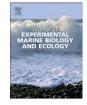
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Resource partitioning by sympatric Steller sea lions and northern fur seals as revealed by biochemical dietary analyses and satellite telemetry

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ABSTRACT

Over 1000 endangered Steller sea lions (SSL, Eumetopias jubatus Schreber, 1776) and approximately 14000 northern fur seals (NFS, Callorhinus ursinus L, 1758) breed sympatrically at the Lovushki Island complex, located in the northern Kuril Island chain in the Russian Far East, creating the potential for inter-specific competition for prey resources. The diets and foraging locations of both species were examined through the analysis of δ^{15} N and δ^{13} C stable isotope (SI) ratios of vibrissae, fatty acid (FA) profiles of blubber biopsies, and telemetry data collected during the breeding seasons of 2007 and 2008. There were significant differences in the mean δ^{15} N and δ^{13} C values between SSL and NFS. Adult female SSL were significantly enriched in both δ^{15} N and δ^{13} C over adult female NFS (by 2.04% \pm 0.23% and 0.83% \pm 0.12%, respectively), which indicates that the sea lions were feeding at a higher trophic level and in a different geographical location than the fur seals. The higher mean δ^{13} C levels found in the sea lion vibrissae suggest that they fed nearshore and benthically, while fur seals fed primarily offshore and pelagically. There were significant differences in the blubber FA profiles between SSL and NFS, indicating that the two species have different foraging strategies with respect to the types and/or proportions of prey items consumed. Foraging behavior analysis also indicated that SSL foraged nearshore and benthically and breeding NFS foraged primarily offshore and pelagically. The combination of these methodologies suggests breeding NFS and SSL partition their forage resources by prey type, as well as spatially, which likely reflected the differences in provisioning strategies of the adults and the fasting abilities of their pups.

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1. Introduction

Steller sea lions (SSL, *Eumetopias jubatus* Schreber, 1776) breed sympatrically with northern fur seals (NFS, *Callorhinus ursinus* L., 1758) on four rookeries in the Russian Far East, including Lovushki Island (48.5436° N, 153.6736° E) in the Kuril Island chain (Fig. 1). Approximately 43% of the total SSL pup production in Russian waters occurs on these rookeries (Burkanov and Loughlin, 2005). Similar to the Western stock of SSL in North American waters, the Asian stock of SSL experienced a dramatic decline and has been unstable for the past four decades (Burkanov and Loughlin, 2005; Loughlin et al., 1992). Although the cause has not been determined, one hypothesis for the decline in North American waters is nutritional stress due to

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changes in the prey base composition (Calkins and Goodwin, 1988; DeMaster and Atkinson, 2002; NMFS, 1995). After experiencing an approximate 80% decline in population from 1955 to 1989, followed by a slight increase, the abundance of non-pup SSL on Lovushki Island has remained relatively stable at an average of 1039 SSL from 1995 to 2005 (Burkanov and Loughlin, 2005). After a slow recovery from eradication in the late 19th century, the NFS population also experienced a period of relative stability from approximately 1978–1988 (Kuzin, 1999); however, a rapid increase in NFS population numbers ensued during the early 21st century, and the pup population grew to 12180 pups by 2006 (Burkanov et al., 2007), placing the non-pup population on Lovushki Island at an estimated 28420 adult and juvenile NFS when pups are assumed to comprise 30% of the total population (Kuzin, 1999).

Non-interbreeding species occupying the same ecological niche and exploiting the same limited resources must modify how they exploit the available resources in order to reduce inter-specific competition that may cause the absolute exclusion of one of the species. SSL and NFS are both piscivorous, sexually dimorphic pinnipeds with similar ecological requirements and life history traits. With a 2–3 month overlap in breeding seasons (May–August) and pup nursing,

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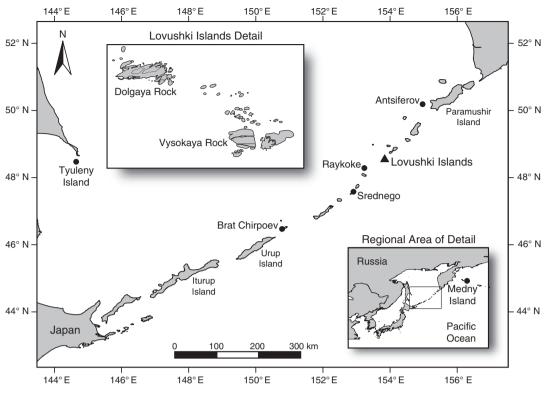


Fig. 1. Location of study site.

foraging could become competitive as adult females of both species are central place foragers, alternating between periods of foraging at sea and nursing their pups on land (Gentry, 2002; Gentry and Kooyman, 1986; Mathisen et al., 1962; Pitcher and Calkins, 1981).

To assess the level of dietary overlap, and thus competition for prey between two sympatric species, it is often necessary to consider foraging behavior and prey consumption over a range of time scales. Distribution of prey items may change over the course of the breeding season, prompting a change in foraging effort by one or more of the resident predator species. Further, any one particular sampling effort may occur during an anomalous and/or ephemeral influx of a specific prey type, and depending on the type of sample collected, inferences regarding the overall dietary composition for the entire breeding season based on such samples may be erroneous.

The composition of SSL and NFS diets has been determined primarily through the analysis of undigested prey remains recovered from stomach and intestinal contents, scats, and spews (Gudmundson et al., 2006; Trites et al., 2007; Waite and Burkanov, 2006; Waite et al., 2012; Zeppelin and Ream, 2006). However, there are a number of biases implicit to these techniques (Arim and Naya, 2003; Dellinger and Trillmich, 1988; Gales and Cheal, 1992; Harvey and Antonelis, 1994; Staniland, 2002). On Lovushki Island, where inter-specific spatial mixing of sympatric species occurs, it can be difficult to distinguish between scats of different predator species without molecular techniques (Waite et al., 2011). Determination of diet among different age and reproductive groups can also be difficult when relying on scats. Furthermore, analysis of samples from a single collection effort only provides information on prey consumed during the animal's most recent foraging trip and results may be biased by opportunistic feeding during the return trip from the primary foraging grounds or from voiding of gastrointestinal contents while at sea.

Naturally occurring stable nitrogen (¹⁵N) and carbon (¹³C) isotopes (SI) in pinniped tissues have been used successfully for the reconstruction of diets and trophic position (Dehn et al., 2007; Hall-Aspland et al., 2005; Hobson et al., 1997), estimation of foraging location (Aurioles et al., 2006; Burton and Koch, 1999), and investigation of physiological condition and maternal strategies (Newsome et al., 2006; Sinisalo et al., 2008). The stepwise enrichment of ¹⁵N in tissues of ~3–5‰ per trophic level allows for the estimation of an organism's relative trophic position in a food web (DeNiro and Epstein, 1981; Minagawa and Wada, 1984). Carbon isotope ratios are less significant in determining trophic position in marine mammals because of the weak isotopic fractionation of ¹³C (~0.1–1.1‰) across trophic levels of higher level consumers (DeNiro and Epstein, 1978; Hirons et al., 2001a; Kurle and Worthy, 2001), but δ^{13} C levels can be used to determine relative foraging location (France, 1995; Hobson, 1999; Kurle and Gudmundson, 2007; Kurle and Worthy, 2002).

Isotopic signatures of metabolically active tissues reflect recent feeding activity, whereas tissues with slower biochemical turnover rates integrate SI from the diet over longer periods of time (Hobson and Clark, 1992; Kurle and Worthy, 2002; Lesage et al., 2002). Serum has one of the fastest isotopic turnover rates (Lesage et al., 2002) and its SI signature corresponds to dietary assimilation from feeding activity within the previous 10-20 days (Hilderbrand et al., 1996; MacAvoy et al., 2006). However, the collection of serum (as well as most other tissues) is an invasive procedure and the compilation of large sample sizes may prove difficult. The isotopic composition of the biologically active portion of vibrissae (i.e., the root) reflects that of serum and corresponds to the previous 10–20 days of feeding activity for SSL (Stegall et al., 2008). While SI analysis of vibrissae does not identify specific prey species, it can provide a time-integrated record of a predator's trophic level and general foraging location, possibly over the entire lifespan of the animal (Hirons et al., 2001b).

Fatty acids (FA) are the primary constituents of lipids, and when consumed, can provide an index of seasonal, sex, geographic as well as inter/intraspecific dietary differences (Beck et al., 2005; Grahl-Nielsen et al., 2005; Iverson et al., 1997; Meynier et al., 2008; Møller et al., 2000; Thiemann et al., 2008). The period represented by the FA profile in the blubber of fur seals and sea lions may depend on the physiological condition of the animal at the time of sampling. During periods of heavy feeding and weight gain, usually outside of the breeding season, the FA profile may reflect either the current

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