

The interaction of intraspecific competition and habitat on individual diet specialization: a near range-wide examination of sea otters

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Abstract The quantification of individuality is a common research theme in the fields of population, community, and evolutionary ecology. The potential for individuality to arise is likely context-dependent, and the influence of habitat characteristics on its prevalence has received less attention than intraspecific competition. We examined individual diet specialization in 16 sea otter (*Enhydra lutris*) populations from southern California to the Aleutian Islands in Alaska. Because population histories, relative densities,

and habitat characteristics vary widely among sites, we could examine the effects of intraspecific competition and habitat on the prevalence of individual diet specialization. Using observed diet data, we classified half of our sites as rocky substrate habitats and the other half containing a mixture of rocky and unconsolidated (soft) sediment substrates. We used stable isotope data to quantify population- and individual-level diet variation. Among rocky substrate sites, the slope [\pm standard error (SE)] of the positive significant relationship between the within-individual component (WIC) and total isotopic niche width (TINW) was shallow (0.23 ± 0.07) and negatively correlated with sea otter density. In contrast, the slope of the positive WIC/TINW relationship for populations inhabiting mixed substrate habitats was much higher (0.53 ± 0.14), suggesting a low degree of individuality, irrespective of intraspecific competition. Our results show that the potential for individuality to occur as a result of increasing intraspecific competition is context-dependent and that habitat characteristics, which ultimately influence prey diversity, relative abundance, and the range of skillsets required for efficient prey procurement, are important in determining when and where individual diet specialization occurs in nature.

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Introduction

The conventional calculation of a population's dietary breadth, its realized niche, integrates prey selection across all individuals in the population and, thus, subsumes any inter- and intraindividual variation in diet. A rapidly growing body of literature published over the past decade,

however, has shown that individual dietary specialization is pervasive in many animal taxa and communities (Bolnick et al. 2003; Araújo et al. 2011) and likely has important implications for population and community ecology (Kondoh 2003; Bolnick et al. 2010). Individual diet specialization may even contribute to interindividual variation in fitness and ultimately result in phenotypic diversification and speciation on evolutionary timescales (Annett and Pierotti 1999; Bolnick et al. 2003; Svanbäck and Bolnick 2005; Agashe and Bolnick 2010).

A variety of factors influence the likely ecological contexts in which individual diet specialization may arise (Araújo et al. 2011). Perhaps the most studied mechanism is intraspecific competition (Svanbäck and Persson 2004; Svanbäck and Bolnick 2005, 2007; Tinker et al. 2008; Agashe and Bolnick 2010), which results in an increase in the total niche width (TNW) of a population and a concomitant decrease in individual niche width, often defined as the within-individual component (WIC) of dietary variation (Bolnick et al. 2003). Such a pattern is to be expected on theoretical grounds so long as phenotypic variation exists among individual consumers with respect to their preference ranking for various prey types, where preference is assumed to reflect realized profitability (Svanbäck and Bolnick 2005). The realized profitability of a particular prey type reflects that prey's intrinsic (nutritional) value, its abundance, and the energetic costs associated with its capture, processing, and assimilation. Differences among individual foragers with respect to handling efficiency, capture success, and/or energetic costs of capturing and consuming specific prey can, thus, lead to interindividual variation in diet composition, with different prey specialists experiencing roughly similar foraging success (in terms of energetic benefits). Dietary specialists may have higher fitness than generalists because trade-offs can exist between individual diet breadth and the ability to maintain specialized skills required to profit from low-ranked prey (Partridge and Green 1985).

A second ecological factor important for promoting individuality that has received considerably less attention than intraspecific competition is the diversity of prey species that are available to consumers. Araújo et al. (2011) identified prey diversity as an important component of ecological opportunity, which is typically cast in the context of interspecific competition and assumed to reduce the diversity of resources available to any single species and, thus, limit the potential for individual diet specialization. A limited number of field-based empirical studies, however, have reported a positive relationship between individual diet specialization and prey diversity. In both wolves (*Canis lupus*; Darimont et al. 2009) and fruit bats (*Rousettus aegyptiacus*; Gerardo Herrera et al. 2008), individual diet specialization was most pronounced in situations where consumers had

access to higher prey diversity. In the latter study, resource diversity was driven by seasonal variation in the diversity of fruits available to bats, which highlights the potentially strong but unresolved connection between temporal resource variation and individual diet specialization.

Habitat characteristics exert a strong influence on the composition and structure of communities, and, thus, impact the diversity of available prey, depending on the spatial scale of habitat heterogeneity and the patch size(s) utilized by consumers. For example, intraspecific morphological variation in several species of freshwater fish has been linked to enhanced ability to efficiently forage distinct prey types associated with benthic versus pelagic habitats (Matthews et al. 2010; Siwertsson et al. 2013). But note that morphological variation is not a necessary requirement to exploit prey found in different habitats. For example, Layman et al. (2007) found that a reduction in prey diversity and niche collapse of a dominant top predator, the gray snapper (*Lutjanus griseus*), was linked to microhabitat variation resulting from anthropogenic fragmentation of shallow wetland ecosystems.

Many terrestrial and marine carnivores classified as dietary generalists occupy a wide variety of habitats, in which the diversity and availability of prey vary considerably. For example, many species of North American canids (foxes, coyotes, wolves) occur in habitats that range from tundra to deserts. While body size is an important factor in determining prey preferences (Peters 1983; Cohen et al. 1993), the generalist and, in some cases, omnivorous dietary strategies used by canids are perhaps one reason why many members of this group have large geographic ranges and may be more locally abundant relative to other more specialized carnivores of similar size, such as wolverines (*Gulo gulo*) or badgers (*Taxidea taxus*) (Brown 1984; Brown et al. 1995). The same is true for marine carnivores, especially those that occur in nearshore environments that contain a more heterogeneous mix of microhabitats than offshore pelagic areas. For example, sea otters (*Enhydra lutris*) occur in nearshore marine environments from southern California to northern Japan and primarily consume benthic invertebrates in a variety of habitats, ranging from unconsolidated (soft) sediment substrates (mud to cobble) to rocky substrates that support kelp forests. A recent dietary census utilizing data from >20 sea otter populations along the northeast Pacific margin (Tinker and Bodkin, unpublished data) shows that the number of distinct invertebrate prey type taxa consumed by sea otters occurring in areas that predominantly contain soft-sediment substrate habitats in Alaska (100 prey taxa) was similar to the diversity of prey consumed by sea otters that occur in rocky substrate habitats in California (98 prey taxa).

The taxonomic diversity of prey assemblages, however, tells only part of the story. Specifically, the relationship

between species diversity and the diversity of distinct functional roles is likely positive but noisy, and, in certain habitats, this relationship may be especially weak. For example, soft-sediment habitats in nearshore marine environments may contain a diverse community (≥ 8 –10 species) of infaunal bivalves that all occupy the same basic functional role (filter feeders). This is important in regards to consumer prey choice because it is a prey's functional role rather than its specific identity that may exert the strongest influence on its availability, the costs associated with its procurement and processing, and, hence, its preference rank as a resource. Furthermore, the specialized hunting and handling skills that individuals use to efficiently capture and process prey, which is believed to be an important mechanism in maintaining individuality, may segregate with prey function rather than with taxonomic classification, which largely dictates where and how often that prey is encountered in the environment.

As keystone predators in nearshore marine communities (Power et al. 1996), sea otters provide a unique opportunity to explore the ecological mechanisms responsible for the promotion and maintenance of individuality in wild animal populations. Since sea otters are capable of limiting the abundance of some of their most-preferred prey taxa, such as sea urchins (*Strongylocentrotus* spp.) and abalone (*Haliotis* spp.), individual foraging success is negatively density-dependent (Estes et al. 1982; Estes 1990, 1996; Garsheles et al. 1986; Bodkin et al. 2000; Tinker et al. 2008). As populations attain equilibrium densities, there is typically an increase in dietary diversity (Estes et al. 1982; Ostfeld 1982), as has been observed in other predator–prey systems (Krebs et al. 1977; Thompson and Colgan 1990) and is theoretically predicted based on the reduced per-capita availability of preferred prey taxa (Pulliam 1974; Schoener 1971). Work on sea otter populations occurring at various densities in rocky substrate habitats in California show that increases in the population-level diet niche width are primarily driven by increased individual dietary specialization, as opposed to an expansion of individual dietary breadth (Tinker et al. 2008, 2012).

Unlike the rocky substrate nearshore habitats of central California or the Aleutian Islands, where the majority of research on sea otter diet has been conducted, sea otters in many areas of the Alaska Peninsula, south central Alaska, southeast Alaska, and even the Pacific Northwest (British Columbia and Washington) occur in mixed substrate habitats containing a combination of rocky and soft-sediment substrates. While the preferred prey of sea otters that occur in rocky substrate habitats are typically sea urchins, abalone, and large decapods, sea otters in mixed substrate habitats consume a high proportion of infaunal bivalves (Kvitek and Oliver 1988; Doroff and DeGange 1994; Dean et al. 2002; Wolt et al. 2012). These mixed substrate

habitats can support sea otter densities that are equivalent to those observed in rocky habitats, but it is unclear whether increased intraspecific competition results in a greater degree of individual dietary specialization in these areas, as it does in rocky substrate habitats (Estes et al. 2003; Tinker et al. 2008).

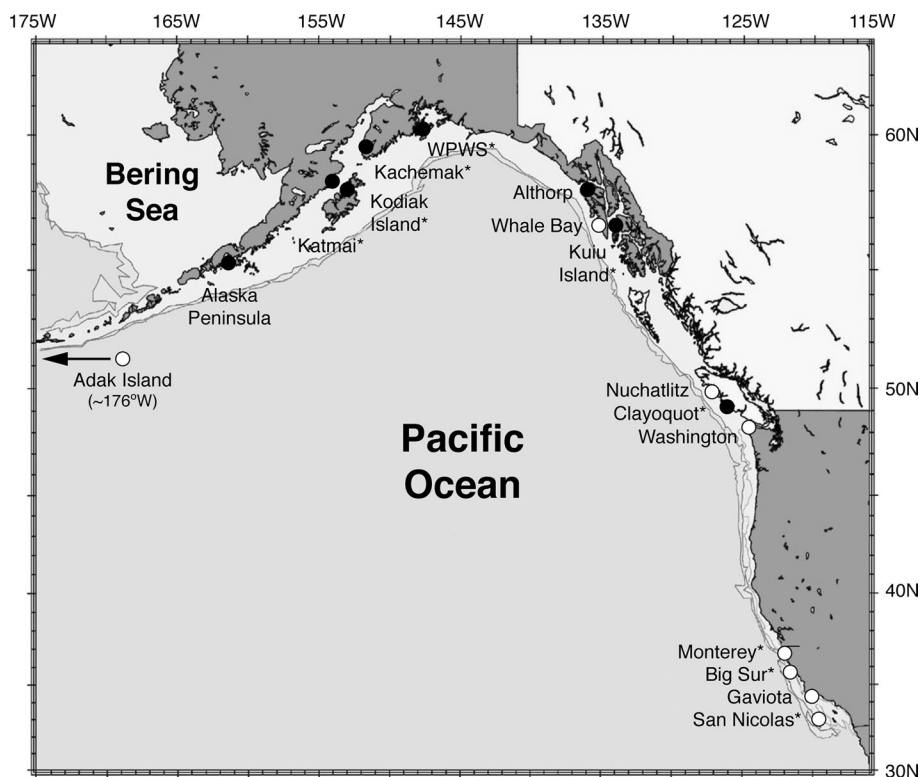
Here, we examine the prevalence of individual diet specialization among 16 sea otter populations across the northeast Pacific Ocean that vary in relation to equilibrium density and occur in different habitats, ranging from rocky to mixed substrate sites. We aim to address three questions regarding the prevalence of individual diet specialization: (1) Does the positive relationship between intraspecific competition and individuality previously recognized in California sea otter populations apply to populations farther north that occur in a more heterogeneous habitat containing a mixture of rocky and soft-sediment substrates? (2) What is the relative importance of taxonomic richness versus prey functional diversity in creating ecological opportunity for individual diet specialization across habitat types? We use observed diet data collected at the population level to first classify the habitat(s) each sea otter population utilizes and then estimate each population's rate of biomass intake (g/min) as a proxy for resource availability. To quantify individual diet specialization, we use a stable isotope approach previously applied to California sea otter populations (Newsome et al. 2009, 2010) that corroborates results gleaned from rich but cost- and time-intensive observational datasets (Estes et al. 2003; Tinker et al. 2008).

Materials and methods

Sample collection

Figure 1 shows the distribution of sea otter populations examined in this study. Vibrissae were collected from captured adult sea otters during population assessments by a variety of state and government agencies, including the U.S. Geological Survey, U.S. Fish and Wildlife Service, California Department of Fish and Game, Fisheries and Oceans Canada, as well as private organizations, including the Monterey Bay Aquarium and Seattle Aquarium. Vibrissae from most (12/16) populations were collected recently from 2009–13. Nearly all vibrissae were collected from live-captured adult sea otters, the only exception being Kachemak Bay, where 27 of the 43 vibrissae analyzed were sourced from stranded sea otters that died from blunt trauma ($n = 13$) or endocarditis ($n = 14$). Table 1 presents the number of male and female vibrissae collected and the year(s) of collection from each sea otter population.

Fig. 1 Map of the northeast Pacific Ocean showing the approximate location of sites where sea otters ($n = 16$) and potential prey ($n = 9$) were collected for stable isotope analysis; the white and black circles represent rocky and mixed substrate habitats, respectively, based on habitat scores reported in Table 1. The asterisks denote sites where standard ellipse areas of potential prey were calculated (Table 1)



Invertebrates were collected during diving and shore-based sampling from a selected number of sites at approximately the same time that vibrissae were collected; the only exception is Kodiak Island, AK, where vibrissae were collected in 2004–05 and prey collections were made in 2010–11. We used observational data on diet composition to select which invertebrates to collect for stable isotope analysis, and only included prey species that represented >5 % of estimated biomass consumed at the population level to generate standard ellipse areas (SEA) of isotopic space occupied by potential prey (Table 1).

Observational data and habitat assessment

We used population-level observed diet data to classify the general habitats utilized by each sea otter population. Data on foraging behavior and prey consumption by sea otters were collected and analyzed as previously described (Tinker et al. 2008, 2012). Briefly, after locating a feeding sea otter, observers initiated a period of intensive observations, recording a contiguous sequence of ≥ 20 feeding dives, referred to as a bout. For each dive, observers recorded location, dive duration (time underwater searching for prey), surface interval (time on the surface between dives handling and consuming prey), and dive outcome (whether or not any prey was captured). For each successful prey capture, we also recorded the prey type identified to the lowest possible taxonomic level, number of prey

items, and prey size. The size of each prey was recorded as a categorical variable corresponding to the number of paw widths (~ 5 cm) spanned by the maximum linear dimension of the prey item, with each class further subdivided into three equal subclasses. The biomass for each item was then estimated using taxa-specific power functions for converting the prey diameter to wet edible biomass (Ofteidal et al. 2007).

We assigned a habitat code to each prey species that was consumed by sea otters at each site where observed diet data were obtained. The assigned habitat codes were based on where each prey species were typically found in subtidal scuba surveys, and ranged from zero (representing unconsolidated substrate with fine to course sediments) to one (consolidated rocky substrate). For example, exclusively infaunal invertebrates such as Nuttall's cockle (*Clinocardium nuttallii*), butter clams (*Saxidomus giganteus*), and fat innkeeper worms (*Urechis caupo*) were assigned habitat codes of zero. In contrast, invertebrates that occur exclusively on rocky substrates, such as kelp crabs (*Pugettia* spp.), abalone, and sea urchins, were assigned a habitat code of one. Invertebrates that were found in both general habitat types received a score of 0.5. The mean habitat scores for each site were calculated by multiplying the proportion of the diet represented by each prey (in terms of consumed biomass) by its habitat code, and then summing this product across all prey types. Thus, sites dominated by mixed sediment substrates had habitat scores ranging from

Table 1 Sea otter densities, population status relative to carrying capacity (K), sample sizes, habitat assessment, biomass intake rates, individual diet specialization metrics (WIC, TINW, WIC/TINW), and standard ellipse areas (SEA in % c^2) of potential invertebrate prey for the sites examined in this study

Site	Density (otters/km ²)	K (= or <)	N (M:F; N_{segments})	General habitat	Habitat score	Biomass intake rate (g/min)	WIC (\pm SE)	TINW (\pm SE)	WIC/TINW (\pm SE)	Prey SEA (\pm SD)
Monterey Bay (2006–2007)	4.6	=	(0:35; 460)	Rocky	0.765	13.5	0.315 (0.017)	1.042 (0.060)	0.302 (0.001)	6.8 (0.4)
Big Sur (2010)	4.2	=	(10:36; 672)	Rocky	0.826	12.9	0.288 (0.033)	1.101 (0.190)	0.262 (0.016)	6.8 (0.4)
Nuchatlitz (2010)	2.1	=	(13:17; 542)	Rocky	0.931	11.2	0.214 (0.003)	0.674 (0.016)	0.318 (0.012)	–
Washington (2011)	1.4	<	(11:19; 487)	Rocky	0.918	23.3	0.328 (0.020)	0.963 (0.382)	0.340 (0.136)	–
Whale Bay (2011)	1.3	<	(6:24; 516)	Rocky	0.801	10.5	0.181 (0.017)	0.384 (0.087)	0.470 (0.024)	–
Gaviota (2012–2013)	0.9	<	(23:17; 687)	Rocky	0.923*	14.4*	0.425 (0.033)	0.908 (0.362)	0.468 (0.040)	–
Adak Island (1997)	0.4	<	(5:15; 440)	Rocky	0.788	36.1	0.170 (0.003)	0.328 (0.036)	0.518 (0.075)	–
San Nicolas Island (2004)	0.3	<	(7:6; 193)	Rocky	0.787	21.3	0.259 (0.020)	0.643 (0.019)	0.402 (0.054)	6.3 (0.9)
Katmai (2009)	7.2	<	(11:17; 611)	Mixed	0.652	15.1	0.117 (0.012)	0.167 (0.002)	0.702 (0.066)	7.2 (0.6)
Kachemak Bay (2008)	3.9	<	(28:15; 803)	Mixed	–	–	0.177 (0.057)	0.376 (0.126)	0.474 (0.006)	7.2 (0.7)
Prince William Sound (2010)	2.8	=	(6:19; 469)	Mixed	0.624	10.7	0.596 (0.105)	0.835 (0.190)	0.722 (0.039)	7.7 (1.0)
Kuiu Island (2011)	2.1	<	(16:15; 651)	Mixed	0.668	17.8	0.119 (0.008)	0.178 (0.008)	0.672 (0.075)	8.3 (0.6)
Althorp (2011)	1.1	=	(7:23; 580)	Mixed	0.486	9.5	0.320 (0.058)	0.710 (0.017)	0.453 (0.093)	–
Kodiak Island (2004–2005)	1.0	<	(16:26; 729)	Mixed	0.487	18.3	0.174 (0.052)	0.353 (0.036)	0.483 (0.098)	4.1 (0.4)
Alaska Peninsula (2009)	1.0	<	(17:15; 630)	Mixed	0.655	23.6	0.435 (0.155)	0.831 (0.222)	0.510 (0.050)	–
Clayoquot (2010–2011)	0.2	<	(8:17; 485)	Mixed	0.505	20.5	0.156 (0.015)	0.622 (0.274)	0.298 (0.107)	5.5 (0.5)

For population status relative to carrying capacity, an equals sign (=) denotes populations at or near equilibrium density and the less than (<) symbol represents populations below equilibrium density. Years in parentheses adjacent to sites denote the time periods otters were captured and invertebrates collected. Sample sizes denote the number of male (M) and female (F) whiskers and the total number of subsampled vibrissae segments (N_{segments}) analyzed from the entire sea otter population at a particular site. The prey biomass intake rate estimated as the wet biomass consumption per unit time foraging (g/min) is used as an index of relative prey abundance. The *asterisk* denotes that a limited amount of observational dietary data are available for the sea otter population at Gaviota, CA, so the habitat score and biomass intake rate for this site is preliminary

0.4 to 0.6, while rocky substrate sites had habitat scores ranging from 0.7 to 0.9 (Table 1). We recognize that this method for evaluating foraging habitat does not provide an estimate of available habitat, but, rather, a measure of the range of habitats actually utilized by each sea otter population.

Sea otter density and population status relative to carrying capacity

The status of the sea otter populations at each site was classified using two approaches: (1) a measure of relative density and (2) a subjective assessment of whether the population was at or near local carrying capacity. The relative density (otters/km² of benthic habitat between the low tide line and the 40 m bathymetric contour) was calculated for each site based on the most recent abundance surveys, and areas with >2 otters/km² were categorized as high density, while areas with <2 otters/km² were categorized as low density. To assess whether a given population was at (or very near) carrying capacity, we evaluated a suite of metrics, including the relative body condition of captured wild sea otters, the duration (years) sea otters had occupied that site, and long-term population trends. For example, if sea otters had been established in an area for >20 years, exhibited low rates of population growth (or stability), and exhibited relatively poor body condition based on comparisons of age-specific body mass and total length, then the population would be classified as being at or near carrying capacity (*K*). Based on these combined metrics, each population was readily classified as either at *K* or well below *K*. Note that there was correlation but not perfect correspondence between the metrics of density and status with respect to *K* (Table 1).

Biomass intake rates

Estimates of the rate of biomass intake—grams of edible biomass consumed per minute of time spent feeding—were calculated from observational data on feeding behavior using a Monte Carlo simulation algorithm that has been described in previously published studies (Tinker et al. 2008, 2012). Briefly, the analysis takes advantage of the strong correlations that exist among recorded dive parameters to account for incomplete data records (e.g., records where prey type, size, or number of items were unidentified or unrecorded) and known biases inherent in observational datasets (e.g., small prey are more likely to be unrecognized than larger prey). All the available data are used to fit appropriate probability distributions for each parameter as well as covariance between parameters, and then Monte Carlo simulations are run that maintain these observed distributions and covariance structures, resulting in unbiased

estimates of prey-specific intake rates and associated uncertainty measures.

Stable isotope analysis

For carbon ($\delta^{13}\text{C}$) and nitrogen ($\delta^{15}\text{N}$) analysis, sea otter vibrissae were rinsed with a 2:1 chloroform:methanol solvent solution to remove surface contaminants. Cleaned vibrissae were then subsampled into ~0.5–0.6-mg segments using nail clippers. The total number of vibrissae segments (N_{segments}) sampled from each sea otter population is presented in Table 1; on average, the number of subsampled segments obtained from each vibrissa ranged from 15 to 20 among sea otter populations. Dried sea otter vibrissae segments (~0.5–0.6 mg) were sealed into 3 × 5-mm tin capsules and carbon ($\delta^{13}\text{C}$) and nitrogen ($\delta^{15}\text{N}$) isotope values were determined using a Costech 4010 (Costech, Valencia, CA) elemental analyzer interfaced with a ThermoFinnigan Delta Plus XL mass spectrometer (Thermo Scientific, Bremen, Germany). Stable isotope results are expressed as δ values, $\delta^{13}\text{C}$ or $\delta^{15}\text{N} = 1,000 \times [(R_{\text{sample}} - R_{\text{standard}})/R_{\text{standard}} - 1]$, where R_{sample} and R_{standard} are the $^{13}\text{C}/^{12}\text{C}$ or $^{15}\text{N}/^{14}\text{N}$ ratios of the sample and standard, respectively. The internationally accepted standards are Vienna Peedee Belemnite limestone (V-PDB) for carbon and atmospheric N_2 for nitrogen. The units are expressed as parts per thousand, or per mil (‰). The within-run standard deviation of multiple organic reference materials was ≤ 0.2 ‰ for both $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values. As a control for the quality of keratin, we also measured the weight percent [C]/[N] ratios of each subsample, which were 3.3–3.5 and within the range expected of unaltered protein (Ambrose 1990).

Potential prey items were rinsed of sediment and/or detritus, weighed, and measured using digital calipers. Inedible portions of prey such as the spines and tests of sea urchins, carapace of large crabs and lobsters, and snail and abalone shells were removed prior to lyophilization. The dried edible portion was homogenized by grinding to a coarse powder in a Wiley mill. We then divided the sample into two subsamples and lipid-extracted one portion via three sequential soaks in 2:1 chloroform:methanol solvent solution over a ~72-h period (Bligh and Dyer 1959). Lipid-extracted subsamples were then rinsed in deionized water and lyophilized. Approximately 0.5–0.6 mg of the dry homogenized powder was sealed into tin capsules for isotopic analysis on the mass spectrometer system described above. We only used isotope values for lipid-extracted samples to calculate the SEA of potential prey (Table 1; Fig. 5).

Prey used in the calculation of SEA varied from site to site. A total of 45 prey samples were used to calculate the prey SEA for San Nicolas Island (CA), including sea urchins (*Strongylocentrotus franciscanus* and *S.*

purpuratus, $n = 18$), *Cancer* crabs (*Cancer antennarius* and *C. productus*, $n = 8$), northern kelp crabs (*Pugettia producta*, $n = 5$), snails (*Tegula eiseni*, *T. funebris*, *T. regina*, $n = 5$), bivalves (*Mytilus californianus* and *Crassadoma gigantea*, $n = 5$), and spiny lobsters (*Panulirus interruptus*, $n = 4$). A total of 256 prey samples were used to calculate the prey SEA for Monterey and Big Sur (CA), including bivalves (*Mytilus californianus*, *Tresus nuttallii*, *Leukoma staminea*, *Saxidomus nuttallii*, *Macoma nasuta*, $n = 74$), sea urchins (*Strongylocentrotus franciscanus* and *S. purpuratus*, $n = 35$), *Cancer* crabs (*Cancer antennarius*, *C. productus*, *Metacarcinus magister*, $n = 34$), northern kelp crabs (*Pugettia producta*, $n = 27$), snails (*Tegula funebris*, *T. pulligo*, *T. brunnea*, *T. montereyi*, $n = 24$), Pacific sand crabs (*Emerita analoga*, $n = 24$), abalone (*Haliotis cracherodii* and *H. rufescens*, $n = 22$), and fat innkeeper worms (*Urechis caupo*, $n = 16$). A total of 117 prey samples were used to calculate the prey SEA for Clayoquot (BC), including bivalves (*Mytilus californianus*, *Crassadoma gigantea*, *Leukoma staminea*, *Saxidomus gigantea*, *Pododesmus macroschisma*, $n = 47$), sea urchins (*Strongylocentrotus droebachiensis*, *S. franciscanus*, *S. purpuratus*, $n = 29$), *Cancer* crabs (*Cancer productus*, $n = 13$), snails (*Astraea gibberosa*, *Tegula funebris*, $n = 11$), northern kelp crabs (*Pugettia producta*, $n = 8$), polychaete worms (*Nephtys* spp., $n = 6$), and sea cucumbers (*Parastichopus californicus*, $n = 3$). A total of 173 prey samples were used to calculate the prey SEA for Kuiu Island (AK), including bivalves (*Mytilus trossulus*, *Leukoma staminea*, *Saxidomus gigantea*, *Clinocardium nuttallii*, *Crassadoma gigantea*, *Tresus capax*, *Mya truncata*, and *Macoma* spp., $n = 94$), sea urchins (*Strongylocentrotus droebachiensis* and *S. franciscanus*, $n = 55$), crabs (*Metacarcinus magister*, $n = 13$), and sea cucumbers (*Parastichopus californicus*, $n = 11$). A total of 56 prey samples were used to calculate the prey SEA for west Prince William Sound (AK), including bivalves (*Mytilus trossulus*, *Leukoma staminea*, *Saxidomus gigantea*, *Clinocardium nuttallii*, $n = 30$) and crabs (*Telmessus cheiragonus* and *Cancer magister*, $n = 26$). A total of 103 prey samples were used to calculate the prey SEA for Kachemak Bay (AK), including bivalves (*Mytilus trossulus*, *M. californianus*, *Leukoma staminea*, *Saxidomus gigantea*, *Hiatella arctica*, $n = 59$), crabs (*Telmessus cheiragonus*, *Chionoecetes bairdi*, *Cancer magister*, $n = 30$), and sea urchins (*Strongylocentrotus droebachiensis* and *S. franciscanus*, $n = 14$). A total of 98 prey samples were used to calculate the prey SEA for Kodiak Island (AK), including bivalves (*Mytilus trossulus*, *Leukoma staminea*, *Saxidomus gigantea*, *Hiatella arctica*, *Mya truncata*, $n = 59$), crabs (*Telmessus cheiragonus* and *Chionoecetes bairdi*, $n = 21$), Pacific octopus (*Enteroctopus dofleini*, $n = 10$), and green sea urchins (*Strongylocentrotus droebachiensis*, $n = 8$). A total of 146 prey samples were used to calculate the prey

SEA for Katmai (AK), including bivalves (*Mytilus trossulus*, *Saxidomus gigantea*, *Macoma* spp., $n = 110$), crabs (*Telmessus cheiragonus*, $n = 4$), and green sea urchins (*Strongylocentrotus droebachiensis*, $n = 32$).

Statistical methods

The ability to differentiate between ecological mechanisms potentially driving population-level diet diversity requires longitudinal dietary records compiled at the individual level. Unfortunately, such data are either prohibitively labor- and cost-intensive or impossible to obtain via direct observation for most terrestrial and marine consumers. Our previous work on sea otters shows that $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ stable isotope analysis provides an efficient tool for measuring individual- and population-level dietary breadth and seasonal shifts in the diet of individuals (Newsome et al. 2009). Our isotopic approach follows the theoretical conventions outlined by Roughgarden (1972) and Bolnick et al. (2003) and the isotopic framework presented by Bearhop et al. (2004) and Newsome et al. (2009). We define a dietary specialist as an individual whose isotopic niche width is considerably narrower than its population's total isotopic niche width (TINW). The TINW is the sum of two components: (1) the WIC, which we define as the average isotopic variance within an individual, and (2) the between-individual component (BIC), which represents the inter-individual isotopic variation. We used variance components analysis performed in JMP (SAS Institute Incorporated, v10.0.2) to determine the WIC and BIC of each sea otter population, which were summed to calculate the TINW. These components were calculated separately for vibrissa $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ data; the results presented in Table 1 are the mean of $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ WIC, BIC, and WIC/TINW ratio, with error bars representing the standard error (SE). The degree of intrapopulation specialization is reflected by the WIC/TINW ratio; as the WIC/TINW ratio decreases, the degree of individual specialization increases.

We used a nonparametric Kruskal–Wallis one-way test with a Chi-square (χ^2) approximation to assess statistical differences in individual specialization metrics (TINW and WIC/TINW) and biomass intake rates among sea otter populations. We contrasted these data using two separate categorical factors in each habitat type. The first categorized populations based on relative density (otters/km²), with high density defined as >2 otters/km² and low density defined as <2 otters/km². The second approach used population status as a categorical factor, with populations at equilibrium density (carrying capacity) or well below carrying capacity. Note that the density and population status approaches produced similar results for rocky substrate sites because these two factors separated the populations in a similar fashion (Table 1). For mixed substrate habitats,

the density and population status did not always agree, so we present statistical tests for both approaches when examining populations from mixed substrate habitats. Note that we only identified two populations (Prince William Sound and Althorp) as being at equilibrium density in mixed substrate habitats.

We used linear regression to characterize the relationship between TINW and WIC (Fig. 3), sea otter density and WIC/TINW ratios (Fig. 4a), sea otter density and biomass intake rates (Fig. 4b), as well as TINW and the SEA of potential prey (Fig. 5). We also used a nonlinear power function of the form $y = a(x)^b$ to describe the negative relationship between sea otter density and biomass intake rates (Fig. 4b). We used the program Stable Isotope Bayesian Ellipses in R (SIBER; Jackson et al. 2011) to calculate the SEA of the isotope space (‰) defined by the potential prey available to a particular sea otter population (Fig. 5). One advantage of SIBER over other spatial metrics (e.g., convex hull) used to estimate isotopic variation is that SEA are insensitive to sample sizes >20 (Jackson et al. 2011).

Results

Habitat scores

We designated sites as rocky substrate habitats if their habitat score ranged from 0.765 to 0.931, while sites were designated mixed substrate habitats if their score ranged from 0.486 to 0.668. Using this criterion, seven sites contained predominantly mixed substrate habitats (Table 1): Clayoquot (BC), Kuiu Island (AK), Althorp (AK), Prince William Sound (AK), Kodiak Island (AK), Katmai (AK), and Alaska Peninsula (AK). Eight sites contained predominantly rocky substrate habitats: San Nicolas Island (CA), Gaviota (CA), Big Sur (CA), Monterey Bay (CA), Washington (WA), Nuchatlitz (BC), Whale Bay (AK), and Adak Island (AK). No directly comparable population-level observational diet data were available for Kachemak Bay, so we did not calculate a habitat score, but based on limited observational diet data (Doroff et al. 2012; Stewart et al. 2014), we are confident that Kachemak Bay would be classified as a mixed substrate habitat.

Biomass intake rates

Biomass intake rates (g/min) varied widely among populations from 9.5 (Althorp, AK) to 36.1 (Adak Island, AK) g/min (Table 1; Fig. 4b). We found no significant differences in the mean (\pm SD) biomass intake rates between rocky (17.9 ± 8.7 g/min) and mixed (16.5 ± 5.1 g/min) substrate habitats; Kruskal–Wallis, $\chi^2 = 0.0_{1,15}$; $P = 1.00$. Combining data from both habitats, we found a significant

negative nonlinear (power function) relationship between sea otter density and biomass intake rate (Fig. 4b); $R^2 = 0.31$, $P < 0.05$. Within habitats, we found no significant differences in the biomass intake rates between high (>2 otters/ km^2) and low (<2 otters/ km^2) density sea otter populations; rocky habitats: Kruskal–Wallis, $\chi^2 = 1.80_{1,8}$; $P = 0.18$, mixed habitats: Kruskal–Wallis, $\chi^2 = 0.50_{1,7}$; $P = 0.48$. Repeating this analysis using population status as the categorical factor instead of density in mixed substrate habitats, sea otter populations that were classified as being at or near carrying capacity had significantly lower biomass intake rates than populations classified as below carrying capacity, irrespective of the substrate type; Kruskal–Wallis, $\chi^2 = 3.75_{1,8}$; $P = 0.05$. Sea otter populations from rocky substrate habitats occurring at or near equilibrium density had low mean (\pm SD) biomass intake rates of 12.5 ± 1.2 g/min, while intake rates for low-density populations below carrying capacity were generally higher but ranged from 10.5 g/min (Whale Bay) to 36.1 g/min (Adak Island). For mixed substrate habitats, populations at equilibrium density also had low mean (\pm SD) biomass intake rates of 10.1 ± 0.8 g/min relative to populations below carrying capacity, which ranged from 15.1 g/min (Katmai) to 23.6 g/min (Alaska Peninsula).

Individual diet specialization metrics

The results of the variance component analyses are presented in Table 1 and Figs. 2 and 3. There was no significant difference in the TINW of sea otter populations from rocky versus mixed substrate habitats (Kruskal–Wallis one-way test, $\chi^2 = 2.48_{1,16}$; $P = 0.12$) or between sea otter populations occurring at high (>2.0 otters/ km^2) versus low (<2.0 otters/ km^2) density in either rocky (Kruskal–Wallis, $\chi^2 = 2.69_{1,8}$; $P = 0.10$) or mixed (Kruskal–Wallis, $\chi^2 = 0.33_{1,8}$; $P = 0.56$) substrate habitats (Fig. 2a, b). Likewise, the TINW of sea otter populations at equilibrium density were not significantly different to populations below carrying capacity in mixed substrate habitats (Kruskal–Wallis, $\chi^2 = 2.77_{1,8}$; $P = 0.10$).

The mean (\pm SD) ratio of the WIC to that of the TINW was significantly lower in sea otter populations from rocky (0.387 ± 0.090) versus mixed (0.539 ± 0.147) substrate habitats (Fig. 2c, d); Kruskal–Wallis, $\chi^2 = 3.98_{1,16}$; $P = 0.04$. For sea otter populations that occupy rocky substrate habitats, the mean WIC/TINW ratio was significantly lower (0.299 ± 0.020) for high-density (>2.0 otters/ km^2) populations than for those that occurred at low density (0.440 ± 0.068); Kruskal–Wallis, $\chi^2 = 5.00_{1,8}$; $P = 0.03$. For sea otter populations that occupy mixed substrate habitats, there were no differences in the mean WIC/TINW ratios for populations that occurred at high versus low density (Kruskal–Wallis,

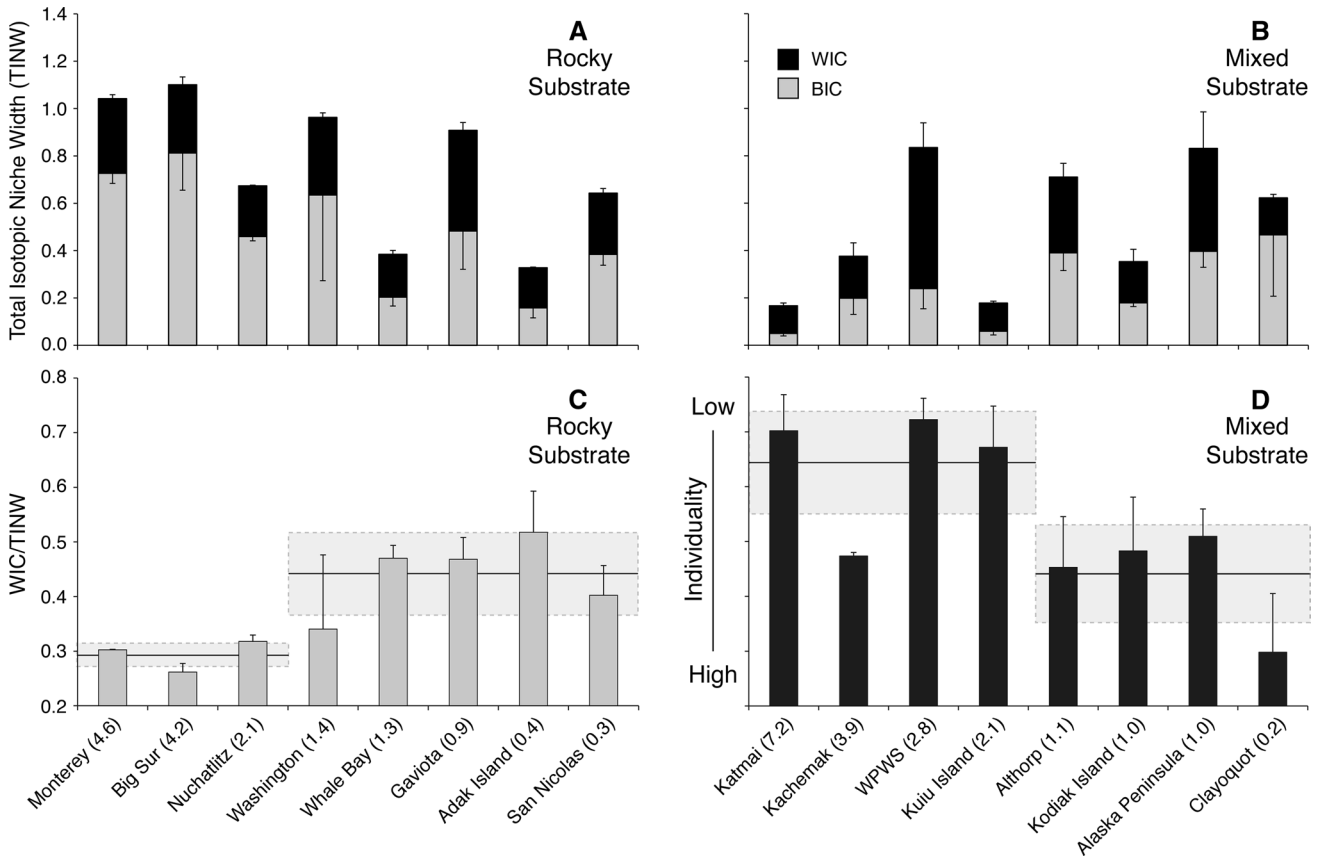
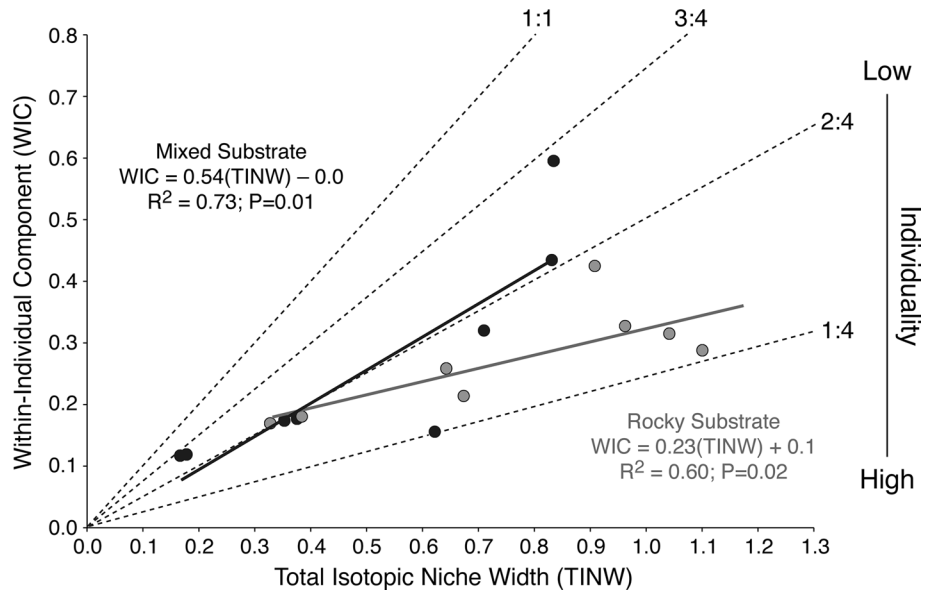


Fig. 2 Total isotopic niche width (TINW) for sea otter populations from rocky (a) and mixed (b) substrate habitats. The errors bars for the within-individual (WIC, black) and between-individual (BIC, gray) components of TINW represent the standard error. c, d Ratio of the WIC to the TINW for sea otter populations from rocky (c) and mixed (d) substrate habitats. Populations in each panel are organized

from the highest to the lowest sea otter density (otters/km²), as indicated in parentheses. The mean WIC/TINW ratios for high- versus low-density populations in each habitat type are indicated by the horizontal lines in c and d, and the shaded area represents the standard deviation

Fig. 3 The relationship between the TINW and WIC for sea otter populations from rocky (gray circles, n = 8) and mixed (black circles, n = 8) substrate habitats. The slope of the relationship for sea otter populations from rocky substrate sites (gray line) is significantly lower than that for populations from mixed substrate sites (black line)



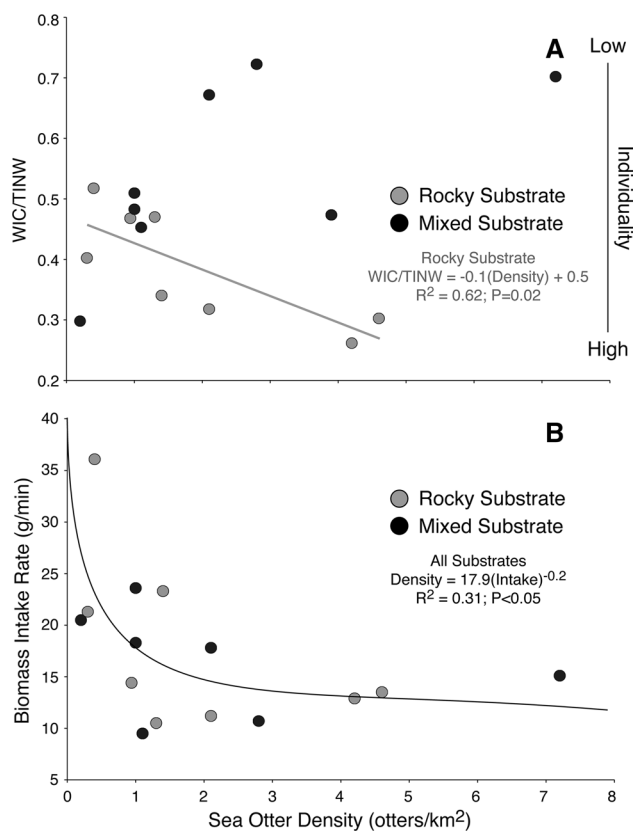


Fig. 4 Relationship between sea otter density (otters/km²) and (a) individual diet specialization (WIC/TINW) and (b) biomass intake rates (g/min) for rocky (gray circles, *n* = 8) and mixed (black circles, *n* = 8) substrate habitats. In a, a negative and significant linear relationship is shown for rocky substrate habitats; the relationship for mixed substrate habitats is not significant. In b, a negative log-linear relationship is shown for combined data from both habitats

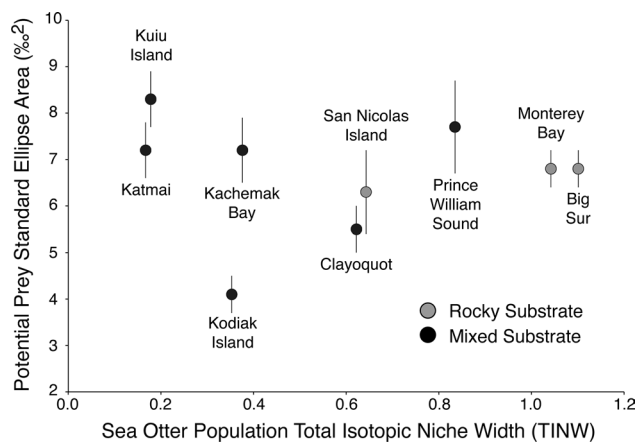


Fig. 5 Relationship between sea otter population TINW and the SEA (‰²) of potential prey available to that population (*n* = 9)

$\chi^2 = 1.33_{1,8}; P = 0.25$). Repeating this analysis with population status as the categorical factor instead of density, there were no differences in the mean WIC/TINW

ratios for populations that occurred at or below carrying capacity in mixed substrate habitats (Kruskal–Wallis, $\chi^2 = 0.11_{1,8}; P = 0.74$).

The slope (\pm SE) of the relationship between the WIC and the TINW was lower for sea otter populations occupying rocky substrate ($0.23 \pm 0.07; R^2 = 0.60, F_{1,7} = 9.1, P = 0.02$) than mixed substrate ($0.54 \pm 0.14; R^2 = 0.73, F_{1,7} = 14.2, P = 0.000$) habitats; equations for each relationship are presented in Fig. 3. Again, a lower slope between the TINW and the WIC implies a higher degree of individuality. The linear relationship between sea otter density (otters/km²) and the WIC/TINW ratio was negative and significant for sea otter populations from rocky substrate habitats (Fig. 4a); $R^2 = 0.62, F_{1,7} = 10.0, P = 0.02$. In contrast, the WIC/TINW ratio increased with increasing sea otter density for populations from mixed substrate habitats; however, this relationship was not significant ($R^2 = 0.40, F_{1,7} = 4.0, P = 0.09$), likely because of values for a single site (Kachemak Bay).

SEA of potential prey

The mean (\pm SD) SEA of potential prey from eight sites are presented in Table 1. Invertebrate species collected from Big Sur and Monterey Bay had statistically indistinguishable isotope values, so data were pooled from these two areas to estimate the SEA of potential prey available to sea otter populations from each site. Since sea otters at the sites of Whale Bay and Althorp likely consume similar species of prey (e.g., red and green sea urchins) associated with rocky substrates found elsewhere in southeast Alaska, the SEA of potential prey at Kuiu Island is likely a good surrogate for other sites in this region. Likewise, the SEA of potential prey at Clayoquot (BC) is likely a good surrogate for Nuchatlitz (BC), which, like the southeast Alaska sites, are in close proximity to one another (<100 km). However, we chose not to extrapolate SEAs among sites in close proximity. The mean (\pm SD) SEA of potential prey among sites varied by a factor of two from 4.1 ± 0.4 ‰ for Kodiak Island to 8.3 ± 0.6 ‰ for Kuiu Island, both of which were classified as mixed substrate habitats according to their habitat scores (Table 1). To assess whether the TINW of sea otter populations was related to the isotopic variance of potential prey available to each population, we compared the mean TINW and SEA (Fig. 5) and found no significant relationship between these metrics ($R^2 = 0.00, F_{1,7} = 0.0, P = 0.96$). Furthermore, the relationship between SEA and habitat score was not significant ($R^2 = 0.26, F_{1,7} = 2.1, P = 0.20$). These nonsignificant relationships suggest that the amount of isotopic variation among available prey is not the principal driver of the observed variation in TINW among populations.

Discussion

The patterns we observe in sea otter individuality between rocky and mixed substrate habitats provide new insights into how ecological factors impact individual diet specialization in natural settings. Possible driving mechanisms for the evolution and maintenance of individuality have been discussed elsewhere; see Bolnick et al. (2003) and Araújo et al. (2011) for multitaxa reviews. Foraging preferences associated with intra- or interspecific morphological variation offer classic examples of individuality (Van Valen 1965; Schluter et al. 1985; Svanbäck and Bolnick 2007); however, a growing number of studies document individual differences in foraging behavior in situations where physical characteristics of the consumer do not appear to play a significant role (e.g., Werner and Sherry 1987; Tinker et al. 2008). Interspecific competition and predation are assumed to play minimal roles in the driving patterns of individuality within sea otter populations, while intraspecific competition and ecological opportunity are believed to be important (Estes et al. 2003; Tinker et al. 2012). Our nearly range-wide, species-level perspective supports the importance of intraspecific competition as a mechanism that promotes individuality, but only under certain ecological conditions. Our study also uniquely demonstrates that habitat characteristics, which control the composition and relative abundance of prey, play an important role in enabling or limiting individual diet specialization.

Isotopic variation among available prey in different habitats

In contrast to traditional approaches used to quantify individuality that define prey diversity as the number of distinct species utilized by a consumer (Roughgarden 1972; Bolnick et al. 2002), our approach relies on the isotopic variation of available prey sources. A potential pitfall of using this approach to examine individuality among populations is that the amount of isotopic variation among prey is not necessarily correlated with the diversity of prey available to any given consumer. Instead, the isotopic composition of animals is primarily driven by (1) their functional roles and (2) isotopic variation of primary producers at the base of a food web. Nearshore marine ecosystems in the northeast Pacific Ocean are characterized by a large degree of isotopic variation among dominant primary producers (macroalgae and phytoplankton; Page et al. 2008) and high functional diversity among primary and secondary invertebrate consumers. This combination yields a large degree of isotopic variation among invertebrates consumed by apex consumers such as sea otters (Page et al. 2008; Newsome et al. 2009, 2010, unpublished data) and California sheep head (*Semicossyphus pulcher*; Hamilton et al. 2011, 2014).

Given the major factors driving isotopic variation, one might hypothesize that rocky substrate habitats host greater invertebrate functional diversity and, thus, may inherently have higher amounts of isotopic variation than areas where soft-sediment substrates substantially contribute to local habitat heterogeneity. The majority of invertebrate biomass in soft-sediment habitats consists of burrowing bivalves, which are predicted to have low isotopic variation because they all fill a similar general functional role as infaunal filter feeders. Contrary to this expectation, our analysis revealed no correlation between the amount of isotopic space (SEA) occupied by invertebrates available in rocky versus mixed substrate habitats and the TINW of the sea otter populations utilizing those habitats (Fig. 5). This result suggests that the observed pattern in individuality among populations is not simply a manifestation of the isotopic variation in prey available to sea otters that inhabit rocky versus mixed substrate habitats.

Intraspecific competition

Several previous observational and experimental studies have found a positive relationship between intraspecific competition and individual specialization (Svanbäck and Persson 2004; Huss et al. 2008; Svanbäck et al. 2008; Tinker et al. 2008; Svanbäck 2009). Especially pertinent to our study is previous work examining individual diet specialization in sea otter populations from rocky substrate habitats in California (Estes et al. 2003; Tinker et al. 2008, 2012; Newsome et al. 2009). Using a unique observational dataset, Tinker et al. (2008) found a greater degree of individuality in sea otters from the central California mainland that occurred at or near equilibrium density relative to a population on San Nicolas Island (SNI) that occurred well below equilibrium density. While sea otters at SNI spend less time searching for food than their mainland counterparts, they are able to consume a greater amount of food per unit time (biomass intake rate) than sea otters in Monterey Bay or Big Sur (Table 1). Differences in sea otter density among sites are, thus, associated with corresponding differences in per capita food availability (and intraspecific competition for those limited resources), and otters in high-density areas must exert greater foraging effort and rely more heavily on low-quality prey types to meet caloric needs. These patterns suggest that intraspecific competition is the most important factor driving differences in individual dietary specialization among populations in the rocky substrate habitats of California.

Our results show that the relationship between intraspecific competition and individual specialization among California sea otter populations holds for other sites farther north that are similarly dominated by rocky substrate habitats. Sea otter populations from densely populated

rocky substrate habitats have the largest measured TINWs observed among populations (Fig. 2a). The increase in the population-level niche width appears to reflect increased individual specialization, since the WIC/TINW ratios are significantly but negatively related to the sea otter density in rocky substrate habitats (Fig. 4a). A low-density (1.4 otters/km²) site in Washington, where sea otters are believed to be below carrying capacity, is the only location that does not fit this pattern. Dissimilarity in $\delta^{13}\text{C}$ (0.997) and $\delta^{15}\text{N}$ (0.273) based estimates of the BIC of diet for the Washington sea otter population yields large error in the estimated WIC/TINW ratio (Fig. 2c). Further, the $\delta^{15}\text{N}$ estimate for the WIC (0.308) at this site was slightly larger than that for the BIC (0.273), suggesting that many sea otters at this site are generalists and switch among prey that occupy different trophic levels.

While data from rocky substrate habitats show that increases in intraspecific competition correspond to increased TINW accompanied by increased individual specialization, the relationship between intraspecific competition and individuality in mixed substrate habitats is clearly different. Our data show that intraspecific competition in mixed substrate habitats is associated with a decrease in TINW and a corresponding increase in WIC/TINW ratios. High-density sea otter populations in mixed substrate habitats have higher WIC/TINW ratios than populations that occur at lower densities (Fig. 3), opposite from the pattern observed in rocky substrate habitats. While this pattern might be explained by an expansion of individual dietary niche breadth (WIC) at high sea otter densities, such an increase would also result in an expansion of the population TINW. In contrast, many of the sea otter populations that occur at high densities in mixed substrate habitats have the lowest TINWs of any (rocky or mixed substrate) population examined in this study (Figs. 2b, 5). The combination of high WIC/TINW ratios but low TINW of sea otter populations from mixed substrate habitats suggests that sea otters at these sites are specialists at the population rather than individual level. In other words, these populations appear to consume a single prey type in high proportion.

Prey abundance, energetic value, and variation in foraging skillsets required among habitats

Why does intraspecific competition promote individuality in rocky substrate habitats but not in mixed substrate habitats? Differences in relative prey abundance, variation in the intrinsic (nutritional) content among prey, as well as the skillsets required to efficiently procure and process different prey are likely important factors that influence the habitat-specific trends in individuality. The relationship between density and biomass intake rates are similar between habitats, suggesting similar trends in relative prey

abundance (Table 1; Fig. 4b). With the exception of Kuiu Island (17.8 g/min), all populations from rocky or mixed substrate habitats with >2 otters/km² have biomass intake rates that range from ~10 to 15 g/min, while intake rates for low-density populations from both habitat types range from ~10 to 35 g/min, and most estimates exceed 15 g/min. Thus, both habitat types conform to expectations regarding reduced per-capita prey availability with increasing intraspecific competition. However, sea otters appear to respond to reduced prey availability differently in rocky versus mixed substrate habitats.

As discussed above, increased intraspecific competition in rocky substrate habitats results in greater population-level dietary diversity (TINW) and individuality (lower WIC/TINW ratios). In contrast, individuality metrics (low TINW and higher WIC/TINW ratios) for sea otters that occur at high density in mixed substrate habitats suggest these populations are consuming a high proportion of prey from a single functional group (Fig. 2b, d). Our observational data and previous studies of sea otters in Alaska (Kvitek and Oliver 1992; Doroff and DeGange 1994; Dean et al. 2002; Wolt et al. 2012) show that infaunal bivalves can represent 50–75 % of population-level diet composition for sea otters in mixed substrate habitats. Infaunal bivalves can be much more abundant than many other prey types available in either mixed or rocky substrate habitats, especially when considering differences in the amount of edible biomass contained in individual bivalves versus small snails (e.g., *Tegula*) and crabs (e.g., *Pugettia*). For example, geoduck (*Panopea abrupta*) densities at sites with sea otters in British Columbia ranged from 0.5 to 2.2 clams/m² (Reidy and Cox 2013), and the mean edible biomass of a geoduck can exceed 1 kg (Ofstedal et al. 2007). Likewise, densities of smaller littleneck clams (*Leukoma staminea*; edible biomass: 8–10 g/individual) in Kachemak Bay, AK, can range from 10 to 20 individuals/m² (Gustafson 1996).

Due to the macromolecular composition of their invertebrate prey, sea otters are likely never protein limited; however, prey items high in fat content (e.g., echinoderms) are preferred because they supply a readily accessible fuel that satisfy an otter's high metabolic demands (Costa and Kooyman 1982). Moreover, the energetic cost of procurement and processing of echinoderms is low relative to infaunal bivalves (see below). For example, sea otters that occur at low density in rocky substrate habitats in southern California and the central Aleutian Islands in Alaska largely consume sea urchins (Watt et al. 2000; Tinker et al. 2008), which have the highest fat content among available prey, ranging between 15 and 35 % on a dry mass basis (Ofstedal et al. 2007). Interestingly, lipid-rich sea urchins are also the preferred prey of sea otters that have recently colonized mixed substrate habitats, such as those found in southeast

Alaska (Kvitek et al. 1992; Kvitek and Oliver 1992). However, sea otters in these mixed substrate areas are able to rapidly deplete urchin populations to very low densities, and, thus, have to switch to alternate prey to meet their high energetic demands (Kvitek and Oliver 1992).

Even though sea urchins and large crabs (*Cancer*) are the preferred resource regardless of habitat, these lipid- and, hence, calorie-rich resources can be quickly depleted by sea otter predation. Infaunal bivalves can also be reduced in size and abundance by sea otter predation (Kvitek and Oliver 1988; Kvitek et al. 1992); however, due to the nature of their microhabitat (buried in sediments), this type of prey has a built-in refuge and can sustain relatively high levels of sea otter predation over many years without becoming extremely depleted. Consequently, in mixed substrate habitats, we expect epifaunal prey types to become disproportionately depleted by increasing sea otter populations, eventually resulting in a heavy reliance on infaunal bivalves. This pattern contrasts with rocky substrate habitats, where depletion of preferred prey leads to an expansion of population dietary niche breadth to include more diverse epifaunal benthic prey species (Estes et al. 1981, 2003; Tinker et al. 2008). While infaunal bivalves have a lower fat content, they have similar energy densities as echinoderms and decapods because they contain higher amounts of protein. Infaunal bivalves in the genera *Saxidomus*, *Leukoma*, *Tresus*, *Panopea*, and *Clinocardium* collected from California and Alaska had energy densities ranging from 0.4 to 0.7 kcal/g wet edible biomass (Oftedal et al. 2007). Energy densities of co-occurring sea urchins range from 0.2 to 0.6 kcal/g and only abalone, some decapods (*Cancer* and *Pugettia*), and small gastropods (*Tegula*) have energy densities similar to infaunal bivalves.

Habitat-based differences in prey assemblages may also dictate the range of distinct skillsets required to efficiently extract energy from the environment. Greater variation in the skills required to succeed in a given setting provides the raw material required for the potential emergence of individual diet specialization. In mixed substrate habits, where sea otters at high densities rely heavily on a single abundant and energy-rich prey functional group (infaunal bivalves), individuals may need a narrower range of hunting and processing skills to acquire the energy needed to fuel their high metabolic demands, and, thus, there is little selection for diversified individual skillsets. In contrast, local depletion of preferred prey in rocky substrate habitats results in dietary diversification to many different prey functional groups because there is no single functional group of prey as abundant or nutritionally adequate as infaunal bivalves in mixed substrates, and, thus, a more diverse array of hunting and processing skillsets is required (Estes et al. 2003; Tinker et al. 2008). This fundamental difference between habitats may act to promote and maintain individuality in

rocky substrate habitats but dampen individuality in mixed substrate habitats.

Prey functional diversity versus richness

Our results suggest that prey functional diversity may be a more suitable metric for quantifying individuality than the number of prey species consumed, at least in environments where a diverse set of specialized hunting and processing skills are passed via learning from parent to offspring (Caro and Hauser 1992; Estes et al. 2003). The selective pressures favoring dietary specialization are not dependent on the number of different prey species a consumer encounters, but, instead, on the number of distinct combinations of prey biomass, morphology, protective armoring, and distribution in the environment, as it is these suites of characteristics that dictate the range of necessary foraging skills. For example, to efficiently find, dig out, and capture infaunal bivalves from unconsolidated sediments and then pry open the valves to extract soft tissue, a sea otter predator requires a very different set of sensory, motor, and handling skills than it needs to efficiently find and pry sea urchins out of crevices in rocks, and then extract soft tissue from a spine-protected exoskeleton. As such, individuality is likely promoted and maintained at the functional rather than at the species level, and these two ecological classifications are not necessarily tightly correlated. An individual sea otter inhabiting a mixed substrate habitat may encounter 6–8 species of infaunal bivalves in a single foraging bout, during which it must dig through large amounts of sediment to locate prey. In this scenario, the individual may capture and consume all of the clams encountered and based on traditional metrics, this individual would be classified as a dietary generalist relative to a sea urchin specialist that consumes (at most) only 2–3 species of *Strongylocentrotus*. We, therefore, suggest that prey functional diversity in addition to prey richness should be considered when examining the ecological causes of individual diet specialization.

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Island, AK. The findings and conclusions in this article are those of the authors and do not necessarily represent the views of the U.S. Fish and Wildlife Service. Any use of trade, product, or firm names in this publication is for descriptive purposes only and does not imply endorsement by the U.S. government.

References

- Agashe D, Bolnick DI (2010) Intraspecific genetic variation and competition interact to influence niche expansion. *Proc Biol Sci* 277:2915–2924
- Ambrose SH (1990) Preparation and characterization of bone and tooth collagen for isotopic analysis. *J Archaeol Sci* 17:431–451
- Annett CA, Pierotti R (1999) Long-term reproductive output in western gulls: consequences of alternate tactics in diet choice. *Ecology* 80:288–297
- Araújo MS, Bolnick DI, Layman CA (2011) The ecological causes of individual specialisation. *Ecol Lett* 14:948–958
- Bearhop S, Adams CE, Waldron S, Fuller RA, MacLeod H (2004) Determining trophic niche width: a novel approach using stable isotope analysis. *J Anim Ecol* 73:1007–1012
- Bligh EG, Dyer WJ (1959) A rapid method of total lipid extraction and purification. *Can J Biochem Physiol* 37:911–917
- Bodkin JL, Burdin AM, Ryazanov DA (2000) Age- and sex-specific mortality and population structure in sea otters. *Mar Mamm Sci* 16:201–219
- Bolnick DI, Yang LH, Fordyce JA, Davis JM, Svanbäck R (2002) Measuring individual-level resource specialization. *Ecology* 83:2936–2941
- Bolnick DI, Svanbäck R, Fordyce JA, Yang LH, Davis JM, Hulsey CD, Forister ML (2003) The ecology of individuals: incidence and implications of individual specialization. *Am Nat* 161:1–28
- Bolnick DI, Ingram T, Stutz WE, Snowberg LK, Lau OL, Paull JS (2010) Ecological release from interspecific competition leads to decoupled changes in population and individual niche width. *Proc Biol Sci* 277:1789–1797
- Brown JH (1984) On the relationship between abundance and distribution of species. *Am Nat* 124:255–279
- Brown JH, Mehlman DW, Stevens GC (1995) Spatial variation in abundance. *Ecology* 76:2028–2043
- Caro TM, Hauser MD (1992) Is there teaching in nonhuman animals? *Q Rev Biol* 67:151–174
- Cohen JE, Pimm SL, Yodzis P, Saldaña J (1993) Body sizes of animal predators and animal prey in food webs. *J Anim Ecol* 62:67–78
- Costa DP, Kooyman GL (1982) Oxygen consumption, thermoregulation, and the effect of fur oiling and washing on the sea otter, *Enhydra lutris*. *Can J Zool* 60:2761–2767
- Darimont CT, Paquet PC, Reimchen TE (2009) Landscape heterogeneity and marine subsidy generate extensive intrapopulation niche diversity in a large terrestrial vertebrate. *J Anim Ecol* 78:126–133
- 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, DeGange AR (1994) Sea otter, *Enhydra lutris*, prey composition and foraging success in the Northern Kodiak Archipelago. *Fish Bull* 92:704–710
- Doroff A, Badajos O, Corbell K, Janski D, Beaver M (2012) Assessment of sea otter (*Enhydra lutris kenyoni*) diet in Kachemak Bay, Alaska (2008–2010). *IUCN Otter Spec Group Bull* 29:15–23
- Estes JA (1990) Growth and equilibrium in sea otter populations. *J Anim Ecol* 59:385–401
- Estes JA (1996) The influence of large, mobile predators in aquatic food webs: examples from sea otters and kelp forests. In: Greenstreet SPR, Tasker ML (eds) *Aquatic predators and their prey*. Fishing News Books, Oxford, pp 65–72
- Estes JA, Jameson RJ, Johnson AM (1981) Food selection and some foraging tactics of sea otters. In: Chapman JA, Pursley D (eds) *Worldwide furbearer conference proceedings, vol 1*. University of Maryland Press, Baltimore, pp 606–641
- Estes JA, Jameson RJ, Rhode EB (1982) Activity and prey election in the sea otter: influence of population status on community structure. *Am Nat* 120:242–258
- 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
- Garshelis DL, Garshelis JA, Kimker AT (1986) Sea otter time budgets and prey relationships in Alaska. *J Wildlife Manage* 50:637–647
- Gerardo Herrera ML, Korine C, Fleming TH, Arad Z (2008) Dietary implications of intrapopulation variation in nitrogen isotope composition of an old world fruit bat. *J Mamm* 89:1184–1190
- Gustafson R (1996) Kachemak Bay littleneck clam assessments, 1995. Alaska Department of Fish and Game, Division of Commercial Fisheries Management and Development. Regional Information Report No. 2A96-12
- Hamilton SL, Caselle JE, Lantz CA, Egloff TL, Kondo E, Newsome SD, Loke-Smith K, Pondella II DJ, Young KA, Lowe CG (2011) Extensive geographic and ontogenetic variation characterizes the trophic ecology of a temperate reef fish on southern California (USA) rocky reefs. *Mar Ecol Prog Ser* 429:227–244
- Hamilton SL, Newsome SD, Caselle JE (2014) Dietary niche expansion of a kelp forest predator recovering from intense commercial exploitation. *Ecology* 95(1):164–172
- Huss M, Byström P, Persson L (2008) Resource heterogeneity, diet shifts and intra-cohort competition: effects on size divergence in YOY fish. *Oecologia* 158:249–257
- Jackson AL, Inger R, Parnell AC, Bearhop S (2011) Comparing isotopic niche widths among and within communities: SIBER—Stable Isotope Bayesian Ellipses in R. *J Anim Ecol* 80:595–602
- Kondoh M (2003) Foraging adaptation and the relationship between food-web complexity and stability. *Science* 299:1388–1391
- Krebs JR, Erichsen JT, Weber MI, Charnov EL (1977) Optimal prey selection in the great tit (*Parus major*). *Anim Behav* 25:30–38
- Kvitek RG, Oliver JS (1988) Sea otter foraging habits and effects on prey populations and communities in soft-bottom environments. In: VanBlaricom GR, Estes JA (eds) *The community ecology of sea otters*. Springer-Verlag, Berlin, pp 22–47
- Kvitek RG, Oliver JS (1992) Influence of sea otters on soft-bottom prey communities in southeast Alaska. *Mar Ecol Prog Ser* 82:103–113
- Kvitek RG, Oliver JS, DeGange AR, Anderson BS (1992) Changes in Alaskan soft-bottom prey communities along a gradient in sea otter predation. *Ecology* 73(2):413–428
- Layman CA, Quattrochi JP, Peyer CM, Allgeier JE (2007) Niche width collapse in a resilient top predator following ecosystem fragmentation. *Ecol Lett* 10:937–944
- Matthews B, Marchinko KB, Bolnick DI, Mazumder A (2010) Specialization of trophic position and habitat use by sticklebacks in an adaptive radiation. *Ecology* 91:1025–1034
- Newsome SD, Tinker MT, Monson DH, Oftedal OT, Ralls K, Staedler MM, Fogel ML, Estes JA (2009) Using stable isotopes to investigate individual diet specialization in California sea otters (*Enhydra lutris nereis*). *Ecology* 90:961–974
- Newsome SD, Bentall GB, Tinker MT, Oftedal OT, Ralls K, Estes JA, Fogel ML (2010) Variation in $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ diet-vibrissae trophic discrimination factors in a wild population of California sea otters. *Ecol Appl* 20:1744–1752

- Oftedal O, 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 Nicolas Island, California and Glacier Bay, Alaska. Final report to the Monterey Bay National Marine Sanctuary and the Marine Mammal Commission, 23 pp
- Ostfeld RS (1982) Foraging strategies and prey switching in the California sea otter. *Oecologia* 53:170–178
- Page HM, Reed DC, Brzezinski MA, Melack JM, Dugan JE (2008) Assessing the importance of land and marine sources of organic matter to kelp forest food webs. *Mar Ecol Prog Ser* 360:47–62
- Partridge L, Green P (1985) Intraspecific feeding specializations and population dynamics. In: Sibley RM, Smith RH (eds) *Behavioural ecology*. Blackwell Press, Oxford, pp 207–226
- Peters RH (1983) The ecological implications of body size. Cambridge University Press, Cambridge, 333 pp
- Power ME, Tilman D, Estes JA, Menge BA, Bond WJ, Mills LS, Daily G, Castilla JC, Lubchenco J, Paine RT (1996) Challenges in the quest for keystones. *Bioscience* 46:609–620
- Pulliam HR (1974) On the theory of optimal diets. *Am Nat* 108:59–74
- Reidy RD, Cox SP (2013) Geoduck clam (*Panopea abrupta*) demographics and mortality rates in the presence of sea otters (*Enhydra lutris*) and commercial harvesting. *Open Fish Sci J* 6:28–40
- Roughgarden J (1972) Evolution of niche width. *Am Nat* 106:683–718
- Schluter D, Price TD, Grant PR (1985) Ecological character displacement in Darwin's finches. *Science* 227:1056–1059
- Schoener TW (1971) Theory of feeding strategies. *Annu Rev Ecol Syst* 2:369–404
- Siwertsson A, Knudsen R, Præbel K, Adams CE, Newton J, Amundsen PA (2013) Discrete foraging niches promote ecological, phenotypic, and genetic divergence in sympatric whitefish (*Coregonus lavaretus*). *Evol Ecol* 27:547–564
- Stewart NL, Konar B, Doroff A (2014) Sea otter (*Enhydra lutris*) foraging in a heterogeneous environment in Kachemak Bay, Alaska. *Bulletin of Marine Science*
- Svanbäck R, Bolnick DI (2005) Intraspecific competition affects the strength of individual specialization: an optimal diet theory method. *Evol Ecol Res* 7:993–1012
- Svanbäck R, Bolnick DI (2007) Intraspecific competition drives increased resource use diversity within a natural population. *Proc Biol Sci* 274:839–844
- Svanbäck R, Persson L (2004) Individual diet specialization, niche width and population dynamics: implications for trophic polymorphisms. *J Anim Ecol* 73:973–982
- Svanbäck R, Persson L (2009) Population density fluctuations change the selection gradient in Eurasian perch. *Am Nat* 173:507–516
- Svanbäck R, Eklöv P, Fransson R, Holmgren K (2008) Intraspecific competition drives multiple species resource polymorphism in fish communities. *Oikos* 117:114–124
- Thompson ID, Colgan PW (1990) Prey choice by marten during a decline in prey abundance. *Oecologia* 83:443–451
- Tinker MT, Bentall G, Estes JA (2008) Food limitation leads to behavioral diversification and dietary specialization in sea otters. *Proc Natl Acad Sci U S A* 105:560–565
- Tinker MT, Guimaraes Jr PR, Novak M, Marquitti FMD, Bodkin JL, Staedler M, Bentall G, Estes JA (2012) Structure and mechanism of diet specialisation: testing models of individual variation in resource use with sea otters. *Ecol Lett* 15:475–483
- Van Valen L (1965) Morphological variation and width of ecological niche. *Am Nat* 99:377–390
- Watt J, Siniff DB, Estes JA (2000) Inter-decadal patterns of population and dietary change in sea otters at Amchitka Island, Alaska. *Oecologia* 124:289–298
- Werner TK, Sherry TW (1987) Behavioral feeding specialization in *Pinaroloxias inornata*, the “Darwin's Finch” of Cocos Island, Costa Rica. *Proc Natl Acad Sci U S A* 84:5506–5510
- Wolt RC, Gelwick FP, Weltz F, Davis RW (2012) Foraging behavior and prey of sea otters in a soft- and mixed-sediment benthos in Alaska. *Mamm Biol* 77:271–280