

Seasonal Differences in Prey Availability Around a Steller Sea Lion Haulout and Rookery in the Gulf of Alaska

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Abstract

Abundance and distribution of fish biomass were surveyed around a Steller sea lion (*Eumetopias jubatus*) haulout (nonbreeding) and rookery (breeding) site in the Gulf of Alaska to test the hypothesis that seasonal occupation of either site was related to the availability of prey. The haulout and rookery are located 30 nmi (55.56 km) apart at Long Island and Marmot Island in the Central Gulf of Alaska region where the Steller sea lion population is slowly recovering from a severe decline. Surveys conducted in May and November of 2002 (just before and after the breeding season) showed significantly higher prey energy density (total fish biomass density \times energy content; kJ nmi⁻²) around the Long Island haulout than around the Marmot Island rookery. A survey conducted in July of 2002 (during breeding season) showed prey energy densities that were not significantly different between Long Island and Marmot Island but that were more concentrated in a single area by Marmot Island. Major prey species groups in all surveys were arrowtooth flounder, walleye pollock, cod, and soles; all are known prey of Steller sea lions in this area. Steller sea lion counts at Long Island during nonbreeding seasons from 2000 to 2004 correlated significantly with midwater prey energy densities. Steller sea lion counts at Marmot Island over the same period did not correlate with midwater prey energy densities in either breeding or nonbreeding seasons. The results of the study indicate that prey availability may be an important factor in the choice of haulout sites by Steller sea lions, and the higher prey availability at rookery sites provides some advantage.

Key Words: Steller sea lion, *Eumetopias jubatus*, prey availability, haulout, rookery, Gulf of Alaska

Introduction

Since 1990, management of Alaska's groundfish fisheries has been driven largely by concern for recovery of Steller sea lions (*Eumetopias jubatus*), whose numbers declined 80% in the 1980s and 1990s (Trites & Larkin, 1996; Loughlin, 1998). This drastic and unexplained decline led to the listing of Steller sea lions as Threatened under the Endangered Species Act (ESA) of 1973 in 1990 (55 FR 12645). Steller sea lions west of 144° W longitude ("western stock") were subsequently listed as Endangered in 1997 (62 FR 30772). Causes of this decline remain unclear, but reductions in prey abundance, availability, or quality may have led to nutritional stress (Merrick et al., 1987, 1997; Springer, 1992; Trites & Donnelly, 2003) and reduced pup survival (York, 1994). As a result, a variety of protective measures have been implemented to reduce the potential adverse effects of commercial fishing (National Marine Fisheries Service [NMFS], 2001, 2003) on Steller sea lions and their prey resources within designated Critical Habitat. Potential adverse effects include disturbance at haulouts, dispersal of fish schools, and depletion of fish species that are sea lion prey (Fritz et al., 1995; Fritz & Ferrero, 1998; Cornick et al., 2006). Critical Habitat for Steller sea lions, defined by the ESA and designated in 1993 (58 FR 45269) includes all major rookeries (sites used for breeding and pup rearing), haulouts (sites used for resting), waters within 20 nmi of those sites, and three recognized foraging areas (ESA 50 CFR 226.202).¹

Steller sea lions are opportunistic feeders, known to prey upon a variety of demersal, semi-demersal, and pelagic species, including Pacific sand lance (*Ammodytes hexapterus*), walleye

¹NOAA Fisheries, National Marine Fisheries Service, Alaska Regional Office (www.fakr.noaa.gov/protected_resources/stellers/habitat.htm)

pollock (hereafter referred to as “pollock”; *Theragra chalcogramma*), herring (*Clupea pallasii*), salmon (*Oncorhynchus* spp.), arrowtooth flounder (*Atherestes stomias*), Pacific cod (*Gadus macrocephalus*), and cephalopods (Mathison et al., 1962; Fiscus & Baines, 1966; Merrick et al., 1997; Sinclair & Zeppelin, 2002; Trites et al., 2007a; McKenzie & Wynne, 2008). Steller sea lions are central place foragers (Orians & Pearson, 1979; Raum-Suryan et al., 2004) whose haulout and rookery sites are likely chosen, in part, for their proximity to prey resources (NMFS, 2001; Ban & Trites, 2007). Foraging trips made in summer by adult females are limited by their need to return to young pups, and these trips were found to average 18 ± 3 h in duration and 17 ± 5 km distance from rookeries (Merrick & Loughlin, 1997; Milette & Trites, 2003; Davis et al., 2006). Females move to haulouts by late summer when their pups are able to accompany them (Raum Suryan et al., 2004), then forage for up to 204 ± 105 h and 133 ± 60 km from haulouts through the winter (Merrick & Loughlin, 1997) as pups mature. Weaning occurs in April or May, usually just prior to the pups’ first (occasionally second or third) birthday, and is marked by abrupt changes in its foraging distance and dive characteristics (Trites & Porter, 2002; Loughlin et al., 2003; Raum-Suryan et al., 2004; Briggs, 2005). Telemetry studies by NMFS (2001) suggested that 75% of foraging by juveniles

occurred within 10 nmi (18.5 km) from shore, and Raum-Suryan et al. (2004) reported that 90% of roundtrips made by pups and juveniles were less than 15 km from their haulouts, suggesting that nearshore waters may be particularly important for pups as they develop foraging skills, and for inexperienced, newly weaned juveniles meeting the high energy demands of growth.

Since 2000, Steller sea lion numbers have stabilized or increased throughout most of Alaska (Sease & Gudmundson, 2002; Fritz & Stinchcomb, 2005). Numbers in the Central Gulf of Alaska, however, have been slow to recover, sparking interest in monitoring Steller sea lion abundance and assessing their foraging environment in this region. Terrestrial sites around Kodiak Island in the Central Gulf of Alaska have been surveyed repeatedly since 1999 to monitor temporal patterns of Steller sea lion distribution, variability in terrestrial site occupation, and potential sources of vulnerability in the Steller sea lion population’s survival and reproductive success (Wynne, 2005b).

In this paper, the authors examine the relationship between site occupation and prey abundance and quality in waters surrounding two sites east of Kodiak: (1) Long Island and (2) Marmot Island (Figure 1). Long Island is a haulout used from fall through spring; it is generally vacated at the onset of the breeding season in May. Although used by

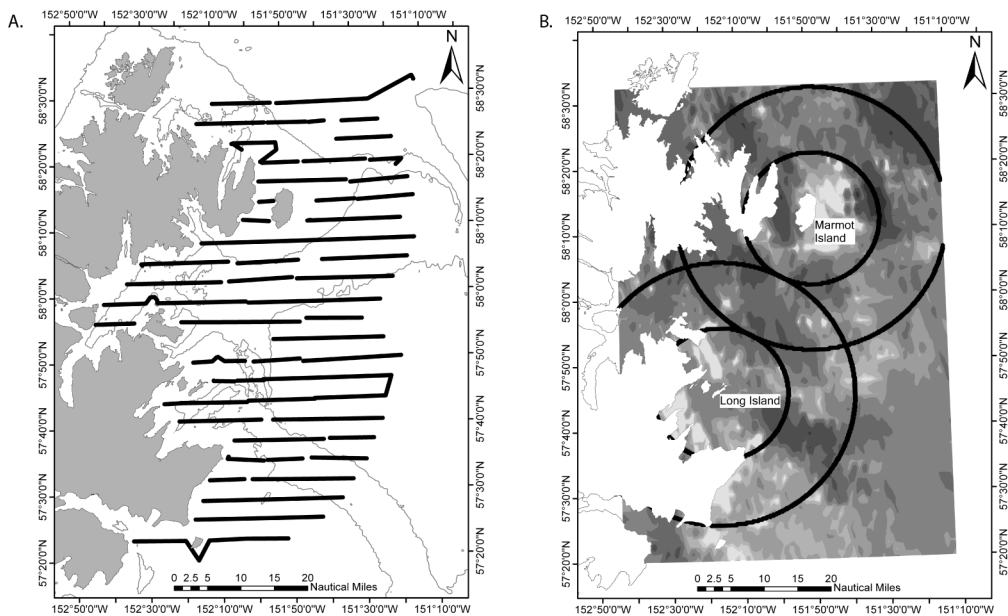


Figure 1. Survey area around Long Island and Marmot Island in the Gulf of Alaska with (A) the acoustic transects overlaid on the 100-m depth isobath and (B) the 10- and 20-nmi zone perimeters around either site overlaid on a krige surface of biomass density of fish (in this example, walleye pollock in July) derived from the acoustic data

some males, this haulout is used predominantly by females with pups and subadults of both sexes. Marmot Island is used as a rookery during the breeding season (May to August) and pup-rearing season (into September), and as a haulout throughout the remainder of the year (Wynne, 2005b). Since 2001, a complex and dynamic series of restrictions under the Critical Habitat designation have prohibited the commercial harvest of groundfish year-round within 0 to 10 nmi of the Long Island haulout, and seasonally up to 20 nmi from Marmot Island (50 CFR 679). The two sites are separated by only 30 nmi (55.56 km). Peak counts of Steller sea lions on Marmot Island generally coincide with lowest counts on Long Island, suggesting a high interchange between the two sites (Wynne, 2005b). Monitoring of individually identifiable (branded) sea lions and their breeding activity verify that many—but not all—animals using Long Island as a winter haulout were bred or born on Marmot Island rookery (Wynne, unpub. data). The cycle of seasonal occupation of Long and Marmot Islands suggests that some habitat value of the two sites changes throughout the year.

The authors hypothesized that the habitat value relates to differences in foraging potential (prey abundance and quality) in the waters surrounding the haulout at Long Island and the rookery at Marmot Island. First, the seasonal relationship between site occupation and prey abundance/quality was examined in a comparative study between sites in May, July, and November 2002 to test the null hypothesis that foraging potential within 20 nmi of a haulout and a rookery does not differ before, during, and after the breeding season. Prey abundance and distribution by species within 0 to 10 vs 10 to 20 nmi of Long Island and Marmot Island were analyzed to test the null hypothesis that prey available to Steller sea lions does not differ significantly on this scale of distance from the sites. Second, counts of Steller sea lions recorded at Long Island and Marmot Island between 2000 and 2004 were compared with fish energy densities recorded at the same time in the surrounding waters to test for long-term (more than 1 y) relationships between sea lion attendance and the prey energy available at each site.

Materials and Methods

Surveys

The Long Island haulout is located at 57° 45.5' N, 152° 16.0' W. The Marmot Island rookery extends from 58° 14.5' N, 151° 47.5' W to 58° 10.0' N, 151° 51.0' W (Figure 1). Greater than 95% of the water depths within 20 nmi of the Long Island and Marmot Island sites were < 200 m deep and were

assumed to be accessible to foraging Steller sea lions (Merrick & Loughlin, 1997; Loughlin et al., 1998, 2003; Pitcher et al., 2005).

For the comparative study between the two sites, the areas surrounding Long Island and Marmot Island were surveyed in 2002 from 17 to 24 May, 19 to 29 July, and 12 to 24 November as part of the Gulf Apex Predator-prey (GAP) project (Foy, 2005). The May (late spring) and July (summer) survey periods correspond to approximately the start and end of breeding season; November (late fall) is in the nonbreeding season (Chumbley et al., 1997; Sease & York, 2003). All three surveys were conducted from the chartered stern trawler *F/V Laura*.

The surveys collected active acoustic data at 38 kHz with a SIMRAD EK60 echo-sounder system along east-west parallel transects 5,600 m apart (Figure 1A) to assess fish abundance and distribution. Acoustic backscatter ≥ -70 dB re: 1 m⁻¹ volume backscattering strength (S_v) was echo-integrated over 0.1 nmi (185.2 m) along-transect horizontal bins from 5 m below surface to 0.5 m above sea bottom. Echo-integrations were screened using Grubbs' (1969) test for outliers ($\{X - \text{mean}(X)\}/\text{SD}(X) > 4$), which occasionally occurred when the acoustic algorithm failed to exclude a section of sea bottom, resulting in very strong misclassified backscatter. Midwater trawls (39-m headrope length, 20-m vertical opening, 2.22-cm codend liner) were deployed along-transect opportunistically (6 to 9/survey) when strong aggregations or pattern changes in the acoustic backscatter were detected, to apportion species composition to the backscatter. Bottom trawls (22.3-m mean net spread, 2.22-cm codend liner) were deployed at 23 to 28 locations per survey, stratified-random by depth (< and \geq 100 m) and distance (< and \geq 10 nmi) to the Steller sea lion sites, to sample near-bottom species. Catches of both midwater and bottom trawls were counted by species, then randomly subsampled to measure and weigh up to 30 fish per species for length-frequency and length-weight distributions. All fish of a species were measured and weighed if \leq 30 occurred in the subsample. Single species counts in excess of 500 were approximated by volumetric subsamples (Foy, 2005).

Midwater species that made up \geq 1% of catch weight in a trawl were apportioned to acoustic backscatter. Nine species in total were retained for acoustic backscatter analysis: pollock, capelin (*Mallotus villosus*), eulachon (*Thaleichthys pacificus*), Pacific herring, king salmon (*O. tshawytscha*), chum salmon (*O. keta*), pink salmon (*O. gorbuscha*), Pacific sand lance, and majestic squid (*Berryteuthis magister*). The salmon were grouped together for this study. Fish and squid lengths

(L), obtained from length-frequency distribution modes of the midwater trawl samples, were converted to estimates of average individual target strength (TS) by the standard regression equation (MacLennan & Simmonds, 1992):

$$TS = 20 \log L \text{ (cm)} + b$$

Regression slope 20 implies proportionality between the backscattering cross-section ($\sigma_{bs} = 10^{TS/10} \text{ m}^2$) and square of total length (Love, 1977). Regression intercepts b were assigned to species from published values (Table 1). For sand lance, the published intercept b had been calculated from 120 kHz rather than 38 kHz measurements (Thomas et al., 2002). It was assumed that this difference would cause only minor discrepancy in TS estimation. Results by Gauthier & Horne (2004) suggest that average TS of eulachon and Atka mackerel (*Pleurogrammus monopterygius*), two species which, like sand lance, do not have swimbladders, are not significantly different between 38 and 120 kHz relative to intraspecific and tilt angle variability. For majestic squid, intercept b was inferred from TS data of the similar-sized (Okutani, 1983; Arkhipkin et al., 1996) Japanese common squid (*Todarodes pacificus*) (Kawabata, 2005). For salmon, echo-sounding at sea is not commonly practiced, and a value of intercept b was chosen from TS data published for acoustically similar fish (i.e., the approach used by Mulligan & Kieser, 1986). Salmon are similar to pollock in size and similar to herring in physiology, including the presence of a swimbladder, and were assigned an intercept value of $b = -66.0$. The value -66.0 is the same as used for pollock (Table 1) and is intermediate among published b values for herring: -71.9 (Foote, 1987), -67.3 (Ona, 2003), and -65.1 (Gauthier & Horne, 2004). All values of intercept b (Table 1) represent dorsal normal aspect measurements (lateral axis of the fish body perpendicular to the incident acoustic front; Gauthier & Horne, 2004). Acoustic detectability of fish can change with diurnal changes in fish behavior and vertical positioning (Shackell et al., 1994; Lawson & Rose, 1999; Hjellvik et al., 2004). Therefore, acoustic data were only collected between dawn and dusk. Since changes in fish position are not instantaneous between day and night, potential time-of-day bias was additionally tested for by calculating regressions of acoustic fish densities per 0.1 nmi along-transect bin vs time difference to sun transit (i.e., true local noon²) from when the transect bin was echo-sounded.

²As determined for each date and latitude and longitude coordinate from the U.S. Naval Observatory website: aa.usno.navy.mil.

Table 1. TS-length regression b intercepts (TS = 20 log L + b) of midwater trawl-caught species

Species	Intercept b	Source
Walleye pollock	-66.0	Foote & Traynor (1988)
Capelin	-69.3	Gauthier & Horne (2004)
Eulachon	-84.5	Gauthier & Horne (2004)
Herring	-65.1	Gauthier & Horne (2004)
Salmon ¹	-66.0	approximated ²
Sand lance	-80.0	Thomas et al. (2002) ³
Majestic squid	-73.1	Kawabata (2005) ⁴

¹King, chum, and pink salmon

²Approximated from similarities to walleye pollock and herring

³Measured at 120 kHz

⁴Japanese common squid

Bottom trawls captured pollock, flatfish, Pacific cod, Tanner crabs (*Chionoecetes bairdi*), greenlings (*Hexagrammos* spp.), rockfish (*Sebastes* spp.), sablefish (*Anoplopoma fimbria*), skates (*Raja* and *Bathyraja* spp.), and sculpins (Cottidae). Greenlings, rockfish, skates, and sculpins, respectively, were grouped for this study. A small number of Pacific tomcod (*Microgadus proximus*) were caught in November and grouped with Pacific cod. Flatfish were grouped according to the classification used by Wynne (2005a) for Steller sea lions' diet: arrow-tooth flounder, Pacific halibut (*Hippoglossus stenolepis*), and soles (*Hippoglossoides*, *Pleuronectes*, and *Psettichthys* spp). Bottom fish cannot be significantly correlated with water column acoustic backscatter, and, therefore, densities of bottom trawl catches were quantified directly. Bottom trawls were standardized to approximately 10 min (exact time at fishing depth was measured for each trawl), which at a trawl speed of 3 kts gives ~0.50 nmi distance covered. Distances covered were multiplied by the average width of the net opening (22.40 m) to give an area swept (m²). Areas swept were not adjusted for trawl depths, of which 92% were < 200 m. Catch weight per species was then divided by area swept to calculate density.

For the analysis of long-term (more than 1 y) relationships between Steller sea lion attendance and prey availability, various acoustic/trawl surveys from the GAP project were used opportunistically if they came within both 0 to 10 and 10 to 20 nmi of Long Island and Marmot Island. Eleven acoustic/trawl surveys between 2000 and 2004 met this criterion (Table 2), in addition to the three-site comparison surveys in 2002. Acoustic and catch data from the opportunistic surveys were processed as described above. However, bottom trawls had not been taken in all of these opportunistic surveys and, therefore, only midwater species were included in this portion of the study.

Table 2. Summary of acoustic/trawl surveys conducted by the GAP project within range (20 nmi) of the Long Island and Marmot Island sites; the three surveys in 2002 that were conducted specifically for comparing Long Island and Marmot Island are in boldface text.

Survey dates	Survey vessel	Midwater trawls	Area (nmi ²) within 20 nmi of	
			Long Island	Marmot Island
6/3 - 13/3 2000	<i>Peggy Jo</i>	2	223.4	187.9
18/5 - 28/5 2000	<i>Peggy Jo</i>	9	605.5	289.1
16/5 - 25/5 2001	<i>Alaska Beauty</i>	6	806.9	403.0
18/7 - 31/7 2001	<i>Alaska Beauty</i>	11	787.2	1,201.4
6/11 - 15/11 2001	<i>Alaska Beauty</i>	7	800.5	336.0
1/4 - 5/4 2002	<i>Laura</i>	6	650.0	249.8
17/5 - 24/5 2002	Laura	6	772.1	1,036.5
19/7 - 29/7 2002	Laura	7	799.8	1,212.0
11/9 - 13/9 2002	<i>Alaskan</i>	4	377.7	110.5
12/11 - 24/11 2002	Laura	9	673.8	1,031.0
5/3 - 9/3 2003	<i>Laura</i>	2	451.2	183.5
1/8 - 17/8 2003	<i>Laura</i>	4	671.0	1,229.7
16/5 - 1/6 2004	<i>Laura</i>	14	671.1	1,235.2
26/7 - 8/8 2004	<i>Laura</i>	8	778.0	1,236.1

Mass Energy Density

Mass energy densities of species groups were determined from fish collected in the trawls during the May, July, and November 2002 surveys. The mass energy density values (kJ g⁻¹ wet weight) were calculated as

$$\text{Energy density (kJ g}^{-1}\text{)} = (\% \text{ protein}/100) \times 20.10 + (\% \text{ lipid}/100) \times 36.43$$

where the energy equivalent values for protein (20.10 kJ g⁻¹) and lipid (36.43 kJ g⁻¹) were taken from Brett (1995). Protein and lipid content were determined by proximate composition analysis of individual species. Fish specimens caught during each survey were frozen at sea and returned to the laboratory for analysis. Protein content was quantified in three replicate aliquots (0.5 to 1.0 g) of homogenized tissues from each fish specimen by combustion at 1100° C in a LecoTM - FP2000 protein analyzer measuring nitrogen concentration. The nitrogen concentration was multiplied by a factor of 6.25 to calculate percent protein (Dowgiallo, 1975). Lipid content was quantified in two replicate aliquots (3 g) of homogenized tissue from each fish specimen. Lipids were extracted in dichloromethane under nitrogen at 70° C in an Accelerated Solvent Extractor (DionexTM) for 12 min, followed by solvent removal under a nitrogen stream on a Turbo Vap LV (ASE Compatible, ZymarkTM). After the proximate composition analysis, percent protein and percent lipid were averaged among replicates per specimen, then averaged among specimens per species group.

Data Analyses

Midwater and bottom densities were expressed per unit area. Count densities (numbers nmi⁻²) of fish and squid were multiplied by mean length distributions from the trawls and converted to biomass densities (kg nmi⁻²) using length-weight power equations ($w = al^b$), which were also calculated from the trawl samples.

Biomass densities per species group were cumulative-summed in rank order (highest to lowest in each survey), and for analysis, those species groups were included that added to the 95th percentile in at least one survey, or to the 99th percentile in all three surveys. Pollock was the only species caught extensively in both midwater and bottom trawls (in > 60% of trawls; no other species was > 10%). For analysis, the pollock midwater/acoustic data were used since these showed higher total biomass and occupied the greater extent of the water column. However, midwater data potentially underestimate pollock densities since adult pollock are known to associate with the sea bottom (Wilson et al., 2003); and for this study, acoustic backscatter was integrated to 0.5 m above bottom.

Steller sea lions consume pollock primarily in the length range of 5 to 60 cm (Winship & Trites, 2003), and juvenile Steller sea lions, in particular, prefer fish < 30 cm (Merrick & Calkins, 1996). Among the species groups in this study, pollock, salmon, arrowtooth flounder, and cod were found to have extensive size ranges (Figure 2). Therefore, in addition to total densities for all sizes, densities of these four species groups were calculated

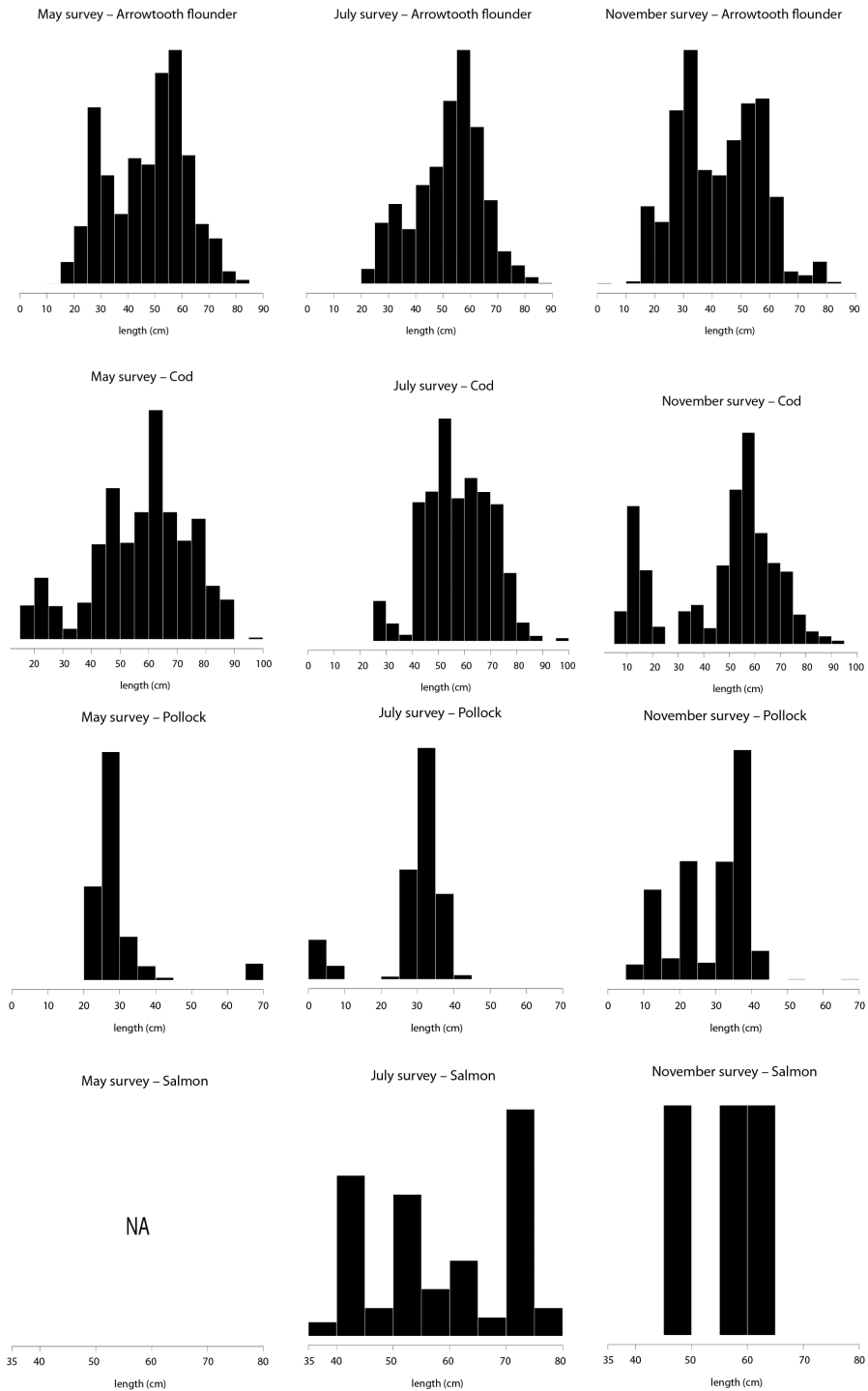


Figure 2. Length mode distributions of arrowtooth flounder, cod, pollock, and salmon; the four prey species groups with extensive size ranges in the May, July, and November 2002 surveys. Length modes were calculated from weighted averages of midwater or bottom trawls. Heights of the bars are arbitrarily standardized.

from length modes restricted to the intervals of 5 to 60 cm and 5 to 30 cm to reflect the putative size preferences.

Species group biomass densities were estimated across the survey area by kriging in 0.1 nmi² area units (Figure 1B). Kriging is a geostatistical interpolation method that uses the spatial autocorrelation among measured points to generate a prediction surface (e.g., Petitgas, 1996). For this study, ordinary co-kriging with a spherical model and anisotropic function was used, calculated in *ArcMAP* software (ESRI Inc., Redlands, CA, USA). Bottom depth was used as the co-kriging co-variate since pollock and capelin were observed during the surveys to occupy areas above distinct bottom depths (generalized additive relationships between bottom depth and pollock or capelin biomass: $p < 0.001$ in each survey), even if the fish did not descend to those depths. *ArcMAP* outputs a point value and SE at every area unit (0.1 nmi²) of the kriged surface.

Estimating uncertainty from multiple sources is recommended for acoustic survey data (Rose et al., 2000). To provide a measure of uncertainty for biomass densities in this study, 1,000 random simulations of each species group's kriged surface were run with the standard error of the area units drawn from the normal distribution. For example, if a given random simulation generated "+0.8," then each area unit of the kriged surface was recalculated as the point value plus 0.8 of its standard error (whereby the standard errors themselves varied considerably as a function of the area units' positions on the kriged surface). Error distributions of species groups' weight estimates were assessed by calculating the standard error of the length-weight equations, then also drawing 1,000 random simulations of the standard errors from the normal distribution. Uncertainty of trawl catch composition (a measure of the stochasticity of what is caught by any given trawl) was approximated by randomly resampling each trawl composition, with replacement, until the same total weight as the original trawl was reached. This could represent substantial variation in trawls where, for example, few large fish had been caught among many small fish. In most resamples, the few large fish were absent, but when they occurred, they made up the major part of the biomass. Each of the 1,000 simulations of the kriged, length-weight, and trawl composition errors was then expressed as the ratio of the simulation to the original empirical value, and the three error sources were multiplied together ($E_{i[\text{krige}]} \times E_{i[\text{length-weight}]} \times E_{i[\text{trawl composition}]}$, $i = 1$ to 1,000) to estimate uncertainty simultaneously from the different terms of the acoustic analysis.

To compare the potential Steller sea lions' prey energy available among surveys, biomass

densities (kg nmi⁻²) per prey species group were multiplied by mass energy density (kJ g⁻¹) of the species group. The resulting areal energy densities (kg nmi⁻² × kJ g⁻¹ × 1,000 = kJ nmi⁻²) could then be summed across species per survey. Differences in areal energy density were examined between the Long Island and Marmot Island sites, and between the zones of 0 to 10 nmi and 10 to 20 nmi within sites (Figure 1B). Statistical significance of differences was evaluated by taking as a threshold the 90th quantile of total areal energy density per survey, then calculating the number of random simulations of areal energy density (out of 1,000) for which (for example) the 0 to 10 nmi zone around Long Island had a higher proportion (to the nearest 0.001) of unit areas above the threshold than the 0 to 10 nmi zone around Marmot Island. This number [LI > MA] was subtracted from the number of simulations for which the 0 to 10 nmi zone around Marmot Island had a higher proportion of unit areas above threshold than the 0 to 10 nmi zone around Long Island [MA > LI]. A resulting score ([LI > MA] - [MA > LI]) of < 100 or > 900 was statistically significant at $\alpha = 0.10$. The choice of the 90th quantile threshold was based on the high areal aggregation of energy densities—a common observation in fish distributions. Gutierrez et al. (2007) used a 90th quantile threshold for indexing the concentration of anchovy and sardine backscatter in the Humboldt Current system. To examine possible effects of different levels of prey size on total energy density, the statistical calculations were made with the inclusion of pollock, salmon, arrowtooth flounder, and cod biomass densities from (1) all length modes, (2) length modes restricted from 5 to 60 cm (*cf.* Winship & Trites, 2003), and (3) length modes restricted from 5 to 30 cm (*cf.* Merrick & Calkins, 1996).

The levels of concentration, or dispersal, of energy around the Long Island and Marmot Island sites were examined by calculating in each survey the minimum proportions of kriged 0.1 nmi² area units (i.e., ranked highest to lowest) that included 50 and 75% of the aggregate areal energy within 20 nmi of either site. The minimum proportions were calculated for all simulations in each survey, and differences between the two sites were analyzed by *t*-test. Since 20 nmi zones around the two sites overlap (Figure 1B), the minimum proportions were also calculated for the combined zone around both sites in each survey to visualize the overall areal energy distribution.

The long-term relationship between Steller sea lion attendance and prey availability was examined by calculating regressions of Steller sea lion counts on midwater prey energy densities from the 14 GAP surveys summarized in Table

2. Most of these 14 surveys (except for the three site comparison surveys in 2002) had not been specifically designed to compare Long Island and Marmot Island, and their area coverage was uneven. Therefore, each survey in a regression was weighted by the area (nmi^2) it covered around either Long Island or Marmot Island. Long Island and Marmot Island, and breeding and nonbreeding season, were regressed separately.

Total Steller sea lion counts were obtained from 55 aerial surveys made between September 1999 and September 2004 (Wynne, 2005b, unpub. data). When aerial survey dates did not overlap with fish survey dates, they were interpolated (the average interpolation offset was 6.25 d).

Results

On average, > 99% of midwater fish distributions occurred shallower than 200 m and > 60% occurred shallower than 100 m at the time of the survey. Estimates of mean biomass density for major fish species groups (i.e., species groups cumulative-summing to the 95th or 99th percentile) showed that four species groups (pollock, arrowtooth flounder, cod, and soles) together comprised between 76 and 92% of total biomass density in all surveys (May, July, and November) and zones (0 to 10 and 10 to 20 nmi around Long Island and Marmot Island) (Figure 3). These four species groups are known to be important in the diet of Steller sea lions in Kodiak and the Gulf of Alaska (Sinclair & Zeppelin, 2002; McKenzie & Wynne, 2008). Preponderance in biomass density shifted from arrowtooth flounder in May to pollock in November (Figure 3).

Average total biomass densities (all major species groups combined) were greater around Long Island than Marmot Island in May (179 ± 287 vs $101 \pm 296 \times 103 \text{ kg nmi}^{-2}$) and November (124 ± 210 vs $88 \pm 217 \times 103 \text{ kg nmi}^{-2}$), but greater around Marmot Island in July (206 ± 533 vs $260 \pm 552 \times 103 \text{ kg nmi}^{-2}$). Interseasonally, average total biomass densities in the entire survey area increased from May to July, then decreased to November (May, July, November: 128 ± 294 , 239 ± 546 , $101 \pm 216 \times 103 \text{ kg nmi}^{-2}$). Regressions for time-of-day bias found no significant relationships ($p > 0.1$) between pollock densities and time difference to sun transit.

Average mass energy densities from proximate composition analysis were lowest in May (compared to July and November) for all species groups except skates and soles (Table 3). Long Island had significantly higher areal energy density (at $p < 0.10$) than Marmot Island in both zones in May and in the 0 to 10 nmi zone in November (Tables 4 to 6). Marmot Island had the highest single

areal energy density (in July, 10 to 20 nmi zone; Table 5), but was not significantly higher than Long Island in any comparison (Tables 4 to 6). Around Long Island, the inshore zone had significantly higher energy density than offshore in November, while around Marmot Island, the offshore zone had significantly higher energy density than inshore in May and November. Biomass densities (kg nmi^{-2} , Figure 3) of the four dominant species groups (pollock, arrowtooth flounder, cod, and soles) varied much more than their energy densities (3.5 to 6.0 kJ g^{-1} ; Table 3), and, therefore, the differences in total areal energy density were primarily due to biomass differences. In effect, all of the interzone or intersite differences found to be statistically significant at $p < 0.10$ (Tables 4 to 6) would have been significant also with calculations including only biomass densities (i.e., with energy densities set to a constant; data not shown).

Plots of 50 and 75% of total areal energy for the three surveys showed that energy shifted offshore, east of Marmot Island, from May to July (primarily driven by arrowtooth flounder and cod), then inshore again toward November (primarily pollock) (Figure 4). In May, 0.16 ± 0.14 proportion of energy in the survey area occurred east of $151^\circ 47.5 \text{ W}$ (the longitude of the Marmot Island rookery), whereas 0.58 ± 0.19 and 0.27 ± 0.13 proportion of energy occurred in this area in July and November, respectively. When calculated separately around Long Island and Marmot Island, energy was more dispersed (higher proportion of area summing to 50% of total areal energy) around Long Island than Marmot Island in May (t -test; $t = 1.654$, $p = 0.098$) and July ($t = 2.534$, $p = 0.011$), and more aggregated in November ($t = 1.908$, $p = 0.057$) (Table 7).

The 5- to 60-cm length mode restriction on arrowtooth flounder, cod, pollock, and salmon lowered areal energy densities to between 0.65 and 0.94 of their total (no length restriction) values. Differences between zones and between sites under this restriction were similar to those of total areal energy densities, but they were significant only in the November survey (compare Table 8 with Tables 3, 4 & 5). The 5- to 30-cm length mode restriction lowered areal energy densities to between 0.15 and 0.59 of their total values. No comparisons between sites or zones were statistically significant under the 5- to 30-cm restriction (Table 8).

Steller sea lion counts from 1999 to 2004 peaked at Marmot Island during or just after breeding seasons, and they peaked at Long Island during nonbreeding seasons (Figure 5A). The linear regression between Steller sea lion counts and midwater prey energy density was marginally significant at Long Island among September to

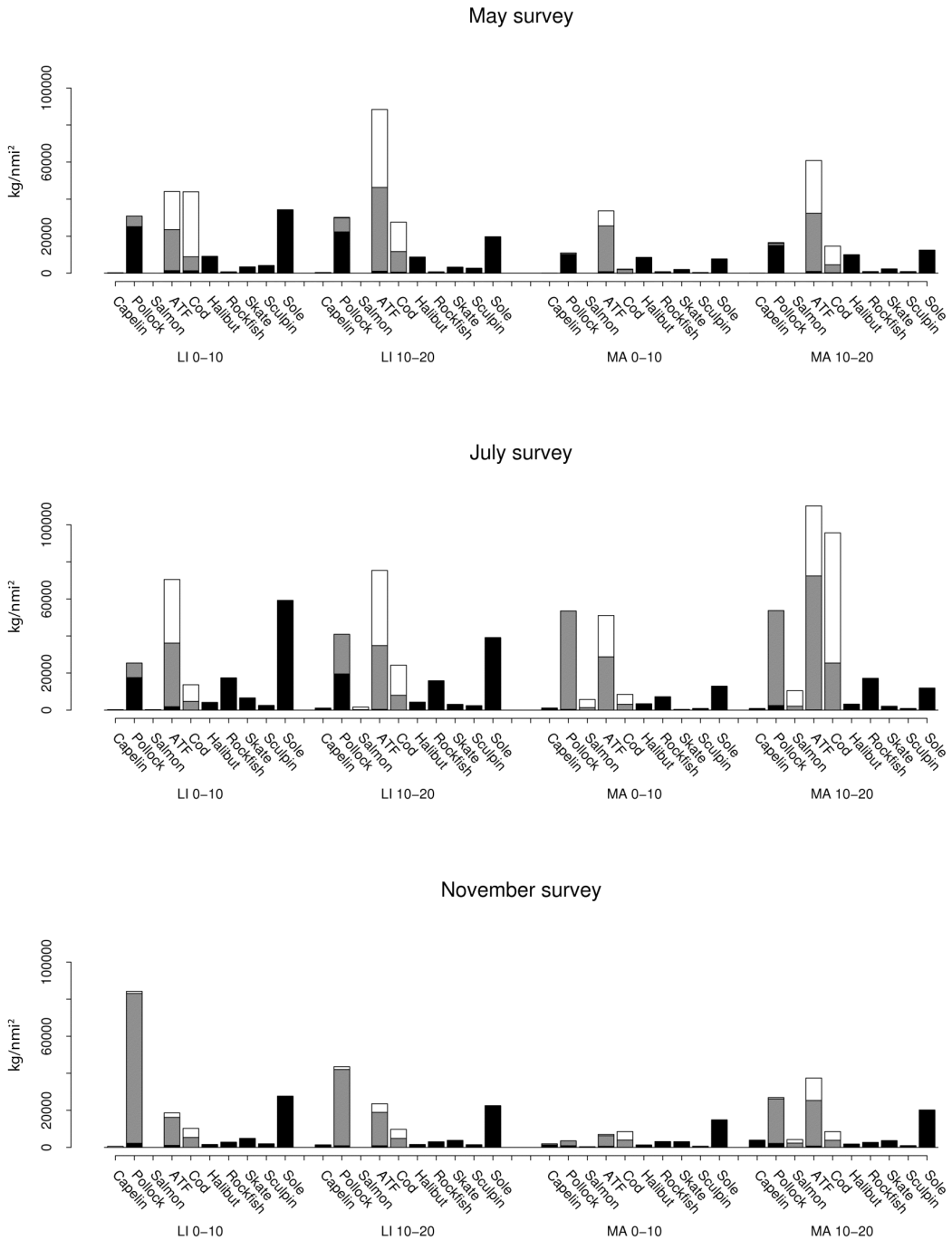


Figure 3. Mean biomass densities (kg nmi⁻²) of major prey species groups in the May, July, and November 2002 surveys, 0 to 10 and 10 to 20 nmi around Long Island (LI) and Marmot Island (MA) in the Gulf of Alaska; for species groups pollock, salmon, arrowtooth flounder (ATF), and cod, gray segments represent densities with the 5- to 60-cm length mode restriction, and black bars represent the 5- to 30-cm length mode restriction.

Table 3. Average mass energy densities ($\text{kJ g}^{-1} \pm 1 \text{ SD}$) used to calculate areal energy densities (kJ nmi^{-2}) of major prey species groups caught in midwater and bottom trawls; for arrowtooth flounder, cod, pollock, and salmon species groups, mass energy densities of the 5- to 60- and 5- to 30-cm length mode restrictions are listed in boldface.

Species group	Mass energy density, $\text{kJ g}^{-1} \pm 1 \text{ SD}$ (no. specimens)					
	May		July		November	
Arrowtooth flounder	4.8 ± 1.3	(55)	5.9 ± 1.5	(45)	5.2 ± 0.8	(64)
5 to 60 cm	4.7 ± 1.2	(41)	6.0 ± 1.5	(29)	5.2 ± 0.8	(58)
5 to 30 cm	3.8 ± 0.8	(20)	4.0 ± 0.5	(8)	4.4 ± 0.5	(35)
Capelin	5.2 ± 0.5	(266)	5.6 ± 0.6	(374)	7.8 ± 0.8	(341)
Cod	3.6 ± 0.2	(59)	4.0 ± 0.5	(40)	4.3 ± 0.8	(126)
5 to 60 cm	3.6 ± 0.3	(41)	4.0 ± 0.5	(21)	4.3 ± 0.9	(99)
5 to 30 cm	3.5 ± 0.2	(12)	3.8 ± 0.3	(10)	3.8 ± 0.2	(57)
Halibut	4.3 ± 0.8	(34)	5.3 ± 1.1	(14)	4.5 ± 1.3	(43)
Walleye pollock	3.8 ± 0.5	(207)	4.8 ± 0.8	(501)	5.4 ± 1.0	(268)
5 to 60 cm	3.8 ± 0.5	(180)	4.8 ± 0.8	(465)	5.3 ± 1.0	(241)
5 to 30 cm	3.8 ± 0.5	(113)	4.3 ± 0.5	(375)	4.8 ± 0.9	(208)
Rockfish	4.9 ± 0.9	(44)	6.7 ± 0.1	(28)	6.0 ± 1.0	(30)
Salmon	--	(0)	6.6 ± 0.7	(525)	8.5 ± 0.2	(7)
5 to 60 cm	--	(0)	6.0 ± 0.4	(514)	8.1 ± 0.4	(6)
Sculpin	3.8 ± 0.6	(34)	4.3 ± 1.0	(29)	3.9 ± 0.6	(53)
Skate	4.8 ± 0.5	(4)	4.2 ± 0.3	(8)	5.0 ± 0.4	(12)
Sole	4.9 ± 1.4	(236)	5.4 ± 1.6	(142)	4.3 ± 0.9	(236)

Table 4. May survey: Mean and 90% CI for total areal energy densities ($\times 10^6 \text{ kJ nmi}^{-2}$) of major prey species groups, by zone (0 to 10 and 10 to 20 nmi) per site (Long Island and Marmot Island); parameters and significance (p) values calculated from randomized simulations of the kriged surfaces.

Zone	Long Island		Marmot Island		p
	Mean	90% CI	Mean	90% CI	
0-10 nmi	755	[0, 2728]	310	[0, 2319]	0.066
10-20 nmi	821	[0, 2793]	543	[0, 2607]	0.027
p	0.872		0.046		

April nonbreeding seasons ($n = 6$, $p = 0.052$, $R^2 = 0.65$; Figure 5B). Data included in that regression were from March 2000; November 2001; April, September, and November 2002; and March 2003 surveys. Linear regressions between Steller sea lion counts and mid-water prey energy density were not significant at Long Island among breeding seasons, or at Marmot Island for either breeding or nonbreeding seasons (Figure 5B).

Discussion

The attraction of Steller sea lions to high prey densities has been observed in other areas of their range (Sigler et al., 2004; Gende & Sigler, 2006; Hoshino et al., 2006; Maniscalco et al., 2006; Womble et al., 2009), but this study presents a first

Table 5. July survey: Mean and 90% CI for total areal energy densities ($\times 10^6 \text{ kJ nmi}^{-2}$) of major prey species groups, by zone (0 to 10 and 10 to 20 nmi) per site (Long Island and Marmot Island); parameters and significance (p) values calculated from randomized simulations of the kriged surfaces.

Zone	Long Island		Marmot Island		p
	Mean	90% CI	Mean	90% CI	
0-10 nmi	1,132	[0, 5782]	794	[0, 5488]	0.821
10-20 nmi	1,148	[0, 5795]	1,598	[0, 6473]	0.149
p	0.778		0.128		

Table 6. November survey: Mean and 90% CI for total areal energy densities ($\times 10^6 \text{ kJ nmi}^{-2}$) of major prey species groups, by zone (0 to 10 and 10 to 20 nmi) per site (Long Island and Marmot Island); parameters and significance (p) values calculated from randomized simulations of the kriged surfaces.

Zone	Long Island		Marmot Island		p
	Mean	90% CI	Mean	90% CI	
0-10 nmi	745	[0, 2661]	230	[0, 2187]	0.029
10-20 nmi	555	[0, 2454]	584	[0, 2557]	0.855
p	0.034		0.065		

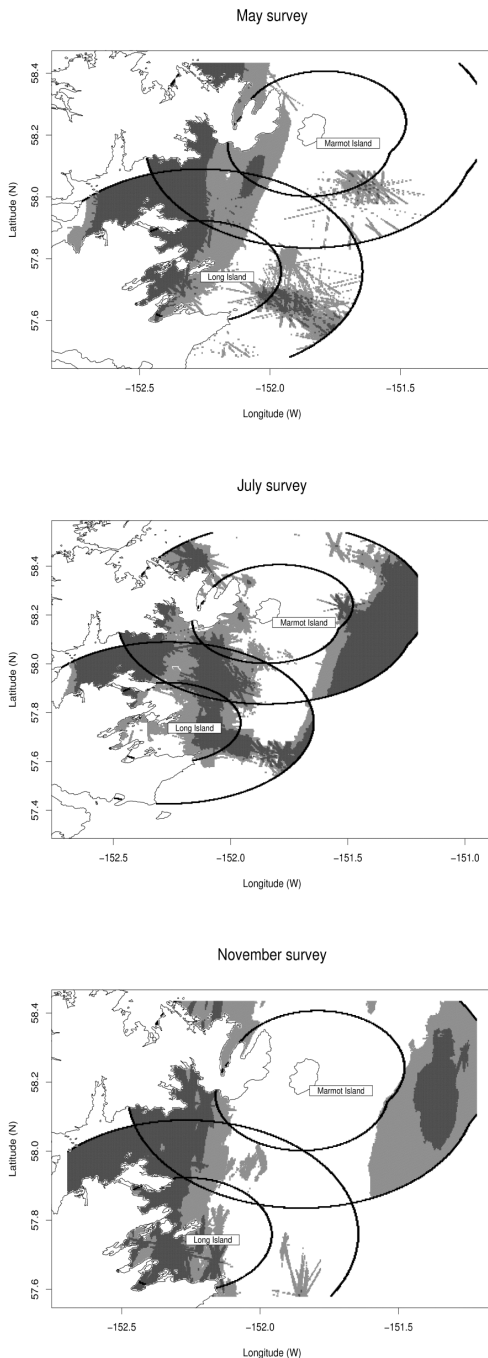


Figure 4. Distributions of kriged area units that sum to 50% (dark gray) and 75% (light gray) of the aggregate areal energy of fish in the survey area; black lines show 10 and 20 nmi perimeters around the Long Island and Marmot Island sites in the Gulf of Alaska.

Table 7. Minimum proportions of the number of 0.1 nmi² area units that sum to 50 and 75% of the total areal energy of major prey species groups, within 20 nmi of Long Island (LI) or Marmot Island (MA), ± 1 SD.

Survey	Long Island		Marmot Island	
	50%	75%	50%	75%
May	0.19 ± 0.13	0.36 ± 0.24	0.18 ± 0.15	0.34 ± 0.27
July	0.23 ± 0.17	0.40 ± 0.28	0.21 ± 0.15	0.38 ± 0.26
Nov.	0.18 ± 0.13	0.35 ± 0.24	0.20 ± 0.15	0.36 ± 0.27

direct comparison of seasonal changes between a haulout and a rookery. Wynne (2005b) reported that Marmot Island functions as a rookery from June to September, and as a haulout from October to May, while relatively few sea lions actually use the site between January and May. That pattern of seasonal migration is consistent with the areal energy density comparisons of this study, which suggest that Steller sea lions gain an advantage of food abundance and proximity by residing at Long Island rather than Marmot Island from November to May. The few (primarily subadult) animals that do use the Long Island haulout site during the breeding season could benefit from the relatively high prey energy density present near Long Island in summer.

Results of these energy density comparisons suggest that factors other than prey energy density result in the redistribution of Steller sea lions to the Marmot Island rookery during summer. Areal energy density was highest overall around Marmot Island in the July survey (10 to 20 nmi zone), but the difference between Marmot Island and Long Island was not statistically significant. Factors such as traditional use, substrate, and topography of the shoreline are likely more important in the choice of the Marmot Island site for summertime breeding and pupping (Call & Loughlin, 2005; Ban & Trites, 2007).

However, the distribution of prey energy density around a rookery may be important in allowing sea lions to make efficient foraging trips. The high energy densities in July were most concentrated in one area within 20 nmi of Marmot Island but were more fragmented within 20 nmi of Long Island. Sinclair & Zeppelin (2002) suggested that Steller sea lions depend on targeting large, dense prey aggregations. Access to such prey aggregations may be particularly important for lactating females, whose foraging trip durations are limited by the need to attend to pups on shore (Trites & Porter, 2002; Davis et al., 2006). Merrick & Loughlin (1997) recorded a maximum trip length of 49 km (26.5 nmi) for tagged adult females in summer, so the large prey field east of

Table 8. Summary of areal energy densities ($\times 10^6$ kJ nmi⁻²) of major prey species groups and [90% CI] with arrowtooth flounder, cod, walleye pollock, and salmon prey species groups restricted to 5- to 60- and 5- to 30-cm length modes.

Survey	Length restriction	Long Island				Marmot Island			
		0-10 nmi		10-20 nmi		0-10 nmi		10-20 nmi	
May	5-60 cm	527	[0, 2203]	557	[0, 2234]	269	[0, 1963]	367	[0, 2096]
	5-30 cm	370	[0, 1481]	269	[0, 1380]	139	[0, 1260]	195	[0, 1324]
July	5-60 cm	890	[0, 4660]	832	[0, 4605]	608	[0, 4411]	1032	[0, 4922]
	5-30 cm	614	[0, 2904]	478	[0, 2779]	158	[0, 2467]	234	[0, 2567]
Nov.	5-60 cm	703 ^{1,2}	[0, 2393]	502 ²	[0, 2181]	200 ^{1,3}	[0, 1932]	477 ³	[0, 2220]
	5-30 cm	210	[0, 809]	178	[0, 778]	135	[0, 737]	189	[0, 793]

¹Significantly different at $p = 0.018$

²Significantly different at $p = 0.019$

³Significantly different at $p = 0.051$

Marmot Island would be well within the foraging range of females on that rookery.

High prey energy density concentrations by Marmot Island were primarily offshore, and only one interzone comparison (Long Island in November) revealed higher areal energy densities within 0 to 10 nmi than 10 to 20 nmi. Data from this study therefore did not suggest that 0- to 10-nmi inshore zones have higher forage potential than 10- to 20-nmi offshore zones. The predominance of foraging observed nearshore, especially for juvenile sea lions (NMFS, 2001; Raum-Suryan et al., 2004), is more likely due to their inexperience at diving or to a lack of necessity for traveling further. Interzone comparisons of forage potential are somewhat limited by how close trawl vessels can approach to shore (> 1 nmi), and, thus, trawls potentially miss shallow water fish assemblages. Hegwer (2004) found that rockfish and greenlings were the most abundant species groups sighted by dive surveys within 100 m of shore (and 33 m depth) at four sites east of Kodiak, including Long Island. In this study, rockfish were of minor importance, and greenlings were negligible in the trawl catches. Dive and trawl surveys are likely to have different sampling biases. Nevertheless, the count densities reported by Hegwer (2004) suggest that total biomass densities were not significantly higher in the nearshore than those extrapolated from the acoustic/trawl surveys in this study, aside from differences in species composition.

The species group length restrictions based on prey size preferences described by Winship & Trites (2003) and Merrick & Calkins (1996) showed few significant differences in prey areal energy densities, and only where the differences were significant without length restriction anyway. This may be due to the fact that most fish of the dominant species were between 30 and 60 cm in length so that the 5- to 60-cm restriction changed too little, and the 5- to 30-cm restriction

left too little biomass to represent the structure of the species distributions. Recent studies found evidence of size-selectivity for juvenile pollock in Steller sea lion scats from the western stock (Zeppelin et al., 2004) but not in scats from the eastern stock (Tollit et al., 2004). Scat analyses from samples near Kodiak showed highest occurrences of pollock in the size range 21 to 34 cm but highest occurrences of arrowtooth flounder, cod, and salmon above 30 cm (McKenzie & Wynne, 2008). The results suggest that sea lions (especially juveniles; Merrick & Calkins, 1996) exhibit size preferences when a range of sizes is available to choose from but that prey size is not otherwise a constraint on foraging ability.

Most prey species groups showed lower energy content in May (generally the post-spawning period) than in July and November (resting and developing periods) consistent with other studies on fish energy content in Alaskan waters (Montevecchi & Piatt, 1984; Smith et al., 1990; Payne et al., 1999; Anthony et al., 2000; Logerwell & Schaufler, 2005). The four predominant species groups observed in this study—pollock, arrowtooth flounder, cod, and soles—have relatively low mass energy densities (compared to capelin and salmon), and correspond to what is termed junk food in the diet of Steller sea lions (Rosen & Trites, 2000). Biomasses of these low energy density groundfish are reported to have increased in the Gulf of Alaska since the 1980s (Anderson & Piatt, 1999), and their increased consumption as “junk” food is hypothesized to have resulted in chronic nutritional stress, contributing to the decline of the Steller sea lion population (Trites & Donnelly, 2003). Over the same time period, biomasses of nutritionally valuable, high energy density forage³ species reportedly decreased in the

³Schooling fishes that correspond to the description of Springer & Speckman (1997).

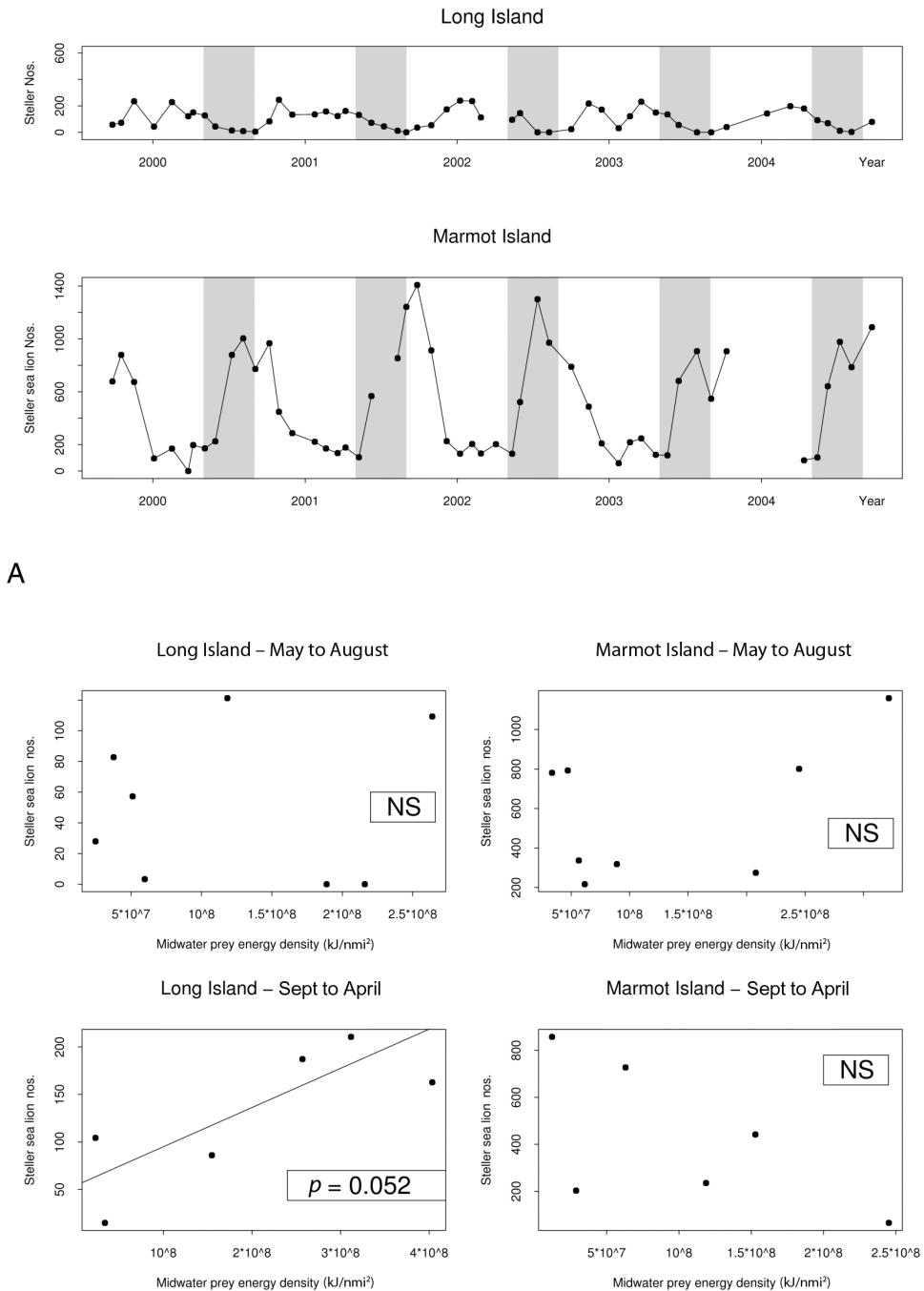


Figure 5. (A) Number of Steller sea lions from aerial surveys at Long Island and Marmot Island between 1999 and 2004; gray undershading represents the May to August breeding season. (B) Significance of linear regression of Steller sea lion numbers vs midwater prey energy density from 14 acoustic/trawl surveys between 1999 and 2004; regressions were separated by Long Island and Marmot Island (midwater prey energy density within 20 nmi of either site) and by breeding (May to August) and nonbreeding (September to April) seasons.

Gulf of Alaska (Anderson et al., 1997; Anderson & Piatt, 1999). Trites et al. (2007b) proposed that ocean climate changes in the North Pacific may be the ultimate cause of species shifts and reduced foraging value for Steller sea lions. However, the actual importance of biomass shifts from high to low energy species, as well as their impact on Steller sea lion diets, have been questioned (Fritz & Hinckley, 2005).

Analyses of scat samples collected around Kodiak from 1999 to 2005 revealed that the high energy forage species capelin, herring, and sand lance had high indices of importance (occurrence + abundance) in Steller sea lion scats, similar to those of several groundfish species (McKenzie & Wynne, 2008). These indices of importance suggest that Steller sea lions positively selected high energy forage species. Alternatively, the (smaller) forage fish may have been underrepresented in the trawl catches used in this study. Midwater trawls did capture low numbers of capelin, and lower numbers of herring and sand lance (not shown), but were not deployed in a manner that would have sampled these species efficiently. Sand lance, for example, either burrow in bottom sand or swim in large schools near the surface (Eschmeyer et al., 1983; Robards et al., 1999). Around Kodiak, sand lance occur primarily inshore (Dick & Warner, 1982) and migrate seasonally (Blackburn & Anderson, 1997). Capelin likewise migrate seasonally (Eschmeyer et al., 1983) and had an 8% frequency of occurrence in stomachs of large arrowtooth flounder east of Kodiak in August 2002 (Knoth, 2006). Since arrowtooth flounders are opportunistic predators (Yang & Livingston, 1986), this 8% frequency of occurrence suggests that capelin abundance was higher than represented by the trawl catches. The overall quantification of prey energy value may additionally be complicated by differences in the foraging costs of pursuing and capturing different species (Winship & Trites, 2003), and by potential dietary differences between males and females (Trites & Calkins, 2008). As noted by Winship & Trites (2003), data on foraging costs to Steller sea lions of different prey species are currently limited but should be incorporated into bioenergetic models as they become available.

Despite these limitations, this study showed a positive relationship between site usage by Steller sea lions of a haulout (Long Island) and a nearby rookery (Marmot Island), and the seasonal density of prey around either site. This suggests that Steller sea lions may respond to differences in prey availability on a spatial scale as small as 30 nmi. In particular, results of the study suggest that greater energy density of prey close to Long Island, compared to Marmot Island, may influence the

movement of animals to Long Island following the breeding season when social behavior restraints (i.e., the need to breed and give birth) no longer restrict animals to remain on Marmot Island. Conversely, the proximity to Marmot Island of densely aggregated prey fields during breeding season may provide an energetic advantage to animals occupying the rookery, but the importance of such prey aggregation patterns in the choice of Marmot Island as a rookery is not clear.

Differences in areal prey energy density (kJ nmi^{-2}) between Long Island and Marmot Island in 2002 were significant despite high estimated variability around both sites (e.g., the 90% CI for energy density simulations included zero in every case) and despite relatively modest seasonal differences in mean energy density. Mean energy densities differed seasonally between surveys by a maximum factor of 3.45 (obtained in the Marmot Island 0 to 10 nmi zone: $794 \times 10^6 \text{ kJ nmi}^{-2}$ in July vs $230 \times 10^6 \text{ kJ nmi}^{-2}$ in November). By contrast, Womble & Sigler (2006) reported > 15x changes in energy density within a single year at Benjamin Island haulout in southeast Alaska, where counts of Steller sea lions were also correlated with prey biomass. At Benjamin Island, prey biomass was dominated by one fish species: herring (Womble & Sigler, 2006). The coastal waters near Kodiak have four dominant species groups, and five species of secondary importance. The comparison between Long Island and Marmot Island, therefore, gives evidence that site selection by Steller sea lions in relation to prey availability can occur in areas of high fish diversity.

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Literature Cited

- Anderson, P. J., & Piatt, J. F. (1999). Community reorganization in the Gulf of Alaska following ocean climate regime shift. *Marine Ecology Progress Series*, 189, 117-123.

- Anderson, P. J., Blackburn, J. E., & Johnson, B. A. (1997). Declines of forage species in the Gulf of Alaska, 1972-1995, as an indicator of regime shift. In *Forage fishes in marine ecosystems. Proceedings of the International Symposium on the Role of Forage Fishes in Marine Ecosystems* (Report No. 97-01) (pp. 531-543). Fairbanks: University of Alaska Sea Grant College Program. 816 pp.
- Anthony, J. A., Roby, D. D., & Turco, K. R. (2000). Lipid content and energy density of forage fishes from the northern Gulf of Alaska. *Journal of Experimental Marine Biology and Ecology*, 248, 53-78.
- Arkhipkin, A. I., Bizikov, V. A., Krylov, V. V., & Nesis, K. N. (1996). Distribution, stock structure, and growth of the squid *Berryteuthis magister* (Berry, 1913) (Cephalopoda, Gonatidae) during summer and fall in the western Bering Sea. *Fishery Bulletin, U.S.*, 94, 1-30.
- Ban, S., & Trites, A. W. (2007). Quantification of terrestrial haul-out and rookery characteristics of Steller sea lions. *Marine Mammal Science*, 23, 496-507.
- Blackburn, J. E., & Anderson, P. J. (1997). Pacific sand lance growth, seasonal availability, movements, catch variability, and food in the Kodiak-Cook Inlet area of Alaska. In *Forage fishes in marine ecosystems. Proceedings of the International Symposium on the Role of Forage Fishes in Marine Ecosystems* (Report No. 97-01) (pp. 409-426). Fairbanks: University of Alaska Sea Grant College Program. 816 pp.
- Brett, J. R. (1995). Energetics. In C. Groot, L. Margolis, & W. C. Clarke (Eds.), *Physiological ecology of Pacific salmon* (pp. 3-68). Vancouver: UBC Press. 384 pp.
- Briggs, H. B. (2005). *Characterizing the winter movements and diving behavior of subadult Steller sea lions (Eumetopias jubatus) in the northcentral Gulf of Alaska*. Master of Science thesis, Texas A&M University, Galveston. 58 pp.
- Call, K. A., & Loughlin, T. R. (2005). An ecological classification of Alaskan Steller sea lion (*Eumetopias jubatus*) rookeries: A tool for conservation/management. *Fisheries Oceanography*, 14, 212-222.
- Chumbley, K., Sease, J. L., Strick, M., & Towell, R. (1997). *Field studies of Steller sea lions (Eumetopias jubatus) at Marmot Island, Alaska, 1979 through 1994* (NOAA Technical Memorandum NMFS-AFSC-77). Washington, DC: U.S. Department of Commerce. 99 pp.
- Cornick, L. A., Neill, W., & Grant, W. E. (2006). Assessing competition between Steller sea lions and the commercial groundfishery in Alaska: A bioenergetics modelling approach. *Ecological Modelling*, 199, 107-114.
- Davis, R. W., Brandon, E. A. A., Calkins, D. G., & Loughlin, T. R. (2006). Female attendance and neonatal pup growth in Steller sea lions (*Eumetopias jubatus*). In A. W. Trites, S. K. Atkinson, D. P. DeMaster, L. W. Fritz, T. S. Gelatt, L. D. Rea et al. (Eds.), *Sea lions of the world* (AK-SG-06-01) (pp. 13-29). Fairbanks: Alaska Sea Grant Publications. 653 pp.
- Dick, M. H., & Warner, I. M. (1982). Pacific sand lance, *Ammodytes hexapterus* Pallas, in the Kodiak Island group, Alaska. *Syesis*, 15, 43-50.
- Dowgiallo, A. (1975). Chemical composition of an animal's body and of its food. In W. Grodzinski, R. Z. Klekowski, & A. Duncan (Eds.), *Methods for ecological bioenergetics* (IBP Handbook No. 24) (pp. 169-199). Oxford, UK: Blackwell Scientific. 367 pp.
- Eschmeyer, W. N., Herald, E. S., & Hammann, H. (1983). *A field guide to Pacific coast fishes. The Peterson field guide series*. Boston: Houghton Mifflin Company. 336 pp.
- Fiscus, C. H., & Baines, G. A. (1966). Food and feeding behavior of Steller and California sea lions. *Journal of Mammalogy*, 47, 195-200.
- Foote, K. G. (1987). Fish target strengths for use in echo integrator surveys. *Journal of the Acoustical Society of America*, 82, 981-987.
- Foote, K. G., & Traynor, J. J. (1988). Comparison of wall-eye pollock target strength estimates determined from in situ measurements and calculations based on swim-bladder form. *Journal of the Acoustical Society of America*, 83, 9-15.
- Foy, R. J. (2005). Steller sea lion prey availability in the Long Island critical habitat (2000-2003). In *Gulf Apex predator-prey study final report FY2001-2003* (NOAA Grant NA16FX1270) (pp. 6-14). Washington, DC: U.S. Department of Commerce. 241 pp.
- Fritz, L. W., & Ferrero, R. C. (1998). Options in Steller sea lion recovery and groundfish fishery management. *Biosphere Conservation*, 1, 7-19.
- Fritz, L. W., & Hinckley, S. (2005). A critical review of the regime shift—"junk food"—nutritional stress hypothesis for the decline of the western stock of Steller sea lion. *Marine Mammal Science*, 21, 476-518.
- Fritz, L. W., & Stinchcomb, C. (2005). *Aerial, ship, and land-based surveys of Steller sea lions (Eumetopias jubatus) in the western stock in Alaska, June and July 2003 and 2004* (NOAA Technical Memorandum NMFS-AFSC-153). Washington, DC: U.S. Department of Commerce. 56 pp.
- Fritz, L. W., Ferrero, R. C., & Berg, R. J. (1995). The threatened status of Steller sea lions, *Eumetopias jubatus*, under the Endangered Species Act: Effects on Alaska groundfish fisheries management. *Marine Fisheries Review*, 57, 14-27.
- Gauthier, S., & Horne, J. K. (2004). Acoustic characteristics of forage fish species in the Gulf of Alaska and Bering Sea based on Kirchhoff-approximation models. *Canadian Journal of Fisheries and Aquatic Sciences*, 61, 1839-1850.
- Gende, S. M., & Sigler, M. F. (2006). Persistence of forage fish "hot spots" and its association with foraging Steller sea lions (*Eumetopias jubatus*) in southeast Alaska. *Deep-Sea Research II*, 53, 432-441.
- Grubbs, F. E. (1969). Procedures for detecting outlying observations in samples. *Technometrics*, 11, 1-21.
- Gutierrez, M., Swartzman, G., Bertrand, A., & Bertrand, S. (2007). Anchovy (*Engraulis ringens*) and sardine (*Sardinops sagax*) spatial dynamics and aggregation patterns in the Humboldt Current ecosystem, Peru, from 1983-2003. *Fisheries Oceanography*, 16, 155-168.

- Hegwer, C. L. (2004). *The seasonal abundance and diversity of nearshore fishes around Steller sea lion haulouts of Kodiak Island*. Master of Science thesis, University of Alaska, Fairbanks.
- Hoshino, H., Isono, T., Takayama, T., Ishinazaka, T., Wada, A., & Sakurai, Y. (2006). Distribution of the Steller sea lion *Eumetopias jubatus* during winter in the northern Sea of Japan, along the west coast of Hokkaido, based on aerial and land sighting surveys. *Fisheries Science*, 72, 922-931.
- Hjellvik, V., Godø, O. R., & Tjøstheim, D. (2004). Diurnal variation in acoustic densities: Why do we see less in the dark? *Canadian Journal of Fisheries and Aquatic Sciences*, 61, 2237-2254.
- Kawabata, A. (2005). Target strength measurements of suspended live ommastrephid squid, *Todarodes pacificus*, and its application in density estimations. *Fisheries Science*, 71, 63-72.
- Knoth, B. A. (2006). *Arrowtooth flounder *Atheresthes stomias* diet and prey consumption near Kodiak Island, Alaska*. Master of Science thesis, University of Alaska, Fairbanks.
- Lawson, G. L., & Rose, G. A. (1999). The importance of detectability to acoustic surveys of semi-demersal fish. *ICES Journal of Marine Science*, 56, 370-380.
- Logerwell, E. A., & Schaufler, L. E. (2005). New data on proximate composition and energy density of Steller sea lion (*Eumetopias jubatus*) prey fills seasonal and geographic gaps in existing information. *Aquatic Mammals*, 31(1), 62-82.
- Loughlin, T. R. (1998). The Steller sea lion: A declining species. *Biosphere Conservation*, 1, 91-98.
- Loughlin, T. R., Perlov, A. S., Baker, J. D., Blokhin, S. A., & Makhnyr, A. G. (1998). Diving behavior of adult female Steller sea lions in the Kuril Islands, Russia. *Biosphere Conservation*, 1, 21-31.
- Loughlin, T. R., Sterling, J. T., Merrick, R. L., Sease, J. L., & York, A. E. (2003). Diving behavior of immature Steller sea lions (*Eumetopias jubatus*). *Fishery Bulletin*, U.S., 101, 566-582.
- Love, R. H. (1977). Target strength of an individual fish at any aspect. *Journal of the Acoustical Society of America*, 62, 1397-1402.
- MacLennan, D. N., & Simmonds, E. J. (1992). *Fisheries acoustics*. New York: Chapman and Hall. 325 pp.
- Maniscalco, J. M., Parker, P., & Atkinson, S. (2006). Interseasonal and interannual measures of maternal care among individual Steller sea lions (*Eumetopias jubatus*). *Journal of Mammalogy*, 87, 304-311.
- Mathison, O. A., Baade, R. T., & Lopp, R. J. (1962). Breeding habits, growth and stomach contents of the Steller sea lion in Alaska. *Journal of Mammalogy*, 43, 469-477.
- McKenzie, J., & Wynne, K. M. (2008). Spatial and temporal variation in the diet of Steller sea lions in the Kodiak Archipelago, 1999 to 2005. *Marine Ecology Progress Series*, 360, 265-283.
- Merrick, R. L., & Calkins, D. G. (1996). Importance of juvenile walleye pollock, *Theragra chalcogramma*, in the diet of Gulf of Alaska Steller sea lions, *Eumetopias jubatus*. In R. D. Brodeur, P. A. Livingston, T. R. Loughlin, & A. B. Hollowed (Eds.), *Ecology of juvenile walleye pollock (Theragra chalcogramma)* (NOAA Technical Report 126) (pp. 153-166). Washington, DC: U.S. Department of Commerce. 200 pp.
- Merrick, R. L., & Loughlin, T. R. (1997). Foraging behavior of adult female and young-of-the-year Steller sea lions in Alaskan waters. *Canadian Journal of Zoology*, 75, 776-786.
- Merrick, R. L., Chumbley, M. K., & Byrd, G. V. (1997). Diet diversity of Steller sea lions (*Eumetopias jubatus*) and their population decline in Alaska: A potential relationship. *Canadian Journal of Fisheries and Aquatic Sciences*, 54, 1342-1348.
- Merrick, R. L., Loughlin, T. R., & Calkins, D. G. (1987). Decline in abundance of the northern sea lion, *Eumetopias jubatus*, in Alaska, 1956-86. *Fishery Bulletin*, U.S., 85, 351-365.
- Millette, L. L., & Trites, A. W. (2003). Maternal attendance patterns of Steller sea lions (*Eumetopias jubatus*) from stable and declining populations in Alaska. *Canadian Journal of Zoology*, 81, 340-348.
- Montevocchi, W. A., & Piatt, J. (1984). Composition and energy contents of mature inshore spawning capelin (*Mallotus villosus*): Implications for seabird predators. *Comparative Biochemistry and Physiology*, 78A, 15-20.
- Mulligan, T. J., & Kieser, R. (1986). Comparison of acoustic population estimates of salmon in a lake with a weir count. *Canadian Journal of Fisheries and Aquatic Sciences*, 43, 1373-1385.
- National Marine Fisheries Service (NMFS). (2001). *Section 7 consultation—Biological opinion and incidental take statement on the authorization of Bering Sea /Aleutian Islands groundfish fisheries based on the Fishery Management Plan for the Bering Sea /Aleutian Islands Groundfish as modified by amendments 61 and 70; and authorization of Gulf of Alaska groundfish fisheries based on the Fishery Management Plan for Groundfish of the Gulf of Alaska as modified by amendments 61 and 70. Parallel fisheries for pollock, Pacific cod, and Atka mackerel, as authorized by the State of Alaska within 3 nm of shore*. Silver Spring, MD: Office of Protected Resources, NMFS.
- NMFS. (2003). *Supplement to the Section 7 consultation—Biological opinion and incidental take statement on the authorization of Bering Sea /Aleutian Islands groundfish fisheries based on the Fishery Management Plan for the Bering Sea/Aleutian Islands Groundfish as modified by amendments 61 and 70; and authorization of Gulf of Alaska groundfish fisheries based on the Fishery Management Plan for Groundfish of the Gulf of Alaska as modified by amendments 61 and 70. Parallel fisheries for pollock, Pacific cod, and Atka mackerel, as authorized by the State of Alaska within 3 nm of shore*. Silver Spring, MD: Office of Protected Resources, NMFS.

- Okutani, T. (1983). *Todarodes pacificus*. In P. R. Boyle (Ed.), *Cephalopod life cycles*. Vol. I: Species accounts (pp. 201-214). London: Academic Press. 475 pp.
- Ona, E. (2003). An expanded target-strength relationship for herring. *ICES Journal of Marine Science*, 60, 493-499.
- Orians, G. J., & Pearson, N. E. (1979). On the theory of central place foraging. In D. J. Horn & R. D. Mitchell (Eds.), *Analysis of ecological systems* (pp. 155-177). Columbus: Ohio State University Press. 312 pp.
- Payne, S. A., Johnson, B. A., & Otto, R. S. (1999). Proximate composition of some north-eastern Pacific forage fish species. *Fisheries Oceanography*, 8, 159-177.
- Petitgas, P. (1996). Geostatistics and their applications to fisheries survey data. In B. A. Megrey & E. Moksness (Eds.), *Computers in fisheries research* (pp. 113-142). London: Chapman and Hall. 224 pp.
- Pitcher, K. W., Rehberg, M. J., Pendleton, G. W., Raum-Suryan, K. L., Gelatt, T. S., Swain, U. G., et al. (2005). Ontogeny of dive performance in pup and juvenile Steller sea lions in Alaska. *Canadian Journal of Zoology*, 83, 1214-1231.
- Raum-Suryan, K. L., Rehberg, M. J., Pendleton, G. W., Pitcher, K. W., & Gelatt, T. S. (2004). Development of dispersal, movement patterns, and haul-out use by pup and juvenile Steller sea lions (*Eumetopias jubatus*) in Alaska. *Marine Mammal Science*, 20, 823-850.
- Robards, M. D., Piatt, J. F., & Rose, G. A. (1999). Maturation, fecundity, and intertidal spawning of Pacific sand lance in the northern Gulf of Alaska. *Journal of Fish Biology*, 54, 1050-1068.
- Rose, G. A., Gauthier, S., & Lawson, G. (2000). Acoustic surveys in the full monte: Simulating uncertainty. *Aquatic Living Resources*, 13, 367-372.
- Rosen, D. A. S., & Trites, A. W. (2000). Pollock and the decline of Steller sea lions: Testing the junk-food hypothesis. *Canadian Journal of Zoology*, 78, 1243-1250.
- Sease, J. L., & Gudmundson, C. J. (2002). *Aerial and land-based surveys of Steller sea lions (Eumetopias jubatus) from the western stock in Alaska, June and July 2001 and 2002* (NOAA Technical Memorandum NMFS-AFSC-131). Washington, DC: U.S. Department of Commerce. 45 pp.
- Sease, J. L., & York, A. E. (2003). Seasonal distribution of Steller's sea lions at rookeries and haul-out sites in Alaska. *Marine Mammal Science*, 19, 745-763.
- Shackell, N. L., Carscadden, J. E., & Miller, D. S. (1994). *Diel vertical migration of capelin (Mallotus villosus) and its effect on acoustic estimates of density* (ICES-CM-1994/Mini: 5).
- Sigler, M. F., Womble, J. N., & Vollenweider, J. J. (2004). Availability to Steller sea lions (*Eumetopias jubatus*) of a seasonal prey resource: A prespawning aggregation of eulachon (*Thaleichthys pacificus*). *Canadian Journal of Fisheries and Aquatic Sciences*, 61, 1475-1484.
- Sinclair, E. H., & Zeppelin, T. K. (2002). Seasonal and spatial differences in diet in the western stock of Steller sea lions (*Eumetopias jubatus*). *Journal of Mammalogy*, 83, 973-990.
- Smith, R., Paul, A., & Paul, J. (1990). Seasonal changes in energy and the energy cost of spawning of Gulf of Alaska Pacific cod. *Journal of Fish Biology*, 36, 307-316.
- Springer, A. M. (1992). A review: Walleye pollock in the North Pacific—How much difference do they really make? *Fisheries Oceanography*, 1, 80-96.
- Springer, A. M., & Speckman, S. G. (1997). A forage fish is what? Summary of the symposium. In *Forage fishes in marine ecosystems. Proceedings of the International Symposium on the Role of Forage Fishes in Marine Ecosystems* (Report No. 97-01) (pp. 773-805). Fairbanks: University of Alaska Sea Grant College Program. 816 pp.
- Thomas, G. L., Kirsch, J., & Thorne, R. E. (2002). Ex situ target strength measurements of Pacific herring and Pacific sand lance. *North American Journal of Fisheries Management*, 22, 1136-1145.
- Tollit, D. J., Heaslip, S. G., & Trites, A. W. (2004). Sizes of walleye pollock (*Theragra chalcogramma*) consumed by the eastern stock of Steller sea lions (*Eumetopias jubatus*) in southeast Alaska from 1994 to 1999. *Fishery Bulletin, U.S.*, 102, 522-532.
- Trites, A. W., & Calkins, D. G. (2008). Diets of mature male and female Steller sea lions (*Eumetopias jubatus*) differ and cannot be used as proxies for each other. *Aquatic Mammals*, 34(1), 25-34.
- Trites, A. W., & Donnelly, C. P. (2003). The decline of Steller sea lions in Alaska: A review of the nutritional stress hypothesis. *Mammal Review*, 33, 3-28.
- Trites, A. W., & Larkin, P. A. (1996). Changes in the abundance of Steller sea lions (*Eumetopias jubatus*) in Alaska from 1956 to 1992: How many were there? *Aquatic Mammals*, 22(3), 153-166.
- Trites, A. W., & Porter, B. T. (2002). Attendance patterns of Steller sea lions (*Eumetopias jubatus*) and their young during winter. *Journal of Zoology*, 256, 546-556.
- Trites, A. W., Calkins, D. G., & Winship, A. J. (2007a). Diets of Steller sea lions (*Eumetopias jubatus*) in southeast Alaska, 1993-1999. *Fishery Bulletin, U.S.*, 105, 234-248.
- Trites, A. W., Miller, A. J., Maschner, H. D. G., Alexander, M. A., Bograd, S. J., Calder, J. A., et al. (2007b). Bottom-up forcing and the decline of Steller sea lions (*Eumetopias jubatus*) in Alaska: Assessing the ocean climate hypothesis. *Fisheries Oceanography*, 16, 46-67.
- Wilson, C. D., Hollowed, A. B., Shima, M., Walline, P., & Stienessen, S. (2003). Interactions between commercial fishing and walleye pollock. *Alaska Fishery Research Bulletin*, 10, 61-77.
- Winship, A. J., & Trites, A. W. (2003). Prey consumption of Steller sea lions (*Eumetopias jubatus*) off Alaska: How much prey do they require? *Fishery Bulletin, U.S.*, 101, 147-167.
- Womble, J. N., & Sigler, M. F. (2006). Seasonal availability of abundant, energy-rich prey influences the abundance and diet of a marine predator, the Steller sea lion

- Eumetopias jubatus*. *Marine Ecology Progress Series*, 325, 281-293.
- Womble, J. N., Siler, M. F., & Willson, M. F. (2009). Linking seasonal distribution patterns with prey availability in a central-place forager, the Steller sea lion. *Journal of Biogeography*, 36, 439-451.
- Wynne, K. M. (2005a). Preliminary assessment of the diet of Steller sea lions in the Kodiak area, 1999-2003. In *Gulf Apex predator-prey study final report FY2001-2003* (NOAA Grant NA16FX1270) (pp. 70-78). Washington, DC: U.S. Department of Commerce. 241 pp.
- Wynne, K. M. (2005b). Aerial monitoring of terrestrial habitat use by Steller sea lions in the Kodiak Archipelago, 1999-2003. In *Gulf Apex predator-prey study final report FY2001-2003* (NOAA Grant NA16FX1270) (pp. 79-92). Washington, DC: U.S. Department of Commerce. 241 pp.
- Yang, M. S., & Livingston, P. A. (1986). Food habits and diet overlap of two congeneric species, *Atheresthes stomias* and *Atheresthes evermanni*, in the eastern Bering Sea. *Fishery Bulletin, U.S.*, 82, 615-662.
- York, A. (1994). The population dynamics of the northern sea lions, 1975-1985. *Marine Mammal Science*, 10, 38-51.
- Zeppelin, T. K., Tollit, D. J., Call, K. A., Orchard, T. J., & Gudmundson, C. J. (2004). Sizes of walleye pollock (*Theragra chalcogramma*) and Atka mackerel (*Pleurogrammus monopterygius*) consumed by the western stock of Steller sea lions (*Eumetopias jubatus*) in Alaska from 1998 to 2000. *Fishery Bulletin, U.S.*, 102, 509-521.