



MARINE MAMMAL SCIENCE, 28(1): 1–15 (January 2012)
© 2011 by the Society for Marine Mammalogy
DOI: 10.1111/j.1748-7692.2011.00463.x

Prey selection of subadult male northern fur seals (*Callorhinus ursinus*) and evidence of dietary niche overlap with adult females during the breeding season

KATHERINE A. CALL

ROLF R. REAM

NOAA, National Marine Fisheries Service,
Alaska Fisheries Science Center,
National Marine Mammal Laboratory
7600 Sand Point Way NE,
Seattle, Washington 98115, U.S.A.
E-mail: kate.call@noaa.gov

ABSTRACT

During the breeding season northern fur seals (*Callorhinus ursinus*) congregate on the Pribilof Islands in large numbers creating the potential for intraspecific competition. Due to the declining trend in the Pribilof Islands population of fur seals, it is important to understand how prey resources are partitioned among the population. Fur seals exhibit a high degree of sexual dimorphism resulting in energetic differences among age and sex classes. Therefore, we hypothesized that subadult male and adult female fur seals would differ in the type and size of prey consumed. We examined the diets of subadult male (age 2–8; mean mass 28–176 kg) and adult female (age ≥ 3 yr; mean mass 13–50 kg) seals on St. Paul Island from 1992 to 2000. Prey remains found in fecal samples were compared using niche overlap indices. There was nearly complete dietary niche overlap between subadult male and adult female fur seals. Walleye pollock (*Theragra chalcogramma*), Pacific salmon (*Oncorhynchus* spp.), Pacific herring (*Clupea pallasii*), and cephalopods were common prey items found in the diets of both groups. We found differences in the size of pollock consumed and that geographic location of sample collection may be important in determining diet differences. Our results indicate high levels of dietary overlap among subadult male and adult female fur seals.

Key words: northern fur seal, *Callorhinus ursinus*, niche overlap, Bering Sea, pinnipeds, foraging behavior.

How colonial breeders partition prey during the breeding season, when large numbers of individuals are vying for resources, remains an important area of ecological research. To maximize success individuals may consume similar prey in different proportions (Whitehead *et al.* 2003), shift prey types (Clarke *et al.* 1998), or partition habitats (Schoener 1970). In extreme cases, competition for resources may lead to the exclusion of one group from the contested habitat (Kruuk *et al.* 1994) but more

often, individuals modify their behaviors, such as alternating the niche they exploit in order to coexist (Loveridge and Macdonald 2003).

Niche theory provides a framework for examining competition within ecological communities (Pianka 1975, Bolnick *et al.* 2003). Niche metrics have been used by ecologists to describe both interspecific differences in feeding among sympatric species (Dellinger and Trillmich 1999, Wathne *et al.* 2000, Elmhagen *et al.* 2002, Page *et al.* 2005) and among individuals within populations that utilize the same foraging habitats (Sol and Lefebvre 2000, Field *et al.* 2005, Page *et al.* 2005, Breed *et al.* 2006). Individuals within a population may vary in the way they exploit prey resources to reduce competition (Charnov *et al.* 1976, Grant 1986) and therefore availability of resources may dictate prey preference and foraging behavior. Segregation of trophic, temporal, and spatial niches reduces competition and allows individuals to coexist.

Northern fur seals (*Callorhinus ursinus*) are widely distributed throughout the North Pacific Ocean and Bering Sea. The Pribilof Islands population accounts for over half of all breeding northern fur seals in the world and is an important component of the Bering Sea ecosystem during summer and fall months. The Pribilof Islands population of *C. ursinus* have experienced a significant decline since the mid-1980s and recent estimates indicate that pup production has declined 5.8% per year since 1998 (Towell *et al.* 2006). The cause of the decline is unknown and contributing factors may include climate change (York 1995), predation (Springer *et al.* 2003) and interactions with commercial fisheries (Trites 1992).

During the summer months, northern fur seals congregate in large breeding areas (rookeries) where females give birth to a single pup that is nursed for several months. During this time adult female fur seals behave as central place foragers (Orians and Pearson 1979), alternating foraging trips with periods of nursing. Subadult males are nonbreeding, typically range from 2 to 8 yr of age and occupy haul-out sites adjacent to their natal rookeries until they reach breeding status (Scheffer and Wilke 1953, Johnson 1968, Gentry 1998). Haul-out sites are structured based on male size and age and provide a setting where young males acquire fighting and territorial maintenance skills (Gentry 1998). Subadult males also behave as central place foragers during the breeding season, alternating feeding bouts with time ashore where ontogenetic changes in young male behavior occurs (Gentry 1979, Sterling and Ream 2004). Telemetry studies revealed that both juvenile male and adult female fur seals exhibit colony-specific foraging site fidelity and that diving bouts are associated with bathymetric features of the continental shelf (Robson *et al.* 2004, Sterling and Ream 2004, Call *et al.* 2008). Because nonbreeding males are not restricted by dependent young or bound to defend breeding territories, they tend to travel farther from shore and remain at sea longer than adult females (Sterling and Ream 2004). Adult males fast while holding territories and are therefore removed from utilizing prey resources during the breeding season.

Intraspecific differences in foraging niche and habitat requirements may be related to an individual's age and social status (Polis 1984, Sol and Lefebvre 2000, Field *et al.* 2007), body size (Shine *et al.* 2002, Woodward and Hildrew 2002, Wikelski *et al.* 2003, Radloff and Du Toit 2004, Field *et al.* 2005), and sex (Page *et al.* 2005, Beck *et al.* 2007). In association with their polygynous mating system, *C. ursinus* display a high degree of sexual dimorphism (Scheffer and Wilke 1953) resulting in energetic differences between males and females (Costa and Gentry 1986, Ono and Boness 1996, Winship *et al.* 2002). In species such as *C. ursinus*, where the degree of sexual dimorphism is pronounced, young males need to grow rapidly to

maximize their lifetime reproductive success, while ontogenetic changes in females are less profound and their social role is established at a younger age (Gentry 1998). As a result, *C. ursinus* may show sex-specific niche segregation which maximizes the foraging success of each sex and age class (Shine *et al.* 2002, Beck *et al.* 2003, Field *et al.* 2007).

The diet of adult female *C. ursinus* has been studied extensively by identifying prey items from stomachs (Wilke and Kenyon 1957, Perez and Bigg 1986, Sinclair *et al.* 1994), fecal samples (Sinclair *et al.* 1996, Antonelis *et al.* 1997, Zeppelin and Ream 2006), regurgitations (Gudmundson *et al.* 2006), and stable isotope analysis (Kurle and Worthy 2001). Juvenile walleye pollock (*Theragra chalcogramma*) and gonatid squid species are the dominant prey of adult female *C. ursinus* (Zeppelin and Ream 2006). While the diet of adult females is well documented, there is little information available on the diet of subadult male fur seals. Kiyota *et al.* (1999) examined 19 scats and 6 regurgitations collected from subadult males and found walleye pollock, Pacific sand fish (*Trichodon trichodon*), and gonatid squid to be major components of these samples.

We describe the diet of subadult male *C. ursinus* from fecal samples collected over a number of years to determine the degree of overlap in prey type and prey size consumed by both subadult male and adult female *C. ursinus* on St. Paul Island during the breeding season. We hypothesize that differences in energetic costs related to sex-specific reproductive requirements, differences in body size, and ontogenetic changes will be reflected in patterns of prey exploitation. Understanding the extent of dietary niche overlap is important to assess resource utilization in fur seals and any possible effects on a declining population.

METHODS

We examined fecal samples (scats) collected during the breeding season from 13 rookeries and neighboring male haul-out sites on St. Paul Island, between 1992 and 2000 (Fig. 1). Scats were collected during biennial population assessments and, therefore, not all sites were sampled in all years. Samples were only included if they were collected in years where there was overlap between rookery and subadult male hauling ground sample collections. During the peak of breeding, when scats are collected, there is a clear division between rookeries and haul-out sites (Fig. 2). Long-term studies document the consistency of these areas overtime (Gentry 1998) and researchers collecting scats are aware of the boundaries between rookeries and male haul-out sites (hauling grounds) (Fig. 2). Due to the structure of territories on rookeries during the breeding season, samples collected from haul-out sites on the periphery of the breeding territories are assumed to be from subadult males (age 2–8; mean mass range 28–176 kg, Lander 1981) and those collected in areas where mating occurs are assumed to be from reproductively mature females (age ≥ 3 yr; mean mass range 13–50 kg, Lander 1981).

Scats were stored in plastic bags and frozen before they were processed in the laboratory. Each sample was rinsed through a series of nested mesh sieves measuring 4.8, 1.7, 0.7, and 0.5 mm. Dietary summaries of prey consumed were created using all prey remains (cephalopod beaks, fish bones, and otoliths) identified to the lowest taxa using a comparative reference collection. Niche statistical analysis requires that prey be identified to the lowest common taxonomic denominator. Therefore identifiable prey remains were grouped by family because not all prey items could be identified

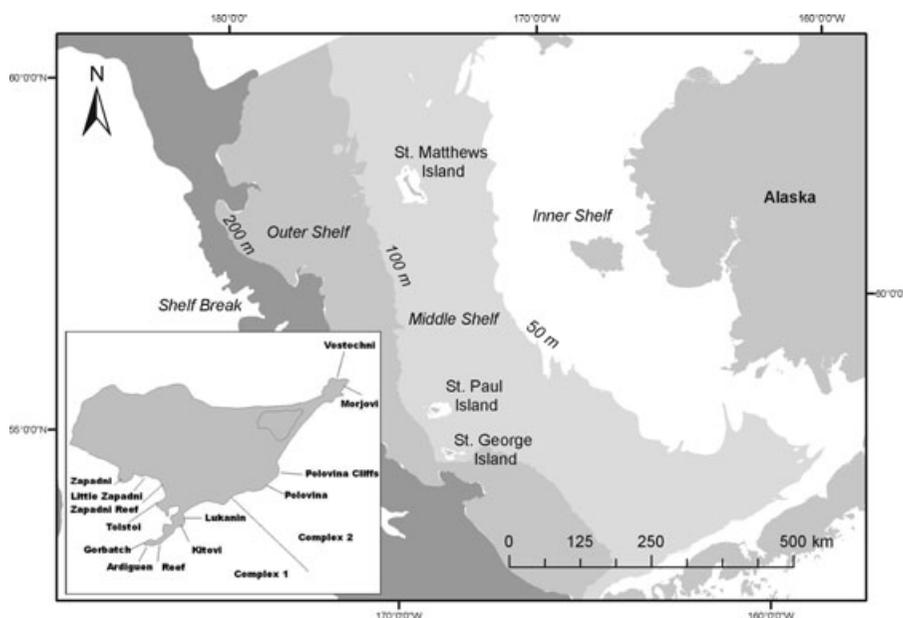


Figure 1. Map of St. Paul Island and the location *C. ursinus* breeding rookeries and haul-out sites ($n = 13$) where fecal samples were collected. Bering Sea shelf domains used to describe foraging habitat are also identified as inner shelf (<50 m), middle shelf (51–100 m), outer shelf (101–200 m), shelf break (201–1,000 m), and oceanic (>1,000 m).

to species. In addition to identification, fish bones, otoliths, and cephalopod beaks were separated and stored for measurement. Due to structural similarities of beaks among some squid species, taxonomic resolution is difficult. As a result, we grouped *Gonatopsis borealis* with *Beryteuthis magister* (*G.b./B.m.*), and *Gonatus middendorffi* with *Gonatus madokai* (*G.m./G.m.*) according to Sinclair *et al.* (1994).

Only scats containing identifiable prey remains were used to calculate frequency of occurrence (FO). Each scat was treated as an independent sample and the importance of each prey item was based on the relative frequency it occurred in the scats. Percent FO of prey was calculated by dividing the number of scats in which a prey species occurred by the total number of scats containing identifiable prey remains. All samples for each sex were pooled for FO calculations within multiple years and among multiple collection sites only after chi-square tests on the prey occurrence greater than 1% showed no difference in occurrence among years for either sex.

Recent studies have demonstrated fur seal rookeries located in close geographic proximity to one another can be grouped based on similarities in the FO of primary prey consumed (Zeppelin and Ream 2006). Furthermore, telemetry studies show that females tracked from these rookery complexes share common foraging locations and these distinct rookery-specific foraging areas persist over time (Robson *et al.* 2004, Call *et al.* 2008). In general rookeries located on the northeastern side of St. Paul Island can be distinguished from rookeries located on the southwestern side by both the types of prey consumed and by foraging locations. Based on these findings scats collected from rookeries and haul-out sites on the southwest side of the island (Complex 1) were grouped separately from scats collected from sites on the northeast

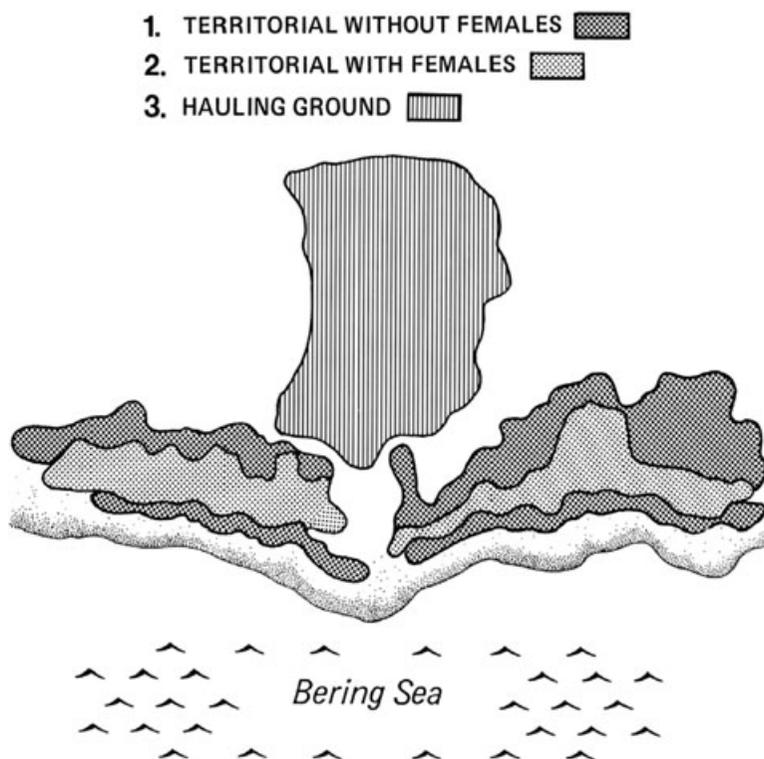


Figure 2. Example depicting the structure of a typical fur seal rookery and haul-out area during the breeding season. The division among area 1 (idle bulls) and area 2 (breeding grounds) are separated from area 3, the hauling grounds where subadult males spend their time on shore.

side (Complex 2) to determine if the geographic location of rookery or haul-out sites was a factor in determining niche separation (Fig. 1). FO and niche overlap measures were calculated for each sex separately regardless of sample collection location, for each sex grouped by geographic area (complex), and by combining both sexes within each geographic area.

For each sample we determined the size of walleye pollock ingested by first counting the number of right and left otoliths, and then selecting and measuring the side with the greatest number. Because the body-shape of walleye pollock is symmetrical the left and right otoliths are mirror images and no significant difference has been found in the number or size of right compared to left otoliths recovered in scats. Pollock otoliths recovered were assigned a condition grade based the digestive wear on distinctive features (Sinclair *et al.* 1994, Antonelis *et al.* 1997, Tollit *et al.* 2004). Those in “good” or “fair” condition were measured to the nearest 0.1 mm using hand-held digital calipers. A condition-specific correction factor was applied to the “fair” grade otoliths to account for wear (Tollit *et al.* 2004). Otoliths determined to be in poor condition were not used. Fork length (FL) was determined using the quadratic equation presented in Zeppelin *et al.* (2004), which describes the relationship between otolith length and fork length.

To determine the size of *G.b./B.m.* and *G.m./G.m.* consumed, we measured the lower rostral length (LRL) of beaks recovered from the scats. Dorsal mantle length (DML) of each squid was then estimated from the LRL using regression equations (Gudmundson *et al.* 2006, Zeppelin and Ream 2006). Only beaks in good condition (not eroded or broken) were measured and therefore a correction factor for erosion was not needed.

Niche Overlap Indices

To quantify the dietary overlap between prey types, prey size, and geographic location of sample collection among subadult male and adult female *C. ursinus* we used the niche overlap index (O) developed by Schoener (1968):

$$O = 1 - 0.5 * |p_{ij} - p_{ik}| \quad (1)$$

where p_{ij} and p_{ik} are the FO of the type or size of the i th prey item consumed by males (j) and females (k). The result is a value ranging between 0 (no overlap) and 1 (complete overlap). A value greater than 0.60 suggests a biologically significant overlap in the resources examined (Wallace 1981).

Foraging niche breadth for the types of prey and the size of pollock and squid consumed was calculated using Levin's (1968) niche breadth:

$$B = \frac{1}{\sum_{i=1}^n p_i^2} \quad (2)$$

where p_i is the proportion of prey item i consumed or the occurrence of a particular size of prey found in the diet and n is the number of prey groups or size classes. The number varies between one and the total number of prey (or size classes) found in the diet. The more evenly the prey type or size of prey are consumed, the greater the niche breadth. For the purpose of niche overlap calculations, prey type was identified to the lowest taxonomic denominator (family) and we assumed that all resources were equally available among subadult males and adult females.

RESULTS

We analyzed a total of 3,568 scats with prey remains collected from subadult male ($n = 1,225$) and adult female ($n = 2,343$) *C. ursinus* on St. Paul Island between 1992 and 2000. An additional 834 samples were collected, but contained no prey remains (Table 1). There was almost complete dietary niche overlap in the prey types consumed by subadult male and adult female fur seals based on Schoener's index ($O = 0.91$). Walleye pollock was the dominant prey species for both groups. Other top prey included cephalopods, Pacific salmon (*Oncorhynchus* spp.), sand lance (*Ammodytes hexapterus*), and Pacific herring (Table 1). Pacific sand fish (*Trichodon trichodon*) and polychaete worms were the only prey to be consumed nearly exclusively by males, whereas females consumed a higher frequency of herring and salmon (Table 1). Subadult males consumed a slightly broader range of prey ($B = 1.8$) compared to females ($B = 1.4$).

Although still significant, niche overlap measures based on the geographic location of sample collection resulted in less diet overlap within each sex grouped by

Table 1. Summary of identifiable prey remains found in subadult male and adult female *C. ursinus* scats. Frequency of occurrence was determined to the lowest taxonomic distinctions possible and limited to prey occurring in amounts greater than 1%.

	Subadult male	Adult female
Scats containing identifiable prey	1,225	2,343
Blank samples	321	513
Prey items	% frequency of occurrence	
Family Gadidae		
<i>Theragra chalcogramma</i> (walleye pollock)	68.9	66.1
<i>Gadus macrocephalus</i> (Pacific cod)	2.7	1.1
Gadidae, not hake	19.7	34.2
Gadidae, unidentified	2.9	5.9
Class Cephalopoda (squids and octopus)		
<i>Gonatopsis borealis/Berryteuthis magister</i>	5.3	3.9
<i>Gonatus madokai/Gonatus middendorfi</i>	6.8	7.2
Squid spp.	1.5	1.6
Squid/octopus	1.6	1.5
Family Trichodontidae		
<i>Trichodon trichodon</i> (Pacific sandfish)	10.2	2.3
Family Ammodytidae (sand lances)		
<i>Ammodytes hexapterus</i>	8.5	8.4
Family Salmonidae		
<i>Oncorhynchus</i> spp. (Pacific salmon spp.)	6.0	8.5
Family Clupeidae		
<i>Clupea pallasii</i> (Pacific herring)	4.4	9.6
Family Hexagrammidae (greenlings)		
<i>Pleurogrammus monoptyerygius</i> (Atka mackerel)	0.9	1.5
<i>Hexagrammos</i> spp. (rock greeling)	1.2	1.4
Unidentified greenling	2.4	1.6
Order Polychaeta	2.5	<1
Family Anoplopomatidae		
<i>Anoplopoma fimbria</i> (sablefish)	1.4	1.5
Unidentified Anoplopomatidae		
Order Pleuronectiformes (flatfishes)		
Unidentified Pleuronectiformes	1.0	<1
Family Bathylagidae (deep sea smelts)		
Bathylagidae		
<i>Leuroglossus schmidti</i> (northern smoothtongue)	1.0	1.1
Family Myctophidae (lanternfishes)	1.1	1.1

complex (subadult male $O = 0.74$; adult female $O = 0.75$), and among sex compared by complex ($O = 0.83$), than between sex when all samples were pooled across geographic regions ($O = 0.91$). Scats collected from rookeries and haul-out sites within complex 1 (southwest side of the island) contained greater relative amounts of pollock, cephalopods, and salmon compared to scats collected from complex 2 (northeast side of the island), which contained greater frequencies of sand lance, sand fish, and herring (Table 2). In addition, we found that scats collected from the SW side of the island had a slightly narrower niche breadth for all groups examined; within subadult males ($B = 1.4$), within females ($B = 1.4$), and for subadult males and females combined ($B = 1.4$), than complex 2; within subadult males ($B = 2.2$),

Table 2. Frequency of occurrence of prey found in amounts >1% determined to the lowest common taxonomic denominator (family). Prey occurrences were determined among and within geographic location of sample collection and by sex. Complex 1 includes scat samples collected from rookeries and haul-out sites located on the southwest side of the island and Complex 2 includes samples collected from sites on the northeast side.

Prey	Subadult			Subadult		
	male Complex 1	Female Complex 1	Both sexes Complex 1	male Complex 2	Female Complex 2	Both sexes Complex 2
Pollock	80.0	81.9	81.3	73.0	82.9	78.8
Cephalopods	17.4	16.7	17.0	9.5	5.9	7.4
Salmon	7.2	9.2	8.4	4.7	7.5	6.3
Sand lance	6.5	3.9	4.9	10.7	10.3	10.5
Herring	2.4	9.7	6.9	6.6	9.4	8.2
Atka Mackerel	2.4	3.2	2.9	2.8	3.4	3.2
Sandfish	1.7	1.8	1.8	19.4	2.8	10.0
Smoothtongue	1.5	1.7	1.6	0.7	0.4	0.5
Sablefish	2.0	1.2	1.5	1.2	1.8	1.5
Flatfishes	1.5	0.7	1.0	0.9	1.2	1.1
Lanternfishes	0.4	1.2	1.0	0.7	0.2	0.4
Polychaete	0.9	0.1	0.4	4.3	0.2	1.9

within females ($B = 1.9$), and between subadult males and females combined ($B = 2.0$).

The majority of the pollock otolith samples used to determine size distribution ($n = 2,576$) were from scats collected between 1998 and 2000 ($n = 326$, subadult male; $n = 2,250$, female). We did not find a biologically significant dietary niche overlap in the size distribution of pollock consumed ($O = 0.54$) and our results indicate subadult male and adult female fur seals consumed different sizes of pollock. The mean size of pollock consumed by subadult males ($\bar{x} = 10.5 \text{ cm} \pm 6.2 \text{ cm}$) was significantly smaller than pollock consumed by adult females (FL = 15.7 cm \pm 9.4 cm, two-tailed t -test, $P < 0.0001$ cm). In addition, adult females consumed greater relative numbers of age-0 (FL ≤ 10 cm) and age-2 (FL = 20–27 cm) pollock, while subadult males consumed greater relative numbers of age-1 (FL = 11–19 cm) and mature sized (FL > 27cm) fish (Fig. 3) Young males consumed a broader size range of pollock ($B = 2.0$) compared to adult females ($B = 1.7$).

Squid size was estimated from a total of 1,146 cephalopod beaks (subadult male, $n = 340$; female, $n = 806$). There was a biologically significant dietary niche overlap ($O > 0.60$) in the size distribution of squids consumed ($O = 0.83$), although subadult males tended to eat larger squids (mean DML = 71.7 cm \pm 21.9 cm), on average, than did adult females (mean DML = 64.3 \pm 17.9 cm, Fig. 4). Subadult males also consumed a broader range of sizes of cephalopods ($B = 5.8$) compared to females ($B = 4.3$).

DISCUSSION

This is the first study to present a comprehensive analysis of subadult male *C. ursinus* diet and compare the extent of dietary niche overlap between subadult males and adult females. We expected that differences in energetic requirements

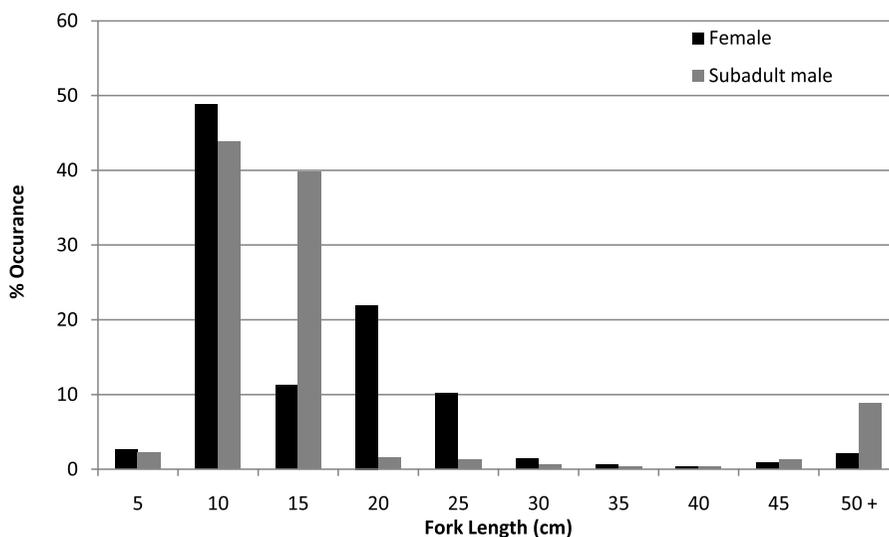


Figure 3. Fork length distribution of walleye pollock consumed by subadult male and adult female northern fur seals based on the frequency of occurrence of individuals recovered from scats collected on rookeries and haul-out sites on St. Paul Island.

related to sex specific reproductive requirements, in body size, accelerated growth rate of males after age five (Gentry 1998), and foraging experience, would lead to differential prey selection between subadult male and adult female fur seals. Contrary to our expectations we found almost complete overlap in the types of prey consumed by subadult male and adult female *C. ursinus* ($O = 0.91$). Both subadult male and adult female fur seals summer diets showed a strong preference for walleye pollock and cephalopods. Our findings are similar to previously published work on adult female *C. ursinus* diets (Kajimura 1984, Perez and Bigg 1986, Sinclair *et al.* 1996, Antonelis *et al.* 1997, Zeppelin and Ream 2006). High energy fish (Iverson *et al.* 2002) including salmon and herring were important for females, whereas, Pacific sand fish and polychaete worms were found almost exclusively in male diets.

In pinnipeds, a seal's body size is correlated with its oxygen stores (Mori 2002). As a result, larger animals should be able to expand their foraging niche by diving deeper for longer durations. Northern fur seals show a high degree of sexual dimorphism (Scheffer and Wilke 1953) and subadult males occupying haul-out sites may be 1.5–4.5 times larger than breeding females on rookeries (Lander 1981). Therefore, we might expect that subadult males are able to access and handle larger prey when compared to their smaller female counterparts (Kooyman *et al.* 1981). However, when we examined the dietary niche overlap in the size of the top two prey types consumed by *C. ursinus*, we did not find evidence that young males consistently target larger prey. We found significant niche overlap in the size of squid consumed by both groups ($O = 0.60$), indicating subadult males and adult females select similar sizes of squid prey (Fig. 4). However, we found evidence that males and females target different sizes of walleye pollock ($O < 0.60$, Fig. 3), highlighting some subtle differences in the seemingly near complete overlap in the prey resources exploited. Subadult males, on average consumed significantly smaller pollock than

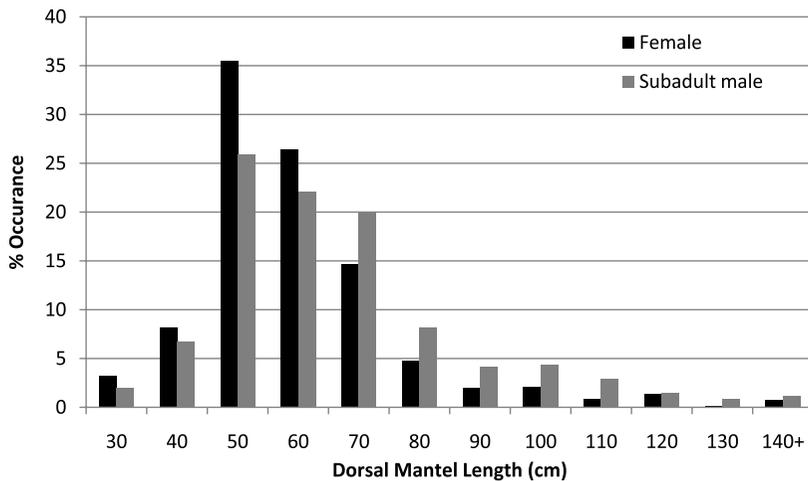


Figure 4. Size distribution of cephalopod species consumed by subadult male and adult female northern fur seals recovered from scats collected on rookeries and haul-out sites on St. Paul Island.

adult females and more than 80% of otoliths recovered from both sexes (Fig. 3) were from either age-0 or age-1 fish. In addition, mature pollock (FL \geq 30 cm) comprised 10% of the otoliths found in male diets and only 3% of female samples. Our results show some subtle partition in the size of prey consumed but not in the expected direction. This is interesting since we expect the larger predator to take larger prey. Subadult males and adult females select the size of pollock which is most available to them and clear size segregation between the sexes is not evident in the samples we examined.

Our findings are consistent with previous studies that found adult female and juvenile male fur seals consume primarily pollock measuring 3–20 cm and classified as age-0 or age-1 (Sinclair *et al.* 1996, Kiyota *et al.* 1999). In addition, recent studies demonstrate foraging behavior of both juvenile male (Sterling and Ream 2004) and adult female (Goebel *et al.* 1991) *C. ursinus* is associated with bathymetric features of the Bering Sea continental shelf and mean dive depths for both sexes are less than 40 m (Goebel *et al.* 1991, Sterling and Ream 2004). Furthermore, these dive patterns can be related to the movement of juvenile pollock (FL < 20 cm) into the upper 40 m of the water column at night (Bailey 1989, Schabetsberger *et al.* 2000), where they are easily assessable to fur seals (Goebel *et al.* 1991, Sinclair *et al.* 1996, Sterling and Ream 2004). Our mixed results on the differences in the size of pollock consumed by subadult male and adult female fur seals could be confounded by energetic demands related to reproductive status and by the level of foraging experience associated with age. However, it is difficult to distinguish among the possible effects of these factors on *C. ursinus* prey choice because individuals on haul-outs represent a range of body sizes, ages and development.

We have shown that the geographic location of haul-out and rookery sites may be important in determining niche segregation among *C. ursinus*. When prey were grouped based on geographic location of sample collection there was less dietary niche overlap than when prey were compared regardless of collection site. The differences we observed in subadult male prey consumption between geographic

locations were strikingly similar to previous reports of differences in prey consumption that distinguished female diet groups (Zeppelin and Ream 2006). Like females, dietary differences related to the geographic location of subadult male haul-outs are also reflected in their foraging patterns. Telemetry studies suggest juvenile males and adult females display similar patterns of rookery-specific foraging. In general, individuals tracked from rookeries and haul-sites on the SW side of the island forage in the deep waters off the continental shelf and those tracked from the NE side forage in the shallow waters over the continental shelf (Sterling and Ream 2004, Call *et al.* 2008). However, compared to adult females that are caring for a dependent pup, subadult males travel farther from shore (subadult male, $\bar{x} = 961 \pm 67$ km; female, $\bar{x} = 483 \pm 168$ km) and spend more time at sea (subadult male, $\bar{x} = 17 \pm 1$ d; female, $\bar{x} = 7.2 \pm 1.6$ d) (Sterling and Ream 2004, Call *et al.* 2008). Although subadult males and adult females tend to consume the same prey types subadult males travel farther from the island to forage (Sterling and Ream 2004). Similar patterns of spatial segregation of foraging habitats among different age and sex classes has also been demonstrated in New Zealand fur seals (*Arctocephalus australis forsteri*) where adult females typically foraged closer to shore than did adult and juvenile males (Page *et al.* 2006).

Even though non-breeding males are not restricted to a particular haul-out site they tend to be loyal to one area, presumably the haul-out adjacent to their birth rookery (Gentry 1998) and subadult male site fidelity increases as males reach sexual maturity (Baker *et al.* 1995). When subadult male prey remains were grouped based on location of haul-out location we found the lowest dietary niche overlap ($O = 0.74$) of any group. Subadult males from haul-outs located on the SW side of the island had high occurrences of prey species associated with the deep waters off the continental shelf including, pollock, squid, and salmon. Whereas, males from haul-outs located on the NE side of the island consumed greater frequencies of prey found in the shallow waters over the continental shelf, including sand fish, sand lances and polychaete worms (Table 2). The decreased niche overlap we observed among geographic area reflects differences in FO of prey and may indicate individuals from different haul-out locations use spatially segregated foraging areas.

Scats are abundant, easy to collect, minimally invasive and have proven to be a reliable method for assessing fur seal diets. However, there are inherent biases associated with using scats to assess the diets of pinnipeds (Bigg and Fawcett 1985, Pierce and Boyle 1991, Bowen 2000), including differential digestion among prey species (Harvey 1989, Tollit *et al.* 1997), varying passage rates due to differences in prey size (Gales *et al.* 1993) and bias towards near shore prey. We recognize that because of the biases associated with using scats to describe diet, our results may underestimate the types and sizes of prey consumed and may over represent prey taxa consumed near shore. These biases may be greater for subadult males because they spend more time at sea and may go through multiple feeding cycles before returning to shore. However, pinniped diet studies have demonstrated differences in prey consumed among seals with varying foraging ranges (Field *et al.* 2007) and we identified 33 prey families, consisting of benthic fish, pelagic fish and squid species, many of which occur in offshore waters several hundred km from shore. Although some prey species and large-sized pollock may be underrepresented in scat samples we feel it is an effective tool for examining fur seal diets.

Niche theory predicts that when resources are limited, to reduce intra-specific competition and maximize fitness, males and females will forage in different locations, on different species, or both (Schoener 1970, Charnov *et al.* 1976). Although subadult

male and adult female fur seals have different morphology, growth rates, and foraging experience, we found they have nearly complete dietary niche overlap. In addition, it appears that subadult males are opportunistic foragers feeding on the types and sizes of prey that are most accessible to them. We also presented evidence that subadult male and adult female fur seals may use similar strategies to partition prey resources by spatially segregating foraging habitats. However, further study is needed to establish that haul-out specific foraging areas exist among subadult male fur seals and that these areas are similar to the rookery-specific foraging areas which have already been defined for adult females (Robson *et al.* 2004, Zeppelin and Ream 2006, Call *et al.* 2008). Additional diet studies to obtain a more complete picture of subadult male foraging should include: the collection of regurgitations to accurately determine the distribution of larger prey (Gudmundson *et al.* 2006), information regarding prey availability, and telemetry studies of subadult males to document their winter migration and to assess if spatial partitioning of habitats occurs outside of the breeding season.

ACKNOWLEDGMENTS

We would like to thank all the field and laboratory personal who have collected and processed scat samples and identified and measured remains, making this study possible. Especially, S. Finneseth, C. Gundmundson, and J. Thomason. All samples were collected according to approved methods listed in our current northern fur seal research permit No. 782-1705-05 and according to internal animal care and handling procedures. We thank T. Zeppelin H. Fearnbach, Dr. K. Ono, and three anonymous reviewers for their helpful comments. We sincerely appreciate the thorough review of our manuscript by the reviewers. Their thoughtful suggestions greatly improved this manuscript.

LITERATURE CITED

- Antonelis, G. A., E. H. Sinclair, R. R. Ream and B. W. Robson. 1997. Inter-island variation in the diet of female northern fur seals, (*Callorhinus ursinus*) in the Bering Sea. *Journal of Zoology (London)* 242:435–451.
- Bailey, K. M. 1989. Interaction between the vertical distribution of juvenile walleye pollock *Theragra chalcogramma* in the eastern Bering Sea, and cannibalism. *Marine Ecology Progress Series* 53:205–213.
- Baker, J. D., G. A. Antonelis and A. E. York. 1995. Natal site fidelity in northern fur seals, *Callorhinus ursinus*. *Animal Behavior* 50:237–247.
- Beck, C. A., S. J. Iverson, W. D. Bowen and W. Blanchard. 2007. Sex differences in grey seal diet reflect seasonal variation in foraging behaviour and reproductive expenditure: Evidence from quantitative fatty acid signature analysis. *Journal of Animal Ecology* 76:490–502.
- Beck, C. A., W. D. Bowen and S. J. Iverson. 2003. Sex differences in seasonal patterns of energy storage and expenditure in a phocid seal. *Journal of Animal Ecology* 72:280–291.
- Bigg, M. A., and I. Fawcett. 1985. Two biases in diet determination of northern fur seals (*Callorhinus ursinus*). Pages 284–291 in J. R. Beddington, R. J. H. Beverton, and D. M. Lavigne, eds. *Marine mammals and fisheries*. George Allen and Unwin, London, U.K.
- Bolnick, D. I., R. Svanbäck, J. A. Fordyce, L. H. Yang, J. M. Davis, C. D. Hulsey and M. L. Forrester. 2003. The ecology of individuals: Incidence and implications of individual specialization. *American Naturalist* 161:1–29.
- Bowen, W. D. 2000. Reconstruction of pinniped diets: Accounting for complete digestion of otoliths and cephalopod beaks. *Canadian Journal of Fishery Aquatic Sciences* 57:898–905.

- Breed, G. A., W. D. Bowen, J. I. McMillan and M. L. Leonard. 2006. Sexual segregation of seasonal foraging habitats in a non-migratory marine mammal. *Proceedings of the Royal Society B: Biological Sciences* 273:2319–2326.
- Call, K. A., R. R. Ream, D. Johnson, J. T. Sterling and R. G. Towell. 2008. Foraging route tactics and site fidelity of adult female northern fur seal (*Callorhinus ursinus*) around the Pribilof Islands. *Deep-Sea Research II* 55:1883–1896.
- Charnov, E. L., G. H. Orians and K. Hyatt. 1976. Ecological implications of resource depression. *American Naturalist* 110:247–259.
- Clarke, J., B. Manly, K. Kerry, E. Franchi, S. Corsolini and S. Focardi. 1998. Sex differences in Adelie penguin foraging strategies. *Polar Biology* 20:248–258.
- Costa, D. P., and R. L. Gentry. 1986. Free-ranging energetic of pinnipeds: Implications for life history patterns. Pages 79–101 in R. L. Gentry and G. L. Kooyman, eds. *Fur seals: Maternal strategies on land and at sea*. Princeton University Press, Princeton, NJ.
- Dellinger, T., and F. Trillmich. 1999. Fish prey of sympatric Galapagos fur seals and sea lions: Seasonal variation and niche separation. *Canadian Journal of Zoology* 77:1204–1216.
- Elmhagen, B., M. Tannerfeldt and A. Angerbjorn. 2002. Food-niche overlap between arctic and red foxes. *Canadian Journal of Zoology* 80:1274–1285.
- Field, I. C., C. J. A. Bradshaw, J. Van Den Hoff, H. R. Burton and M. A. Hindell. 2007. Age-related shifts in the diet composition of southern elephant seals expand overall foraging niche. *Marine Biology* 150:1441–1452.
- Field, I. C., C. J. A. Bradshaw, H. R. Burton, M. D. Sumner and M. A. Hindell. 2005. Resource partitioning through oceanic segregation of foraging juvenile southern elephant seals. *Oecologia* 142:127–135.
- Gales, R., D. Pemberton, C. C. Lu and M. R. Clarke. 1993. Cephalopod diet of the Australian fur seal: Variation due to location, season and sample type. *Australian Journal of Marine and Freshwater Research* 44:657–671.
- Gentry, R. L. 1979. Land-sea movements of juvenile males. Marine Mammal Division, Fur Seal Investigations, 1978. U.S. Department of Commerce, NMFS, NWAFSC Processed Report. 84 pp.
- Gentry, R. L. 1998. Behavior and ecology of the northern fur seal. Princeton University Press, Princeton, NJ.
- Goebel, M. E., J. L. Bengtson, R. L. DeLong, R. L. Gentry and T. R. Loughlin. 1991. Diving patterns and foraging locations of female northern fur seals. *Fishery Bulletin* 89:171–179.
- Grant, P. R. 1986. The ecology and evolution of Darwin's finches. Princeton University Press, Princeton, NJ.
- Gudmundson, C. J., T. K. Zeppelin and R. R. Ream. 2006. Application of two methods for determining diet in northern fur seals (*Callorhinus ursinus*). *Fishery Bulletin* 104:445–455.
- Harvey, J. T. 1989. Assessment of errors associated with harbor seal (*Phoca vitulina*) fecal sampling. *Journal of Zoology (London)* 219:101–111.
- Iverson, S. J., K. J. Frost and S. L. C. Lang. 2002. Fat content and fatty acid composition of forage fish and invertebrates in Prince William Sound, Alaska: Factors contributing to among and within species variability. *Marine Ecology Progress Series* 241:161–181.
- Johnson, A. M. 1968. Annual mortality of territorial male fur seals and its management significance. *Journal of Wildlife Management* 32:94–99.
- Kajimura, H. 1984. Opportunistic feeding of the northern fur seal, *Callorhinus ursinus*, in the North Pacific Ocean and eastern Bering Sea. U.S. Department of Commerce, NOAA Technical Report, NMFS SSRF-779. 49 pp.
- Kiyota, M., C. Kawai and N. Baba. 1999. Estimation of the diet of male northern fur seals (*Callorhinus ursinus*) based on analysis of fecal and regurgitated materials. *Bulletin of National Research Institute of Far Seas Fisheries* 36:1–7.
- Kooyman, G. L., M. A. Castellini and R. W. Davis. 1981. Physiology of diving in marine mammals. *Annual Review of Physiology* 43:343–356.

- Kruuk, H., B. Kanchanasaka, S. O'Sullivan and S. Wanghangsa. 1994. Niche separation in 3 sympatric otters *Lutra perspicillata*, *L. lutra* and *Aonyx cinerea* in Hai Kha Khaeng, Thailand. *Biology Conservation* 69:115–120.
- Kurle, C. M., and G. A. J. Worthy. 2001. Stable isotope assessment of temporal and geographic differences in feeding ecology of northern fur seals (*Callorhinus ursinus*) and their prey. *Oecologia* 126:254–265.
- Lander, R. H. 1981. A life table and biomass estimate for Alaskan fur seals. *Fisheries Research (Amsterdam)* 1:55–70.
- Levin, R. 1968. Evolution in changing environments. Monographs in population biology. Princeton University Press, Princeton, NJ.
- Loveridge, A. J., and D. W. Macdonald. 2003. Niche separation in sympatric jackals (*Canis mesomelas* and *Canis adustus*). *Journal of Zoology* 259:143–153.
- Mori, Y. 2002. Optimal diving behavior for foraging in relation to body size. *Journal of Evolutionary Biology* 15:269–276.
- Ono, K. A., and D. J. Boness. 1996. Sexual dimorphism in sea lion pups: Differential maternal investment, or sex-specific differences in energy allocation? *Behavioral Ecology and Sociobiology* 38:31–41.
- Orians, G. H., and N. E. Pearson. 1979. On the theory of central place foraging. Pages 155–177 in D. J. Horn, G. R. Stairs, and R. D. Mitchell, eds. *Analysis of ecological systems*. Ohio State University Press, Columbus, OH.
- Page, B., J. McKenzie and S. D. Goldsworthy. 2005. Dietary resource partitioning among sympatric New Zealand and Australian fur seals. *Marine Ecology Progress Series* 293:283–302.
- Page, B., J. McKenzie, M. D. Sumner, M. Coyne and S. D. Goldsworthy. 2006. Spatial separation of foraging habitats among New Zealand fur seals. *Marine Ecology Progress Series* 323:263–279.
- Perez, M. A., and M. A. Bigg. 1986. Diet of northern fur seals, *Callorhinus ursinus*, off western North America. *Fishery Bulletin* 84:957–971.
- Pianka, E. R. 1975. Niche relations of desert lizards. Pages 292–319 in M. L. Cody and J. M. Diamond, eds. *Ecology and evolution of communities*. Harvard University Press, Cambridge, MA.
- Pierce, G. J., and P. R. Boyle. 1991. A review of methods for diet analysis in piscivorous marine mammals. *Oceanography Marine Biology Annual Review* 29:409–486.
- Polis, G. A. 1984. Age structure component of niche width and intraspecific resource partitioning: Can age groups function as ecological species? *American Naturalist* 123:541–564.
- Radloff, F. G. T., and J. T. Du Toit. 2004. Large predators and their prey in southern African savanna: A predator's size determines prey size. *Journal of Animal Ecology* 73:410–423.
- Robson, B. W., M. E. Goebel, J. D. Baker *et al.* 2004. Separation of foraging habitat among breeding sites of a colonial marine predation, the northern fur seal (*Callorhinus ursinus*). *Canadian Journal of Zoology* 82:20–29.
- Schabestberger, R., R. Brodeur, L. Ciannelli, J. M. Napp and G. L. Swartzman. 2000. Diel vertical migration and interaction of zooplankton and juvenile walleye pollock (*Theragra chalcogramma*) at a frontal region near the Pribilof Islands, Bering Sea. *ICES Journal of Marine Science* 57:1283–1295.
- Scheffer, V. B., and F. Wilke. 1953. Relative growth in the northern fur seal. *Growth* 17:129–145.
- Schoener, T. W. 1968. The *Anolis* lizards of Bimini: Resource partitioning a complex fauna. *Ecology* 65:1820–1827.
- Schoener, T. W. 1970. Nonsynchronous spatial overlap of lizards in patchy habitats. *Ecology* 51:408–418.
- Shine, R., R. N. Reed, S. Shetty and H. G. Cogger. 2002. Relationship between sexual dimorphism and niche partitioning within a clade of sea snakes (Laticaudinae). *Oecologia* 133:45–53.

- Sinclair, E. H., T. R. Loughlin and W. G. Pearcy. 1994. Prey selection by northern fur seals (*Callorhinus ursinus*) in the Bering Sea. *Fishery Bulletin* 92:144–156.
- Sinclair, E. H., G. A. Antonelis, B. W. Robson, R. R. Ream and T. R. Loughlin. 1996. Northern fur seal, *Callorhinus ursinus*, predation on juvenile walleye pollock, *Theragra chalcogramma*. Pages 167–178 in R. D. Brodeur, P. A. Livingston, T. R. Loughlin, and A. B. Hollowed, eds. *Ecology of walleye pollock, Theragra chalcogramma*. U.S. Department of Commerce, NOAA Technical Report NMFS-126.
- Sol, D., and L. Lefebvre. 2000. Behavioral flexibility predicts invasion success in birds introduced to New Zealand. *Oikos* 90:599–605.
- Springer, A. M., J. A. Estes, G. B. van Vliet, T. M. Williams, D. F. Doak, E. M. Danner, K. A. Forney and B. Pfister. 2003. Sequential megafaunal collapse in the North Pacific Ocean: An ongoing legacy of industrial whaling? *Proceedings of the National Academy of Sciences* 100:12223–12228.
- Sterling, J. T., and R. R. Ream. 2004. At-sea behavior of juvenile male northern fur seals. *Canadian Journal of Zoology* 82:1621–1637.
- Tollit, D. J., S. G. Heaslip, T. K. Zeppelin, R. Joy, K. A. Call and A. E. Trites. 2004. A method to improve size estimates of walleye Pollock (*Theragra chalcogramma*) and Atka mackerel (*Pleurogrammus monpterygius*) consumed by pinnipeds: Digestion correction factors applied to bones and otoliths recovered from scats. *Fishery Bulletin* 102:498–508.
- Tollit, D. J., M. J. Steward, P. M. Thompson, G. J. Pierce, M. B. Santos and S. Hughes. 1997. Species and size differences in the digestion of otoliths and beaks: Implications for estimates of pinniped diet composition. *Canadian Journal of Fisheries Aquatic Sciences* 54:105–119.
- Towell, R. G., R. R. Ream and A. E. York. 2006. Decline in northern fur seal (*Callorhinus ursinus*) pup production on the Pribilof Islands. *Marine Mammal Science* 22:486–491.
- Trites, A. W. 1992. Northern fur seals: Why have they declined? *Aquatic Mammals* 18:3–18.
- Wallace, R. K. 1981. An assessment of diet-overlap indexes. *American Fishery Society* 110:72–76.
- Wathne, J. A., T. Haug and C. Lydersen. 2000. Prey preference and niche overlap of ringed seals *Phoca hispida* and harp seals *P. groenlandica* in the Barents Sea. *Marine Ecology Progress Series* 194:233–239.
- Whitehead, H., C. D. MacLeod and P. Rodhouse. 2003. Differences in niche breadth among some teuthivorous mesopelagic marine mammals. *Marine Mammal Science* 19:400–405.
- Wikelski, H., C. D. MacLeod and P. Rodhouse. 2003. Niche expansion, body size and survival in Galapagos marine iguanas. *Oecologia* 124:107–115.
- Wilke, F., and K. W. Kenyon. 1957. The food of the fur seal in the Bering Sea. *Journal of Wildlife Management* 21:237–238.
- Winship, A. J., A. W. Trites and D. A. S. Rosen. 2002. A bioenergetic model for estimating the food requirements of Steller sea lions *Eumetopias jubatus* in Alaska, USA. *Marine Ecology Progress Series* 229:291–312.
- Woodward, G., and A. G. Hildrew. 2002. Body-size determinants of niche overlap and intraguild predation within a complex food web. *Ecology* 71:1063–1074.
- York, A. E. 1995. The relationship of several environmental indices to the survival of juvenile male northern fur seals (*Callorhinus ursinus*) from the Pribilof Islands. Pages 317–327 in R. J. Beamish, ed. *Climate change and northern fish populations*. Canadian Special Publication of Fisheries and Aquatic Sciences 121.
- Zeppelin, T. K., and R. R. Ream. 2006. Foraging habitats based on the diet of female northern fur seals (*Callorhinus ursinus*). *Canadian Journal of Zoology* 270:565–576.
- Zeppelin, T. K., D. J. Tollit, K. A. Call, T. J. Orchard and C. J. Gudmundson. 2004. Sizes of walleye pollock (*Theragra chalcogramma*) and Atka mackerel (*Pleurogrammus monpterygius*) consumed by the western stock of Steller sea lions (*Eumetopias jubatus*) in Alaska from 1998–2000. *Fishery Bulletin* 102:509–521.

Received: 24 September 2009

Accepted: 16 November 2010