Prey competition between sympatric Steller sea lions (*Eumetopias jubatus*) and northern fur seals (*Callorhinus ursinus*) on Lovushki Island, Russia

J.N. Waite, V.N. Burkanov, and R.D. Andrews

Abstract: Approximately 1 000 Steller sea lions (*Eumetopias jubatus* (Schreber, 1776); SSL) and 14 000 northern fur seals (*Callorhinus ursinus* (L., 1758); NFS) breed sympatrically on Lovushki Island in the Russian Far East, creating the potential for interspecific competition for prey. An additional 13 000 – 14 000 juvenile NFS are present during the breeding season. The diets of breeding SSL and both breeding and juvenile NFS were examined through analysis of scats and spews collected during the breeding seasons of 2003, 2005, and 2007–2008. There were significant overlaps in the prey species and size selection of SSL and juvenile NFS. There were significant differences between the diets of SSL and breeding NFS. SSL and juvenile NFS fed primarily on Atka mackerel (*Pleurogrammus monopterygius* (Pallas, 1810)), while breeding NFS fed on cephalopods, salmon (genus *Oncorhynchus* Suckley, 1861), Atka mackerel, and northern smoothtongue (*Leuroglossus schmidti* Rass, 1955). The partitioning of resources between breeding animals has allowed both species to coexist within the same region and likely reflected differences in foraging abilities and provisioning strategies of the adults and the fasting abilities of their pups. However, continued growth of the NFS population may lead to the exclusion of SSL owing to interspecific competition for prey.

Résumé : Environ 1 000 lions de mer de Steller (*Eumetopias jubatus* (Schreber, 1776); SSL) et 14 000 otaries à fourrure du Nord (*Callorhinus ursinus* (L., 1758); NFS) se reproduisent en sympatrie sur l'île Lovushki dans l'Extrême-Orient russe, créant une situation potentielle de compétition pour les proies. De plus, 13 000 – 14 000 jeunes NFS sont aussi présents durant la saison de reproduction. Nous avons déterminé le régime alimentaire des SSL en reproduction et des NFS reproducteurs et jeunes par l'examen des défécations et des vomissements récoltés durant les saisons de reproduction de 2003, 2005 et 2007–2008. Il y a des chevauchements significatifs dans la sélection des espèces et des tailles de proies par les SSL et les jeunes NFS. Il existe des différences significatives de régime alimentaire entre les SSL et les NFS en reproduction. Les SSL et les jeunes NFS se nourrissent surtout de maquereaux d'Atka (*Pleurogrammus monopterygius* (Pallas, 1810)), alors que les NFS en reproduction s'alimentent de céphalopodes, de saumons (genre *Oncorhynchus* Suckley, 1861), de maquereaux d'Atka et de leuroglosses luisants (*Leuroglossus schmidti* Rass, 1955). Le partage des ressources entre les animaux reproducteurs permet aux deux espèces de cohabiter dans la même région et reflètent vraisemblablement des différences dans les habiletés de recherche de nourriture et les stratégies d'approvisionnement des adultes et les capacités de leurs petits à jeûner. Cependant, une croissance continue de la population de NFS pourrait mener à l'exclusion de SSL à cause de la compétition interspécifique pour les proies.

[Traduit par la Rédaction]

Introduction

The competitive exclusion principle postulated by Gause (1934) maintains that one of two non-interbreeding species occupying the same ecological niche and the same geographical territory will be displaced if population growth is not the same between species. Therefore, competition will result in the absolute exclusion of one of the species unless this species is able to modify how it exploits the available resources.

Many species of marine mammals successfully coexist through spatial or temporal partitioning of foraging grounds (González-Solís et al. 2000; Kronfeld-Schor and Dayan 2003; Bailleul et al. 2005; Friedlaender et al. 2009), segregation of prey species (Page et al. 2005; Sivertsen et al. 2006; Cooper et al. 2009) or prey size consumed (Wathne et al. 2000), or through differences in lactation timing and duration (Robinson et al. 2002). These strategies are also employed to

doi:10.1139/Z11-117

reduce intraspecific competition among age, sex, and reproductive classes (Field et al. 2005; Page et al. 2005).

Steller sea lions (*Eumetopias jubatus* (Schreber, 1776); SSL) breed sympatrically with northern fur seals (*Callorhinus ursinus* (L., 1758); NFS) on four rookeries in the Russian Far East: Medny Island (54.8667°N, 167.3667°E) in the Commander Island group, Srednego (47.5797°N, 152.9083°E) and Lovushki (48.5436°N, 153.6736°E) islands in the Kuril Island chain, and Tyuleny Island (48.5°N, 144.6334°E) in the western Sea of Okhotsk (Fig. 1). Approximately 46% of the total SSL breeding population and approximately 43% of the total SSL pup production in Russian waters occurs on these rookeries (Burkanov and Loughlin 2005). SSL and NFS are both piscivorous, sexually dimorphic pinnipeds with similar ecological requirements and life-history traits. Mass of adult male SSL is up to 1120 kg and females to 350 kg (Loughlin et al. 1987), whereas the mass of adult male NFS is up to 320 kg and females to 71 kg (Scheffer and Wilke 1953). With overlapping breeding periods (May–August), the adults of both species become highly territorial and males vigorously defend harems of breeding females. With a 2–3 month overlap in pup nursing, foraging also becomes competitive because adult females of both species are central place foragers, alternating between periods of foraging at sea and nursing their pups on land (Mathisen et al. 1962; Pitcher and Calkins 1981; Gentry and Kooyman 1986; Gentry 2002).

Ship-based surveys conducted between 2002 and 2005 estimated a range-wide SSL population of 62 000 – 74 000 animals (Burkanov and Loughlin 2005; Pitcher et al. 2007) with approximately 16 000 (22%–25%) located along the coastal waters of Russia and northern Japan (Burkanov and Loughlin 2005). Similarly to the Western SSL stock in Alaska, the Asian stock of SSL experienced a dramatic decline and has been unstable for the past 4 decades (Loughlin et al. 1992; Burkanov and Loughlin 2005). On Lovushki Island, the abundance of nonpup SSL dropped from approximately 4000 in 1955 to approximately 760 by 1989 (Burkanov and Loughlin 2005). After a slight increase, the population has remained relatively stable at 1039 ± 49 SSL (mean ± SE) from 1995 through 2005 (Burkanov and Loughlin 2005). Though the cause for the decline has not yet been determined, one hypothesis for the decrease in North American waters is nutritional stress or food limitation as a result of changes in the quantity and (or) quality of certain prey items (Calkins and Goodwin 1988; NMFS 1995; DeMaster and Atkinson 2002; Trites and Donnelly 2003).

Prior to eradication owing to unregulated harvesting in the late 19th century, the nonpup population of NFS in the Kuril Islands was at least 15 000 (Snow 1897). A slow re-establishment of breeding colonies occurred in the early 20th century, and surveys conducted in 1955–1956 counted approximately 2000 fur seals on Lovushki Island and an additional 800–900 on Srednego Island (Klumov 1957). The nonpup population in this region continued to grow at 19.9% per year until 1978 and then remained relatively stable at 8063 ± 379 (mean ± SD) for the next decade (Kuzin 1999). A rapid increase in NFS population numbers ensued during the early 21st century with pup counts on Lovushki Island increasing to approximately 12 180 pups by 2006 (Burkanov et al. 2007). Using a method of estimating total abundance

wherein pups are considered to be a mean of 30% of the total population (Kuzin 1999), the total nonpup NFS population in 2006 on Lovushki Island alone was estimated at 28 420.

Historic data on the diet of SSL and NFS in Russian waters is sparse. Based on analyses of stomach contents, the diets of NFS and SSL on their allopatric sites in the Kuril Islands were similar in the 1950s and 1960s (Panina 1964, 1966; Belkin 1966; Kuzin et al. 1977), with walleye pollock (*Theragra chalcogramma* (Pallas, 1814)) accounting for the majority of the NFS and SSL diet. Rockfish (genus *Sebastes* Cuvier, 1829), Okhotsk Atka mackerel (*Pleurogrammus azonus* Jordan and Metz, 1913), Pacific sand lance (*Ammodytes hexapterus* Pallas, 1814), and cephalopods (class Cephalopoda) were also predominant (Belkin 1966). Kuzin et al. (1977) described a partitioning of diet between the two pinniped species in the early 1970s on sympatric rookeries in the Kuril Islands: the frequency of occurrence of prey remains recovered from stomachs of NFS was 75.8% Commander squid (*Berryteuthis magister* (Berry, 1913)), 27.6% Japanese flying squid (*Todarodes pacificus* (Steenstrup, 1880)), and 3.4% walleye pollock, whereas stomachs of SSL contained 70.7% walleye pollock, 26.8% Octopoda (Leach, 1818), 31.7% Commander squid, 12.1% Japanese flying squid, and 7.3% Hexagrammidae. During this period, the population of NFS was relatively low and outnumbered SSL at less than 2.5:1 (Kuzin et al. 1977), compared with the 28:1 ratio in 2006.

The North Pacific and Bering Sea experienced oceanographic regime shifts in 1976–1977 and 1989 that resulted in marked changes in the abundance and distribution of the primary prey of both SSL and NFS (Anderson and Piatt 1999; Benson and Trites 2002; Conners et al. 2002). Waite and Burkanov (2006) presented the most recent data on SSL prey selection on allopatric sites throughout the majority of their Russian range and suggested that while pollock had been one of the major prey items, it had been replaced by salmon and Atka mackerel (*Pleurogrammus monopterygius* (Pallas, 1810)) as the dominant prey items of SSL on rookeries in the Kuril Islands.

Recent studies on NFS diet in Russian waters are extremely limited. However, data from other regions of the northern Pacific Ocean indicate some dietary overlap between the two species. Stomachs from juvenile and adult NFS captured off the Pacific coast of northern Japan in 1997–1998 contained primarily squid, smelt, Japanese anchovy (*Engraulis japonicas* Temminck and Schlegel, 1846), headlightfish (genus *Diaphus* Eigenmann and Eigenmann, 1890), and lampfish (family Myctophidae) (Yonezaki et al. 2003). Prey items found in SSL scats collected on haul-outs in the southern Kuril Islands near Japan were similar, consisting of large numbers of Japanese anchovy, gadids (family Gadidae), and squid (Waite and Burkanov 2006). Walleye pollock and Atka mackerel were important prey items for both NFS and SSL in the Aleutian and Pribilof islands from 1981 to 2005 (Sinclair et al. 1994; Merrick et al. 1997; Zeppelin and Ream 2006; McKenzie and Wynne 2008).

Antonelis et al. (1997) found that NFS on Medny Island in 1988 consumed primarily squid and relatively little Atka mackerel, while Waite and Burkanov (2006) found that SSL on Medny Island in 2001 consumed exclusively Atka mack-

Fig. 1. Location of study site.
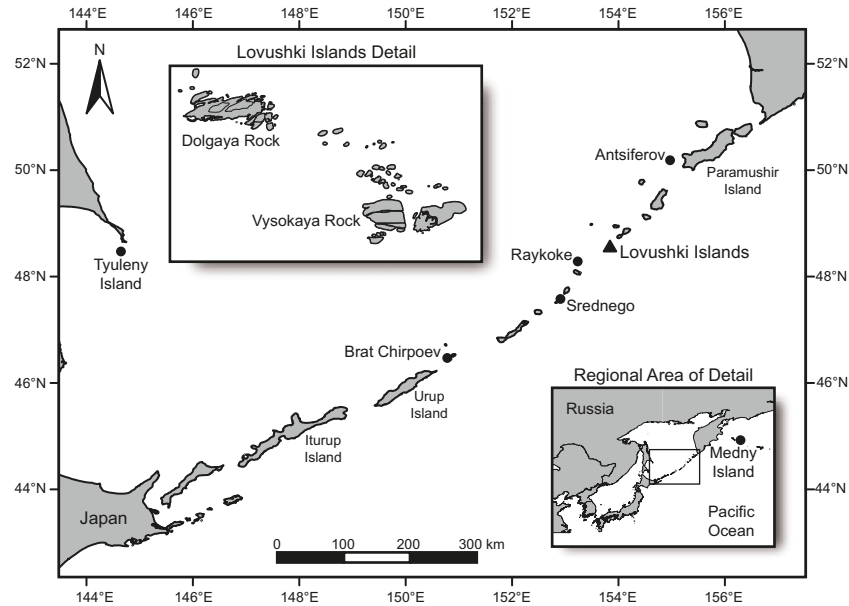
erel ($n = 12$). There are no known published studies containing recent data on SSL or NFS diets on the remaining three sympatric rookeries, primarily owing to difficulties in distinguishing between the scats of the two species. Therefore, very little is known regarding prey selection trends, diet diversity, or level of competition for prey resources with commercial fisheries over the last several decades for a substantial portion of the SSL and NFS population. With NFS outnumbering SSL by an order of magnitude on Lovushki Island, we hypothesized that interspecific competition for prey resources might be limiting the recovery of the SSL population. Similar life-history traits and ecological requirements, along with recent growth in the NFS population, suggest the potential for elevated interspecific competition. Therefore, we combined the identification of predator scat using fecal DNA and the analysis of undigested prey remains to examine the use of prey resources by SSL and NFS on Lovushki Island and to assess the potential for interspecific competition for prey.

Materials and methods

Sample collection and processing

During the breeding seasons (June through August) of 2003, 2005, 2007, and 2008, we collected a total of 495 scats and 44 spews from SSL and NFS on both the breeding and nonbreeding portions of the rookery at Lovushki Island. We obtained an additional six fecal samples via enema (Yonezaki et al. 2004), five fecal samples via normal defecation, and two stomach content samples via gastric lavage (Antonelis et al. 1987) from breeding female fur seals while they were immobilized by isoflurane anesthesia (Heath et al. 1996) during concurrent research projects.

Scat and spew (regurgitate) samples were collected opportunistically when the rookery was disturbed for concurrent research projects. On the most densely populated portions of the rookery, breeding SSL segregate into groups, which were usually surrounded by groups of breeding NFS. These areas

were visually monitored by field observers present on the rookery for the duration of the breeding season. Only fresh scats were collected in these areas to maximize the likelihood that we could positively identify which species had deposited the fecal samples. Because the boundaries of these groups were plastic, scats collected near the edges were subsampled for genetic analysis to verify pinniped species ($n = 51$). In locations where significant species mixing occurred, each scat was subsampled for genetic analysis before removal from the substrate ($n = 63$). Samples collected in these areas were considered to be from breeding animals. The remainder of the samples collected from nonbreeding portions of the rookery and outlying rocks inhabited exclusively by NFS were considered to be from nonbreeding, juvenile NFS. All scat and spew samples collected from breeding portions of the rookery were assumed to be from females.

The genetic subsamples were collected and stored according to Murphy et al. (2002), wherein 1–2 mL of fecal material per scat was collected, placed in 95% ethanol at a 4:1 (ethanol:feces) ratio by volume, and stored either at room temperature or at –80 °C. Fecal genetic samples were analyzed to determine the species of origin by the University of Idaho (Moscow, Idaho, USA) according to Waite et al. (2011).

Each scat was placed in a separate plastic bag and processed onboard a support vessel. The plastic bags were filled with water and a mild detergent and allowed to soak for 24–48 h while being agitated by the movement of the vessel. The resulting slurry was rinsed through a series of three nested mesh sieves (1.0 mm, 710 μm, and 500 μm). Solid fecal material was gently manipulated with a soft brush and rinsed with water until it passed through the sieves (Treacy and Crawford 1981).

Prey species were enumerated and identified to the lowest possible taxonomic group by Pacific Identifications, Inc. (Victoria, British Columbia, Canada) from the dried hard parts. All identifiable skeletal structures (instead of only otoliths) were used to reduce the problems associated with dif-

ferential digestion of smaller or more delicate prey items (Browne et al. 2002; Tollit et al. 2006). The minimum number of individuals (MNI) consumed for each prey type was estimated by counting a variety of key diagnostic structures. Prey size was estimated and grouped into species-specific size categories based on an extensive reference collection of skeletal remains.

Statistical analysis

For general diet descriptions, data from scats and spews were pooled to accurately assess frequency of occurrence, prey size, and total number of prey. Pooling scat and spew data also reduces the biases associated with analyzing scat or spew separately (Page et al. 2005; Gudmundson et al. 2006), as spews often contain prey remains too large to pass through the pyloric sphincter and increased numbers of cephalopod beaks that had accumulated in the folds of the stomach lining (Jobling and Breiby 1986; Harvey and Antonelis 1994). For comparisons between scats and spews, enema samples were grouped with scats and stomach samples were grouped with spews. The relative importance of each prey type was calculated using (1) simple frequency of occurrence (FO):

$$[1] \qquad \text{FO}_i = \left(\frac{n_i}{n_t}\right) \times 100$$

where n_i is the number of samples containing prey type i and n_t is the total number of samples examined, and (2) percent numerical abundance (NA), a measure of dominance:

$$[2] \qquad \text{NA}_i = \left(\frac{\text{MNI}_i}{\text{MNI}_t}\right) \times 100$$

where MNI_i is the minimum number of individuals of prey type i consumed and MNI_t is the minimum number of all prey items consumed. NA_i was calculated for spew and scat samples combined and for scat samples only (NA_i^s). An adjusted MNI_i (MNI) was calculated for each prey type by applying numerical correction factors (NCF) published for Steller sea lions (Tollit et al. 2007) to scat samples to account for species-specific differences in complete prey digestion. Adjusted NA_i values (NA_i^*) and 95% confidence intervals were computed. There are no current published prey-specific correction factors developed for NFS using multiple prey elements.

The proportion of total biomass consumed contributed by each major prey species consumed (BM) was estimated for each predator group using a variable biomass reconstruction index (Joy et al. 2006). Lengths of individual Atka mackerel, pollock, and salmon were estimated using the mean length for each species grouped into species-specific size categories. Mean squid length was estimated from data on stomach contents of NFS caught in the western North Pacific (Mori et al. 2001) and mean northern smoothtongue length was estimated from trawl data collected along the Kuril Island Chain and Kamchatka Peninsula (Nagasawa et al. 1996). Prey length to mass predictive equations for Atka mackerel, walleye pollock (Orlov and Binohlan 2009), pink salmon (*Oncorhynchus gorbuscha* (Walbaum, 1792); Erokhin 1990), and northern smoothtongue (Orlov and Binohlan 2009), and dorsal mantle length to total mass for boreopacific gonate squid (Kubodera 1986) were selected from studies that took place as close to

Lovushki Island as possible. Pink salmon was selected as the representative salmon species because they have historically been the most abundant of the salmon species in the region (Temnykh and Marchenko 2002) and were repeatedly observed being consumed by both SSL and NFS during the study.

Binary logistic regression models were used to determine if the occurrence of prey varied by predator species, reproductive group, or sample type. The presence or absence of each prey type was modeled as a binary response variable with species-reproductive group (breeding SSL, breeding NFS, and juvenile NFS), sample type (scat or spew), and the interaction between group and sample type as explanatory variables. If a significant interaction term was added to the model, sample types within each group were compared.

Fligner–Policello tests were performed to test for differences in number of prey species and MNI_i found in individual samples between scats and spews, predator species, and reproductive groups. The Fligner–Policello statistic tests for differences in central tendency among samples with unequal variances and was selected owing to its robustness concerning violations of the assumption of symmetrical distributions (Fligner and Policello 1981).

To quantify the dietary overlap among reproductive and species groups, we calculated Pianka's niche overlap index (O_{jk}) (Pianka 1973):

$$[3] \qquad O_{jk} = \frac{\displaystyle\sum_{i=1}^{m}(p_{ij} \times p_{ik})}{\sqrt{\displaystyle\sum_{i=1}^{m} p_{ij}^2 \times \sum_{i=1}^{m} p_{ik}^2}}$$

where p_{ij} and p_{ik} are the percent numerical abundance (NA) of the ith prey type for the predator groups j and k being compared. The index O_{jk} ranges from 0 to 1, where 0 indicates no dietary resource sharing between the two groups and 1 indicates a complete overlap in their diet. A value greater than 0.6 is considered to be a "biologically significant" overlap (Zaret and Rand 1971; Mathur 1977; Wallace 1981). The niche overlap index for each pair of groups was calculated based on NA_i, NA_i^s, and NA_i^*. Pearson's χ^2 contingency table analyses were performed to test for differences in the size of prey items consumed between predator groups with a biologically significant niche overlap index. When a contingency table contained a cell size of <5, p values were computed for a Monte Carlo test using 1000 replicates (Hope 1968). Contingency table tests were only performed for prey species that occurred in ≥5% of scats.

The diversity of the diet of each species and reproductive group was calculated using Shannon's index of diversity:

$$[4] \qquad H = -\sum_{i=1}^{k} p_i \ln p_i$$

where p_i is the numerical abundance of the ith prey type (NA_i) and k is the number of prey types.

Associations between prey types found in individual samples were examined by calculating Pearson partial correlation coefficients for each pair of prey types within each predator species and reproductive group. Partial correlation takes into

account the interactions of other prey types on the two species under consideration. Correlations between prey species were illustrated with a dendrogram produced through an agglomerative hierarchical cluster analysis. Clustering method was set to "average" and the distance between prey types was set to one minus the Pearson partial correlation coefficient of those two items (McGarigal et al. 2000).

Unless otherwise noted, all statistical analyses and calculation of indices were performed using five prey groups which consisted of species that occurred in ≥5% of all samples: Atka mackerel, salmon, walleye pollock, cephalopods, and northern smoothtongue. Scats that were without hard parts or remains that could not be identified to at least family level were not included in the analyses. Adequacy of sample size to describe diet across all years was verified by creating mean percent numerical abundance curves. Curves were created for each of the three predator species – age combinations by repeatedly resampling, with replacement, successively larger numbers of samples from the data and estimating the mean percent numerical abundance for each of the five major prey groups. In all cases, the variances stabilized and the curves reached an asymptote, verifying the adequacy of total sample size for each group. Sample size was considered to be insufficient to test for differences between years based on analyses by Trites and Joy (2005). Simple bootstrapping was used to estimate 95% confidence intervals (CI) around the overlap and diversity indices. Differences between the bootstrapped confidence intervals were calculated to test for differences in indices among groups. All values are reported as means ± SD unless otherwise indicated. Statistical analyses were performed using R version 2.9.2 (The R Foundation for Statistical Computing, Vienna, Austria) and SAS version 9.1 (SAS Institute Inc., Cary, North Carolina, USA).

All work was conducted under permits from the Russian regional permitting agency SakhalinVetSanNadzor and was approved by the Alaska SeaLife Center (ASLC) Institutional Animal Care and Use Committee (IACUC), approved protocol numbers 06-004 and 07-001. All biological samples were imported into the United States under National Marine Fisheries Service permit #881-1724 issued to the ASLC under the authority of the United States Marine Mammal Protection Act.

Results

Genetic analysis

Of the 114 fecal subsamples genetically analyzed to determine species, 28 were determined to be from fur seals and 76 from sea lions. A total of 10 samples could not be identified to species because of problematic DNA extractions or amplification failure and were not included in the analyses. Of the 51 scat samples that were collected near the boundary between groups of SSL and NFS, approximately 12% ($n = 6$) had been initially incorrectly identified in the field based on collection location before subsequent correct identification using molecular techniques, emphasizing the importance of genetic testing.

Fur seal diet

Of the 242 scats and 45 spews collected from NFS, 198 scats (81.8%) and 43 spews (95.5%) contained prey remains that could be minimally identified to the family level. No prey remains were found in 13 (5.4%) of the scats. The remaining scats (12.8%) and spews (4.5%) contained unidentifiable prey remains. A total of 21 different prey types were identified with 9 identified to species. Overall, the most common NFS prey items, in order of frequency of occurrence, were Atka mackerel (50.0%), salmon (37.6%), cephalopods (28.5%; primarily *Gonatopsis* sp. cf. *Gonatopsis borealis* Sasaki, 1923), walleye pollock (26.3%), and northern smoothtongue (17.5%). The most dominant prey items, in order of numerical abundance, were cephalopods (27.0%), northern smoothtongue (25.8%), Atka mackerel (19.2%), walleye pollock (12.6%), and salmon (8.7%) (Fig. 2, Table 1A).

Diet composition varied between reproductive groups. Salmon (FO = 43.4%, BM = 28.2%), cephalopods (FO = 41.4%, BM = 25.6%), and Atka mackerel (FO = 31.7%, BM = 21.1%) were the most frequently occurring taxa in the breeding NFS diet and represented the taxa with the highest proportions of biomass; however, northern smoothtongue (NA = 40.9%, BM = 14.4%) and cephalopods (NA = 31.5%) were the most numerically dominant (Table 1B). The most frequently occurring taxa in the juvenile NFS diet (Table 1C) were Atka mackerel (FO = 69.1%, BM = 53.1%), pollock (FO = 36.0%, BM = 26.5%), and salmon (FO = 31.6%, BM = 11.2%), which also represented the taxa with the highest biomass; however, cephalopods (NA = 23.0%, BM = 5.9%) were more numerically abundant than salmon (NA = 7.9%). Based on the frequency of occurrence, breeding NFS consumed significantly more cephalopods ($\chi^2 = 29.76$, $p < 0.001$), northern smoothtongue ($\chi^2 = 20.41$, $p < 0.001$), and salmon ($\chi^2 = 6.70$, $p = 0.010$) than juvenile NFS. Juvenile NFS consumed significantly more Atka mackerel ($\chi^2 = 39.13$, $p < 0.001$) and pollock ($\chi^2 = 10.18$, $p = 0.001$) than breeding NFS.

Diet composition varied between scats and spews. The occurrence of pollock ($\chi^2 = 11.18$, $p < 0.001$) and cephalopods ($\chi^2 = 5.58$, $p = 0.018$) was significantly higher in spews than in scats. Atka mackerel ($\chi^2 = 4.38$, $p = 0.036$) and northern smoothtongue ($\chi^2 = 4.43$, $p = 0.039$; Fisher's exact test) occurred more frequently in scats than in spews. The application of numerical correction factors to the scat MNI values resulted in a change in dominance ranks (Table 2).

Scats from breeding and juvenile NFS contained 2.1 ± 1.0 and 1.7 ± 1.1 prey species and 5.2 ± 8.0 and 2.7 ± 3.1 individual prey items, respectively. Neither difference was significant ($p > 0.05$; Fligner–Policello tests). Nearly identical percentages (49.1%) of the scats from breeding NFS and juvenile (48.8%) NFS contained only 1 prey species. The majority of scats from breeding NFS (80.9%) contained ≤5 individual prey items and 7.2% contained between 20 and 53 individual prey items. The majority of scats from juvenile NFS (87.2%) contained ≤3 individual items with a maximum number of individual items in a single scat equaling 15. The number of prey species contained in spews from breeding (3.4 ± 0.7) and juvenile (2.3 ± 0.6) NFS was not significantly different; also, there were no significant differences in the number of individual prey items found in spews from breeding (2.6 ± 0.3) and juvenile (3.1 ± 0.6) NFS ($p > 0.05$; Fligner–Policello tests).

The MNI of prey items differed between scats and spews

Fig. 2. Frequency of occurrence, numerical abundance, and proportion of total biomass consumed of prey items found in scats and spews of Steller sea lions (*Eumetopias jubatus*) and northern fur seals (*Callorhinus ursinus*) collected from Lovushki Island, Russia, during the breeding seasons of 2003, 2005, 2007, and 2008. Atka, Atka mackerel (*Pleurogrammus monopterygius*); Pol, walleye pollock (*Theragra chalcogramma*); Sal, salmon (*Onchorhynchus* sp.); Ceph, cephalopods; NST, northern smoothtongue (*Leuroglossus schmidti*).
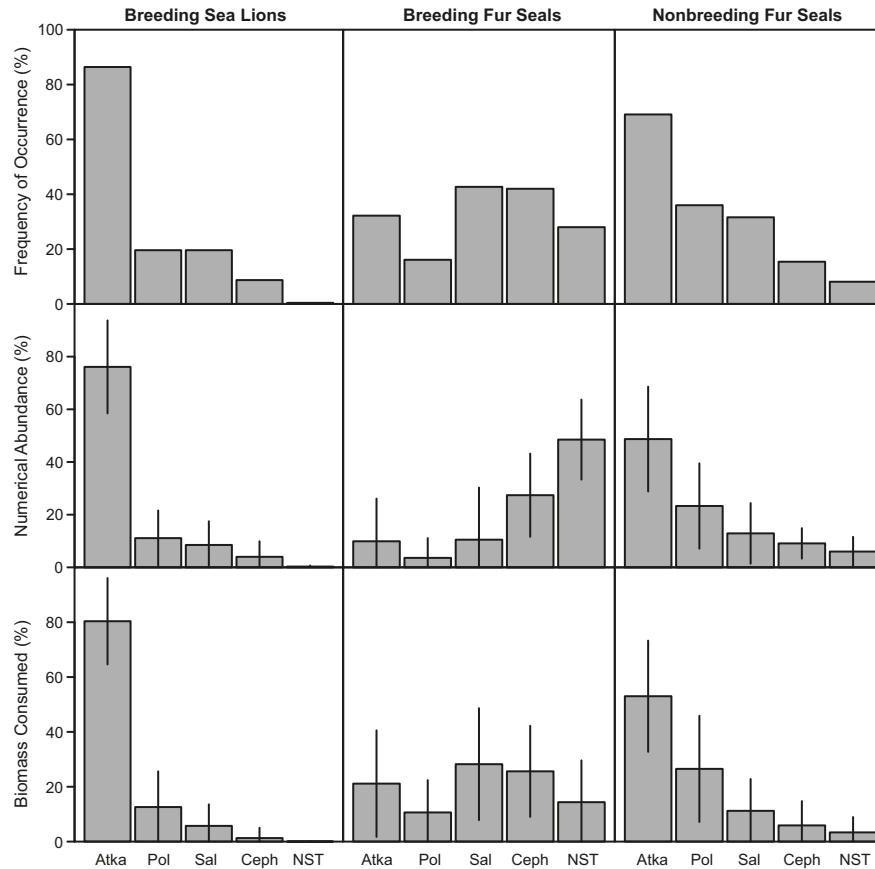
(Table 3). The MNI of Atka mackerel ($\hat{U} = -3.15$, $p = 0.002$), cephalopods ($\hat{U} = -3.99$, $p < 0.001$), and pollock ($\hat{U} = -4.56$, $p < 0.001$) consumed were significantly higher in spews than in scats. Scats contained a significantly higher number of northern smoothtongue than spews ($\hat{U} = 2.60$, $p = 0.009$). There was no difference in salmon MNI between scats and spews ($\hat{U} = 1.88$, $p = 0.060$). Atka mackerel was the prey type found in 71.4% of scats from juvenile NFS that contained only one species, while scats from breeding NFS that contained only one prey type were more likely to contain salmon (40.7%) than any other species.

In samples from breeding NFS, the occurrence of Atka mackerel was significantly negatively correlated with the occurrence of cephalopods ($r = -0.23$, $t_{0.05(3),124} = -2.58$, $p = 0.010$; Fig. 3) and salmon ($r = -0.26$, $t_{0.05(3),124} = -2.94$, $p = 0.003$), and positively correlated with pollock ($r = 0.24$, $t_{0.05(3),124} = 2.67$, $p = 0.008$). In samples from juvenile NFS, Atka mackerel was negatively correlated with pollock ($r = -0.43$, $t_{0.05(3),118} = -5.02$, $p < 0.001$). Northern smoothtongue was positively correlated with cephalopods in samples from both breeding ($r = 0.30$, $t_{0.05(3),124} = 3.38$, $p = 0.001$) and juvenile ($r = 0.24$, $t_{0.05(3),122} = 2.68$, $p = 0.007$) NFS.

Sea lion diet

Of the 271 scats collected from SSL, 247 (91.1%) contained prey remains that could be minimally identified to the

family level. A total of 14 different prey were identified with 6 prey to species. The most common prey items (Table 1D), in order of both frequency, abundance, and biomass, were Atka mackerel (FO = 87.1%, NA = 71.8%, BM = 80.4%), walleye pollock (FO = 19.6%, NA = 10.2%, BM = 12.7%), salmon (FO = 19.2%, NA = 7.8%, BM = 5.6%), and cephalopods (FO = 8.5%, NA = 3.8%, BM = 1.2%). The primary squid species consumed was *Gonatopsis* sp. cf. *G. borealis*.

Scats from SSL contained 1.6 ± 1.5 prey species and 3.1 ± 1.6 individual prey items. Over half (57.7%) of the scats contained only one prey species, and of these, 94.1% contained Atka mackerel. The majority of scats (89.4%) contained ≤5 individual prey items. The occurrence of Atka mackerel was significantly negatively correlated with the occurrence of pollock ($r = -0.29$, $t_{0.05(3),256} = -4.86$, $p < 0.001$; Fig. 3), salmon ($r = -0.30$, $t_{0.05(3),256} = -5.06$, $p < 0.001$), and northern smoothtongue ($r = -0.56$, $t_{0.05(3),256} = -10.66$, $p < 0.001$). Northern smoothtongue was significantly correlated with pollock ($r = 0.21$, $t_{0.05(3),256} = 3.40$, $p = 0.001$) and salmon ($r = 0.18$, $t_{0.05(3),256} = 2.87$, $p = 0.004$).

Niche overlap and diet diversity

SSL consumed significantly more Atka mackerel (based on numerical abundance) than both breeding ($\chi^2 = 94.91$, $p < 0.001$) and juvenile ($\chi^2 = 7.53$, $p = 0.006$) NFS. Breeding NFS consumed significantly more cephalopods ($\chi^2 = 55.94$,

Table 1. Minimum number of individuals consumed (MNI), percent numerical abundance (NA), and percent frequency of occurrence (FO) of prey taxa found in scats and spews from (A) total northern fur seals (*Callorhinus ursinus*), (B) breeding northern fur seals, (C) juvenile northern fur seals, and (D) breeding Steller sea lions (*Eumetopias jubatus*).

(A) Total diet of northern fur seals.

Prey type	2003 (n = 42/35)			2005 (n = 48/48)			2007 (n = 105/98)			2008 (n = 93/93)			Total (n = 288/274)		
	MNI	NA	FO	MNI	NA	FO	MNI	NA	FO	MNI	NA	FO	MNI	NA	FO
Fish	**112**	**85.5**	**97.1**	**220**	**71.4**	**95.8**	**254**	**89.4**	**98.0**	**330**	**66.9**	**93.5**	**916**	**73.0**	**96.0**
Unidentified fish	6	4.6	17.1	5	1.6	10.4	23	8.1	23.5	15	3.0	16.1	49	3.9	17.9
Hexagrammidae	**34**	**26.0**	**57.1**	**37**	**12.0**	**37.5**	**82**	**28.9**	**52.0**	**89**	**18.1**	**51.6**	**242**	**19.3**	**50.0**
Atka mackerel	34	26.0	57.1	37	12.0	37.5	82	28.9	52.0	88	17.8	51.6	241	19.2	50.0
Rock greenling										1	0.2	1.1	1	0.1	0.4
Gadidae	**2**	**1.5**	**5.7**	**1**	**0.3**	**2.1**	**40**	**14.1**	**28.6**	**118**	**23.9**	**46.2**	**161**	**12.8**	**27.0**
Unidentified gadid				1	0.3	2.1				1	0.2	1.1	2	0.2	0.7
Walleye pollock	2	1.5	5.7				40	14.1	28.6	116	23.5	45.2	158	12.6	26.3
Pacific cod										1	0.2	1.1	1	0.1	0.4
Salmon	18	13.7	48.6	37	12.0	75.0	26	9.2	25.5	28	5.7	26.9	109	8.7	37.6
Northern smoothtongue	26	19.8	17.1	140	45.5	39.6	81	28.5	7.1	77	15.6	17.2	324	25.8	17.5
Other fish species	**26**	**19.8**	**34.3**				**2**	**0.7**	**2.0**	**3**	**0.6**	**2.2**	**31**	**2.5**	**5.8**
Sculpin sp.	12	9.2	14.3										12	1.0	1.8
Irish lord sp.	1	0.8	2.9										1	0.1	0.4
Herring	1	0.8	2.9										1	0.1	0.4
Lampfish sp.							1	0.4	1.0				1	0.1	0.4
High cockscomb							1	0.4	1.0	1	0.2	1.1	2	0.2	0.7
Prickleback sp.										2	0.4	1.1	2	0.2	0.4
Sand lance	2	1.5	2.9										2	0.2	0.4
Snailfish sp.	2	1.5	2.9										2	0.2	0.4
Stone cockscomb	8	6.1	22.9										8	0.6	2.9
Cephalopods	**19**	**14.5**	**25.7**	**88**	**28.6**	**41.7**	**30**	**10.6**	**14.3**	**201**	**40.8**	**37.6**	**338**	**27.0**	**28.5**
Unidentified cephalopod	1	0.8	2.9	46	14.9	20.8	6	2.1	5.1	40	8.1	14.0	93	7.4	10.6
Squid sp.	18	13.7	22.9	42	13.6	37.5	24	8.5	11.2	160	32.5	30.1	244	19.5	23.7
Octopus sp.										1	0.2	1.1	1	0.1	0.4
Other prey*	**2**		**5.7**	**83**		**33.3**	**3**		**3.1**	**11**		**9.7**	**99**		**10.9**
Bird sp.	1		2.9										1		0.4
Polychaete worm	1		2.9	83		33.3	3		3.1	11		9.7	98		10.6

(B) Diet of breeding northern fur seals.

Prey type	2003 (n = 12/11)			2005 (n = 36/36)			2007 (n = 48/46)			2008 (n = 51/51)			Total (n = 148/145)		
	MNI	NA	FO	MNI	NA	FO	MNI	NA	FO	MNI	NA	FO	MNI	NA	FO
Fish	**46**	**71.9**	**90.9**	**167**	**69.6**	**100.0**	**140**	**83.8**	**95.7**	**144**	**57.8**	**88.5**	**497**	**65.6**	**93.8**
Unidentified fish	2	3.1	18.2	5	2.1	13.9	15	9.0	32.6	12	4.8	21.2	34	4.5	22.8
Hexagrammidae	**2**	**3.1**	**18.2**	**5**	**2.1**	**13.9**	**26**	**15.6**	**41.3**	**31**	**12.4**	**38.5**	**64**	**8.4**	**31.7**
Atka mackerel	2	3.1	18.2	5	2.1	13.9	26	15.6	41.3	30	12.0	38.5	63	8.3	31.7
Rock greenling										1	0.4	1.9	1	0.1	0.7
Gadidae	**1**	**1.6**	**9.1**				**4**	**2.4**	**8.7**	**27**	**10.8**	**36.5**	**32**	**4.2**	**16.6**
Unidentified gadid										1	0.4	1.9	1	0.1	0.7

Table 1 (*continued*).

(B) Diet of breeding northern fur seals.

Prey type	2003 (n = 12/11)			2005 (n = 36/36)			2007 (n = 48/46)			2008 (n = 51/51)			Total (n = 148/145)		
	MNI	NA	FO	MNI	NA	FO	MNI	NA	FO	MNI	NA	FO	MNI	NA	FO
Walleye pollock	1	1.6	9.1				4	2.4	8.7	26	10.4	34.6	31	4.1	15.9
Salmon	**7**	10.9	63.6	29	12.1	77.8	14	8.4	30.4	17	6.8	26.9	67	8.8	43.4
Northern smoothtongue	25	39.1	45.5	128	53.3	36.1	80	47.9	13.0	77	30.9	30.8	310	40.9	27.6
Other fish species	**9**	**14.1**	**36.4**				**1**	**0.6**	**2.2**	**1**	**0.4**	**1.9**	**11**	**1.5**	**4.1**
High cockscomb							1	0.6	2.2				1	0.1	0.7
Irish lord, sp.	1	1.6	9.1										1	0.1	0.7
Prickleback sp.										2	0.8	1.9	2	0.3	0.7
Sculpin sp.	2	3.1	18.2										2	0.3	1.4
Snailfish sp.	2	3.1	18.2										2	0.3	1.4
Stone cockscomb	4	6.3	36.4										4	0.5	2.8
Cephalopods	**18**	**28.1**	**72.7**	**73**	**30.4**	**36.1**	**27**	**16.2**	**26.1**	**121**	**48.6**	**51.9**	**239**	**31.5**	**41.4**
Unidentified cephalopod	1	1.6	9.1	41	17.1	22.2	3	1.8	6.5	35	14.1	19.2	80	10.6	15.2
Squid sp.	17	26.6	63.6	32	13.3	33.3	24	14.4	23.9	86	34.5	42.3	159	21.0	35.9
Other prey*	**2**		**18.2**	**55**		**33.3**	**2**		**4.3**	**11**		**17.3**	**70**		**17.2**
Bird	1		9.1										1		0.7
Polychaete worm	1		9.1	55		33.3	2		4.3	11		17.3	69		16.6

(C) Diet of juvenile northern fur seals.

Prey type	2003 (n = 25/31)			2005 (n = 16/16)			2007 (n = 56/52)			2008 (n = 43/43)			Total (n = 157/136)		
	MNI	NA	FO	MNI	NA	FO	MNI	NA	FO	MNI	NA	FO	MNI	NA	FO
Fish	**66**	**98.5**	**100.0**	**95**	**66.9**	**100.0**	**114**	**97.4**	**100.0**	**164**	**67.2**	**97.7**	**439**	**77.0**	**99.3**
Unidentified fish	4	6.0	16.0	1	0.7	6.3	8	6.8	15.4	3	1.2	7.0	16	2.8	11.8
Hexagrammidae	**32**	**47.8**	**72.0**	**35**	**24.6**	**100.0**	**56**	**47.9**	**61.5**	**58**	**23.8**	**65.1**	**181**	**31.8**	**69.1**
Atka mackerel	32	47.8	72.0	35	24.6	100.0	56	47.9	61.5	58	23.8	65.1	181	31.8	69.1
Gadidae	**1**	**1.5**	**4.0**	**1**	**0.7**	**6.3**	**36**	**30.8**	**46.2**	**90**	**36.9**	**55.8**	**128**	**22.5**	**36.8**
Unidentified gadid				1	0.7	6.3							1	0.2	0.7
Walleye pollock	1	1.5	4.0				36	30.8	46.2	90	36.9	55.8	127	22.3	36.0
Pacific cod										1	0.4	2.3	1	0.2	0.7
Salmon	11	16.4	40.0	11	7.7	68.8	12	10.3	21.2	11	4.5	25.6	45	7.9	31.6
Northern smoothtongue	1	1.5	4.0	47	33.1	56.3	1	0.9	1.9				49	8.6	8.1
Other fish species	**17**	**25.4**	**32.0**				**1**	**0.9**	**1.9**	**1**	**0.4**	**2.3**	**19**	**3.3**	**7.4**
Sculpin sp.	10	14.9	12.0										10	1.8	2.2
Herring	1	1.5	4.0										1	0.2	0.7
Lampfish sp.							1	0.9	1.9				1	0.2	0.7
High cockscomb										1	0.4	2.3	1	0.2	0.7
Sand lance	2	3.0	4.0										2	0.4	0.7
Stone cockscomb	4	6.0	16.0										4	0.7	2.9
Cephalopods	**1**	**1.5**	**4.0**	**47**	**33.1**	**62.5**	**3**	**2.6**	**3.8**	**80**	**32.8**	**18.6**	**131**	**23.0**	**15.4**
Unidentified cephalopod				23	16.2	25.0	3	2.6	3.8	5	2.0	7.0	31	5.4	6.6
Squid sp.	1	1.5	4.0	24	16.9	56.3				74	30.3	11.6	99	17.4	11.0

Table 1 (*concluded*).

(C) Diet of juvenile northern fur seals.

Prey type	2003 (*n* = 25/31)			2005 (*n* = 16/16)			2007 (*n* = 56/52)			2008 (*n* = 43/43)			Total (*n* = 157/136)		
	MNI	NA	FO	MNI	NA	FO	MNI	NA	FO	MNI	NA	FO	MNI	NA	FO
Octopus sp.										1	0.4	2.3	1	0.2	0.7
Other prey*				**29**		**31.3**	**1**		**1.9**				**30**		**4.4**
Bird sp.															
Polychaete worm				29		31.3	1		1.9				30		4.4

(D) Diet of breeding Steller sea lion.

Prey type	2003 (*n* = 32/32)			2005 (*n* = 53/53)			2007 (*n* = 111/111)			2008 (*n* = 75/75)			Total (*n* = 271/271)		
	MNI	NA	FO	MNI	NA	FO	MNI	NA	FO	MNI	NA	FO	MNI	NA	FO
Fish	**73**	**98.6**	**100.0**	**170**	**97.1**	**100.0**	**308**	**98.1**	**100.0**	**216**	**91.9**	**100.0**	**767**	**96.4**	**99.6**
Unidentified fish	4	5.4	12.5	2	1.1	3.8	8	2.5	7.2	8	3.4	10.8	22	2.8	8.1
Hexagrammidae	**57**	**77.0**	**84.4**	**118**	**67.8**	**77.4**	**245**	**78.0**	**91.0**	**154**	**65.5**	**90.5**	**574**	**72.1**	**87.1**
Atka mackerel	56	75.7	84.4	118	67.8	77.4	244	77.7	91.0	154	65.5	90.5	572	71.9	87.1
Greenling sp.	1	1.4	3.1				1	0.3	0.9				2	0.3	0.7
Gadidae	**5**	**6.8**	**12.5**	**18**	**10.3**	**26.4**	**24**	**7.6**	**13.5**	**42**	**17.9**	**32.4**	**89**	**11.3**	**21.0**
Unidentified gadid										1	0.4	1.4	1	0.1	0.4
Walleye pollock	3	4.1	9.4	16	9.2	24.5	24	7.6	13.5	38	16.2	29.7	81	10.2	19.6
Pacific cod	2	2.7	3.1	2	1.1	3.8				4	1.7	5.4	8	1.0	2.6
Salmon	5	6.8	15.6	29	16.7	41.5	24	7.6	18.9	4	1.7	5.4	62	7.8	19.2
Northern smoothtongue										2	0.9	1.4	2	0.3	0.4
Other fish species	**2**	**2.7**	**3.1**	**3**	**1.7**	**5.7**	**7**	**2.2**	**5.4**	**7**	**3.0**	**9.5**	**19**	**2.4**	**6.3**
Antlered sculpin							1	0.3	0.9				1	0.1	0.4
Sculpin sp.										1	0.4	1.4	1	0.1	0.4
Herring	1	1.4	3.1										1	0.1	
Irish lord sp.				1	0.6	1.9	1	0.3	0.9	1	0.4	1.4	3	0.4	1.1
Flatfish sp.	1	1.4	3.1							2	0.9	2.7	3	0.4	1.1
Northern lampfish				1	0.6	1.9				2	0.9	2.7	3	0.4	1.1
Lampfish sp.							1	0.3	0.9				1	0.1	0.4
Prickleback sp.				1	0.6	1.9	1	0.3	0.9	1	0.4	1.4	3	0.4	1.1
Sand lance							1	0.3	0.9				1	0.1	0.4
Snailfish sp.							2	0.6	1.8				2	0.3	0.7
Cephalopods	**1**	**1.4**	**3.1**	**5**	**2.9**	**9.4**	**6**	**1.9**	**5.4**	**17**	**7.2**	**14.9**	**29**	**3.6**	**8.5**
Unidentified cephalopod				4	2.3	7.5	2	0.6	1.8	4	1.7	5.4	10	1.3	3.7
Squid sp.	1	1.4	3.1	1	0.6	1.9	4	1.3	3.6	12	5.1	9.5	18	2.3	4.8
Octopus sp.										1	0.4	1.4	1	0.1	0.4
Other prey*	**1**		**3.1**	**3**		**3.8**	**5**		**2.7**				**9**		**2.2**
Bird sp.							1		0.9				1		0.4
Polychaete worm	1		3.1	3		3.8	4		1.8				8		1.8

Note: The total number of samples collected and the total number of samples with prey remains are in parentheses. Grouped totals are in boldface type.

*Polychaete worms and birds were considered to be secondary or accidental prey items and therefore not included in the calculations of percent numerical abundance.

Table 2. Summary of adjusted numerical abundance (NA*) based on prey- and size-specific numerical correction factors (NCF) applied to the minimum number of individuals of each of the five most commonly occurring prey types, ranked based on frequency of occurrence (FO), numerical abundance based on scats only (NA^s), and adjusted numerical abundance (NA*).

Prey type	Breeding northern fur seals			Juvenile northern fur seals			Steller sea lions		
	NA^s	NA* (95% CI)	Rank FO/NA^s/NA*	NA^s	NA* (95% CI)	Rank FO/NA^s/NA*	NA^s	NA* (95% CI)	Rank FO/NA^s/NA*
Atka mackerel	9.9	11.7 (9.1, 15.5)	3 / 4 / 3	48.7	53.0 (41.1, 70.2)	1 / 1 / 1	76.8	79.5 (62.0, 100.0)	1 / 1 / 1
Cephalopods	27.4	18.1 (17.7, 18.6)	2 / 2 / 2	9.1	5.4 (5.4, 5.7)	4 / 4 / 5	3.9	2.3 (2.2, 2.3)	4 / 4 / 4
Northern smoothtongue	48.4	55.1 (46.7, 67.7)	4 / 1 / 1	6.0	6.4 (5.4, 7.7)	5 / 5 / 4	0.3	0.3 (0.2, 0.3)	5 / 5 / 5
Pollock	3.6	3.9 (2.2, 6.4)	5 / 5 / 5	23.3	22.9 (13.6, 38.3)	2 / 2 / 2	10.9	10.4 (6.2, 18.0)	2 / 2 / 2
Salmon	10.8	11.2 (8.2, 17.7)	1 / 3 / 4	12.9	12.3 (9, 19.5)	3 / 3 / 3	8.2	8.2 (5.4, 11.7)	3 / 3 / 3

Note: 95% CI, 95% confidence intervals.

Table 3. Summary of the mean minimum number of individual prey items consumed between northern fur seals (*Callorhinus ursinus*; NFS) and Steller sea lions (*Eumetopias jubatus*; SSL).

Prey	NFS				Fligner–Policello test					
	Spew (range)	Scat (range)	Total (range)	SSL total (range)	NFS scat vs. spew		NFS scat vs. SSL scat		NFS total vs. SSL scat	
					$\hat{U}$	p	$\hat{U}$	p	$\hat{U}$	p
Atka mackerel	2.9±3.1 (1, 9)	1.5±1.1 (1, 6)	1.8±1.7 (1, 9)	2.5±2.9 (1, 10)	−3.15	0.002	−6.21	<0.001	−5.68	<0.001
Cephalopod	8.2±16.3 (1, 35)	3.0±6.2 (1, 23)	4.2±10.3 (1, 35)	1.3±0.2.9 (1, 5)	−3.99	<0.001	5.66	<0.001	8.01	<0.001
Northern smoothtongue	1.3±1.7 (1, 2)	7.4±22.9 (1, 53)	6.8±23.5 (1, 53)	2.0±0.0 (2, 2)	2.60	0.009	na	na	na	na
Pollock	3.3±3.6 (1, 11)	1.6±3.8 (1, 12)	2.2±4.2 (1, 12)	1.6±2.3 (1, 5)	−4.56	<0.001	−0.98	0.328	1.30	0.195
Salmon	1.00±0.00 (1, 1)	1.1±0.4 (1, 3)	1.1±0.5 (1, 3)	1.2±1.1 (1, 3)	1.88	0.060	−2.29	0.022	−2.45	0.014

Note: Values are mean ± SD. na, not applicable.

Fig. 3. Clustering dendrograms of prey groups found in scats of Steller sea lions (*Eumetopias jubatus*) and northern fur seals (*Callorhinus ursinus*) collected on Lovushki Island, Russia, during the breeding seasons of 2003, 2005, 2007, and 2008.
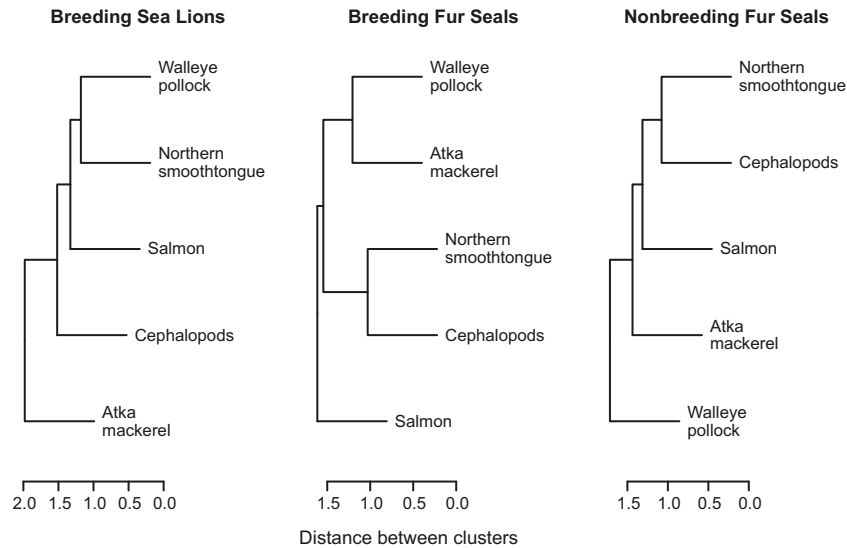

Table 4. Summary of Pianka's niche overlap indices calculated using three different measures of numerical abundance for breeding (B) and juvenile (J) northern fur seals (*Callorhinus ursinus*; NFS) and Steller sea lions (*Eumetopias jubatus*; SSL).

| Groups (i, h) | Niche overlap index (O_{jk}) (95% CI) | | |
	NA	NA^s	NA*
SSL, NFS	0.539 (0.324, 0.650)	0.539 (0.324, 0.650)	0.520 (0.324, 0.696)
SSL, NFS-B	0.218 (0.124, 0.305)	0.227 (0.107, 0.330)	0.230 (0.086, 0.352)
SSL, NFS-J	0.831 (0.710, 0.974)	0.937 (0.877, 1.000)	0.947 (0.896, 1.000)
NFS-B, NFS-J	0.468 (0.287, 0.673)	0.385 (0.228, 0.529)	0.359 (0.293, 0.679)

Note: NA, numerical abundance; NA^s, numerical abundance for scat samples only; NA*, adjusted numerical abundance.

$p < 0.001$), northern smoothtongue ($\chi^2 = 22.02$, $p < 0.001$), and salmon ($\chi^2 = 34.07$, $p < 0.001$) than SSL. Juvenile NFS consumed significantly more smoothtongue ($\chi^2 = 7.49$, $p = 0.006$) and salmon ($\chi^2 = 7.89$, $p = 0.005$) than SSL.

Pianka's niche overlap index for breeding and juvenile fur seals based on scats and spews combined was 0.468. Breeding and juvenile NFS had niche overlap indices of 0.385 and 0.359 when based on NA^s and NA*, respectively. The niche overlap index was 0.230 for SSL and breeding NFS based on scats alone and 0.947 for SSL and juvenile NFS. These two overlap index values were significantly different ($p < 0.05$). All overlap indices differed only slightly when based on NA^s instead of NA* (Table 4).

The sizes of prey items occurring in $\geq 5\%$ of scats did not differ between SSL and juvenile NFS when only scats were considered (Atka mackerel: $\chi^2 = 4.47$, $p = 0.502$; pollock: $\chi^2 = 1.12$, $p = 0.812$; salmon: $\chi^2 = 3.60$, $p = 0.152$). The sizes of Atka mackerel consumed by SSL and juvenile NFS were significantly different when both scats and spews were considered ($\chi^2 = 11.77$, $p = 0.035$), with SSL consuming a higher proportion of small (16–20 cm) Atka mackerel ($\chi^2 = 6.46$, $p = 0.011$) and NFS consuming a higher proportion of medium–large (29–35 cm) Atka mackerel ($\chi^2 = 5.86$, $p = 0.015$). There were no differences in sizes of salmon ($\chi^2 = 3.23$, $p = 0.219$) or pollock ($\chi^2 = 2.54$, $p = 0.519$) consumed when both scats and spews were considered (Fig. 4).

Shannon's diet diversity index for breeding and juvenile NFS, based on scats and spews, was 1.321 and 1.378, respectively. Overall, NFS had a diet diversity index of 3.085 based on scats and spews. Based on scats alone, breeding and juvenile NFS had a diet diversity index of 1.296 and 1.341, respectively. The overall diet diversity index for NFS based on scats alone was 3.389. SSL had a diet diversity index of 0.794, which was significantly different from the diet diversity indices of both breeding and juvenile NFS (Table 5).

Discussion

Interspecific competition

This study found significant differences between the diets of breeding NFS and SSL, both in terms of numerical abundance and estimated percent biomass. This difference in prey selection between NFS and SSL is likely reflective of the different diving abilities and provisioning strategies of the two species, as well as the fasting abilities of their dependent young (Costa et al. 2004). By both measures, the diet of SSL consisted primarily of Atka mackerel. The diet of breeding NFS was numerically dominated by northern smoothtongue and cephalopods, while salmon, cephalopods, and Atka mackerel contributed the most biomass. However, Joy et al. (2006) found that biomass reconstruction indices may substantially underestimate the biomass contributed by

Fig. 4. Sizes of prey items consumed by juvenile northern fur seals (*Callorhinus ursinus*) (black bars) and Steller sea lions (*Eumetopias jubatus*) (grey bars). Asterisks indicates a significant difference.
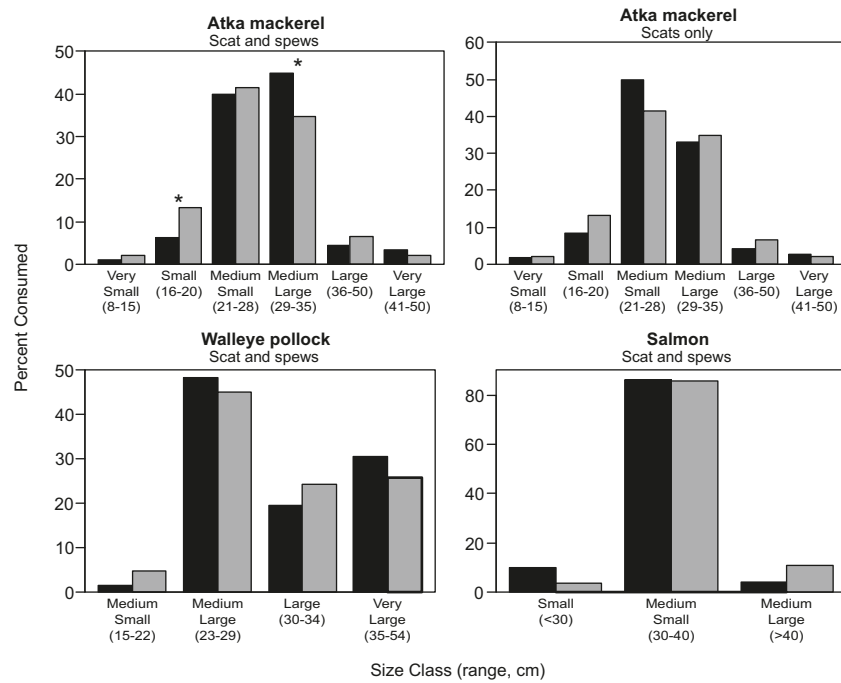

Table 5. Summary of Shannon's index of diversity calculated for breeding (B) and juvenile (J) northern fur seals (*Callorhinus ursinus*; NFS) and Steller sea lions (*Eumetopias jubatus*; SSL) using numerical abundance of prey remains calculated from all samples (NA) and from scat samples only (NA[s]).

| Group | Diet diversity (*H*) (95% CI) | |
	NA	NA[s]
SSL	0.794 (0.698, 0898)	0.794 (0.698, 0898)
NFS	3.085 (2.310, 5.000)	3.389 (2.333, 5.000)
NFS-B	1.321 (1.255, 1.434)	1.296 (1.213, 1.432)
NFS-J	1.378 (1.277, 1.542)	1.341 (1.200, 1.527)

smaller species eaten in large numbers, while overestimating the biomass contributed by species eaten in fewer numbers owing to differences in bone recovery rates. This may be further compounded by an increased chance of at-sea voiding of prey remains owing to longer transit durations from the foraging grounds. Tollit et al. (2003) found the initial defecation time for a meal fed to captive SSL to be between 2 and 56 h and skeletal elements from prey items were found in scats in increasingly lower numbers up to 148.3 h after feeding. The final defecation time for a single meal was 82 ± 41 h. As foraging trips by NFS from Lovushki Island can exceed this time frame (Waite 2010), meals consumed during the early stages of foraging are more likely to be voided at sea. Scats and spews that are deposited on land, therefore, contain significantly fewer prey remains from meals consumed at the primary foraging grounds; thus, they may be more reflective of meals consumed during the later stages of the foraging trip or of prey items consumed on the return trip. Depending on the distance traveled, meals consumed at the primary foraging location may be entirely voided prior to returning to the

rookery. Based on the significantly higher number of smoothtongue and squid consumed by breeding NFS, as well as the increased foraging trip distances that would be required to forage on these taxa, it is likely that the estimated biomass of these prey items consumed was substantially underestimated. As such, the biomass estimates presented in the current study should be interpreted with caution.

Larger diving animals have greater oxygen stores and lower mass-specific rates of oxygen consumption and, therefore, make longer and deeper dives than smaller divers. A model by Mori (2002) predicts that, to forage optimally, smaller divers should seek prey at shallower depths. Additionally, small pinnipeds are adapted to exploiting locally abundant and predictable sources of prey, while larger pinnipeds are more adapted to exploiting more dispersed prey (Costa 1993). Thus, NFS that prey on abundant prey species such as cephalopods and northern smoothtongue that aggregate in large numbers near the surface at night may be optimizing their foraging strategy, leaving nonschooling prey items that occur at deeper depths, such as Atka mackerel, to the larger SSL.

To maximize their fitness, central place foragers must maximize their energy intake while minimizing their energy expenditure to deliver the maximum amount of nutrients and energy to their dependent pups (Pyke et al. 1977). However, fitness is not always maximized by feeding on the most energy-dense prey species. In addition to choosing which species to consume, an optimally foraging predator may also modify its behavior to choose the optimal foraging location (Pyke et al. 1977). Optimal foraging location may be selected as a consequence of either reduced foraging costs or a reduction in the local availability of prey, which might occur when competition levels are high. To maintain a consistent supply of energy to their young, a central place forager must deliver more energy per foraging trip as the distance to the foraging

grounds and trip duration increases (Arnould and Boyd 1995). A patch of prey with a lower net rate of energy gain may be selected by central place foragers if it is close to the rookery, thereby reducing overall energy expenditure through a reduced cost of transport (Staniland et al. 2007). Atka mackerel are a medium-energy prey species; specimens collected in the western Aleutian Islands, with a mean mass of 694.8 g contained a mean of 5.6 kJ·g^{-1} (wet mass) of energy and 6.9% lipid (Logerwell and Schaufler 2005). Atka mackerel are pelagic throughout most of the year but become demersal and migrate to shallow waters in the summer to spawn, living at depths from the intertidal zone to <200 m (Gorbunova 1962; McDermott and Lowe 1997). Atka mackerel are a relatively cryptic species, often hiding among the rocks and kelp during the spawning season (Gorbunova 1962), which may increase the amount of time required to be located and captured by predators (Bowen et al. 2002). Thus, although SSL foraging on Atka mackerel may have a relatively lower rate of energy gain on a per-dive basis, their cost of foraging can be reduced by foraging close to the rookery and they can therefore deliver energy in the form of milk to their pups on a more frequent basis. However, to support this foraging strategy, sea lions require a locally abundant prey source (Boyd 1998). We suggest that the local abundance of Atka mackerel is relatively high because we observed a low diet diversity index for SSL, which suggests a high abundance of the preferred food item and, therefore, greater specialization (Pyke et al. 1977; Waite and Burkanov 2006).

In contrast, squid and northern smoothtongue that numerically dominated the NFS diet in this study are mid-water shelf and mesopelagic prey items located relatively farther offshore, requiring longer foraging trip durations and, therefore, higher levels of energy expenditure associated with travel costs. As foraging trip duration increases, it is necessary for NFS to acquire more energy per trip to maintain a constant supply of energy to their pups. Additionally, pinnipeds on longer foraging trips spend proportionately less time diving and thus need to increase the net energy gained per dive (Staniland et al. 2007). Northern smoothtongue are a smelt with a high energy density; samples collected in the central Bering Sea in June of 2000 had a mean energy density of 8.37 kJ·g^{-1} wet mass (Davis 2003). Smoothtongue are located at depths of 200–1000 m during the day but migrate to the 0–200 m at night (Sobolevskii and Sokolovskaya 1994; Sobolevskii et al. 1996). Commander squid collected in the western Aleutian Islands were of a lower energy value, containing a mean of 3.95 kJ·g^{-1} (wet mass) of energy and 3.65% lipid (Logerwell and Schaufler 2005). Like smoothtongue, many squid species migrate vertically and aggregate in large numbers at the surface at night, especially during spawning (Moiseev 1991; Lapko 1996; Watanabe et al. 2006), and although they are not as energy-dense, large numbers can be easily captured in a short amount of time. Between the high-energy smoothtongue and the abundant squid, it is likely that NFS have a relatively high rate of energy gain per dive.

In response to reduced prey availability, such as might occur when competition for prey resources is high, predators can choose to either modify their prey choice or foraging location, or increase their foraging effort. Costa and Gentry

(1986) found that during periods of reduced prey availability, northern fur seals on St. George Island, Alaska, increased their foraging effort rather than trip duration, the latter of which should be done only as a last resort (Costa 2008). However, optimal patch choice is partly decided by the extent of competition for prey within a given area (Pyke et al. 1977) and the ability of fur seals to modify foraging behavior varies between rookeries (Costa 2008). Therefore, the breeding NFS in this study may have chosen to increase their trip duration to reach more distant yet richer prey sources in response to competition with the larger SSL or the abundant juvenile NFS.

There was a biologically significant overlap in the diets of SSL and juvenile NFS, indicating the potential for strong interspecific competition for food resources. When only scats were considered, there were no significant differences in the sizes of prey consumed by SSL and juvenile NFS. When both scats and spews are considered, significantly more Atka mackerel in the 29–35 cm size class were found in NFS samples. This may be an artifact of larger prey items being regurgitated rather than passing through the gastrointestinal tract. However, an organism's niche is a multidimensional concept that includes variables such as prey selection, foraging location, and time budgets. Niche overlap indices, such as Pianka's niche overlap index, take into account only a single dimension at a time and may not closely relate to the true overall niche overlap. Therefore, a strong overlap in prey selection may not necessarily indicate strong competition if there is little overlap between other niche dimensions, such as foraging location. Further studies on these other dimensions, such as the deployment of satellite-linked time–depth recorders on both groups, or detailed examination of the energetic requirements of both groups, need to be completed before the potential level of competition between these two groups can be fully assessed.

Although the biomass, and thus the importance, of Atka mackerel consumed by breeding NFS is likely to have been overestimated, it is clear from the data that some Atka mackerel are being consumed by the breeding NFS population. Given that breeding NFS outnumber SSL by an order of magnitude, the relatively small proportion of Atka mackerel consumed by breeding NFS could add up to a substantial amount of biomass being removed from the prey base available to SSL. We estimated the total amount of Atka mackerel consumed daily by all three predator and age-class combinations using daily gross energy requirements (GER; Winship et al. 2002) and estimated proportion of Atka mackerel in the diet. All parameter values presented in Winship et al. (2002) were used in the calculation of GER for SSL, except for proportion of time spent in the water, which was estimated from SSL maternal attendance patterns on Lovushki Island (Burkanov et al. 2011).

For NFS, GER was estimated by substituting NFS-specific parameter values for body mass, daily body mass growth increment, and proportion of time spent in the water. To estimate the masses of breeding NFS, we first modeled the age structure by drawing from a normal sampling distribution whose mean and standard deviation (11.1 ± 4.6 years) were estimated from the NFS population on Bering Island, Russia (Boltnev et al. 1998). Masses were then estimated from the ages using a predictive equation (Boltnev et al. 1998) and

daily growth was estimated by calculating the mass of each animal at +1 year of age and dividing the difference by 365. The proportion of time spent in the water (71.1% ± 14.9%) was estimated from NFS foraging studies conducted on San Miguel Island, California (Gentry 1998), and St. Paul and St. George islands, Alaska (Gentry 1998; Call et al. 2008). The sex ratio of juvenile NFS was assumed to be 50:50. The age structure, body mass, and daily growth was modeled using parameters based on the juvenile male NFS population on St. Paul Island (Baker et al. 1994). The age structure of juvenile female NFS was assumed to be equal proportions of 2-, 3-, and 4-year-olds. Body mass and daily growth was estimated as for breeding female NFS. We used the proportion of time spent in water presented for juvenile SSL (Winship et al. 2002).

The estimated GER for breeding female SSL, breeding female NFS, and juvenile NFS was 88.1 ± 18.0, 22.1 ± 4.7, and 25.5 ± 5.7 MJ·d^{-1}, respectively. Based on these values and the estimated proportions of total biomass consumed represented by Atka mackerel, we estimate that the population of 1000 SSL on Lovushki Island consumed 31.7% (16.9 ± 7.5 metric ton) of the total Atka mackerel removed each day, whereas the 14 000 breeding NFS consumed only 15.6% (13.2 ± 20.4 metric ton) per day. In contrast, the 14 000 juvenile NFS consume an estimated 52.7% (43.3 ± 3.4 metric ton) per day. Although the density of Atka mackerel around Lovushki Island is currently not known, and assuming an overestimation of Atka mackerel biomass consumed by breeding NFS, it is clear that SSL face stronger competition for Atka mackerel from juvenile NFS than from breeding NFS.

Intraspecific competition

There was a clear difference between the diets of breeding and juvenile fur seals. This is possibly a reflection of the difference in energetic and time constraints between the two groups rather than a direct means by which to reduce intraspecific competition. Lactating females need to carefully balance their time and energy budgets to meet their basic nutritional demands, as well provide sufficient energy to their dependent pups. Juvenile animals have fewer restrictions with regards to the resources they can exploit and the amount of time spent doing so.

Study biases

Studies conducted on a variety of captive pinnipeds have confirmed the use of scat and spew analyses as a practical and accurate means by which to assess prey selection and numerical proportion of different prey species (Dellinger and Trillmich 1988; Fea and Harcourt 1997; Orr and Harvey 2001; Tollit et al. 2003). However, the use of undigested prey remains recovered from scats and spews has inherent biases that need to be taken into consideration during data analysis and interpretation. Of primary concern are the digestibility differences among prey species. Most empirical studies show that smaller prey species are more likely subject to complete digestion, which may lead to prey underrepresentation (Dellinger and Trillmich 1988; Gales and Cheal 1992). Skeletal elements from larger prey remains may accumulate in the stomach over time before being regurgitated. Therefore, spew samples may provide an overes-

timation of larger prey items or prey with especially robust skeletal elements. Combining data from scats and spews has been reported to reduce these errors (Gudmundson et al. 2006). The application of numerical correction factors (NCFs) may also help minimize the bias associated with differential digestion (Bowen 2000; Orr and Harvey 2001; Lundström et al. 2007). We applied NCFs developed by Tollit et al. (2007) through experiments with captive SSL to SSL scat samples collected for this study. These particular correction factors were chosen because they were based on the recovery of all identifiable skeletal elements, rather than relying solely on recovered otoliths, and are therefore applicable to samples where only nonotolith elements were recovered. There are currently no published NCFs based on all skeletal elements developed specifically for northern fur seals for the range of prey species identified in the samples collected on Lovushki Island. Correction factors are available for other fur seal species; however, they are either based only on recovered otoliths or were developed for fur seal species that forage on a substantially different prey (Bowen 2000; Staniland 2002). Therefore, because of their similar diets and digestive physiologies (Ridgway 1972), as well as the fact that the majority of prey items were identified using skeletal elements other than otoliths, the NCFs developed for SSL were also applied to the NFS scat samples.

Digestion rates are also affected by meal size, feeding frequency, diet mixing, and prey quality (Hunt and Stubbs 1975; Markussen 1993; Trumble et al. 2003; Trumble and Castellini 2005). Smaller meals, meals consisting primarily of prey with lower energy densities, or infrequent meals, may move through the gastrointestinal tract at a slower rate to maximize the absorption of nutrients into the body. Thus, skeletal elements of prey items in the throughput of smaller meals are subjected to higher levels of erosion. In contrast, larger meals, meals consisting of higher energy density prey, or frequent meals have decreased transit times, thereby increasing the likelihood of passing hard parts intact. This may be an especially important consideration when comparing the diets of lactating and nonlactating central place foragers. Breeding females must maximize their energy intake to provide enough energy to their young, as well as to meet their own energetic requirements. It would be logical to assume that between fasting periods on the rookery, females may attempt to maximize their meal size and the quality of prey items during intermittent foraging. Juvenile and other nonbreeding animals are not under such energetic and time constraints and could therefore consume several smaller, more frequent meals over a period of time to meet their energetic requirements.

Other potential biases include partial consumption of prey items, deposition of remains from a single meal over multiple samples, and voiding of scats and spews while at sea. Larger prey items, especially salmon (Hauser et al. 2008), are often brought to the surface and torn apart prior to consumption. In many of these cases, the head is discarded, emphasizing the importance of using elements other than otoliths for prey identification (Hauser et al. 2008). Unfortunately, many of the skeletal elements, such as vertebrae, are not useful for the enumeration of prey items consumed. Thus, the number of prey items eaten in this fashion may be underestimated.

Conclusions

The SSL on Lovushki Island have a very specialized diet. This is illustrated in both the high frequency of occurrence and numerical dominance of their primary prey item, Atka mackerel, as well as in their foraging tactics inferred from both the location of their primary prey and the negative correlation between the occurrence of Atka mackerel in SSL scat and all other prey types. The diet of breeding NFS, while more diverse than SSL, suggests a specialization on squid and northern smoothtongue. This clear partitioning of prey items and foraging location between breeding animals allows both to coexist within the same geographical region despite an increase in the population of both predator species.

The diet of juvenile NFS is more representative of a generalist predator, but there is a significant overlap with SSL in prey species and prey sizes consumed. If the total available biomass of Atka mackerel far exceeds the amount taken by SSL and NFS combined, then the effect of diet overlap may not negatively impact the population of either species. However, as juvenile NFS outnumber the SSL by an order of magnitude, there is substantial potential for interspecific competition for dietary resources between these two groups if prey resources are limiting. Although juvenile NFS may have greater flexibility to modify their foraging strategy owing to differences in energetic demands, a continued rapid increase in the NFS population could bring about localized shortages in the primary prey items of SSL, forcing the SSL to either increase their nearshore foraging efforts or to begin foraging farther offshore on more pelagic prey species. Either option would cause the SSL to expend larger amounts of energy over the course of a foraging trip and would increase the amount of time the SSL pups must fast between meals. Additionally, an expanded foraging range and increase in the consumption of other prey items by SSL may increase the dietary niche overlap and interspecific competition with breeding NFS and may have negative consequences for the population of either species. Therefore, continued growth of the NFS population on Lovushki Island may lead to the competitive exclusion of SSL owing to interspecific competition for food resources.

References

Anderson, P.J., and Piatt, J.F. 1999. Community reorganization in the Gulf of Alaska following ocean climate regime shift. Mar. Ecol. Prog. Ser. **189**: 117–123. doi:10.3354/meps189117.

Antonelis, G.A., Lowry, M.S., Demaster, D.P., and Fiscus, C.H. 1987. Assessing northern elephant seal feeding habits by stomach lavage. Mar. Mamm. Sci. **3**(4): 308–322. doi:10.1111/j.1748-7692.1987.tb00318.x.

Antonelis, G.A., Sinclair, E.H., Ream, R.R., and Robson, B.W. 1997. Inter-island variation in the diet of female northern fur seals (*Callorhinus ursinus*) in the Bering Sea. J. Zool. (Lond.), **242**(3): 435–451. doi:10.1111/j.1469-7998.1997.tb03847.x.

Arnould, J.P.Y., and Boyd, I.L. 1995. Temporal patterns of milk production in Antarctic fur seals (*Arctocephalus gazella*). J. Zool. (Lond.), **237**(1): 1–12. doi:10.1111/j.1469-7998.1995.tb02741.x.

Bailleul, F., Luque, S., Dubroca, L., Arnould, J.P.Y., and Guinet, C. 2005. Differences in foraging strategy and maternal behaviour between two sympatric fur seal species at the Crozet Islands. Mar. Ecol. Prog. Ser. **293**: 273–282. doi:10.3354/meps293273.

Baker, J.D., Fowler, C.W., and Antonelis, G.A. 1994. Body weight and growth of juvenile male northern fur seals, *Callorhinus ursinus*. Mar. Mamm. Sci. **10**(2): 151–162. doi:10.1111/j.1748-7692.1994.tb00257.x.

Belkin, A.N. 1966. Summer distribution, stocks, prospects of harvest, and some features of biology of the sea lions inhabiting the Kuril Islands. Inz. Tikhookeanskogo Nauchno-Issled. Inst. Rybn. Khoz. i Okeanografii, **58**: 69–95.

Benson, A.J., and Trites, A.W. 2002. Ecological effects of regime shifts in the Bering Sea and eastern North Pacific Ocean. Fish Fish. **3**: 95–113.

Boltnev, A.I., York, A.E., and Antonelis, G.A. 1998. Northern fur seal young: interrelationships among birth size, growth, and survival. Can. J. Zool. **76**(5): 843–854. doi:10.1139/z98-010.

Bowen, W.D. 2000. Reconstruction of pinniped diets: accounting for complete digestion of otoliths and cephalopod beaks. Can. J. Fish. Aquat. Sci. **57**(5): 898–905. doi:10.1139/f00-032.

Bowen, W.D., Tully, D., Boness, D.J., Bulheier, B.M., and Marshall, G.J. 2002. Prey-dependent foraging tactics and prey profitability in a marine mammal. Mar. Ecol. Prog. Ser. **244**: 235–245. doi:10.3354/meps244235.

Boyd, I.L. 1998. Time and energy constraints in pinniped lactation. Am. Nat. **152**(5): 717–728. doi:10.1086/286202. PMID:18811346.

Browne, P., Laake, J.L., and DeLong, R.L. 2002. Improving pinniped diet analyses through identification of multiple skeletal structures in fecal samples. Fish. Bull. (Wash., D.C.), **100**(3): 423–433.

Burkanov, V.N., and Loughlin, T.R. 2005. Distribution and abundance of Steller sea lions, *Eumetopias jubatus*, on the Asian coast, 1720's–2005. Mar. Fish. Rev. **67**(2): 1–62.

Burkanov, V., Altukhov, A., Andrews, R., Calkins, D., Gurarie, E., Permyakov, P., Sergeev, S., and Waite, J. 2007. Northern fur seal (*Callorhinus ursinus*) pup production in the Kuril Islands, 2005–2006. Paper presented at the 17th Biennial Conference of the Biology of Marine Mammals. Society for Marine Mammalogy, Cape Town, South Africa, 29 November – 3 December 2007.

Burkanov, V., Gurarie, E., Altukhov, A., Mamaev, E., Permyakov, P., Trukhin, A., Waite, J., and Gelatt, T. 2011. Environmental and biological factors influencing maternal attendance patterns of Steller sea lions (*Eumetopias jubatus*) in Russia. J. Mammal. **92**(2): 352–366. doi:10.1644/10-MAMM-A-194.1.

Calkins, D.G., and Goodwin, E.A. 1988. Investigation of the decline sea lion population in the Gulf of Alaska. Alaska Department of Fish and Game, Anchorage.

Call, K.A., Ream, R.R., Johnson, D., Sterling, J.T., and Towell, R.G. 2008. Foraging route tactics and site fidelity of adult female northern fur seal (*Callorhinus ursinus*) around the Pribilof Islands. Deep Sea Res. Part II Top. Stud. Oceanogr. **55**(16–17): 1883–1896. doi:10.1016/j.dsr2.2008.04.022.

Conners, M.E., Hollowed, A.B., and Brown, E. 2002. Retrospective analysis of Bering Sea bottom trawl surveys: regime shift and ecosystem reorganization. Prog. Oceanogr. **55**(1–2): 209–222. doi:10.1016/S0079-6611(02)00079-4.

Cooper, M.H., Budge, S.M., Springer, A.M., and Sheffield, G. 2009. Resource partitioning by sympatric pagophilic seals in Alaska: monitoring effects of climate variation with fatty acids. Polar Biol. **32**(8): 1137–1145. doi:10.1007/s00300-009-0614-5.

Costa, D.P. 1993. The relationship between reproductive and foraging energetics and the evolution of the Pinnipedia. Symp. Zool. Soc. Lond. No. 66. pp. 293–313.

Costa, D.P. 2008. A conceptual model of the variation in parental attendance in response to environmental fluctuation: foraging energetics of lactating sea lions and fur seals. Aquat. Conserv. **17**(Suppl. 1): S44–S52. doi:10.1002/aqc.917.

Costa, D.P., and Gentry, R.L. 1986. Reproductive energetics of the northern fur seal. *In* Fur seals: maternal strategies on land and at sea. *Edited by* R.L. Gentry and G.L. Kooyman. Princeton University Press, Princeton, N.J. pp. 79–101.

Costa, D.P., Kuhn, C.E., Weise, M.J., Shaffer, S.A., and Arnould, J.P.Y. 2004. When does physiology limit the foraging behaviour of freely diving mammals? Int. Congr. Ser. **1275**: 359–366. doi:10.1016/j.ics.2004.08.058.

Davis, N.C.D. 2003. Feeding ecology of Pacific salmon (*Oncorhynchus* spp.) in the central North Pacific Ocean and central Bering Sea, 1991–2000. Ph.D. dissertation, Hokkaido University, Hakodate, Hokkaido, Japan.

Dellinger, T., and Trillmich, F. 1988. Estimating diet composition from scat analysis in otariid seals (Otariidae): is it reliable? Can. J. Zool. **66**(8): 1865–1870. doi:10.1139/z88-269.

DeMaster, D., and Atkinson, S. (*Editors*). 2002. Steller sea lion decline: is it food II. University of Alaska Sea Grant Report AK-SG-02-02, Fairbanks.

Erokhin, V.G. 1990. Distribution and biological characteristics of pink salmon *Oncorhynchus gorbuscha* in the ocean. J. Ichthyol. **30**(6): 1031–1036.

Fea, N.I., and Harcourt, R. 1997. Assessing the use of faecal and regurgitate analysis as a means of determining fur seal diet. *In* Marine mammal research in the southern hemisphere. Vol. 1. Status, ecology and medicine. *Edited by* M. Hindell and C. Kemper. Surrey Beatty and Sons, Sydney, N.S.W., Australia. pp. 143–150.

Field, I.C., Bradshaw, C.J.A., Burton, H.R., Sumner, M.D., and Hindell, M.A. 2005. Resource partitioning through oceanic segregation of foraging juvenile southern elephant seals (*Mirounga leonina*). Oecologia (Berl.), **142**(1): 127–135. doi:10.1007/s00442-004-1704-2. PMID:15365810.

Fligner, M.A., and Policello, G.E., II. 1981. Robust rank procedures for the Behrens–Fisher problem. J. Am. Stat. Assoc. **76**(373): 162–168. doi:10.2307/2287062.

Friedlaender, A.S., Lawson, G.L., and Halpin, P.N. 2009. Evidence of resource partitioning between humpback and minke whales around the western Antarctic Peninsula. Mar. Mamm. Sci. **25**(2): 402–415. doi:10.1111/j.1748-7692.2008.00263.x.

Gales, N.J., and Cheal, A.J. 1992. Estimating diet composition of the Australian sea lion (*Neophoca cinerea*) from scat analysis: an unreliable technique. Wildl. Res. **19**(4): 447–456. doi:10.1071/WR9920447.

Gause, G.F. 1934. The struggle for existence. Williams and Wilkins, Baltimore, Md.

Gentry, R.L. 1998. Behavior and ecology of the northern fur seal. Princeton University Press, Princeton, N.J.

Gentry, R.L. 2002. Northern fur seals. *In* Encyclopedia of marine mammals. *Edited by* W.F. Perrin, B. Würsig, and J.G.M. Thewissen. Academic Press, San Diego, Calif. pp. 813–817.

Gentry, R.L., and Kooyman, G.L. 1986. Fur seals: maternal strategies on land and at sea. Princeton University Press, Princeton, N.J.

González-Solís, J., Croxall, J.P., and Wood, A.G. 2000. Foraging partitioning between giant petrels *Macronectes* spp., and its relationship with breeding population changes at Bird Island, South Georgia. Mar. Ecol. Prog. Ser. **204**: 279–288. doi:10.3354/meps204279.

Gorbunova, N.N. 1962. Razmnozhenie i razvite ryb semeistva terpugovykh (Hexagrammidae) [Spawning and development of greenlings (family Hexagrammidae)]. Akademii Nauk SSSR, **59**: 118–182. [In Russian and translated by the Israeli Program for Scientific Translations, 1970, pp. 121–185.] *In* Greenlings: taxonomy, biology, interoceanic transplantation. *Edited by* T.S. Rass. National Technological Information Service, Springfield, Va.

Gudmundson, C.J., Zeppelin, T.K., and Ream, R.R. 2006. Application of two methods for determining diet of northern fur seals (*Callorhinus ursinus*). Fish. Bull. (Wash., D.C.), **104**(3): 445–455.

Harvey, J.T., and Antonelis, G.A. 1994. Biases associated with non-lethal methods of determining the diet of northern elephant seals. Mar. Mamm. Sci. **10**(2): 178–187. doi:10.1111/j.1748-7692.1994.tb00259.x.

Hauser, D.D.W., Allen, C.S., Rich, H.B., Jr., and Quinn, T.P. 2008. Resident harbor seals (*Phoca vitulina*) in Iliamna Lake, Alaska: summer diet and partial consumption of adult sockeye salmon (*Oncorhynchus nerka*). Aquat. Mamm. **34**(3): 303–309. doi:10.1578/AM.34.3.2008.303.

Heath, R.B., Calkins, D., McAllister, D., Taylor, W., and Spraker, T. 1996. Telazol and isoflurane field anesthesia in free-ranging Steller's sea lions (*Eumetopias jubatus*). J. Zoo Wildl. Med. **27**(1): 35–43.

Hope, A.C.A. 1968. A simplified Monte Carlo significance test procedure. J. R. Stat. Soc. B Methodol. **30**(3): 582–598.

Hunt, J.N., and Stubbs, D.F. 1975. The volume and energy content of meals as determinants of gastric emptying. J. Physiol. **245**(1): 209–225. PMID:1127608.

Jobling, M., and Breiby, A. 1986. The use and abuse of fish otoliths in studies of feeding habits of marine piscivores. Sarsia, **71**: 265–274.

Joy, R., Tollit, D.J., Laake, J.L., and Trites, A.W. 2006. Using simulations to evaluate reconstructions of sea lion diet from scat. *In* Sea lions of the world. *Edited by* A.W. Trites, S.K. Atkinson, D.P. DeMaster, L.W. Fritz, T.S. Gelatt, L.D. Rea, and K.M. Wynne. Alaska Sea Grant College Program, Anchorage. pp. 205–222.

Klumov, S.K. 1957. Beregovye lezhbishcha kotikov i mesta obitaniya kalanov na Kuril'skikh ostrovakh i orientirovochnoe opredelenie ikh chislennosti [Shore rookeries of northern fur seals and habitats of sea otters on the Kuril Islands and tentative assessment of their abundance]. Doklady Akademii Nauk USSR, **117**(1): 153–156.

Kronfeld-Schor, N., and Dayan, T. 2003. Partitioning of time as an ecological resource. Annu. Rev. Ecol. Evol. Syst. **34**(1): 153–181. doi:10.1146/annurev.ecolsys.34.011802.132435.

Kubodera, T. 1986. Squids in the food chain. Report of development of ecosystem modeling in the subarctic Pacific. Fisheries Agency, Japan. [In Japanese.]

Kuzin, A.E. 1999. The northern fur seal. Russian Marine Mammal Council, Pacific Fishery and Oceanography Research Center (TINRO-Center), Moscow, Russia.

Kuzin, A.E., Panina, G.K., and Perlov, A.S. 1977. The abundance and interrelationships of Steller's sea lions and northern fur seals on common rookeries of the Kuril Islands. *In* Marine mammals of the Pacific, issue 1, Vladivostok. [In Russian and translated by S. Pearson, National Marine Mammal Laboratory, National Marine

Fisheries Service, 7600 Sand Point Way NE, Seattle, WA 98115, USA.] pp. 50–66.

Lapko, V.V. 1996. The role of squids in the Sea of Okhotsk communities. Oceanology (Mosc.), **35**(5): 672–677. [English translation.]

Logerwell, E.A., and 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. Aquat. Mamm. **31**(1): 62–82. doi:10.1578/AM.31.1. 2005.62.

Loughlin, T.R., Perez, M.A., and Merrick, R.L. 1987. *Eumetopias jubatus*. Mamm. Species No. 283: 1–7. doi:10.2307/3503908.

Loughlin, T.R., Perlov, A.S., and Vladimirov, V.A. 1992. Range-wide survey and estimation of total number of Steller sea lions in 1989. Mar. Mamm. Sci. **8**(3): 220–239. doi:10.1111/j.1748-7692.1992. tb00406.x.

Lundström, K., Hjerne, O., Alexandersson, K., and Karlsson, O. 2007. Estimation of grey seal (*Halichoerus grypus*) diet composition in the Baltic Sea. NAMMCO Sci. Publ. **6**: 177–196.

Markussen, N.H. 1993. Transit time of digesta in captive harbor seals (*Phoca vitulina*). Can. J. Zool. **71**(5): 1071–1073. doi:10.1139/ z93-144.

Mathisen, O.A., Baade, R.T., and Lopp, R.J. 1962. Breeding habits, growth and stomach contents of the Steller sea lion in Alaska. J. Mammal. **43**(4): 469–477. doi:10.2307/1376909.

Mathur, D. 1977. Food habits and competitive relationships of the bandfin shiner in Halawakee Creek, Alabama. Am. Midl. Nat. **97**(1): 89–100. doi:10.2307/2424687.

McDermott, S.F., and Lowe, S.A. 1997. The reproductive cycle of Atka mackerel (*Pleurogrammus monopterygius*) in Alaskan waters. Fish. Bull. (Wash., D.C.), **96**: 321–333.

McGarigal, K., Cushman, S., and Stafford, S. 2000. Multivariate statistics for wildlife and ecology research. Springer Science +Business Media, LLC, New York.

McKenzie, J., and Wynne, K.M. 2008. Spatial and temporal variation in the diet of Steller sea lions in the Kodiak Archipelago, 1999 to 2005. Mar. Ecol. Prog. Ser. **360**: 265–283. doi:10.3354/ meps07383.

Merrick, R.L., Chumbley, M.K., and Byrd, G.V. 1997. Diet diversity of Steller sea lions (*Eumetopias jubatus*) and their population decline in Alaska: a potential relationship. Can. J. Fish. Aquat. Sci. **54**(6): 1342–1348. doi:10.1139/f97-037.

Moiseev, S.I. 1991. Observation of the vertical distribution and behavior of nektonic squids using manned submersibles. Bull. Mar. Sci. **49**(1–2): 446–456.

Mori, Y. 2002. Optimal diving behaviour for foraging in relation to body size. J. Evol. Biol. **15**(2): 269–276. doi:10.1046/j.1420-9101. 2002.00382.x.

Mori, J., Kubodera, T., and Norihisa, B. 2001. Squid in the diet of northern fur seals, *Callorhinus ursinus*, caught in the western and central North Pacific Ocean. Fish. Res. (Amst.), **52**(1–2): 91–97. doi:10.1016/S0165-7836(01)00233-8.

Murphy, M.A., Waits, L.P., Kendall, K.C., Wasser, S.K., Higbee, J.A., and Bogden, R. 2002. An evaluation of long-term preservation methods for brown bear (*Ursus arctos*) faecal DNA samples. Conserv. Genet. **3**(4): 435–440. doi:10.1023/ A:1020503330767.

Nagasawa, K., Ueno, Y., Azuma, T., Ogura, M., Startsev, A.V., Ivanova, I.M., and Morris, J.F.T. 1996. Distribution and biology of epipelagic animals in the northern North Pacific Ocean and adjacent seas. I. Fishes and squids in the southern Okhotsk Sea and western North Pacific Ocean off the Kuril Islands in the autumn of 1993. Bull. Natl. Res. Inst. Far Seas Fish. **33**: 149–170.

NMFS. 1995. Status review of the United States Steller sea lion (*Eumetopias jubatus*) population. National Marine Fisheries Service (NMFS), National Marine Mammal Laboratory, Seattle, Wash.

Orlov, A., and Binohlan, C. 2009. Length-weight relationships of deep-sea fishes from the western Bering Sea. J. Appl. Ichthyol. **25**(2): 223–227. doi:10.1111/j.1439-0426.2009.01215.x.

Orr, A.J., and Harvey, J.T. 2001. Quantifying errors associated with using fecal samples to determine the diet of the California sea lion (*Zalophus californianus*). Can. J. Zool. **79**(6): 1080–1087.

Page, B., Mckenzie, J., and Goldsworthy, S.D. 2005. Dietary resource partitioning among sympatric New Zealand and Australian fur seals. Mar. Ecol. Prog. Ser. **293**: 283–302. doi:10.3354/ meps293283.

Panina, G.K. 1964. Pitanie kotikov v Yaponskom more [Feeding of northern fur seals in the Sea of Japan]. Inz. Tikhookeanskogo Nauchno-Issled. Inst. Rybn. Khoz. i Okeanografii, **54**: 67–73.

Panina, G.K. 1966. Diet of Steller sea lion and seals on Kuril Islands. Inz. Tikhookeanskogo Nauchno-Issled. Inst. Rybn. Khoz. i Okeanografii, **58**: 235–236.

Pianka, E.R. 1973. The structure of lizard communities. Annu. Rev. Ecol. Syst. **4**(1): 53–74. doi:10.1146/annurev.es.04.110173. 000413.

Pitcher, K.W., and Calkins, D.G. 1981. Reproductive biology of Steller sea lions in the Gulf of Alaska. J. Mammal. **62**(3): 599–605. doi:10.2307/1380406.

Pitcher, K.W., Olesiuk, P.F., Brown, R.F., Lowry, M.S., Jeffries, S.J., Sease, J.L., Perryman, W.L., Stinchcomb, C.E., and Lowry, L.F. 2007. Abundance and distribution of the eastern North Pacific Steller sea lion (*Eumetopias jubatus*) population. Fish. Bull. (Wash., D.C.), **107**: 102–115.

Pyke, G.H., Pulliam, H.R., and Charnov, E.L. 1977. Optimal foraging: a selective review of theory and tests. Q. Rev. Biol. **52**(2): 137–154. doi:10.1086/409852.

Ridgway, S.H. 1972. Mammals of the sea: biology and medicine. Charles C. Thomas Publisher Ltd., Springfield, Ill.

Robinson, S.A., Goldsworthy, S.G., Hoff, J.V.D., and Hindell, M.A. 2002. The foraging ecology of two sympatric fur seal species, *Arctocephalus gazella* and *Arctocephalus tropicalis*, at Macquarie Island during the austral summer. Mar. Freshw. Res. **53**(7): 1071–1082. doi:10.1071/MF01218.

Scheffer, V.B., and Wilke, F. 1953. Relative growth in the northern fur seal. Growth, **17**(3): 129–145. PMID:13108094.

Sinclair, E., Loughlin, T., and Pearcy, W. 1994. Prey selection by northern fur seals (*Callorhinus ursinus*) in the eastern Bering Sea. Fish. Bull. (Wash., D.C.), **92**(1): 144–156.

Sivertsen, S.P., Pedersen, T., Lindstrom, U., and Haug, T. 2006. Prey partitioning between cod (*Gadus morhua*) and minke whale (*Balaenoptera acutorostrata*) in the Barents Sea. Mar. Biol. Res. **2**(2): 89–99. doi:10.1080/17451000600670952.

Snow, H.J. 1897. Notes on the Kuril Islands. Royal Geographic Society, London.

Sobolevskii, E.I., and Sokolovskaya, T.G. 1994. New data on the biology of the smoothtongue, *Leuroglossus schmidti* (Bathylagidae), in the Northwestern Pacific. J. Ichthyol. **34**(3): 20–27.

Sobolevskii, E.I., Sokolovskaya, T.G., Balanov, A.A., and Senchenko, I.A. 1996. Distribution and trophic relationships of abundant mesopelagic fishes of the Bering Sea. *In* Ecology of the Bering Sea: a review of Russian literature. *Edited by* O.A. Mathisen and K.O. Coyle. University of Alaska, Fairbanks. pp. 159–167.

Staniland, I.J. 2002. Investigating the biases in the use of hard prey remains to identify diet composition using Antarctic fur seals (*Arctocephalus gazella*) in captive feeding trials. Mar. Mamm. Sci. **18**(1): 223–243. doi:10.1111/j.1748-7692.2002.tb01030.x.

Staniland, I.J., Boyd, I.L., and Reid, K. 2007. An energy-distance

trade-off in a central-place forager, the Antarctic fur seal (*Arctocephalus gazella*). Mar. Biol. **152**(2): 233–241. doi:10.1007/s00227-007-0698-9.

Temnykh, O.S., and Marchenko, S.L. 2002. Variability of the pink salmon sizes in relation with abundance of Okhotsk Sea stocks. PICES Sci. Rep. No. 20.

Tollit, D.J., Wong, M., Winship, A.J., Rosen, D.A.S., and Trites, A.W. 2003. Quantifying errors associated with using prey skeletal structures from fecal samples to determine the diet of Steller's sea lion (*Eumetopias jubatus*). Mar. Mamm. Sci. **19**(4): 724–744. doi:10.1111/j.1748-7692.2003.tb01127.x.

Tollit, D., Heaslip, S., Deagle, B., Iverson, S., University, D., Joy, R., Rosen, D., and Trites, A. 2006. Estimating diet composition in sea lions: which technique to choose? *In* Sea lions of the world. *Edited by* A.W. Trites, S.K. Atkinson, D.P. DeMaster, L.W. Fritz, T.S. Gelatt, L.D. Rea, and K.M. Wynne. Alaska Sea Grant College Program, Anchorage. pp. 293–307.

Tollit, D.J., Heaslip, S.G., Barrick, R.L., and Trites, A.W. 2007. Impact of diet-index selection and the digestion of prey hard remains on determining the diet of the Steller sea lion (*Eumetopias jubatus*). Can. J. Zool. **85**(1): 1–15. doi:10.1139/z06-174.

Treacy, S.D., and Crawford, T.W. 1981. Retrieval of otoliths and statoliths from the gastro-intestinal tracts and scats of marine mammals. J. Wildl. Manage. **45**(4): 990–993. doi:10.2307/3808110.

Trites, A.W., and Donnelly, C.P. 2003. The decline of Steller sea lions *Eumetopias jubatus* in Alaska: a review of the nutritional stress hypothesis. Mammal Rev. **33**(1): 3–28. doi:10.1046/j.1365-2907.2003.00009.x.

Trites, A.W., and Joy, R. 2005. Dietary analysis from fecal samples: how many scats are enough? J. Mammal. **86**(4): 704–712. doi:10.1644/1545-1542(2005)086[0704:DAFFSH]2.0.CO;2.

Trumble, S.J., and Castellini, M.A. 2005. Diet mixing in an aquatic carnivore, the harbour seal. Can. J. Zool. **83**(6): 851–859. doi:10.1139/z05-069.

Trumble, S.J., Barboza, P.S., and Castellini, M.A. 2003. Digestive constraints on an aquatic carnivore: effects of feeding frequency and prey composition on harbor seals. J. Comp. Physiol. B Biochem. Syst. Environ. Physiol. **173**(6): 501–509. doi:10.1007/s00360-003-0358-4. PMID:12856134.

Waite, J.N. 2010. Resource partitioning among sympatric Steller sea lions and northern fur seals on Lovushki Island, Russia. Ph.D. dissertation, School of Fisheries and Ocean Sciences, University of Alaska, Fairbanks.

Waite, J.N., and Burkanov, V.N. 2006. Steller sea lion feeding habits in the Russian Far East, 2000–2003. *In* Sea lions of the world. *Edited by* A.W. Trites, S.K. Atkinson, D.P. DeMaster, L.W. Fritz, T.S. Gelatt, L.D. Rea, and K.M. Wynne. Alaska Sea Grant College Program, Anchorage. pp. 223–234.

Waite, J.N., Waits, L.P., Bozza, M., and Andrews, R.D. 2011. Differentiating between Steller sea lion (*Eumetopias jubatus*) and northern fur seal (*Callorhinus ursinus*) scats through analysis of faecal DNA. Mol. Ecol. Resour. **11**(1): 166–170. doi:10.1111/j.1755-0998.2010.02874.x. PMID:21429117.

Wallace, R.K., Jr. 1981. An assessment of diet-overlap indexes. Trans. Am. Fish. Soc. **110**(1): 72–76. doi:10.1577/1548-8659(1981)110<72:AAODI>2.0.CO;2.

Watanabe, H., Kubodera, T., Moku, M., and Kawaguchi, K. 2006. Diel vertical migration of squid in the warm core ring and cold water masses in the transition region of the western North Pacific. Mar. Ecol. Prog. Ser. **315**: 187–197. doi:10.3354/meps315187.

Wathne, J.A., Haug, T., and Lydersen, C. 2000. Prey preference and niche overlap of ringed seals *Phoca hispida* and harp seals *P. groenlandica* in the Barents Sea. Mar. Ecol. Prog. Ser. **194**: 233–239. doi:10.3354/meps194233.

Winship, A.J., Trites, A.W., and Rosen, D.A.S. 2002. A bioenergetic model for estimating the food requirements of Steller sea lions *Eumetopias jubatus* in Alaska, USA. Mar. Ecol. Prog. Ser. **229**: 291–312. doi:10.3354/meps229291.

Yonezaki, S., Kiyota, M., Baba, N., Koido, T., and Takemura, A. 2003. Size distribution of the hard remains of prey in the digestive tract of northern fur seal (*Callorhinus ursinus*) and related biases in diet estimation by scat analysis. Mammal Study, **28**(2): 97–102. doi:10.3106/mammalstudy.28.97.

Yonezaki, S., Kiyota, M., Baba, N., Koido, T., and Takemura, A. 2004. An enema technique to collect dietary information from northern fur seals (*Callorhinus ursinus*) at sea. Aquat. Mamm. **30**(2): 284–288. doi:10.1578/AM.30.2.2004.284.

Zaret, T.M., and Rand, A.S. 1971. Competition in tropical stream fishes: support for the competitive exclusion principle. Ecology, **52**(2): 336–342. doi:10.2307/1934593.

Zeppelin, T.K., and Ream, R.R. 2006. Foraging habitats based on the diet of female northern fur seals (*Callorhinus ursinus*) on the Pribilof Islands, Alaska. J. Zool. (Lond.), **270**(4): 565–576. doi:10.1111/j.1469-7998.2006.00122.x.