Fig. 2.8). Combination of the maturity and sine equations for mass and food intake provide a way of quantifying both the average annual increase in these measurements and the seasonal oscillations present (Fig. 2.8). The concept of these combined models could be used in future bioenergetic modeling to predict wild food intake. Bioenergetic models enhance understanding of Steller sea lions energetic requirements by incorporating the seasonal costs associated with thermoregulation and reproduction.

The Steller Sea Lion Recovery Plan highlights winter as a critical foraging period for Steller sea lions and recommends minimizing interactions with fisheries during this season (NMFS 2008). However, evidence from our and other studies points to summer as an additional period in which the potential for nutritional stress is high (Kumagai et al. 2006, Rea et al. 2007, Jeanniard du Dot et al. 2008, Rosen & Kumagai 2008). Understanding Steller sea lion food intake was limited by a lack of wild animal data on body size from the winter and spring (Winship et al. 2002), and has been augmented by data from our captive animals. In particular, the captive Steller sea lions showed that seasonal highs and lows in mass and food intake are not concurrent, and that multiple influences combine to produce these offset patterns. Such asynchronous patterns may apply to other animal groups that have seasonal oscillations. Our captive sea lions also revealed specific differences between male and female sexual maturity, non-reproductive and reproductive animals, and growth and food intake in all seasons that can benefit the management of this species and improve our understanding of seasonal food requirements of Steller sea lions.

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Chapter 3: The influence of testosterone on the mass and food intake of Steller sea lions[2]

Introduction

Much of what is known about the effects of testosterone on the male reproductive cycle has come from correlative studies that relate circulating levels of testosterone with time of year and morphometric changes (e.g., Dufour et al. 1984, Atkinson & Gilmartin 1992, Bartsh et al. 1992, Rhim et al. 1993, Tsubota et al. 1997, Stewardson et al. 1998, Gardiner et al. 1999). Studies of sexually dimorphic mammals have tended to show that naturally occurring testosterone concentrations are highest prior to breeding, and correspond with increased aggression, testicular recrudescence, and increases in gonadal mass and sperm production. Other studies have intentionally altered testosterone levels to determine the effects of testosterone in small mammals irrespective of season, and have shown that injections of low-dose testosterone cause an increase in mass growth and food intake in female and castrated male hamsters (*Mesocricetus auratus*) and rats (*Rattus norvegicus*) (Gentry & Wade 1976, Wade & Gray 1979, Slusser & Wade 1981, Kuchár et al. 1982). Experimental and observational data thus indicate that testosterone influences long-term body growth and food intake, as well as short-term reproductive behavior and sexual

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organ maturity.

Male pinnipeds, especially the highly dimorphic Steller sea lions (*Eumetopias jubatus*), attain large adult size and undergo rapid mass increases prior to the breeding season (Chapter 2; Pitcher & Calkins 1981, McLaren 1993, Atkinson 1997, Winship et al. 2001). Adult male Steller sea lions consume little if any food during the breeding period and must rely on increased stamina and competitive success associated with large body size to defend their territories from other males where females will give birth and mate (Pitcher & Calkins 1981, Weckerly 1998, Winship et al. 2002). Testosterone may be the driving force that links reproduction, consumption, and mass growth of male sea lions both during sexual maturity and in subsequent breeding periods. However, long-term research into the effects of testosterone on growth and food intake of sea lions has not been conducted.

An alternative to measuring testosterone levels or injecting pinnipeds to obtain information on the role of testosterone is to examine differences between intact and neutered males in a controlled setting. This technique has been successfully applied to study the effect of male reproductive hormones on growth and food intake of cervids and rodents (Ryg 1982, Ryg & Jacobsen 1982, Dark & Zucker 1985, Canguilhem et al. 1988), and can be used for marine mammals at aquariums that commonly neuter males to reduce aggression and avoid unwanted pregnancies (Siebert et al. 2007). Removing the testes, which is the main source of testosterone, should reduce body size, lower food intake, and disrupt seasonal cycles.

The goal of our study was to determine the extent to which gonadal activity, thus testosterone, was linked with seasonal changes in mass and food intake of male Steller sea lions. We also sought to assess the effect of testosterone on the attainment of sexual maturity. We compared records of body mass and food intake from captive Steller sea lions that were castrated (neutered) and uncastrated (intact).

Materials and methods

Data were collected from captive male Steller sea lions housed at 6 aquariums (Vancouver Aquarium, Canada; Mystic Aquarium, USA; Dolfinarium Harderwijk, the Netherlands; Futami Sea Paradise, Japan; Kamogawa Sea World, Japan; and Izu-Mito Sea Paradise, Japan). Mass and food intake were recorded on a regular basis from 17 males of which 5 were neutered (Appendix 1). One male ("Boris") was neutered during his 5th year, while the age of castration for the remaining males is unknown. Fish consumption of all males was recorded, and mass was measured from 3 neutered and 5 intact animals.

Data were analyzed using non-linear mixed-effect models from the nlme package in R 2.8.0 (Pinheiro et al. 2008, R Development Core Team 2008). Mass growth and annual increases in food intake were mathematically described using the "maturity" growth model:

$$1. \qquad S_t = [\frac{1}{3}k(\frac{1-e^{-h(t-a)}}{h} + a) + {w_0}^{1/3}]^3$$

where α is the age at sexual maturity, h is a value that scales the rate of exponential decline in growth following sexual maturity, and w_0 is the size at age zero (Day & Taylor 1997). We tested whether the growth and food intake models differed significantly between intact and neutered males using an ANOVA likelihood test (Pinheiro et al. 2008). We fixed the α parameter in the maturity model at age 5 y — the age at which the youngest male among our study animals successfully impregnated a female. We also explored seasonality in consumption and mass fluctuations using a sine equation:

$$\text{2.} \qquad A_{mp} \times \sin[2 \times pi \times \Omega(t - H)] + v$$

where A_{mp} is the amplitude of the wave, H is the horizontal shift, v is the vertical shift in the position of the wave, and one wavelength equaled $2 \times pi \times \Omega$. We set Ω to 1 y because seasonal wave patterns in the data occurred on a yearly basis. We further refined the models by including a random effects structure that allowed the fixed effects k and w_0 in the maturity equation, and the parameters A_{mp}, H and v in the sine equation to vary by individual animal. The random effects of the aquariums that housed these animals and whether the animals were born in captivity or in the wild were tested for inclusion with animal into the random effects structure. There was never a significant difference between any of these models ($p > 0.05$), so the more simplistic model with just animal as the random effects was chosen in all cases. We also incorporated a first-order autocorrelation function (corAR1) in all models to correct for serial correlation that occurs from repeated measurements of the same animals. All

Table 3.1: Parameter estimates (±CI) of models describing the mass growth (kg) and food intake (kg d^{-1}) of intact and neutered male Steller sea lions. The maturity model describes growth from age 1.5 y onwards, and the sine model describes seasonal oscillations in mass from age 5 y onwards. All model parameters were significant ($p<0.001$). There was no significant difference in food intake data from intact and neutered animals ($p=0.541$).

Meas.	Model	Status	n	Parameters ± CI
Mass (kg)	maturity	Intact	5	$h=0.1321 \pm 0.0115$; $k=1.4835 \pm 0.2561$; $w_0=75.2630 \pm 21.5184$; ($a = 5$)
		Neutered	3	$h=0.2372 \pm 0.0458$; $k=1.3092 \pm 0.2839$; $w_0=71.1274 \pm 52.4821$; ($a = 5$)
	sine	Intact	5	$A_{mp} = -100.2413 \pm 45.2916$; $H=7.6734 \pm 4.2556$; $v=574.9260 \pm 74.1087$
		Neutered	3	$A_{mp} = -31.7320 \pm 11.7210$; $H=2.6252 \pm 3.2997$; $v=392.6731 \pm 64.2994$
Food Intake (kg d^{-1})	maturity	Intact	12	$h=0.3882 \pm 0.1427$; $k=0.2328 \pm 0.0406$; $w_0=7.3827 \pm 1.1330$; ($a = 5$)
		Neutered	5	$h=0.3512 \pm 0.2028$; $k=0.2711 \pm 0.1098$; $w_0=5.8353 \pm 2.2967$; ($a = 5$)
	sine	Intact	10	$A_{mp} = -3.9700 \pm 1.1712$; $H= -7.4330 \pm 2.0440$; $v=17.6210 \pm 2.7302$
		Neutered	5	$A_{mp} = -2.4532 \pm 0.8337$; $H= -7.6359 \pm 2.9261$; $v=15.0312 \pm 1.7006$

model parameters were assessed for significance using Wald F-tests, and model assumptions were tested using graphical applications from the package nlme in R 2.8.0 (Pinheiro & Bates 2002, Pinheiro et al. 2008, R Development Core Team 2008). Confidence intervals (95%) for the models were determined using hierarchical bootstrapping on individual animal residual variance from the model.

Results

Males attained sexual maturity at age 5 y and increased in mass throughout adulthood (Fig. 3.1). However, we could not include an autocorrelation function in the mass models because of convergence failure due to large variability of the data, and exclusion of this function tended to inflate the asymptote. Growth rates increased from age 5 to 7 y, during the time of sexual maturity. Seasonally, the mass of intact males increased 200 kg from a low at

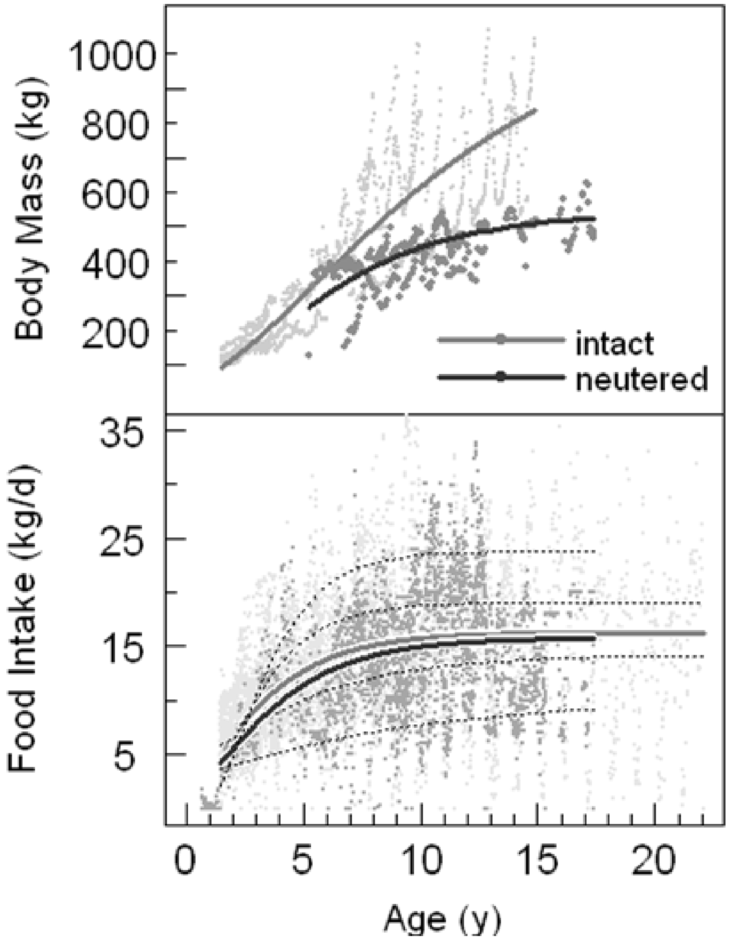

Fig. 3.1. Body mass (top) and food intake (bottom) of intact (lighter points and lines; n_{mass}=5; n_{food}=15) and neutered (darker points and lines; n_{mass}=3; n_{food}=5) male Steller sea lions. Body mass was described by the maturity equation (Table 3.1) and differed significantly between neutered and intact males ($p<0.001$). There was no significant difference between the food intake of intact and neutered males ($p=0.541$). Dotted lines indicate 95% confidence intervals. Confidence intervals are not included in the mass models because they did not include an autocorrelation function.

the end of October to a peak in late April, although changes within individual animals were much larger than predicted by the model (Fig. 3.2).

Growth of neutered males differed significantly from that of intact males (all parameters: $p < 0.001$; Table 3.1; Fig. 3.1). Intact males were ~50 kg or 17% larger than neutered animals at age 5 y, with the disparity increasing to a

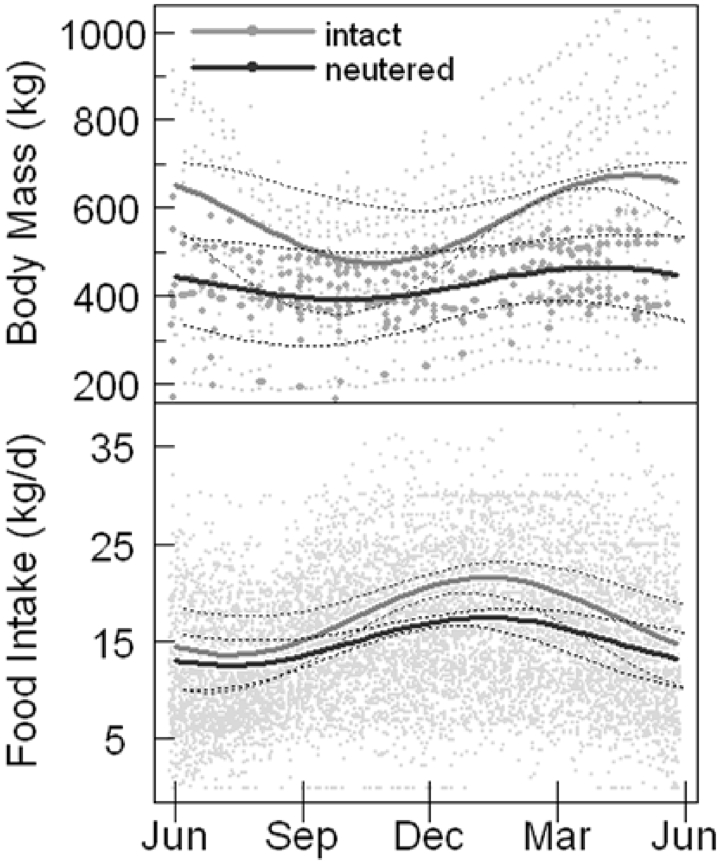

Fig. 3.2. Seasonal changes in the body mass and food intake of neutered and intact Steller sea lions as described by the sine equation. The sine function predicted that intact male mass (*n*=5) oscillated 140 kg more than neutered males (*n*=3) per year and reached peak mass in late April. There was no significant difference in the seasonal patterns of food intake between the two groups (n_{intact} =10, $n_{neutered}$ =5; p=0.541). Peak consumption occurred in December and both groups decreased consumption by 5 to 8 kg d^{-1} to a low in late June. Dotted lines indicate 95% confidence intervals.

difference of 200 kg per year (34%) as the animals aged. The mass of neutered males also changed seasonally but the oscillations were dampened compared to those of intact males (all parameters: p<0.001; Table 3.1; Fig. 3.2). Mass of neutered males peaked in the spring but oscillated only ~60 kg; which was about 140 kg (57%) less than the change in mass of intact males. Neutered males did not experience the large growth spurts characteristic of breeding male Steller sea lions. However, food intake was similar between the two groups of males (p=0.541; Figs. 3.1 and 3.2).

Discussion

Testosterone is an anabolic steroid hormone that regulates the reproductive cycle in male mammals by affecting puberty, gonadal development, sexual aggressiveness, spermatogenesis and the size of the testes (e.g., Dufour et al. 1984, Bartsh et al. 1992, Striera et al. 1999). Among species that are seasonal breeders, testosterone concentrations rise and fall in tandem with the breeding period. Testosterone levels tend to be high at the beginning of the breeding season, and fall to low levels at the time of mating (Dufour et al. 1984, Atkinson & Gilmartin 1992, Bartsh et al. 1992, Rhim et al. 1993, Tsubota et al. 1997, Roelants et al. 2002). Other hormones that influence the male reproductive cycle include gonadotropin-releasing hormone (GnRH), luteinizing hormone (LH), and follicle-stimulating hormone (FSH) (Rhim et al. 1993, Roelants et al. 2002). Changes in testosterone and other related hormones may be under photoperiodic control (Canguilhem et al. 1988, Boyd 1991, Rhim et al. 1993, Stewardson et al. 1998, Delgadillo et al. 1999).

Pinnipeds are seasonal breeders and many are highly sexually dimorphic (McLaren 1993, Atkinson 1997). As with most mammals, testosterone is central in the development of sexual maturity of male pinnipeds, and affects territorial behavior and gonadal mass and development (Atkinson 1997, Stewardson et al.

1998). Testosterone levels of Hawaiian monk seals (*Monachus schauinslandi*) and Weddell seals (*Leptonychotes weddelli*) increase during the breeding season (Atkinson & Gilmartin 1992, Bartsh et al. 1992) and correlate with larger male Weddell seals winning more breeding territory disputes (Bartsh et al. 1992).

It is likely that the sexual size dimorphism in Steller sea lions (McLaren 1993, Weckerly 1998, Winship et al. 2001) is mediated by gonadal hormones. Increased growth during puberty has been linked with testicular growth and thus testosterone production in mammals, allowing males to attain larger size than females (Slob & van der Werff Ten Bosch 1975, Kuchár et al. 1982, Bartsh et al. 1992). This is consistent with observations of cattle castrated at young ages that failed to develop some characteristically male traits and reached an adult size halfway between intact males and females (Biagini & Lazzaroni 2007, Micol et al. 2009). The marked growth spurt of intact Steller sea lion males at sexual maturity was much smaller in neutered males, as shown by the marked divergence of their growth curves during sexual maturity (Fig. 3.1). Although it was difficult to assess earlier growth trends in our data because mass was only available from neutered males aged 5 y and above, castrates were ~22% smaller than intact males by age 7 y.

The smaller size of neutered Steller sea lions agrees with castration studies of a wide range of sexually dimorphic mammals including rodents (Slob & van der Werff Ten Bosch 1975, Gentry & Wade 1976, Dark & Zucker 1985, Canguilhem et al. 1988, Kriegsfeld & Nelson 1996), ruminants (Ryg 1982, Ryg & Jacobsen 1982, Webster 1993, Walkden-Brown et al. 1997, Solanas et al. 2005, Biagini & Lazzaroni 2007, Lazzaroni & Biagini 2008, Micol et al. 2009) and boars (*Sus scrofa*; FlorCruz & Lapwood 1978). These studies have shown that negligible testosterone secretion from the testes following castration reduces growth rate and adult size of sexually dimorphic mammals. Conversely, injection of androgens into female and castrated male rodents and ruminants causes growth rate to increase (Gentry & Wade 1976, Ryg 1982, Ryg & Jacobsen 1982, Canguilhem et al. 1988, Walkden-Brown et al. 1997). Thus, gonadal secretions in both male and female mammals likely drive patterns of sexual dimorphism: rising gonadal steroids during puberty either decreases female growth (estrogen) or increases male growth (testosterone) (Slob & van der Werff Ten Bosch 1975, Gentry & Wade 1976, Wade & Gray 1979, Kuchár et al. 1982).

On a seasonal basis, mature male Steller sea lions gain mass prior to breeding in order to attain a size advantage to compete for and defend breeding territory, and use this mass as a lipid reserve to meet energetic demands associated with breeding (Nitto et al. 1998, Winship et al. 2001, Chabot & Stenson 2002, Beck et al. 2003). Both intact and castrated males demonstrated these seasonal mass changes although the oscillation in the latter group was smaller (Fig. 3.2), suggesting that gonadal steroid levels alone do not fully mediate mass growth. This pattern of decreased mass oscillations in gonadectomized males is typical in ruminants, and points to alternative endogenous mechanisms driving these patterns (Ryg 1982, Ryg & Jacobsen 1982, Walkden-Brown et al. 1997). Changes in mass are correlated with seasonal food intake oscillations in many mammals (e.g., Loudon 1994).

However, species such as ground squirrels (*Spermophilus spp.*), Siberian hamsters (*Phodopus sungorus*) and red deer (*Cervus elaphus*) display an offset in the voluntary food intake and mass similar to that noted in our study (Fig. 3.2), with both mass and food displaying distinct cycles that are resistant to experimental manipulation (Loudon 1994). Hence, seasonal mass changes are likely mediated by factors other than gonadal hormone concentration or changes in food intake.

Unlike mass, quantity of food consumed by Steller sea lions did not seem to be influenced by levels of testosterone. The slightly lower food intake of castrated sea lions did not differ significantly from that of intact males, which means that castrated males actually consumed more food per unit body mass than did the intact males (Fig 3.1). This finding differs from the significantly lower food consumption noted in castrated California sea lions (*Zalophus californianus*, Kastelein et al. 2000) and cervids (Ryg 1982, Ryg & Jacobsen 1982), but is similar to the slightly reduced food intake patterns seen in castrated cattle (Andersen & Ingvartsen 1984, Solanas et al. 2005, Biagini & Lazzaroni 2007, Lazzaroni & Biagini 2008). Castrated animals generally have lower muscle mass and a higher fat content and greater fat deposition rate than their intact counterparts because testosterone increases muscle mass and decreases adiposity. Fat deposition is more costly than building muscle, and may explain why castrated animals consumed similar amounts of food as did intact males despite their smaller body size, although this may be counteracted because of the higher cost of maintaining muscle versus fat tissue (Wade & Gray 1979, Andersen & Ingvartsen 1984, Solanas et al. 2005, Biagini & Lazzaroni 2007, Lazzaroni & Biagini 2008). The positive relationship between gonadal hormones and muscle mass deposition may thus help explain why castrated animals consumed more food per unit body mass than did the intact Steller sea lions.

Testosterone may affect adiposity (Wade & Gray 1979, Ryg & Jacobsen 1982, Webster 1993, Solanas et al. 2005, Biagini & Lazzaroni 2007, Lazzaroni & Biagini 2008), but does not appear to affect seasonal cycles in food intake in Steller sea lions since both intact and castrated males increased their food intakes in winter and decreased consumption to low levels in summer (Fig. 3.2). This seasonal pattern of food intake of captive sea lions compares favorably with that reported for wild sea lions, with the lowest levels of consumption corresponding with the summer breeding season while breeding males are on shore (Winship et al. 2002). Decreasing food intake levels correlate with increasing gonadal hormone concentrations in many ruminant species during the breeding period (Ryg & Jacobsen 1982, Miquelle 1990, Loudon 1994, Newman et al. 1998). However, this does not hold for species whose cycles of mass change and food intake are offset such that changes in gonadal hormone cycles correspond with changes in mass but not correspond with changes in food intake patterns (Miquelle 1990, Loudon 1994). The lack of significant differences in our study between intact and castrated males in either total food intake or seasonal patterns in food consumption indicate that gonadal hormones likely do not influence food intake in Steller sea lions.

In conclusion, castration, and thus cyclical levels of circulating testosterone, affected mass growth but not food intake in male Steller sea lions. These findings point to control mechanisms other than testosterone that influence changes in body mass and hunger levels. Photoperiodicity is one such possible control mechanism that has been shown to affect secretions of melatonin from the pineal gland, which correlates with seasonal changes in mass of some species by influencing endogenous factors involved in growth (i.e. growth hormone) and food intake (i.e. leptin) (Dark & Zucker 1985, Loudon 1994, Kriegsfeld & Nelson 1996, Peltier et al. 2003). However, body mass and food intake cycles are independent of photoperiod in other species, where circadian rhythms appear to affect circulating hormone levels and match reproductive timing with the availability and intake of food (Dark & Zucker 1985, Loudon 1994, Kriegsfeld & Nelson 1996, Peltier et al. 2003). Photoperiodic manipulation experiments with pinnipeds have shown that light levels partially drive reproductive cycles of females, and suggest that the primary mechanism controlling changes in body mass and food intake is endogenous and likely hereditary (Spotte & Adams 1981, Temte 1991). While it is unknown whether the same conclusions regarding the affects of photoperiod apply to male pinnipeds, male cervids are known to use light levels to match growth and consumption with the timing of important life history events (Ryg & Jacobsen 1982, Miquelle 1990, Peltier et al. 2003). Such uncertainties point to the need to better understand the mechanisms that mediate seasonal changes in body size and food intake in Steller sea lions.

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Chapter 4: Conclusions

The goals of our study were to quantify seasonal changes in length, mass and food intake of Steller sea lions (*Eumetopias jubatus*), and to compare the patterns of growth and consumption found in castrated and intact males and in non-reproductive, pregnant and lactating females. To do so, we used a large data set from captive Steller sea lions collected from all time periods and life stages, and fit growth and oscillating sine curves to evaluate the influences of sexual maturity, activity, and environmental conditions on growth and food intake.

Summary of findings

Our study derived equations that quantified Steller sea lion food intake and growth in length and mass. They showed pups and juveniles grew rapidly, and that males and females differed in mass beginning in their first year of life, while length could be differentiated one year later. All animals continued to grow throughout adulthood in both length and mass (i.e., growth was indeterminate). Males achieved a much larger size than females by having a longer growth period in length and mass and through a growth spurt that occurred at the time of sexual maturity between ages 5 to 7 y. This pattern was driven in part by testosterone, as the mass increase occurred during puberty when testosterone levels are known to rise in pinnipeds (Atkinson 1997, Stewardson et al. 1998). Females grew in mass and length for a shorter period of time, and reached adult length just following sexual maturity at age ~5.5 y, and adult mass four years later. These patterns were expected in this sexually dimorphic species.

Breeding size of females in a sexually dimorphic species was presumably reached at a younger age than males in order to maximize the number of offspring they can have in their lifetime. Males do not reach reproductive size until a number of years later because of the need to be larger to successfully compete for breeding opportunities (Weckerly 1998, Cassini 1999, Isaac 2005). Food intake followed similar patterns to those of length and mass, because females reached asymptotic consumption during their fourth year at the approximate age of sexual maturity, while males continued to increase their intake ~2 years following sexual maturity.

We found significant seasonal oscillations in male and female mass and food intake data, but not in the lengths of either sex. Males gained mass from the late fall into spring, highlighting the importance of large body size for breeding. A decrease in the amplitude of seasonal oscillations in the mass of neutered males indicated that testosterone was involved in driving these mass increases prior to the breeding season, but was not the only controlling factor. Non-reproductive and lactating females followed a similar pattern, although the amplitudes of their oscillations were much less than that of males. Lactating females were ~80 kg larger than females that did not reproduce. Pregnant female mass reflected fetal growth and weight gain preceding lactation, as they gained mass from the time of implantation to just prior to parturition.

We detected seasonality in food intake, with all groups reaching peak consumption in the winter, and decreasing intake in summer. Unlike for mass, testosterone levels did not influence food intake seasonality given that intact and neutered male food intake consumption and seasonal patterns were identical. Lactating females consumed 40% more food than pregnant and non-pregnant females during winter, but had similar levels of consumption following parturition and prior to the next breeding season. Oscillations in mass and food intake of all age groups were offset, with peaks in food intake occurring in winter ~3 to 4 months before the peaks in mass were achieved. Female mass was likely influenced by both reproduction and a need to store fat during winter. The same may be true for males since testosterone levels, and thus the reproductive cycle, affected mass but not food intake. Food intake following breeding increased in all animals into winter as they replenished stores lost during reproduction and combated thermoregulatory costs. Summer to winter was identified as a period where sufficient energy intake was important for the continued health of the animals because of low mass following breeding, and increases in thermoregulatory costs (and pup costs for lactating females) in the fall and winter. Thus, quantifying seasonality allowed us to determine the influence of thermoregulation and reproduction on mass and food intake.

Strengths and weaknesses

Most of the strengths and weaknesses in our study resulted from collecting data from captive animals. Data collection in wild Steller sea lions has been limited by sampling difficulties of collecting animals from all times of the year and from a range of age groups and sizes. It is also limited by available funds and restrictions on the types of data that can be collected from declining populations under the Endangered Species Act (NMFS 2008). The captive animal data we used is an alternate source of growth and food intake data, and was collected year-round with each season equally represented. We also had a better sample of large breeding males that are difficult to capture in the wild, and did not have the cohort effect found in the data collected from wild sea lions during two different time periods (Calkins et al. 1998). The main benefits of using captive data were that we had year-round data, and were able to examine actual food intake of Steller sea lions.

Many benefits resulted from using captive-animal data, but there were weaknesses as well. Many animals were the siblings and offspring of other animals in the data, and relatedness is a determinant of growth patterns (Lindström 1999). However, environmental influences also impact growth, and the large sample size we had likely negated any effects of this bias. In addition, two facilities (Vancouver and Mystic Aquariums) conducted research and periodically restricted the amounts of food they gave their animals, unlike the other facilities that had limited training regimes and were able to feed animals until satiation. While non-research facilities fed their animals more fish overall, this “aquarium effect” did not have any statistical significance likely due to high individual animal variability, and thus did not significantly affect the growth and food intake equations. Lastly, diet composition and activity differences between these captive animals and their wild counterparts precluded directly applying the food intake of captive sea lions to the wild Steller sea lion population. Patterns in food intake presented in our study are more useful for extrapolation to the wild population, but elements of these must be viewed with caution. Mainly, wild diet availability could influence food intake in alternate ways than presented in our study, and complications arising in lactating animals from increased foraging costs may amplify their energetic costs above what we presented. Seasonal patterns in food intake likely reflect the minimum metabolic requirements of Sea lions throughout the year. Wild animals likely face additional foraging and breeding costs.

Implications and future research

Our results have implications for understanding nutritional studies in Steller sea lions. The decline of the population in Alaska has been linked with a reduction in fish availability and quality causing a delay in the sexual maturity of juvenile animals and a lengthening of the lactation period (Alverson 1992, Rosen et al. 2000, National Research Council 2003, Trites et al. 2007, NMFS 2008). Thus, recent research on Steller sea lions has focused on nutrition deficits, especially in a seasonal context. These studies have collectively identified summer and winter as times when animals may have problems increasing mass following both fasting and food restriction (Rea et al. 1999, Kumagai et al. 2006, Rea et al. 2007, Jeanniard du Dot et al. 2008, Rosen & Kumagai 2008). However, available information from growth models and bioenergetic estimations of energy requirements predict that winter is a critical time for juveniles and lactating females. Seasonal oscillations were not found in the mass growth of non-reproductive wild females, and estimated energy requirement oscillations in wild animals did not match the timing or amplitude calculated from our models (Winship et al. 2001, Winship et al. 2002). Our seasonal mass and food intake models highlighted the importance of summer, fall and winter in terms of food intake, because animals were replenishing stores following breeding, preparing for increased thermoregulatory costs in winter, and in lactating females, facing increased energy costs due to suckling pups. Our study thus has two main implications for past Steller sea lion research. First, we determined seasonal patterns in mass and actual food intake from data collected during all seasons; and second, we found that these patterns were asynchronous. Studies on nutrition in Steller sea lions should address and account for seasonal effects inherent in growth and consumption.

Limitations in our understanding of food intake could be improved through the use of data loggers attached to wild animals. Stomach temperature recorders have been used to determine food intake of marine mammals and birds. While there is error associated with using these recorders, they provide a method to determine actual food intake in wild Steller sea lions (Gremillet & Pios 1994, Hedd et al. 1996, Bost et al. 1997, Austin et al. 2006, Kuhn & Costa 2006). The main issue in using our data to understand wild animal food intake, and the largest source of error in the bioenergetic model, was problems with animal activity (Winship et al. 2002). Activity may be best-studied through the use of attachable devices such as time-depth recorders and satellite tags, which can record diverse data such as swim speed and location. Such tags carried by different reproductive groups can give information on the activity differences in foraging between animals (Boyd et al. 1991, Costa 1991, Merrick et al. 1994, Boyd et al. 1997, Williams et al. 2004). The use of data loggers is one way to collect updated information on actual food intake and activity levels of wild animals.

A less expensive way to improve understanding of wild Steller sea lion food intake would be to update bioenergetic models using growth and seasonal intake information from our study and dietary and activity data from field and captive research. Recent studies on Steller sea lion diving suggest that foraging may be less costly than previously predicted (Hastie et al. 2007, Fahlman et al. 2008a, Fahlman et al. 2008b). As well, advancements have been made in understanding the diet composition of these animals (Deagle & Tollit 2007, McKenzie & Wynne 2008, Trites & Calkins 2008, Tollit et al. in press). Combining new information on diving metabolism and activity, diet composition and evidence from our study of asynchronous seasonal patterns in male and female mass growth in an update of the current bioenergetic model (Winship et al. 2002) would produce better estimates of wild animal energy requirements. Ideally, future Steller sea lion research will focus on refining our understanding of metabolism, exploring technology that allow recording of activity and food intake in wild animals and improving bioenergetic models to enhance our understanding of Steller sea lion energy requirements.

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Appendix 1: Summary of animal data

Table A1.1: Description of data collected from each animal. Animals with an * are listed in two facilities because they were transferred. L= length (cm), M=mass (kg), F=food intake (kg d^{-1}).

Facility	Animal	Sex	Age span of data (y)	Parents (♀,♂)	Reproductive status	Age at pup birth (♀) or fertilization of egg (♂)	Data used in pup graphs	Data used in juvenile models	Data used in main models	Data used in sine models
Vancouver Aquarium	Adak*	♂	0 - 4	Wild	intact			L,M,F	L,M,F	M,F
	Ashby	♀	0 - 5	Wild	non-reprod.			L,M,F	L,M,F	M,F
	Boni	♀	0 - 8	Wild	non-reprod.			L,M,F	L,M,F	M,F
	Eden	♀	0 - 8	Wild	non-reprod.			L,M,F	L,M,F	M,F
	Hazy	♀	0 - 11	Wild	non-reprod.			L,M,F	L,M,F	M,F
	Izzy	♀	0 - 5	Wild	non-reprod.			L,M,F	L,M,F	M,F
	Kiska	♀	0 - 5	Wild	non-reprod.			L,M,F	L,M,F	M,F
	Kodiak*	♂	0 - 5.5	Wild	non-reprod.			L,M,F	L,M,F	M,F
	Mara	♀	0 - 5	Wild	non-reprod.			L,M,F	L,M,F	M,F
	Nuka	♀	0 - 6	Wild	non-reprod.			L,M,F	L,M,F	M,F
	Rogue	♀	0 - 5	Wild	non-reprod.			L,M,F	L,M,F	M,F
	Sade*	♀	0 - 3	Wild	non-reprod.			L,M,F	L,M,F	M,F
	Sitka	♀	0 - 11	Wild	non-reprod.			L,M,F	L,M,F	M,F
	Sugar	♀	0 - 5	Wild	non-reprod.			L,M,F	L,M,F	M,F
	Tasu	♀	0 - 8	Wild	non-reprod.			L,M,F	L,M,F	M,F
	Tag	♂	0 - 14.5	Wild	non-reprod.			L,M,F	L,M,F	M,F
	Timber	♂	0 - 2.5	Wild	non-reprod.			L,M,F	L,F	
	Willo	♀	0 - 5	Wild	non-reprod.			L,M,F	L,M,F	M,F
	Woody	♂	0 - 5	Wild	non-reprod.			L,M,F	L,M,F	M,F
	Yasha	♀	0 - 8	Wild	non-reprod.			L,M,F	L,M,F	M,F
Mystic Aquarium	Augustus	♂	6.5 - 15.5	Stella, unknown	neutered				F (neut.)	F (neut.)
	Jezebel	♀	21 - 29	Wild	reproductive	10, 11				F
	Julius	♂	7 - 13	Banchee, unknown	neutered				F (neut.)	F (neut.)
	Juneau	♀	10 - 24	Jezebel, Kojak	non-reprod.					F
	Kodiak*	♂	5.5 - 10.5	Wild	non-reprod.				M,F	M,F
	LA	♀	7 - 20	Lucia, Unknown	non-reprod.					F

Table A1.1: Continued

Facility	Animal	Sex	Age span of data (y)	Parents (♀,♂)	Reproductive status	Age at pup birth (♀) or fertilization of egg (♂)	Data used in pup graphs	Data used in juvenile models	Data used in main models	Data used in sine models
Mystic Aquarium continued	Lucia	♀	12 - 25	Banchee, Cyrus	reproductive	5				F
	Stella	♀	14 - 24	Banchee, Cyrus	reproductive	7				F
Dolfinarium Harderwijk	Aafke	♀	0 - 2	Lammechein, Bart	non-reprod.		F			
	Adak*	♂	4 - 15	Wild	reproductive	5,8,9,11,13			M,F	M.F
	Bart	♂	0 - 22	Wild	reproductive	6-8,10-15,18,19,20			F	F
	Boris	♂	0 - 15.5	Snibbechien, Bart	neutered				M, F (neut.)	M, F (neut.)
	Chiswell	♀	0 - 4	Ida, Adak	non-reprod.		M,F	M	M,F	
	Dirk	♂	0 - 3	Snibbechien, Bart	non-reprod.		F		F	
	Frederika	♀	0 - 11	Snibbechien, Bart	reproductive	4,6,8	F		F	F
	Icy	♀	0 - 2	Olympia, Adak	non-reprod.		M,F	M		
	Ida	♀	0 - 15	Snibbechien, Bart	reproductive	14	F		F	M,F
	Jaap	♂	0 - 3	Snibbechien, Bart	non-reprod.		F		F	
	Lammechien	♀	0 - 24	Wild	reproductive	7,15,17			F	F
	Laska	♂	0 - 8	Olympia, Adak	non-reprod.		M,F	M	M,F	M,F
	Martine	♀	0 - 5	Snibbechien, Bart	non-reprod.		F		F	
	Matushka	♀	0 - 6	Sade, Adak	non-reprod.		M,F	M	M,F	M,F
	Molly	♂	0 - 6	Snibbechien, Bart	non-reprod.		F		F	F
	Olympia	♀	0 - 16	Frederika, Bart	reproductive	5,13	F		M,F	M,F
	Sade*	♀	3 - 14	Wild	reproductive	4,7,11			M,F	M,F

Table A1.1: Continued

Facility	Animal	Sex	Age span of data (y)	Parents (♀,♂)	Reproductive status	Age at pup birth (♀) or fertilization of egg (♂)	Data used in pup graphs	Data used in juvenile models	Data used in main models	Data used in sine models
Dolfinarium Harderwijk continued	Sitka2	♀	0 - 2	Sade, Adak	non-reprod.		M,F	M		
	Snibbechein	♀	0 - 29	Wild	reproductive	4,8,10-14,17,19			F	F
	Teun	♂	0 - 13	Lammechein, Bart	non-reprod.		F		F	M,F
	Yvonne	♀	0 - 17.5	Snibbechien, Bart	reproductive	6			F	M,F
Futami Sea Paradise	Akina	♀	13 - 23	Wild						F
	Futa	♂	5.5 - 22.5	Wild	reproductive	9,12-15				F
	Haruna	♀	0 - 9.5	Akina, Yudai	reproductive	8	F		F	F
	Komachi	♀	0 - 3	Nana, Futa	non-reprod.		F		F	
	Konami	♀	0 - 5	Nana, Futa	non-reprod.		F		F	F
	Kotetsu	♂	0 - 4	Nana, Futa	reproductive	5,8,9	F		F	
	Nana	♀	2.5 - 9	Captive, Unknown	reproductive	4,5,6,7			F	
	Yae	♀	2.5 - 6	Captive, Unknown	reproductive	7,10,11			F	F
	Yudai	♂	10.5 - 18	Wild	reproductive	11				F
	Yukina	♀	17.5 - 24	Wild	non-reprod.					F
Kamogawa	Mori	♀	2 - 9	Wild	non-reprod.				M,F	M,F
	Nosa	♂	15 - 23	Wild	reproductive	16				F
	Rei	♀	0 - 5	Captive, Unknown	non-reprod.			M	M,F	
	Rui	♀	2.5 - 9	Captive, Unknown	reproductive	4			M,F	M,F
Izumito Sea Paradise	Genn	♂	10 - 17.5	Wild	neutered				M,F (neut.)	M,F (neut.)
	Wann	♂	5 - 13	Unknown	neutered				M,F (neut.)	M,F (neut.)

Male length

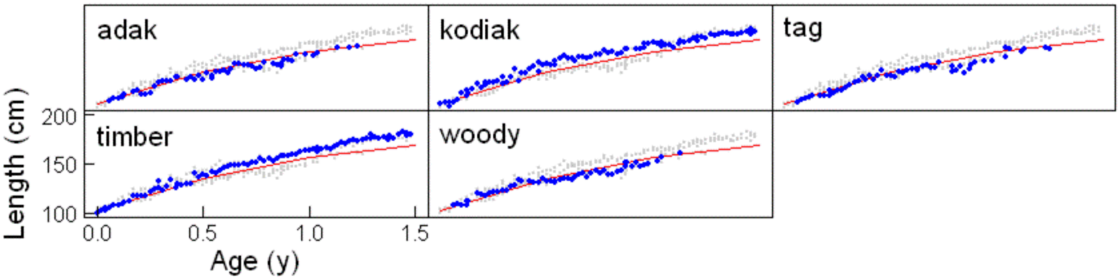

Fig. A1.1. Intact male length data from animals aged 0 to 1.5 y. Data from all animals is in gray and individual data points for each animal are in blue. The red line is the juvenile von Bertalanffy model for intact male length (Table 2.1).

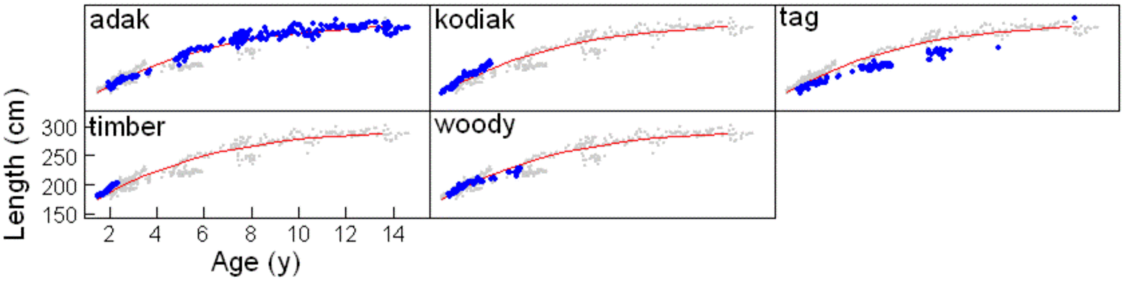

Fig. A1.2. Intact male length data from animals aged 1.5 to 15 y. Data from all animals is in gray and individual data points for each animal are in blue. The red line is the main von Bertalanffy model for intact male length (Table 2.1).

Female length

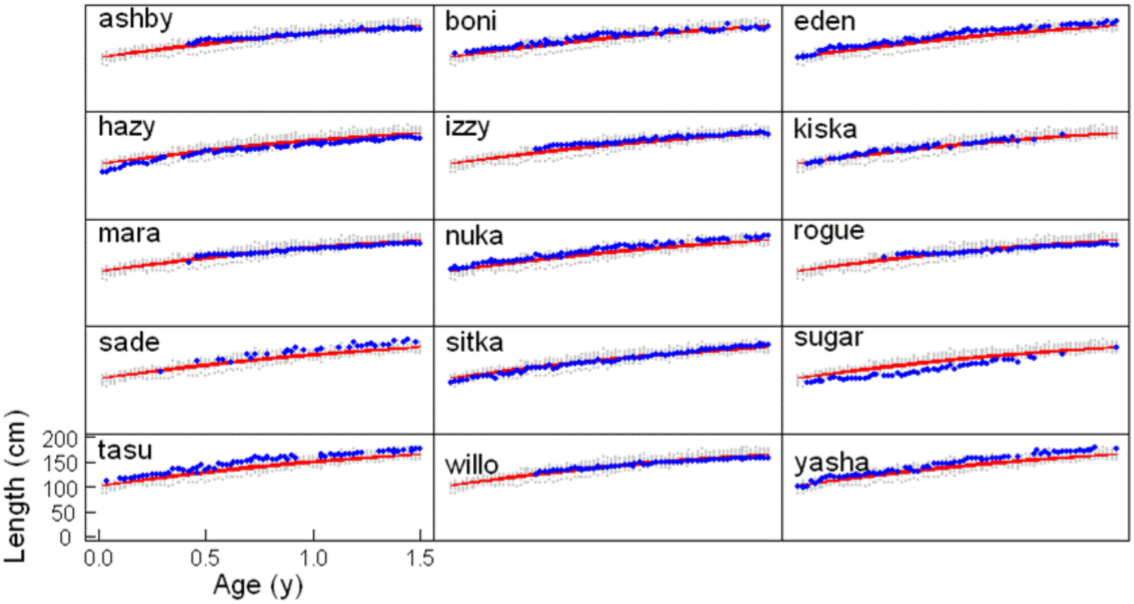

Fig. A1.3. Female length data from animals aged 0 to 1.5 y. Data from all animals is in gray and individual data points for each animal are in blue. The red line is the juvenile von Bertalanffy model for female length (Table 2.1).

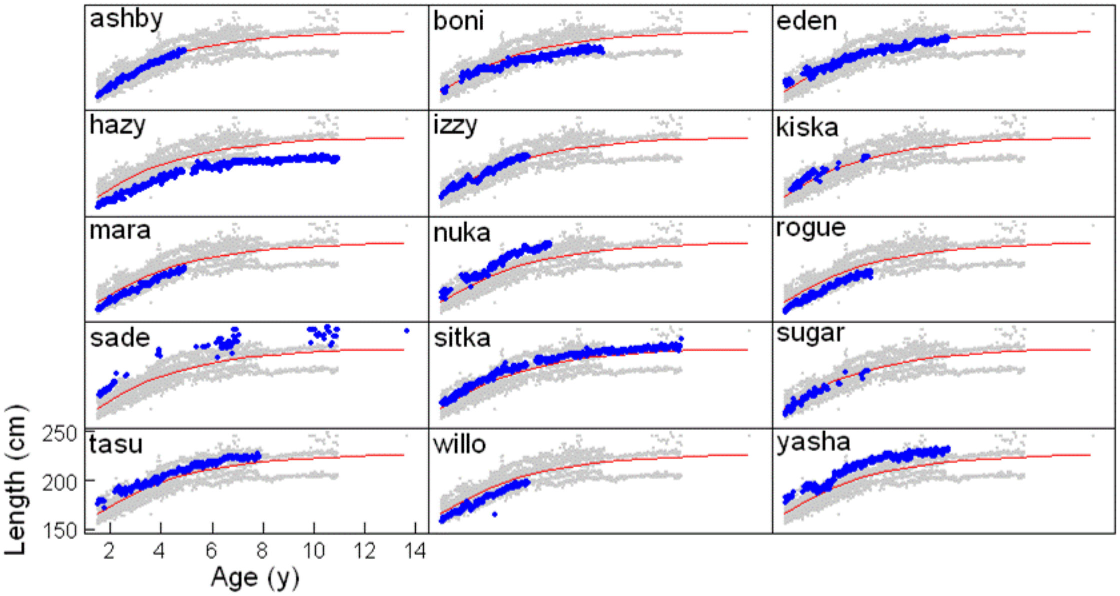

Fig. A1.4. Female length data from animals aged 1.5 to 15 y. Data from all animals is in gray and individual data points for each animal are in blue. The red line is the main von Bertalanffy model for female length (Table 2.1).

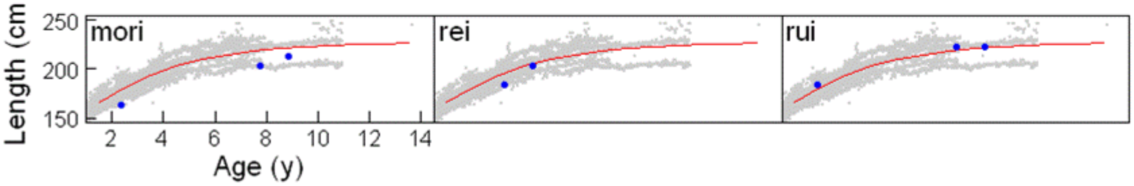

Fig. A1.5. Female length data excluded from the main model. Data from all animals is in gray and individual data points for each animal are in blue.

Male mass

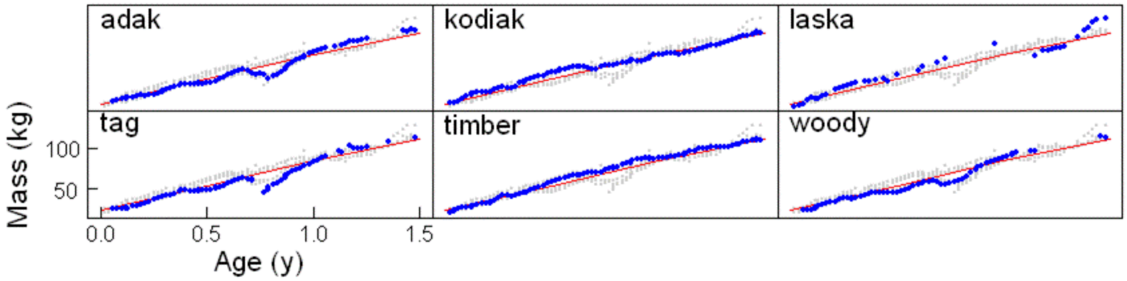

Fig. A1.6. Intact male mass data from animals aged 0 to 1.5 y. Data from all animals is in gray and individual data points for each animal are in blue. The red line is the juvenile Maturity model for intact male mass (Table 2.1).

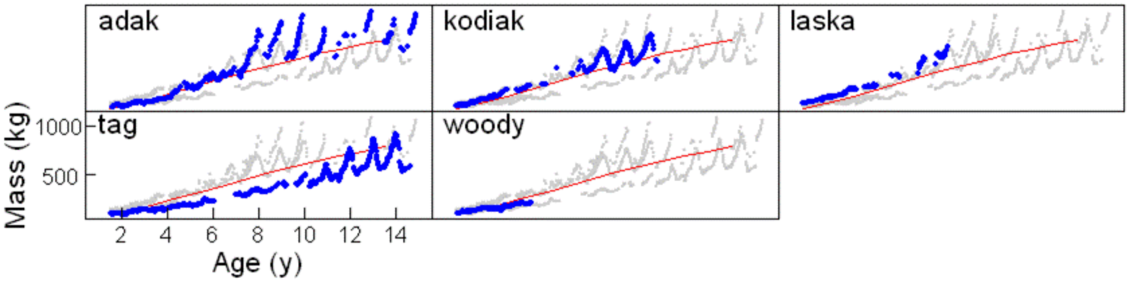

Fig. A1.7. Intact male mass data from animals aged 1.5 to 15 y. Data from all animals is in gray and individual data points for each animal are in blue. The red line is the main Maturity model for intact male mass (Table 2.1).

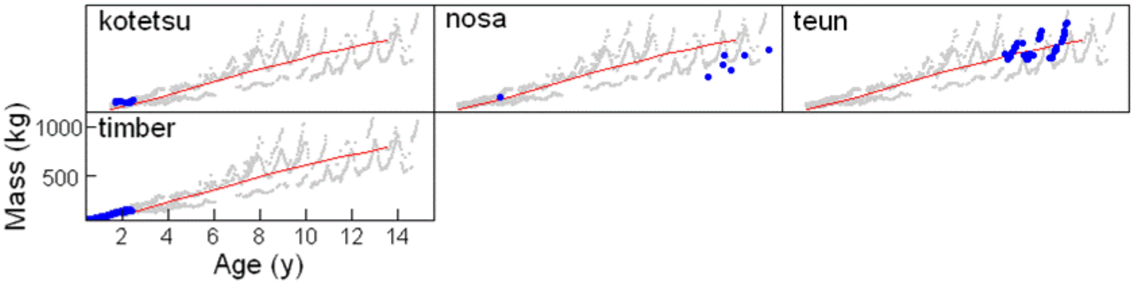

Fig. A1.8. Intact male mass data excluded from the main model. Data from all animals is in gray and individual data points for each animal are in blue.

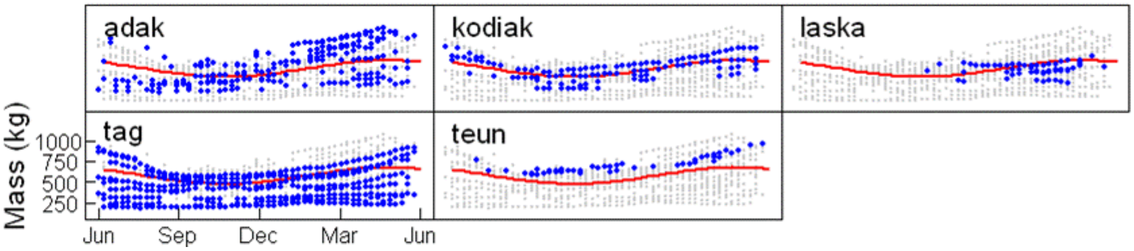

Fig. A1.9. Intact male mass data used in the sine model. Data from all animals is in gray and individual data points for each animal are in blue. The red line is the sine model for intact adult male mass (Table 2.1).

Female mass

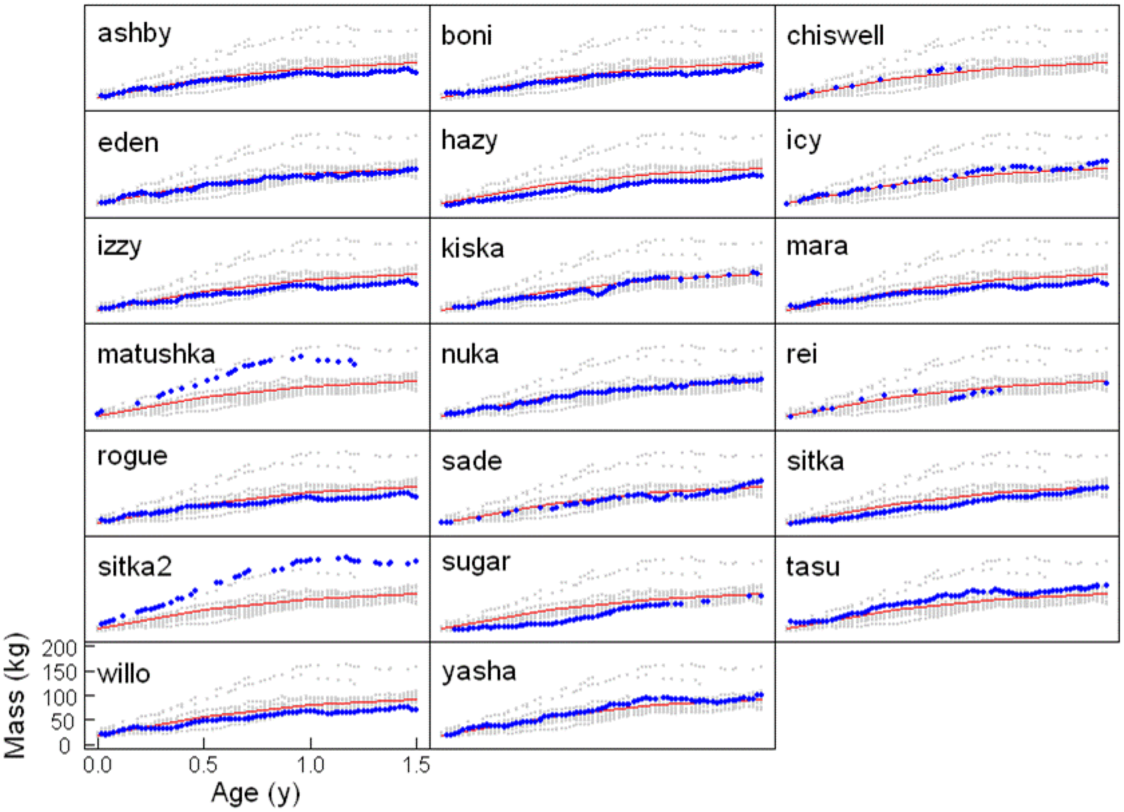

Fig. A1.10. Female mass data from animals aged 0 to 1.5 y. Data from all animals is in gray and individual data points for each animal are in blue. The red line is the juvenile Maturity model for female mass (Table 2.1).

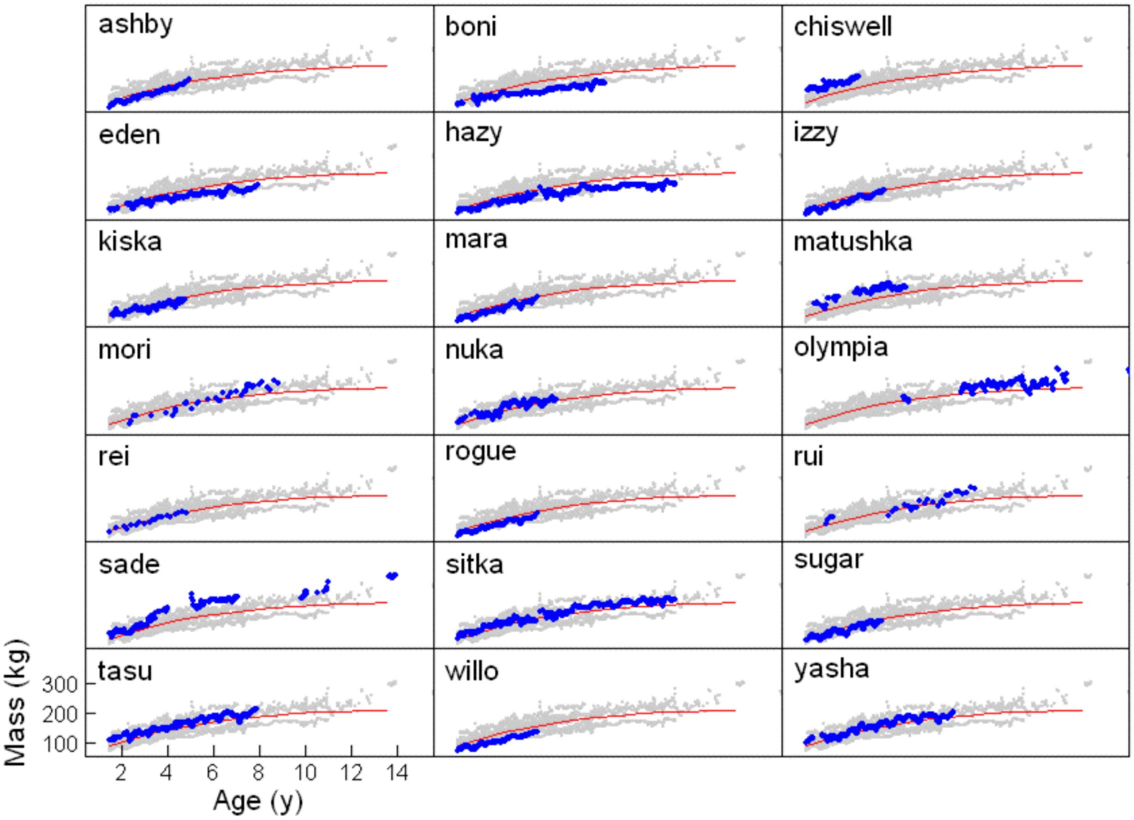

Fig. A1.11. Female mass data from animals aged 1.5 to 15 y. Data from all animals is in gray and individual data points for each animal are in blue. The red line is the main Maturity model for female mass (Table 2.1).

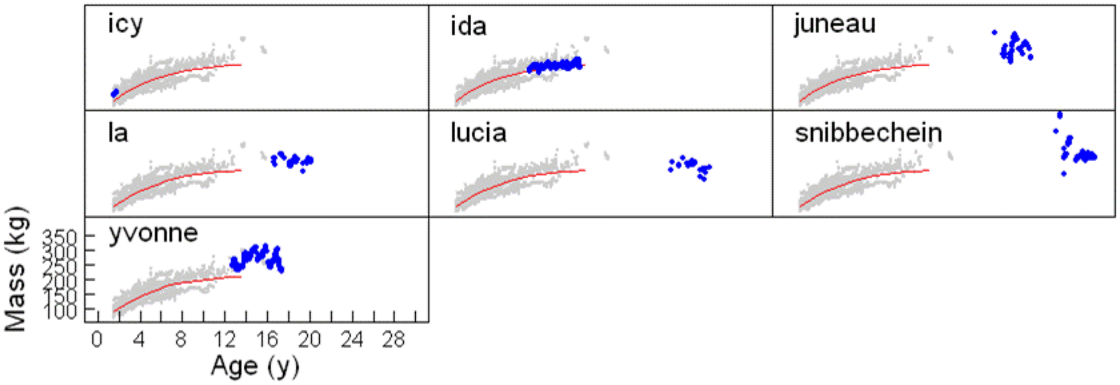

Fig. A1.12. Female mass data excluded from the main model. Data from all animals is in gray and individual data points for each animal are in blue.

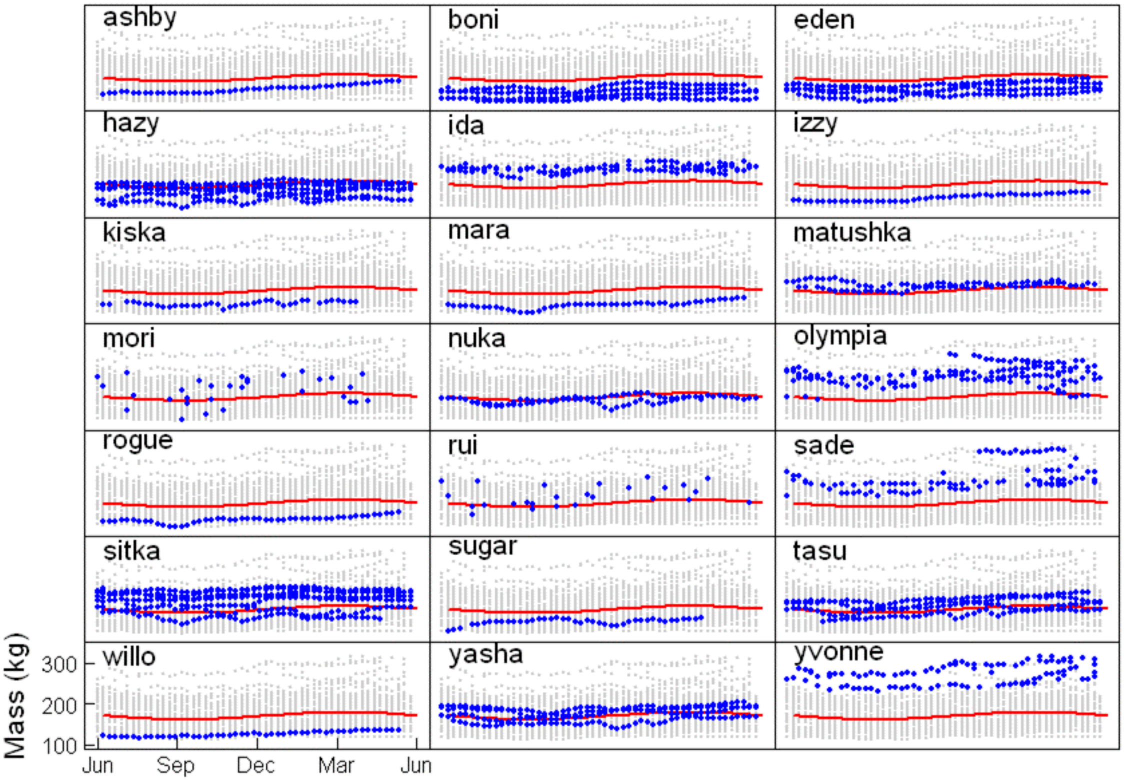

Fig. A1.13. Female mass data used in the sine model. Data from all animals is in gray and individual data points for each animal are in blue. The red line is the sine model for adult female mass (Table 2.1).

Male food intake

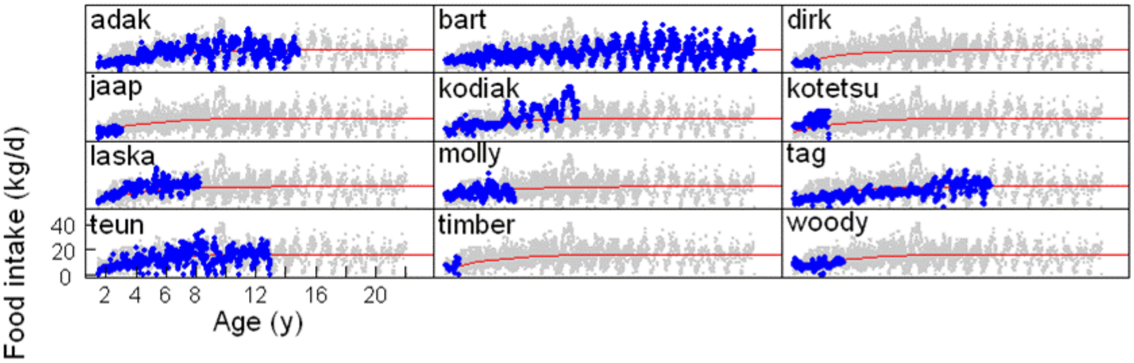

Fig. A1.14. Intact male food intake data from animals aged 1.5 to 25 y. Data from all animals is in gray and individual data points for each animal are in blue. The red line is the main Maturity model for intact male food intake (Table 2.1).

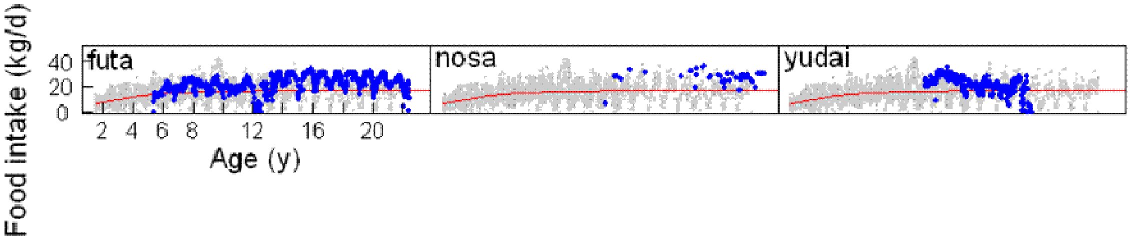

Fig. A1.15. Intact male food intake data excluded from the main model. Data from all animals is in gray and individual data points for each animal are in blue.

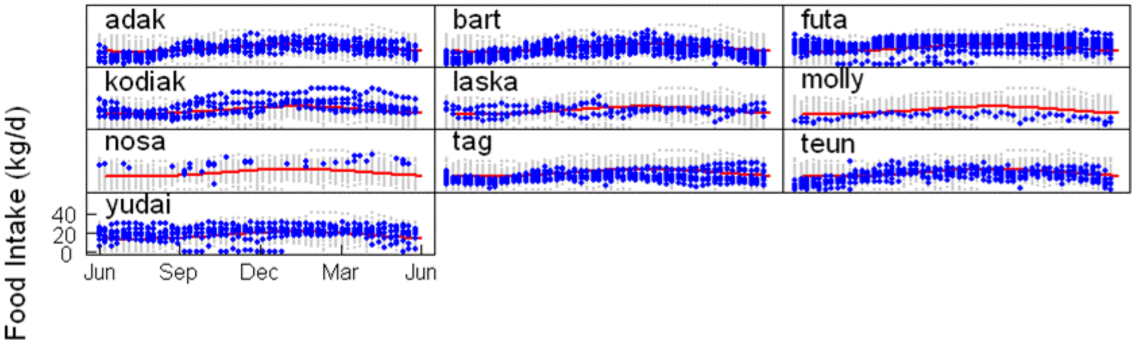

Fig. A1.16. Intact male food intake data used in the sine model. Data from all animals is in gray and individual data points for each animal are in blue. The red line is the sine model for intact adult male food intake (Table 2.1).

Female food intake

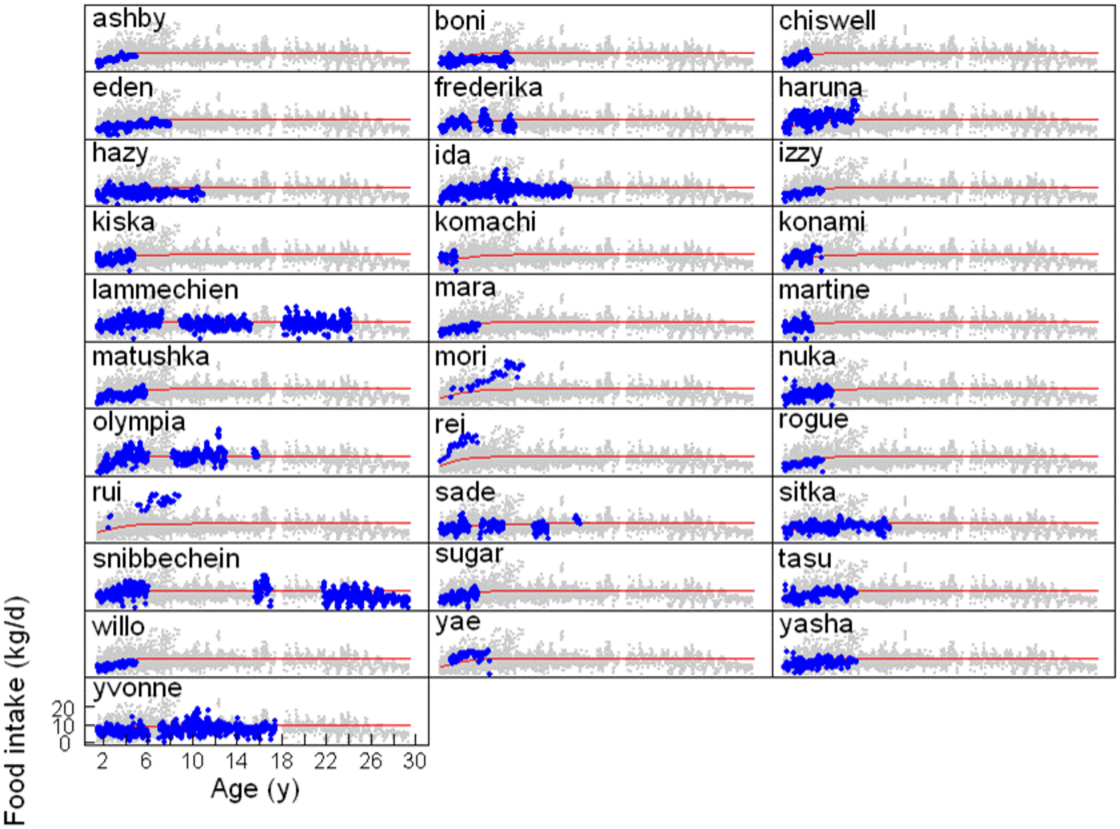

Fig. A1.17. Female food intake data from animals aged 1.5 to 30 y. Data from all animals is in gray and individual data points for each animal are in blue. The red line is the main Maturity model for female food intake (Table 2.1).

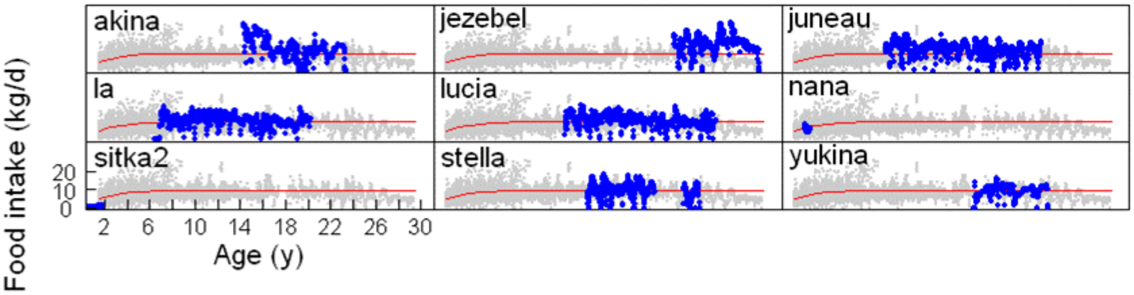

Fig. A1.18. Female food intake data excluded from the main model. Data from all animals is in gray and individual data points for each animal are in blue. The red line is the main Maturity model for female food intake (Table 2.1).

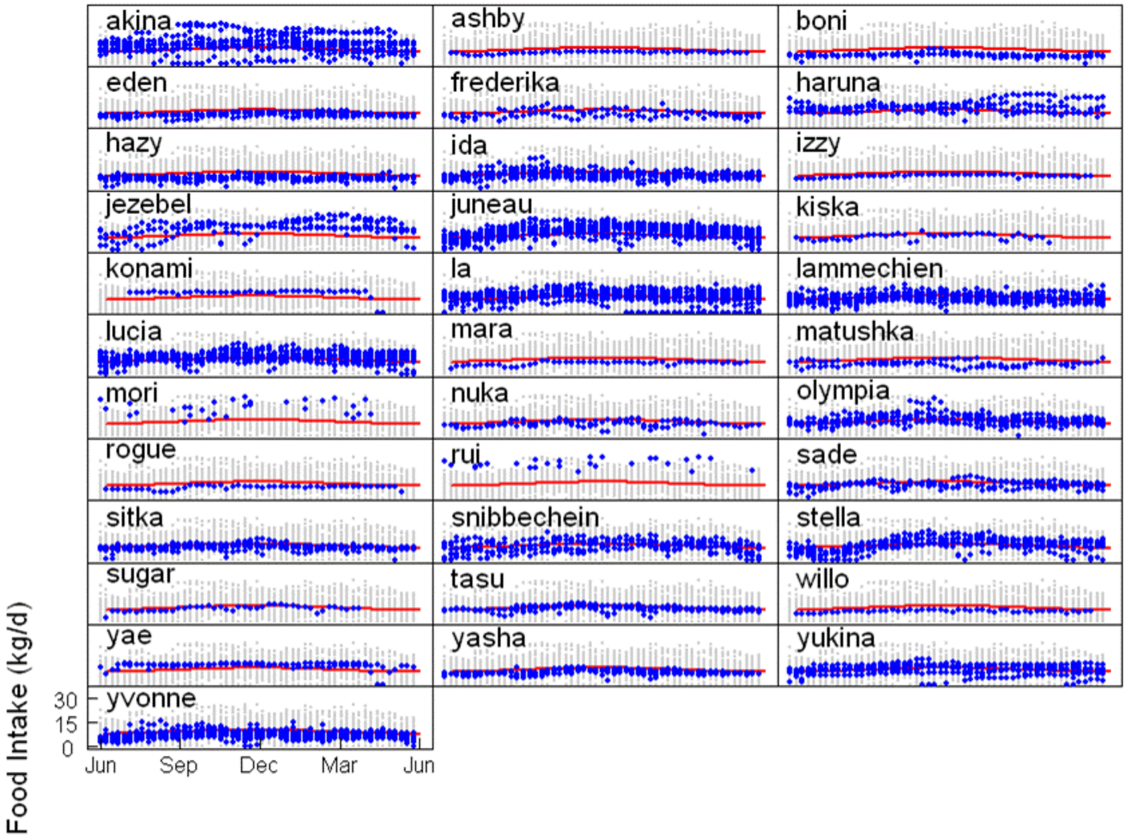

Fig. A1.19. Female food intake data used in the sine model. Data from all animals is in gray and individual data points for each animal are in blue. The red line is the sine model for adult female food intake (Table 2.1).

Pup mass

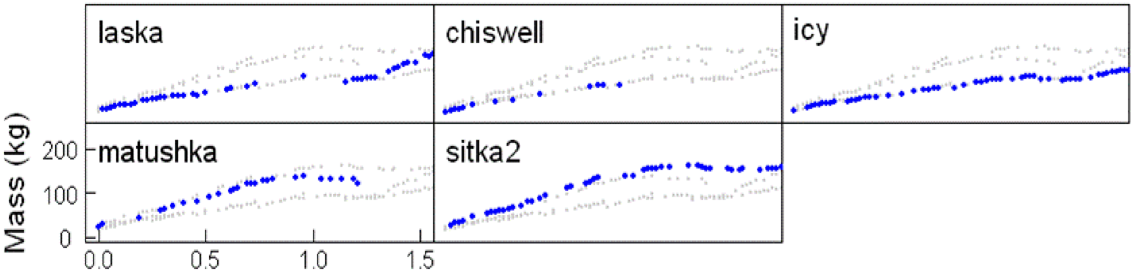

Fig. A1.20. Mass data from pups. Data from all pups is in gray and individual data points for each animal are in blue.

Pup fish intake

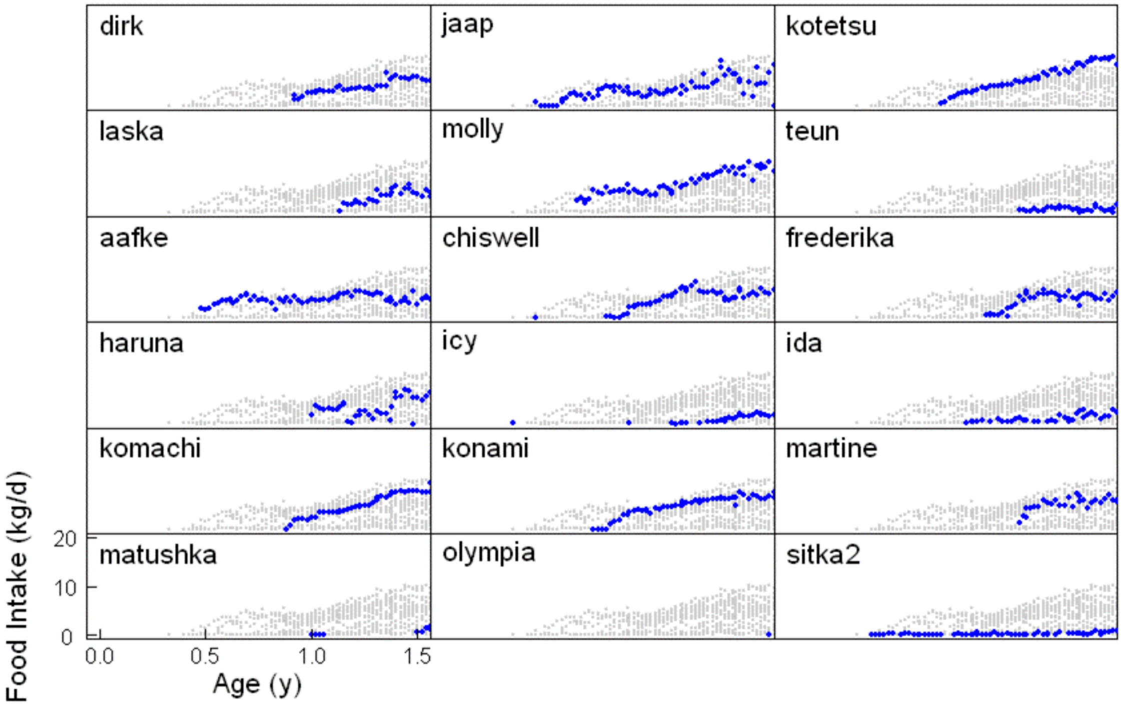

Fig. A1.21. Fish intake data from pups. Data from all pups is in gray and individual data points for each animal are in blue.

Pregnant female mass

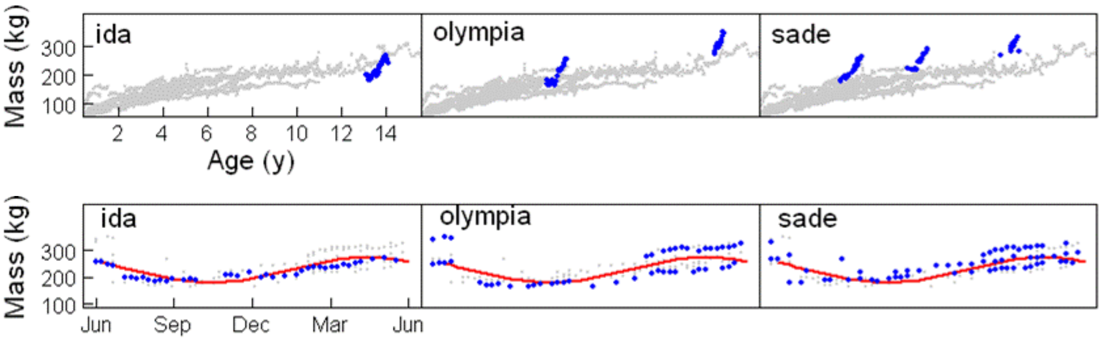

Fig. A1.22. Pregnant female mass. Top: Pregnant female mass data in blue with data from all non-reproductive animals in gray. Bottom: Pregnant female mass data used in the sine model (red line; Table 2.1).

Pregnant female food intake

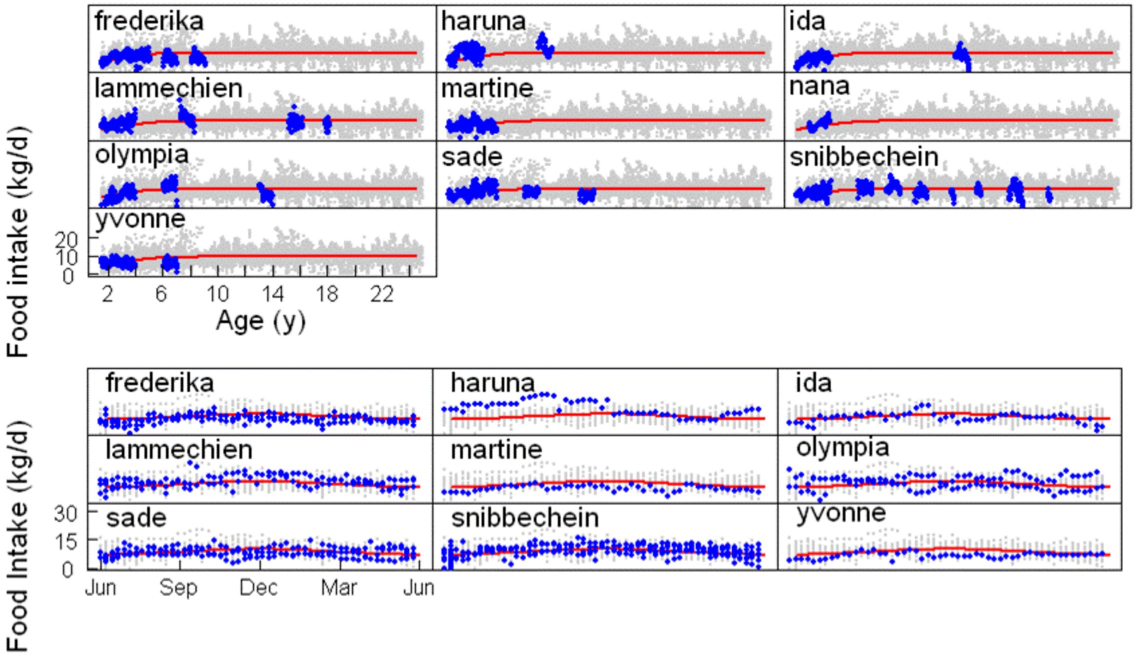

Fig. A1.23. Pregnant female food intake.
Top: Pregnant female food intake data in blue with data from all non-reproductive animals in gray. The red line is the main Maturity model for pregnant female food intake (Table 2.1).
Bottom: Pregnant female food intake data used in the sine model (red line; Table 2.1).

Lactating female mass

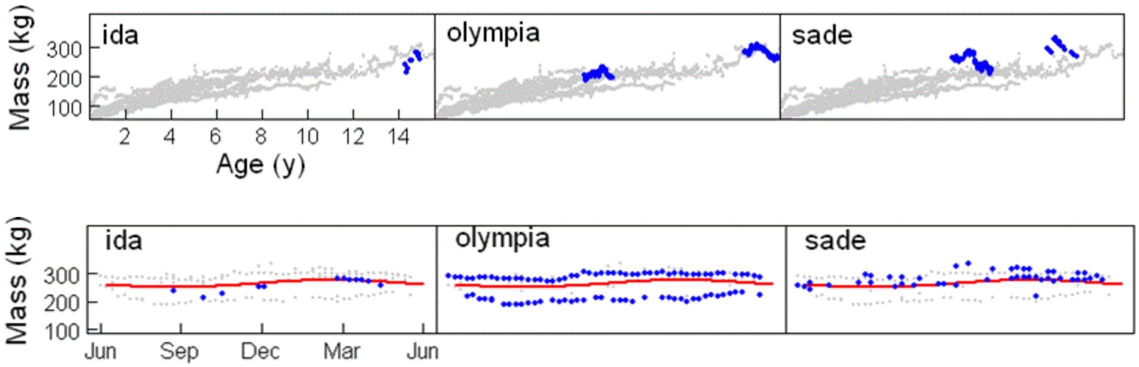

Fig. A1.24. Lactating female mass. Top: Lactating female mass data in blue with data from all non-reproductive animals in gray. Bottom: Lactating female mass data used in the sine model (red line; Table 2.1).

Lactating female food intake

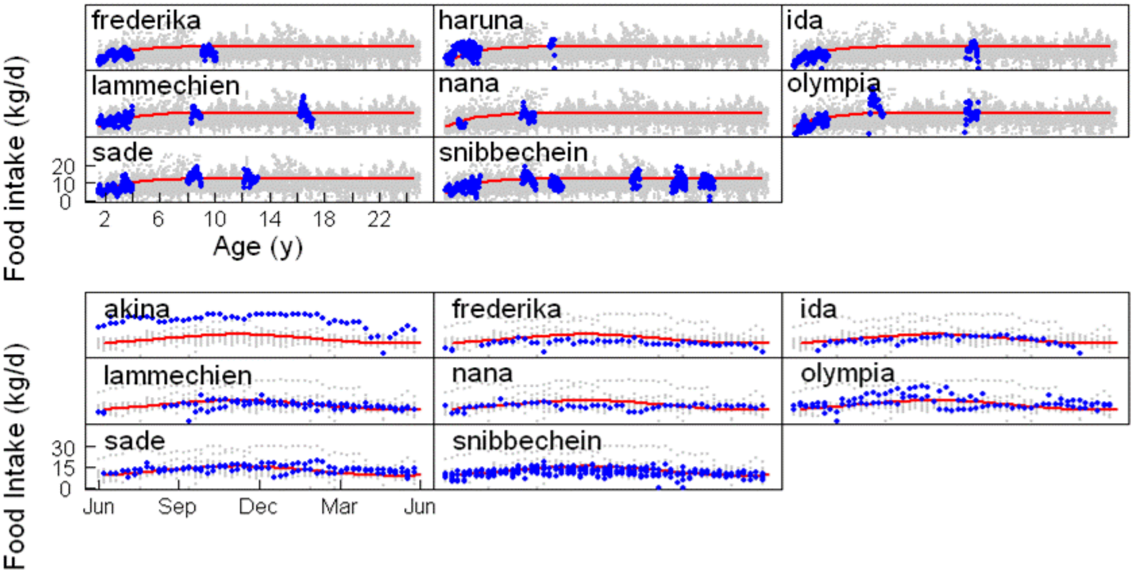

Fig. A1.25. Lactating female food intake.
Top: Lactating female food intake data in blue with data from all non-reproductive animals in gray. The red line is the main Maturity model for lactating female food intake (Table 2.1).
Bottom: Lactating female food intake data used in the sine model (red line; Table 2.1).

Neutered male mass

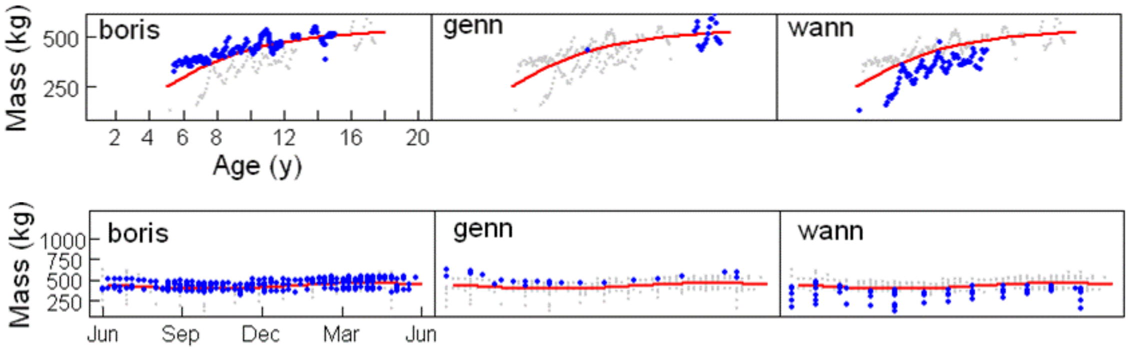

Fig. A1.26. Neutered male mass data. Top: Neutered male mass data in blue with data from all neutered animals in gray. The red line is the main Maturity model for neutered male mass (Table 2.1). Bottom: Neutered male mass data used in the sine model (red line; Table 2.1).

Neutered male food intake

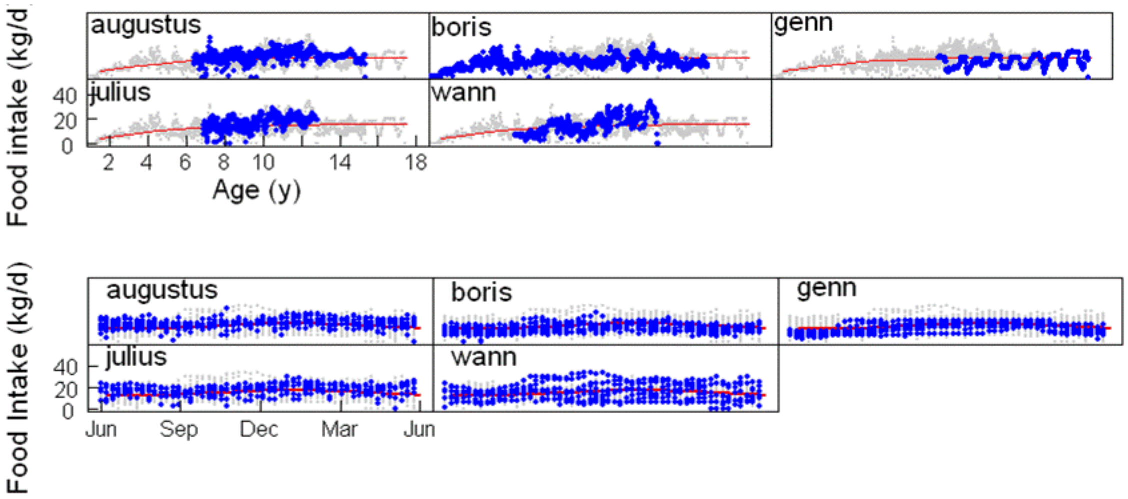

Fig. A1.27. Neutered male food intake data. Top: Neutered male food intake data in blue with data from all neutered animals in gray. The red line is the main Maturity model for neutered male food intake (Table 2.1). Bottom: Neutered male food intake data used in the sine model (red line; Table 2.1).

Appendix 2: Fish energetic composition of all prey species fed at all facilities. Vancouver and Mystic Aquariums analyzed the composition of fish fed to Steller sea lions using proximate composite analysis.

Facility	Prey Species	Mean Prey Energy Content (kJ/g wet mass)	Percent of Food Intake	% of Energy Intake	Source
Vancouver Aquarium	Pacific herring, *Clupea palasii*	7.794	88	94	Analyzed by facility
	Squid, *Illex spp.*	2.600	4	2	
	Pollock, *Theragra chalcogramma*	4.358	3	2	
	Capelin, *Mallotus villosus*	3.573	3	1	
	Pink salmon, *Oncorhynchus gorbuscha*	5.330	2	1	
Mystic Aquarium	Herring, *Clupea harengus*	5.311	61		Analyzed by facility
	Capelin, *Mallotus villosus*	3.679	21		
	Squid, *Loligo brevis*	4.034	13		
	High-fat herring, *Clupea harengus*	7.662	3		
	Mackerel, *Scomber scombrus*	7.080	2		
Dolfinarium Harderwijk	Atlantic herring, *Clupea harengus*	9.366	73		(Maartensson et al. 1996)
	Horse mackerel, *Trachurus trachurus*	5.650	25		(Balmelli & Wickens 1994)
	Sprat, *Sprattus sprattus*	4.500	2		(Arrhenius 1998)
Futami Sea Paradise	Atka mackerel, *Pleurogrammus monopterygius*	6.329*	73		Vancouver and Mystic Aquariums
	Okhostk atka mackerel, *Pleurogrammus azonus*	6.610	21		(Perez & Bigg 1986)
	Surf smelt, *Hypomesus pretiosus*	4.390	4		(Anthony et al. 2000)
	Squid, *Illex illecebrosus* & *Gonatus fabricii*	6.400**	2		(Lawson et al. 1998)
Izumito Sea Parasise	Chub mackerel, *Scomber japonicus*	7.060	76		(Eder & Lewis 2005)
	Arabesque greenling, *Pleurogrammus azonus*	3.450	24		(Van Pelt et al. 1997)
Kamogawa Sea World	Unknown	6.252	100	100	Weighted mean of fish energy from Futami and Izumito

*Taken as an average of the values from both facilities; **Taken as an average between the two species

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