

# Seasonal availability of abundant, energy-rich prey influences the abundance and diet of a marine predator, the Steller sea lion *Eumetopias jubatus*

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**ABSTRACT:** Steller sea lions *Eumetopias jubatus* are central-place foragers that forage in the marine environment while using terrestrial sites to rest and care for young. Some terrestrial sites are used seasonally; however, the reasons for doing so are not fully understood. We addressed the hypothesis that seasonal availability of prey influences seasonal abundance and diet of sea lions. We quantified monthly prey availability and sea lion abundance and quarterly diet composition at Benjamin Island in SE Alaska (2001–2004). Large numbers of sea lions occupied Benjamin Island during the non-breeding season from October to April when Pacific herring *Clupea pallasii* biomass was highest. Herring was the most common species in sea lion diet (frequency of occurrence [FO] = 90%) and comprised over 81% of the available pelagic prey biomass and 96% of the energy encountered during pelagic surveys. Walleye pollock *Theragra chalcogramma* accounted for 19% of the available prey biomass but was only slightly less common in sea lion diet (FO = 88%) than herring. Herring biomass was correlated with the number of sea lions; in contrast, there was no relationship between pollock biomass and number of sea lions. Several fish species were found in nearshore areas, but were uncommon in sea lion diet. Sea lions consumed the available pelagic prey but little of the available nearshore prey. The FO of herring and pollock in sea lion diet did not differ significantly between seasons; however, the FO of other seasonal prey species differed between seasons. Seasonal occupation of Benjamin Island by sea lions is influenced by seasonally available, densely aggregated, energy-rich prey.

**KEY WORDS:** Seasonal · Prey availability · Abundance · Diet · Energy · *Eumetopias jubatus* · *Clupea pallasii* · *Theragra chalcogramma*

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## INTRODUCTION

The ideal free distribution predicts that the distribution of organisms among foraging sites should match the distribution of resources. Spatial and temporal changes in resource availability can influence prey density (Fretwell 1972), which in turn influences predator density (Carbone & Gittleman 2002). In the marine environment, changes in resource availability can influence all trophic levels, ranging from plankton to top marine predators (Croxall 1992). For upper-

trophic level marine predators that exhibit a central-place foraging strategy, such as pinnipeds or seabirds (Orlans & Pearson 1977), the availability of resources around a colony can influence their distribution, abundance, survival, and foraging behavior (e.g. Boyd et al. 1998, Soto et al. 2004).

The Steller sea lion *Eumetopias jubatus* is an otariid found throughout the North Pacific Rim that relies on the marine environment to meet its energetic and nutritional demands while using terrestrial sites to rest, breed, care for young, and avoid predators, hence

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exhibiting a central-place foraging strategy (Orians & Pearson 1977). In contrast to capital breeders, which depend upon stored body reserves to nourish offspring (Jönsson 1997), adult female Steller sea lions rely upon intermittent foraging trips during an extended lactation period (10 mo to >3 yr) to deliver energy to their dependent young (Pitcher & Calkins 1981).

In SE Alaska, during the breeding season from mid-May through late July (Pitcher et al. 2001), sea lions typically make seasonal migrations to rookeries, which are located along the outer coast. After the breeding season, females with dependent young depart rookeries and migrate to terrestrial haulout sites (Calkins & Pitcher 1982). The availability of seasonally predictable prey resources near a terrestrial haulout site may be critical in order to decrease energy spent traveling to foraging sites and increase energy allocated to the female and ultimately delivered to offspring during the extended lactation period.

Several seasonally available prey species are abundant and densely aggregated during the non-breeding season of Steller sea lions and can be seasonally important to the foraging ecology and reproductive success of Steller sea lions. In SE Alaska, sea lions are seasonally associated with spring-spawning aggregations of eulachon *Thaleichthys pacificus* (Marston et al. 2002, Sigler et al. 2004) and herring *Clupea pallasii* (Womble et al. 2005), and in Prince William Sound, sea lions are associated with overwintering herring schools (Thomas & Thorne 2001).

Prey consumption patterns of Steller sea lions in the western stock suggest that sea lions forage on seasonally abundant and densely aggregated prey (Sinclair & Zeppelin 2002); however, the influence of seasonal prey availability on sea lion diet and abundance has yet to be quantified. Thus, our objectives were to assess the seasonal abundance and diet of Steller sea lions in relation to seasonal prey availability. Specifically, we predicted that sea lion abundance and diet would vary depending on seasonally available prey biomass and associated energy density around a terrestrial haulout site during the non-breeding season of Steller sea lions. We examined the hypothesis that the seasonal availability of prey influences the seasonal abundance and seasonal diet of Steller sea lions at Benjamin Island, SE Alaska. We tested the following predictions: (1) the number of sea lions at Benjamin Island is correlated with the biomass of herring; (2) the number of sea lions at Benjamin Island is correlated with the biomass of walleye pollock *Theragra chalcogramma*; (3) the frequency of occurrence of prey species in sea lion diet reflects changes in seasonal availability of pelagic and nearshore prey; and (4) diet diversity increases in spring when forage fish are spawning.

## MATERIALS AND METHODS

**Sea lion seasonal abundance at Benjamin Island and along transects.** Aerial surveys were used to count the number of sea lions at Benjamin Island, SE Alaska (58° 33.7' N, 134° 54.8' W) (Fig. 1) from March 2001 to May 2004. Surveys were conducted monthly from a floatplane (Cessna 206) between 09:00 and 14:00 h and, when possible, within 3 h of low tide. The observer-photographer sat in the front seat and photographed sea lions on shore through an open window from an altitude of 250 to 300 m and at a speed of 183 to 210 km h<sup>-1</sup>.

Photographic images of haulouts were taken using a 35 mm autofocus camera (Nikon 8008S) with a motor drive equipped with a 70–210 mm zoom lens and a 35 mm autofocus digital camera (Nikon D1X) equipped with a 70–300 mm zoom lens. Overlapping images were taken if more than 1 image was needed to cover the entire site. The clearest image was projected and each sea lion in the image was counted. Each image was counted twice by an experienced counter.

In addition to counting the number of sea lions ashore at Benjamin Island, we also enumerated sea lions along acoustic transects which were conducted monthly. An observer stationed on the bridge of the 11 m commercial fishing vessel FV 'Williwaw' used Nikon 7 × 50 binoculars to scan for sea lions in the water along the transect route (Fig. 1). All surveys occurred during daylight hours to facilitate sea lion observations.

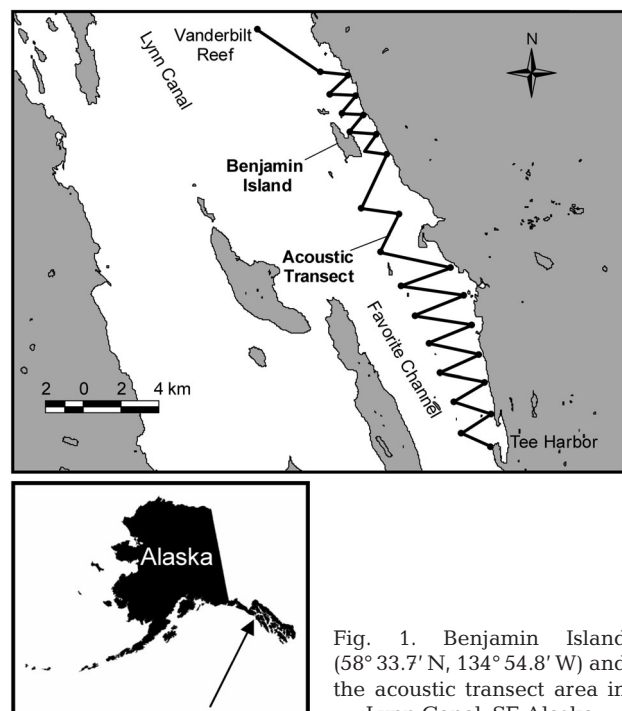


Fig. 1. Benjamin Island (58° 33.7' N, 134° 54.8' W) and the acoustic transect area in Lynn Canal, SE Alaska

**Sea lion diet.** Steller sea lion scat samples (total  $n = 787$ ) were collected during 2001 ( $n = 252$ ), 2002 ( $n = 213$ ), 2003 ( $n = 213$ ), and 2004 ( $n = 109$ ). Samples were collected during February, April, October, and December each year to determine the seasonal changes in sea lion diet. During 2004, samples were only collected in February and April. Samples were not collected during the breeding season, as Benjamin Island is not typically used by sea lions at that time.

Only fresh scat samples that had obviously come from 1 animal were collected. Samples were collected with a spoon, stored in plastic bags, and frozen immediately until processing. Each sample was thawed in water and washed through an elutriator (Bigg & Oleksiuk 1990) or a 0.495 mm sieve. All prey remains (fish bones, otoliths, cartilaginous parts, lenses, teeth, and cephalopod beaks, lenses, and pens) were recovered, dried, and stored in petri dishes. Using a reference collection, prey remains were identified to the lowest possible taxon by Pacific Identifications, Victoria, BC, Canada. The all-structures identification technique was used to identify all skeletal fragments and other hard parts to account for prey with completely digested otoliths or prey that might not be otherwise represented by otoliths (Lance et al. 2001, Browne et al. 2002).

Relative importance of each prey species was based on the frequency of occurrence (FO) in scat samples, calculated as the percentage of all scats in which a prey species occurred. Percentage FO was calculated by dividing the number of scats in which a prey item occurred by the total number of scats that contained identifiable prey remains and multiplying by 100% (Lance et al. 2001). Chi-square analysis was used to test for differences in FO of prey species in scat samples between seasons from 2001 to 2003. The analysis was limited to prey items occurring in at least 5% of scats across years. Diet diversity was calculated for each year and each season using Shannon's index of diversity ( $H$ ) where  $p_i$  is the proportion of the  $i$ th species in the sample (Zar 1999).

$$H = -\sum_{i=1}^k p_i \ln p_i$$

The fork length (FL) of herring and pollock consumed by sea lions was estimated by comparing sizes of bone structures found in scat with those of a reference collection maintained by Pacific Identifications. The FL estimates were generated by comparison with the same structure from comparative specimens of known size from the reference collection and grouped into size classes.

**Prey availability—pelagic prey.** Acoustic surveys were conducted near Benjamin Island in Favorite Channel, in Lynn Canal, SE Alaska (Fig. 1), monthly

from June 2001 to May 2004 to estimate the availability of pelagic prey to Steller sea lions (Sigler & Csepp in press). The transects occurred between Tee Harbor (58° 25' N, 134° 46' W) and Vanderbilt Reef (58° 36' N, 135° 01' W) and included pelagic and nearshore habitats with an average depth of 60 m (depth range = 5 to 305 m). Prey availability was estimated using a portable 38 kHz Simrad echo-integration system with a 12° beam angle towed beside an 11 m commercial fishing vessel, FV 'Williwaw', at 11 km h<sup>-1</sup>. Acoustic transect routes were georeferenced using a Garmin global positioning system with ±10 m accuracy. All surveys began in the morning after daybreak and concluded before dark to account for diel variation in acoustic density estimates (Huse & Korneliusen 2000, Hjellvik et al. 2004) and to facilitate observations of foraging sea lions while collecting acoustic data. Midwater trawls from commercial fishing vessels were conducted quarterly to identify acoustic targets in the echograms and to collect length, weight, and species composition data.

The acoustic data were analyzed with an echo-integrator that was used to sum the returning echoes from fish observed beneath the vessel. Acoustic data were classified by 0.183 km length intervals and 10 m depth intervals, and corrected for instrument calibration using the echo-integration software SonarData Echoview. The output of acoustic scattering (nautical area scattering coefficient, NASC) was used to compute fish density (MacLennan & Simmons 1992). Average fish density was computed by substrata to account for differences in fish density within the survey area. Fish biomass equals average fish density in weight multiplied by the size of the substrata. Further details of methodology can be found in Sigler & Csepp (in press).

Seasonal values of herring and pollock energy density (J. J. Vollenweider unpubl. data) were multiplied by monthly estimates of herring and pollock biomass, respectively, to obtain estimates of the total available energy per month available from herring and pollock. Available prey energy was compared to estimates of individual sea lion energy demands per day (Sigler et al. 2004), which were derived from consumption estimates and bioenergetic models for Steller sea lions (Winship et al. 2002). The estimated daily food ration was obtained by dividing the total food requirement of sea lions in Alaska by the estimated population size of sea lions (Winship et al. 2002). The estimated daily food ration (15.6 kg d<sup>-1</sup>) was converted to daily energy ration using diet composition and prey density values from Winship et al. (2002) resulting in a computed ration of 79464 kJ d<sup>-1</sup> (Sigler et al. 2004).

**Prey availability–nearshore prey.** A companion study conducted nearshore prey surveys at 13 sites around Benjamin Island in winter (February to March) and summer (July) to estimate availability of nearshore prey species to Steller sea lions (Thedinga et al. 2006). Surveys were conducted in March (2002 and 2003) and July (2001, 2002, 2003) using a combination of seining, jigging, and remotely operated vehicle (ROV). Sampling areas included intertidal and subtidal areas up to 100 m in depth and within 350 m of shore. Sites were selected in areas that could be seined, and were spatially distributed throughout the study area. The beach seine was 37 m long with variable mesh that tapered from 5 m wide at the center to 1 m wide at the ends. Jigging occurred at a depth range of 5 to 115 m at 18 stations at Benjamin Island with 3 people jigging at each station for 15 min. Captured fish were identified to species, enumerated, and weighed to the nearest 0.1 kg. FL was measured to the nearest mm for up to 50 individuals of the selected species that were important in the diet of sea lions. An ROV was used to survey for fish that might not have been captured by jigging or seining. ROV dives were conducted at a depth of 125 to 255 m and extended towards the shore. Further details of methodology can be found in Thedinga et al. (2006).

## RESULTS

### Sea lion seasonal abundance at Benjamin Island and along transects

Benjamin Island was occupied by sea lions from October until June (Fig. 2) primarily by adult females with dependent young, juveniles, subadults and a few adult males. The pattern of sea lion occupation was consistent among years, with sea lions typically absent during summer and early fall, usually between July and September. The maximum number of sea lions ashore (range = 747 to 803) at Benjamin Island occurred between October and December (Fig. 2). Beginning in April in all years, the numbers of sea lions ashore at Benjamin Island began to decrease. Sea lions returned to Benjamin Island in October after the breeding season.

Steller sea lions were commonly observed in the water during acoustic surveys. A total of 366 Steller sea lions were observed on 61 occasions (Table 1). Steller sea lions were most common during fall and winter and infrequent during summer. Overall, 98% of Steller sea lion observations occurred from October to February.

### Sea lion diet

A total of 56 prey items were identified from sea lion scat samples ( $n = 787$ ) collected at Benjamin Island (2001 to 2004); however, only 12 species occurred in at least 5% of scat samples. The 2 most common prey species found in scat samples, when pooled across years and seasons, were Pacific herring (FO = 90%) and walleye pollock (FO = 88%) followed in importance by skate *Raja* sp. (FO = 19%), Pacific cod *Gadus macrocephalus* (FO = 18%), capelin *Malloctus villosus* (FO = 17%), Pacific salmon *Oncorhynchus* sp. (FO = 16%), cephalopods (FO = 14%), northern lampfish *Stenobrachius leucopsarus* (FO = 12%), sculpins (Cottidae) (FO = 10%), arrowtooth flounder *Atheresthes stomias* (FO = 8%), eulachon (FO = 8%), and Pacific hake *Merluccius productus* (FO = 5%) (Table 2, Fig. 3).

The FO of salmon, capelin, northern lampfish, sculpins, arrowtooth flounder, eulachon, and hake differed significantly among seasons; however, the FO of herring, pollock, skate, Pacific cod, and cephalopods did not differ significantly among seasons (Table 3, Fig. 3). The FO of salmon in scat was highest during October and December. The FO of capelin, northern lampfish, eulachon, and Pacific cod increased during April (Table 2).

The mean number of prey species per scat sample was  $3.3 \pm 2.1$  (SD) and ranged from 1 to 13 species. There was a high co-occurrence of herring and pollock in the same scat sample (77.6%). Diet diversity was higher in 2002 ( $H = 2.1$ ) than in 2001 ( $H = 1.8$ ) and 2003 ( $H = 1.8$ ). Seasonal diet diversity was slightly higher in February ( $H = 1.9$ ) and April ( $H = 2.1$ ) than in October ( $H = 1.8$ ) and December ( $H = 1.8$ ).

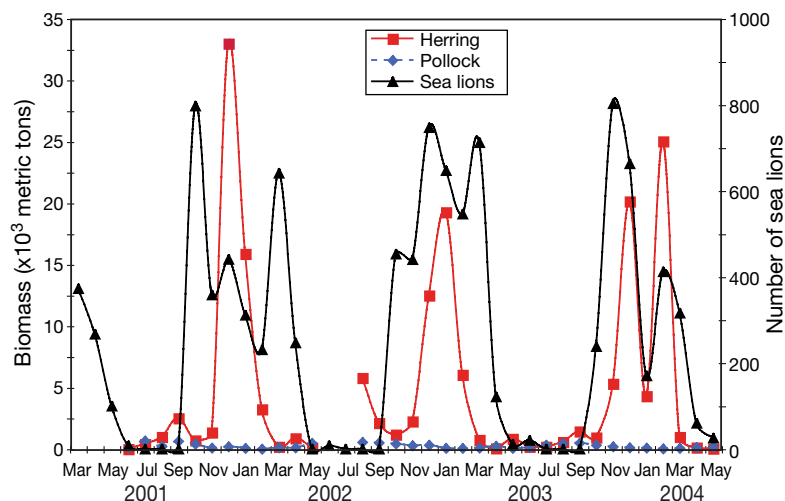


Fig. 2. *Clupea pallasii*, *Theragra chalcogramma* and *Eumetopias jubatus*. Monthly biomass of Pacific herring and walleye pollock and the number of sea lions ashore at Benjamin Island from March 2001 to May 2004

Table 1. Number and percent of Steller sea lions counted in the water during monthly acoustic surveys. ns = no survey

Month	2001	2002	2003	2004	Total	% of total
Jan	ns	44	88	21	153	41.8
Feb	ns	18	9	54	81	22.1
Mar	ns	0	0	0	0	0.0
Apr	ns	0	0	3	3	0.8
May	ns	2	1	0	3	0.8
Jun	0	0	0	ns	0	0.0
Jul	0	0	0	ns	0	0.0
Aug	0	0	1	ns	1	0.3
Sep	1	0	0	ns	1	0.3
Oct	0	0	14	ns	14	3.8
Nov	20	12	4	ns	36	9.8
Dec	1	36	37	ns	74	20.2
Total	22	112	154	78	366	1

A total of 5684 bone structures (including otoliths) from sea lion scat samples were compared to a reference collection of fish of known size to estimate FL of herring and pollock. Herring remains found in sea lion scat were predominantly of adult size (96%) and ranged from 11 to 35 cm FL based on 3813 bone structures. Pollock remains found in sea lions scat included adult pollock (36%) ranging from 34 to 54 cm FL, juvenile pollock (51%) ranging from 20 to 34 cm FL, and young-of-year pollock (10%) ranging from 8 to 30 cm FL based on 1871 bone structures.

**Prey availability**

Pelagic prey biomass varied dramatically by month and by species. Herring and pollock were the most commonly detected prey species during acoustic surveys; however, herring occurred at densities several orders of magnitude greater than pollock. Herring biomass ranged from 6 t (June 2001) to 32 976 t (December 2001). The biomass of herring exceeded 10 000 t in December and January in 2001/2002 and 2002/2003, and in December and February in 2003/2004 (Table 4). In contrast, pollock biomass ranged from 3 t (February 2002) to 655 t (July 2001) (Table 4). Although herring and walleye pollock dominated the surveys, the seasonality of the 2 species differed (Fig. 2). Large schools of herring began to form in November and were present through February in all years. In contrast, pollock was available throughout the year but did not vary as dramatically as herring (Fig. 2). Maximum pollock biomass occurred in late spring and summer. Averaged across all months, herring represented 81% of available biomass, whereas walleye pollock accounted for only 19% of the biomass. Hake contributed to the remaining 1% in several months.

Table 2. Frequency of occurrence (FO, in %) of prey species in sea lion scat samples from Benjamin Island 2001 to 2004. Samples were collected in February, April, October, and December. Only prey species that occur in ≥5% of scat samples across years are shown here. Average % of FO and total numbers of scat yr<sup>-1</sup> given in **bold**

Prey species	2001 to 2004				2001				2002				2003				2004			
	Feb	Apr	Oct	Dec	FO	Feb	Apr	Oct	Dec	FO	Feb	Apr	Oct	Dec	FO	Feb	Apr	Oct	Dec	FO
Pacific herring	<b>90.0</b>	92.0	95.7	86.7	98.2	<b>92.1</b>	96.2	70.4	86.8	100.0	<b>88.3</b>	88.7	68.6	88.9	96.4	<b>85.9</b>	98.1	94.5	94.5	<b>96.3</b>
Walleye pollock	<b>87.5</b>	82.0	89.4	90.8	71.9	<b>84.5</b>	88.7	88.9	77.4	92.5	<b>86.9</b>	83.0	86.3	98.1	92.7	<b>90.1</b>	94.4	87.3	90.8	<b>90.8</b>
Skates ( <i>Raja</i> sp.)	<b>19.4</b>	28.0	29.8	16.3	8.8	<b>19.4</b>	24.5	22.2	20.8	18.9	<b>21.6</b>	9.4	21.6	18.5	12.7	<b>15.5</b>	22.2	23.6	<b>22.9</b>	<b>22.9</b>
Pacific cod	<b>17.5</b>	4.0	34.0	11.2	10.5	<b>13.9</b>	13.2	24.1	18.9	18.9	<b>18.8</b>	22.6	11.8	13.0	18.2	<b>16.4</b>	16.7	34.5	<b>25.7</b>	<b>25.7</b>
Capelin	<b>17.2</b>	24.0	48.9	1.0	0.0	<b>14.3</b>	13.2	22.2	18.9	9.4	<b>16.0</b>	26.4	17.6	13.0	3.6	<b>15.0</b>	25.9	34.5	<b>30.3</b>	<b>30.3</b>
Pacific salmon	<b>15.6</b>	14.0	12.8	25.5	21.1	<b>19.8</b>	7.5	3.7	30.2	22.6	<b>16.0</b>	7.5	3.9	11.1	25.5	<b>12.2</b>	14.8	9.1	<b>11.9</b>	<b>11.9</b>
Cephalopods	<b>13.9</b>	4.0	19.1	14.3	3.5	<b>10.7</b>	11.3	24.1	13.2	17.0	<b>16.4</b>	11.3	5.9	13.0	14.5	<b>11.3</b>	24.1	18.2	<b>21.1</b>	<b>21.1</b>
Northern lampfish	<b>12.1</b>	10.0	12.8	3.1	1.8	<b>6.0</b>	5.7	37.0	18.9	26.4	<b>22.1</b>	9.4	11.8	11.1	7.3	<b>9.9</b>	5.6	16.4	<b>11.0</b>	<b>11.0</b>
Sculpins (Cottidae)	<b>9.9</b>	4.0	4.3	9.2	12.3	<b>7.9</b>	5.7	22.2	5.7	17.0	<b>12.7</b>	5.7	13.7	7.4	7.3	<b>8.5</b>	11.1	12.7	<b>11.9</b>	<b>11.9</b>
Arrowtooth flounder	<b>8.1</b>	8.0	17.0	15.3	3.5	<b>4.8</b>	9.4	5.6	18.9	9.4	<b>10.8</b>	13.2	9.8	7.4	1.8	<b>8.0</b>	9.3	12.7	<b>11.0</b>	<b>11.0</b>
Eulachon	<b>8.0</b>	0.0	19.1	0.0	1.8	<b>4.0</b>	7.5	24.1	17.0	17.0	<b>16.4</b>	0.0	13.7	7.4	3.6	<b>6.1</b>	1.9	7.3	<b>4.6</b>	<b>4.6</b>
Pacific hake	<b>4.8</b>	2.0	0.0	5.1	3.5	<b>3.2</b>	7.5	0.0	1.9	17.0	<b>6.6</b>	13.2	2.0	1.9	1.8	<b>4.7</b>	5.6	5.5	<b>5.5</b>	<b>5.5</b>
n	<b>787</b>	50	47	98	57	<b>252</b>	53	54	53	53	<b>213</b>	53	51	54	55	<b>213</b>	54	55	<b>109</b>	<b>109</b>

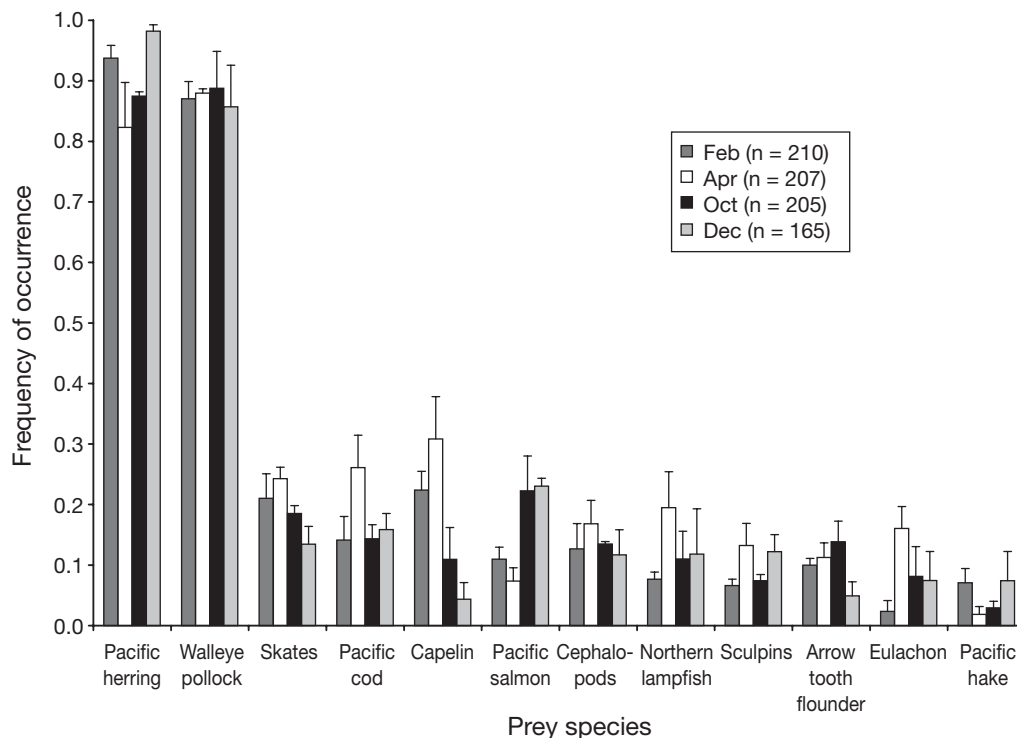


Fig. 3. *Eumetopias jubatus*. Frequency of occurrence of prey species in Steller sea lion scat samples collected in February, April, October and December (2001 to 2004) from Benjamin Island. Only prey species that occur in  $\geq 5\%$  of scat samples across years are shown

Midwater trawls targeting herring and pollock were dominated by catches of these species. Herring comprised 87% of the catch by weight when herring was targeted and pollock comprised 84% of the catch by weight when pollock was targeted (Sigler & Csepp in press). Herring caught in trawl surveys ranged from 8 to 27 cm FL ( $n = 2809$ ) and available pollock size ranged from 10 to 69 cm FL ( $n = 15\,873$ ).

Table 3. Difference in frequency of occurrence of prey species in Steller sea lion scat samples between February, April, October, and December during 2001–2003. Chi-square analysis was limited to prey species occurring in  $\geq 5\%$  of scat samples across years.  $\chi^2_{0.05,3} = 7.815$

Prey species	$\chi^2$	p
Pacific herring	4.03	0.26
Walleye pollock	0.29	0.96
Skates	5.00	0.17
Pacific cod	6.00	0.11
Capelin	42.00	<0.001
Pacific salmon	23.00	<0.001
Cephalopods	4.00	0.26
Northern lampfish	13.00	<0.005
Sculpins	7.85	<0.05
Arrowtooth flounder	16.00	<0.005
Eulachon	28.00	<0.001
Pacific hake	11.25	<0.025

Herring accounted for the majority of energy available to sea lions in most months. Energy available from herring was highest from December to February (Fig. 4). During winter, herring accounted for 99% of the energy available from pelagic prey surveys (Sigler & Csepp in press). The maximum value of available herring energy along transects was 285 Tera Joules ( $TJ = 10^{12} J$ ), equivalent to 3.6 million daily rations for sea lions (Table 4). The seasonal occupation of Benjamin Island by sea lions coincided with peaks in estimated energy available from herring (Fig. 4). In contrast, the maximum value of energy available from pollock was 2.8 TJ, equivalent to 35 000 daily rations for sea lions (Table 4). Although the contribution of pollock to the total energy content was orders of magnitude less than herring, pollock alone could provide enough daily rations for sea lions at Benjamin Island.

Nearshore prey catches were much greater during summer than in winter around Benjamin Island (Thedinga et al. 2006). Rock sole *Lepidopsetta bilineata*, buffalo sculpin *Enophrys bison*, and pink salmon *Oncorhynchus gorbuscha* were the most common species in seine catches in winter and were the most frequent species captured by jigging. In summer, pollock, herring, and Pacific sand lance *Ammodytes hexapterus* were the most common species in seine catches, whereas armorhead sculpin *Gymnocanthus galeatus*

Table 4. Biomass, total energy content, and the estimated number of daily energy rations of herring and pollock available to Steller sea lions at Benjamin Island, SE Alaska

Date	Herring biomass (t)	Pollock biomass (t)	Herring energy content (TJ)	Pollock energy content (TJ)	No. of daily energy rations from herring (thousands)	No. of daily energy rations from pollock (thousands)
<b>2001</b> June	6	102	0.1	0.4	1	5
July	406	655	3.7	2.7	46	34
August	994	225	9.0	1.0	113	12
September	2506	637	22.6	2.8	284	35
October	716	415	6.5	1.7	81	21
November	1347	79	11.6	0.4	146	4
December	32976	199	284.9	0.9	3585	12
<b>2002</b> January	15835	73	136.8	0.3	1722	4
February	3367	3	19.3	0.0	243	0
March	203	104	1.2	0.4	15	5
April	883	113	5.1	0.4	64	6
May	139	473	0.8	1.7	10	22
August	5795	553	61.4	2.4	772	30
September	2129	523	22.6	2.3	284	29
October	1173	422	12.4	1.8	156	23
November	2245	287	19.5	1.3	245	16
December	12492	319	108.3	1.4	1363	18
<b>2003</b> January	19272	74	167.1	0.3	2103	4
February	6117	55	35.1	0.2	442	3
March	757	86	4.3	0.3	55	4
April	59	242	0.3	0.9	4	11
May	837	61	4.8	0.2	60	3
June	186	126	1.1	0.5	13	6
July	191	321	1.9	1.3	23	17
August	580	457	5.6	1.9	71	24
September	1448	455	14.1	1.9	177	24
October	941	313	9.2	1.3	115	16
November	5309	203	47.2	0.9	594	12
December	20139	106	179.0	0.5	2253	6
<b>2004</b> January	4319	80	38.4	0.4	483	4
February	25026	21	143.7	0.1	1808	1
March	988	60	5.7	0.2	71	3
April	128	126	0.7	0.4	9	6
May	39	177	0.2	0.6	3	8

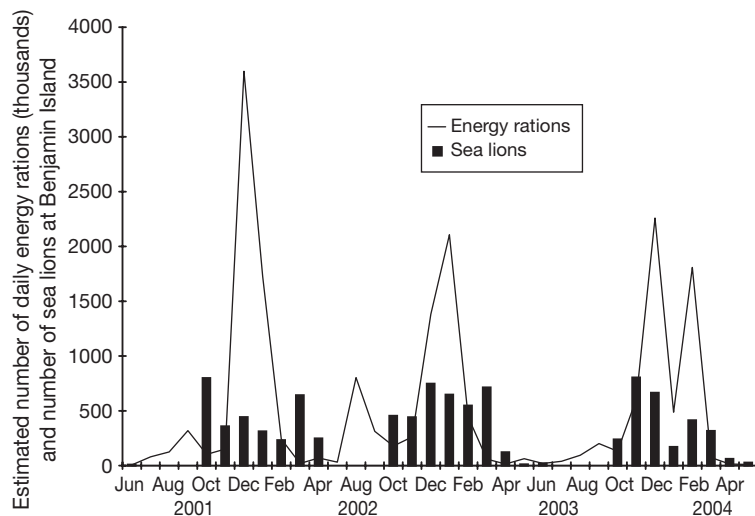


Fig. 4. *Clupea pallasii*, *Theragra chalcogramma*, and *Eumetopias jubatus*. Estimated number of sea lion daily energy rations available from herring and pollock in relation to the number of sea lions hauled out at Benjamin Island from March 2001 to May 2004

was the most frequently captured by jigging (Thedinga et al. 2006). Most species captured by seining were <17 cm FL, yet sea lions at Benjamin Island consumed few species that were <17 cm FL.

The most common species observed from the ROV included juvenile gadids, Pacific sand lance, dusky rockfish *Sebastes ciliatus*, and Pacific snake pricklebacks *Lumpenus sagitta*. Seven species were observed with the ROV that were not captured either by seining or jigging and included Atka mackerel *Pleurogrammus monoptyerygius*, Puget Sound rockfish *S. emphaeus*, silvergray rockfish *S. brevispinus*, tiger rockfish *S. nigrocinctus*, yelloweye rockfish *S. ruberrimus*, rex sole *Glyptocephalus zachirus*, and Alaska skate *Bathyraja parmifera* (Thedinga et al. 2006).

### Seasonal abundance and diet of sea lions in relation to prey availability

Large numbers of sea lions occupied Benjamin Island during the non-breeding season when herring biomass was highest. Peaks in sea lion abundance at Benjamin Island and in the water along acoustic transects occurred between October and March. Pacific herring was the most common prey species in sea lion diet and comprised over 81 % of the available pelagic prey biomass and 96 % of the energy encountered during pelagic surveys near Benjamin Island. In contrast, walleye pollock accounted for 19% of the available prey biomass but was only slightly less common in sea lion diet than Pacific herring. For all years combined, there was a significant relationship between (log) number of sea lions and (log) herring biomass (t) ( $r^2 = 0.55$ ,  $F_{1,23} = 27.11$ ,  $p < 0.0001$ ) (Fig. 5a), but there was no relationship with (log) pollock biomass ( $r^2 = 0.01$ ,  $F_{1,23} = 0.25$ ,  $p = 0.62$ ) (Fig. 5b). Pollock biomass increased when sea lions were absent from Benjamin Island from May through September (Fig. 2). As her-

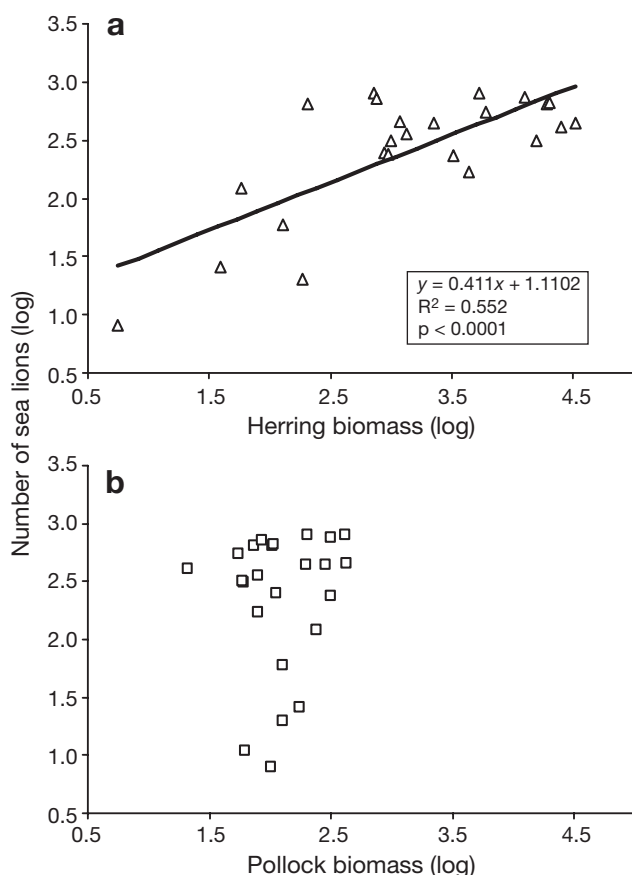


Fig. 5. *Eumetopias jubatus*, *Clupea pallasii* and *Theragra chalcogramma*. Relationship between (a) herring biomass (log) and (b) pollock biomass (log) and number of Steller sea lions (log) at Benjamin Island

ring biomass began to decline in late winter, spring-spawning prey species such as Pacific cod, capelin, northern lampfish, and eulachon increased in FO in the diet of sea lions and herring decreased (Fig. 3). When herring biomass declined around Benjamin Island in spring, the number of sea lions declined (Fig. 2); however, the number of sea lions increased in Berners Bay, located approximately 22 km north of Benjamin, which is the site of a spring-spawning aggregation of eulachon (Sigler et al. 2004).

The size of herring consumed by sea lions (8 to 27 cm FL) overlapped with the size of herring detected during trawl surveys (11 to 35 cm FL). The majority of pollock consumed by sea lions (20 to 54 cm FL) was similar to the size of pollock detected by trawls (10 to 69 cm FL); however, there were smaller pollock (<20 cm FL) detected by trawls that were not found in sea lion scat.

Few fish species in seine catches in nearshore areas were found in the sea lion diet samples and most fish species were smaller (Thedinga et al. 2006) than the average size of prey consumed by sea lions at Benjamin Island. Juvenile pink salmon (<10 cm FL) comprised 12.3 and 16.2% of nearshore seine catch in March of 2002 and 2003, respectively, but sea lions consume Pacific salmon ranging from 16 to 90 cm FL. Sea lions consumed Pacific cod ranging from 16 to 80 cm FL; however, 96% were of adult size. Pacific cod captured by jigging in nearshore areas ranged from 14 to 49 cm FL, whereas cod from seine catches were primarily juveniles (3 to 19 cm FL). Fish species such as cottids were found in seine catches and occurred in sea lion diet (Thedinga et al. 2006). The most common cottids found in sea lion scat samples were Pacific staghorn sculpin *Leptocottus armatus* (FO = 3.9%) and great sculpin *Myoxocephalus polyacanthocephalus* (FO = 2.2%). Most staghorn sculpins (84%) consumed by sea lions were adults and ranged between 20 and 44 cm FL and overlapped with the size (16 to 30 cm FL) of staghorn sculpins caught in nearshore seine catches. Great sculpins found in sea lion scat were also primarily adults (16 to 64 cm FL); however, adult fish (25 to 47 cm FL) were only captured in nearshore jig sampling.

## DISCUSSION

### Seasonal availability of prey resources for sea lions

Large numbers of sea lions occupied Benjamin Island during the non-breeding season from October to April, when herring biomass was highest, and there was a positive correlation with the biomass of herring and the number of sea lions. The seasonal use of Benjamin Island by sea lions is associated with the avail-



ability of densely aggregated, overwintering herring. Herring is available for several months, around Benjamin Island, and can sustain sea lions that come ashore at Benjamin Island for up to 6 mo (October to March). The energy density of herring is highest in fall and early winter (Vollenweider 2005), when herring are most abundant near Benjamin Island and thus may confer energetic benefits to sea lions. In April, when herring biomass decreases and herring energy density decreases, the number of sea lions begins to decrease. Herring provides an abundant, densely aggregated, high-energy resource for sea lions close to the terrestrial haulout site, which may be particularly important for adult females with dependent pups.

Overwintering herring were seasonally predictable near Benjamin Island from 2001 to 2004. Furthermore, aggregations of overwintering herring were documented in the same general area from 1973 to 1975 (Carlson 1980), suggesting that herring have been using the same area for at least 3 decades. Herring usually follow the same migration paths and use the same overwintering areas year after year (Corten 2002). In spring, between March and May in SE Alaska, herring move to spawning areas (Carlson 1980). During summer, herring typically move to feeding areas, many of which are located along the outer coast of SE Alaska (Rounsefell 1930).

Although there was no relationship between the biomass of pollock and the number of sea lions, pollock was only slightly less common than herring in sea lion diet. The availability of pollock throughout the year may provide a maintenance diet for sea lions when other seasonal prey resources are not available. Pollock may be consumed by sea lions for much of the year; however, when herring are aggregated in areas close to Benjamin Island, herring may be more energetically rewarding than pollock because they are more densely aggregated and higher in energy density and lipid content than pollock (Iverson et al. 2002, Vollenweider 2005). Furthermore, a mixed diet of pollock and herring may confer benefits over a single-species diet by increasing digestible energy intake (Trumble & Castellini 2005).

Pollock occurred in much lower biomass than did herring, particularly in winter when sea lions were at Benjamin Island, yet pollock was one of the most common prey consumed and were present throughout the winter. Possible explanations include different spatial distributions of pollock and herring in the survey area. The survey area is an important herring overwintering area and herring are concentrated there seasonally, whereas pollock are common both inside and outside the survey area (based on limited sampling outside the survey area). In addition, captive studies have shown that pollock remains occur in significantly more sea

lion scats than other prey species and recovery rates for pollock are 3-fold that of herring (Tollit et al. 2003). Cottrell & Trites (2002) found that on the average the number of pollock hard parts recovered from the scat of captive sea lions was 31.2 per pollock, in contrast to only 7.9 per herring. Passage rates are higher for pollock than herring, which may tend to overestimate pollock and underestimate herring in sea lion diet. Pollock typically have larger more robust otoliths that are able to withstand the digestive process better than the smaller otoliths of herring (Tollit et al. 2003).

Although pollock biomass increased primarily during summer at Benjamin Island, the energy density of pollock is highest in winter (Vollenweider 2005), when sea lions occupy Benjamin Island. In other areas of Alaska, pollock was the dominant prey species of sea lions (Pitcher 1981, Merrick et al. 1997, Sinclair & Zepelin 2002); however, small schooling fish, not pollock, were the dominant prey items found in sea lions taken in Alaska from 1958 to 1962 (Fiscus & Baines 1966).

The size of prey consumed by pinnipeds is likely underestimated due to erosion of hard parts during the digestive process (e.g. da Silva & Neilson 1985, Tollit et al. 2004). Underestimation of prey size, which is influenced by fish species and size (Bowen 2000), may account for differences observed in the size of prey consumed in relation to the available detected during trawl surveys. Although the size of pollock consumed by sea lions was similar to the size of pollock available in trawl surveys, the average size reduction for different pollock structures ranged from 12.2 to 24.7% in captive feeding trials with Steller sea lions (Tollit et al. 2004).

### Importance of other seasonally occurring prey species

Although pollock and herring dominated the diet of sea lions during all seasons, other seasonally available prey species, such as spring-spawning forage fish and Pacific salmon, were important for shorter periods. The frequency of occurrence of forage fish species, with the exception of herring, increased in the sea lion diet during April and consequently prey diversity increased. Spawning aggregations of forage fish provide densely aggregated, high-energy prey for Steller sea lions for brief time periods and may influence haulout use by sea lions (Sigler et al. 2004, Womble et al. 2005). The spawning season of many forage fish species occurs between March and May in SE Alaska just prior to the breeding season of Steller sea lions.

Eulachon provide an important high-energy prey pulse for Steller sea lions at Benjamin Island when herring biomass begins to decrease in spring. Other than northern lampfish, eulachon are higher in lipid content than any other sea lion prey item (Iverson et al. 2002,

Vollenweider 2005). Mean lipid content for eulachon in SE Alaska was  $16.30 \pm 4.10\%$  and was as high as 28.9% (Vollenweider 2005). Overall, eulachon were found in only 8% of scat samples from 2001 to 2004, although during April 2002 the frequency of occurrence of eulachon in sea lion scat was as high as 24.1%. Eulachon may be underestimated in scat samples from Benjamin Island because sea lions raft near spawning aggregations and may not regularly return to the haulout to defecate (Womble et al. 2005). In addition, during captive feeding trials with California sea lions the average recovery rate for eulachon otoliths was only 46.5% ( $\pm 13.7$ ) (Orr & Harvey 2001) further contributing to the underestimation of eulachon in the sea lion diet.

Although eulachon does not appear to be an important prey item for sea lions in other areas of Alaska (Pitcher 1981, Merrick et al. 1997, Sinclair & Zeppelin 2002), observations from Lynn Canal near Benjamin Island suggest that eulachon may play an important role in the seasonal foraging ecology of sea lions in the area (Marston et al. 2002, Sigler et al. 2004, Womble et al. 2005). In 2004, eulachon were found in 100% of scat samples ( $n = 10$ ) (J. N. Womble unpubl. data) collected at a terrestrial haulout site in Berners Bay in Lynn Canal near a spawning aggregation of eulachon. In addition, juvenile sea lions captured and tagged at Benjamin Island were observed to move to areas of known high eulachon concentrations in Berners Bay and northern Lynn Canal during the spring spawning season of 2003 (National Marine Fisheries Service [NMFS] unpubl. data).

Capelin was seasonally important in sea lion diet in April (up to FO = 48.9%) and overall occurred in 17% of scat samples. Although not as high in energy content as eulachon and herring, the mean energy value of capelin in SE Alaska was  $4.51 \pm 1.04 \text{ kJ g}^{-1}$  (Vollenweider 2005). As with eulachon, the smaller and more fragile otoliths of capelin were recovered at a much lower rate ( $10.0 \pm 7.1\%$ ) in captive trials with California sea lions (Orr & Harvey 2001); therefore it is likely

the use of capelin by sea lions at Benjamin Island may be underestimated. Capelin spawn in spring and summer in SE Alaska (Table 5) and spawning occurs in northern Lynn Canal in spring (K. Brownlee pers. comm. 2002). In Prince William Sound, capelin was primarily consumed by sea lions in spring and summer (Pitcher 1981). Prior to the 1970s, capelin was an important component of sea lion diet in the Gulf of Alaska and Unimak Pass (Fiscus & Baines 1966, Pitcher 1981); however, in sea lion scat samples collected from 1990 to 1998, capelin occurred in low frequencies (Sinclair & Zeppelin 2002).

Northern lampfish occurrence in sea lions scats also increased during spring with a particularly dramatic increase in April 2002 (FO = 37%). Northern lampfish have the highest lipid content ( $46.3 \pm 4.40\%$  dry mass) (Anthony et al. 2000) of any sea lion prey species and are one of the most abundant species caught in trawls in the mesopelagic zone of the Gulf of Alaska (Purcell 1996). Typically they inhabit depths of 300 to 600 m during the day with vertical migrations to 50 m at night (Frost & McCrone 1979). We commonly detected northern lampfish in our acoustic surveys, but we did not estimate their abundance because they were mixed with Pacific hake and have low acoustic reflectivity.

Northern lampfish may play an important seasonal role in the foraging ecology of sea lions, given their extremely high lipid content and accessibility. In Muir Inlet, a glacial fiord west of Lynn Canal, northern lampfish have been found as shallow as 10 to 15 m during the day (Abookire et al. 2001), which would make them easily accessible to Steller sea lions. In other areas, such as the Southern Ocean, myctophids are high in lipid content, exploited by several predators, and play an important role in food webs (Lea et al. 2002).

The FO of salmon increased in October and December and coincided with the run timing of fall spawning salmon (Table 5). During fall and early winter (September to December) coho salmon *Oncorhynchus kisutch* and chum salmon *O. keta* are returning to rivers in

Table 5. Prey species that differed significantly in frequency of occurrence by season, month of maximum frequency of occurrence (FO<sub>max</sub>), and the season during which each species spawns

Prey species	— 2001 —		— 2002 —		— 2003 —		Spawning season	Source
	Month	FO <sub>max</sub>	Month	FO <sub>max</sub>	Month	FO <sub>max</sub>		
Capelin	Apr	48.9	Apr	22.2	Feb	26.4	Spring and Summer	M. Arimitsu (USGS-BRD, Juneau, AK) pers. comm.
Pacific salmon	Oct	25.5	Oct	30.2	Dec	25.5	Summer and fall	Groot & Margolis (1991)
Northern lampfish	Apr	12.8	Apr	37.0	Apr	11.8	Winter to spring	Smoker & Pearcy (1970)
Sculpins	Dec	12.3	Apr	22.2	Apr	13.7	Winter	Hart (1973)
Arrowtooth flounder	Apr	17.0	Oct	18.9	Feb	13.2	Winter	Rickey (1995)
Eulachon	Apr	19.1	Apr	24.1	Apr	13.7	Spring	Hart (1973)
Hake	Oct	5.1	Dec	17.0	Feb	13.2	Winter	Hart (1973)

northern Lynn Canal to spawn (Cline 1982) and are available to sea lions as high-energy prey. Sea lions may intercept salmon as the fish migrate by Benjamin Island en route to spawning rivers in northern Lynn Canal. In contrast, in both Prince William Sound and in the western Alaska, salmon were consumed by sea lions primarily in summer, likely reflecting the spawning period of salmon in those areas (Pitcher 1981, Sinclair & Zeppelin 2002). The importance of salmon in the diet may be underestimated because the recovery rate (13 to 86%) of salmon structures in scat was much lower than that of pollock (22 to 156%) from a captive study of Steller sea lions (Tollit et al. 2003).

Skates (*Raja* sp.) were the third most common prey group and were typically more common in February and April. During pelagic prey surveys, there was no directed sampling for on-bottom species such as skates near Benjamin Island; however, in Frederick Sound, approximately 160 km south of Benjamin Island, sandpaper skates *Bathyraja interrupta*, Alaska skates *B. parmifera*, longnose skates *Raja rhina*, and big skates *R. binoculata*, were the most frequently caught species in longline catches (M. F. Sigler unpubl. data). Although skates were a common diet item for sea lions, the energy content of skates is relatively low compared to herring (Logerwell & Schaufler 2005).

#### Foraging tactics and energetic costs

Although herring and pollock were the primary pelagic species available to sea lions and corresponded to the most common prey species in sea lion diet, sea lions likely use different foraging tactics for each of these species. Foraging for different prey types can influence foraging strategies and encounter rates (Engen & Stenseth 1984), which ultimately influence foraging costs. For example, the foraging tactics of harbor seals *Phoca vitulina* differed among prey types and these tactics had energetic consequences that likely affected prey profitability (Bowen et al. 2002). Pursuit/handling time for harbor seals was greater for demersal flounder than for schooling sand lance (Bowen et al. 2002).

Ultimately, given the differences in prey density, energy density, and depth ranges for herring and pollock, it would be necessary to determine the cost of foraging for each of these prey types, as the foraging tactics employed by sea lions are likely to be different, thus influencing prey profitability. Herring are schooling fish that are typically found in densely aggregated schools along the bottom or in the water column. In contrast, juvenile pollock are more loosely aggregated. Average depths for herring and juvenile pollock were <100 m water depth, whereas adult pollock aver-

age depths were from 150 to 200 m (Sigler & Csepp in press).

In contrast to herring, most of the nearshore fish species are not densely aggregated and may require a different foraging tactic for sea lions in nearshore areas. Although some prey species, such as Pacific cod, skates, and sculpins, found in nearshore areas were common in the sea lion diet, in general there was very little overlap with fish species or fish size caught in nearshore areas and the fish species found in sea lion scat. Nearshore seine and jig catches in winter around Benjamin Island contained far fewer fish than seine and jig catches in summer (Thedinga et al. 2006), suggesting that the nearshore area may not be a cost-efficient place to forage in winter.

#### Implications of seasonal availability of prey to marine predators

If prey patches are profitable season after season, experience could allow predators to locate prey patches more efficiently in following trips (Miliniski 1994), as marine predators may use a combination of local enhancement and memory to locate prey patches around a central place (Davoren et al. 2003). Experimental studies with California sea lions have demonstrated that individual sea lions have the ability to remember over several years (Reichmuth Kastak & Schusterman 2002). Herring return to the same wintering grounds year after year (Carlson 1980); therefore, it is likely that individual sea lions may learn and remember where the highly predictable prey patches are located and return to a terrestrial haulout site close to the prey patches. Observations of adult female Steller sea lions with pups that were permanently marked at their birth rookeries suggest that some of the same sea lions return to Benjamin Island year after year (K. W. Pitcher pers. comm. 2004). Given the lengthy lactation period of Steller sea lions, access to predictable densely aggregated prey resources in winter around Benjamin Island may be critical as energetic demands increase for females with growing dependent pups during winter and spring (Winship et al. 2002). In Tysfjord, Norway, killer whales *Orcinus orca* return to feed on spring-spawning Atlantic herring *Clupea harengus* year after year (Similä et al. 1996). Other pinniped species, including Antarctic fur seals *Arctocephalus gazella* and northern elephant seals *Miromunga angustirostris*, make foraging trips to the same areas year after year (LeBoeuf et al. 2000, Bonadonna et al. 2001).

The seasonal availability of densely aggregated, energy-rich prey resources influences the seasonal abundance and diet of sea lions at Benjamin Island.

Sea lions exhibit similar patterns of seasonal occupation at other terrestrial haulout sites in SE Alaska (Womble 2003) and these patterns may be related to the seasonal movement of herring or other seasonally available prey species. The availability of prey resources can vary temporally and spatially at various scales, so further integrated, fine-scale investigations of the influence of prey abundance and availability on sea lion abundance, distribution, diet, and movements are warranted throughout their range. Elucidating factors that may influence the abundance and distribution of sea lions may provide insight into declines of sea lions in other parts of their range. Marine predators likely depend upon seasonally available prey to meet energy demands throughout the year. Ultimately, understanding the role that the seasonal availability of prey species plays in the ecology of marine predators is an important step in furthering our understanding of factors that may regulate marine predator populations.

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