Oecologia
DOI 10.1007/s00442-014-3149-6

BEHAVIORAL ECOLOGY - ORIGINAL RESEARCH

Testing the nutritional-limitation, predator-avoidance, and storm-avoidance hypotheses for restricted sea otter habitat use in the Aleutian Islands, Alaska

Nathan L. Stewart · Brenda Konar · M. Tim Tinker

Received: 26 December 2013 / Accepted: 10 November 2014
© Springer-Verlag Berlin Heidelberg 2014

Abstract Sea otters (*Enhydra lutris)* inhabiting the Aleutian Islands have stabilized at low abundance levels following a decline and currently exhibit restricted habitat-utilization patterns. Possible explanations for restricted habitat use by sea otters can be classified into two fundamentally different processes, bottom-up and top-down forcing. Bottom-up hypotheses argue that changes in the availability or nutritional quality of prey resources have led to the selective use of habitats that support the highest quality prey. In contrast, top-down hypotheses argue that increases in predation pressure from killer whales have led to the selective use of habitats that provide the most effective refuge from killer whale predation. A third hypothesis suggests that current restricted habitat use is based on a need for protection from storms. We tested all three hypotheses for restricted habitat use by comparing currently used and historically used sea otter foraging locations for: (1) prey availability and quality, (2) structural habitat complexity, and (3) exposure to prevailing storms. Our findings suggest that current use is based on physical habitat complexity and not on prey availability, prey quality, or protection from storms, providing further evidence for killer whale predation as a cause for restricted sea otter habitat use in the Aleutian Islands.

Keywords Prey quality · Habitat complexity · Predation risk

Communicated by Helene Marsh.

N. L. Stewart
School of Fisheries and Ocean Sciences, University of Alaska Fairbanks, 245 O'Neill Building, Fairbanks, AK 99775, USA
e-mail: nlstewar@bu.edu

B. Konar (✉)
School of Fisheries and Ocean Sciences, University of Alaska Fairbanks, 217 O'Neill, P.O. Box 757220, Fairbanks, AK 99775, USA
e-mail: bhkonar@alaska.edu

M. T. Tinker
US Geological Survey Western Ecological Research Center, Long Marine Laboratory, 100 Shaffer Road, Santa Cruz, CA 95060, USA
e-mail: ttinker@usgs.gov

Introduction

Many factors contribute to the selective use of habitats by animals, including habitat suitability, prey quality, and predation risk (Sih 1987; Lima 1998; Andruskiw et al. 2008). Of particular interest are situations where habitats with high food availability also have high predation risk. In the absence of predators, consumers are expected to select foraging habitat based on net realized profitability. However, under the risk of predation there exists a fundamental trade-off between foraging profitability and safety from predators, which can lead to the selection of more highly restricted habitat [e.g., shifting activity toward safer but less rewarding food patches (Sih 1980; Brown 1999; Oksanen et al. 1995)]. Both theoretical (McNamara and Houston 1992; Bolker et al. 2003) and empirical studies (Gilliam and Fraser 1987; Stein and Magnuson 1976) have shown that animals will under-utilize habitats with high food availability if these same habitats are associated with higher predation risk. Therefore, determining the cause of restricted habitat use in populations where there is potential for prey availability-predator avoidance trade-offs requires the careful investigation of prey abundance, prey quality, and predation risk (Sih 1980; Lima 1998; Heithaus and Dill 2006).

Sea otter (*Enhydra lutris)* populations in the Aleutians declined precipitously during the early 1990s (Estes et al.

Published online: 22 November 2014

1998; National Research Council 1996, 2003) and have remained at or near their minimum for nearly two decades (Doroff et al. 2003; Estes et al. 2005). During the decline, sea otters shifted from the broad use of all available nearshore habitats to the selective use of very few nearshore habitats (Estes et al. 2010a). This pattern of restricted habitat use (sensu Brown 1984) is characteristic of populations that have stabilized at low abundances following a decline (Norris 2004). The causes for this shift have been attributed to three fundamentally different processes: nutritional limitation, predator avoidance, or the need for protection from storms (Estes et al. 1998, 2009, 2010a; Laidre et al. 2006; Kuker and Barrett-Lennard 2010) and remain actively contested.

Arguments for nutritional limitation propose that restricted habitat use by sea otters is due to changes in the availability or quality of prey (Kuker and Barrett-Lennard 2010) as has been posited for other marine vertebrate species in southwest Alaska (Alverson 1992; Trites and Donnelly 2003). Unlike changes observed in forage fishes in offshore habitats [the junk food hypothesis (Alverson 1992; Rosen and Trites 2000)], nearshore habitats support diverse populations of sea otter prey species (Simenstad et al. 1978; Estes et al. 2010b) and exhibited increases in sea urchin (*Strongylocentrotus polyacanthus*) biomass over the course of the sea otter decline (Estes et al. 1998). Despite evidence against nutritional limitation, Kuker and Barrett-Lennard (2010) have argued that increases in sea urchin biomass alone do not provide sufficient evidence against nutrition limitation because sea otters have a diverse diet (Estes et al. 2003). The potential relationship between prey quality and sea otter use of more highly restricted habitats remains to be tested.

In contrast to the nutrition-limitation hypothesis, a number of independent lines of evidence suggest that increased predation by killer whales may be influencing current sea otter habitat selection (Estes et al. 2010a). Coastal habitats in the Aleutians vary from steep, exposed coastlines to shallow, reef-dominated areas to inner bays (McNab and Avers 1996). These habitats have been shown to differ in terms of protection from predation: sea otters inhabiting a highly protected lagoon experienced lower mortality rates and a significantly lower rate of decline than otters in a nearby open bay, a finding attributed to the lagoon's inaccessibility to killer whales (Estes et al. 1998). In studies of other marine mammal species it has been shown that complex or shallow habitat structures in nearshore waters may provide some degree of refuge from killer whale predation (Vila et al. 2008). If the current use of restricted habitat is predator mediated, we would expect current foraging areas to be more shallow or have greater three-dimensional complexity (the presence of habitat features that might limit access by killer whales) than historical foraging areas.

An alternative explanation for restricted habitat use by sea otters is the need for protection during storms (Kuker and Barrett-Lennard 2010). The storm-avoidance argument proposes that habitats that provide shelter from storms and are prey rich should be the first areas occupied by expanding populations and the last areas inhabited by post-decline populations (Kuker and Barrett-Lennard 2010). Sea otters have been observed to utilize sheltered areas during rough weather (Kenyon 1969; Rotterman and Simon-Jackson 1988), generally occupying waters <40 m deep and within 400 m from the shoreline (Burn et al. 2003). If the current use of restricted habitat is driven by storm avoidance, we expect preferred habitats to include inner bay locations sheltered from prevailing weather and exclude locations with high exposure to prevailing winds and waves.

In this study we examined currently used and historically used sea otter foraging habitats in the Aleutians to determine if recent restricted habitat use by sea otters can be attributed to nutritional limitation, predator avoidance, or the need for protection from storms. We tested these alternative hypotheses:

1. Currently used sea otter foraging habitats will provide greater prey availability and/or prey quality than historically used habitats.
2. Currently used sea otter foraging habitats will provide greater structural complexity (i.e., protection from predators) than historically used habitats.
3. Currently used foraging sites will provide greater protection from prevailing weather.

To test these hypotheses, we quantified and compared sea otter prey abundance, biomass, potential energy density, habitat structural complexity, and site exposure at currently used and historically used sea otter foraging locations.

Materials and methods

We conducted this study in nearshore habitats in the inner bay (51°48′19N, 176°47′53W) and surrounding headlands of the Bay of Islands, Adak, Alaska (Fig. 1). To determine if the differences in current and historical sea otter foraging site selection could be attributed to differences in prey availability, prey quality, habitat complexity, or storm avoidance, we utilized a design I study for evaluating resource selection (Manly et al. 2002). Resource use is based on unmarked individuals and is quantified on the basis of information gathered via surveys within plots and availability is characterized at the level of the study area. We sampled a total of 22 sites, 11 currently used and 11 historically used sea otter foraging locations (Fig. 1). We randomly selected currently used sites from a database of

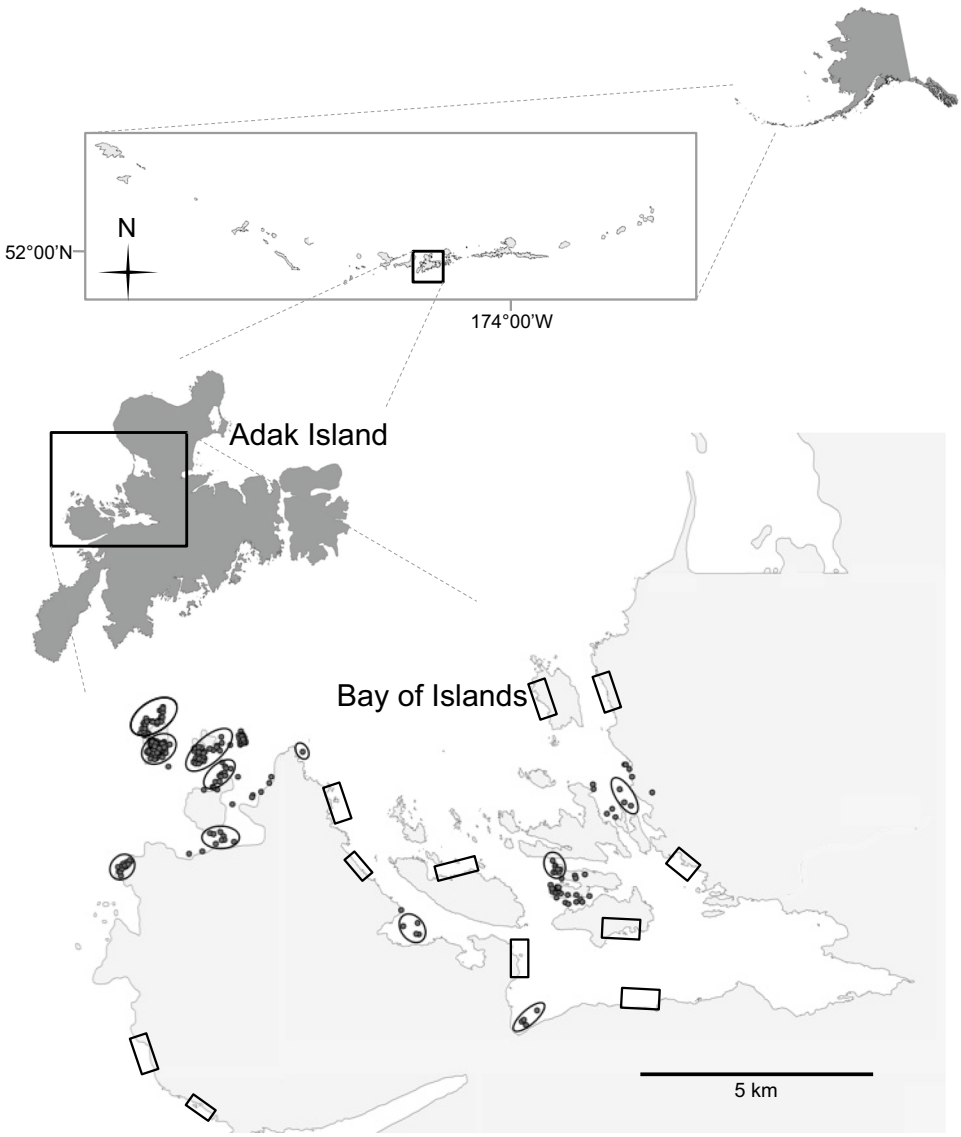

Fig. 1 Map of the Aleutian Islands, Alaska (*inset*) indicating the location of Adak Island and the study area in the Bay of Islands. *Each dot* indicates a site where a series of feeding dives were recorded during a focal observation conducted in summer 2008. *Open circles* ($n = 11$) indicate currently used sea otter foraging locations. *Open rectangles* ($n = 11$) indicate historically used foraging locations, areas where otters were regularly seen but have not been observed since the early 1990s

observed sea otter foraging locations recorded during an intensive shore and boat-based focal observation study conducted in July and August 2008 (Fig. 1; Estes and Tinker, unpublished data) and used these points as centroids for our sampling sites. We selected historically used foraging sites, areas where otters have not been observed since 2005 but where otters were regularly seen foraging through the mid 1990s, using data collected during sea otter foraging surveys conducted between 1993 and 1996. We filtered historical locations to remove points that were less than 1,000 m from any observed otter locations recorded during whole-island surveys conducted after 2005 and less than 1,000 m from any observed locations recorded during the 2008 intensive foraging observations. We then selected 11 of these points at random and used them as the centroids for historically used sites. Sites were located using a geographic information system (ArcGIS 10; Environmental Systems Research Institute, Redlands, CA), were approximately 1,000 m × 500 m in size (0.5 km^2), and included both inner and outer bay locations.

To determine if currently used sea otter foraging locations provide comparable prey abundance and size to historical foraging areas, we sampled sea otter prey species at each site using diver visual surveys in July 2010. We

evaluated invertebrate prey using three 20-m transects and fish prey were evaluated using one 50-m × 2-m × 2-m transect oriented at random compass headings and secured to a haphazardly placed anchor at each site. Our target sampling depth contour was 5–15 m based on mean sea otter foraging depths (Bodkin et al. 2004) and the observation that sea otter prey distribution patterns in the Aleutians are generally similar across this depth range (Estes et al. 2009). We sampled invertebrate prey using three 0.25-m^2 quadrats placed randomly along each transect ($n = 9$ quadrats per site), inside which we counted all potential invertebrate prey, identified them to species, and measured them to the nearest millimeter (test or shell maximum linear length). We counted fish observed along the fish sampling transect, identified them to species, and estimated their length to the nearest centimeter. We predetermined random transect compass headings and quadrat locations using a random number table.

In addition to count and size measurements within quadrats, we collected a subsample of sea urchins ($n = 10$ per site) and other invertebrate prey species ($n = 3$ per species per site due to lower abundances) from each quadrat (Alaska Department of Fish and Game Permit no. CF-10-072) to measure energy density and edible biomass. We collected only the largest individuals of each species occurring within quadrats to simulate size-selective foraging behavior exhibited by sea otters (Ostfeld 1982; Estes and Duggins 1995). We collected fish ($n = 3$ per species per historically used and currently used sites) using scuba and baited hook and line (Freiwald et al. 2009; IACUC 163475-2, University of California, Santa Cruz). We calculated biomass per unit area for wet matter (WM) (g WM 0.25 m^{-2}) using species-specific size to biomass conversion factors (Dean et al. 2002; Oftedal et al. 2007) calibrated with specimens collected in this study (test or shell-free wet weight for invertebrates and whole wet weight for fish). To determine if sea otter prey composition changed during the shift from historical to current foraging site we compared historical and current sea otter diet composition data collected during intensive sea otter foraging surveys from 1993 to 1997 (1,127 h of observation and 35,992 dives) and 2008 [168 h of observation and 6,953 dives (Estes and Tinker, unpublished data)].

To determine if currently used sea otter foraging locations provide comparable potential energy density to historically used sites, we analyzed the caloric value of all sea otter prey species collected during this study using bomb calorimetry. We regarded weight loss from ashing as organic content and used it to express the caloric content in terms of ash-free dry weight. We then multiplied energy from dry matter (DM) (cal g^{-1} DM) by the proportion of dry matter in the wet mass to express energy density in terms of wet mass (kcal g^{-1} WM). We calculated potential prey energy density per unit area (kcal g^{-1} WM 0.25 m^{-2}) using species-specific biomass to energy density conversion factors (Dean et al. 2002; Oftedal et al. 2007) calibrated with specimens collected in this study. Although wet mass is influenced by ash and water dilution, it is a better representation of the actual prey biomass as consumed by sea otters (Oftedal et al. 2007).

To determine if the selection of currently used sea otter foraging sites can be attributed to predator avoidance, we used multiple approaches to quantify structural complexity at currently used and historically used locations. We quantified coastal habitat features that increase the three-dimensional complexity of the foraging area (at the ca. 0.5-km^2 scale). Although it is unknown which physical habitat features prevent killer whale predation on sea otters in typical coastal habitats, it is thought that increasingly complex depth profiles and increases in the size and number of pinnacles may inhibit killer whale movement and hence the probability of predation (C. Matkin, personal communication). Measures of habitat complexity included: (1) water depth variation, (2) percent cover of persistently exposed rock pinnacles, and (3) the number of pinnacles per unit area. To measure depth variation, we used a handheld depth sounder (Speedtech SM-5, 400 kHz; Laylin, Unionville, VA) to record depth at 5-m × 5-m intervals in a 1,125-m^2 grid located haphazardly in the foraging site. We recorded a depth measurement at each grid intersection point ($n = 45$ per site) and compared currently used ($n = 11$) and historically used ($n = 11$) site bathymetries as spatially explicit three-dimensional surfaces. We estimated percent cover of exposed rock per site by track-line tracing the periphery of the entire site and all persistently exposed rock outcrops occurring within the site (e.g., habitat features that remain above water-line throughout the tidal cycle). We calculated the areal dimension of a site and the areal extent of exposed rock within the site using ArcGIS 10. In addition to estimating the percent cover of exposed rock, we counted the number of independent pinnacles that occurred within a site and present them as pinnacles per unit area. Both attributes are important to the relative provision of refugia due to the functional differences between a site characterized by a high percent cover of exposed rock and a small number of pinnacles per unit area (e.g., a single large exposed island) vs. a site characterized by a high percent cover of exposed rock and a large number of pinnacles per unit area (e.g., a field of rock spires and surge channels consisting of ca. ten to 15 exposed pinnacles).

To determine if the selection of restricted habitats can be attributed to protection from storms, we related the relative location and aspect of currently used and historically used sea otter foraging sites to dominant weather patterns affecting the Bay of Islands, in northwestern Adak (Fett et al. 1993). We determined foraging site exposure to prevailing

Table 1 Statistical tests of the three major hypotheses for sea otter restricted habitat use in the Aleutian Islands, Alaska

Hypothesis	Measure	Test	Result
Nutrition limitation	Prey abundance	ANOVA	Invertebrates: $n = 22$, $F = 0.71$, $p = 0.41$
			Fishes: $n = 22$, $F = 0.68$, $p = 0.34$
	Prey size	*t*-test	Invertebrates: $t\,(22) = 0.86$, $p = 0.43$
			Fishes: $t\,(22) = 1.06$, $p = 0.33$
	Prey biomass	ANOVA	Invertebrates: $n = 22$, $F = 0.84$, $p = 0.31$
			Fishes: $n = 22$, $F = 0.61$, $p = 0.27$
	Potential energy density	ANOVA	Invertebrates: $n = 22$, $F = 0.54$, $p = 0.47$
			Fishes: $n = 22$, $F = 0.74$, $p = 0.43$
Predator avoidance	Water depth variation	One-sided *t*-test	$t\,(22) = 8.33$, $p < 0.0001$*
	Exposed pinnacles (% cover)	ANOVA	$n = 22$, $F = 55.4$, $p < 0.0001$*
	Pinnacles per unit area	ANOVA	$n = 22$, $F = 26.3$, $p < 0.0001$*
Storm refuge	Exposure to prevailing weather	χ^2	c2(1, $n = 22$) = 0.84, $p = 0.37$

Results indicate differences in sea otter prey species and physical habitat characteristics between currently used (2008) and historically used foraging areas (1993–1997)

* $p < 0.05$

westerly/northwesterly weather using compass bearing functions in ArcGIS 10. We considered sites with ≥50 % of the area exposed to westerly/northwesterly directions exposed sites. We considered all inner bay locations and southern/southeastern aspects in outer bay locations protected from storms in the Bay of Islands. Although southeasterly storms do affect the Aleutians, these weather patterns are rare events. Given the mobility of sea otters and their capability of responding to infrequent southeasterly storms, prevailing weather patterns likely have a greater influence on sea otter resource selection.

Data analysis

We examined differences in the abundance, biomass, and energy density of prey species among sites with ANOVA and considered *P*-values <0.05 significant in all tests. We tested for differences in invertebrate and fish prey size using paired *t*-tests of mean prey sizes from currently used and historically used sites and considered *P*-values <0.05 significant. We presented prey abundance, biomass, and energy density in terms of current vs. historic use and their inner vs. outer bay location to address potential spatial bias. We used similarity analysis and multidimensional scaling (MDS) to determine if current sea otter use was attributable to prey availability or prey quality [PRIMER-E version 6 (Lutton, UK); Clarke and Warwick 2001; Clarke and Gorley 2006]. We used similarity percentages analysis (SIMPER) to determine which of the above variables contributed most to the observed similarity between currently used and historically used locations. We examined the similarity between inner and outer bay locations in terms of prey characteristics and habitat complexity measures using analysis of similarity. We calculated the variation in depth between foraging sites by finding the sample variance from depths recorded in the 5 × 9 grids ($n = 45$ depths) from each current ($n = 11$) and each historic ($n = 11$) location. We log-transformed sample variances and used a one-sided *t*-test to determine if mean variability between currently used and historically used sites was significantly different at *P*-values <0.05. We created three-dimensional surface plots of the sample variance in depth recorded at each spatially explicit grid cell to graphically compare the variance in depth at currently used and historically used sites. We used binary classification to classify sites as refuge from prevailing storms or exposed to storms based on site location and aspect and present them as a percent of the total sites sampled. We performed a χ^2-test of independence between sea otter use and protected vs. non protected site locations with *P*-value <0.05 considered significant.

Results

Prey characteristics

There was no statistical difference in prey abundance between currently used and historically used sea otter foraging sites (Table 1). Although we noted slight differences in species assemblages between inner bay and outer bay habitats, differences were not significant (ANOVA, $n = 22$, $F = 1.88$, $p = 0.73$; Table 2). Inner bay prey assemblages were dominated by *Strongylocentrotus polyacanthus*, followed by gastropods, chitons, and crabs. Outer bay prey assemblages were also dominated by *S. polyacanthus*; however, the next most common species were *Pododesmus*

Table 2 The abundance (individuals 0.25 m^{-2}), available biomass (g wet mass 0.25 m^{-2}), and potential energy density (*ED*) per unit area (kcal g wet mass 0.25 m^{-2}) of various sea otter prey species at currently used and historically used sea otter foraging locations in the Bay of Islands, Adak, Alaska

Prey species	All sites		Inner bay		Outer bay	
	Current ($n = 11$)	Historic ($n = 11$)	Current ($n = 4$)	Historic ($n = 4$)	Current ($n = 7$)	Historic ($n = 7$)
Strongylocentrotus polyacanthus						
Abundance	27.1 ± 10.2	31.6 ± 9.7	24.2 ± 11.1	27.3 ± 9.1	31.1 ± 9.8	34.8 ± 10.1
Biomass	542.3 ± 204.1	632.2 ± 194.2	484.7 ± 221.5	546.4 ± 183.4	622.2 ± 196.3	696.7 ± 203.8
ED	130.1 ± 48.9	152.7 ± 46.6	116.3 ± 53.2	131.8 ± 44.2	149.3 ± 47.1	167.2 ± 48.9
Pododesmus machrochisma						
Abundance	2.3 ± 2.1	3.1 ± 2.2	0.7 ± 0.5	1.1 ± 0.6	2.6 ± 0.7	3.3 ± 1.1
Biomass	86.3 ± 78.7	116.2 ± 82.5	26.3 ± 18.7	41.3 ± 22.5	97.5 ± 26.3	123.7 ± 41.2
ED	71.6 ± 65.3	96.4 ± 68.4	21.8 ± 15.5	34.2 ± 18.6	80.9 ± 21.8	102.6 ± 34.1
Mytilus trossulus						
Abundance	1.7 ± 0.6	2.1 ± 0.7	0.9 ± 0.5	1.1 ± 0.7	2.1 ± 0.3	2.5 ± 0.5
Biomass	19.7 ± 6.9	24.3 ± 8.1	10.4 ± 5.8	12.7 ± 8.2	24.3 ± 3.5	29.1 ± 5.7
ED	9.8 ± 3.4	12.1 ± 4.0	5.2 ± 2.9	6.4 ± 4.1	12.2 ± 1.7	14.6 ± 2.8
Gastropod spp.						
Abundance	1.9 ± 0.5	2.2 ± 0.4	2.1 ± 0.3	2.5 ± 0.3	1.7 ± 0.4	1.5 ± 0.2
Biomass	56.8 ± 14.9	65.7 ± 11.9	62.7 ± 8.9	74.4 ± 7.9	50.8 ± 11.9	44.7 ± 5.9
ED	73.8 ± 19.3	85.4 ± 15.4	81.5 ± 11.5	96.3 ± 10.2	66.3 ± 15.4	58.1 ± 7.6
Chiton spp.						
Abundance	1.2 ± 0.3	1.4 ± 0.4	1.6 ± 0.2	1.9 ± 0.3	0.9 ± 0.1	0.7 ± 0.2
Biomass	23.6 ± 5.9	27.6 ± 7.8	31.5 ± 3.9	37.4 ± 5.9	17.7 ± 1.9	13.7 ± 3.9
ED	21.2 ± 5.3	24.8 ± 7.0	28.3 ± 3.5	33.6 ± 5.3	15.9 ± 1.7	12.3 ± 3.4
Crab spp.						
Abundance	1.2 ± 1.1	1.5 ± 1.3	1.3 ± 1.1	1.6 ± 1.4	1.1 ± 1.0	1.4 ± 0.9
Biomass	78.8 ± 71.5	97.5 ± 84.5	84.6 ± 70.7	104.1 ± 91.2	71.5 ± 64.6	91.6 ± 58.1
ED	54.3 ± 49.3	67.3 ± 58.3	58.5 ± 48.7	71.6 ± 62.9	49.3 ± 44.5	63.2 ± 40.1
Fish spp.						
Abundance	0.05 ± 0.05	0.07 ± 0.06	0.02 ± 0.03	0.04 ± 0.04	0.06 ± 0.05	0.07 ± 0.05
Biomass	12.5 ± 12.2	17.5 ± 15.7	7.6 ± 7.5	11.9 ± 10.1	14.4 ± 12.3	16.9 ± 13.1
ED	17.2 ± 16.8	24.1 ± 21.6	10.5 ± 10.3	16.4 ± 13.9	19.8 ± 16.9	23.3 ± 18.0
Total						
Abundance	35.4 ± 14.8	41.9 ± 14.7	30.8 ± 13.7	35.5 ± 12.4	39.5 ± 12.3	44.2 ± 13.0
Biomass	820.0 ± 394.3	981.0 ± 419.4	777.8 ± 337.0	828.2 ± 329.2	898.4 ± 316.8	1,016 ± 331.7
ED	378.0 ± 208.3	462.8 ± 221.3	322 ± 145.6	390 ± 159.2	393 ± 149.1	441 ± 154.9

Abundance, biomass, and potential ED are expressed as mean ± SD from current ($n = 11$) and historical ($n = 11$) sites. No significant differences in prey abundance, biomass, or energy density were detected between current and historical sites (ANOVA, $p < 0.05$)

machrochisma, *Mytilus trossulus*, and gastropods. Crabs were patchy in abundance and were represented primarily by individual *Paralithodes rathbuni* and *Phyllolithodes papillosus*. Fish species occurred in low abundances in both inner and outer bay locations and no significant difference between fish abundances in currently used and historically used locations were detected (Table 1). The most common fish species in the inner bay were *Hexagrammos decagrammus*, *Lepidopsetta polyxystra,* and *Bathymaster caeruleofasciatus* and in the outer bay were *H. decagrammus*, *Hemilepidotus jordani,* and *B. caeruleofasciatus*; however, differences were not significant (ANOVA, $n = 22$, $F = 0.91$, $p = 0.51$). Although we did not record large schools of atka mackerel, *Pleurogrammus monopterygius*, during fish surveys conducted in this study, we observed several massive schools at outer bay locations and believe they are likely an important prey species when present (Anthony et al. 2008).

There was no statistical difference in available prey biomass between currently used and historically used sea otter foraging sites (Table 1). *Strongylocentrotus polyacanthus* contributed the greatest available biomass per unit area followed by gastropods in the inner bay and *Pododesmus machrochisma* in the outer bay (Table 2).

There was no statistical difference in potential energy density per unit area between currently used and historically used sea otter foraging sites (Table 1). The highest potential energy density prey sampled in this study were fish followed by *Pododesmus machrochisma* and crabs (Table 2). We detected no significant differences in potential prey density between the inner and outer bay (ANOVA, $n = 22$, $F = 0.74$, $p = 0.53$). Due to low abundances and comparable energy density per unit of tissue, we grouped individual fish species for all biomass and potential energy density comparisons.

We did not detect significant differences in prey size for any invertebrate or fish prey species between currently used and historically used foraging areas (Table 1). Although mean sea urchin size was somewhat larger at historically used foraging areas in relation to currently used foraging areas (Table 3), we did not detect significant differences between urchin standing stock biomass (ANOVA, $n = 22$, $F = 1.39$, $p = 0.27$). Sea otter diet composition was similar before and after the decline, with sea urchins constituting approximately 60 % of prey consumed during both time periods (Table 4).

Currently used and historically used sea otter foraging locations do not show a clear separation in terms of relative prey abundance, size, biomass, and energy density using multidimensional scaling analyses (MDS; Fig. 2). Available prey biomass (SIMPER 11 %) and potential energy density (SIMPER 13 %) do not contribute to the dissimilarity between current and historic foraging sites, as indicated by SIMPER.

Habitat complexity

Depth was significantly more variable at currently used sites ($\sigma^2 = 1.92 \pm 0.1$ SD) than at historically used sites ($\sigma^2 = 1.62 \pm 0.1$ SD), as indicated by a *t*-test of sample variances from each location (Table 1). Spatially explicit surface plots of sample variances from each grid cell from currently used sites exhibited greater variation in depth than grid cells at historical sites (Fig. 3). Currently used sites had significantly more exposed rock and more pinnacles per unit area than historical sites (Table 1).

Storm avoidance

Currently used and historically used sites do not differ in terms of their location in inner bay or outer bay habitats or in relation to their exposure to synoptic weather patterns. Currently used foraging areas consist of locations directly exposed to westerly/northwesterly prevailing weather conditions and both inner and outer bay habitats in the Bay of Islands. Of the 22 sites sampled in this study, 13 sites were located in the inner bay (four currently used and nine historically used sites) and nine sites were located in the outer bay (seven currently used and two historically used sites). Only two currently used sites were located in the inner bay with eastern/southeastern aspects. Of the outer bay locations, only one currently used site was situated with a southeasterly aspect; however, it should be noted that this site experiences extremely high currents during regular tidal exchanges (Fett et al. 1993). We found no relationship between sea otter use and protected vs. non-protected site locations (Table 1).

Discussion

The use of restricted habitats by sea otters currently inhabiting the Bay of Islands, Adak, does not appear to be driven by prey depletion or the need for protection from storms. Instead, our findings suggest that restricted habitat use is predator mediated, with otters utilizing habitats that would be expected to provide the greatest refuge from killer whale predation. The principal difference between currently and historically used sea otter foraging locations is structural complexity. Currently used locations are typically associated with highly rugose and irregular coastlines that divide large portions of the available foraging habitat into channels and pinnacles. In contrast, historically used foraging locations were typically associated with broad open coastlines, gradual seafloor relief and very few or no pinnacles. During the past two decades, sea otters appear to have shifted from the broad use of available nearshore habitats to the selective use of very few highly complex habitats.

Table 3 Sea otter prey sizes at currently used and historically used foraging sites in the Bay of Islands, Adak, Alaska

Prey species	*n*		Size (mm or cm)			
			Inner bay		Outer bay	
	Current	Historic	Current	Historic	Current	Historic
Invertebrates						
S. polyacanthus	2,938	3,128	53.1 ± 15.3	58.4 ± 7.3	59.7 ± 6.7	55.4 ± 11.8
P. machrochisma	288	307	61.6 ± 9.2	54.5 ± 12.1	51.1 ± 13.3	63.6 ± 7.7
Mytilus trossulus	208	189	65.5 ± 26.7	56.6 ± 21.5	59.3 ± 17.4	68.6 ± 28.1
Gastropod spp.	198	217	31.1 ± 16.8	26.3 ± 13.2	33.2 ± 11.2	24.7 ± 17.1
Chiton spp.	117	138	24.3 ± 6.4	22.2 ± 9.3	26.3 ± 10.1	19.3 ± 6.2
Crab spp.	114	129	44.7 ± 11.6	47.4 ± 12.3	49.9 ± 15.4	41.9 ± 13.5
Fishes						
Bathymaster caeruleofasciatus	15	16	52.3 ± 6.6	56.1 ± 5.3	48.6 ± 9.3	52.2 ± 8.1
Lepidopsetta polyxystra	6	9	78.2 ± 7.3	69.5 ± 4.7	68.3 ± 11.2	73.4 ± 9.5
Hexagrammos lagocephalus	29	31	93.3 ± 9.5	97.8 ± 6.8	101.3 ± 14.6	91.7 ± 13.0
Sebastes ciliatus	14	17	74.5 ± 6.1	78.3 ± 5.1	69.7 ± 9.6	76.1 ± 7.4
Hemilepidotus jordani	18	21	101.6 ± 14.2	107.3 ± 16.9	97.3 ± 13.3	104.2 ± 11.6
Hemilepidotus hemilepitodus	17	19	75.7 ± 9.3	80.5 ± 7.0	71.7 ± 9.2	78.4 ± 8.8
Enophrys bison	13	9	51.4 ± 8.7	57.2 ± 11.3	49.3 ± 10.1	59.0 ± 11.3
Eumicrotremus orbis	3	5	11.1 ± 4.1	13.6 ± 6.0	14.8 ± 6.6	16.6 ± 7.3
Total	3,978	4,235				

Prey size is recorded as the maximum linear length of the test or shell (mm) in invertebrates and as total length in fish (cm) and is expressed as mean ± SD from current ($n = 11$) and historical ($n = 11$) sites. No significant differences in prey size were detected between current and historical sites (paired *t*-test, $P < 0.05$)

Table 4 Sea otter diet composition before (1993–1997) and after (2008) the sea otter population decline in Adak, Alaska

Time period	Obs. hours	Dives	Sea otter diet composition									
			Urchin	Clam	Mussel	Fish	Crab	Worm	Sea star	Snail	Octopus	Other
1993–1997	1,126.7	35,992	0.656	0.171	0.020	0.079	0.025	0.008	0.012	0.000	0.002	0.026
2008	168.4	6,953	0.589	0.176	0.125	0.047	0.020	0.000	0.004	0.005	0.001	0.033
Total	1,295.2	42,945	0.623	0.173	0.073	0.063	0.023	0.004	0.008	0.002	0.001	0.030

Sample sizes of annual sea otter foraging surveys are presented in terms of the number of person-hours of focal observation and dives completed during pre-decline (3 people × 8 days per month for 12 months, 1995–1996; and 2 people × 8 days per month for 2 months in 1997) and post-decline sampling periods (2 people × 10 days each month for 2 months in 2008)

Obs. Observed

The shift to more highly complex habitats is often predator mediated and may represent increased use of escape terrain (Stein and Magnuson 1976; Sih 1980, 1982; Vila et al. 2008). The concept of escape terrain is not well defined for sea otters, unlike it is in other terrestrial predator–prey interactions (Fox et al. 1992). The structural similarities within currently used foraging locations sampled in this study suggest that sea otters prefer sites with highly variable seafloor bathymetry, 13–28 % exposed rock, and from ten to 28 pinnacles per 20,000 m^2. There are several critical assumptions in assessing current sea otter restricted habitat as escape terrain, including: (1) that predators continue to affect sea otters in this area, (2) that sea otters that once associated with historical locations have either moved to current locations or were killed, and (3) that remaining sea otters have successfully avoided predation by associating with these current locations.

Changes in prey abundance [acute nutritional stress (Trites and Donnelly 2003)] or prey quality (chronic nutritional stress) are an unlikely cause of restricted habitat use in the nearshore Aleutians given the comparable abundance and quality of prey resources available to sea otters at historically and currently used foraging locations and the stability of the urchin-dominated community for the past two decades (Estes et al. 1998, 2005, 2010a). We observed a tenfold increase in available biomass of sea urchins in

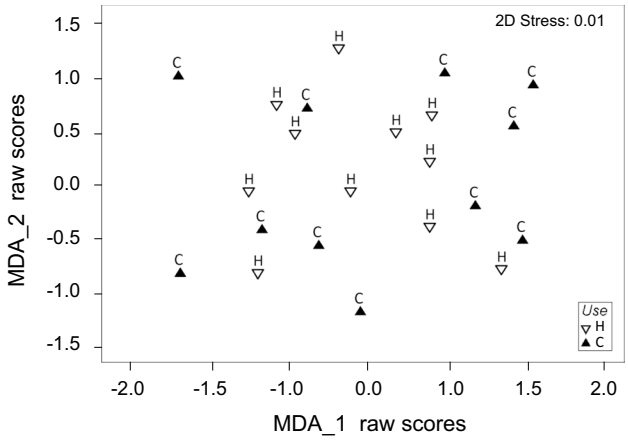

Fig. 2 Multidimensional scaling ordination derived from Bray-Curtis similarities of the square-root transformed contributions of sea otter prey size, abundance, biomass, and energy density to the gradient in separation in currently used (*C*) and historically used (*H*) habitats in the Bay of Islands, Adak, Alaska. *MDA* Multiple discriminant analysis

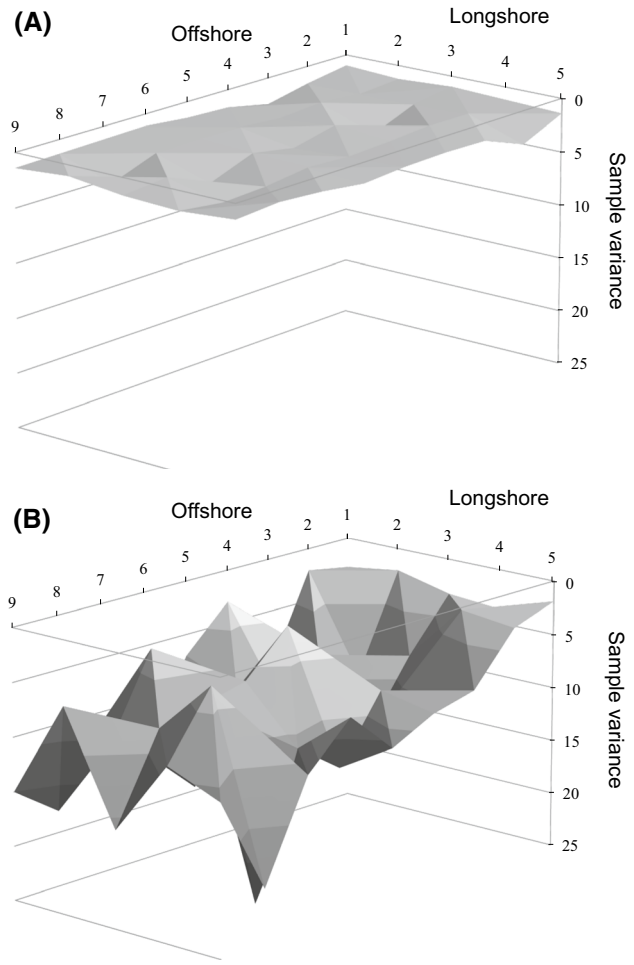

Fig. 3 Variance in depth from **a** historically used and **b** currently used sea otter foraging locations in the Bay of Islands Adak, Alaska. Surface plots were generated using sample variances from each spatially explicit grid coordinate ($n = 45$) from 11 historically used and 11 currently used locations. Offshore and longshore axes are in units of meters

nearshore habitats at Adak between 1987 and 1997 (Estes et al. 1998) and a consistent increase in sea otter body condition and size during the period of sea otter decline (Laidre et al. 2006). Sea urchin biomass continues to be much higher in areas that experienced a decline in sea otter population and the estimated rate of energy gain of sea otters foraging at Bay of Islands at Adak in 2008 (20 kcal min^{-1}) is the highest we have seen in any other population, including the rapidly expanding populations in Glacier Bay and British Columbia (Estes et al. 2010a). Although the lack of kelp does affect benthic productivity (Duggins et al. 1990) and urchin barrens are generally associated with poor nutritional resources (Harrold and Reed 1985), the shift to an urchin-dominated system, in itself, was not enough to nutritionally compromise sea otters (Stewart and Konar 2012) nor does it explain their current use of restricted habitats.

The alternative explanation for the use of more highly protective habitats is as refuge from storms (Kuker and Barrett-Lennard 2010). This can be disregarded because currently used sites are predominantly exposed rocky headlands or the outer coasts of islands. These areas are directly exposed to the prevailing weather patterns impacting the Bay of Islands within northwestern Adak. The sites of greatest storm protection in the study area are in the inner bay or are situated at aspects where few sea otters are currently found. We do not find support for the hypothesis that habitats that provide shelter from storms and are prey rich should be the last areas inhabited by post-decline populations, as suggested by Kuker and Barrett-Lennard (2010).

If killer whale predation is mediating sea otter habitat selection in the Bay of Islands, sea otter prey availability is likely to change over time due to over-exploitation (Brown et al. 1999). Intense predation pressure can generate a fundamental trade-off between food and protection, forcing prey species to balance habitat selection between safe and productive locations (Sih 1980; Brown 1999). Sea otters are known to preferentially select the largest and most calorically rich prey first before switching to smaller and less valuable prey (Ostfeld 1982; Garshelis 1983). Depending on prey choices associated with restricted habitats and the mobility of sea otters under the risk of predation, prey depletion and nutritional stress represent potential outcomes of long-term habitat restriction. Areas close to escape terrain are often heavily used for foraging compared to areas located further away (Pfitsch and Bliss 1985). Since intensive grazing or browsing can greatly reduce forage abundance and quality (Cote et al. 2004; Schoenecker et al. 2004), areas near escape terrain may be less

productive due to local grazing stress. Should sea otters continue to be restricted to a limited foraging habitat due to predation pressure from killer whales, further sea otter population decline could result from prey overexploitation.

In conclusion, the sea otters currently inhabiting the Bay of Islands, Adak, have shifted their habitat to use areas of greater structural complexity, a change that is most consistent with selection of habitat that provides greater protection from killer whale predation. This conclusion is supported by:

1. Currently used sea otter foraging locations providing similar prey quantity and quality to historically used habitats.
2. Currently used foraging sites showing more structural complexity than historical sites.
3. Currently used foraging locations predominantly being situated in areas exposed to prevailing weather.

Increasing predation pressure by killer whales (Estes et al. 1998) has potentially resulted in the selective use of areas with abundant escape terrain, and such areas represent a limited sub-set of otherwise suitable sea otter foraging habitat. Over time it is possible that sea otters will deplete prey in the currently used areas, with implications for the trade-off between food abundance and predator avoidance. As we have demonstrated, understanding the processes limiting wildlife populations under prey availability-predator avoidance trade-offs requires careful analyses of prey distribution, prey quality, and predation risk.

Acknowledgments We would like to thank J. A. Estes for valuable comments and logistical support during this study. Contributions from D. M. Thomas, B. P. Kelly, and M. J. Wooller contributed greatly to earlier drafts of this manuscript. Special thanks to T. Efird, M. Stewart, S. Beaudreault, and J. P. Smelter for their assistance in the field. This research was primarily funded by the National Science Foundation (to B. K., award no. 0647635). Other financial support (to N. S.) was provided by the Robert Byrd Research Award, the Frances and Alfred Baker Memorial Scholarship in Marine Biology, and the Ken Turner Memorial Research Grant. This work would not have been possible without the support of the Alaska Maritime Wildlife Refuge, the R/V Tiglax, and US Fish and Wildlife Service staff at the Adak field office. All work reported in this paper was done in compliance with US law. Any use of trade, product, or firm names in this publication is for descriptive purposes only and does not imply endorsement by the US government.

References

Alverson DL (1992) A review of commercial fisheries and the Steller sea lion (*Eumetopias jubatus*): the conflict arena. Rev Aquat Sci 6:203–256

Andruskiw M, Fryxell JM, Thompson ID, Baker JA (2008) Habitat-mediated variation in predation risk by the American marten. Ecology 89:2273–2280

Anthony RG, Estes JA, Ricca MA, Miles AK, Forsman ED (2008) Bald eagles and sea otters in the Aleutian Archipelago: indirect effects of trophic cascades. Ecology 89:2725–2735

Bodkin JL, Esslinger G, Monson DH (2004) Foraging depths of sea otters and implications to coastal marine communities. Mar Mamm Sci 20:305–321

Bolker B, Holyoak M, Krivan V, Rowe L, Schmitz O (2003) Connecting theoretical and empirical studies of trait-mediated interactions. Ecology 84:1101–1114

Brown JS (1984) On the relationship between abundance and distribution of species. Am Nat 124:255–279

Brown JS (1999) Vigilance, patch use and habitat selection: foraging under predation risk. Evol Ecol Res 1:49–71

Brown JS, Laundre JW, Gurung M (1999) The ecology of fear: optimal foraging, game theory, and trophic interactions. J Mamm 80:385–399

Burn DM, Doroff AM, Tinker TM (2003) Carrying capacity and pre-decline abundance of sea otters (*Enhydra lutris kenyoni*) in the Aleutian Islands. Northwest Nat 84:145–148

Clarke KR, Gorley RN (2006) PRIMER v6: user manual/tutorial. PRIMER-E, Plymouth, pp 1–192

Clarke KR, Warwick RW (2001) Change in communities: an approach to statistical analysis and interpretation, 2nd edn. PRIMER-E, Plymouth, pp 1–172

Cote SD, Rooney TP, Tremblay J-P, Dussault C, Waller DM (2004) Ecological impacts of deer overabundance. Annu Rev Ecol Evol S 35:113–114

Dean TA, Bodkin JL, Fukuyama AK, Jewett SC, Monson DH, O'Clair CE, VanBlaricom GR (2002) Food limitation and the recovery of sea otters following the 'Exxon Valdez' oil spill. Mar Ecol Prog Ser 241:255–270

Doroff AM, Estes JA, Tinker MT, Burn DM, Evans TJ (2003) Sea otter population declines in the Aleutian archipelago. J Mamm 84:55–64

Duggins DO, Eckman JE, Sewell AT (1990) Ecology of understory kelp environments. II. Effects of kelps on recruitment of benthic invertebrates. J Exp Mar Biol Ecol 143:27–45

Estes JA, Duggins DO (1995) Sea otters and kelp forests in Alaska—generality and variation in a community ecological paradigm. Ecol Monogr 65:75–100

Estes JA, Tinker MT, Williams TM, Doak DF (1998) Killer whale predation on sea otters linking oceanic and nearshore ecosystems. Science 282:473–476

Estes JA, Riedman ML, Staedler MM, Tinker MT, Lyon BE (2003) Individual variation in prey selection by sea otters: patterns, causes and implications. J Anim Ecol 72:144–155

Estes JA, Tinker MT, Doroff AM, Burn DM (2005) Continuing sea otter population declines in the Aleutian archipelago. Mar Mamm Sci 21:169–172

Estes JA, Doak DF, Springer AM, Williams TM (2009) Causes and consequences of marine mammal population declines in southwest Alaska: a food-web perspective. Philos Trans R Soc B 364:1647–1658

Estes JA, Bodkin JL, Tinker MT (2010a) Threatened southwest Alaska sea otter stock: delineating the causes and constraints to recovery of a keystone predator in the North Pacific Ocean, North Pacific Research Board final report 717, p 117

Estes JA, Tinker MT, Bodkin JL (2010b) Using ecological function to develop recovery criteria for depleted species: sea otters and kelp forests in the Aleutian Archipelago. Conserv Biol 24:852–860

Fett RW, Englebretson RE, Perryman DC (1993) Basic weather regimes of the Aleutian Islands. In: RW Fett, RE Englebretson, DC Perryman (eds) Forecasters Handbook for the Bering Sea, Aleutian Islands, and Gulf of Alaska. Naval Research Laboratory report NRL/PU/7541–93–006. Naval Research Laboratory, Monterey, CA, p (4)1–23

Fox JL, Sinha SP, Chundawat RS (1992) Activity patterns and habitat use of ibex in the Himalaya Mountains of India. J Mamm 73:527–534

Freiwald J, Stewart NL, Yates DC, Bernardi G (2009) Isolation and characterization of nine polymorphic microsatellite loci of the kelp greenling, *Hexagrammos decagrammus*, a temperate reef fish. Mol Ecol Resour 9:563–565

Garshelis DL (1983) Ecology of sea otters in Prince William Sound, Alaska. PhD dissertation, University of Minnesota, Minneapolis, MN

Gilliam JF, Fraser DF (1987) Habitat selection under predation hazard: test of a model with forging minnows. Ecology 68:1856–1862

Harrold C, Reed DC (1985) Food availability, sea urchin grazing, and kelp forest community structure. Ecology 66:1160–1169

Heithaus MR, Dill LM (2006) Does tiger shark predation risk influence foraging habitat use by bottlenose dolphins at multiple spatial scales? Oikos 114:257–264

Kenyon KW (1969) The sea otter in the Eastern Pacific Ocean. Dover Publications, New York

Kuker K, Barrett-Lennard L (2010) A re-evaluation of the role of killer whales *Orcinus orca* in a population decline of sea otters *Enhydra lutris* in the Aleutian Islands and a review of alternative hypotheses. Mamm Rev 40(2):1–22

Laidre KL, Estes JA, Tinker MT, Bodkin J, Monson D, Schneider K (2006) Patterns of growth and body condition in sea otters from the Aleutian archipelago before and after the recent population decline. J Anim Ecol 75:978–989

Lima SL (1998) Stress and decision making under the risk of predation: recent developments from behavioral, reproductive, and ecological perspectives. Adv Study Behav 27:215–290

Manly BFJ, McDonald LL, Thomas DL, McDonald TL, Erickson WP (2002) Resource selection by animals: statistical design and analysis for field studies, 2nd edn. Kluwer Academic, Boston

McNab WH, Avers PE (1996) Ecoregional Subregions of the United States. United States Forest Service rport WO–WSA–5. United States Department of Agriculture, Washington, DC

McNamara JM, Houston AI (1992) Risk-sensitive foraging: a review of the theory. B Math Biol 54:355–378

National Research Council (1996) The Bering Sea ecosystem. National Academy Press, Washington, DC, p 320

National Research Council (2003) The decline of the Steller sea lion in Alaskan waters: untangling food webs and fishing nets. National Academy Press, Washington, DC, p 204

Norris K (2004) Managing threatened species: the ecological toolbox, evolutionary theory and declining-population paradigm. J Appl Ecol 41:413–426

Oftedal OT, Ralls K, Tinker MT, Green A (2007) Nutritional constraints on the southern sea otter in the Monterey Bay National Marine Sanctuary and a comparison to sea otter populations at San Nicholas Island, California and Glacier Bay, Alaska. Joint final report to the Monterey Bay National Marine Sanctuary, Monterey Bay, CA

Oksanen T, Power ME, Oksanen L (1995) Habitat selection and consumer resources. Am Nat 146:565–583

Ostfeld RS (1982) Foraging strategies and prey switching in the California sea otter. Oecologia 53:170–178

Pfitsch WA, Bliss LC (1985) Seasonal forage availability and potential vegetation limitations to a mountain goat population, Olympic National Park. Am Midl Nat 113:109–121

Rosen DAS, Trites AW (2000) Pollock and the decline of Steller sea lions: testing the junk food hypothesis. Can J Zool 78:1243–1250

Rotterman LM, Simon-Jackson T (1988) Sea otter. In: Lentfer JW (ed) Selected marine mammals of Alaska: species accounts with research and management recommendations. Marine Mammal Commission, Washington, DC, pp 237–271

Schoenecker KA, Singer FJ, Zeigenfuss LC, Binkley D, Menezes RSC (2004) Effects of elk herbivory on vegetation and nitrogen processes. J Wildl Manage 68:837–849

Sih A (1980) Optimal behavior: can foragers balance two conflicting demands? Science 210:1041–1043

Sih A (1982) Optimal patch use: variation in selective pressure for efficient foraging. Am Nat 120:666–685

Sih A (1987) Predators and prey lifestyles: an evolutionary and ecological overview. In: Sih A (ed) Predation: direct and indirect impacts on aquatic communities. University Press of New England, Hanover, pp 203–224

Simenstad CA, Estes JA, Kenyon KW (1978) Aleuts, sea otters, and alternate stable-state communities. Science 200:403–411

Stein RA, Magnuson JJ (1976) Behavioral response of crayfish to a fish predator. Ecology 57:751–761

Stewart NL, Konar B (2012) Kelp forests versus urchin barrens: alternate stable states and their effect on sea otter prey quality in the Aleutian Islands. J Mar Biol 2012:1–12

Trites AW, Donnelly CP (2003) The decline of Steller sea lions *Eumetopias jubatus* in Alaska: a review of the nutritional stress hypothesis. Mamm Rev 33:3–28

Vila AR, Campagna C, Iñíguez M, Falabella V (2008) South American sea lions (*Otaria flavescens*) avoid killer whale (*Orcinus orca*) predation. Aquat Mamm 34:317–330