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Influence of occupation history and habitat on Washington sea otter diet

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ABSTRACT

Habitat characteristics are primary determinants of nearshore marine communities. However, biological drivers like predation can also be important for community composition. Sea otters (*Enhydra lutris* ssp.) are a salient example of a keystone species exerting top-down control on ecosystem community structure. The translocation and subsequent population growth and range expansion of the northern sea otter (*Enhydra lutris kenyoni*) in Washington State over the last five decades has created a spatio-temporal gradient in sea otter occupation time and density, and acts as a natural experiment to quantify how sea otter population status and habitat type influence sea otter diet. We collected focal observations of sea otters foraging at sites across the gradient in varying habitat types between 2010 and 2017. We quantified sea otter diet composition and diversity, and long-term rates of energy gain across the gradient. We found that sea otter diet diversity was positively correlated with cumulative sea otter density, while rate of energy gain was negatively correlated with cumulative density. Additionally, we found that habitat type explained 1.77 times more variance in sea otter diet composition than sea otter cumulative density. Long-term diet studies can provide a broader picture of sea otter population status in Washington State.

Key words: sea otter, foraging, *Enhydra lutris kenyoni*, diet composition, cumulative density gradient, energy intake, diet diversity, habitat, occupation history, population status.

Understanding how organisms interact with the biotic and abiotic environment is among the fundamental goals of ecology (Sutherland *et al.* 2013). Habitat characteristics are often primary determinants of nearshore marine communities (*e.g.,* Sebens 1991), while biological drivers like predation can also be important determinants of community composition (*e.g.,* Paine 1966). In some cases habitat characteristics can also mediate the effects of predation on community structure (*e.g.,* Menge 1978). Marine mammals are often important predators in shaping marine ecosystems (Bowen 1997) and sea otters (*Enhydra lutris ssp.)* are a salient example of a keystone species exerting top-down control on ecosystem community structure (*e.g.*, Estes and Palmisano 1974, Garshelis *et al.* 1986, Riedman and Estes 1990, Estes and Duggins 1995). Sea otters are top predators with small home ranges and differ from most marine mammals in that they forage in shallow nearshore coastal waters and bring captured prey to the surface to handle and consume, allowing for direct observation (Riedman and Estes 1990). Within the nearshore marine environment, sea otters forage in a variety of habitat types, including rocky- and soft-bottom habitat, with and without surface kelp canopy (Riedman and Estes 1990). Therefore, sea otters are ideally suited for ecological studies investigating the interplay of biotic and abiotic drivers of organisms, setting the groundwork for understanding the drivers of marine mammals more broadly, especially those that may not lend themselves to comparative foraging studies.

Sea otters (*Enhydra lutris* spp.) were heavily exploited during the maritime fur trade from the mid-1700s until the early 1900s, resulting in their extirpation from extensive portions of their range, including the northern sea otter (*E. l. kenyoni*) from Washington State (Scheffer 1940, Kenyon 1969). Following the translocation of 59 sea otters from Amchitka Island, Alaska in 1969 and 1970 to the central portion of the Olympic Coast of Washington State (Jameson *et al.* 1982), Washington’s sea otter population grew rapidly from a founding population estimated to be as few as 10 individuals (10%–21% per year, Jameson *et al.* 1982, 1986; Bodkin *et al.* 1999). Between the late 1970s and early 1990s, the sea otter population range was limited to the outer coast of Washington between Makah Bay and Destruction Island (Fig. 1), apparently reaching equilibrium levels in core parts of the range (between Petroleum Creek and Little James Island) around the mid-1990s (Laidre *et al.* 2002). Sea otters temporarily expanded their range north and eastward into the Strait of Juan de Fuca, with small numbers of animals sighted in the area in the winter of 1995, and sighting frequency and group sizes increasing until 2000, when more than 100 animals were noted in the Strait of Juan de Fuca (Laidre and Jameson 2006). Sighting frequency and group sizes in the Strait decreased after 2000, and have remained low. Beginning in the mid-2000s, sea otters began to expand their range southward from their established range (Jameson and Jeffries 2005), and since 2002 the majority of the population has occurred in the southern portion of the range, south of La Push (Fig. 1). The estimated number of sea otters in Washington State is now over 2,058 individuals (Jeffries *et al.* 2017).

The sea otter diet spans a diverse array of prey (Kenyon 1969, Riedman and Estes 1990, Estes 2015), primarily consisting of benthic marine invertebrates including mollusks, crustaceans, and echinoderms. Previous research has shown that sea otter diet selection, including prey type and size, depends on location, habitat type, season, and relative abundance of preferred prey types (*e.g.,* Estes and Duggins 1995, Watt *et al.* 2000, Tinker *et al.* 2012). Previous research also suggests that sea otter foraging site selection is based on habitat complexity (Stewart 2011), and that shoreline complexity (used to approximate sea otter proximity to diverse habitat types) likely mediates how sea otter foraging affects coastal communities (Hessing-Lewis *et al.* 2018).

The sea otter's nearshore distribution and foraging behavior allows a land-based observer with a high-powered telescope to estimate sea otter prey size, number, and type through direct observation, as well as to estimate energy intake rates (Dean *et al.* 2002, Tinker *et al.* 2008*a*). As a result, sea otter diets have been more closely studied than almost any other carnivore species (Tinker 2015). The relationship between population status and foraging behavior has been studied in various taxa, including birds (*e.g.,* Lewis *et al.* 2001, Ballance *et al.* 2009, Newsome *et al.* 2015), insects (*e.g.,* Kelly *et al.* 1996), and mammals, such as sea otters (*Enhydra lutris*; see review in Monson and Bowen 2015), Galapagos sea lions (*Zalophus* *wollebaeki*; Páez-Rosas and Aurioles-Gamboa 2010), white tailed deer (*Odocoileus virginianus*; Taillon *et al.* 2006), and reindeer (*Rangifer tarandus platyrhynchus*; Skogland 1985). Generally as populations approach environmental carrying capacity, competition for food increases and/or food becomes harder to find, leading to increased individual foraging effort, decreased energy intake rates, increased diet diversity and/or individual diet specialization (*e.g.,* Kelly *et al.* 1996, Lewis *et al.* 2001, Bolnick *et al.* 2002, Svanbäck and Bolnick 2005, Ballance *et al.* 2009, Páez-Rosas and Aurioles-Gamboa 2010, Tinker *et al.* 2012, Visser and Fiksen 2013). These individual effects eventually result in changes to population level demographic rates (*e.g.,* Skogland 1985) and declines in the intrinsic rate of population growth (Monson and Bowen 2015). Sea otter population growth and range expansion and associated dietary changes have been well documented. For example, sea otters exhibit different feeding habits depending on their occupation time in a given habitat; in many cases these predictable changes are a response to reduced abundance of preferred prey types, which are depleted by sea otter predation (Estes *et al.* 1981, Garshelis *et al.* 1986, Watt *et al.* 2000, Laidre and Jameson 2006, Tinker *et al.* 2008*a*). Optimal foraging theory predicts that animals forage to optimize their net energy intake per unit time (Macarthur and Pianka 1966). Thus, sea otters in newly occupied, food-rich areas, often target large, energy-rich, and abundant prey items (Estes *et al.* 1982, Ostfeld 1982, Garshelis *et al.* 1986, Laidre and Jameson 2006). In contrast, sea otters in longer occupied, food-poor areas focus on a wider variety of smaller, less abundant prey items (Estes *et al.* 1981; Kvitek *et al.* 1993; Laidre and Jameson 2006; Tinker *et al.* 2008*a*, 2012).

Northern sea otters in Washington State are listed as State Endangered, and both state and federal agencies have endeavored to monitor the population status through annual population counts to produce population indices since 1977 (Jeffries *et al.* 2017). In addition, studies of Washington sea otter foraging have been undertaken to understand their food habits and activity-time budgets as an indication of habitat quality, resource use, and population status (*e.g.,* Bowlby *et al.* 1988, Laidre and Jameson 2006, Walker *et al.* 2008). The continued growth and range expansion of the Washington State sea otter population provides an opportunity to explore the interplay between habitat type and sea otter occupation history as drivers of sea otter diet, and to expand upon previous sea otter foraging studies in Washington State (*e.g.,* Bowlby *et al.* 1988, Laidre and Jameson 2006, Walker *et al.* 2008) to estimate metrics of population status, including calorie intake rate and diet diversity. The population growth and range expansion of sea otters in Washington has created a spatial gradient in sea otter occupation time and density, with regions of the outer coast of Washington differing in their recent history of sea otter predation levels. In this study, we utilize this gradient to assess how sea otter diet composition and diversity, and energy intake rate change as a function of sea otter occupation history and quantify the effects of sea otter cumulative density and habitat type on sea otter diet.

METHODS

Sea Otter Population Indices

Range-wide population surveys have been conducted annually in Washington State since 1977, in late June or early July (excluding 1978–1980, 1982, 1984, 1986, 1988, 1997, 2009).

Aerial and ground-based surveys were conducted concurrently, following Jeffries *et al.* (2017). Each annual survey ideally resulted in 3 d of surveys, with up to two flight passes per day, and included aerial, photo, and ground estimates. The final index of sea otter abundance was a combination of aerial, photo, and ground counts, following Jeffries *et al.* (2017).

Sea Otter Distribution and Density

We used the digitized annual indices of sea otter abundance and positions from 1977–2017 population surveys to create a continuous smoothed 2-D raster surface representing cumulative sea otter density using the krnel density estimate (KDE) tool in ArcGIS 10.1, following Weitzman (2013). Kernel density calculates the density of point features (in this case otter positions and associated number of otters) around each output raster cell by fitting a kernel surface over each point. The surface value is highest at the point, and decreases with increasing radial distance from the point, reaching zero at the search radius. The volume under the surface equals the number of otters counted at that point. The density at each output raster cell is calculated by summing the values of all the kernel surfaces that overlay that raster cell center. Annual kernel densities were calculated and summed to create cumulative density surfaces for 1977–2017. We used a raster cell size of 25 m^2, and a search radius of 5 km, as this distance has been found to produce an appropriate level of smoothing in previous analyses (*e.g.,* Weitzman 2013, Tinker *et al.* 2008*b*). The year of occupation was calculated as the first year in which sea otters were counted during the annual summer survey within 5 km of a site, and rate of population change was calculated by fitting a linear model to the last 3 yr of counts (2015–2017) and determining the slope (Table 1). This method generates three important metrics of sea otter occupation, including: (1) the cumulative number of sea otters that were at a site, (2) the length of time that sea otters have been at a site, and (3) the current trend in counts of sea otters at the site.

Sea otter cumulative densities were extracted from raster cells corresponding to general foraging areas observable from previously established land-based observation sites (*n* = 29) to identify sea otter foraging observation sites used for this study. Sea otter foraging observation sites were then chosen across a gradient of sea otter cumulative density (0–233 cumulative sea otters/km^2) from the 29 previously established land-based observation sites.

Sea Otter Foraging Observations

Foraging data collected prior to 2014 were collected as a part of the USGS Pacific Nearshore Project[2] and other studies[3] and were used in addition to data collected in 2014–2017. We identified eight land-based sea otter foraging observation sites across the gradient of sea otter cumulative density (Fig. 1). Other criteria for site selection, in addition to sea otter cumulative density, included ease of access and permitting restrictions. Sea otter cumulative densities at the sites ranged from 0 to 51.50 cumulative sea otters/km^2 in 2010 and 0.03 to 64.16 cumulative sea otters/km^2 in 2017 (Table 1). At these eight sites, sea otters foraged in a range of habitats, from rocky, sand-bottom, to mixed habitats, with and without kelp canopies.

Foraging data were collected opportunistically from unmarked foraging sea otters from October 2010 to October 2017 with spotting scopes (Field Model, 53-80× magnification, Questar Corp., New Hope, PA; Victory Diascope 65 T* FL, 15-56×

magnification, Carl Zeiss Inc., Chesterfield, VA) at each of the sites following standard protocols established and used in studies of sea otters throughout their range in North America (Dean *et al.* 2002, Tinker *et al.* 2008*a*, Esslinger *et al.* 2014, Tinker 2015). By the nature of observing unmarked individuals on subsequent days, data from some individuals may be overrepresented. After locating a foraging sea otter, observers initiated focal observations for a continuous sequence of foraging dives, referred to as a foraging bout. For each foraging dive, observers recorded key variables: dive duration (time underwater searching for prey), surface duration (time on surface between dives, usually spent consuming prey), and dive outcome (whether prey was successfully captured). For each successful foraging dive, observers identified prey type to the lowest possible taxonomic level, number of prey items, and prey size. Prey size was estimated in relation to average sea otter forepaw width (5 cm; Kvitek *et al.* 1993), where size 1 prey were <5 cm (smaller than sea otter forepaw width), size 2 prey were >5 cm <10 cm (larger than 1 sea otter forepaw width, but smaller than 2), size 3 prey were >10 cm <15 cm (larger than two sea otter forepaw widths, but smaller than 3), and size 4 prey were >15 cm (larger than three sea otter forepaw widths) (VanBlaricom 1987). Prey size categories (1, 2, 3, and 4) were further split into size category qualifiers *a*, *b*, and *c*, where *a* was the smallest 1/3 of the size class, *b* was the middle 1/3 of the size class, and *c* was the largest 1/3 of the size class.

Sea Otter Foraging Data Analysis

As with previous studies of sea otter foraging, the raw data contained missing or unobserved variables for many dives, and these missing values were often biased towards small prey or short surface durations. To account for these biases and associated uncertainty in parameter estimates, we used a Monte Carlo resampling algorithm (Dean *et al.* 2002; Tinker *et al.* 2008*a*, 2012) to estimate sea otter rate of energy intake and diet diversity. This algorithm, as described in detail by Tinker (2015), consisted of 1,000 iterations of simulated foraging bouts, with dive variables drawn from appropriate density functions fit to our raw data. To parameterize distributions of prey biomass and energy density, we used previously assembled information on diameter-biomass relationships and calorific densities for each prey type (Oftedal *et al.* 2007), following Tinker *et al.* (2008*a*).

Multivariate statistics were used to determine correlations between habitat type, sea otter cumulative density, and sea otter diet composition. We summarized diet composition using the raw data in terms of the average proportion of dives on which 5 general prey classes occurred (clam, cancer crab, other crab, snail, and other) per site for each year and habitat type. Habitat type for each foraging bout was determined by observers in the field concurrent with foraging observations and was determined based on surface features and location of the area proximate to the foraging sea otter (*e.g.,* floating kelp canopy, protruding rocks). Habitat types were defined as intertidal, open water, emergent rock, and kelp canopy, depending on the habitat in which the focal sea otter had begun its foraging bout. For foraging bouts that did not have habitat data recorded, but did have sea otter position recorded, we assigned the habitat type *post hoc* based on the location of the foraging sea otter in relation to environmental layers, including annual kelp layers from Washington State DNR (Van Wagenen 2015) and a digital bathymetry model (Weatherall *et al.* 2015) in ArcGIS 10.1. Foraging bouts that did not have habitat data or sea otter position data recorded were not included in the multivariate diet composition analysis. We calculated assemblage dissimilarity using Bray-Curtis distance and applied nonmetric multidimensional scaling (NMDS) to visualize relationships among diet composition, habitat type, and sea otter cumulative density in ordination space. Multivariate analyses were performed using R version 3.2.4 (R Core Team 2016) with the vegan *package*, version 2.4-6 (Oksanen *et al.* 2018). We used the adonis2() function from the vegan library to fit a linear model to the distance matrix and conducted a permutation test with pseudo *F*-ratios to determine the influence of habitat type and sea otter cumulative density on diet composition. As we could not include site as a random effect in the model due to the nature of a permutation test, we defined the model to respond similarly with site as a fixed effect.

RESULTS

Foraging Data

Foraging records consisted of 5,573 individual foraging dives from 461 sea otter foraging bouts collected between 18 October 2010 and 16 October 2017 (Table 1). Of the data collected, 64% of dives (3,730 dives) were collected from females, 8% (490 dives) from males, and 28% (1,636 dives) from individuals of unknown sex. Approximately 77% of dives resulted in successful prey capture. The average dive duration was 50.40 ± 30.71 s, and the average surface duration was 38.90 ± 51.72 s. Aggregated prey diversity, as calculated by the Shannon Wiener diversity index (Shannon and Weaver 1949), for all observed foraging bouts was 1.38, and long term average rate of energy gain was 13.86 kcal/min.

Sea otters were observed to consume a total of 43 prey taxa. When prey selection was examined irrespective of habitat type or site, the dominant prey taxa in the diet of sea otters (prey taxa making up more than 5% of diet) were kelp crabs (*Pugettia spp*., percent of diet: 14.69%, mass intake: 2.43 g/min), followed by unidentified crabs (percent of diet: 13.71%, mass intake: 2.27 g/min), razor clams (*Siliqua patula*, percent of diet: 10.56%, mass intake: 1.75 g/min), Dungeness crabs (*Cancer magister*, percent of diet: 9.20%, mass intake: 1.52

g/min), red rock crabs (*Cancer productus*, percent of diet: 8.19%, mass intake: 1.35 g/min), unidentified snails (percent of diet: 7.09%, mass intake: 1.17 g/min), unidentified clams (percent of diet: 6.61%, mass intake: 1.09 g/min), butter clams (*Saxidomus gigantea,* percent of diet: 6.18%, mass intake: 1.02 g/min), and graceful kelp crabs (*Pugettia gracilis,* percent of diet: 5.51%, mass intake: 0.91 g/min).

Geographic Differences

The primary prey taxa in the diet of sea otters at each site were as follows: Koitlah Point, butter clam (*Saxidomus gigantea*, 4.82 g/min); Beach 4, Pacific razor clam (*Siliqua patula*, 19.26 g/min); Giants Graveyard, red rock crab (*Cancer productus*, 6.88 g/min); Norwegian Memorial, Dungeness crab (*Cancer magister*, 4.55 g/min); Sand Point, unidentified snail (4.48 g/min); Yellow Banks, kelp crab (*Pugettia* spp., 3.46 g/min); Duk Point, unidentified clam (8.18 g/min); and Cannonball, unidentified crab (rate of mass gain = 5.74 g/min). The relative abundance of sea otter prey classes (urchin, bivalve, cancer crab, other crab, snail, and other) are reported in Table 2.

In general, sea otter rate of energy gain was negatively correlated with sea otter cumulative density (Fig. 2A, residual SE: 7.392 on five degrees of freedom), and sea otter prey diversity was positively correlated with sea otter cumulative density (Fig. 2B, residual SE: 0.3582 on five degrees of freedom). Energy recovery rates decreased with increasing sea otter cumulative density from approximately 27.71 ± 2.66 kcal/min at 5.63 otters/km^2 to approximately 15.51 ± 1.79 kcal/min at 64.16 otters/km^2 (Fig. 2A). An analysis of the frequency of size classes consumed by sea otters across the gradient of sea otter occupation demonstrated that sea otter prey size generally decreased with increasing sea otter cumulative density (Fig. 3). Sea otters at sites with sea otter cumulative densities of 0.03–27.14 otters/km^2 primarily consumed larger prey items (mode: size 1C, 33.3–50 mm), while sea otters at sites with sea otter cumulative densities of 41.26–64.16 otters/km^2 consumed smaller prey items (mode: size 1B, 16.7–33 mm).

Multivariate Analyses

NMDS ordination of sea otter diet composition converged on a stable, 2-D solution (stress = 0.16) and indicated moderate separation of diet composition at high cumulative density sites from low cumulative density sites along NMDS1 (Fig. 4A, C). We observed no differentiation of diet composition by habitat type (Fig. 4B) or site. Sea otter prey categorized as “other” were negatively correlated with NMDS1, while “other crabs” were positively correlated with NMDS1 (Fig. 4C). Cancer crabs were positively correlated with NMDS2, while clams and snails were negatively correlated with NMDS2 (Fig. 4C). The NMDS also suggested that higher sea otter cumulative density was correlated with a higher proportion of “other crabs” in sea otter diet, while the proportion of clams was negatively correlated with cumulative density (Fig. 4C). The NMDS also suggested that snail prey was mostly associated with intertidal habitat, clams and cancer crabs mostly associated with open water habitat, and prey categorized as “other crabs” and “other” mostly associated with kelp canopy habitat (Fig. 4D). A test of multivariate homogeneity of group dispersions indicated homogeneity of dispersion (P = 0.129). perMANOVA analysis indicated that all three covariates were significant in explaining the dissimilarity in sea otter diet composition, including site ($P = 0.001$), cumulative density ($P = 0.017$), and habitat type ($P = 0.03$). Of the variance explained by the model (50%), site explained 75.1% of the variance in sea otter diet composition ($r^2 = 0.376$), while habitat type explained 16.02% ($r^2 = 0.08$) and sea otter cumulative density explained 9.04% ($r^2 = 0.045$).

DISCUSSION

Sea Otter Diving

Our study demonstrated that current sea otter foraging dive parameters, including dive success, dive duration, and surface duration were similar to those reported previously for Washington State in 1993–1999 (Laidre and Jameson 2006) and 2003–2004 (Walker *et al.* 2008). Approximately 77% of dives resulted in successful prey capture in our study, compared to a 77% success rate reported in 1993–1999 and 81.4% in 2003–2004. Average dive duration (irrespective of dive success) in Washington in the 1990s was 55 ± 1 s and 36.5 ± 19.9 s in 2003–2004, compared to 50.40 ± 30.71 s in our study. Average surface duration in the 1990s was 45 ± 2 s compared to the 38.90 ± 51.72

s in our study. The similarities between dive parameters in our study and those reported in Laidre and Jameson (2006) and Walker *et al.* (2008), as well as those reported in other areas (Ralls *et al.* 1995, Bodkin *et al.* 2004), suggest that Washington sea otters have similar foraging habits to other sea otter populations, at least at shallow depths.

Previous research of sea otter foraging depths in Southeast Alaska has shown that for deep foraging dives (38.5–49 m), sea otters exhibit almost double the dive and surface duration when compared to shallow foraging dives (7.1–8.1 m), and exhibit similar dive durations to those observed in this study (59–64 s for shallow dives in SE Alaska, *vs.* 50.40 s in this study) (Bodkin *et al.* 2004). The similarity between observed dive durations and shallow dive durations in southeast Alaska, in combination with subsequent work by Laidre *et al.* (2009) that found time spent foraging was minimal beyond 40 m depth in Washington, suggests that the majority of foraging observations in this study occurred at shallow depths, well below 40 m offshore depth. While previous radiotelemetry studies have shown that foraging sea otters in Washington average 717–1,163 m from shore depending on sex and age class (Laidre *et al.* 2009), offshore foraging may be particularly important for sea otters south of Cape Flattery on the outer coast of Washington, as the continental shelf provides usable foraging habitat to 40 m offshore depth and extends as much as 15 km offshore, compared to the Strait of Juan de Fuca where the 40 m depth contour extends as much as 1 km offshore. However, we are limited in our ability to observe sea otters foraging at deeper depths offshore by the viewing distance of spotting scopes (our maximum viewing distances averaged approximately 1 km). As such, our foraging observations are limited to a small proportion of available forage habitat and should not be considered representative of all sea otter diet in Washington. If sea otters in Washington are foraging throughout the total available habitat to 40 m offshore depth, their energy recovery rates may be lower than what we observed in this study. However, this also depends on their prey items, as there would be energy tradeoffs between diving to deeper depths and the energy intake from the prey recovered.

Previous studies of foraging sea otters have also shown that males typically dive to deeper depths farther offshore (Bodkin *et al.* 2004, Laidre *et al.* 2009), with adult females foraging 60% of the time between 0 m and 10 m offshore depth and negligible time spent foraging beyond 30 m, and adult males foraging between 0-10 m 22% of the time, and 32%–34% of the time between 10 m and 30 m, indicating that our foraging data may be biased towards females who forage closer to shore. Our findings suggest this may be the case as well: 64% of dives (3,730 dives) were collected from females, 8% (490 dives) from males, and 28% (1,636 dives) from individuals of unknown sex. This is likely due in part to the fact that sea otters sex segregate; male areas generally occur at the geographic range edges while female and pup areas occur in the core of the geographic range (Riedman and Estes 1990). Six of our eight sites were located in female/pup areas. Additionally, as foraging observations were collected from unmarked individuals on subsequent days, our data may overrepresent the diet of some individuals. Thirty sea otters were flipper tagged in 2011 as a part of the USGS Pacific Nearshore Project;[4] however, we were unable to collect foraging data from these individuals during the course of our study.

Although this is a potential bias of our study, previous foraging studies of unmarked sea otters have been used to assess the population status of various sea otter populations (see review of approaches to evaluating the status of individuals and populations in Monson and Bowen 2015). Additionally, the potential overrepresentation of some individuals was likely partially ameliorated, as we collected foraging data throughout the year, and in multiple years.

Sea Otter Diet

It has previously been established that sea otter diet diversity in Washington State is lower in recently occupied areas than in areas within the established sea otter population range (Laidre and Jameson 2006), and our study further demonstrated that at a finer geographic scale and across a gradient of occupation time and density. We also found that sea otter rate of energy gain is generally negatively correlated with sea otter cumulative density, and sea otters foraging at sites with low sea otter cumulative density consumed larger prey than sea otters foraging in areas with medium and high sea otter occupation time and density. Although these results are not surprising and suggest that Washington State sea otters are consistent with patterns established in other areas, they allow us to make informed predictions of future foraging patterns.

In the temporary absence of sea otters after their extirpation from portions of their range, high-value invertebrate fisheries developed that target many of the same calorically rich prey preferred by sea otters. The recolonization and reintroduction of sea otters to areas of historical sea otter occupation, that now cooccur spatially with fisheries, has led to conflicts between sea otters and fisheries along the North American Pacific Coast (*e.g.,* Estes and VanBlaricom 1985, Reidy 2011, USFWS 2012, Larson *et al.* 2013, Honka 2014, Hoyt 2015), and in some cases has had measurable impacts on fisheries species (Fanshawe *et al.* 2003, Larson *et al.* 2013, Hoyt 2015). As the Washington State sea otter population continues to grow and expand its range, managers are faced with managing sea otters and fisheries that have never coexisted, similar to other areas of sea otter recolonization. Further research is needed to elucidate the potential interactions between sea otters and fisheries in Washington to set the ground work for predictive modeling necessary to inform management strategies. Sea otters in Washington have been observed consuming fishery species, including Dungeness crab, sea cucumbers, razor clams, and urchins (JH, personal observation). Despite this, there is a need for a formal evaluation of the potential impact of sea otters on these fished invertebrate populations and for a quantitative assessment of whether sea otter predation impacts are of sufficient magnitude to threaten the harvests of these species.

Interestingly, our observations of sea otters foraging primarily on Pacific razor clams (65% of diet in 2010–2017) near the southern extent of the current population range draws a parallel with past sea otter range expansion into the Strait of Juan de Fuca in 1995. When sea otters temporarily expanded their range into the Strait, they began occupying urchin-rich habitat that they historically had not occupied since the beginning of the 20th century (Laidre and Jameson 2006). When sea otters first expanded their range into the Strait, their diet consisted almost exclusively (85%–90%) of red urchins, an important commercial and tribal fishery until 1997. After 1995, urchin monitoring surveys reported a 71% decline in sea urchins over 1 yr, and subsequent to this decrease in biomass, the fishery district was closed to commercial harvest by Tribal–State harvest agreement (Laidre and Jameson 2006). The percent of red urchins in sea otter diet decreased subsequent to their initial expansion into the Strait, from 85%–90% in 1995 and 1996, to 60% in 1997, and 40% in 1998 and 1999 (Laidre and Jameson 2006). Sea otter predation was never formally implicated in the decline and subsequent fishery closure (Laidre and Jameson 2006). Sighting frequency and group sizes of sea otters in the Strait have remained low after 2000 and urchins now (2010-2017) comprise 15% of sea otter diet at Koitlah Point in the Strait of Juan de Fuca. In Southeast Alaska, sea otters have been found to consume the highest proportion of commercially important species in recently colonized, low density areas (Hoyt 2015), likely as a result of sea otters preferentially consuming large, energy-rich, and abundant prey items. In Washington, we observed sea otters primarily consuming razor clams near the southern range extent at Beach 4, as well as at other areas near Kalaloch Beach. While the diet of sea otters immediately following their occupation (2005-2009) of this area is unknown, our results suggest that sea otters in this area are preferentially consuming a fishery species in recently occupied habitat as they did previously when they temporarily expanded their range into the Strait. While the impact of sea otters on razor clam populations and fisheries is currently unknown in Washington, and it is possible that sea otter consumption of razor clams may not conflict with the success of razor clam fisheries, there is a need for additional research given the majority of the sea otter population growth has occurred in the southern portion of the range (south of La Push) since 2002, the area where sea otters are spatially cooccurring with razor clam fisheries. As such, the potential for conflict between sea otters and razor clam fisheries, an important recreational and tribal fishery, should be evaluated.

Drivers of Sea Otter Diet Composition

As sea otter diet spans a diverse array of prey, a variety of factors can influence their specific prey choice, including sea otter occupation history and density, habitat type, prey size and density, and prey recruitment patterns and growth. Our analysis indicated that site, habitat type, and sea otter cumulative density explained approximately 50% of the variation in sea otter diet composition, and that of the covariates included in the model, site was the most important in explaining variation in sea otter diet composition. This may be reflective of the fact that sea otter diet composition is influenced by other environmental variables in the area surrounding a site, such as exposure or coastline complexity. In Southeast Alaska, exposure has been identified as an important variable describing sea otter diet (Hoyt 2015), and in British Columbia recent research has shown that coastline complexity, used to approximate sea otter proximity to shelter and diverse habitat types, is a driver of sea otter foraging (Hessing-Lewis *et al.* 2018). As sea otters in Washington experience a spatial gradient in shoreline complexity and exposure, with more complex shorelines to the north, and less complex, more exposed shorelines to the south, future research should investigate the relationship between shoreline complexity and exposure and sea otter diet composition in Washington. The availability of greater habitat diversity in other areas may also reduce the importance of habitat type on sea otter diet composition. We found that habitat type explained 1.77 times more variation in sea otter diet composition in Washington than sea otter cumulative density. Current research on drivers of sea otter diet in British Columbia has shown that sea otter occupation time is an important driver of diet, with the niches occupied by sea otters expanding at long occupation times to include more diverse prey items and habitats.[5] Occupation time may be a particularly important driver of sea otter diet in British Columbia because the coastline is more complex than Washington, and as a result sea otters can forage in diverse habitats in close proximity to each other (Hessing-Lewis *et al.* 2018), whereas habitats in Washington may be more spatially segregated.

Our determination of habitat type based on surface features where sea otters begin their foraging bouts may not necessarily reflect the diversity of habitat beneath the surface. The presence of a kelp canopy is reasonable evidence of consolidated substrate, however, the absence of surface canopy kelp says little about the underlying substrate or biogenic habitat like kelp and seagrass. Additionally, some species of kelp are seasonal and have reduced algal cover in the winter, adding to our inability to determine underlying substrate from surface features. As our study found that of the variance explained by the model (50%), habitat type explained 16.02% of variation in sea otter diet composition, accurate habitat classification when collecting sea otter foraging data will be important in future research. Prey recovered by sea otters may be an alternative to subjective habitat classification.[6] For example, clams and Dungeness crab (*Cancer magister)* are typically associated with unconsolidated, sandy substrate, and could be used as indicators of unconsolidated substrate, while kelp crabs (*Pugettia spp.)*, urchins, and chitons may be used to predict rocky substrate. However, in this case, classifying habitat type by prey would lead to circular logic when investigating habitat as a driver of sea otter diet.

Energy Intake Rate as Metric of Population Status

Evaluating population status is a fundamental aspect of the management and recovery of species. Population status can be defined based on the trend in abundance of the population or the population’s probability of persistence (Morris and Doak 2002).

Population status can also be defined ecologically, such as the population status relative to environmental carrying capacity (Monson and Bowen 2015). When population size is small relative to carrying capacity, individuals are expected to more easily acquire the resources they need to survive, often manifested as little time and/or effort spent foraging, which can lead to a cascade of individual and population level effects. Individuals are predicted to be able to acquire excess onboard energy stores (stored as blubber or lipid), which is then reflected in individual body condition which can translate to improved reproductive and survival rates (Monson and Bowen 2015). Life history and demographic metrics can thus be used as indicators of population status (Eberhardt 1977*a*, *b*; Fowler 1987), as individual status is intrinsically linked to population status. Various life history and demographic metrics have been used to infer the status of marine mammal populations, including (1) individual body condition (*e.g.,* fin whale, *Balaenoptera physalus*; Williams *et al.* 2013); (2) time spent foraging (*e.g.,* sea otter, *Enhydra lutris*; Estes *et al.* 1982); (3) age at maturity (*e.g.,* crabeater seal, *Lobodon carcinophagus*; Bengtson and Laws 1985); (4) reproductive rate (*e.g.,* hooded seal, *Cystophora cristata*; Frie *et al.* 2012); and (5) survival rate (*e.g.,* northern fur seal, *Callorhinus ursinus*; Fowler 1990). While these metrics can be more labor intensive and expensive to estimate than population abundance, they reflect population status at different temporal scales, providing managers with additional evidence and potentially advanced warning of changes in population status that are not yet reflected as changes in abundance (Monson and Bowen 2015). These indices can also shed light onto the mechanisms behind potential changes in population abundance, rather than just identifying the current trend in abundance or probability of persistence (Monson and Bowen 2015). Population status metrics are especially useful in the absence of frequent population monitoring. In the case of Washington sea otters, no population survey was conducted in 2018, and in the absence of an updated population abundance index, metrics of population status like energy intake rate and diet diversity can provide another line of evidence for sea otter population status.

Previous research has demonstrated generalizable trends in sea otter rate of energy intake and diet diversity across a gradient of sea otter population growth rate and density (Tinker 2015, Coletti *et al.* 2016). While our results indicated that, in general, sea otter foraging patterns in Washington follow traditional patterns established from well-studied areas, our study also highlights the importance of replicated studies of sea otter foraging in similar systems across a variety of geographic areas. Our study demonstrated two important deviations from traditional patterns. While we observed decreasing energy intake rates with increasing sea otter cumulative density, we also observed much higher energy intake rates than we would have expected based on population status. Typical energy intake rates range from 12 kcal/min to 21 kcal/min in recently established and rapidly growing populations throughout the sea otter’s North Pacific range, compared to energy intake rates ranging from 7 kcal/min to 11 kcal/min in long established, stable or slowly increasing populations where resource abundance is thought to be limiting further growth (Tinker *et al.* 2013, Tinker 2015, Coletti *et al.* 2016). As reported in Laidre *et al.* (2002), sea otters in Washington were apparently reaching equilibrium levels in core part of the range (between Petroleum Creek and Little James Island) around the mid-1990s. Therefore, we would expect the energy recovery rates of sea otters in that core area to reflect this equilibrium. Instead we observed energy intake rates ranging from 10.79 kcal/min to 15.76 kcal/min, compared to the typical 7–11 kcal/min. Similarly, we observed higher than expected energy intake rates ranging from 21.20 kcal/min to 27.71 kcal/min for sea otters foraging south of the core area, compared to the typical 12–21 kcal/min.

Sea otter populations have been shown to exhibit fairly uniform patterns of density-dependent growth (Estes 1990, Estes *et al.* 1996), best described by a logistic growth model when it is fit to populations at biologically meaningful spatial scales (Bodkin 2015, Tinker 2015, Tinker *et al.* 2017). As equilibrium density has been defined as the number of otters that can be supported by the habitat (Estes 1990), it logically follows that the density at which sea otter populations reach equilibrium varies with habitat characteristics and prey productivity (Laidre *et al.* 2001, 2002; Burn *et al.* 2003; Gregr *et al.*, 2008). Laidre *et al.* (2002) estimated the carrying capacity of Washington State sea otters by using sea otter densities in rocky habitat believed to be at equilibrium and calculating proportional densities for sandy and mixed areas based on current counts in the rocky equilibrium region and from previous calculations done in California (Laidre *et al.* 2001). The carrying capacity of Washington sea otters ranged from 1,372 (CV 0.13) to 2,734 (CV 0.13) (Laidre *et al.* 2002), compared to the current population index of 2,058 (Jeffries *et al.* 2017). These calculations were based on the assumptions that (1) sea otters in the rocky equilibrium area (Petroleum Creek to Little James Island) were at equilibrium, and (2) that when sea otters reached carrying capacity in sandy and mixed habitats that they would use those habitats similarly to sea otters in California. The high energy intake rates estimated in our study may be indicative of the Washington coast’s ability to support a higher number of sea otters than previously thought, largely as a consequence of abundant prey in relatively close proximity offshore, especially on the outer coast where the 40 m depth contour lies as far as 15 km offshore. In addition, previous radiotelemetry work in Washington demonstrates movements of animals throughout the occupied range (Laidre *et al.* 2009), compared to the small home ranges reported in long established sea otter populations at equilibrium densities (Bodkin 2015), suggesting that sea otters in Washington may not have been at environmental carrying capacity in the rocky equilibrium area at the time of the study. As these data were collected from 1992 to 1999, and there is no recent radiotelemetry data available for Washington sea otters, further research is needed to determine if sea otters in Washington State are at equilibrium in portions of their range as previously suggested, or are still below equilibrium densities as our energy intake rates suggest.

We found that the higher than expected energy intake rates were due in part to the estimated input of calories from kelp crabs (*Pugettia* spp.). Washington sea otters appear to be eating a kelp crab of a given size class almost twice as fast as in California[7] and British Columbia.[8] As kelp crabs are the primary prey item of sea otters in Washington State (14.69% of the diet), the net outcome of these faster kelp crab handling times is higher energy intake rate estimates. This faster kelp crab handling time in Washington was consistent across multiple independent observers during our study period (2010-2017), and across previous studies in the 1990s (Laidre and Jameson 2006). We explored this phenomenon by repeating our analysis after adjusting kelp crab edible biomass recovered per unit handling time to what we would expect for sea otters in British Columbia and California. We used a proportional reduction to adjust the edible biomass for kelp crab species and found the rate of energy gain across the gradient of sea otter occupation was more similar to those reported for California and British Columbia (Fig. S1). This exercise demonstrated that the higher than expected energy intake rates were in part a result of kelp crab consumption. Further research into the faster kelp crab handling time phenomenon will be important to understanding Washington sea otter foraging ecology, as previous research has assumed uniformity in sea otter prey, foraging behavior, and data collection methods.

The second deviation from previously established patterns in our study was at Koitlah Point, located near Neah Bay in the Strait of Juan de Fuca. Koitlah Point had the lowest cumulative sea otter density (0.03 sea otters/km^2) of any of our sites, and as such we expected it to have the highest energy intake rate and lowest prey diversity. However, Koitlah Point had the lowest energy intake rate (6.99 kcal/min) and a higher diet diversity (1.25) than expected based on Koitlah's sea otter occupation history that is reflected in the annual sea otter survey data. When we removed Koitlah Point from our models of energy intake rate and diet diversity, the model fits were more similar to the relationships that have been found in other areas (Fig. S2A, B). Sea otters at Koitlah Point had the longest dive and surface durations of any site, with a mean dive duration of 83.49 ± 36.69 s (1.76 times the average dive duration of all other sites of 47.55 s), and an average surface duration of 48.59 ± 49.03 s (1.27 times the average surface duration of all other sites of 38.23 s). As male sea otters are known to dive deeper than females (Bodkin *et al.* 2004, Laidre *et al.* 2009) and congregate at range edges (Riedman and Estes 1990), and Koitlah Point is near the northeastern most edge of the Washington sea otter range, we explored the possibility that this longer observed average dive duration could be a result of sex bias in our data.

When we compared the average percent of dives across all sites made by females (62%), males (10%), and by individuals of unknown sex (28%) with dives made at Koitlah Point by females (58%), males (3%), and individuals of unknown sex (38%), we did observe a smaller proportion of dives by females and a larger proportion of dives by individuals of unknown sex. It is possible that those individuals of unknown sex could be males foraging farther from shore, where it is difficult to observe morphological indications of sex. As sea otters at Koitlah Point were primarily consuming clams equal or less than one sea otter paw width in size (≤size 1C), we hypothesize that the energetic demand of making deep dives for small clams resulted in a lower kilocalorie intake rate than expected based on the sea otter cumulative density data at this site. In addition, Koitlah Point was the only site located in the Strait of Juan de Fuca (all other sites were on the outer coast of the Olympic Peninsula), thus the difference in kilocalorie intake rate and diet diversity may also be indicative of spatial variation in the sustainable carrying capacity of sea otters. Other explanations for this include the possibility that the cumulative density, calculated from the annual sea otter survey data, is not accurately reflecting the use of this site by sea otters. As the annual sea otter survey is conducted in late June or early July each year, the surveys may not be reflective of seasonal changes in occupancy. In contrast to the outer coast, sea otters appear to seasonally occupy Koitlah Point, with anecdotally more individuals in early spring when compared to summer and fall (JH, personal observation). As a result, the survey may be underestimating the actual densities of sea otters in this area in non-summer months. Future research is needed to investigate the intra-annual variation in sea otter occupation of Koitlah Point.

Many previous studies of sea otter diet have taken advantage of spatial and temporal gradients in sea otter recolonization and have used space-for-time substitutions to infer a temporal trend in sea otter diet with varying sea otter occupation dates (Kvitek 1989; Kvitek *et al.* 1992, 1998; Singh *et al.* 2013; Honka 2014). However, space-for-time substitutions fail to take into account varying degrees of occupation (*i.e.*, population density) and the fact that areas can become unoccupied (*i.e.*, the persistence of occupation). Cumulative density analyses, however, account for both potential changes in occupation status and abundance (Larson *et al.* 2013, Weitzman 2013), providing a more accurate measure of sea otter occupation history over time. An alternative metric of sea otter impact that accounts not only for sea otter persistence and degree of occupation, but also for the availability of potential foraging habitat, will be important as sea otter equilibrium densities have been shown to be spatially variable and will influence how the sea otter use metric is interpreted.

Our study highlights the importance of replicated studies of sea otter foraging in similar systems across a variety of geographic areas, and suggests that drivers of sea otter diet vary between geographic regions. Understanding the drivers of sea otter diet, in combination with predictive population modeling, could provide valuable insight into potential interactions between sea otters and fishery species and assist management decisions. Northern sea otters play a critically important ecological and cultural role on the Olympic Coast of Washington State, and this research contributes to a better understanding of the effect of sea otters on the nearshore marine system, as well as provides another measure of population status of a reintroduced sea otter population.

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SUPPORTING INFORMATION

The following supporting information is available for this article online at http://

Figure S1. Rate of sea otter energy gain (kcal/min) versus sea otter (*Enhydra lutris kenyoni*) cumulative density (otters/km^2) after being adjusted for percent edible biomass of kelp crabs. Error bars indicated standard deviation (Residual SE: 7.292 on five degrees of freedom).

Figure S2. A. Rate of sea otter energy gain (kcal/min) versus sea otter (*Enhydra lutris kenyoni*) cumulative density (otters/km^2) fit with a 3-term exponential model, not including Koitlah Point. Error bars indicate standard deviations (residual SE: 2.849 on four degrees of freedom). B. Sea otter diet diversity versus sea otter cumulative density fit with a 3-term exponential model, not including Koitlah Point (residual SE: 0.315 on four degrees of freedom).

Figure 1. The Olympic Peninsula of Washington State with cumulative density of sea otters (*Enhydra lutris kenyoni*), 1977-2017. Darker shades indicate high sea otter cumulative density; lighter shades indicate low sea otter cumulative density. White callout bubbles indicate sea otter foraging observation sites, including Koitlah Point, Beach 4, Giant’s Graveyard, Norwegian Memorial, Yellow Banks, Sand Point, Duk Point, and Cannonball (cumulative densities in Table 1).

Figure 2. A. Rate of sea otter energy gain (kcal/min) versus sea otter (*Enhydra lutris kenyoni*) cumulative density (otters/km^2) fit with a 3-term exponential model. Error bars indicate standard deviations (residual SE: 7.392 on five degrees of freedom). B. Sea otter diet diversity versus sea otter cumulative density fit with a 3-term exponential model (residual SE: 0.3582 on five degrees of freedom).

Figure 3. The frequency of prey size classes recovered by sea otters (*Enhydra lutris kenyoni*) in Washington State during foraging dives at sites with varying sea otter cumulative densities. Darker shades indicate high sea otter cumulative density, lighter shades indicate low sea otter cumulative

density (cumulative densities in Table 1).

Figure 4. A. NMDS ordination of sea otter (*Enhydra lutris kenyoni*) diet composition based on the average proportion of dives that prey classes occur on from eight observation sites in Washington State, with the gradient of sea otter cumulative density shown. Bubble size corresponds to sea otter cumulative density. B. Ordination with 98% probability ellipses for each habitat type (ER = emergent rock, IN = intertidal, KC = kelp canopy, OW = open water) shown. C. Vectors are shown, scaled by their r^2 value, for each variable (sea otter cumulative density, clam, cancer crab, other crab, snail, other). D. Both habitat ellipses and variable vectors are shown.

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[2] Unpublished data from J. L. Bodkin, U.S. Geological Survey, Alaska Science Center, 4210 University Drive, Anchorage, AK 99508, U.S.A., June 2013.

[3] Unpublished data from S. E. Larson, Seattle Aquarium, 1483 Alaskan Way, Seattle, WA 98101, U.S.A., November 2016 and January 2018.

[3] Unpublish14ed data from S. E. Larson, Seattle Aquarium, 1483

Alaskan Way, Seattle, WA 98101, U.S.A., November 2016 and January 2018.

[4] Unpublished data from J. L. Bodkin, U.S. Geological Survey, Alaska Science Center, 4210 University Drive, Anchorage, AK 99508, U.S.A., March 2016.

[5] Personal communication from E. U. Rechsteiner, Hakai Insitute, End of Kwakshua Channel, Calvert Island, BC, Canada, May 2018.

[6] Personal communication from James Bodkin, U.S. Geological Survey, Alaska Science Center, 4210 University Drive, Anchorage, AK 99508, U.S.A., May 2018.

[7] Unpublished data from M. T. Tinker, Department of Ecology and Evolutionary Biology, University of California, Center for Ocean Health, 100 Scheffer Road, Santa Cruz, CA 95060, U.S.A., August 2017.

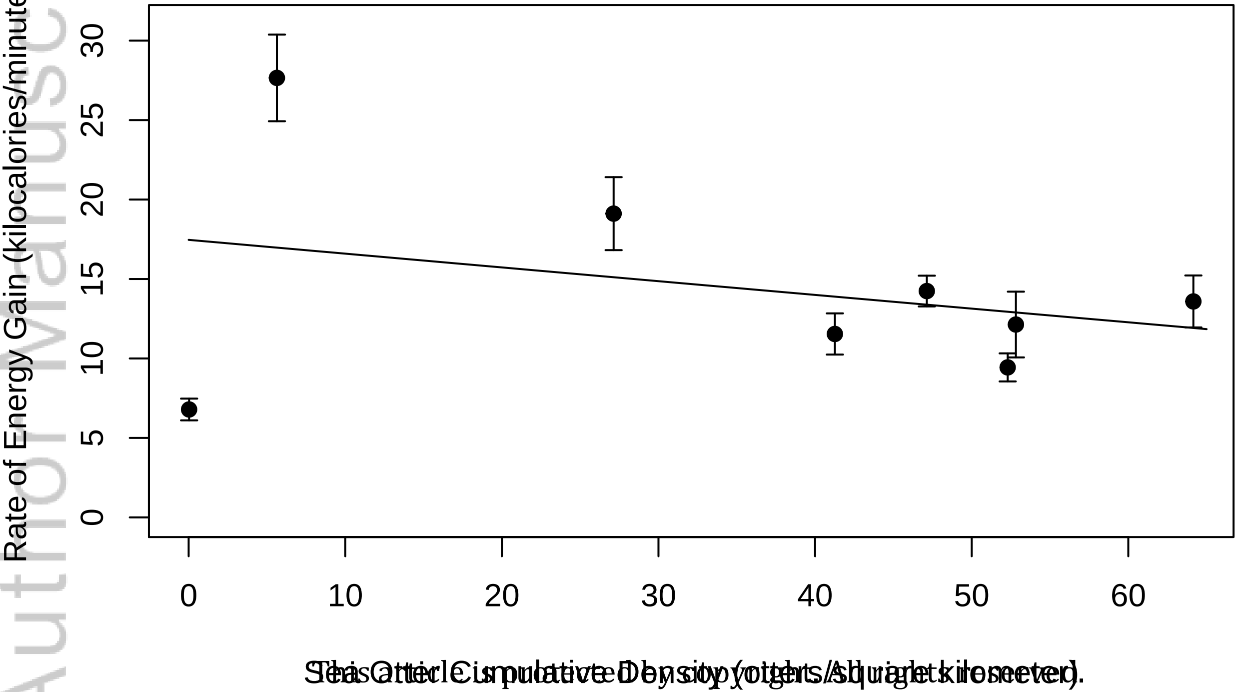
[8] Unpublished data from E. U. Rechsteiner, Hakai Institute, End of Kwakshua Channel, Calvert Island, BC, Canada, July 2018.

Table 1. Cumulative (1977–2017) density of sea otters (*Enhydra lutris kenyoni*) at foraging observation sites along the Washington Coast, year of occupation, rate of change in sea otter numbers, number of sea otter foraging dives and foraging bouts observed at each site, long-term rate of energy gain (kcal/min), and sea otter diet diversity as measured by the Shannon Weiner Index.

Site	Cumulative density (otters/km^2)	Year of occupation	Rate of change, 2015–2017	Number of dives	Number of foraging bouts	Rate of energy gain (kcal/min)	Diet diversity
Koitlah Point	0.03	2011	0	506	69	6.99	1.25
Beach 4	5.63	2005	239	636	47	27.71	0.84
Giants Graveyard	27.14	1977	92.5	721	51	21.2	0.47
Norwegian Memorial	41.26	1977	25.5	530	52	12.8	0.89
Sand Point	47.13	1981	14.5	1059	80	15.76	1.23
Yellow Banks	52.3	1981	24	1067	79	10.79	0.78
Duk Point	52.82	1977	−25	617	51	13.34	1.34
Cannonball	64.16	1977	−34	437	32	15.51	1.28

Table 2. The relative abundance of sea otter prey classes output from the Monte Carlo resampling algorithm.

Site	Urchin	Bivalve	Cancer crab	Other crab	Snail	Other
Koitlah Point	0.16	0.66	0.02	0.08	0.00	0.08
Beach 4	0.00	0.65	0.04	0.24	0.00	0.06
Giants Graveyard	0.00	0.10	0.52	0.36	0.01	0.00
Norwegian Memorial	0.00	0.00	0.33	0.36	0.04	0.27
Sand Point	0.01	0.12	0.04	0.48	0.31	0.03
Yellow Banks	0.00	0.04	0.24	0.53	0.14	0.04
Duk Point	0.02	0.52	0.12	0.25	0.02	0.07
Cannonball	0.06	0.12	0.07	0.58	0.07	0.10


Rate of Energy Gain (kilocalories/minute)
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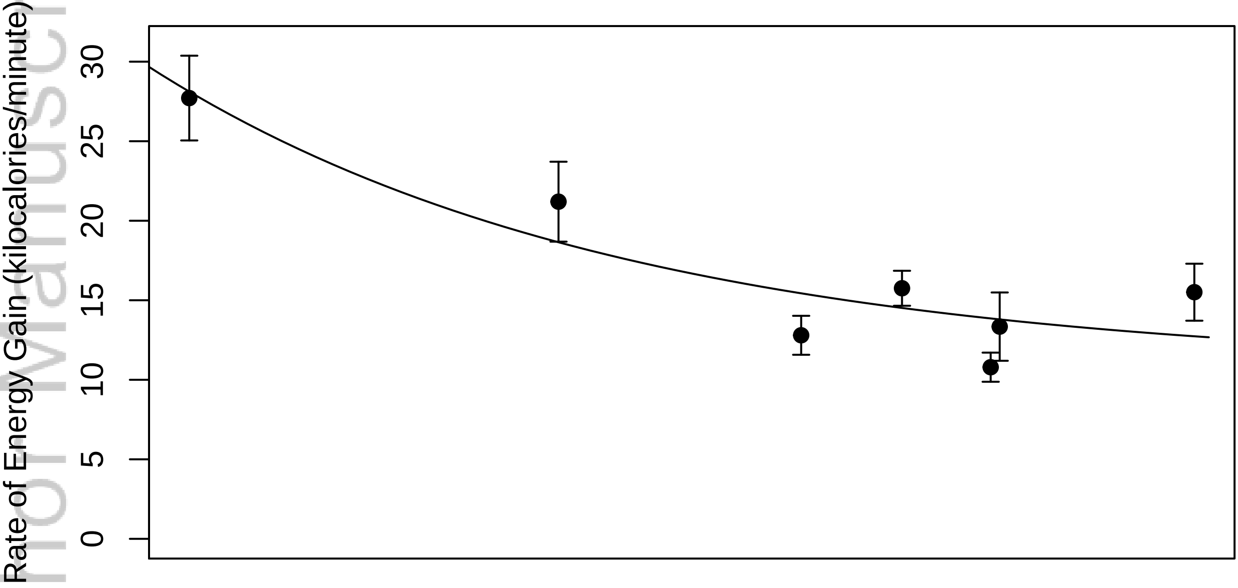
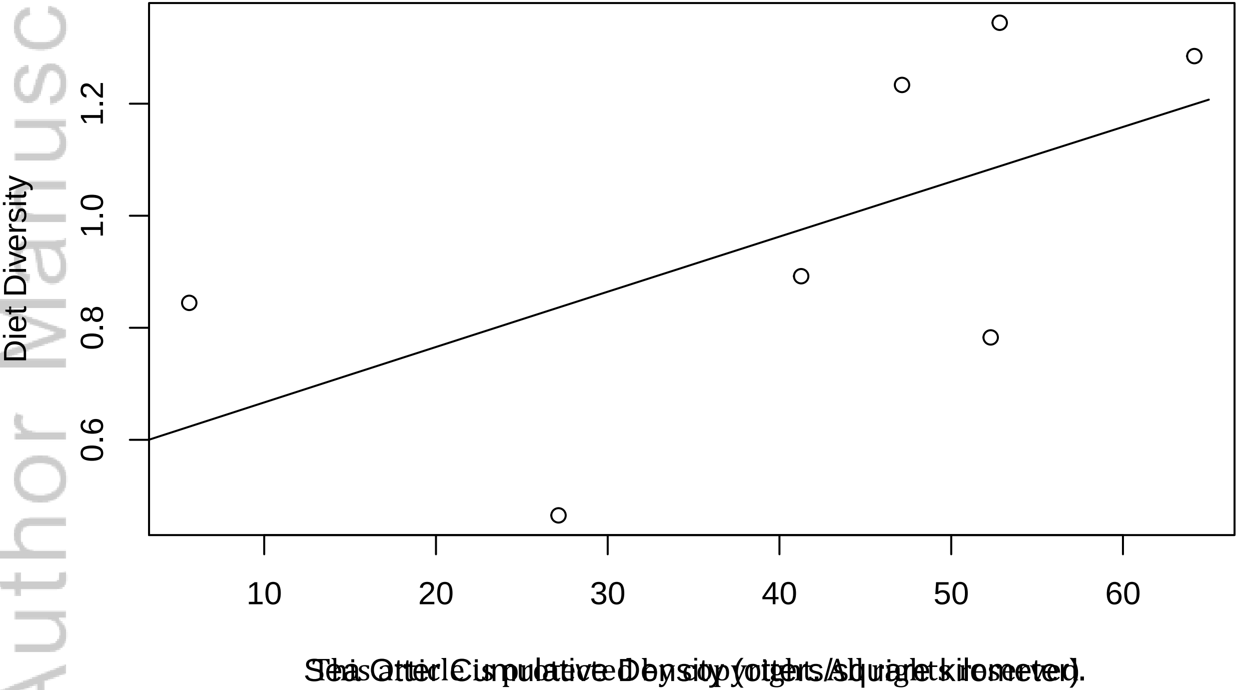
5
10
15
20
25
30
0
10
20
30
40
50
60
Sea Otter Cumulative Density (otters/square kilometer)


Rate of Energy Gain (kilocalories/minute)
30
25
20
15
10
5
0


Diet Diversity
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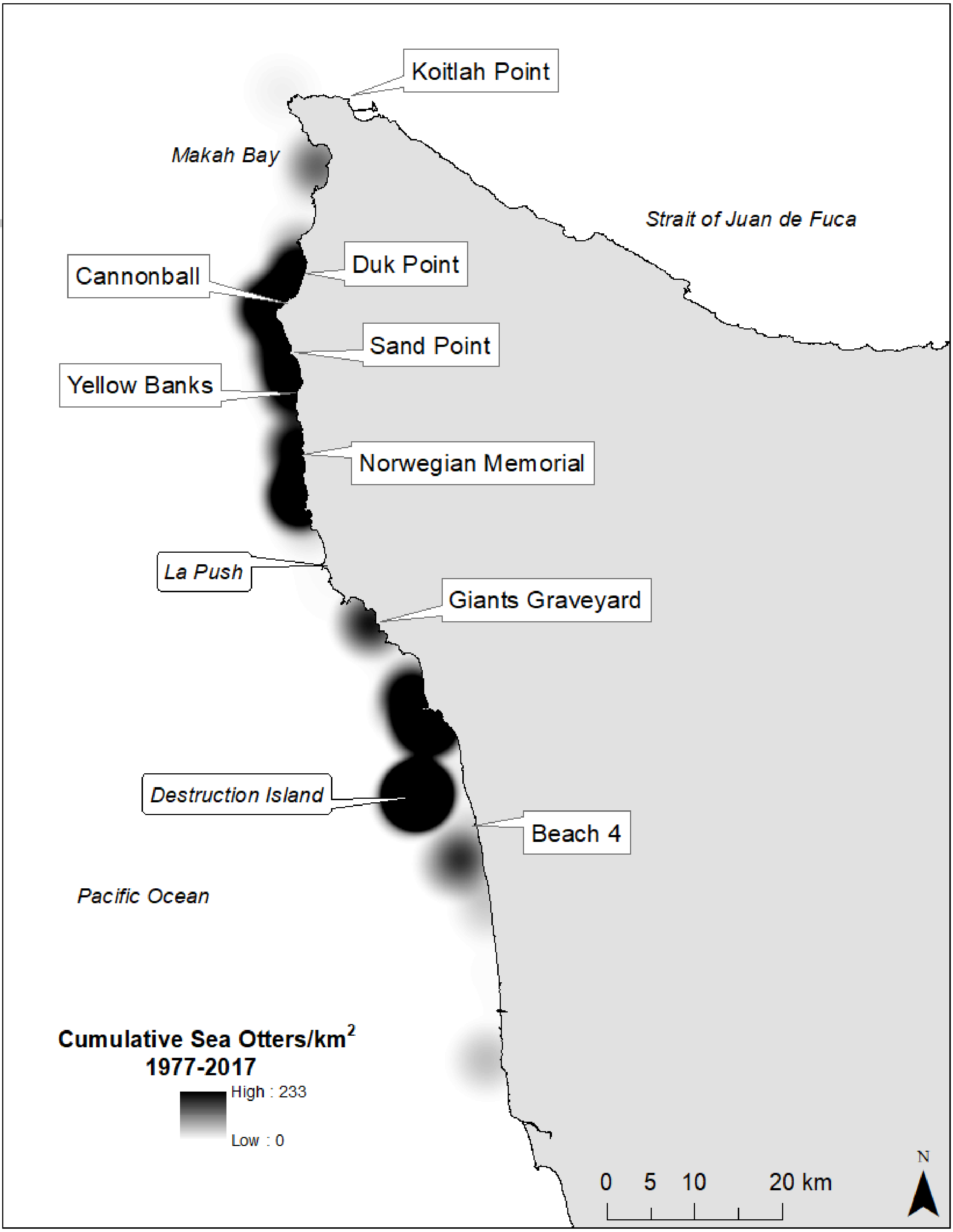
0.8
1.0
1.2
10
20
30
40
50
60
Sea Otter Cumulative Density (otters/square kilometer)



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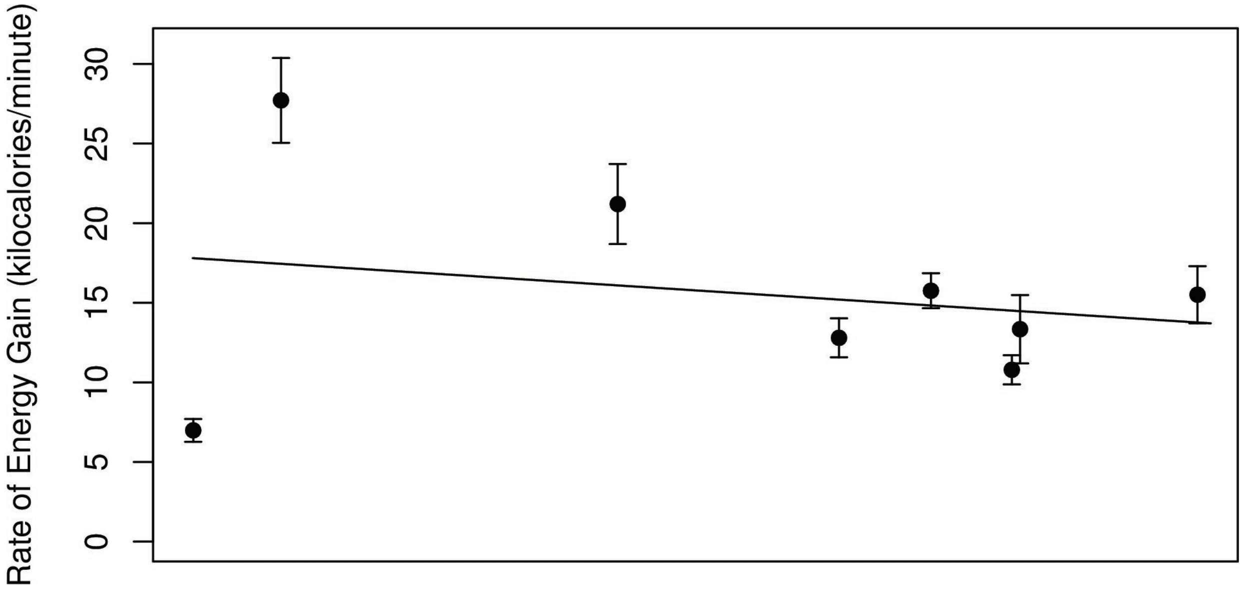

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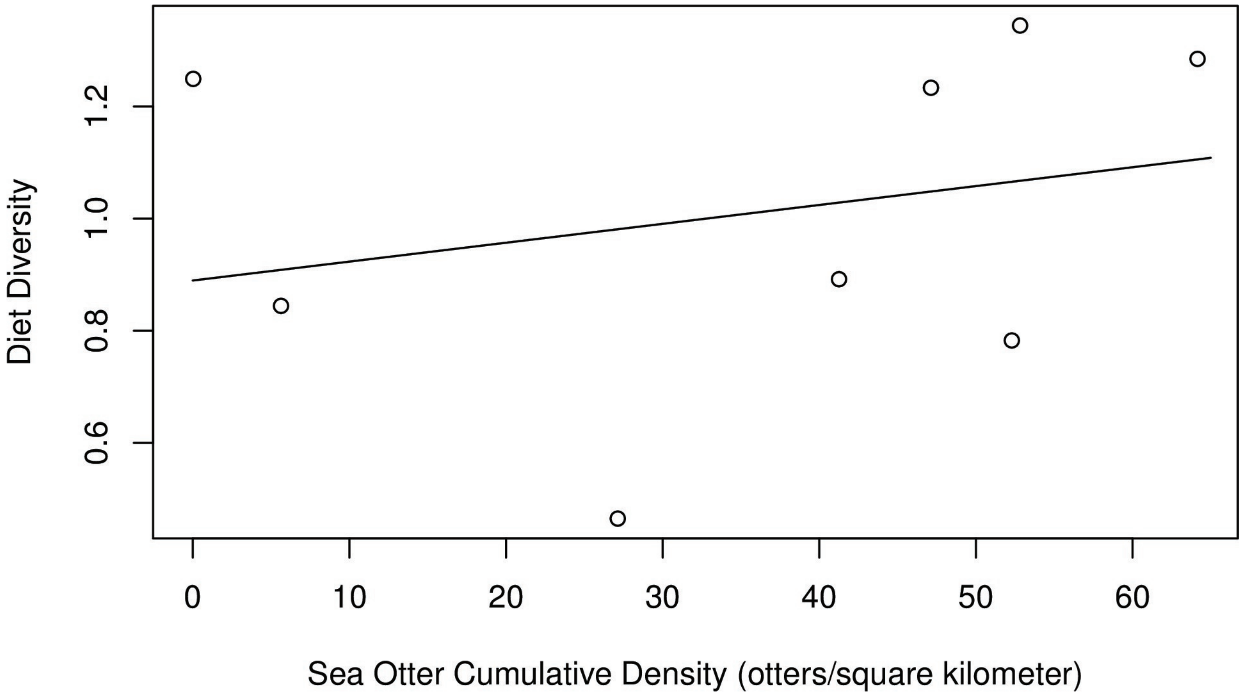

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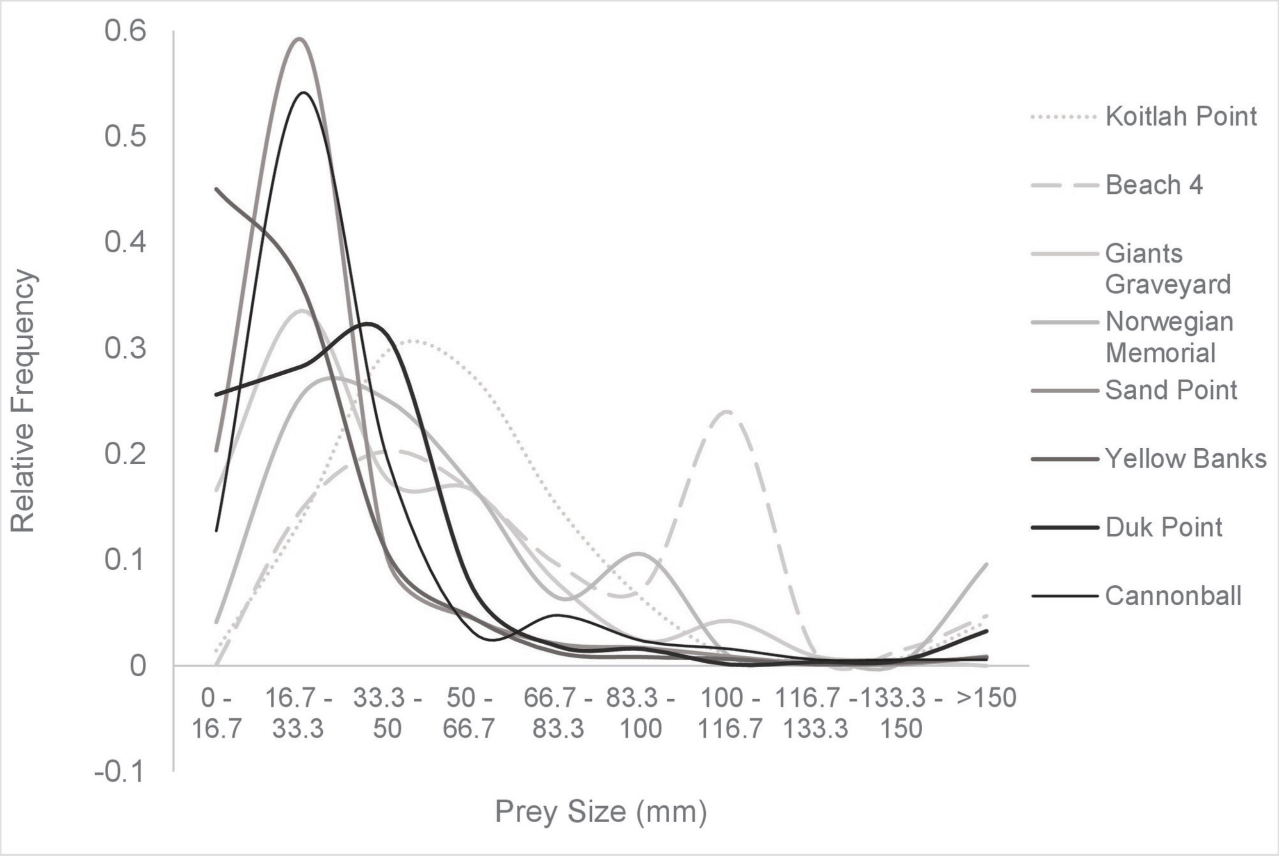

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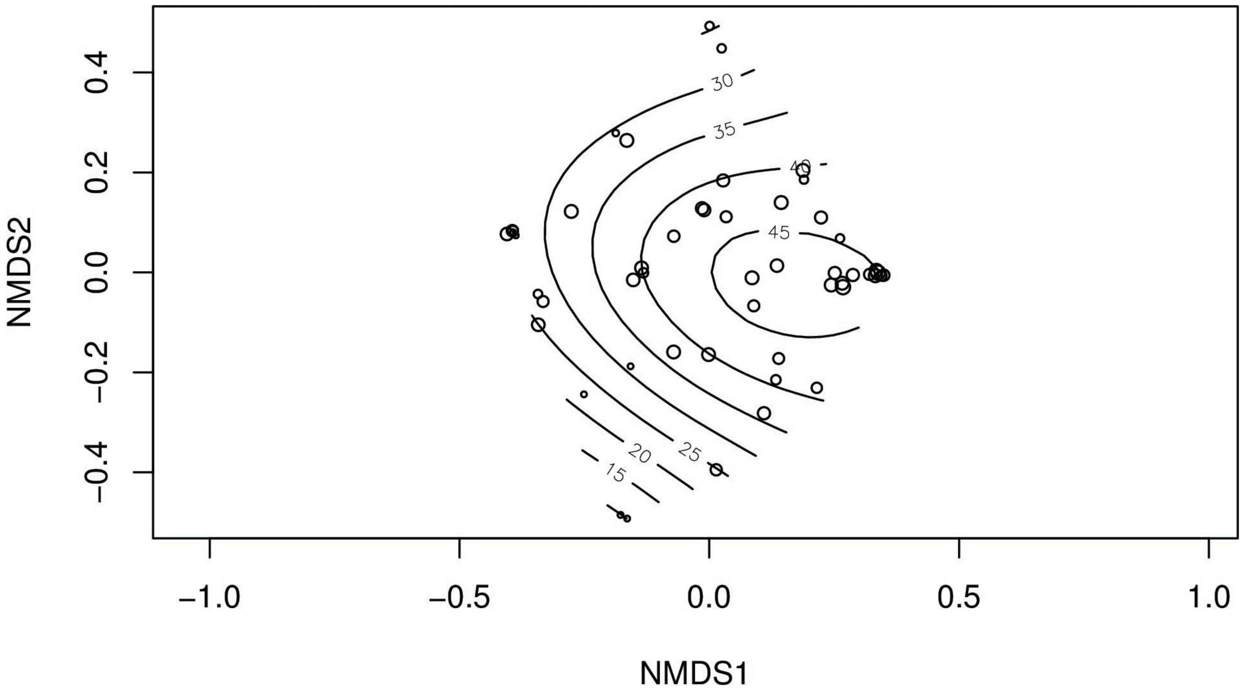

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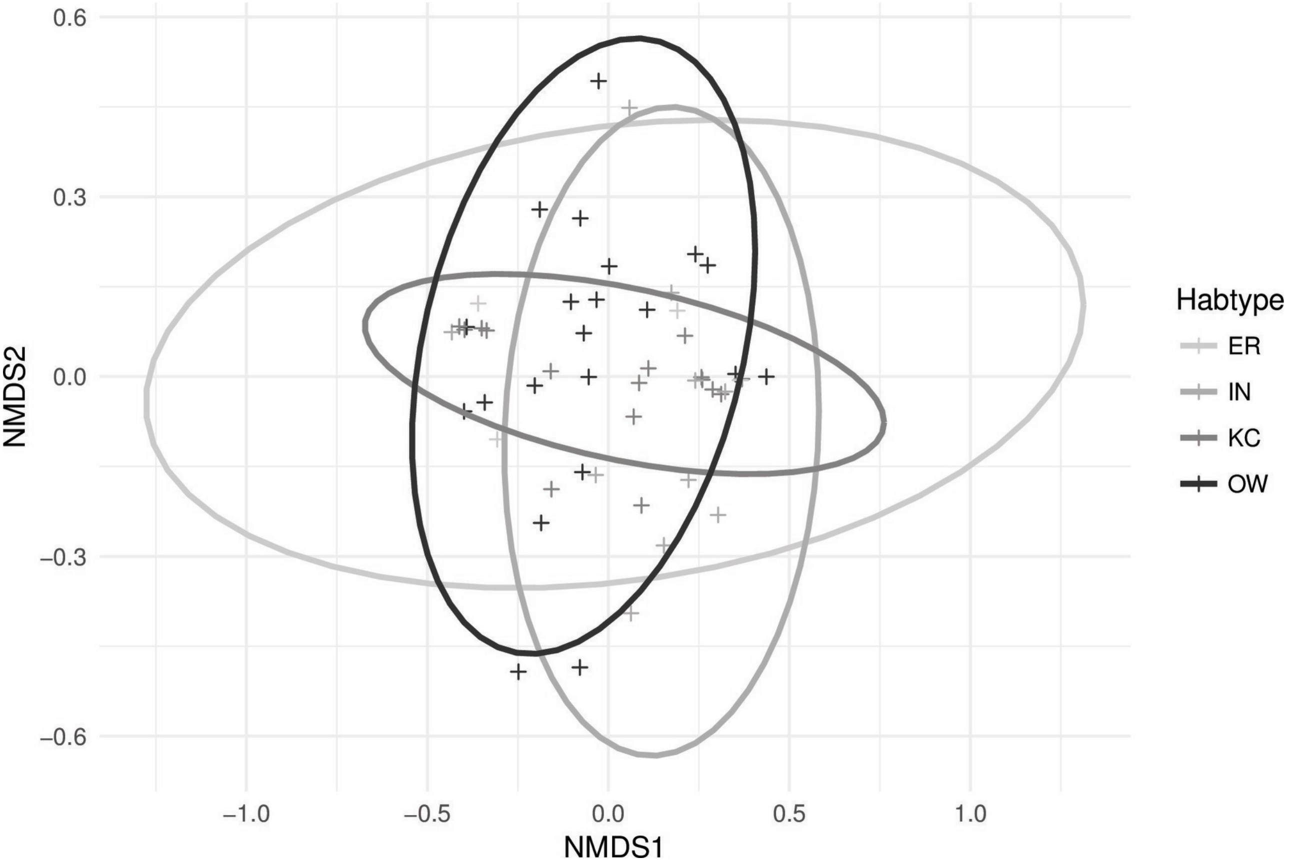

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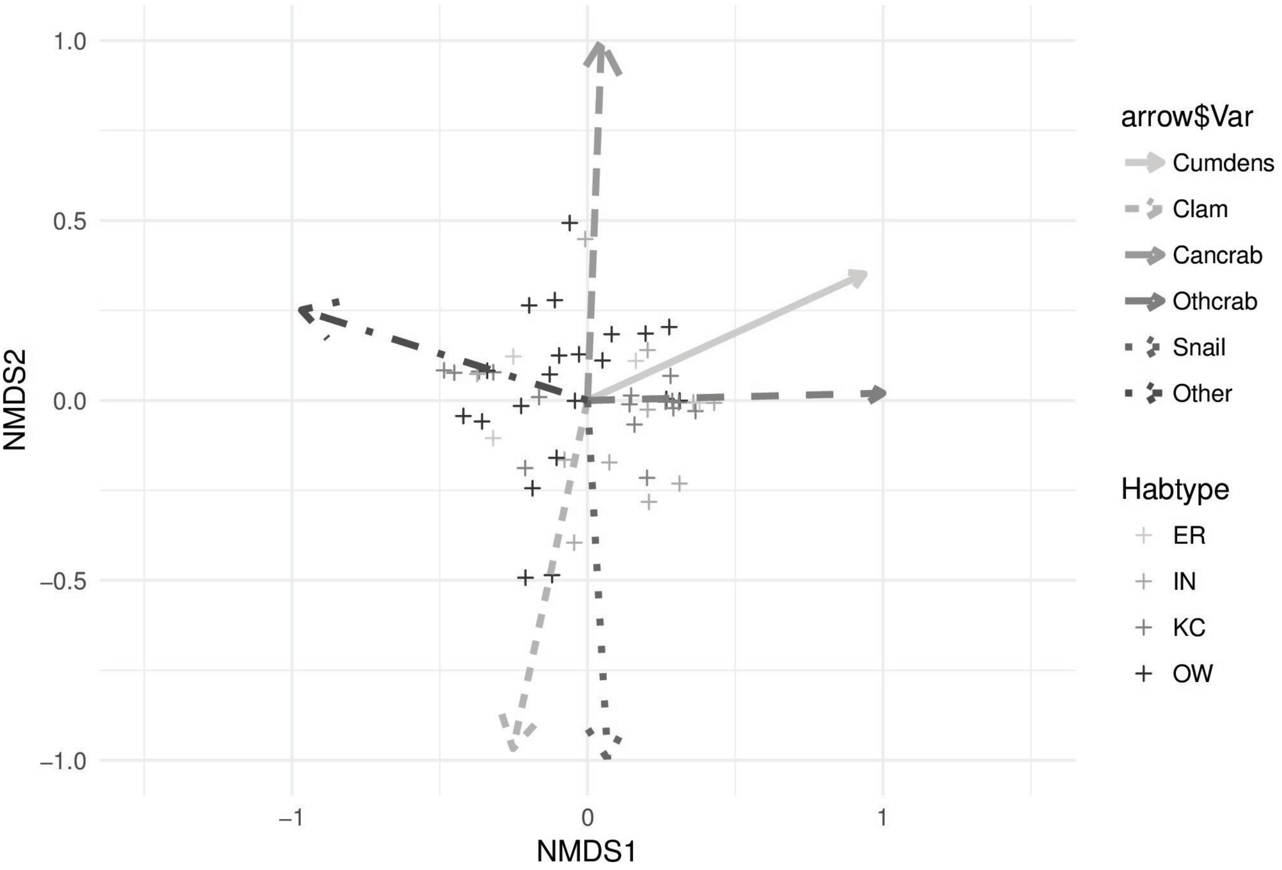

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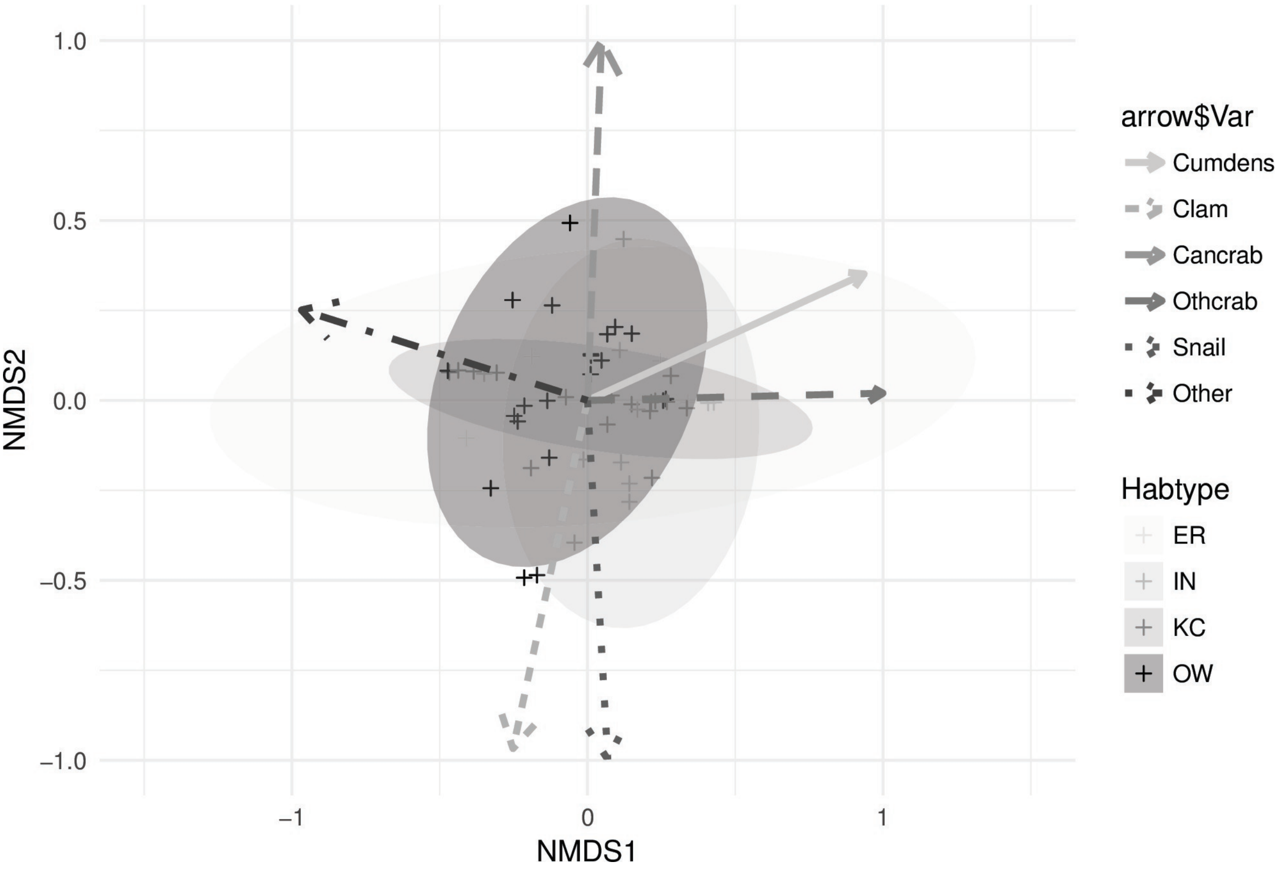

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FIGURES

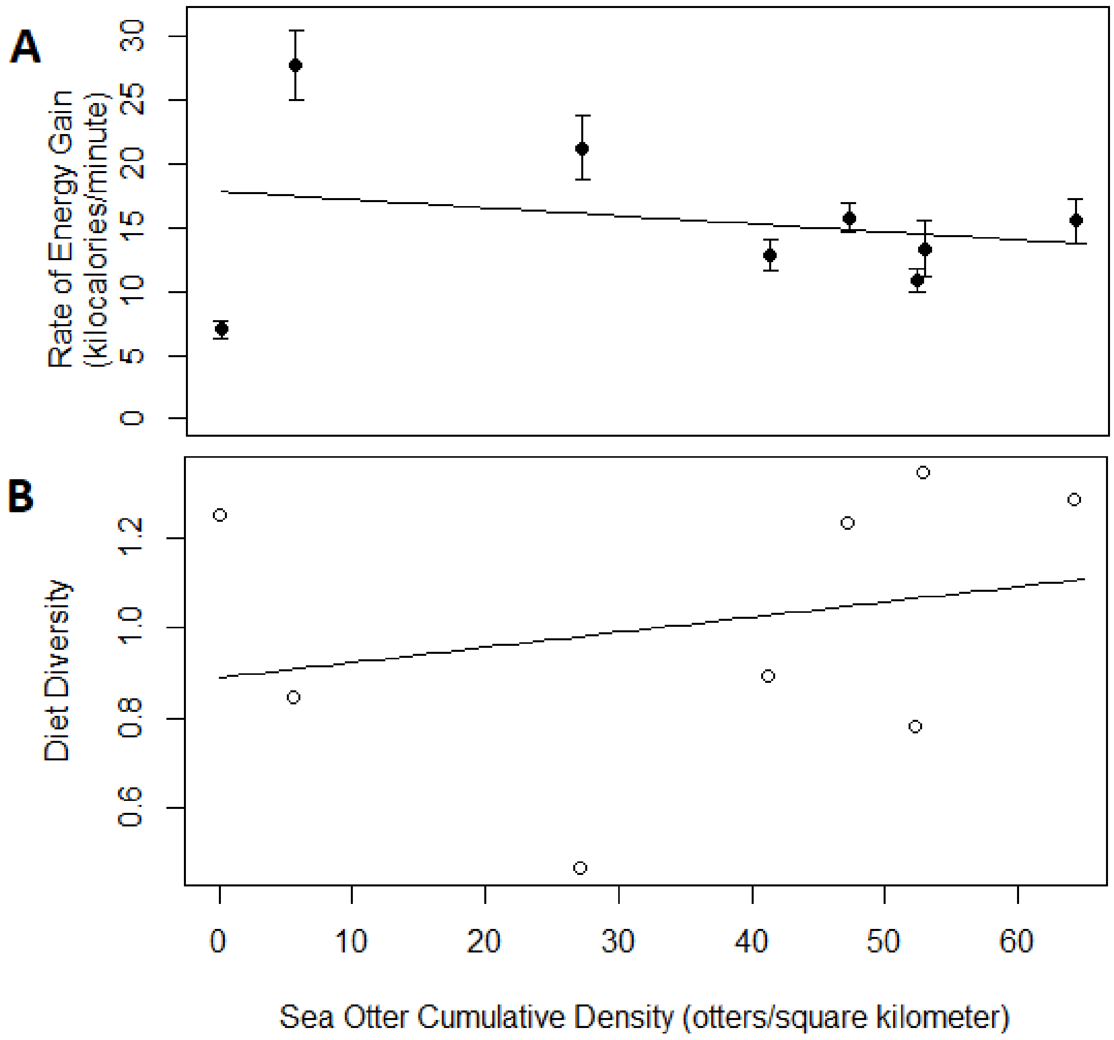
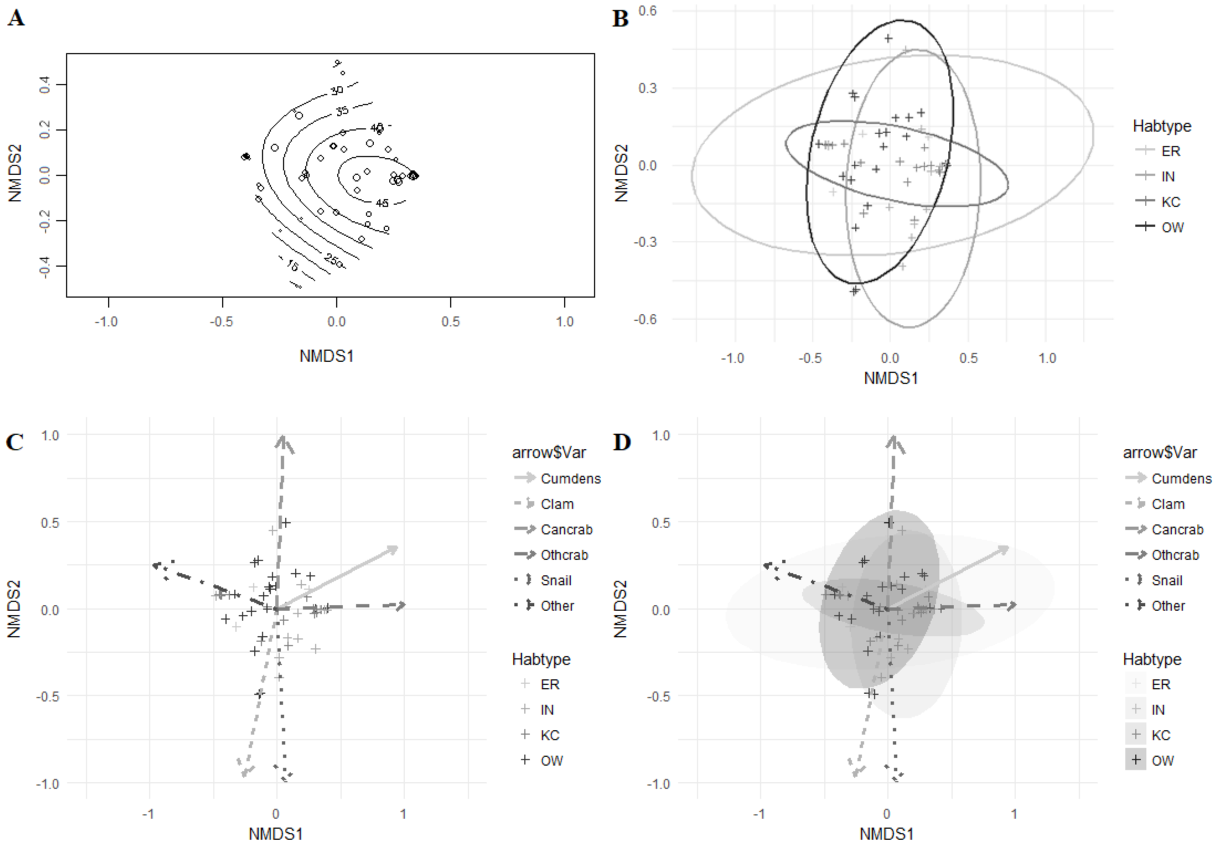


FIGURE 2.


A
NMDS2
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0.2
0.0
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0.0
0.5
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NMDS1
30
35
40
45
25
15
B
0.6
0.3
0.0
-0.3
-0.6
NMDS2
-1.0
-0.5
0.0
0.5
1.0
NMDS1
Habtype
ER
IN
KC
OW
C
1.0
0.5
0.0
-0.5
-1.0
NMDS2
-1
0
1
NMDS1
arrow$Var
Cumdens
Clam
Cancrab
Othcrab
Snail
Other
Habtype
ER
IN
KC
OW
D
1.0
0.5
0.0
-0.5
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NMDS2
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0
1
NMDS1
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OW

FIGURE 4.

APPENDIX FIGURES

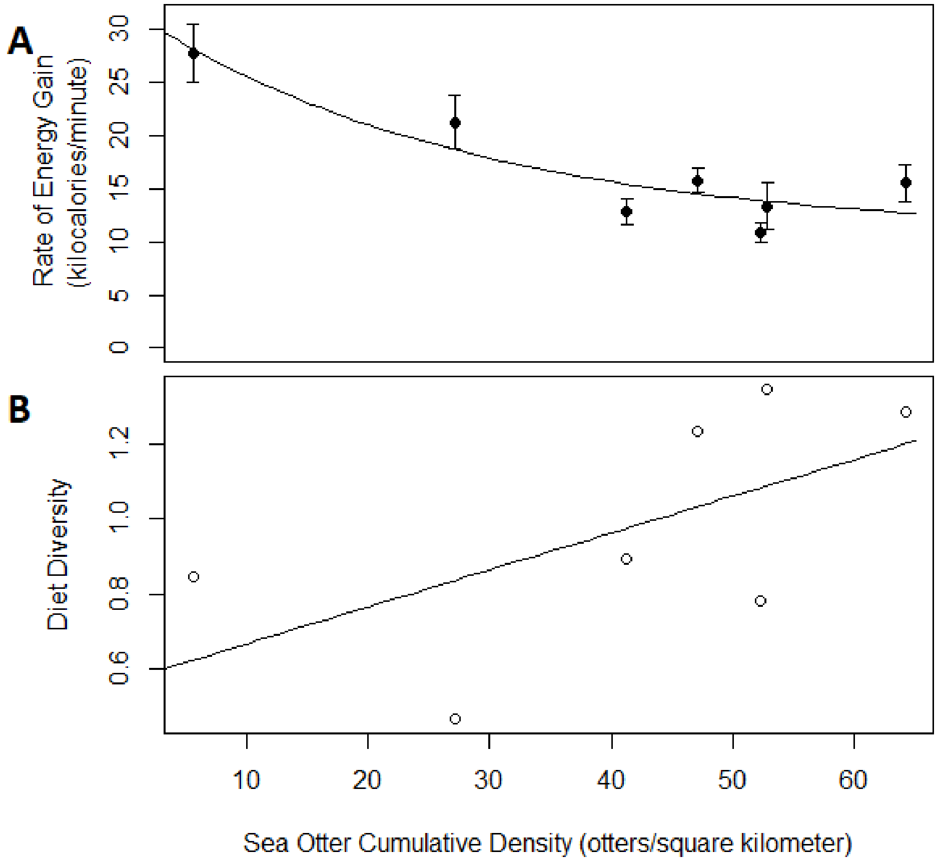

FIGURE 2