

**COMPARING THE NUTRITIONAL QUALITY OF
STELLER SEA LION (*EUMETOPIAS JUBATUS*) DIETS**

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ABSTRACT

Steller sea lions have been declining precipitously within portions of their range over the past three decades and although the primary cause(s) remains unknown, one hypothesis is nutritional stress. Nutritional stress may be attributable to reduced preferred prey availability and/or prey quality and could be the result of commercial fisheries removals or, alternately, environmental changes such as climatic regime shifts. At the Alaska SeaLife Center (ASLC), researchers have formulated three different feeding regimes representative of Steller sea lion diets: prior to their population decline (Gulf of Alaska, 1970s), during their decline (Gulf of Alaska, 1980s), and from a stable or growing population (southeast Alaska, 1990s). The purpose of this project was to compare the nutritional quality of these three Steller sea lion diets that differ in prey species composition. Proximate composition and bomb calorimetry were used to determine energy density of prey species. Variations in the proximate composition of prey species, such as high energy herring and low energy octopus, affected the overall energy densities of the different diets. While the pre-decline and stable diets were composed of more high fat fish such as herring, capelin and pink salmon, the decline diet contained more lower fat prey items, such as octopus, Dover sole and rock sole. The resulting overall energy densities provided by the pre-decline and stable diets are similar to one another and significantly higher in energy density than the decline diet. Assuming that the ten prey species analyzed for this study adequately represent the bulk of prey consumed by Steller sea lions and that these formulated diets are representative of Steller sea lion diets prior to and during their population decline and in stable populations, results from this study are consistent with the possibility that nutritional stress is a cause of the Steller sea lion decline.

TABLE OF CONTENTS

ABSTRACT	iii
LIST OF TABLES	v
LIST OF FIGURES	vi
ACKNOWLEDGMENTS	vii
INTRODUCTION	1
METHODS	4
Sample Collection and Analysis	4
Lipid Extraction Solvent Validation	7
Feeding Regimes	9
Statistical Analysis	10
RESULTS	11
Whole Body Energy Content and Proximate Composition	11
Feeding Regimes	11
DISCUSSION	13
Prey Species	13
Comparing bomb calorimetry with proximate composition	17
Feeding Regimes	19
REFERENCES	21

LIST OF TABLES

Table 1.	Three Steller sea lion feeding regimes: Diet A, western stock prior to population decline and climate shift; Diet B, western stock during decline and after the climate shift; and Diet C, stable eastern stock in Southeast Alaska. Diets are based on feeding studies conducted at the Alaska SeaLife Center (ASLC) from 1998-2001. % Bio = percent biomass (wet). Rock Sole and Dover Sole % Bio are equal divisions of one value for total flatfish % biomass. Rank is decreasing order of percentages. (Source: V. Burkanov and D. Calkins, pers. comm.).....	35
Table 2.	Source information for Steller sea lion prey items subsampled from food fed to Steller sea lions at the ASLC between 1998 and 2001.....	36
Table 3.	Proximate composition (% water, ash, protein and lipid) values (\pm SD) comparing lipid extraction methods and corresponding ranking of each species on a wet mass basis. Rank is decreasing order of percentages.....	37
Table 4.	Comparison of \log_{10} -transformed mean (\pm SD) lipid content between two lipid extraction solvents for Steller sea lion prey species.....	38
Table 5.	Conversion factors between lipid extraction methods. All values are wet mass. Hx:Ia = Hexane/Isopropyl alcohol solvent, Ch:Mth=Chloroform/Methanol solvent, ln=natural log, a=intercept, b=slope	39
Table 6.	P-values comparing \log_{10} -transformed protein and lipid content among species, NS = no significance. Protein comparisons are in the upper triangle and lipid comparisons are in the lower triangle. WP = Walleye Pollock, PH = Pacific herring, OP = Octopus, PS = Pink salmon, PC = Pacific cod, DS = Dover sole, RS = rock sole, SL = sandlance, CP = capelin, SQ = squid.....	40
Table 7.	Comparing month, year, energy density values (wet mass, kcal/g), length, mass, water content (%), and locations of selected Steller sea lion prey species analyzed from literature sources and this study. GOA = Gulf of Alaska, NGOA = Northern Gulf of Alaska, PWS = Prince William Sound, AK = Alaska, AI = Aleutian Islands, CN = Canada, BC = British Columbia. Blank cells represent lack of data. Atlantic herring is included to compare energy densities of different locations.....	41

LIST OF FIGURES

- Figure 1.** Method comparison of mean dry mass energy density (\pm SD) resulting from two methods of lipid extraction and bomb calorimetry of Steller sea lion prey species.....**49**
- Figure 2.** Scatter plot of Pacific sand lance lipid values, chloroform/methanol values along x-axis and hexane/isopropyl alcohol values along y-axis.....**50**
- Figure 3.** Mean lipid and protein values (%) of prey species with standard deviations. Areas above bars represent ash content.....**51**
- Figure 4.** Total energy densities of prey species with relative contributions of lipid and protein energy. Percent water is plotted to demonstrate the inverse relationship with energy density.....**52**
- Figure 5.** Energy densities (wet mass basis) (\pm SD) derived from bomb calorimetry and proximate composition using hexane/isopropanol 7:2 (v:v) lipid extraction solvent for three different Steller sea lion diets.....**53**
- Figure 6.** Comparison of the protein and lipid content % (\pm SD) of Steller sea lion feeding regimes on a wet mass basis.....**54**

INTRODUCTION

Steller sea lions (*Eumetopias jubatus*) inhabit coastal waters of the North Pacific from California through Alaska to the Kuril Islands and northern Japan (Scheffer 1958, Rice 1977) and their numbers have declined precipitously over the past three decades within portions of their range. The worldwide population of Steller sea lions estimated at 240,000 to 300,000 animals in the 1960s, plummeted to approximately 116,000 animals by 1989 (Kenyon and Rice 1961, Loughlin *et al.* 1992). This 39-48% worldwide decline resulted in the listing of Steller sea lions as threatened in 1990 under the Endangered Species Act (ESA) (National Marine Fisheries Service 1997). Between 1956 and 1960, the greatest abundance of Steller sea lions was observed in the western Gulf of Alaska and Aleutian Islands, where over 140,000 animals were counted (Mathisen and Lopp 1963, Merrick *et al.* 1987). The animals in western Alaska have been disappearing rapidly, whereas Steller sea lion numbers between southeast Alaska and northern California have stabilized and even increased (Angliss *et al.* 2001). Regional discrepancies in population dynamics spurred genetic investigations, resulting in splitting the species into eastern and western stocks separated at 144° W longitude (Bickham *et al.* 1996, Loughlin 1997). Due to the disparate population trajectories of the two Steller sea lion stocks, the eastern stock maintains its threatened status while the western stock was reclassified as endangered under the ESA in 1997 (National Marine Fisheries Service 1997).

Although the primary cause(s) of the Steller sea lion decline remains unknown, one hypothesis is nutritional stress. Studies investigating the role of pollution, predation, disease, and subsistence hunts on Steller sea lion populations have shown that none of these are likely to have been the sole cause of the decline (Loughlin and York 2001). Animals require a certain amount of energy to meet metabolic demands, such as thermoregulation, basal metabolism, foraging, growth, and reproduction (Robbins 1993). Without sufficient energy to meet their requirements, an animal or population will experience nutritional stress, which is defined here as the reduced fitness of an organism due to changes in the amount and/or quality of prey available. Thus, reduced reproductive rates and reduced survival of Steller sea lions may be due to decreases in

either or both quantity or quality of Steller sea lion prey caused by commercial fishery interactions and/or climate changes (Braham *et al.* 1980, Loughlin 1984, Merrick *et al.* 1987, Pascual and Adkison 1994, Trites and Larkin 1996, Merrick *et al.* 1997, Loughlin 1998). Environmental fluctuations are known to cause changes in zooplankton and ecosystem compositions (Francis and Hare 1994, McGowan *et al.* 1998). For example, the North Pacific sea surface temperature changed rapidly from a cold-water regime from 1947 through 1976 to a warm water regime from 1977 onward (Royer 1989, Ebbesmeyer *et al.* 1991, Kerr 1992, Francis and Hare 1994, Trenberth and Hurrell 1994, McGowan *et al.* 1998). This regime shift resulted in the abrupt displacement of forage fish species, such as capelin (Van Pelt *et al.* 1997), by gadids, such as walleye pollock (Anderson and Piatt 1999, Payne *et al.* 1999, Mueter and Norcross 2000). Capelin are generally considered a high lipid forage fish, while walleye pollock are regarded as a low lipid species (Van Pelt *et al.* 1997). Such changes in prey availability and subsequent differences in diet quality may help to explain Steller sea lion population declines, consistent with the nutritional stress hypothesis (Merrick *et al.* 1987, Loughlin 1998, Anderson and Piatt 1999).

Steller sea lions are opportunistic predators whose primary prey vary geographically and temporally (Mathisen *et al.* 1962; Fiscus and Baines 1966; Pitcher 1981; Merrick *et al.* 1997). Common prey species include walleye pollock (*Theragra chalcogramma*), Atka mackerel (*Pleurogrammus monopterygius*), Pacific herring (*Clupea pallasii*), Pacific cod (*Gadus macrocephalus*), Pacific sand lance (*Ammodytes hexapterus*), capelin (*Mallotus villosus*), rockfishes (*Sebastes* spp.), flatfishes (Pleuronectidae), sculpins (Cottidae), salmon (*Oncorhynchus* spp.), greenlings (Hexagrammidae), octopus (*Octopus* spp.) and squid (Gonatidae) (Mathisen *et al.* 1962, Fiscus and Baines 1966, Pitcher 1981, Loughlin 1998, Merrick *et al.* 1997).

For this study, I focused on one aspect of nutritional quality, defined here as the energy density, sometimes referred to as gross energy, (kcal/g) of prey items, and further considered proportions of protein and lipid as they contribute to energy density. Energy density can be determined by proximate composition analysis and by bomb calorimetry

(Watt & Merrill 1950). Proximate composition analysis determines the amounts of water and major organic compounds; i.e., dry matter protein, lipid, carbohydrate and ash (Watt and Merrill 1950). Organic energy sources include protein, lipids and carbohydrates (Watt and Merrill 1963). Carbohydrates are regarded as negligible components of fish (Chatfield and Adams 1940, Goodman-Lowe *et al.* 1999, Payne *et al.* 1999) and therefore were not analyzed in the present study. The term 'lipid' refers to water insoluble components also called oil or fat (Watt and Merrill 1975). The energy density of lipid is almost twice as much as that of protein or carbohydrates (Watt and Merrill 1963) and it is therefore more potentially valuable as an energy source. Bomb calorimetry measures the whole body energy content (WBEC) of a sample (Food and Agriculture Organization of the United Nations 1947), which can then be converted to overall energy density and used as a standard for comparison. In this study, overall energy density values calculated from proximate composition analysis were compared to energy density values directly determined by bomb calorimetry and literature values for each species.

The primary objective of this investigation was to compare the nutritional quality of three different diet compositions, formulated to represent diets at times and places of different Steller sea lion population trajectories. To address this objective, it was essential to determine the nutritional quality of each prey species comprising the different diet regimes. To determine the nutritional quality of each prey species, it was first necessary to validate the methodology of our lipid extraction analyses.

METHODS

Sample Collection and Analysis

Three different feeding regimes representative of Steller sea lion diets (1) prior to their population decline (Gulf of Alaska, 1970s), (2) during their decline (Gulf of Alaska, 1980s), and (3) from a stable or growing population (southeast Alaska, 1990s)^{1 2}(Merrick & Calkins 1996, Castellini 2001) (Table 1) were fed to captive sea lions at the ASLC. Each diet differed in composition, frequency of occurrence and biomass of prey species. The diets were determined by Don Calkins (ASLC) and Vladimir Burkanov (National Marine Fisheries Service (NMFS), formerly ASLC), based on Calkins' research (D. G. Calkins and E. A. Goodwin, Investigation of the Declining Sea Lion Population in the Gulf of Alaska, unpublished report, Alaska Department of Fish and Game, Anchorage, AK, 1988; Calkins 1998; Merrick and Calkins 1996) and literature values. The three feeding regimes comprised ten prey species listed in order of decreasing importance, defined as percent biomass in each feeding regime on a wet mass basis: walleye pollock, Pacific herring, octopus, pink salmon (*Oncorhynchus gorbuscha*), Pacific cod, Dover sole (*Microstomus pacificus*), rock sole (*Pleuronectes bilineatus*), Pacific sand lance, capelin, and squid (*Loligo pealei*). Prey items analyzed for this study were randomly sampled from single batches of commercially harvested species which were purchased by the ASLC to feed their captive Steller sea lions (Table 2). Individual prey items were not separated by age or sex classes. The smaller sample sizes of octopus, salmon and Pacific cod are due to the lower numbers of available items of these species. The five octopus were debeaked and eviscerated. Four of the pink salmon were eviscerated and decapitated. All other prey items sampled were whole fish.

Bomb calorimetry energy values and proximate composition estimates of energy density were both determined in this study and compared to one another to cross-check values (Craig *et al.* 1978). Bomb calorimetry of all samples was conducted at the ASLC,

¹ Personal communication from V. Burkanov, Natural Resources Consultants, Inc., contracted by National Marine Mammal Laboratory, National Marine Fisheries Service, NOAA, Seattle, WA, April 2000.

² Personal communication from D. Calkins, Steller sea lion Program Manager, Alaska SeaLife Center, Seward, Alaska. April 2000.

Seward, AK. Seven species were homogenized and lyophilized at the ASLC, Seward, AK between May and August 2000. Due to their large size, the three remaining species (octopus, Pacific cod and pink salmon) were homogenized by commercial grinders and lyophilized at the Fishery Industrial Technology Center (FITC), Kodiak, AK in August 2001. Homogenization and drying of samples were assumed to be of equal quality between the two facilities. Ash and lipid content analyses were conducted both at the Alaska SeaLife Center, Seward, AK from June to August of 2000 and at the University of Alaska Fairbanks, between September 2000 and September 2001. Ashing was assumed to be of equal quality between the two facilities since the muffle furnaces were of the same type and temperature. Lipid content analysis for some samples was repeated at the University of Alaska Fairbanks to check for interlab variability. For species in which significant differences existed, lipid analysis was redone at the University of Alaska Fairbanks and those values were then used for subsequent data analysis. Protein content analysis was conducted by the Soils Laboratory at the University of Alaska Fairbanks between September 2000 and 2001.

Proximate analysis was composed of several steps to determine the nutritional quality of prey items. Partially frozen whole prey items were measured, weighed and homogenized in commercial grinders and food processors. Approximately 20 g wet weight of homogenized samples were collected in duplicate from each individual per species and placed on a Labconco 6-liter benchtop lyophilizer to remove moisture for 3-6 days, or until weight changes were negligible (i.e., less than 0.001g weight change). Water content was determined by calculating the weight difference before and after lyophilizing. Subsequent analyses were conducted using portions of the dried, homogenized samples. Technicians at the ASLC placed approximately 0.5 g of dried sample in a Parr 1261 Isoperibol bomb calorimeter, which oxidizes a sample in a combustion chamber to measure the resulting heat released by the sample. The change in heat is then converted to the dry matter chemical energy (calories) contained in the sample (Robbins 1993). Approximately 0.2 g of each homogenized, dried sample was placed in a LECO model 2000 CNS analyzer to determine dry matter nitrogen content via

a thermal conductivity cell (Nelson and Sommers 1996). Nitrogen values were converted to protein content based on the assumption that protein contains 16% nitrogen (Watt and Merrill 1963) (Equation 1) (Association of Official Analytical Chemists 1990, p. 937).

$$\text{Protein content (\%)} = \text{nitrogen content (\%)} \times 6.25. \quad (1)$$

Ash content refers to mineral content and was determined by placing 0.5 g of dried, pre-weighed sample in a 550°C muffle furnace for 24 hours (Section 938.08, Association of Official Analytical Chemists 1990). The weight of material remaining was considered inorganic dry matter ash content. Lipid content was determined by a difference in weights before and after placing approximately 0.5 g of homogenized, dried sample in a Soxhlet apparatus, which repeatedly immersed samples in a lipid extraction solvent (Helrich 1990). Resulting protein, lipid and ash content values are on a dry matter basis as homogenized dried samples were used for each portion of proximate analysis after lyophilization. Multivariate analysis of variance (MANOVA) was used to analyze variations in water, and dry matter ash, protein and lipid content across species (Johnson and Wichern 1992). General linear model (GLM) procedures were used because of unbalanced data (Cody and Smith 1997). Statistical analyses were performed using SAS 8.2 (1999-2001 SAS Institute, Cary, North Carolina, U.S.A).

Protein and lipid content values were used to calculate whole body energy density estimates for each species as these are the major energy-contributing components of analyzed prey species (Chatfield and Adams 1940, Watt and Merrill 1963, Goodman-Lowe *et al.* 1999, Payne *et al.* 1999). To estimate energy density of prey species, the dry sample mass first had to be converted into wet sample mass (Equation 2). Next, dry protein and lipid mass were converted to wet protein and lipid mass (Equation 3) and then multiplied by their energy equivalents to estimate overall wet mass energy density (Equation 4) (Watt and Merrill 1963).

$$\text{Sample wet mass (g)} = \text{sample dry mass (g)} \div (1 - \text{water content of prey item (g)}) \quad (2)$$

$$X \text{ wet mass (g, \%, or kcal/g)} = X \text{ dry mass (g, \%, or kcal/g)} \div \text{sample wet mass} \quad (3)$$

Where X = protein, lipid, or ash content, or energy density.

$$\begin{aligned} \text{Energy density (} \frac{\text{Kcal}}{\text{g wet mass}} \text{)} = & \text{protein (} \frac{\text{g protein}}{\text{g wet sample}} \text{)} \times 5.65 (\frac{\text{Kcal}}{\text{g protein}} \text{)} + \\ & \text{lipid (} \frac{\text{g lipid}}{\text{g wet mass}} \text{)} \times 9.50 (\frac{\text{Kcal}}{\text{g lipid}} \text{)} \end{aligned} \quad (4)$$

The measured total energy density (cal/g) value from bomb calorimetry for each sample was converted to kcal/g on a wet mass basis (Equations 2, 3, and 4).

Lipid Extraction Solvent Validation

To determine the nutritional composition of prey items, it was first necessary to determine the most accurate method of lipid extraction. Chloroform/methanol (2:1 v:v) has previously been the lipid extraction solvent commonly used with the Soxhlet apparatus (Bligh and Dyer 1959), however this solution is not only highly toxic, but also may overestimate lipid content by removing non-lipid materials (Radin 1981). An alternate lipid extracting solvent is hexane/isopropyl alcohol (7:2 v:v), which is less toxic than chloroform/methanol and reportedly extracts only lipids (Radin 1981).

Duplicate samples of all prey species were placed in both extraction solvents, the resulting lipid content values were used with protein content to calculate overall energy densities on a wet mass basis. They were then compared to converted wet mass bomb calorimetry estimates. The solvent which led to closer approximations of energy density when compared to bomb calorimetry values was considered the more accurate extraction solvent. Multivariate analysis of variance (MANOVA) (Johnson and Wichern 1992) was used to analyze differences between the two lipid extraction methods and bomb calorimetry and statistical significance level was designated as $p < 0.05$. General linear model (GLM) procedures were used because of unbalanced data (Cody and Smith 1997).

Percentages of water, ash, protein and lipid components on a wet mass basis should total 100% body composition of fish (Table 3). Deviations from 100% indicate possible inaccuracies in determining one or more proximate components or carbohydrates

which weren't measured. Proximate analysis values of walleye pollock, Pacific cod, Dover sole, rock sole, sand lance, and capelin totaled less than 99% body mass when hexane/isopropanol was used. When chloroform/methanol was used, only rock sole and sand lance totaled less than 99% body mass and squid totaled more than 101% body mass.

Comparisons between the two lipid extraction solvents resulted in significantly higher measured lipid content for seven species using chloroform/methanol solvent. No differences were detected between the two extraction solvents for Pacific herring ($p=0.526$), Dover sole ($p=0.98$), and pink salmon ($p=0.132$), which were also species containing the highest amounts of lipid (Table 4). Perhaps with higher lipid content, the ratio of lipid to non-lipid components becomes much larger. As a result, if chloroform/methanol is extracting both lipid and non-lipid material, the ratio of lipid to non-lipid material is so high that the non-lipid material fraction, and thus the introduced error, becomes relatively negligible. This might explain the lack of statistically significant differences between extraction methods in prey items with higher lipid content.

Whole body energy density determined by bomb calorimetry was considered the standard with which to compare proximate composition energy density estimates and therefore to validate the accuracy of one lipid extraction solvent over the other. Energy density estimates derived from hexane/isopropanol (7:2 v:v) closely matched bomb calorimetry values for pink salmon ($p=0.296$), Pacific cod ($p=0.174$) and capelin ($p=0.682$). Energy density values for octopus ($p=0.011$), Dover sole ($p=0.0002$) and squid ($p<0.0001$), however, were overestimated by hexane/isopropanol (7:2 v:v) solvent when compared to bomb calorimetry. Rock sole ($p<0.0001$) and sand lance ($p<0.0001$) energy density values were underestimated when comparing these same methods. Calculated energy densities using chloroform/methanol (2:1 v:v) proximate composition measurements were significantly higher than energy density estimates determined by bomb calorimetry for all ten species (p -values ranged from <0.0001 to 0.020) (Figure 1). Based on these results, hexane/isopropyl alcohol (7:2 v/v) was deemed

the more accurate lipid extraction solvent, consistent with Radin (1981). All subsequent analyses and comparisons were made using only hexane/isopropanol (7:2 v:v) solvent and bomb calorimetry values.

It would be helpful to have a conversion factor to allow comparison between previously published literature values and current data based on different extraction methods. Such a conversion factor can be developed using the data on differences in lipid content estimates derived from different lipid extraction solvents. The conversion factor would allow transformation of lipid content values derived from chloroform/methanol solvent into values comparable to lipid content values derived from hexane/isopropyl alcohol extraction. I calculated conversion factors between lipid extraction solvents using linear regressions. One single conversion factor between lipid extraction methods for all species could not be calculated. Rock sole and capelin lipid values did not require any transformations to develop useable conversion equations; the remaining six species were natural log transformed. Lipid content values derived from either chloroform/methanol or hexane/isopropyl alcohol can be converted to values comparable to each other by entering species specific lipid content, slope and intercept values in the equations in Table 5. Instead, conversion factors were calculated based on wet mass values for each species, except for Pacific sand lance ($R^2 = 0.1095$, $F = 2.21$, $p = 0.154$) and octopus ($R^2 = 0.3328$, $F = 3.99$, $p = 0.081$), for which significant statistical relationships did not exist between the two lipid extraction methods (Figure 2).

Feeding Regimes

To compare the overall protein, lipid and energy densities of the three feeding regimes, the corresponding nutritional components of prey species comprising each diet were used from proximate composition and bomb calorimetry analyses. Mean protein and lipid content and energy density values for each feeding regime were calculated using equations 5 and 6 (Franz Mueter, pers. comm.)³.

³ Personal communication from F. Mueter, consultant; Sigma Plus Consulting 697 Fordham Drive, Fairbanks, Alaska 99709; November 2001.

$$X_i = P_1X_{i1} + P_2X_{i2} + P_3X_{i3} + \dots P_yX_{iy} \quad (5)$$

Where X = lipid or protein content (%) or energy density (kcal/g) of prey items, i = regime (pre-decline, decline, stable), P_y = the proportion of prey item “y” within diet i . Variance across species for each diet were calculated as follows:

$$\text{Var}(X_i) = \text{var}(P_1X_{i1} + P_2X_{i2} + \dots P_yX_{iy}) = \text{var}(P_1X_{i1}) + \text{var}(P_2X_{i2}) + \text{var}(P_yX_{iy}) \quad (6)$$

Where var = variance, which was then converted to standard deviation (Equation 7).

$$\text{Standard Deviation}(X_i) = \sqrt{\text{var}(X_i)} \quad (7)$$

Statistical Analysis

Replicate subsamples collected from each individual prey item were averaged to provide a mean value per individual prey item. Data reported within this paper were \log_{10} -transformed to reduce the heterogeneity of values. Outliers were identified as data points falling above 2.5 or below -2.5 on residual plots of log transformed data and were excluded from analyses reported in this study. Statistical analyses were performed using SAS 8.2 (1999-2001 SAS Institute, Cary, North Carolina, U.S.A)

RESULTS

Proximate Composition – Dry Mass Basis

Proximate composition components varied across the ten Steller sea lion prey species analyzed (Table 3). Water content ranged from 64.7% in Pacific herring to 85.6% in octopus. On a dry mass basis, ash content ranged from 5.73% in pink salmon to 13.84% in octopus. Protein content ranged from 43.15% in Pacific herring to 79.17% in squid. Lipid content was lowest in octopus (5.75%) and highest in Pacific herring (48.25%). As lipid content decreased, protein content increased (Figure 2). Water content was negatively correlated to energy density (Figure 3).

Proximate Composition – Wet Mass Basis

On a wet mass basis ash content ranged from 1.7% in squid to 3.6% in rock sole. Protein content ranged from 10.8% in octopus to 19.3% in pink salmon. Lipid content varied from 0.8% in octopus to 17.1% in Pacific herring. Pacific herring ranked lowest in water content (64.7%) and highest in lipid content (17.1%), whereas octopus ranked highest in water content (85.6%) and lowest in lipid content (0.8%). Pink salmon and Dover sole ranked second and third highest in lipid content and ranked next to Pacific herring in having low water content. Pink salmon, sand lance, Dover sole, and Pacific herring had high protein content, defined as $\geq 15\%$ body composition (Stansby 1976). Octopus had the lowest protein content at 10.8%, 8.5% lower than pink salmon.

Feeding Regimes

The pre-decline and stable feeding regimes provided similar energy densities using either proximate composition estimates ($p = 0.084$) or bomb calorimetry values ($p = 0.293$) (Figure 4). The decline diet, however, provided significantly lower energy density compared with the pre-decline and stable diets ($p < 0.0001$) using either value. The two methods of estimating energy density, proximate analysis and bomb calorimetry, were not statistically different for the decline ($p = 0.103$) and stable diets ($p = 0.081$).

Because energy density is calculated from protein and lipid content values, these components were compared across species (Table 6) and across feeding regimes to determine how different species compositions affected proportions of these two sources of energy for each feeding regime (Figure 5). The pre-decline and stable diets provided similar amounts of protein ($p = 0.387$) and lipid ($p = 0.496$) on a dry mass basis. Significantly higher protein was contained in the decline diet than in the pre-decline ($p = 0.020$) and stable ($p = 0.009$) diets. The decline diet simultaneously provided significantly lower lipid content than either the pre-decline ($p = <0.0001$) or stable ($p = <0.0001$) diets.

DISCUSSION

Prey Species

Results from this study show that biochemical compositions, mainly protein and lipid content and energy density, of Steller sea lion prey vary among species. Lipid content, and hence energy density, is highest in Pacific herring but twenty times lower in octopus. Pink salmon, sand lance and Dover sole are high protein prey species whereas octopus, rock sole and capelin are low protein species. Proximate analysis and energy density results from this study complement the growing volume of literature as evidence that opportunistic predators, such as Steller sea lions, are consuming a variety of prey items which each provide different nutritional quality (Ashwell-Erickson and Elsner 1981, Perez 1994, Anthony and Roby 1997, Van Pelt *et al.* 1997, Payne *et al.* 1999, Anthony *et al.* 2000, Rosen and Trites 2000, Worthy 2001).

In addition to overall energy density, our results demonstrate the need for proximate composition analysis to determine protein and lipid content, which are important components of nutritional quality. Although protein and lipid both contribute to the overall energy density of a prey item (Watt and Merrill 1963), protein is a more energetically expensive compound to metabolize, thereby making the net energy gain lower than metabolizing the same amount of lipid (Schmidt-Nielsen 1997). As a result, energy density is primarily related to lipid content (Robbins 1993, Anthony *et al.* 2000, Worthy 2001). In this study capelin and sand lance contain similar overall energy densities and might therefore be considered prey items of similar value. Based on our data, however, sand lance contains almost 30% more protein/gram and nearly 40% less lipid/gram than capelin. If nutritional quality is defined by available energy, then it is important to distinguish between sources of energy, in this case, higher protein sand lance vs. higher lipid capelin, to determine which prey item would provide higher quality nutrition. It is therefore important to consider not only overall energy density but also to determine lipid content.

To balance their nutritional and energetic requirements predators must consume prey in sufficient quantity (Murphy 1994) and/or of sufficient quality (Ricklefs 1979,

Robbins 1993). Assuming that nutritional value is determined by energy density and hence lipid content, our data suggest that Steller sea lions feeding predominantly on high lipid species, (e.g., Pacific herring), are consuming high energy prey items whereas Steller sea lions feeding predominantly on low lipid species, (e.g., octopus), are consuming low energy prey items. Studies suggest that changes in quantity and/or quality of prey due to climate (Shepherd *et al.* 1984, Anderson *et al.* 1997) and/or commercial fisheries removals (Lowry *et al.* 1989), may cause Steller sea lions to change their foraging patterns (Rosen *et al.* 2000). Reduced survival of juvenile Steller sea lions in the 1980s has been attributed to the absence of high energy prey and the coincident lack of alternative prey items (Merrick and Calkins 1996). If, however, in the absence of high energy prey items, lower energy prey items are available, Steller sea lions might be able to consume higher quantities of lower energy prey to compensate for differences in energy density (Stephens and Krebs *et al.* 1986). Our results demonstrate that when considering energy density alone, a Steller sea lion may consume an amount of energy equal to that found in one 100 g herring (250 kcal) by consuming ~130 g of pink salmon, ~220 g of walleye pollock, or ~360 g of octopus. Similarly, a Steller sea lion might receive an equivalent amount of lipid found in a 100 g herring (17 g lipid) by consuming ~200 g of pink salmon, ~540 g of walleye pollock, ~850 g of Pacific cod, or ~2 kg of octopus. These comparisons, however, only consider energy density and lipid content without addressing other nutritional factors such as vitamins or essential amino or fatty acids. They also do not address additional parameters such as limits of satiation, digestive, assimilation, or foraging efficiencies associated with different prey items, or seasonal variations in species composition.

The nutritional composition and energy density of fish species can vary intraspecifically with respect to age, weight, length (Hislop *et al.* 1991, Anthony and Roby 1997), season (Smith *et al.* 1990, Robards *et al.* 1999a, Pedersen and Hislop 2001) and location (Lawson *et al.* 1998, Anthony *et al.* 2000). The relationship between energy density and size is inconsistent across different species (Payne *et al.* 1999, Anthony *et al.* 2000). For walleye pollock, Pacific and Atlantic cod (*Gadus morhua*), energy density

seems independent of size (Lawson *et al.* 1998, Anthony *et al.* 2000), whereas other species, such as Pacific herring, pre-spawning sand lance and pre-spawning capelin exhibit positive relationships between energy density and size (Hislop *et al.* 1991, Anthony *et al.* 2000). Seasonal variations exist in energy density and/or lipid content for Pacific cod (Smith *et al.* 1990), Pacific herring (Hislop *et al.* 1991), Pacific sand lance (Robards *et al.* 1999a), and capelin (Lawson *et al.* 1998, Anthony *et al.* 2000) and appear to be related to spawning (Anthony *et al.* 2000). For example, lipid content of capelin decreased from June through September, coincident with their May to September spawning season (Anthony *et al.* 2000). Similarly, the lipid content of Pacific sand lance was highest in June and steadily declined through September, suggesting that they invest energy in preparation for autumn spawning (Anthony *et al.* 2000). Energy density and lipid content of fish have been found to differ among locations and may be the result of variations in abundance and/or quality of zooplankton consumed (Anthony *et al.* 2000). Limited data suggest species also may exhibit interannual variations in energy density (Lawson *et al.* 1998), perhaps also due to changes in zooplankton availability or quality.

My data contribute to the growing literature addressing nutritional composition of marine organisms. However our results cannot address intraspecific variations in prey quality, as prey items sampled for this study came from single batches of harvested species. Not many proximate composition values exist in the literature for some species such as octopus, Dover sole, rock sole and squid, and so it is difficult to determine how these species' energy densities vary throughout the year. For species that are well studied, data collected throughout the seasons of the year or spanning different age classes allow comparisons to be made. Pacific cod, for example, fluctuates only between 0.7 and 1.0 kcal/g wet mass. Pacific herring, however, exhibits marked variability from 0.9 to 2.8 kcal/g, most likely a reflection of the size of fish or reproductive state rather than time of year. The lack of information on specific and/or comprehensive sampling times in the literature make it difficult to decipher which parameters most strongly affect energy density. The compilation shown in Table 7 demonstrates the need for future studies investigating nutritional quality of Steller sea lion food to consider the size and/or

life history stage of species, along with season and location of sampling, to allow for accurate comparisons of data across studies.

As opportunistic predators, Steller sea lions forage on prey species whose availability can change over time. Pacific cod in the Bering Sea have been found to overwinter offshore where they congregate to spawn and subsequently move inshore as water temperatures warm in spring (Shimada and Kimura 1994). Pacific sand lance in the Gulf of Alaska school nearshore to spawn in mid-autumn, spend the winter in dormant stages with poor energy stores, and then feed on spring plankton blooms (Robards *et al.* 1999b). Such seasonal variations in movement and abundance of prey species may explain seasonal differences in Steller sea lion prey consumption. Salmon and capelin, for example, were present in 12% and 30%, respectively, of 50 Steller sea lion stomachs collected in spring and summer from the Gulf of Alaska, coincident with nearshore, spawning distributions of these species but were mostly absent from stomach contents in fall and winter (Pitcher 1981). Pacific herring were found in 15 of 16 stomachs and squids in 30 of 35 stomachs collected from Steller sea lions in Prince William Sound, but these two prey items were not prominent prey items in other locations (Pitcher 1981). Scat samples collected in the early 1990s identified walleye pollock as the dominant prey species within the Gulf of Alaska and Atka mackerel as the dominant prey species in the central Aleutian Islands (Merrick *et al.* 1997). Therefore, to accurately assess the importance of various prey items to Steller sea lion foraging, it is necessary to recognize how prey abundance varies with season and location.

As a result of nutritional stress being highlighted as one of the more probable causes of the Steller sea lion decline (Loughlin and York 2002), studies such as this one focus on energy and lipid content of prey items, though other bioenergetic parameters require further investigation prior to making any conclusions about the Steller sea lion decline. For example, foraging efficiency suggests that an organism seeks maximum benefits, (i.e., energy), for minimal cost, (i.e., short search times and easy to handle prey) (Stephens and Krebs 1986) and it is therefore important to consider how this affects Steller sea lion prey choice. A comparison of the diets of declining and stable Steller sea

lion populations suggests that at least two primary prey species, such as walleye pollock and Atka mackerel (eastern Aleutians 1990-1993) or walleye pollock and capelin (Kodiak 1975-1978) are necessary to stabilize Steller sea lion populations (Merrick *et al.* 1997). This assumes increased foraging efficiency with a more diverse prey base, translating to more prey patches, increased patch density and higher chances of encountering preferred prey sizes (Merrick *et al.* 1997). In addition, different digestive and assimilation efficiencies are associated with different prey items (Robbins 1993). For example, the presence of larger skeletal structures in species such as walleye pollock suggest lower digestive efficiencies, whereas thinner-boned herring and invertebrate cephalopods (excluding beaks) may be completely digested, resulting in higher digestive efficiencies. Thus, the cost of digestion varies with the prey item for Steller sea lions (Rosen and Trites 2000).

Comparing Bomb Calorimetry with Proximate Composition

Comparisons between bomb calorimetry and proximate composition analysis in this study show that the two methods result in similar estimates of energy densities for eight out of ten species. This suggests that overall energy content or density of a prey item can be adequately estimated from proximate analysis alone for some species. For the two species for which the methods were not comparable, the energy density of sand lance is overestimated by bomb calorimetry and underestimated for squid. The sand lance sampled for this study may have contained energy-contributing components that were not represented by either protein or lipid analysis in proximate composition, such as carbohydrates, but were accounted for in bomb calorimetry, which might explain the difference in energy density values. Bomb calorimetry is the common method of determining whole body energy content (Watt and Merrill 1963, Paul and Willette 1997, Rosen and Trites 2000), but one drawback is that bomb calorimetry does not differentiate between assimilable and nonassimilable components and may therefore overestimate the available energy in prey to consumers (Van Pelt *et al.* 1997). The assumption that carbohydrates are negligible components of fish (Watt and Merrill 1963, Sidwell *et al.*

1974, Stansby 1976, Craig *et al.* 1978, Van Pelt *et al.* 1997, Payne *et al.* 1999, Anthony *et al.* 2000) is currently under debate (Goodman-Lowe *et al.* 2000) and future studies should consider the presence of carbohydrates to try to improve the accuracy of nutritional and bioenergetics studies of marine predators, such as Steller sea lions.

The sum of the proximate composition values for water, protein, ash and lipid contents on a wet mass basis should equal 100% wet body composition; deviations from 100% imply errors in proximate analysis methods, including the presence of carbohydrates. Inaccurate water content values can lead to under- or over-estimates of protein, ash and lipid content estimates on a wet mass basis. Prey samples for this study were frozen and if storage containers are not properly sealed, dehydration of samples can occur, resulting in underestimates of water content and subsequent overestimates of proximate composition components and wet mass energy densities (Montevecchi and Piatt 1984, Hislop *et al.* 1991, Van Pelt *et al.* 1997, Anthony *et al.* 2000). Species containing dense skeletal structures, such as Pacific cod, are harder to fully homogenize than finer boned fish such as Pacific herring. This may lead to more hard parts included in some samples than others, and thus more variability in proximate analysis. Protein content is commonly determined by converting measured nitrogen content into protein content using a 6.25 conversion factor, based on the assumption that protein contains 16% nitrogen (Watt and Merrill 1963). Proteins may vary in nitrogen content, however, and protein content may therefore be over- or under-estimated unless the specific makeup of the protein being estimated is known (Watt and Merrill 1963). Overall nitrogen may include non-protein nitrogen, such as nucleic acids, free amino groups and nucleotides, resulting in overestimates of protein content (Bondi 1987, Goodman-Lowe *et al.* 1999). Similarly, energy density due to lipid content may be overestimated due to the presence of waxes, sterols, phospholipids, and organic acids, which are low energy lipids compared to high energy triglycerides or fats (Bondi 1987, McDonald *et al.* 1981). Although the composition of proteins and lipids was not analyzed for this study, future investigations addressing assimilation efficiencies or biologically valuable nutritional components would need to include such analyses (Goodman-Lowe *et al.* 1999).

Feeding Regimes

The feeding regimes developed by researchers at the ASLC are being used to test the nutritional stress hypothesis by varying diet compositions to reflect differences in the availability of prey species to wild Steller sea lions. While the results of this study are consistent with the nutritional stress hypothesis, the ten species comprising the different feeding regimes are not the only prey items Steller sea lions are known to consume. Additional prey of varying importance identified from Steller sea lion stomach content and scat analyses include sculpins (Cottidae), rockfish (*Sebastes* sp.), greenlings (*Hexagrammidae*), halibut (*Hippoglossus stenolepis*), Pacific hake (*Merluccius productus*), eulachon (*Thaleichthys pacificus*), arrowtooth flounder (*Atheresthes stomias*), skates (*Raja* sp.), Atka mackerel (*Pleurogrammus monopterygius*), crabs, bivalves and other pinniped species (Mathisen *et al.* 1962, Thorsteinson and Lensink 1962, Fiscus and Baines 1966, Pitcher 1981, Merrick *et al.* 1997, Calkins 1998). Flatfish are commonly not identified to species and instead grouped together as “flatfish” (Mathisen *et al.* 1962, Thorsteinson and Lensink 1962, Fiscus and Baines 1966, Pitcher 1981, Merrick *et al.* 1997, Calkins 1998). However, Dover sole and rock sole samples analyzed for this study exhibited significant differences in lipid and protein content and overall energy density, suggesting that different flatfish species provide different nutritional values. In addition, we are assuming that prey items sampled during the present decade are representative of the same prey items from the 1970s. However, environmental changes might cause interannual differences in energy density (Robards *et al.* 1999a) and herring in the 1970s, for example, might have had different nutritional quality than herring in the 1990s.

Conclusion

Results from this study indicate that the prey composition representing a declining Steller sea lion population diet provides lower energy than either the pre-decline or stable population diets. Based on the nutritional quality of prey species analyzed and the feeding regimes formulated for this study, these results are consistent with the possibility

that nutritional stress was a factor contributing to the Steller sea lion decline. The formulated compositions representative of pre-declining, declining and stable Steller sea lion population diets provide generalized hypothesized diets reflecting large-scale temporal shifts in primary prey consumed by Steller sea lions. These feeding regimes do not, however, address seasonal or fine-scale geographic differences in prey consumption. Therefore, when addressing nutritional stress as a factor contributing to the Steller sea lion decline, it is important to recognize how greatly each of the aforementioned caveats contribute to the over- or under- estimation of the nutritional quality of prey consumed by Steller sea lions. Future studies addressing the nutritional stress hypothesis should consider when Steller sea lions depend on various prey resources on a seasonal basis, how dominant prey items consumed vary with location, what the nutritional state of their prey are when they are most heavily consuming them, and the foraging efficiency of consuming various prey items. As studies continue to encompass and account for seasonal and geographic differences in the composition, quantity, quality and foraging efficiency and assimilation of various diets, the better we can address how great a role nutritional stress plays in the decline of Steller sea lions.

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Table 1. Three Steller sea lion feeding regimes: Diet A, western stock prior to population decline and climate shift; Diet B, western stock during decline and after the climate shift; and Diet C, stable eastern stock in Southeast Alaska. Diets are those used in feeding studies conducted at the Alaska SeaLife Center (ASLC) from 1998-2001. % Bio = percent biomass (wet). Rock Sole and Dover Sole % Bio are equal divisions of one value for total flatfish % biomass. Rank is decreasing order of percentages. (Source: V. Burkanov and D. Calkins, pers. comm.).

Diet A (1975-78)	%Bio	Rank	Diet B (1980s)	%Bio	Rank	Diet C (SE AK)	%Bio	Rank
Walleye pollock	60	1	Walleye pollock	50	1	Walleye pollock	30	1
Pacific herring	16	2	Pacific herring	2.7	5	Pacific herring	7	3
Octopus	0	0	Octopus	25	2	Octopus	2.5	5
Pink salmon	6	4	Pink salmon	2	6	Pink salmon	7	3
Pacific cod	0	0	Pacific cod	2	6	Pacific cod	15	2
Dover Sole	0	0	Dover Sole	8.5	3	Dover Sole	6.3	4
Rock sole	0	0	Rock sole	8.5	3	Rock sole	6.3	4
Sandlance	0	0	Sandlance	2	6	Sandlance	7	3
Capelin	11	3	Capelin	0	0	Capelin	0	0
Squids	5	5	Squids	4	4	Squids	2.5	5

(Totals do not add to 100 %, as regime diets presented are theoretical diets and actual amounts fed are dependent on availability or food species harvested and purchased during trial periods).

Table 2. Source information for Steller sea lion prey items subsampled from food fed to Steller sea lions at the ASLC between 1998 and 2001.

Species	Common Name	Sample Size	Date of Harvest	Location of Harvest
<i>Theragra chalcogramma</i>	walleye pollock	10	Late winter 2000	unknown
<i>Clupea pallasii</i>	Pacific herring	10	December 1999	Petersburg-Wrangell, Alaska
<i>Enteroctopus dofleini</i>	octopus	5	February/March 2000	British Columbia
<i>Oncorhynchus gorbuscha</i>	pink salmon	9	July 1999 and 2000	Lower Cook Inlet
<i>Gadus macrocephalus</i>	Pacific cod	5	January 2001	Resurrection Bay
<i>Microstomus pacificus</i>	Dover sole	10	April 2000	Kodiak Island
<i>Pleuronectes bilineatus</i>	rock sole	10	April 2000	Kodiak Island
<i>Ammodytes hexapterus</i>	Pacific sand lance	10	July/August 1999	Prince Edward Island, Canada
<i>Mallotus villosus</i>	capelin	10	January/February 2000	Iceland
<i>Loligo pealei</i>	squid	10	1999	California

Table 3. Wet mass proximate composition (% water, ash, protein and lipid) values (\pm SD) comparing lipid extraction methods and corresponding ranking of each species on a wet mass basis. R and Rk = Rank in decreasing order of percentages.

Species	Rk/Diet			R	Water	R	Ash	R	Protein	R	Lipid			SUM	
	1	2	3								R	Hex/IA	R	Ch/Mth	H:I
Walleye pollock	1	1	1	4	78.28 \pm 0.43	4	2.57 \pm 0.20	6	14.96 \pm 0.42	6	3.15 \pm 0.32	6	4.85 \pm 0.84	99	101
Pacific herring	2	5	3	10	64.68 \pm 2.48	6	2.16 \pm 0.19	4	15.15 \pm 0.56	1	17.14 \pm 2.86	1	18.06 \pm 2.95	99	100
Octopus	0	2	5	1	85.61 \pm 2.21	8	1.96 \pm 0.29	10	10.77 \pm 2.01	10	0.82 \pm 0.09	10	2.06 \pm 0.30	99	100
Pink salmon	4	6	3	9	69.24 \pm 1.46	9	1.76 \pm 0.30	1	19.28 \pm 0.94	2	9.01 \pm 1.88	2	10.22 \pm 1.79	99	101
Pacific cod	0	6	2	3	79.37 \pm 1.56	5	2.54 \pm 0.42	5	15.02 \pm 0.81	9	2.02 \pm 1.02	9	2.72 \pm 1.01	99	100
Dover sole	0	3	4	8	71.32 \pm 0.95	2	3.01 \pm 0.48	3	16.58 \pm 0.83	3	7.79 \pm 1.17	3	8.98 \pm 1.59	99	100
Rock sole	0	3	4	6	73.86 \pm 1.68	1	3.63 \pm 0.63	9	12.54 \pm 0.54	8	2.65 \pm 0.79	7	4.61 \pm 1.04	93	95
Sandlance	0	6	3	7	72.47 \pm 0.40	3	2.61 \pm 0.14	2	17.27 \pm 0.47	5	3.77 \pm 0.40	5	5.73 \pm 0.42	96	98
Capelin	3	0	0	5	76.89 \pm 0.66	7	2.10 \pm 0.16	8	13.37 \pm 0.48	4	6.25 \pm 0.74	4	7.46 \pm 0.74	99	100
Squid	5	4	5	2	81.20 \pm 0.39	10	1.66 \pm 0.05	7	14.89 \pm 0.33	7	2.71 \pm 0.31	8	4.29 \pm 0.50	101	102

Table 4. Comparison of \log_{10} - transformed mean (\pm SD) lipid content values (dry mass) between two lipid extraction solvents for Steller sea lion prey species.

Species	Hexane:Isoprop.	Chloroform	F-value	Pr>F
Walleye Pollock	1.159 \pm 0.04	1.343 \pm 0.07	36.71	<.0001
Pacific herring	1.681 \pm 0.05	1.704 \pm 0.04	0.57	0.4497
Octopus	0.757 \pm 0.06	1.156 \pm 0.04	86.48	<.0001
Pink salmon	1.458 \pm 0.09	1.515 \pm 0.07	3.22	0.0745
Pacific cod	0.952 \pm 0.18	1.097 \pm 0.13	11.44	0.0009
Dover sole	1.430 \pm 0.06	1.490 \pm 0.07	3.91	0.0498
Rock sole	0.991 \pm 0.11	1.237 \pm 0.08	65.68	<.0001
Sandlance	1.134 \pm 0.04	1.318 \pm 0.03	36.51	<.0001
Capelin	1.429 \pm 0.04	1.507 \pm 0.03	6.57	0.0113
Squid	1.156 \pm 0.05	1.355 \pm 0.05	42.94	<.0001

Table 5. Conversion factors between lipid extraction methods. All values are wet mass except squid. Hx:Ia = Hexane/Isopropyl alcohol solvent, Ch:Mth = Chloroform/Methanol solvent, Ln = natural log, a = intercept, b = slope.

Species	Lipid (Hx:Ia) = a + [b * Lipid (Ch:Mth)]	a (std. err)	b (std. err)	R²	F	p
Walleye pollock	$\%(\text{Hx:Ia}) = 0.66077 + [0.53948 * \%(Ch:Mth)]$	0.43519	0.09362	0.6614	33.21	<0.0001
Pacific herring	$\text{Ln}\%(\text{Hx:Ia}) = -0.01912 + [0.98825 * \text{Ln}\%(Ch:Mth)]$	0.18446	0.06393	0.9300	238.99	<0.0001
Pink salmon	$\text{Ln}\%(\text{Hx:Ia}) = -0.54226 + [1.17736 * \text{Ln}\%(Ch:Mth)]$	0.14647	0.06324	0.9559	346.60	<0.0001
Pacific cod	$\text{Ln}\%(\text{Hx:Ia}) = -0.60580 + [1.28636 * \text{Ln}\%(Ch:Mth)]$	0.10146	0.10143	0.9526	160.83	<0.0001
Dover sole	$\text{Ln}\%(\text{Hx:Ia}) = 0.46653 + [0.72244 * \text{Ln}\%(Ch:Mth)]$	0.25507	0.11664	0.6806	38.36	<0.0001
Rock sole	$\%(\text{Hx:Ia}) = 0.30060 + [0.51160 * \%(Ch:Mth)]$	0.56732	0.11844	0.5233	18.66	0.0005
Capelin	$\%(\text{Hx:Ia}) = -4.33830 + [5.28075 * \text{Ln}\%(Ch:Mth)]$	2.27353	1.13279	0.5470	21.73	0.0002
Squid *	$\text{Ln}\%(\text{Hx:Ia}) = -24.94944 + [14.80761 * \%(Ch:Mth)]$	0.52110	0.19570	0.9969	5725.16	<0.0001

* Values reported for squid are dry mass.

Table 6. P-values comparing \log_{10} transformed protein and lipid content among species, NS = no significance. Protein comparisons are in the upper triangle and lipid comparisons are in the lower triangle. WP = Walleye Pollock, PH = Pacific herring, OP = Octopus, PS = Pink salmon, PC = Pacific cod, DS = Dover sole, RS = rock sole, SL = sandlance, CP = capelin, SQ = squid.

		PROTEIN									
		WP	PH	OP	PS	PC	DS	RS	SL	CP	SQ
LIPID	WP		<.0001	NS	0.014	NS	<.0001	0.0008	0.0113	<.0001	<.0001
	PH	<.0001		<.0001	<.0001	<.0001	<.0001	<.0001	<.0001	<.0001	<.0001
	OP	<.0001	<.0001		<.0001	NS	<.0001	<.0001	<.0001	<.0001	NS
	PS	<.0001	<.0001	<.0001		0.0002	NS	NS	NS	NS	<.0001
	PC	<.0001	<.0001	0.0026	<.0001		<.0001	<.0001	0.0002	<.0001	NS
	DS	<.0001	<.0001	<.0001	NS	<.0001		NS	0.0402	NS	<.0001
	RS	<.0001	<.0001	<.0001	<.0001	NS	<.0001		NS	NS	<.0001
	SL	NS	<.0001	<.0001	<.0001	0.0008	<.0001	0.0015		NS	<.0001
	CP	<.0001	<.0001	<.0001	NS	<.0001	NS	<.0001	<.0001		<.0001
	SQ	NS	<.0001	<.0001	<.0001	<.0001	<.0001	0.0001	NS	<.0001	

Table 7. Comparing month, year, energy density values (wet mass, kcal/g), length, mass, water content (%), and locations of selected Steller sea lion prey species analyzed from literature sources and this study. GOA = Gulf of Alaska, NGOA = Northern Gulf of Alaska, PWS = Prince William Sound, AK = Alaska, AI = Aleutian Islands, CN = Canada, BC = British Columbia. Blank cells represent lack of data. Atlantic herring is included to compare energy densities of different locations.

Species	kCal/g	%Water	Mass(g)	Lenth(mm)	Month(s)	Year	Location	Ref(s)
Capelin								
<i>Mallotus villosus</i>	1.4 ± 0.1	76.9 ± 0.7	31.6	149.5	Jan./Feb.	2000	Iceland	1
<i>M. villosus</i>	1.4	78.0 ± 0.7			Feb	1993	GOA	11**
<i>M. villosus</i>	1.3	78.9 ± 0.8			Feb,Jun,Aug	1991-95	GOA	11**
<i>M. villosus</i>	1.6	76.4 ± 0.8			Feb,Jun,Aug	1991-96	Bering Sea	11**
<i>M. villosus</i>	1.0 ± 0.1	77.1 ± 0.5	2.3 ± 0.1	<90 mm	May-Aug	1995-96	NGOA	2*
<i>M. villosus</i>	1.2 ± 0.0	74.7 ± 0.4	9.9 ± 0.5	>90 mm	May-Aug	1995-96	NGOA	2*
<i>M. villosus</i>	0.9 ± 0.2	79.2 ± 1.5	21.9 ± 1.5		May-Sept.	1995	PWS,AK	3*
<i>M. villosus</i>	1.0	81.4 ± 0.6			June	1995	GOA	11**
<i>M. villosus</i>	0.9 ± 0.1	80.2 ± 1.4	42.1 ± 4.2	183 ± 6.2	June	1982	Newfdlnd,CN	7*
<i>M. villosus</i>	1.7	75.1 ± 2.2			Jun-July	1993	GOA	11**
<i>M. villosus</i>	1.7	75.0 ± 1.2			Jun-July	1993	Bering Sea	11**
<i>M. villosus</i>	1.4	78.0 ± 0.6			Jun-July	1994	Bering Sea	11**
<i>M. villosus</i>	1.1 ± 0.1	76.5 ± 1.0	26.2 ± 8.4	158 ± 18.6	July	1982	Newfdland,CN	7*
<i>M. villosus</i>	1.7	72.6	17.7		July	1984	Bering Sea	13
<i>M. villosus</i>	1.1 ± 0.1	77.8 ± 1.0	5.9-6.7	100-113	July/Aug.	1993-94	Kodiak - AI	17*
<i>M. villosus</i>	0.9 ± 0.1	81.3 ± 1.2	7.7-9.8	110-118	July/Aug.	1993-95	Kodiak - AI	17*
<i>M. villosus</i>	1.2 ± 0.1	75.5 ± 1.3	2.0-2.9	80-92	July/Aug.	1993-96	Kodiak - AI	17*
<i>M. villosus</i>	0.9 ± 0.2	80.0 ± 2.6	20.7 ± 5.5	158 ± 12.7	August	1982	Newfdland,CN	7*
<i>M. villosus</i>	1.7	72.3	9.2		August	1984	GOA	13
<i>M. villosus</i>	1.2	79.1 ± 0.7			Aug-Sep.	1993	GOA	11**
Dover sole								
<i>Microstomus pacificus</i>	1.7 ± 0.1	71.3 ± 1.0	400.4	272.3	April	2000	Kodiak, AK	1
<i>M. pacificus</i>	0.7	81.7	10.8	≥ 80 mm	May-Aug	1995-96	NGOA	2*

Table 7 Cont'd.

Species	kCal/g	%Water	Mass(g)	Lenth(mm)	Month(s)	Year	Location	Ref(s)
Octopus								
<i>Enteroctopus dofleini</i>	0.7 ± 0.1	85.6 ± 2.2	7829.7	1298.8	Feb./March	2000	B.C., Can.	1
<i>Octopus cyanea</i>	0.9 ± 0.0	83.1					Hawaii	6****
Pacific cod								
<i>Gadus macrocephalus</i>	1.0 ± 0.1	79.4 ± 1.6	3803.5	638.0	Jan.	2001	Resurrection	1
<i>G. macrocephalus</i>	1.0	77.5	3036 ± 553	618 ± 30.8	March	1987	Kodiak, GOA	16****
<i>G. macrocephalus</i>	1.0	77.6	2842 ± 642	603 ± 47.8	March	1987	Kodiak, GOA	16****
<i>G. macrocephalus</i>	0.9	76.9	2556 ± 545	642 ± 49.5	April	1987	Kodiak, GOA	16****
<i>G. macrocephalus</i>	0.9	78.8	2527 ± 585	643 ± 41.4	April	1987	Kodiak, GOA	16****
<i>G. macrocephalus</i>	0.8	80.2	2559 ± 843	645 ± 75.6	May	1987	Kodiak, GOA	16****
<i>G. macrocephalus</i>	0.9	80.7	1954 ± 478	586 ± 42.1	May	1987	Kodiak, GOA	16****
<i>G. macrocephalus</i>	0.9 ± 0.0	77.8 ± 0.3	3.9 ± 0.2	< 100 mm	May-Aug	1995-96	NGOA	2 *
<i>G. macrocephalus</i>	0.9 ± 0.1	78.9 ± 1.6	15.4 ± 2.1	≥ 100 mm	May-Aug	1995-96	NGOA	2 *
<i>G. macrocephalus</i>	0.7 ± 0.0	83.2 ± 1.2	3.1 ± 1.7		May-Sept.	1995	PWS,AK	3*
<i>G. macrocephalus</i>	0.8 ± 0.1	77.0 ± 1.7	13.2 ± 2.8		May-Sept.	1995	PWS,AK	3*
<i>G. macrocephalus</i>	0.8	80.9	2840 ± 786	657 ± 63.7	July	1987	Kodiak, GOA	16****
<i>G. macrocephalus</i>	0.8	79.7	2367 ± 674	629 ± 58.3	July	1987	Kodiak, GOA	16****
<i>G. macrocephalus</i>	1.0	78.9	183.2		July	1984	Bering Sea	13
<i>G. macrocephalus</i>	0.7 ± 0.0	81.9 ± 0.7	2.0 - 7.8	69-103	July/Aug.	1993-94	Kodiak - AI	17*
<i>G. macrocephalus</i>	0.9	80.0	361.6		August	1984	GOA	13
<i>G. macrocephalus</i>	0.9	78.3	4506 ± 1584	738 ± 78.5	October	1986	Kodiak, GOA	16****
<i>G. macrocephalus</i>	0.9	78.5	3734 ± 1136	696 ± 61.4	October	1986	Kodiak, GOA	16****
<i>G. macrocephalus</i>	0.9	79	3130 ± 1056	635 ± 55.9	November	1986	Kodiak, GOA	16****
<i>G. macrocephalus</i>	1.2	73.9	2857 ± 702	620 ± 44.1	November	1986	Kodiak, GOA	16****
<i>G. macrocephalus</i>	1.0	78	3671 ± 1717	678 ± 93.1	December	1986	Kodiak, GOA	16****
<i>G. macrocephalus</i>	1.1	76.3	2919 ± 1151	622 ± 71.6	December	1986	Kodiak, GOA	16****

Table 7 Cont'd.

Species	kCal/g	%Water	Mass(g)	Lenth(mm)	Month(s)	Year	Location	Ref(s)
Pacific herring								
<i>Clupea pallasii</i>	1.4 ± 0.1			(YOY)	fall	1995	PWS, AK	9*
<i>C. pallasii</i>	1.9 ± 0.3			(1)	fall	1995	PWS, AK	9*
<i>C. pallasii</i>	2.2 - 2.4			(2+)	fall	1995	PWS, AK	9*
<i>C. pallasii</i>	1.1 ± 0.1			(YOY)	spring	1996	PWS, AK	9*
<i>C. pallasii</i>	1.1 ± 0.1			(1)	spring	1996	PWS, AK	9*
<i>C. pallasii</i>	1.2 - 1.5			(2+)	spring	1996	PWS, AK	9*
<i>C. pallasii</i>	1.0			80	February	1997	PWS, AK	5*
<i>C. pallasii</i>	0.9			98	March	1997	PWS, AK	5*
<i>C. pallasii</i>	1.1				May	1996	PWS, AK	8*
<i>C. pallasii</i>	0.8 - 1.4			< 130	May	1997	PWS, AK	8*
<i>C. pallasii</i>	1.4 - 1.9			> 130	May	1997	PWS, AK	8*
<i>C. pallasii</i>	0.9 ± 0.0	77.6 ± 0.2	3.5 ± 0.5	<100	May-Aug	1995-96	NGOA	2 *
<i>C. pallasii</i>	1.4 ± 0.0	72.3 ± 0.3	23.5 ± 1.1	≥100	May-Aug	1995-96	NGOA	2 *
<i>C. pallasii</i>	1.0 ± 0.7	77.6 ± 0.1	3.2 ± 0.6		May-Sept.	1995	PWS, AK	3*
<i>C. pallasii</i>	1.1 ± 0.2	77.9 ± 2.6	13.2 ± 4.0		May-Sept.	1995	PWS, AK	3*
<i>C. pallasii</i>	1.7 ± 0.3	67.7 ± 3.4	18.5 ± 5.1		May-Sept.	1995	PWS, AK	3*
<i>C. pallasii</i>	1.4 ± 0.3	74.2 ± 3.0	36.9 ± 13.3		May-Sept.	1995	PWS, AK	3*
<i>C. pallasii</i>	1.3				June	1996	PWS, AK	8*
<i>C. pallasii</i>	0.6			25 - 35	July	1996	PWS, AK	8*
<i>C. pallasii</i>	1.3			> 80	July	1996	PWS, AK	8*
<i>C. pallasii</i>	0.6			25 - 60	July	1997	PWS, AK	8*
<i>C. pallasii</i>	1.4			> 80	July	1997	PWS, AK	8*
<i>C. pallasii</i>	1.3	75.4	33.0		July	1984	Bering Sea	13
<i>C. pallasii</i>	2.8	61.1	159.4		August	1984	GOA	13
<i>C. pallasii</i>	0.7			20 - 60	August	1996	PWS, AK	8*
<i>C. pallasii</i>	0.8			30 - 65	August	1997	PWS, AK	8*
<i>C. pallasii</i>	1.1			65 ± 13	October	1996	PWS, AK	5*
<i>C. pallasii</i>	1.1			40 - 100	October	1996	PWS, AK	8*

Table 7 Cont'd.

Species	kCal/g	%Water	Mass(g)	Lenth(mm)	Month(s)	Year	Location	Ref(s)
<i>C. pallasi</i>	1.3			60 - 100	October	1997	PWS, AK	8*
<i>C. pallasi</i>	1.2			74 ± 9	November	1996	PWS, AK	5*
<i>C. pallasi</i>	1.1			79 ± 12	December	1996	PWS, AK	5*
<i>C. pallasi</i>	2.5 ± 0.3	64.7 ± 2.5	98.0	196.0	Dec.	1999	Ptrsburg, AK	1
<i>C. pallasi</i>	0.8	84.8					GOA	11
<i>C. pallasi</i>	1.6 ± 0.0	71.7 ± 0.2					Bering Sea	4
<i>C. pallasi</i>	2.1 ± 0.1	66.8 ± 0.5					Bering Sea	4
<i>C. pallasi</i>	2.4 ± 0.0	64.0 ± 0.5					Bering Sea	4
Atlantic herring								
<i>Clupea harengus</i>	1.1			120-149	Feb		North Sea	12*
<i>C. harengus</i>	1.6			200-249	Feb		North Sea	12*
<i>C. harengus</i>	1.1			120-149	Apr - June		North Sea	12*
<i>C. harengus</i>	1.1			150-199	Apr - June		North Sea	12*
<i>C. harengus</i>	1.4			200-249	Apr - June		North Sea	12*
<i>C. harengus</i>	1.2			120-149	July - Sep		North Sea	12*
<i>C. harengus</i>	2.4			150-199	July - Sep		North Sea	12*
<i>C. harengus</i>	2.6			200-249	July - Sep		North Sea	12*
<i>C. harengus</i>	1.5			120-149	Oct - Dec		North Sea	12*
<i>C. harengus</i>	1.7			150-199	Oct - Dec		North Sea	12*
<i>C. harengus</i>	2.0			200-249	Oct - Dec		North Sea	12*
<i>C. harengus</i>	1.8	73.0	86.0	164.0				15*
<i>C. harengus</i>	1.7	72.6	77.0	158.0				15*
Pink salmon								
<i>Oncorhynchus gorbuscha</i>	0.8 ± 0.0	78.7 ± 0.2	7.5 ± 0.4	<100 mm	May-Aug.	1995-96	NGOA	2 *
<i>O. gorbuscha</i>	0.9 ± 0.0	77.3 ± 0.4	14.5 ± 0.9	≥100 mm	May-Aug.	1995-96	NGOA	2 *
<i>O. gorbuscha</i>	2.0 ± 0.2	69.2 ± 1.5	1688.7	45.0 cm	July	1999,2000	Cook Inlet	1
<i>O. gorbuscha</i>	1.3	74.7	1100.0	443.0				15*

Table 7 Cont'd.

Species	kCal/g	%Water	Mass(g)	Lenth(mm)	Month(s)	Year	Location	Ref(s)
Rock sole								
<i>Pleuronectes bilineatus</i>	1.0 ± 0.1	73.9 ± 1.7	448.8	27.8 cm	April	2000	Kodiak, AK	1
Sand lance								
<i>Ammodytes hexapterus</i>	0.8 ± 0.1	79.6 ± 1.8		127 ± 7.7	Feb.	1996	Kchmk Bay, AK	14****
<i>A. hexapterus</i>	0.8 ± 0.1	79.5 ± 2.1		125 ± 8.6	Feb.	1996	Kchmk Bay, AK	14****
<i>A. hexapterus</i>	1.17	78.9 ± 0.4			Apr-May	1994	GOA	11**
<i>A. hexapterus</i>	1.2 ± 0.0	73.1 ± 0.5	2.6 ± 0.1	<100 mm	May-Aug.	1995-96	NGOA	2*
<i>A. hexapterus</i>	1.4 ± 0.0	73.1 ± 0.2	9.7 ± 0.2	≥100 mm	May-Aug.	1995-96	NGOA	2*
<i>A. hexapterus</i>	1.0 ± 0.1	78.4 ± 0.7	1.9 ± 0.5	0+	May-Sept.	1995	PWS,AK	3*
<i>A. hexapterus</i>	1.2 ± 0.1	76.0 ± 1.4	2.0 ± 0.4	0+	May-Sept.	1995	PWS,AK	3*
<i>A. hexapterus</i>	1.5 ± 0.1	71.4 ± 1.1	9.4 ± 0.8	1+	May-Sept.	1995	PWS,AK	3*
<i>A. hexapterus</i>	1.3 ± 0.1	73.8 ± 1.5	16.1 ± 3.9	2+	May-Sept.	1995	PWS,AK	3*
<i>A. hexapterus</i>	1.2 ± 0.1	75.6 ± 1.0	13.6 ± 2.1	2+	May-Sept.	1995	PWS,AK	3*
<i>A. hexapterus</i>	1.3 ± 0.1	73.6 ± 1.5		137 ± 6.0	June	1996	Kchmk Bay, AK	14****
<i>A. hexapterus</i>	1.3 ± 0.1	73.1 ± 1.4		138 ± 4.9	June	1996	Kchmk Bay, AK	14****
<i>A. hexapterus</i>	1.18	78.3 ± 0.5			June-July	1993-94	GOA	11**
<i>A. hexapterus</i>	1.5	75.8 ± 1.0		> 100 mm	June-July	1993-94	BER.	11**
<i>A. hexapterus</i>	1.3 ± 0.0	73.4 ± 1.7		140 ± 9.8	July	1996	Kchmk Bay, AK	14****
<i>A. hexapterus</i>	1.4 ± 0.0	72.7 ± 1.2		140 ± 6.9	July	1996	Kchmk Bay, AK	14****
<i>A. hexapterus</i>	1.3 ± 0.1	72.5 ± 0.4	18.8		July/Aug.	1999	Pr.Ed.Isl., CN	1
<i>A. hexapterus</i>	1.4 ± 0.2	73.2 ± 2.0	12.0-23.7	147-191	July/Aug.	1993-94	Kodiak - AI	17*
<i>A. hexapterus</i>	1.2 ± 0.2	75.5 ± 2.0	3.9-8.4	110-132	July/Aug.	1993-94	Kodiak - AI	17*
<i>A. hexapterus</i>	0.8	80.90	1.5-1.8	80-85	July/Aug.	1993-94	Kodiak - AI	17*
<i>A. hexapterus</i>	1.2 ± 0.0	74.2 ± 0.8		142 ± 11.5	Aug.	1996	Kchmk Bay, AK	14****
<i>A. hexapterus</i>	1.4 ± 0.0	72.0 ± 0.9		144 ± 10.6	Aug.	1996	Kchmk Bay, AK	14****
<i>A. hexapterus</i>	1.37	76.0 ± 0.9			Aug.-Sept.	1992-94	GOA	11**
<i>A. hexapterus</i>	1.1 ± 0.0	75.7 ± 0.8		132 ± 9.9	Sept.	1996	Kchmk Bay, AK	14****
<i>A. hexapterus</i>	1.3 ± 0.1	73.0 ± 1.0		140 ± 11.0	Sept.	1996	Kchmk Bay, AK	14****
<i>A. hexapterus</i>	0.9 ± 0.0	78.9 ± 1.0		144 ± 13.9	Oct.	1996	Kchmk Bay, AK	14****

Table 7 Cont'd.

Species	kCal/g	% Water	Mass(g)	Lenth(mm)	Month(s)	Year	Location	Ref(s)
<i>A. hexapterus</i>	1.0 ± 0.0	77.7 ± 1.9		138 ± 14.2	Oct.	1996	Kchmk Bay, AK	14****
<i>A. hexapterus</i>	0.8 ± 0.0	80.5 ± 1.5		119 ± 12.2	Nov.	1996	Kchmk Bay, AK	14****
<i>A. hexapterus</i>	0.8 ± 0.1	79.9 ± 1.4		129 ± 10.4	Nov.	1996	Kchmk Bay, AK	14****
<i>A. hexapterus</i>	1.2	77.7 ± 0.8		< 100 mm			GOA	11**
<i>A. hexapterus</i>	1.3	77.8 ± 0.4		≥ 100 mm			GOA	11**
Squid								
Gonatidae	0.9 ± 0.1	81.6 ± 0.9	3.5-12.3	71-135	July/Aug.	1993-94	Kodiak - AI	17*
<i>Loligo opalescens</i>	1.1 ± 0.0	81.2 ± 0.4	60.8	103.9		1999	California	1
<i>L. opalescens</i>	0.9	82.5	53.0	152.0				15*
<i>Loligo sp.</i>	0.8 ± 0.0	82.9					Hawaii	6****
Walleye Pollock								
<i>Theragra chalcogramma</i>	1.1 ± 0.0	78.3 ± 0.4	211.0	299.2	winter	2000		1
<i>T. chalcogramma</i>	1.1	77.4	836.0	48.2	March	1984	GOA	13
<i>T. chalcogramma</i>	1.0 ± 0.1			< 80 mm	March	1996	PWS	10*
<i>T. chalcogramma</i>	0.8 ± 0.1			< 70 mm	March	1997	PWS	10*
<i>T. chalcogramma</i>	0.8 ± 0.1			96 mm	March	1997	PWS	10*
<i>T. chalcogramma</i>	1.0 ± 0.1			> 90 mm	May	1996	PWS	10*
<i>T. chalcogramma</i>	0.8 ± 0.0	79.1 ± 0.3	7.9 ± 2.0	<100 mm	May-Aug.	1995-96	NGOA	2*
<i>T. chalcogramma</i>	0.8 ± 0.0	79.2 ± 0.3	29.0 ± 1.7	≥100 mm	May-Aug.	1995-96	NGOA	2*
<i>T. chalcogramma</i>	0.8 ± 0.1	79.3 ± 1.5	1.16 ± 0.4		May-Sep.	1995	PWS, AK	3*
<i>T. chalcogramma</i>	0.9 ± 0.1	78.2 ± 1.1	33.1 ± 7.2		May-Sep.	1995	PWS, AK	3*
<i>T. chalcogramma</i>	0.6 ± 0.1			> 90 mm	June	1996	PWS, AK	10*
<i>T. chalcogramma</i>	1.2	77.0	270.4		July	1984	Bering Sea	13
<i>T. chalcogramma</i>	0.7 ± 0.1	83.7 ± 0.6	0.8-4.7	54-87	July/Aug.	1993-94	Kodiak - AI	17*
<i>T. chalcogramma</i>	1.1	77.7	67.7		August	1984	GOA	13

Table 7 Cont'd.

Species	kCal/g	%Water	Mass(g)	Lenth(mm)	Month(s)	Year	Location	Ref(s)
<i>T. chalcogramma</i>	0.8 ± 0.1			69 mm	August	1996	PWS, AK	10*
<i>T. chalcogramma</i>	0.9 ± 0.7			< 70 mm	October	1995	PWS, AK	10*
<i>T. chalcogramma</i>	0.9 ± 0.1			60–70 mm	October	1996	PWS, AK	10*
<i>T. chalcogramma</i>	0.9 ± 0.1			81 mm	October	1996	PWS, AK	10*
<i>T. chalcogramma</i>	0.9	82.6					GOA	11**
<i>T. chalcogramma</i>	1.0	77.3	1010.0	426.0				15*
* converted wet mass kJ/g → wet mass kcal/g								
** computed wet mass kcal/g from wet mass proximate composition values provided in literature reference								
*** calculated wet mass from % dry mass								
**** calculated wet mass from % dry mass and converted kJ/g → kcal/g								
References:								
1 This study								
2 Anthony <i>et al.</i> 2000								
3 Anthony and Roby 1997								
4 Ashwell-Erickson and Elsner 1981								
5 Foy and Paul 1999								
6 Goodman-Lowe <i>et al.</i> 1999								
7 Montevicchi and Piatt 1984								
8 Paul and Paul 1999								
9 Paul, Paul and Brown 1998								
10 Paul, Paul and Smith 1999								
11 Payne <i>et al.</i> 1999								
12 Pederson and Hislop 2001								
13 Perez 1994								
14 Robards <i>et al.</i> 1999a								
15 Rosen and Trites 2000								
16 Smith <i>et al.</i> 1990								
17 Van Pelt <i>et al.</i> 1997								

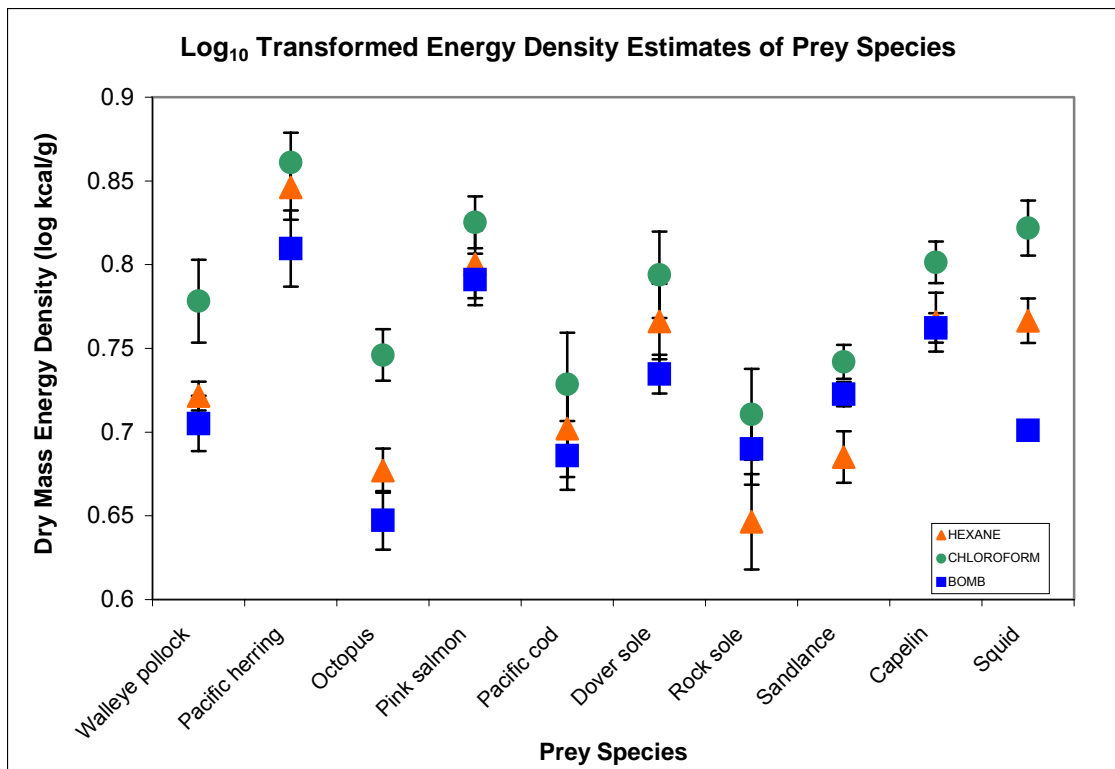


Figure 1. Method comparison of mean dry mass energy density (\pm SD) resulting from two methods of lipid extraction and bomb calorimetry of Steller sea lion prey species.

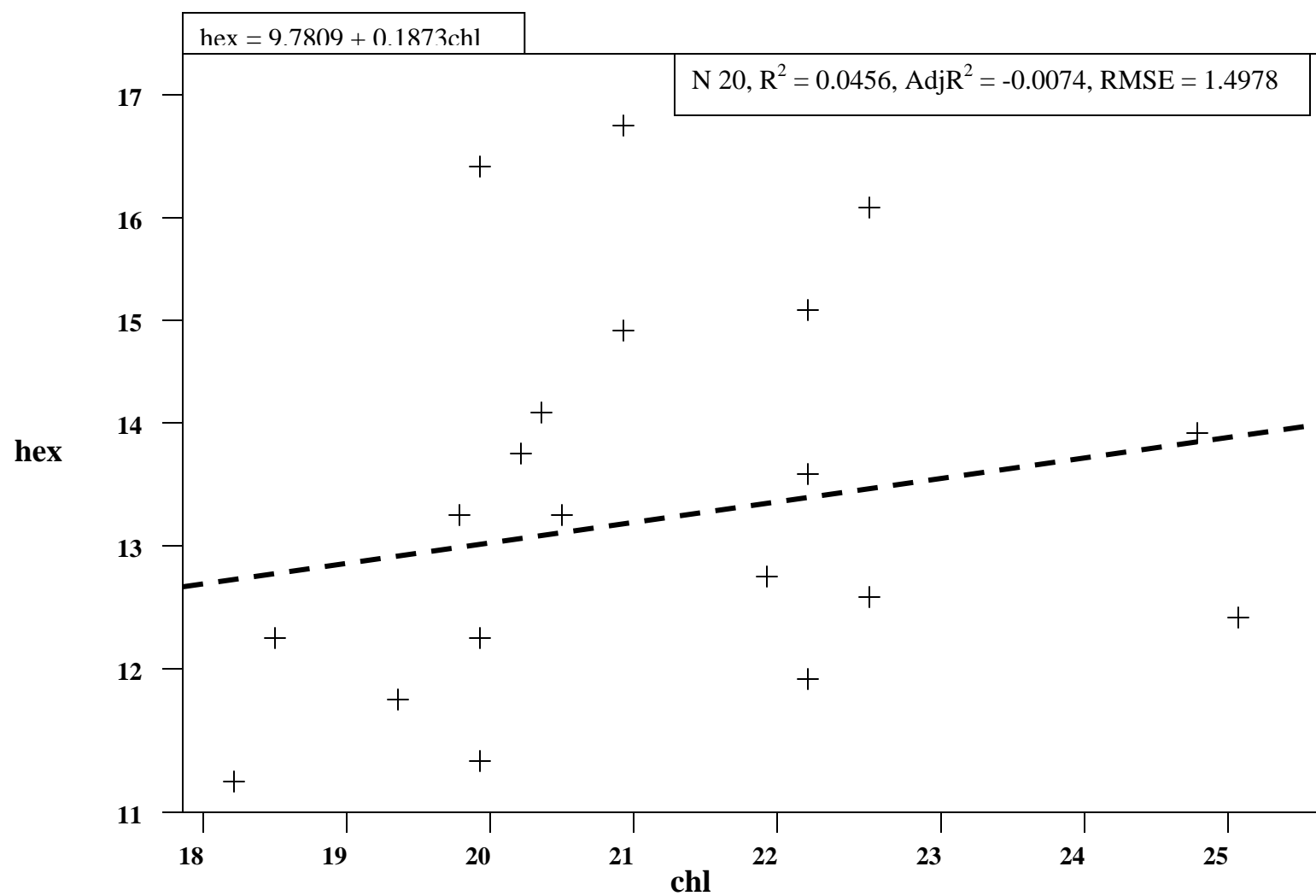


Figure 2. Scatter plot of Pacific sand lance lipid values, chloroform/methanol values along x-axis and hexane/isopropyl alcohol values along y-axis.

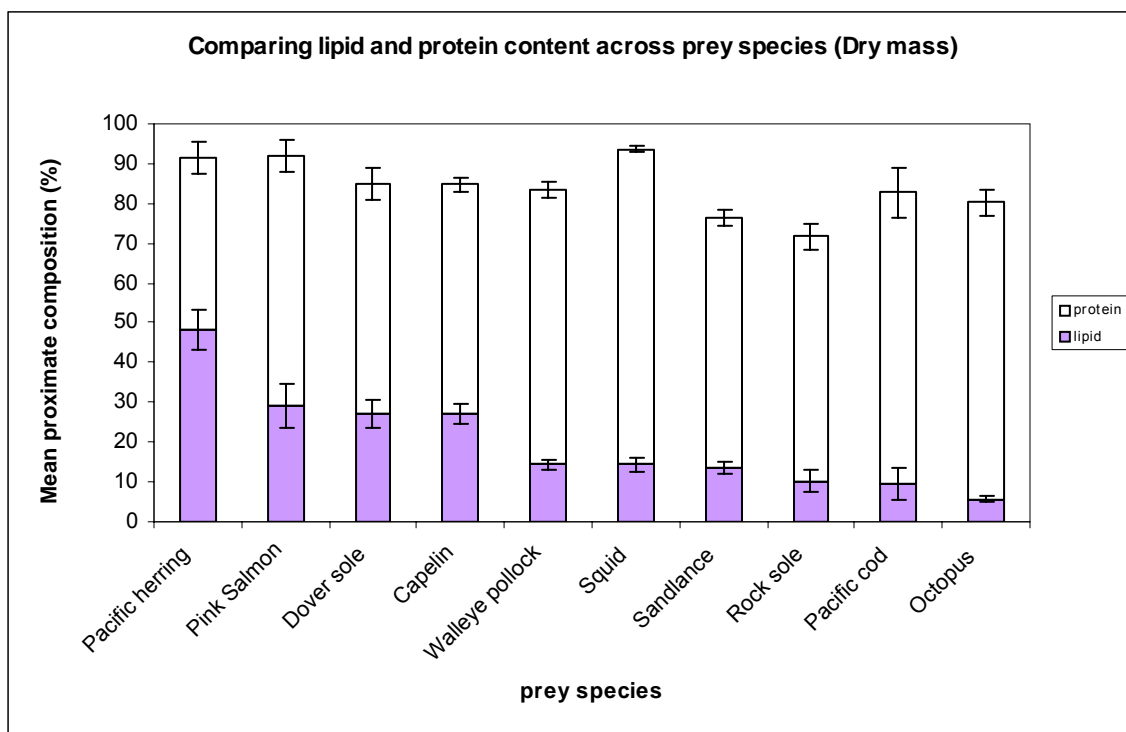


Figure 3. Mean hexane/isopropanol lipid and protein values (%) of prey species with standard deviations. Areas above bars represent the presence of other dry matter components such as ash and possibly carbohydrates.

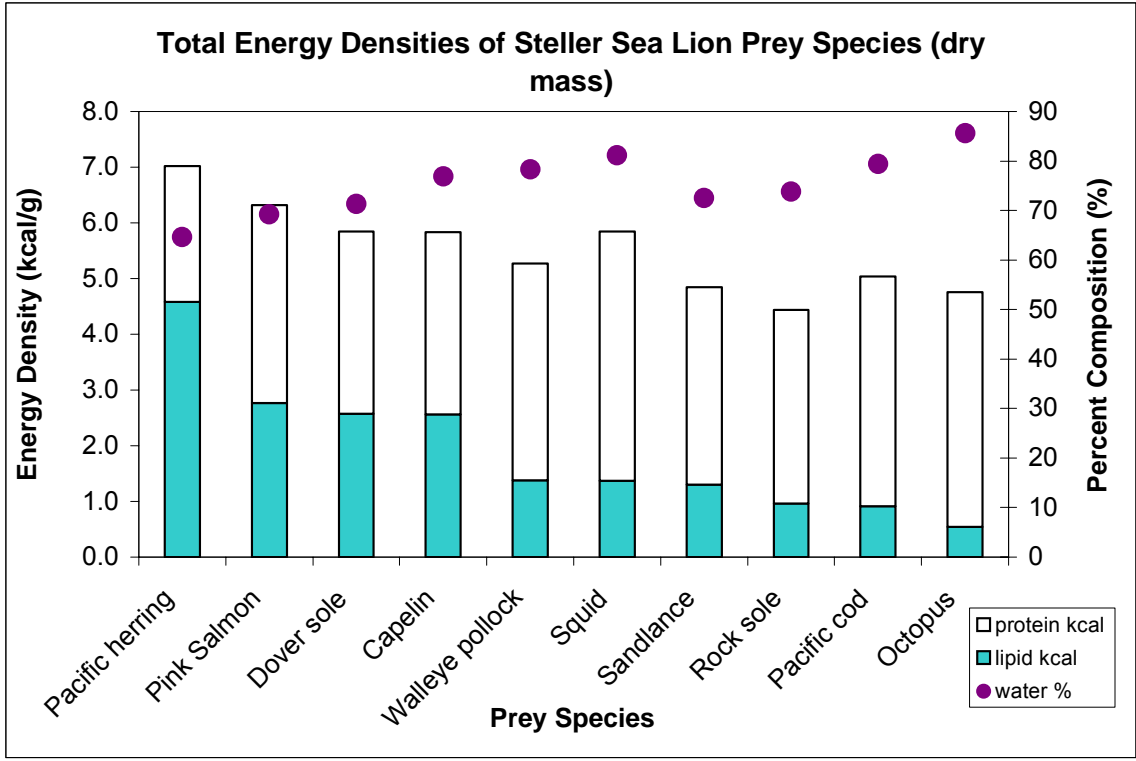


Figure 4. Total energy densities of prey species with relative contributions of lipid and protein energy. Percent water is plotted to demonstrate the inverse relationship with energy density

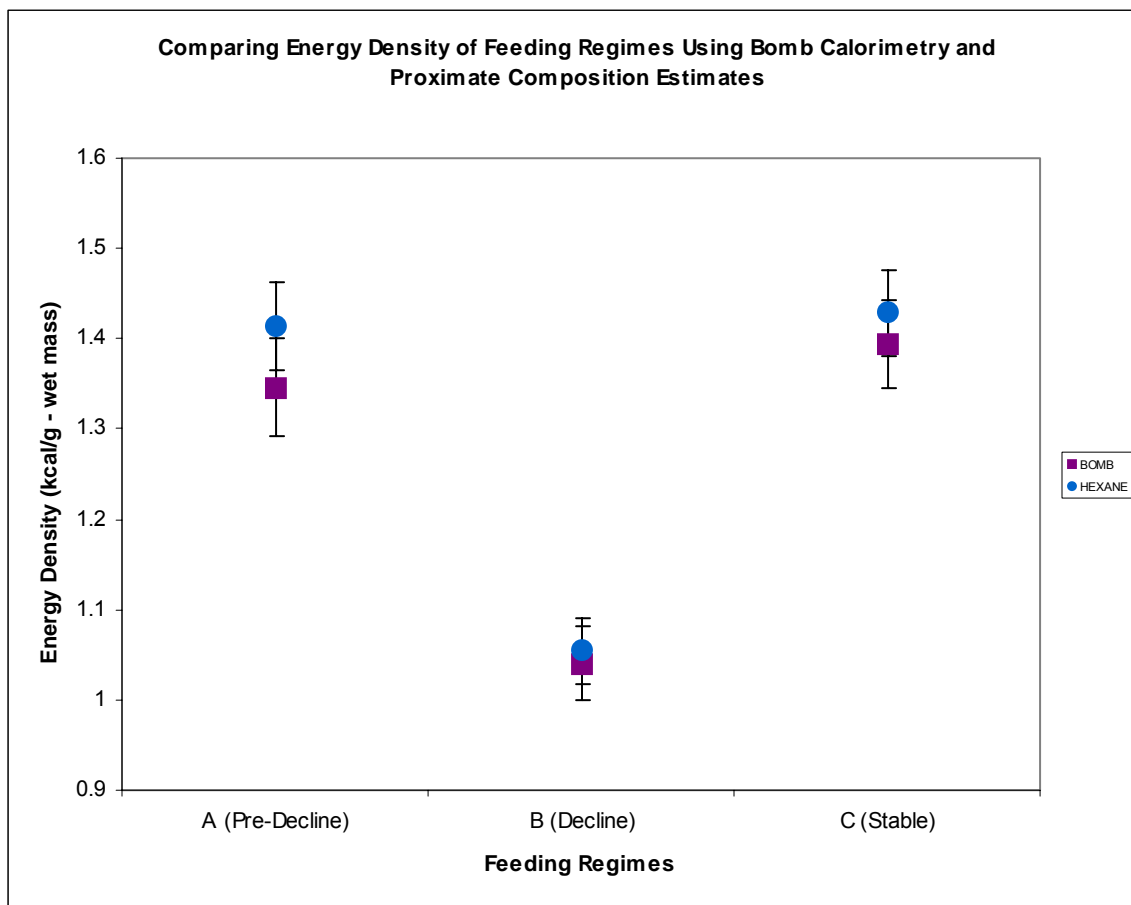


Figure 5. Energy densities (wet mass basis) (\pm SD) derived from bomb calorimetry and proximate composition using hexane/isopropanol 7:2 (v:v) lipid extraction solvent for three different Steller sea lion diets.

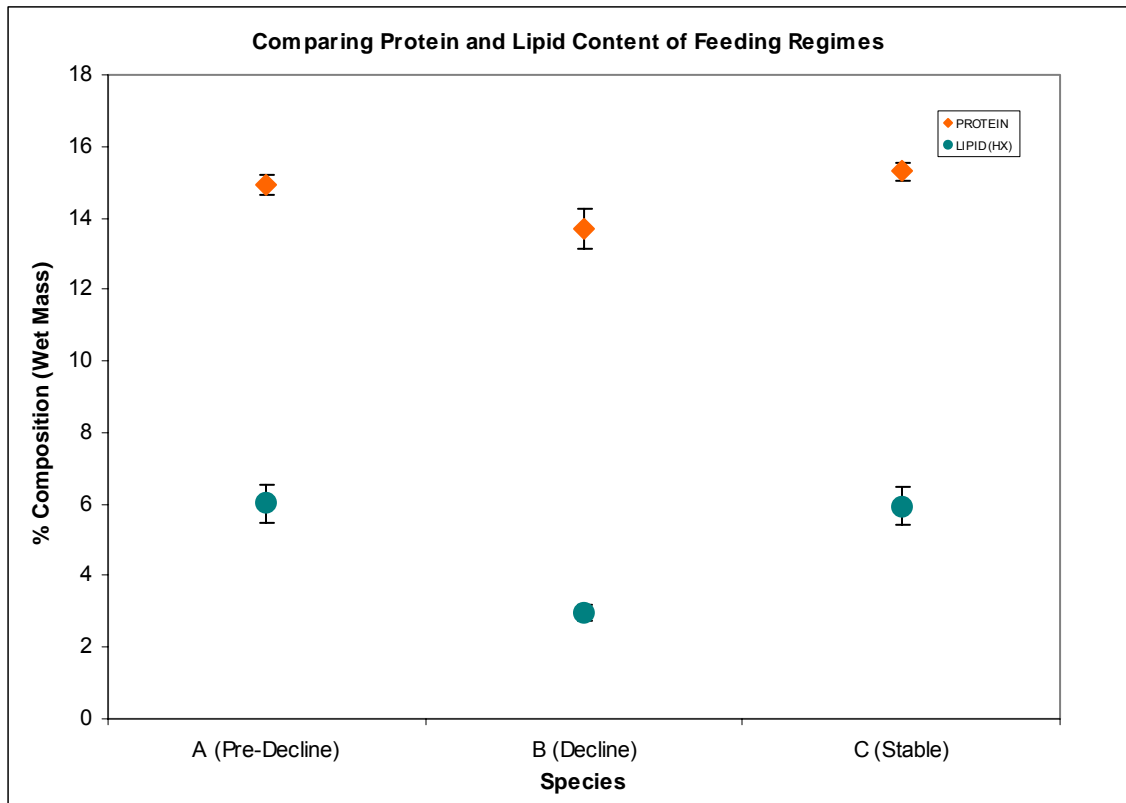


Figure 6. Comparison of the protein and lipid content % (\pm SD) of Steller sea lion feeding regimes on a wet mass basis.

