Steller sea lion foraging response to seasonal changes in prey availability

Michael F. Sigler[1,*]**, Dominic J. Tollit**[2,*]**, Johanna J. Vollenweider**[1]**,**
John F. Thedinga[1]**, David J. Csepp**[1]**, Jamie N. Womble**[1]**, Mandy A. Wong**[2]**,**
Michael J. Rehberg[3]**, Andrew W. Trites**[2]

[1]**National Oceanic and Atmospheric Administration, National Marine Fisheries Service, Alaska Fisheries Science Center, 17109 Point Lena Loop Road, Juneau, Alaska 99801-8626, USA**

[2]**Marine Mammal Research Unit, Fisheries Centre, University of British Columbia, 2202 Main Mall, Vancouver, British Columbia V6T 1Z4, Canada**

[3]**Alaska Department of Fish and Game, Statewide Marine Mammal Program, 525 West 67th Avenue, Anchorage, Alaska 99518-1599, USA**

ABSTRACT: We hypothesized that: (1) Steller sea lion *Eumetopias jubatus* diet choice is a function of prey availability, (2) sea lions move to take advantage of times and locations of seasonal prey concentrations and (3) the number present depends on the amount of prey available (numerical response). Over 3 yr, typically on a quarterly basis, in Frederick Sound, SE Alaska, multiple measurements were taken of Steller sea lion abundance (aerial surveys), diet (scats), dive behavior (satellite telemetry) and prey availability and caloric density (nearshore, pelagic and demersal fish surveys). We found that Steller sea lions shifted diet composition in response to changes in prey availability of pollock *Theragra chalcogramma*, hake *Merluccius productus*, herring *Clupea pallasi* and salmon *Oncorhynchus* spp. They selected intermediate-sized fish and avoided small (<10 cm) and large (>60 cm) fish, and moved between areas as prey became available seasonally. The number of sea lions present depended on the amount of prey available; a standing biomass of 500 to 1700 t of prey in a non-breeding area such as Frederick Sound, depending on species composition, can attract and sustain about 500 sea lions. Pollock was more frequent in sea lion diet in inside waters of SE Alaska — including Frederick Sound, Stephens Passage and Lynn Canal — than anywhere else in Alaska and contributed ~⅓ of the dietary energy in Frederick Sound. This finding implies that a diet with substantial year-round contributions from less nutritious, but abundant prey such as pollock can form part of a healthy diet as long as more nutritious prey such as herring, salmon or eulachon *Thaleichthys pacificus* also are consumed. Our study supports the conclusion that the Steller sea lion is an opportunistic marine predator with a flexible foraging strategy that selects abundant, accessible prey and shifts among seasonally available species.

KEY WORDS: Prey availability · Foraging · Steller sea lion · Prey selection · Diet · Walleye Pollock · Herring

INTRODUCTION

Animals should forage in a way that optimizes their energy intake and, ultimately, fitness. Multiple factors influence foraging behavior, including predation risk and prey availability. Air-breathing mammals and birds foraging underwater are additionally challenged by the need to resupply oxygen stores frequently. Some marine mammals specialize (Ostfeld 1982, Ford & Ellis 2006), while others feed opportunistically on the most abundant prey within a suite of preferred species (Thompson et al. 1991, Bowen & Harrison 1994, Tollit et al. 1997a) and switch prey when prey abundance changes (Bailey & Ainley 1982, Sinclair et al. 1994, Tol-

lit et al. 1997a, Weise & Harvey 2008). Mammalian and avian predators often move to take advantage of daily (Coyle et al. 1992, Hunt et al. 1998) or seasonally abundant prey including Atlantic *Clupea harengus* (Similä et al. 1996, Skov et al. 2000) and Pacific herring *Clupea pallasi* (Womble & Sigler 2006) and anadromous fishes such as salmon *Oncorhynchus* spp. (Willson & Halupka 1995, Middlemas et al. 2006) and eulachon *Thaleichthys pacificus* (Marston et al. 2002, Sigler et al. 2004). A single prey aggregation can attract thousands of individuals and a mixture of predators (Marston et al. 2002), and individual predators may repeatedly return to predictable daily (Irons 1998) and seasonal (Similä et al. 1996) prey aggregations. Diet composition also can be affected by distance from haulouts (Womble et al. 2005), diving ability (Beck et al. 2003) or prey predictability (Gende & Sigler 2006).

An important mammalian predator in the North Pacific Ocean, the western stock of Steller sea lion *Eumetopias jubatus* has declined by more than 80% since the 1960s (Loughlin et al. 1992, Trites & Larkin 1996), whereas the eastern stock has more than doubled (Pitcher et al. 2007). A diet dominated by less nutritious prey may have contributed to the decline of the western stock (junk food hypothesis) (Alverson 1992, Trites & Donnelly 2003) and has also been implicated in the population dynamics of other top marine predators (Österblom et al. 2008). Chronically low juvenile survival was likely a primary driver in the Steller sea lion decline (York 1994, Pascual & Adkison 1994). Adults can meet their daily energy needs eating exclusively low energy prey, but young sea lions cannot and must obtain milk for an extra 1 or 2 yr at the expense of mothers' reproductive rates (Rosen & Trites 2004, Kumagai et al. 2006, Trites et al. 2006). Low lipid diets appear to negatively affect body composition during periods of inadequate intake (Rosen & Trites 2004, 2005, Kumagai et al. 2006), and season affects the sea lions' capacity to recover from these episodes (Jeanniard du Dot et al. 2008). Commercial fisheries also may have reduced the quantity of prey and contributed to lower juvenile survival, episodic adult mortality and reduced fecundity or birth rates (Atkinson et al. 2008b).

In our study we address 3 questions regarding Steller sea lion foraging ecology: (1) do Steller sea lions exhibit a flexible foraging strategy and shift diet composition in response to changes in prey availability; (2) do Steller sea lions move between areas as prey becomes available seasonally and is the number present related to the amount of prey available; and (3) are Steller sea lions susceptible to nutritional stress if they rely on less nutritious species? To answer these questions, we studied Steller sea lions and their prey across 3 yr (2001 to 2004) in Frederick Sound, southeast (SE) Alaska. Frederick Sound is a useful area to learn about Steller sea lion foraging ecology because: (1) several hundred or more sea lions use the area year-round; (2) prey availability and sea lion diet and foraging behavior can be quantified; and (3) study results from this area can be compared to nearby areas used seasonally (Sigler et al. 2004, Womble & Sigler 2006). We completed multiple measurements, typically on a quarterly basis, including Steller sea lion abundance (aerial surveys), diet (scats), dive behavior (satellite telemetry) and prey availability and caloric density (nearshore, pelagic and demersal fish surveys). We compared seasonal changes in prey abundance and Steller sea lion abundance, as well as diet and foraging behavior. With these data, we tested 3 hypotheses: (1) sea lion diet choice is a function of prey availability; (2) sea lions move to take advantage of times and locations of seasonal prey concentrations; and (3) the number of sea lions present depends on the amount of prey available (numerical response).

MATERIALS AND METHODS

Study area. The core study area was a 20 km radius circle centered at the Brothers Islands (56° 16′ N, 133° 52′ W) at the confluence of Stephens Passage and Frederick Sound in SE Alaska, USA, where Steller sea lions use several terrestrial sites (haulouts) to rest and care for young year-round (Fig. 1). This area encompasses a variety of marine habitats (depth ranges between 5 and 480 m) that are typical of areas used by foraging sea lions in SE Alaska (Pitcher et al. 2005). Most trips (>90%) made by juvenile sea lions are <15 km from haulouts (Raum-Suryan et al. 2004), while adult females appear to forage within 15 km during summer and may travel considerably farther during winter (Merrick & Loughlin 1997). The southern Stephens Passage/northern Frederick Sound study area is 1 of 3 study areas that make up a larger SE Alaska Steller sea lion prey study. The 3 study areas include: (1) an area that sea lions use year-round (Frederick Sound); (2) an area used only during late fall and winter (Lynn Canal, 58° 39.0′ N, 135° 04.0′ W) (Womble & Sigler 2006); and (3) an area used only for a short period during spring (Berners Bay, 58° 45.1′ N, 134° 58.5′ W) (Sigler et al. 2004).

Steller sea lion abundance. Sea lions were counted during monthly aerial surveys of terrestrial sites to determine sea lion abundance in our study area (Fig. 1) from March 2001 to May 2004 (Womble et al. 2009). Counts were made by taking oblique angle photographs from an aircraft passing terrestrial sites, which
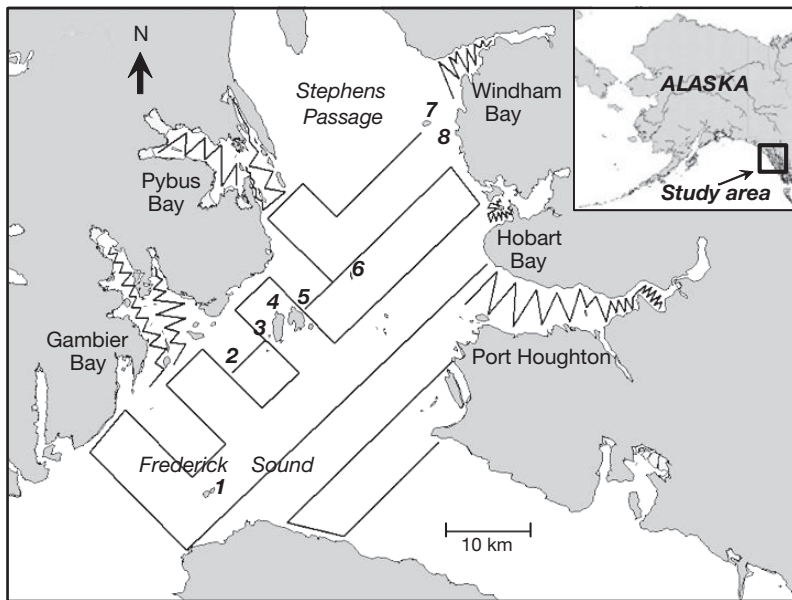
Fig. 1. Acoustic survey transect lines and terrestrial locations (haulouts) where Steller sea lions were counted during aerial surveys. 1: Turnabout Island; 2: Round Rock; 3: Southwest Brothers Island; 4: West Brothers Island; 5: East Brothers Island; 6: Sail Island; 7: Sunset Island; 8: Sunset Point

is a standard method for counting Steller sea lions, but not determining age or sex composition (Pitcher et al. 2007). Surveys were conducted 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 at an oblique angle through an open window from an altitude of 250 to 300 m at an air speed of 183 to 210 km h^{-1}. Photographic images of terrestrial sites were taken using a 35 mm autofocus camera (Nikon 8008S) with a motor drive equipped with a 70 to 210 mm zoom lens and a 35 mm auto-focus digital camera (Nikon D1X) equipped with a 70 to 300 mm zoom lens. Overlapping images were taken if more than one image was needed to cover the entire site. The clearest image was projected and the sea lions in the image were counted twice by an experienced counter.

Steller sea lion diet. Scat samples were collected 5× a yr from May 2001 to March 2004 (n = 15 collections) to determine sea lion diet (Tollit et al. 2008). Collections were concurrent with pelagic and nearshore fish surveys (see below). Scat was collected in March, May, June/July, September and December/January. The 4 sites with the greatest sea lion abundance (Southwest Brothers, West Brothers, Sunset and Sail Islands) were visited consistently. Excluding March 2002 (n = 9), sample size averaged 120 scats (SD = 55, range = 40 to 223) for the 4 haulout sites. For these 9 samples, only

1 sample collection was less than the recommended minimum sample size of 59 for comparing prey occurrence (Trites & Joy 2005). Scats were washed through an elutriator (Bigg & Olesiuk 1990) or a 0.495 mm sieve. Pacific Identifications identified all hard structures (fish bones, otoliths, cartilaginous parts, lenses and teeth, and cephalopod beaks, lenses and pens) to the lowest possible taxon (Olesiuk et al. 1990, Browne et al. 2002) using a reference collection (all-structures approach). Prey numbers were estimated from counts of hard structures and were adjusted for species-specific recovery rates using species-specific numerical correction factors (Tollit et al. 2003, 2007). Prey sizes were estimated from measurements of hard structures and were adjusted for the observed level of wear using species-specific digestion correction factors (Tollit et al. 1997b, 2004).

The overall importance of each prey species (or category) in scat samples was expressed using: (1) frequency of occurrence (FO, %) (Hyslop 1980); (2) reconstructed biomass (BR, %) (Hammond & Rothery 1996); (3) energetic contribution (EC, %) (Vollenweider et al. 2006); and (4) index of relative importance (IRI) (Hyslop 1980), which uses a composite of prey number, FO and BR. Biomass was reconstructed by combining prey numbers and sizes, which were converted to biomass using length–weight relationships. EC was computed from reconstructed biomass and species-specific and seasonal energy density values (Vollenweider et al. 2006). Biomass reconstruction and energy contribution calculations used a weighted or variable method (Lance et al. 2001) and pooled scats for comparability with previous diet studies in the region (Vollenweider et al. 2006, Womble & Sigler 2006). Diet diversity also was calculated to compare across studies (Merrick et al. 1997, Sinclair & Zeppelin 2002, Womble & Sigler 2006, Trites et al. 2007). Chi-squared tests on occurrence data were used to assess differences in diet for the 9 most important prey categories (overall FO ≥5%). The dominant prey species, walleye pollock *Theragra chalcogramma*, also was analyzed by size category (young-of-the-year [YOY]: <20 cm; juvenile: 20 to 34 cm; adult: ≥34 cm) (Tollit et al. 2004).

Captive feeding studies with Steller sea lions have shown that an all-structures approach reliably detects meals of small (10 cm) prey, although the proportion recovered is less than that for larger prey, hence the

need for correction factors (Tollit et al. 2007). Adult gadids have relatively robust skeletal structures with a high likelihood of being recovered in scats, but they also have a greater propensity of being regurgitated (Tollit et al. 2003), as do large cephalopod beaks. Comparisons of hard part identifications with molecular genetic techniques to identify prey from soft tissue in scats tissue indicated the former technique had missed ~20% of recent meals (Tollit et al. 2009). These consisted mainly of salmonids, flatfish, elasmobranches and cephalopods, amounting to 10–15% increases in individual occurrences. Overall, occurrence indices provide a valuable comparative index related to the number of animals eating a prey type. They likely overestimate the relative importance of small or trace prey, while, conversely, biomass-related indices (BR and EC) may often overestimate the importance of large prey (Laake et al. 2002), especially when using a weighted approach and/or small numbers of scats.

A bioenergetic model (Winship et al. 2002) was used to estimate the biomass of prey consumed by Steller sea lions during each of the 5 scat sampling periods. Inputs included sea lion abundance, diet composition and energy content for our study area, and estimated age- and sex-specific energy requirements by date (Winship et al. 2002). A stable age structure was assumed (Winship et al. 2002). The counts were adjusted for the unobserved individuals because sea lions were counted while on land and did not include individuals in the water. The proportion of time Steller sea lions spend ashore varies with time of yr and age/sex classes (lower in winter than summer, lower for juveniles than adults overall) and ranges from 10 to 63% (Holmes et al. 2007). We used the mid-point of this range (37%), so that a count of 370 individuals ashore implied 1000 individuals total. Energy requirements were computed per individual and then multiplied by the maximum sea lion abundance for that sampling period. The values per individual ranged from 67 613 kJ d^{-1} during June/July to 97 568 kJ d^{-1} during May. Total food consumption was calculated by allocating total energy requirements based on energy content and composition of the biomass-reconstructed diet.

Prey selection was assessed by the odds ratio (O) (Fleiss 1981): $O = (p_1 \times q_2)/(p_2 \times q_1)$, where p_1 is the proportion of the diet consisting of a particular prey item, p_2 is the relative abundance as a proportion of this prey item in the environment, q_1 is the proportion of the diet contributed by all other prey items and q_2 is the relative abundance of all the other prey items in the environment. Odds ratios were transformed logarithmically (base 10). Positive values indicate prey that were selected and negative values indicate potential prey that were ignored. Prey size selection was assessed by comparing size frequencies from scats to size frequen-

cies from prey abundance surveys using the Kolmogorov-Smirnov statistical test to determine if the 2 distributions differed significantly.

Steller sea lion dive behavior. Juvenile sea lions were captured throughout SE Alaska and tagged to monitor their movement. Juveniles were tagged because chronically low juvenile survival likely was a primary driver in the decline of the western stock (York 1994, Pascual & Adkison 1994) and no method for tagging adults is considered safe enough for permit approval. Although these tagging results apply only to juveniles, studies of the ontogeny of dive performance show that by 1.5 yr of age, juveniles are capable of sustained periods of long dives. Depths and durations of their dives are similar to adult females (Pitcher et al. 2005) and juveniles and subadults dive to similar depths and durations (Rehberg and Burns 2008). A total of 111 individuals was fitted with satellite dive recorders (SDR, Wildlife Computers) that relayed point location estimates, on-land/at-sea cycles and summarized dive characteristics (Pitcher et al. 2005). For each individual, we linked the on-land/at-sea data to location estimates and used this information to identify which ones were present within the Frederick Sound study area during 6 wk windows centered around scat collections (median dates). Six juvenile sea lions captured during 5 to 15 May 2001 were present in the study area during the May and June/July 2001 scat sampling periods, and 4 juveniles captured during 15 to 20 November 2002 were present during the December 2002 scat sampling period. Their estimated ages at tagging ranged from 17 to 29 mo. Some Steller sea lions are weaned before or on their first birthday, while others continue to suckle until their second birthday or beyond (Pitcher & Calkins 1981, Trites & Porter 2002, Trites et al. 2006). Thus some of these tagged individuals may still have been suckling and dependent on their mother for some portion of their nutrition.

We calculated the proportion of time spent submerged below 4 m for each 6 h summary period provided by the SDRs. We identified whether summary periods were primarily in daylight or darkness using civil twilight (solar angle = –6°) of each date in the study area as the threshold. We also determined the maximum depth reached per 24 h day by each sea lion. Using a generalized linear model (GLM), we examined the effect of season (May–June vs. December) and time of day (day vs. night) and their interaction on time submerged, including individual animal as a random effect. Time submerged was arcsine-root transformed to improve normality, post hoc tests had Bonferroni correction and significance was set at $p < 0.05$.

Prey availability. Prey surveys were conducted in 3 major habitat types in Frederick Sound: pelagic,

demersal and nearshore habitats. Acoustic surveys were conducted quarterly from May 2001 to March 2004 to estimate abundance of pelagic prey. Surveys were conducted during March, May, September and December (except that the December 2003 survey was postponed to January 2004). Prey availability was estimated using a portable 38 kHz Simrad split beam echosounder with a 12° beam angle towed beside a vessel at 11 km h^{-1}, or a 38 kHz Simrad split beam echosounder with a 7° beam angle transducer attached to the hull of a vessel traveling at 15 km h^{-1}. Acoustic transect routes (Fig. 1) were geo-referenced using a Garmin GPS 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 & Korneliussen 2000) and to facilitate observations of foraging sea lions while collecting acoustic data. Midwater trawls were deployed to identify acoustic targets in the echograms and to collect fork length (FL), weight and species composition data.

The acoustic data were analyzed with an echo-integrator that summed the returning echoes from fish observed beneath the vessel. Acoustic data were classified by 183 m 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 & Simmonds 1992). Target strength (TS) refers to the acoustic reflectivity of a single echo or fish and depends on length (L, in cm): TS = 20 $\log_{10}$L + b (MacLennan & Simmonds 1992); for walleye pollock, b = −66 (Traynor 1996), for Pacific hake *Merluccius productus*, b = −68 (Traynor 1996) and for herring, b = −65.4 (Ona 2003). In addition, Pacific herring acoustic estimates were adjusted for depth compression of the air bladder (Ona 2003) and acoustic shadowing (Zhao & Ona 2003, Sigler & Csepp 2007). Hake and pollock sometimes were found in mixed concentrations; the mixed-species NASC was partitioned to species based on each species' average acoustic backscatter and proportional weight in midwater trawl catches (MacLennan & Simmonds 1992, their Eq. 8.8), with equal weight given to the proportions in each catch (MacLennan & Simmonds 1992, their Eq. 8.9). Average fish density was computed by substrata to account for differences in fish density within the survey area. The substrata consisted of the individual bays and the open water at the confluence of Frederick Sound and Stephens Passage. Fish biomass was computed by multiplying average fish density in weight by the aerial size of the substrata.

Longline surveys were conducted during September 2003, February/March 2004 and May 2004 to estimate seasonal trends in relative abundance of demersal prey. Standardized longline gear was used, with #14/0 Mustad hooks spaced 1.6 m apart and baited with chopped squid (mantle length averaging 16.5 cm, 2 to 3 baits per squid including tentacles). The groundline was 0.87 cm diameter and gangions were #66 thread and 25 cm tied length. Fifteen longline sets were completed during each seasonal survey. The location of the first station was randomly chosen, and then the remaining stations were systematically located to cover the survey area. The same 15 locations were sampled each survey period. Depths from 53 to 397 m were sampled. Catch, fork length, weight and effort (number of hooks) data were recorded. Relative abundance was inferred by computing catch (numbers and weight) per 1000 hooks by species.

Nearshore areas were surveyed for prey in winter (March 2002, 2003 and 2004) and summer (July 2001, 2002 and 2003) to estimate seasonal trends in relative abundance of nearshore prey species around the Brothers Islands (Thedinga et al. 2006). Beach seining, jigging and a remotely operated vehicle (ROV) were used for surveys. Intertidal and subtidal areas (<115 m deep, <350 m from shore) were sampled. Depths <5 m were sampled by beach seine at 14 sites, and depths from 5 to 115 m were sampled by jigging at 18 sites. Captured fish were counted and a subsample of most species was measured for fork length; large catches were estimated gravimetrically (Thedinga et al. 2006). The ROV surveyed depths from 1 to 85 m (limit of umbilical cord) at 11 sites for fish not captured by jigging or seining.

Whole fish were frozen during pelagic, nearshore and demersal surveys for measurement of caloric content and protein and fat composition using standard laboratory procedures (Vollenweider et al. 2006). Season- and species-specific values of energy density were multiplied by quarterly biomass measurements from the pelagic surveys to determine available energy per quarter. Available energy was computed only for pelagic prey because biomass was estimable for the acoustic survey, whereas the nearshore and demersal surveys only indexed abundance. Available prey energy was compared to estimates of individual sea lion energy demands per day (annual average of 79 464 kJ d^{-1} per individual) (Sigler et al. 2004), which were derived using bioenergetic models for Steller sea lions (Winship et al. 2002).

Steller sea lion numerical response. We estimated the numerical response of Steller sea lions to variations in prey abundance. A numerical response provides a measure of how Steller sea lion populations will respond to changes in fishing or how ocean conditions modify prey fields. Counts of Steller sea lions were regressed against nutritional energy of pelagic prey.

Both variables were log-transformed to meet the assumption that they were obtained from normal populations. Data from a year-round study at Lynn Canal (Sigler & Csepp 2007) were added to the Frederick Sound data because the Lynn Canal prey and sea lion abundances varied much more and provided more contrast to detect a numerical response. The numerical response was estimated based on pelagic biomass, but not demersal or nearshore biomass which were indexed (catch rates). Steller sea lions counts were adjusted for time spent ashore (37%).

RESULTS

Steller sea lion abundance

Sea lions occupied terrestrial sites (n = 8) in the study area throughout the yr (Table 1). The total number of sea lions of all age classes observed ashore during surveys (n = 39) ranged from 669 (February 2002) to 2374 (August 2002), excluding months when one or more of the 4 most attended sites (Southwest Brothers, West Brothers, Sunset and Sail Islands) were not surveyed

Table 1. *Eumetopias jubatus*. Number of Steller sea lions counted at terrestrial sites during aerial surveys of Frederick Sound, SE Alaska. I. = island, NC: no count

Year and month	Southwest Brothers I.	West Brothers I.	East Brother I.	Turn-about I.	Sunset Island	Sail Island	Round Rock	Sunset Point	Total
2001									
March	NC	NC	NC	28	61	41	30	NC	160
April	168	0	179	1	218	90	16	NC	672
May	489	0	0	0	558	150	6	NC	1203
June	528	0	0	0	478	316	1	NC	1323
July	361	0	0	0	706	5	0	NC	1072
August	1283	0	0	0	19	644	0	0	1946
September	526	8	4	12	120	601	3	0	1274
October	361	421	0	181	62	387	42	0	1454
November	NC	NC	0	NC	NC	NC	NC	NC	0
December	NC	NC	0	NC	NC	NC	NC	NC	0
2002									
January	214	266	0	137	31	48	36	206	938
February	270	0	15	76	77	59	37	135	669
March	364	0	0	124	347	32	57	108	1032
April	269	0	0	21	343	103	45	118	899
May	710	0	0	0	342	160	13	1	1226
June	741	0	NC	0	566	7	0	0	1314
July	NC	0	0	0	NC	3	6	0	9
August	1752	0	0	0	8	614	0	0	2374
September	481	0	0	0	8	1124	21	0	1634
October	684	129	NC	18	267	1110	63	0	2271
November	291	172	0	57	45	222	41	48	876
December	316	291	0	187	54	191	50	15	1104
2003									
January	534	276	0	170	178	163	44	121	1486
February	277	66	0	45	280	124	44	0	836
March	496	0	0	48	600	75	108	66	1393
April	98	2	0	0	318	156	114	5	692
May	759	3	4	0	611	124	8	0	1509
June	1126	0	0	0	522	45	0	0	1693
July	1483	0	0	0	8	248	0	0	1739
August	1457	0	0	3	0	404	0	0	1864
September	911	0	0	0	40	1297	3	0	2251
October	735	0	0	120	177	274	39	0	1345
November	620	308	NC	308	165	313	63	0	1777
December	402	451	0	311	259	248	54	0	1725
2004									
January	311	260	0	179	372	100	38	0	1260
February	392	104	0	162	518	118	94	0	1388
March	392	0	0	95	391	161	81	0	1120
April	127	0	0	0	525	85	35	0	772
May	509	0	0	9	508	1	3	0	1030

due to bad weather. Average abundance was highest during August (2061) and lowest during April (759). Terrestrial sites at Southwest Brothers, Sunset and Sail Islands were occupied throughout the yr. Steller sea lions were most abundant at Southwest Brothers Island, which was occupied by up to 1752 sea lions (August 2002). In contrast, other terrestrial sites were occupied seasonally (Turnabout Island and Round Rock during fall, winter, and spring; West Brothers Island during fall and winter). Sea lions also were observed infrequently at Walter Island in Port Houghton near Frederick Sound (December 2002, October and November 2003). Most sea lions counted on the haulouts likely were juveniles and adult females. Counts from a year-long (July 2004 to July 2005) ground-based study at Southwest Brothers Island found adult females (40%), juveniles and pups (55%) and bulls and subadult males (5%) (Marcotte 2006).

Steller sea lion diet

A total of 59 prey species/categories was identified from scat samples collected during May 2001 to March 2004 (n = 1640 scats with remains, 9739 identified prey items). Nine species occurred in at least 5% of scat samples (Table 2). Walleye pollock dominated prey occurrence (FO = 95%), followed by Pacific herring, Pacific hake and arrowtooth flounder *Atheresthes stomias* (FO = 20 to 40%), and skate (Rajidae), cephalopods, Pacific cod *Gadus macrocephalus*, salmon and rockfish *Sebastes* spp. (FO = 5 to 15%). Pollock (BR = 39%) also dominated prey biomass (particularly juveniles, BR = 22%), followed by arrowtooth flounder and

skate (BR = 11 to 12%), and salmon, cod, herring and hake (BR = 5 to 7%). Each of these 7 species also contributed ≥5% of estimated energetic consumption. For IRI, pollock ranked first, followed by herring, arrowtooth flounder, hake, skate and salmon. Pollock occurrence was consistent year-round (>91%, coefficient of variation [CV] = 2%), whereas salmon occurrence increased each September (to 21–35%, CV = 100%, Fig. 2). Temporal variability of the other key species (FO ≥5%) was intermediate (CV = 47 to 73%), with all species but rockfish showing statistically significant seasonal effects. A wide size range of prey (3 to 111 cm) was consumed, but most (78%) were 10 to 35 cm (Figs. 3 & 4). The heaviest individual prey was an ~8 kg skate.

The number of prey species per scat sample averaged 2.5 ± 1.7 (SD) and ranged from 1 to 14 species. About one-third of the recovered scats contained only one species, which was predominantly pollock (94%). No other prey species exceeded 3% as the sole species. As a result, pollock occurred with 1.6 other species on average, while the remaining key species occurred with between 2.8 (herring) and 3.7 (skate) other species on average. Herring occurred on its own in just 1.3% of cases, co-occurring with pollock in 95% of cases, with hake in 37% of cases and with arrowtooth flounder in 28% of cases. About 28% of the recovered scats contained 2 species. In 92% of the cases, one of the 2 species was pollock.

We computed diet (Shannon's index) diversity 3 different ways to compare our results to those from recent publications on Steller sea lion diet (prey species with FO > 5%, Womble & Sigler 2006; prey family FO, Sinclair & Zeppelin 2002; taxonomic grouping and trophic

Table 2. Key prey species (frequency of occurrence [FO] ≥5%) consumed by Steller sea lions in Frederick Sound, SE Alaska, based on 1640 scats containing hard remains. Estimates for walleye pollock were additionally partitioned by size class (in italics) and FO was modified (FO$_{mod}$) to total 100% for comparison across indices. Biomass reconstruction (BR) and energetic contribution (EC) indices were calculated based on number (N) of fish (adjusted for species-specific recovery rates), prey size estimates (adjusted for observed level of wear of hard structures) and energetic density values. The index of relative importance (IRI) ranks prey based on a composite of N, FO and BR. P-values are based on chi-square analyses of prey occurrence counts that tested for season and year effects

| Species category	N	FO	FO$_{mod}$	BR	EC	IRI	Season		Year	
							χ^2	p	χ^2	p
Pollock overall	5817	95.4	37.8	39.1	33.5	1	0.2	0.99	0.4	0.82
Young-of-the-year	*1238*	*30.7*	*–*	*2.4*	*2.0*	*–*				
Juvenile	*3678*	*76.5*	*–*	*22.4*	*18.9*	*–*				
Adult	*901*	*43.1*	*–*	*14.3*	*12.6*	*–*				
Pacific herring	1277	32.9	13.0	5.7	9.2	2	35.3	<0.001	20.2	<0.001
Pacific hake	532	27.1	10.7	5.3	5.3	4	36.5	<0.001	6.5	0.04
Arrowtooth flounder	376	21.3	8.5	12.2	17.1	3	66.3	<0.001	13.9	<0.001
Skate spp.	235	14.3	5.7	11.2	11.7	5	168.6	<0.001	1.3	0.52
Cephalopod spp.	299	13.9	5.5	1.9	1.8	8	62.0	<0.001	31.2	<0.001
Pacific cod	263	12.5	4.9	6.4	5.3	7	34.8	<0.001	12.8	0.002
Salmonid spp.	236	12.0	4.7	7.3	6.7	6	168.6	<0.001	1.3	0.52
Rockfish spp.	78	4.7	1.9	2.2	2.7	9	7.7	0.10	19.9	<0.001
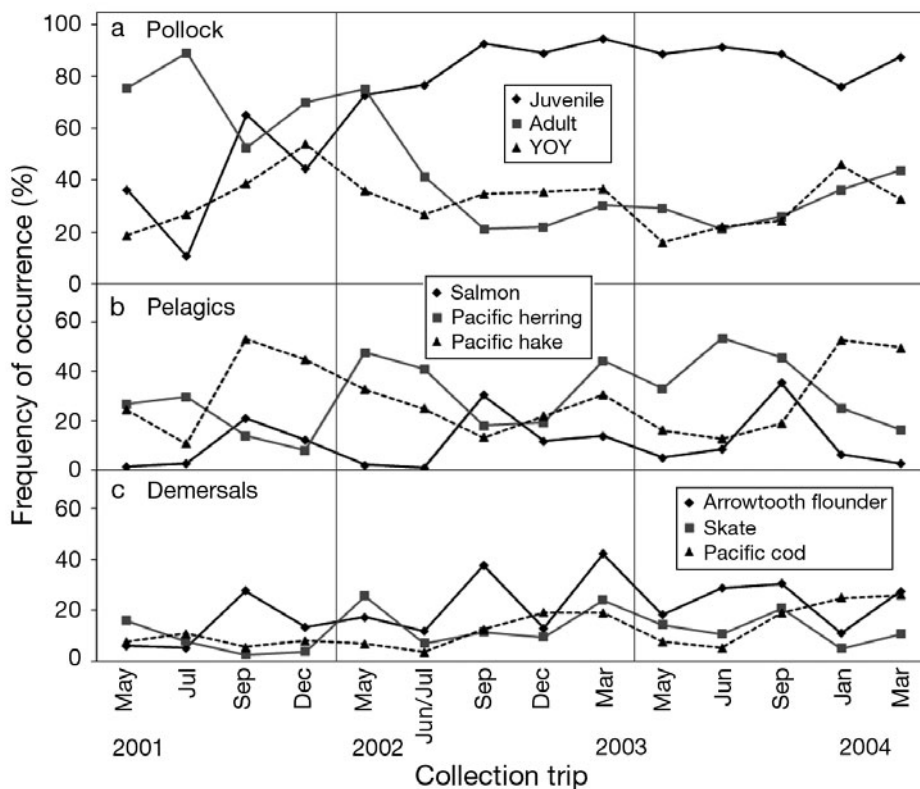
Fig. 2. Temporal changes in the occurrence of key species in Steller sea lion diet in Frederick Sound, SE Alaska (May 2001 to March 2004). (a) Walleye pollock (young-of-the-year [YOY]: <20 cm; juvenile: 20–34 cm; adult: ≥34 cm), (b) pelagic prey (salmon sp., Pacific herring and Pacific hake) and (c) demersal prey (arrowtooth flounder, skate and Pacific cod). Note that the frequencies of occurrences do not sum to 100% and that scats can contain the remains of one or more species (or size class of pollock)

level, Trites et al. 2007). Steller sea lions seem to need a variety of prey available (Merrick et al. 1997). Diet diversity sensu Womble & Sigler (2006) was 2.3 overall. Seasonal diversity was highest in March and September (2.4 to 2.5), with lower values in December, May and June/July (1.8 to 2.1). Diversity values sensu Sinclair & Zeppelin (2002) were 2.3 during May to September and 2.6 during October to April. Diet diversity sensu Trites et al. (2007) was 3.5 overall and also lower in December, May and June/July (2.9 to 3.1) than March and September (4.0 to 4.1) (Tollit et al. 2008).

Estimated average prey consumption for all sea lions in Frederick Sound was 2200 t mo^{-1}, and estimated daily individual consumption was 18.7 kg. Monthly consumption varied seasonally and was lowest in June/July (1700 t) and highest in September (2600 t). The seasonal variation reflected not only variation in sea lion abundance, but also higher proportions of energy-dense prey such as herring during summer. Monthly consumption of pollock (range = 800 to 1200 t) and herring (70 to 190 t) both peaked in May, while consumption of hake (80 to 220 t) peaked in December. Consumption of salmon was 400 to 420 t in September, equivalent to ~27 000 adult pink salmon. Although monthly prey consumption appears large (2200 t mo^{-1}), it represents a small portion of the prey that was available. The number of daily energy rations available from pelagic prey averaged 550 000 per sea lion.

Juvenile Steller sea lion dive behavior

Juvenile Steller sea lions during May–July spent a greater proportion of their time submerged at night (0.66) than during daylight (0.43, $F_1 = 19.095$, p < 0.001). During December, the proportion of time submerged was similar during daytime and nighttime ($F_1 = 2.466$, p = 0.117). The only significant seasonal effect occurred during nighttime, when sea lions spent more time submerged during May–July (0.66) than December (0.36, $F_1 = 29.825$, p < 0.001). Maximum daily depths reached by sea lions averaged 85 ± 42 m (SD) during December and 99 ± 29 m during May–July. The average of maximum dive depths reached by individuals was 215 ± 145 m (maximum = 420) during December and 195 ± 41 m (maximum = 244) during May–July.

Prey availability

Pelagic species

Twelve acoustic surveys were conducted between May 2001 and March 2004, totaling 5437 km of standard acoustic transects and including 319 midwater trawl tows. The largest midwater trawl catches by weight were pollock, hake and herring. Acoustic estimates of abundance were completed for these 3 species because
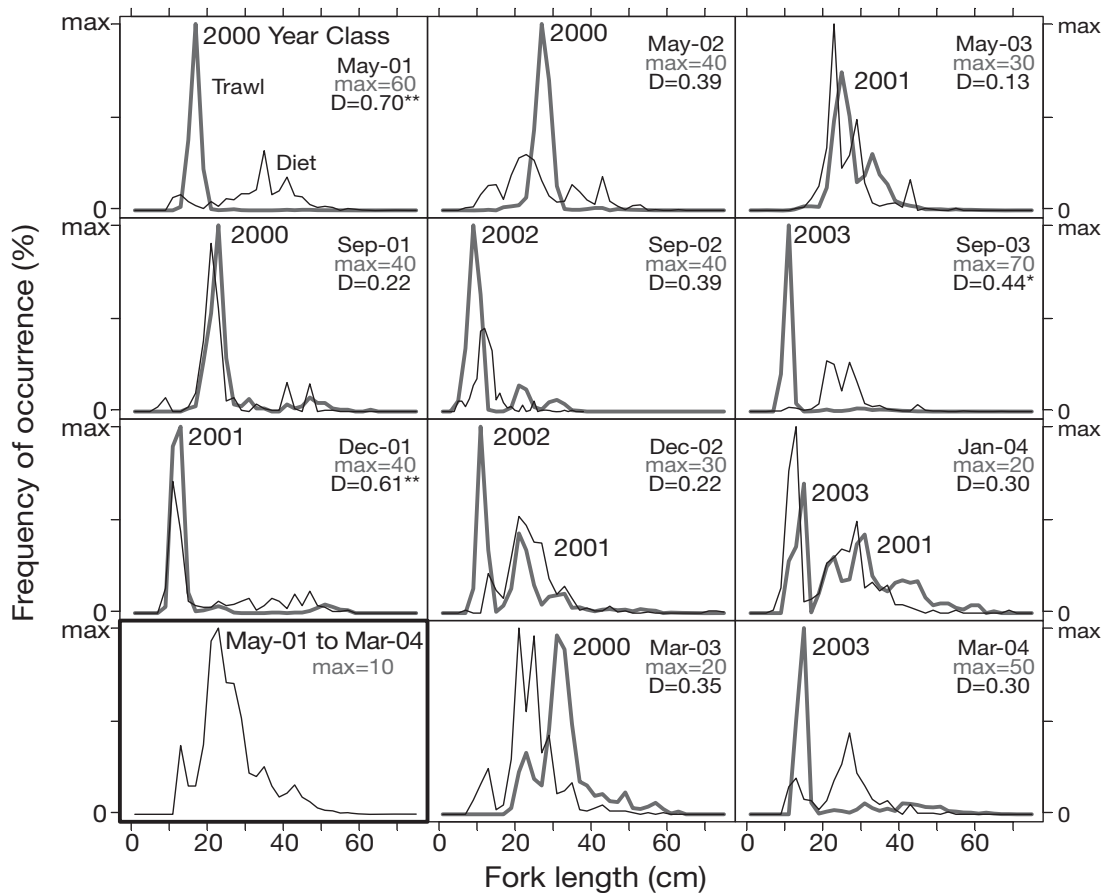
Fig. 3. *Theragra chalcogramma*. Size frequencies of walleye pollock found in the diet of Steller sea lions overall (panel in lower left corner) and compared with sizes found in concurrent midwater trawl sampling in Frederick Sound, SE Alaska. The dominant yr class (yr of recruitment) associated with trawl surveys is indicated in each period. max: maximum frequency of occurrence; D: Kolmogorov-Smirnov statistical result with significance levels of p < 0.05 (*) and p < 0.01 (**) indicated. Three of the 12 sets of compared frequency distributions differed significantly

the catches consistently confirmed delineations of these species in the echograms. Other large catches by weight (>100 kg) or number (>1000) were jellyfish (Scyphozoa), northern lampfish *Stenobrachius leucopsarus*, smooth lumpsucker *Aptocyclus ventricosus*, eulachon, Pacific glass shrimp *Pasiphaea pacifica*, northern shrimp *Pandalus borealis* and northern smoothtongue *Leuroglossus schmidti*. These species plus squid (Teuthida) and Pacific viperfish *Chauliodus macouni* were widely caught (FO > 10%). Pollock were most abundant (average biomass of 9057 t), followed by hake (1715 t) and herring (1176 t) (Table 3). Pollock abundance differed seasonally (p = 0.03) and annually (p = 0.02) (2-way ANOVA, df = 11). In this case, yr refers to survey yr (e.g. survey yr 1 encompasses May 2001 to March 2002). Pollock abundance was higher in May and September than December and March for each survey yr. Pollock abundance was higher in the 2nd survey yr than in the 1st and 3rd survey yr for each season. Neither season nor yr differed for hake or herring (2-way ANOVA, df = 11, p > 0.25).

Demersal species

Three longline surveys were conducted between September 2003 and May 2004, totaling 16 815 hooks. The largest catches were Pacific halibut *Hippoglossus stenolepis*, followed by Pacific cod and sablefish *Anoplopoma fimbria* (Table 4). Arrowtooth flounder and sandpaper skate *Bathyraja interrupta* were also caught frequently. These species together comprised 95% of the total catch by weight for all 3 survey periods combined. Of these 5 species, relative abundance differed seasonally for arrowtooth flounder (p = 0.01), Pacific cod (p < 0.01) and sablefish (p < 0.01) (2-way ANOVA, df = 2). Arrowtooth flounder were most abundant during September, Pacific cod during February and May and sablefish during September. For all species combined, relative abundance was 40% higher in February than September or May, but this difference was not statistically significant (p = 0.23).
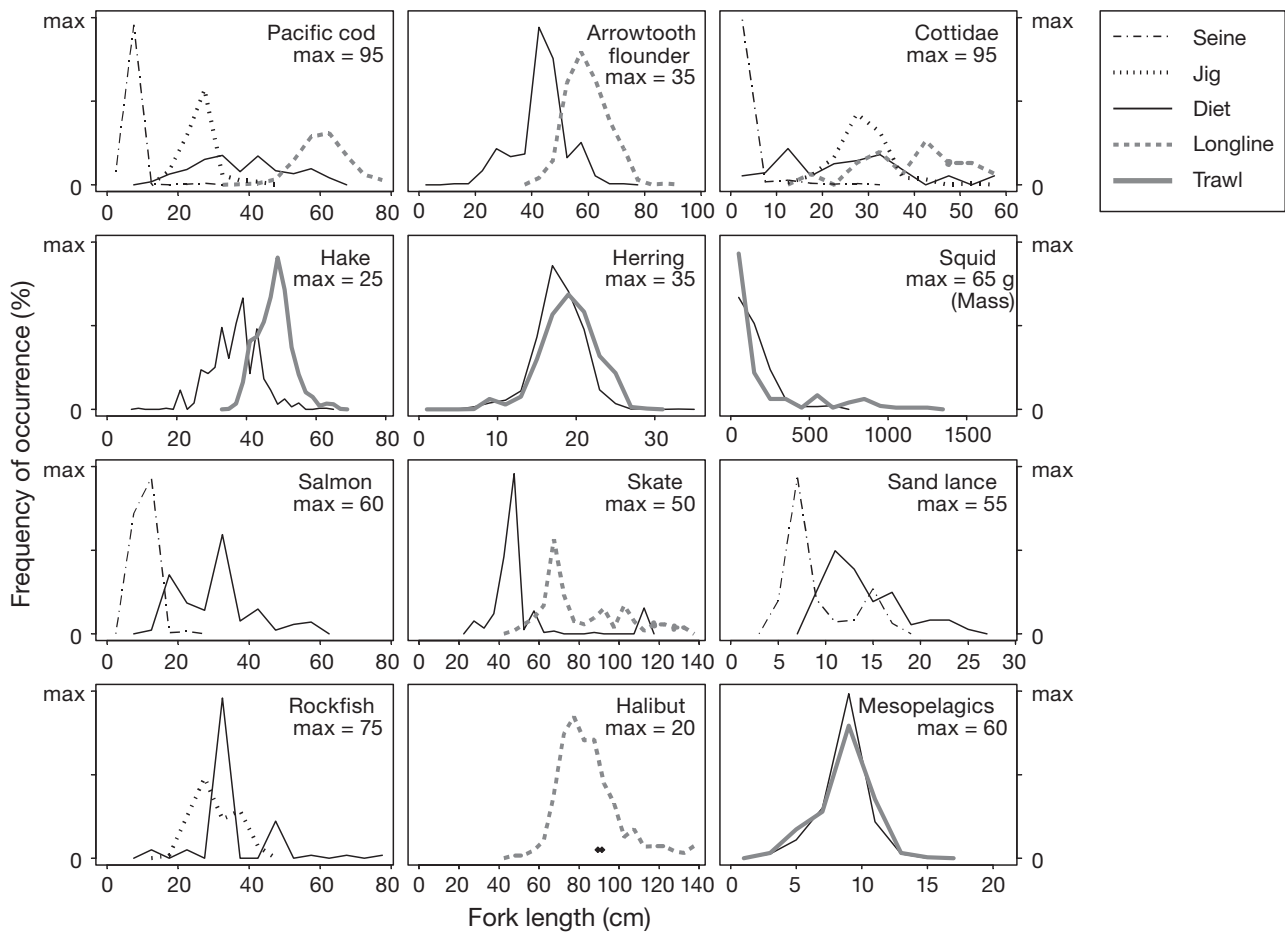
Fig. 4. Size frequencies of several species found in the diet of Steller sea lions compared with sizes found in concurrent midwater trawl, seine, jig and longline surveys of Frederick Sound, SE Alaska. max: maximum frequency of occurrence. Squid measurements are mantle length and black diamonds represent single fish consumed by Steller sea lions

Nearshore species

In summer, a total of 39 beach seine hauls yielded 187613 fish representing 37 species (Thedinga et al. 2006). Total catch was dominated by pollock (85%), Pacific herring and Pacific sand lance *Ammodytes hexapterus*. In winter, 987 fish were captured in 40 beach seine hauls representing 24 species; pink

salmon *Oncorhynchus gorbuscha* fry occurrence was 60%. Seine catch rates were higher during summer than winter (GLM ANOVA of log-transformed values, p < 0.05). Catch varied by yr, especially in summer, because of strong pollock (notably 2001, 2003) and herring (2003) yr classes. A total of 363 fish representing 22 species was captured by jigging; catches were dominated by armorhead sculpin *Gymnocanthus*

Table 3. *Merluccius productus*, *Clupea pallasi* and *Theragra chalcogramma*. Acoustic estimates of abundance (t) of Pacific hake, Pacific herring and walleye pollock during surveys in Frederick Sound, SE Alaska, by yr and mo. p-values for season and year effects are based on a 2-factor ANOVA with no replication

Species	2001			2002				2003			2004		Mean	SD	CV	Season effect p	Year effect p
	May	Sep	Dec	Mar	May	Sep	Dec	Mar	May	Sep	Jan	Mar					
Pacific hake	980	1459	5008	1152	2984	644	1749	2003	978	1237	271	2115	1715	1266	0.74	0.79	0.64
Pacific herring	969	486	1149	583	459	271	1978	3557	505	1331	996	1828	1176	927	0.79	0.29	0.50
Walleye pollock	12148	13073	5403	6010	13752	19603	7367	8816	6009	6929	5677	3895	9057	4636	0.51	0.03	0.02
Juvenile	10027	11042	1064	4735	12635	18891	5050	6800	5732	6138	2096	1178					
Adult	2121	2031	4339	1276	1117	713	2317	2016	277	791	3581	2716					

Table 4. Longline survey estimates of relative abundance (catch in weight and number per 1000 hooks) during surveys of Frederick Sound, SE Alaska, by yr and mo. The other species category cumulatively accounts for less than 5% of the total catch by weight. P-values are based on a 2-factor ANOVA with no replication of relative abundance in weight

Species	——— Catch (kg) per 1000 hooks ———			——— Catch (no.) per 1000 hooks ———			p
	Sep 2003	Feb 2004	May 2004	Sep 2003	Feb 2004	May 2004	
Pacific halibut	387	704	480	44	72	66	0.264
Sablefish	228	102	30	72	41	12	<0.001
Pacific cod	92	219	220	36	88	92	0.001
Arrowtooth flounder	73	16	28	27	7	15	0.012
Sandpaper skate	25	31	23	6	9	6	0.570
Other	34	85	28	15	35	15	0.002
Total	839	1157	809	200	252	206	0.227

galeatus, Pacific cod and dusky rockfish *Sebastes ciliatus*. More fish were captured by jigging in summer (266 fish representing 14 species) than in winter (97 fish representing 13 species). Fish captured by seining mostly were juveniles and were smaller (median size of pollock, Pacific herring, salmon, Pacific sand lance and Pacific cod was ≤80 mm) than those captured by jigging (median size of sculpin, flatfish, Pacific cod, rockfish and greenling was ≥249 mm). Species commonly observed with the ROV were juvenile gadids, Pacific sand lance, dusky rockfish and snake pricklebacks *Lumpenus sagitta*. Mean depth of observation and length of fish observed with the ROV were 43 m and 290 mm FL, respectively.

Seasonal abundance and diet in relation to prey availability

The pelagic species, pollock, herring and hake, were eaten frequently by Steller sea lions. Salmon and certain demersal prey, such as arrowtooth flounder, skates and Pacific cod, were also important in terms of biomass and energetic contribution to the diet, mainly due to their larger sizes. All of the targeted demersal prey were moderately sized and were typically found in shallow to intermediate depths. Small (<8 cm) nearshore species appear to have been ignored.

Pelagic habitat

Pollock, herring and hake generally were selected in Steller sea lion diet in proportion to their abundance in the environment. The overall odds ratio was close to zero, suggesting no general selection or avoidance of pollock, herring or hake for all seasons combined (Table 5). Pollock occurrence in the diet remained high throughout the yr (>90%) (Fig. 2). Pollock was positively selected (odds ratio > 0.5) in 4 periods (December 2001 and 2002, March 2003 and 2004) that were characterized by reduced relative abundance of pollock (<70% of total pelagic prey abundance) and preferential consumption of abundant yr classes (see below). An odds ratio analysis comparing juvenile and adult pollock found that selection for adult pollock in 2001 shifted to selection for juvenile pollock by 2004. In addition, throughout the present study, adults were positively selected only in May and September.

The size of pollock eaten by Steller sea lions varied across collection periods, with YOY, juveniles and adults all consumed (mean ± SD = 25 ± 9 cm, range = 7 to 76 cm, n = 5821; ANOVA, F_{14} = 33.3, p < 0.001). Adult pollock occurred most frequently during the 1st survey yr, after which younger fish dominated, especially juveniles 20 to 34 cm in length (Fig. 2). YOY pollock that were 4 to 6 cm long dominated nearshore beach seine catches (>75%), but these small pollock

Table 5. *Merluccius productus*, *Clupea pallasi* and *Theragra chalcogramma*. Log$_{10}$ odds ratio values comparing 3 key pelagic species in Frederick Sound, SE Alaska, by yr and mo (first 3 rows labeled Pacific hake, Pacific herring and walleye pollock). Ratios were separately computed to compare juvenile and adult walleye pollock (fourth row labeled juvenile pollock). Positive values indicate apparent selection and negative values avoidance. Values exceeding 0.5 are in **bold**

Species	2001			2002			2003			2004		Overall
	May	Sep	Dec	May	Sep	Dec	Mar	May	Sep	Jan	Mar	
Pacific hake	0.2	0.4	−0.4	−0.2	0.2	−0.2	−0.3	−0.4	−0.4	**0.8**	−0.4	−0.1
Pacific herring	0.0	−0.2	**−1.0**	**0.9**	**0.6**	**−0.7**	**−0.7**	0.2	0.1	−0.1	**−0.5**	−0.1
Walleye pollock	−0.1	−0.3	**0.5**	−0.3	−0.4	**0.5**	**0.6**	0.1	0.1	−0.3	**0.6**	0.1
Juvenile pollock	**−1.1**	**−0.6**	0.2	**−1.1**	**−1.0**	0.3	0.1	**−0.7**	−0.3	**0.7**	**1.0**	−0.2

were never found in scat. Instead, sea lions began tar-geting small pollock 4 to 5 mo later during winter (December 2001, January 2004) when these small pol-lock had grown to ~10–12 cm, moved offshore and were detectable by acoustic surveys. Steller sea lions targeted abundant pollock yr classes, most obviously tracking the abundant 2001 yr class through multiple years (December 2001, December 2002, March 2003). Across the 3 yr study period, 3 other yr classes of pol-lock (2000, 2002 and 2003) were targeted (Fig. 3).

In contrast to pollock, the herring sizes consumed by Steller sea lions were very consistent (mean ± SD = 18 ± 3 cm, range = 5 to 34 cm, n = 1277) (Fig. 4). Despite significant statistical differences between collections (ANOVA, F_{14} = 9.8, p < 0.001), the mean size of herring found in scats varied by only 3 cm (from 16 to 19 cm), with fish 14 to 22 cm mostly selected. The nearshore beach seine surveys in July 2003 were dominated (>83%) by 4 to 6 cm herring, but again these small YOY fish were completely ignored by Steller sea lions.

Hake were the largest frequently consumed pelagic species taken by Steller sea lions (mean ± SD = 37 ± 7 cm, range = 9 to 63 cm, n = 532) and, like pollock, the size of hake in the diet differed between collections (ANOVA, F_{14} = 8.8, p < 0.001) (Fig. 4). No hake below 36 cm were found in trawls even though hake less than 20 cm were found in the diet. Overall, hake found in the diet were mainly confined to the smallest fish found in trawls.

A wide size range of salmon was eaten (mean ± SD = 31 ± 12 cm, range = 12 to 63 cm, n = 236) (Fig. 4). DNA analysis identified September 2001 samples primarily as pink salmon and secondarily as coho salmon, and December 2001 samples primarily as chinook salmon and secondarily as pink salmon (Tollit et al. 2008). Cephalopods in the diet ranged widely in size (mean = 141 ± 334 g, range = 1 to 4853 g, n = 299) and encom-passed both small squid and larger octopus. The small-est fish eaten by Steller sea lions were myctophids (mean = 8 ± 2 cm, range = 3 to 12 cm, n = 88) and north-ern smoothtongue (mean = 8 ± 1 cm, range = 7 to 10 cm, n = 29), which were similar to sizes in midwater trawl catches.

Energy density at <30 m water depth diminished during December and March, suggesting that pelagic species vacated shallow depths during winter (Fig. 5). Likewise, nearshore species abundance was signifi-cantly less during December compared to July. How-ever, our sampling focused primarily on daylight hours. Based on occasional qualitative (checking vessel depth sounder while anchored at night) and limited quantita-tive nighttime sampling, pelagic species moved shal-lower during nighttime (Fig. 6).

Demersal and nearshore habitats

Arrowtooth flounder, Pacific cod and skates, but not halibut or sablefish, were important dietary items, even though all 5 species were abundant demersal species (Table 4). Log-odds-ratio analysis was possible for September 2003 and for the combined period Feb-ruary and May 2004. In both periods, arrowtooth floun-der was strongly selected (O = +0.7 and +1.4, respec-tively), skates were selected in September (O = +1.4) but not February/May (O = +0.3) and cod dietary im-portance was proportional to abundance in the envi-ronment in September (O = 0) and February/May (O = +0.3). Halibut and sablefish were avoided. Pacific hali-but and sablefish were common longline-caught spe-cies, but just 2 large (~90 cm) halibut and no sablefish were found in scats. Steller sea lions selected small arrowtooth flounder. Most (81%) arrowtooth flounder (mean ± SD = 43 ± 9 cm, range = 15 to 73 cm, n = 370)
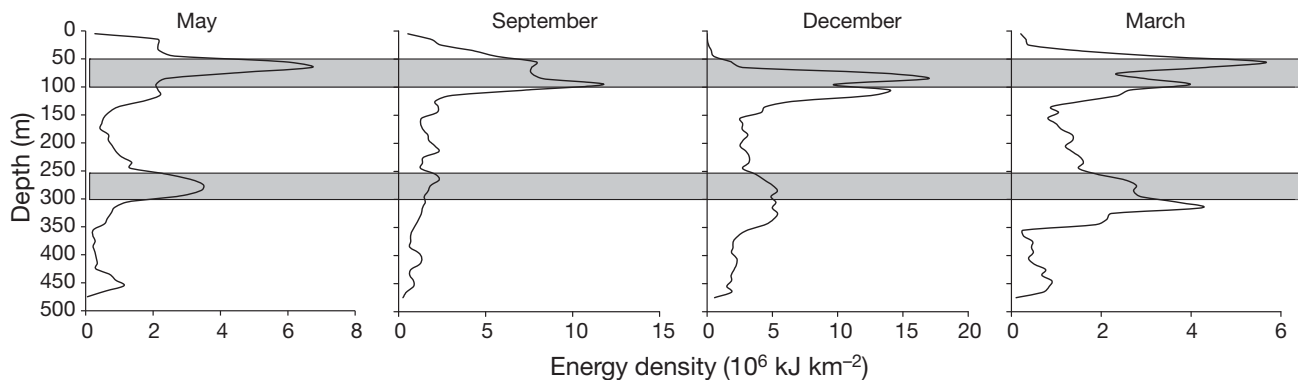

Fig. 5. *Theragra chalcogramma*, *Merluccius productus* and *Clupea pallasi*. Energy density (10^6 kJ km^{-2}) of pelagic species (wall-eye pollock, Pacific hake and Pacific herring) measured by acoustic surveys in Frederick Sound, SE Alaska, during daylight by depth interval (m) and season (May, September, December, March). Light gray shades highlight the bimodal depth distributions that run through all panels
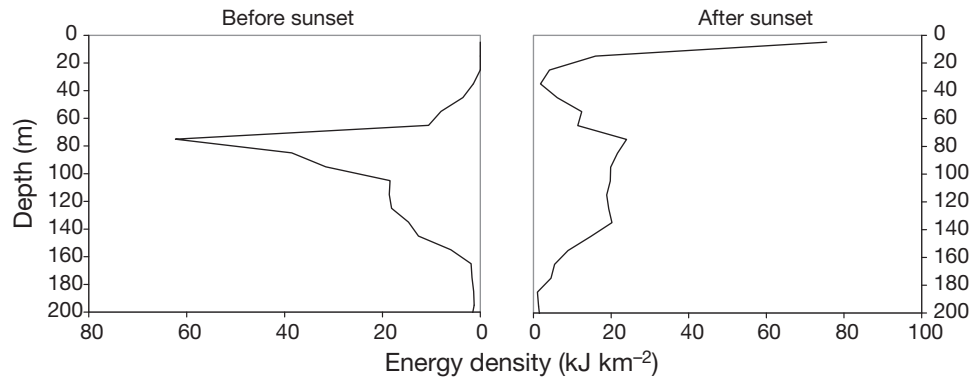
Fig. 6. *Theragra chalcogramma*, *Merluccius productus* and *Clupea pallasi*. Energy density (10^6 kJ km^{-2}) of pelagic species (walleye pollock, Pacific hake and Pacific herring) measured by acoustic surveys in Frederick Sound, SE Alaska, by depth interval (m) from 27 to 28 May 2001 during 4 h (18:00–21:00 h) before and 6 h (22:00–03:00 h) after sunset (21:44 h). Plots are shown as mirror images of each other (using sunset as the line that separates each half)

in scats were 35 to 60 cm in length, whereas most longline sizes were 50 to 75 cm (Fig. 4). Steller sea lions also selected small skates. Most (73%) skates (mean = 48 ± 19 cm, range = 23 to 111 cm, n = 235) were 35 to 50 cm in length, whereas most longline sizes were 55 to 75 cm. Pacific cod were shallower (average depth of 192 m based on longline surveys) than arrowtooth flounder (254 m), halibut (248 m) and sandpaper skate (260 m), which in turn were shallower than sablefish (305 m). Juvenile cod, but no other longline-caught species, were common in nearshore surveys (beach seines <5 m, jigging 5 to 115 m, ROV 1 to 85 m) (Thedinga et al. 2006).
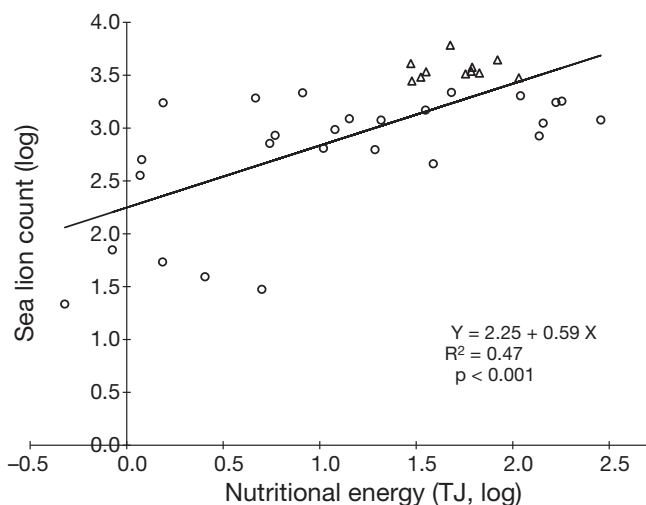

Fig. 7. *Theragra chalcogramma*, *Merluccius productus* and *Clupea pallasi*. Relationship between nutritional energy (TJ, log) of pelagic species (walleye pollock, Pacific hake and Pacific herring) and number (log) of Steller sea lions at 2 areas in SE Alaska: Frederick Sound (△) and Lynn Canal (○)

Rockfish and juvenile Pacific cod, but not small (<10 cm) pollock, herring or Pacific sand lance, were important dietary items, even though all 5 species were abundant nearshore species (Thedinga et al. 2006). Only larger sand lance and Cottidae were present in scats, even though summer beach seine survey catches were dominated by small pollock (4 to 6 cm) and herring (4 to 6 cm), with smaller catches of sand lance, chum salmon, Cottidae and small Pacific cod (<10 cm) (Fig. 4). Pacific cod present in scats encompassed jig and longline survey sizes and were larger than beach seine survey sizes. Rockfish present in scats encompassed jig survey sizes as well as larger fish. Rock sole present in scats were similar to jig survey sizes.

Steller sea lion numerical response

More sea lions were present when more prey was available, demonstrating a numerical response between Steller sea lion abundance and available nutritional energy. There was a significant relationship between log(number of sea lions) and log(nutritional energy of pelagic prey; in TJ) ($R^2 = 0.47$, $F_{1,35} = 30.9$, p < 0.001) (Fig. 7).

DISCUSSION

Diet choice and prey availability

Steller sea lions shifted diet composition in response to changes in prey availability of pollock, hake, herring and salmon. Steller sea lions switched from adult pollock at the start of the study period in 2001 and earlier

(1994 to 1999) (Tollit et al. 2004) to juvenile pollock from 2002 to 2004. They targeted 20 to 34 cm fish and tracked strong yr classes, most obviously the strong 2001 yr class through 3 yr (2001 to 2003, Figs. 2 & 3). Hake consumption expanded from sporadic low-level occurrences in summer and fall only (Trites et al. 2007, Tollit et al. 2008) to year-round (present study) as hake expanded northward during warm El Niño periods in the late 1990s (Ressler et al. 2007) and apparently remained in Frederick Sound (present study). Herring dietary occurrence peaked each yr in May–July (Fig. 2), coincident with herring spawning. Salmon dietary occurrence (September, Fig. 2) and Steller sea lion counts at terrestrial sites (~2000 sea lions, August or September, Table 1) peaked each yr coincident with the run-timing of spawning pink salmon.

Steller sea lions preyed upon the most abundant pelagic prey but ignored some species in demersal and nearshore habitats. In Frederick Sound, pollock were the most abundant pelagic species and were a dietary staple year-round, occurring in 95% of scats and contributing $\frac{1}{3}$ of the diet in terms of energy (Table 2). Hake and herring were on average 5- and 8-fold less abundant than pollock (Table 3) and occurred less frequently in sea lion diets, resulting in biomass contributions that in both cases were ~7-fold less than that of pollock (Table 2). Two demersal species, halibut and sablefish, were ignored, possibly because both are strong swimmers. Additionally, halibut were large (average 8.5 kg) and sablefish were deep (average 305 m). Steller sea lions tended to select intermediate-sized fish and avoid small (<10 cm) and large (>60 cm) fish. Halibut dominated the demersal species abundance, whereas the smaller arrowtooth flounder and skate (average 2.3 and 3.8 kg, respectively) were less common. However, the 2 smaller demersal species were energetically important in sea lion diet (arrowtooth flounder EC = 17%, skate EC = 12%), whereas halibut was strongly avoided.

Small fish, typically in nearshore areas, were also ignored despite periodic abundance. Very few small (<8 cm) fish were found in scats, even when YOY pollock were abundant in summer 2001 (mean catch per beach seine haul = 5878) (Thedinga et al. 2006). Instead, YOY pollock were consumed by sea lions in winter when the fish were larger (10 to 12 cm) and in deeper water. This pattern is not due to Steller sea lions avoiding nearshore areas, as individually tracked juvenile Steller sea lions in SE Alaska preferentially traveled nearshore and minimized the length of open water crossings (B. Wilson & M. A. Lea pers. comm.). Although accessible, the capture cost for many small fish is likely higher than the equivalent biomass of a few large fish.

Steller sea lions sometimes selected less nutritious fish if located nearby their haulouts. Port Houghton forms a main bay with a distinct arm at the back of the main bay (Fig. 1). An occasionally used haulout, Walter Island, is centrally located in the main bay about 9 km away from the arm and is the only known haulout in Port Houghton. In December 2002, the main bay contained 1200 t of pollock, while the arm contained 600 t of herring and 80 t of pollock. During daylight, pollock in the main bay (80 to 130 m) were shallower than herring in the arm (120 to 160 m) and both species were closer to the surface at night. All scats from Walter Island contained pollock and one-quarter also contained herring. The common occurrence of pollock in scats at Walter Island indicates that: (1) even though herring energy density is about 80% greater than pollock (Vollenweider et al. 2006), pollock are worth preying upon; and (2) even when herring are preyed upon, pollock are not avoided. The frequent occurrence of herring in these scats indicates that sea lions periodically chose to travel farther to obtain energy-rich forage fish. Availability also was important for prey selection by harbor seals, which adopted a pelagic foraging strategy when clupeid prey was abundant and switched to a demersal foraging strategy when clupeid abundance was low (Tollit et al. 1997a). Likewise, Steller sea lions in Prince William Sound, Alaska, preyed upon herring when they were less abundant but more accessible than pollock (Thomas & Thorne 2001).

Prey predictability also affects prey selection by Steller sea lions. Herring in Frederick Sound appear less predictable compared to other areas such as Lynn Canal, where herring is far more frequent in sea lion diets (90% FO in Lynn Canal vs. 33% in Frederick Sound). Herring appeared irregularly in satellite bays of Frederick Sound and were abundant in as few as one and as many as 4 bays in a sampling period. In contrast, large, predictable herring schools were present November through February in Lynn Canal (Womble & Sigler 2006, Sigler & Csepp 2007), and their persistence was an important characteristic in determining whether foraging Steller sea lions utilized them (Gende & Sigler 2006).

Juvenile Steller sea lion dive patterns followed seasonal shifts in prey depth distribution. During the day, prey were less abundant at depths <50 m during winter than summer for both pelagic (Fig. 5) and nearshore (Thedinga et al. 2006) species. Individuals reached greater depths during December (maximum daily depth = 99 m) than May–July (85 m). Juvenile Steller sea lions are capable of diving deeper than these depths; their deepest dives reached 200 m by 1 yr of age and exceeded 400 m by 3 yr of age (Pitcher et al. 2005).

Diet diversity in Frederick Sound generally was similar in summer and higher in winter than that found in

several other regions of Alaska. In Frederick Sound, species diversity in Steller sea lion diets peaked in autumn and early spring, reflecting increased contributions from arrowtooth flounder, salmon, hake and Pacific cod. The values were similar to diversity indices calculated using scats collected at other haulouts in SE Alaska (September–May, Frederick Sound = 3.6 vs. other haulouts in southeast Alaska = 4.1), but were lower than the diverse diets at coastal rookeries in southeast Alaska (June–July, Frederick Sound = 2.9 vs. southeast Alaska rookeries = 5.3) (Trites et al. 2007). Prey family diversity in Steller sea lion diets during summer in Frederick Sound (May–September, 2.3) was similar to that in the eastern Aleutians (2.0) and western Gulf of Alaska (2.1) (Sinclair & Zeppelin 2002) and higher than that in the central Gulf of Alaska (1.7) and central and western Aleutians (1.5) (Sinclair & Zeppelin 2002). In winter, prey family diversity in Frederick Sound (October–April, 2.6) was higher than that in the eastern Aleutians and western and central Gulf of Alaska (1.8 to 2.1) and in the central and western Aleutians (1.9) (Sinclair & Zeppelin 2002).

Steller sea lions exhibit a flexible foraging strategy. Their diet composition shifts from a simpler diet dominated by Atka mackerel in the western and central Aleutian Islands to more complex diets with multiple important species (FO > ~35%) in the eastern Aleutian Islands, Gulf of Alaska and SE Alaska (Sinclair & Zeppelin 2002, Trites et al. 2007) (Fig. 2). Salmon and pollock were important in the eastern Aleutian Islands and western Gulf of Alaska, while salmon, pollock, forage fish and arrowtooth flounder were dominant in the central Gulf of Alaska, and salmon, pollock and forage fish occurred most frequently in SE Alaska (Table 2) (Sinclair & Zeppelin 2002, Trites et al. 2007, McKenzie & Wynne 2008).

A flexible foraging strategy confers several advantages. Steller sea lions may take advantage of seasonal prey aggregations that presumably are easier to capture due to high prey density and choose prey with higher energy content (Sinclair & Zeppelin 2002). This strategy buffers Steller sea lions against seasonally varying energetic requirements which vary across seasons due to the demands of pregnancy, lactation and fasting during the breeding period (Winship et al. 2002). For example, energy intake by captive California sea lions *Zalophus californianus* during lactation and immediately post-lactation (August–February) was nearly 4× maintenance levels (Williams et al. 2007). A flexible foraging strategy also buffers Steller sea lions against variation in ocean productivity which varies on decadal (Francis et al. 1998) and longer time scales (Baumgartner et al. 1992) and can affect prey composition and abundance (Anderson & Piatt 1999). California sea lions exhibit annual diet changes corresponding to large-scale ocean climate shifts (Weise and Harvey 2008), similar to the entrance of hake into the diet of Steller sea lions in Frederick Sound. Several life history strategies including longevity, parental investment in offspring, fasting capability (Iverson et al. 2007) and reproductive failure during late gestation (Pitcher et al. 1998) buffer Steller sea lions against variation in ocean productivity. These traits likely help individual Steller sea lions survive periods of reduced prey abundance or quality and, at the population level, dampen swings in Steller sea lion abundance.

Shifts among seasonally available prey

Steller sea lions move between areas as prey becomes available seasonally. Steller sea lions were present in Frederick Sound year-round, whereas they were found in Lynn Canal primarily from November to March (Womble & Sigler 2006) and in Berners Bay only during April and May (Gende et al. 2001, Marston et al. 2002, Sigler et al. 2004). These seasonal changes in location appear related to seasonal differences in prey availability. In Frederick Sound, prey was abundant (e.g. average pelagic fish biomass was 5× higher than the monthly consumption estimate) and pollock and hake were common (Table 3) year-round. In contrast, herring were concentrated in Lynn Canal only during November to April (Sigler & Csepp 2007) and eulachon were concentrated in Berners Bay only during April and May (Marston et al. 2002, Sigler et al. 2004). Diet studies imply that the western population of Steller sea lions also follows strong seasonal patterns in consumption of most species of prey (Sinclair & Zeppelin 2002, Sinclair et al. 2005).

Steller sea lions move from place to place as part of an annual foraging strategy in SE Alaska to forage on herring aggregations in winter, fish spawning aggregations in spring, salmon in summer and fall (depending on species) and pollock and Pacific hake throughout the yr. First described in an analysis of aerial survey data on 28 haulouts in southeast Alaska (Womble et al. 2009), this strategy also is supported by aerial survey, prey and diet data from this study (salmon available in fall, pollock and Pacific hake year-round) and the companion studies in Lynn Canal (herring aggregations in winter) (Womble & Sigler 2006) and Berners Bay (fish spawning aggregations in spring) (Sigler et al. 2004). Moving between areas of seasonal concentrations of high quality prey (multiple central place foraging) also confers the advantage of reducing overall travel costs and providing access to a larger foraging area (Chapman et al. 1989) if prey quantity in one area is insufficient due to depletion or seasonality.

Numerical response

The number of Steller sea lions present depended on the amount of prey available (Fig. 7). This relationship reasonably estimates the nutritional energy necessary to attract and sustain Steller sea lions because the eastern population has grown since the 1970s (Pitcher et al. 2007), which implies nutritional requirements were met. The estimated numerical response implies that 0.3 TJ are sufficient nutritional energy for 100 sea lions, 5 TJ for 500 sea lions and 20 TJ for 1000 sea lions. Translating to biomass and applying the range of energy densities measured in the present study (3 to 10 kJ g^{-1}), the relationship implies that 500 to 1700 t of prey are needed near a terrestrial location where 500 sea lions haul out, depending on the species composition of the prey. 'Near' is loosely defined as the radius of our study area, which was 20 km. These prey amounts far exceed energetic requirements of individual Steller sea lions. For example, assuming a daily ration of 79 464 kJ per sea lion (Sigler et al. 2004), 5 TJ for 500 sea lions provides about 63 000 daily rations. Steller sea lions may require rich foraging locations to thrive, or Frederick Sound may be the most attractive among competing rich foraging locations. The numerical response is nonlinear; more energy per sea lion is necessary to attract many sea lions than few sea lions (0.003, 0.011 and 0.2 TJ per individual for 100, 500 and 1000 sea lions, respectively), and may indicate that foraging costs are density-dependent. Steller sea lion foraging may disrupt fish schools, thus reducing captures in successive foraging bouts. Steller sea lions foraged alone or in small groups (≤20 individuals) in Frederick Sound, though they sometimes cooperatively foraged in large groups of 10s to 100s of individuals for eulachon in Berners Bay (Gende et al. 2001, Sigler et al. 2004).

Nutrition and diet diversity

A diet dominated by less nutritious prey (e.g. gadids such as pollock) was proposed to have caused nutritional stress and contributed to the decline of the western stock of Steller sea lions (Alverson 1992, Trites & Donnelly 2003). In contrast, eastern stock abundance has increased by about 3 % yr^{-1} since the 1970s (Pitcher et al. 2007), yet pollock occurred at higher frequency in Steller sea lion scats in inside waters of SE Alaska, including Frederick Sound, Stephens Passage and Lynn Canal (Table 2) (Womble & Sigler 2006, Trites et al. 2007), than in the coastal rookeries of SE Alaska (~60 %, Trites et al. 2007), the central (~40 to 60 %) and western (~80 %) Gulf of Alaska and eastern (~60 %), central and western (~10 %) Aleutians (Sin-

clair & Zeppelin 2002, McKenzie & Wynne 2008). Pollock comprised 34 % of the energetic contribution and 39 % of the biomass contribution in Frederick Sound, approaching the 45 % biomass contribution of pollock to Steller sea lions in the Kodiak area after sea lion abundance began to decline there (Atkinson et al. 2008a). Together, gadid species contributed 50 % of the biomass and 44 % of the energetic contribution in Frederick Sound. Pollock also may be selected when more nutritious herring are nearby (e.g. Port Houghton) and can commonly occur with herring (~90 %) in sea lion diets, even when herring are more abundant than pollock in an area (Womble & Sigler 2006). Obtaining a healthy diet that is dominated by less nutritious prey likely depends on including a proportion of nutritious prey, as sea lions sometimes traveled farther to obtain herring even when pollock were plentiful nearby (e.g. Port Houghton). These observations imply that a diet with substantial year-round contributions from less nutritious but abundant prey, such as pollock, can form part of a healthy diet as long as more nutritious prey such as herring, salmon or eulachon also are consumed, as in SE Alaska.

The diverse diet (salmon, pollock and forage fish), abundant quantity and presence of some high quality prey (salmon, herring and eulachon) likely sustains the increasing population in SE Alaska. Nearly $\frac{1}{3}$ of all scats collected contained only pollock, but the remainder contained other prey such as herring and arrowtooth flounder, implying sea lions have a flexible foraging strategy, even at the trip level. Seasonal switches to salmon, hake and skate also support the flexible foraging strategy with little direct selection evident beyond accessible prey and fairly broad prey size preferences. Pollock's importance may lie in its steady availability that provides a food source that is always available in case seasonal aggregations show up weak or not at all.

Our study supports the conclusion that a flexible foraging strategy and diverse diet help marine predators compensate for less nutritious prey. Animal species with limited ability to carry food loads back to their young and energetically expensive foraging behavior likely are particularly sensitive to food quality (Österblom et al. 2008). Less nutritious prey and a focus on 1 or 2 prey species led to reproductive failure in the common guillemot *Uria aalge* (Wanless et al. 2005, Österblom et al. 2006). Black-legged kittiwakes *Rissa tridactyla* compensated for food shortages during nesting by increased parental investment, while thick-billed murres *Uria lomvia* did not and chick growth decreased (Kitaysky et al. 2000). In contrast, seal and sea lion species chose the most abundant prey within a suite of preferred species (Thompson et al. 1991, Bowen & Harrison 1994, Tollit et al. 1997a) and switched prey when prey abundance changed (Bailey

& Ainley 1982, Sinclair et al. 1994, Tollit et al. 1997a, Weise and Harvey 2008). We found that Steller sea lions switch prey in response to changes in prey abundance, move to take advantage of seasonally available prey and can rely on less nutritious species as long as more nutritious prey are also consumed.

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