Sea otter diet nutrient composition with respect to recolonization, life history, and season in southern Southeast Alaska

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Abstract

The sea otter (Enhydra lutris) population of Southeast Alaska has been growing at a higher rate than other regions along the Pacific coast. While good for the recovery of this endangered species, rapid population growth of this apex predator can create a human-wildlife conflict, negatively impacting commercial and subsistence fishing. Previous foraging studies throughout the sea otter range have shown they will reduce invertebrate prey biomass when recolonizing an area. The goal of this study was to examine and quantify the energetic content of sea otter diets through direct foraging observations and prey collection. Our study area, Prince of Wales Island in southern Southeast Alaska, exhibits a gradient of sea otter recolonization, thus providing a natural experiment to test diet change in regions with different recolonization histories. Sea otter prey items were collected in three seasons (spring, summer, winter) to measure caloric value and lipid and protein content. We observed 3,523 sea otter dives during the spring and summer. A majority of the sea otter diet consisted of clams. Sea otters in newly recolonized areas had lower diet diversity, higher kcal/gram intake rates, and higher energetic intake rates. Females with pups had the highest diet diversity and the lowest energetic intake rates (calories per gram consumed). Sea otter energetic intake rates were higher in the fall and winter vs. spring and summer. Sea cucumber energy and lipid content appeared to correspond with times when sea otters consumed the highest proportion of sea cucumbers. These caloric variations are an important component of understanding ecosystem level effects sea otters have in the nearshore environment.

1. Introduction

The nutritional ecology of marine predators is poorly understood compared to terrestrial predators. Classic foraging theory suggests that consumers should target prey that maximizes their net rate of energetic gain . As energetic intake was the focus, studies addressed consumers' overall net energetic consumption as a factor in prey selection. However, more recent studies have focused on predators' nutritional needs and how prey choice varies according to macronutrient composition . Consumers may target lower energy prey for various reasons, including reproductive status. For example, Machovsky-Capuska et al. (2018) revealed that male Australasian gannets (*Morus serrator*) consistently foraged for fish with higher protein-to-lipid ratios, whereas females foraged for fish with higher lipid-to-protein ratios. One potential explanation is the differential dietary response by female and male parents according to the changing needs of growing chicks. Similarly, female sea otters (*Enhydra lutris*) will switch their foraging tactics when caring for a pup, which may represent a trade-off between maximizing potential energy return and meeting pup needs .

Sea otters are a dynamic species in which to study nutritional ecology because of their unique adaptations to the marine environment. Unlike most marine mammals, sea otters do not have blubber to keep them warm. Instead, sea otters maintain very high metabolisms . Various studies estimate sea otters consume anywhere from 19 to 39% of their body weight in food per day to sustain these elevated metabolic costs . Because of their voracious appetites, sea otters can exert large effects on the nearshore marine ecosystem within relatively short periods . These effects are particularly evident in kelp forests, where sea otters suppress the grazers, sea urchins (*Strongylocentrotus* spp.), which in turn relieves pressure on kelp. This relief of grazing pressure helps to increase kelp forest density, which has been shown to increase juvenile fish habitat and increase overall species diversity in the system.

Historical records show that sea otters once inhabited nearshore ecosystems of the Pacific Ocean from Japan to Baja California. However, by the late 19th Century, there were only 11 remnant populations within their once continuous distribution due to hunting for the lucrative fur markets in Russia and China. In 1911, sea otters were protected from hunting by the International Fur Seal Treaty. By this time, sea otters were extirpated from Southeast Alaska . To restore sea otters to their historical range, the Alaska Department of Fish and Game and the Atomic Energy Commission initiated a translocation program and, in the 1960s, relocated about 400 sea otters from the Aleutian Islands to six locations in Southeast Alaska. Since the translocation, sea otters have expanded their range and increased in numbers. The most recent range-wide sea otter aerial counts in 2010–2011 estimated that approximately 25,000 sea otters were present in Southeast Alaska . The expansion of sea otters from the six translocation sites in Southeast Alaska into unoccupied habitat over time allows for a ‘space-for-time’ substitution , in which the longer-term effects (positive, neutral, and negative) of sea otters on the nearshore ecosystem can be seen in areas of longer occupation.

Prince of Wales Island (POW), along with its neighboring islands, in southern Southeast Alaska has two original release locations. Hoyt (2015) studied sea otter diets around POW for three years (2010–2012) focusing on sea otter impacts on commercially important species. Hoyt (2015) found that the number of species consumed by sea otters increased as time since recolonization increased, and sea otters reduced the abundance of commercially important species. The sea cucumber (*Apostichopus californicus*) fishery is an example of a commercial shellfishery impacted by sea otters. Previous studies showed that sea otter presence caused a decline of sea cucumbers in all regions where sea otters were present for $>$ 15 years . Many sea cucumber fishery regions have been closed due to declining sea cucumber abundance after sea otters have recolonized the regions .

Measuring sea otter energetic intake rate is a widely used method to measure changes in diet and to assign quantitative values to sea otter nutritional needs . In Alaska, the Alaska Science Center, a part of the United States Geological Survey (USGS), maintains a database on species- and size-specific energetic values for sea otter prey items. Many of these values come from California invertebrate collections and published literature . These values are used to create energetic models and biomass estimates for each sea otter prey species; however, using prey values from other regions could lead to inaccurate consumption estimates for sea otters in Alaska. Similarly, a comprehensive analysis of the biochemical composition of sea otter prey was conducted in varying seasons in California but is absent for Alaskan prey . A preliminary study in Sitka, Alaska, showed that the preferred prey of sea otters (clams) was not highest in overall caloric content or lipid content when compared to all available prey items . This preliminary work is a driver for further investigation of sea otter diet analysis in Southeast Alaska.

Our goal for this study was to analyze the relationship between sea otter diet and prey nutritional composition. Our objectives were to: 1) investigate the macronutrient quality of sea otter prey in southern Southeast Alaska across seasons; and 2) examine diet composition according to prey macronutrient composition across different sea otter metrics: (i) time since recolonization, (ii) sea otter sex and reproductive class, and iii) season. This work increases our understanding of sea otter prey composition according to the energy and macronutrient content in Southeast Alaska, which, in turn, gives us a better understanding of the invertebrates removed from the nearshore system due to sea otter predation, and why. This increases the potential to predict future impacts of sea otters on nearshore ecosystems, including changes to kelp forest cover and reductions in commercial and subsistence species due to sea otter predation.

2. Methods

2.1 Visual foraging observations

We observed sea otter foraging behavior from May to August 2018 on the western side and neighboring islands of POW. Sampling was stratified by time since recolonization, based on US Fish and Wildlife Service (USFWS) aerial surveys. Three periods were denoted from the surveys: zone 1 (> 30 years present), zone 2 (< 30 years and > 15 years present), and zone 3 (< 15 years and > 7 years present) (Fig. 1). In each zone, a minimum of 300 foraging dives were recorded. Because zone 2 makes up a majority of POW, most foraging dives occurred in this zone.

Foraging observations were made from shore to assess sea otter diet composition. Questar telescopes (50X) were used to follow individual sea otters for one foraging bout (up to 20 dives per sea otter). The observer recorded the following foraging metrics: prey item (to species level when possible), prey size (based on an estimated sea otter paw width of 5 cm and categorized into < 1/3 of the paw, > 1/3 and < 2/3 of the paw, or the whole paw), the proportion of the prey item consumed, GPS location (approximated based on GPS location of the telescope and distance/bearing to the sea otter), prey handling time (defined as the amount of time the sea otter spent manipulating and eating the prey), time spent diving, and total time spent at the surface. The following sea otter metrics were also recorded for each foraging bout: sex, reproductive status, and age class. Males were identified by the presence of a penile bulge, whereas females were identified if there was a clear lack of penile bulge, or if they had a pup. If sex was not confirmed, nor pup was observed, the sex was categorized as "unknown." When possible, age class was determined as adult or juvenile by visual assessment of size and amount of grizzled fur .

We calculated the caloric intake for sea otters based on visual foraging observations using the Sea Otter Foraging Analysis (SOFA) program, which is based in Matlab (MathWorks) and maintained by the USGS Alaska Science Center in Anchorage, AK. SOFA uses a Monte Carlo-based simulation to account for unknown prey items and potential sampling bias. SOFA is a Bayesian model that provides the estimated biomass for individual prey types across time since recolonization, reproductive status, and sex. All SOFA outputs are reported as means with standard deviation. The consumption rates for each prey species were assigned for each foraging bout using the estimated prey size relative to a sea otter paw width. Prey diversity for each region was calculated using the Shannon-Wiener Index . Success rate, which is defined as the percentage of dives in a bout where the sea otter came up with food, was calculated for each sea otter metric.

2.2 Prey sampling

Potential prey items to be collected for macronutrient and energetic analyses were selected based on existing literature on sea otter diets in Southeast Alaska . Five functional prey groups (crabs, clams, sea cucumbers, snails, sea urchins) were identified that were composed of 13 target species for analysis. These five functional groups made up 95% of sea otter diets (in terms of biomass) from visual foraging observations. Five individuals of each target species were collected at two sites (Fig. 1) in May 2018, August 2018, and February 2019. All samples were collected in the intertidal zone. Two collection sites were selected that encompassed the foraging observation sites and had reliable access. Craig (Site 1) and Soda Bay (Site 2) represented differences in sea otter occupation time (> 15 years for Craig, and > 7 years for Soda Bay). Where there were more sea otters present, there were less abundant invertebrate species for collection. Additional samples were opportunistically collected around POW if they were not present or in high enough abundance in the two designated sites. Samples were held in seawater-filled buckets, cleaned of sand and dirt, and then frozen at -18°C.

In the lab, samples were thawed, weighed, measured, and separated into edible and inedible tissues. For bivalves, decapods, gastropods, and sea urchins, all hard parts were removed and discarded, as they were considered inedible as the sea otter excretes these contents . For sea cucumbers, the entire organism was considered edible. Only crabs were processed separately by sex. Remaining edible tissues were weighed and homogenized in a Cuisinart Mini-prep food processor. A maximum of 4 g of tissue was dried in a LECO Thermogravimetric Analyzer 701 (TGA) dryer at 135°C, or in a gravity convection oven (VWR Symphony 414004-552) at 70°C. Standards and duplicates were run with each dryer to confirm consistent moisture values.

2.3 Energy content nutritional analysis

We measured energetic value and proximate composition (the proportion of protein content, lipid content, moisture, and percent ash) for sea otter prey items. We used previously established methods to measure energy density using a Parr 6725 semi-micro bomb calorimeter. Standards and replicates were used to confirm consistent calorimeter readings. Lipid content was determined using previously established methods using a sulfo-phospho-vanillin colorimetric analysis. Protein content was estimated by multiplying total nitrogen content by 6.25, which accounts for the nitrogen content of protein . Nitrogen content was measured with a FlashSmart elemental analyzer coupled to a Delta-V continuous-flow isotope ratio mass spectrometer (Thermo Scientific, Waltham, Massachusetts, USA). Carbohydrate content was not assessed as it is assumed to be negligible in marine invertebrates . Ash content was processed at 600°C and measured with a LECO Thermogravimetric Analyzer 701 (TGA) dryer. Only samples with > 1 g of dried material were able to be combusted for percent ash content.

2.4 Statistical analysis of sea otter prey

To test our first objective (investigate the macronutrient quality of sea otter prey across seasons), we calculated the percent protein and lipid of each prey group using the energy equivalents of 9.5 kcal/g for lipid and 5.7 kcal/g for protein . We used PRIMER v7 with a one-way analysis of similarity (ANOSIM) procedure with season as factors for each prey group, excluding crabs ($\alpha = 0.01$). Snails had too few samples to conduct pairwise seasonal comparisons. Mussels were excluded from results because they were a very small portion ($< 1\%$) of the sea otter diet around POW. Crabs were analyzed separately with season and sex as factors, using a two-way ANOSIM ($\alpha = 0.01$).

To test our second objective (compare diet composition and prey macronutrient composition across different sea otter metrics), we calculated regional-level concentrations of macronutrient composition of sea otter diets using established methods . In brief, first, we converted the dry mass average (kcal, lipid, and protein) for each functional prey group to a wet mass value. Second, using the proportion of diet (also in wet mass) from SOFA outputs for each functional prey group and the average prey value (kcal, lipid, and protein), we calculated an average for each prey and macronutrient and added all individual groups together. Finally, we divided this newly calculated wet mass by dry mass to get the nutrient composition of dry mass. Statistical comparisons between sea otter metrics tested were not possible because we were not able to study known individual sea otters and all data were used at a regional scale (Western POW and surrounding islands).

Due to weather and light limitations, it was only possible to conduct visual foraging observations during spring and summer. To estimate year-round diets, we used results from stable isotope analysis . Diets estimates were made using stable isotope (δ^{13}C and δ^{15}N) analysis of both sea otter vibrissae and the prey present around POW using a Bayesian model to estimate percent of total diet for functional prey groups. These diet estimates were used in the calculations for seasonal sea otter macronutrient contribution and comparison to changes in sea otter prey. All datasets are archived in a publicly accessible database with the Knowledge Network for Biocomplexity .

3. Results

3.1 Sea otter diets across Prince of Wales

Foraging records consisted of 362 foraging bouts. In total, 3,523 dives were recorded between May 6, 2018, and August 13, 2018. The overall success rate was 89.9%, and diet diversity (H') was 0.81. Mean dive time was 88.4 seconds (± 44.5), and mean surface time was 56.4 seconds (± 42.3). The mean energy intake rate was 7.3 ± 0.22 Kcal/min. Sea otters were observed to consume a total of 44 prey items. When prey selection was examined irrespective of habitat type or site, the dominant prey categories (making up 97.5% of the total diet by biomass) calculated by SOFA were clams (80.9 ± 2.21%), sea cucumbers (8.5 ± 1.13%), crabs (3.8 ± 0.44%), snails (2.7 ± 0.39%), and sea urchins (1.6% ± 0.28%). Within the clam category, butter clams (*Saxidomus gigantea*) were the predominant species, comprising 36.9 ± 1.61% of the overall diet.

We observed differences in sea otter diets across recolonization zones and reproductive status. Species diversity and intake rate (kcal/min) varied by recolonization zone (Table 1). The newest recolonization zone (> 7 years) had the lowest species diversity (H' = 0.39) and highest intake rate (11.06 ± 0.8 Kcal/min). The zone where sea otters have been present for the longest period of time (> 30 years) had the highest species diversity (H' = 1.19) and lowest intake rate (5.7 ± 0.8 Kcal/min). Clams were the main prey consumed across all recolonization zones (Fig. 2A). Species diversity and intake rate varied by reproductive status (Table 1). Although clams were the dominant prey, sea otter diets varied by reproductive status; females with pups had a more varied diet and higher species diversity than females without pups and males (Table 1, Fig. 2B). Females with pups had the highest species diversity (H' = 1.23) and highest success rate (90%) whereas males had the lowest species diversity (H' = 0.34).

3.2 Macronutrient content in sea otter diets

Energetic intake (kcal/gram) and percent protein composition varied by recolonization zone (Fig. 3A) and reproductive status (Fig. 3B). Energetic intake, percent lipid, and protein composition varied by season (Fig. 3D). For example, fall and winter varied from spring and summer in overall energetic intake (fall: 4.3 Kcal/gram, winter: 4.2 Kcal/gram, spring: 3.8 Kcal/gram, summer: 3.8 Kcal/gram). The variation in energetic intake is driven by both percent protein and percent lipid (fall: 8.0% lipid and 58.4% protein, winter: 8.1% lipid and 58.0% protein, spring: 7.4% lipid and 51.3% protein, summer: 7.5% lipid and 51.1% protein). In contrast, females with and without pups had variation in overall energetic content driven only by the percent protein in the diet (with pup: 3.9 Kcal/gram, 7.2% lipid, and 53.6% protein, without pup: 4.4 Kcal/gram, 7.4% lipid, and 61.2% protein).

3.3 Energetic content of sea otter prey

Overall, sea otter prey had a similar makeup of protein and lipid content; sea urchins were the only prey group significantly different from other prey groups for lipid-to-protein ratio (Fig. 4, $p < 0.01$). Functional prey groups varied in their energy, lipid, and protein content across seasons (Table 2). Across all seasons, sea cucumbers exhibited lower energy than all other prey types (Fig. 5), and their energy and lipid varied significantly by season (Table 2). Sea urchins had significant variability in lipid content across seasons (Table 2). Clams exhibited a significant change in energy and lipid over seasons as well, but R values were low, which means the overall seasonal effect was low (Table 2). Crabs did not vary significantly across seasons or sex. Snails did not vary significantly across seasons. Pairwise comparisons for all prey groups and seasons revealed significant differences in energy for clams and sea cucumbers (Table 3). Lipid varied for clams, sea cucumbers, and sea urchins, whereas protein only varied between seasons for clams. Snails were not compared across seasons due to the small sample size.

When we compared year-round energetic changes in sea otter prey with diet proportion estimates, we found consumption rates of most functional prey groups did not correlate with energy density. Clam consumption, the major diet item for sea otters in this study, did not correspond with changes in energy (Fig. 6A) or lipid (Fig. 6C). Based on LaRoche et al. (2021), sea otters consumed more clams in the fall and winter months, when the energetic and lipid contents of clams were lower than the spring season. Sea cucumber consumption, the second most abundant diet contribution, did appear to correspond with changes in energy (Fig. 6B) and lipid (Fig. 6D). Sea otters decreased their consumption of sea cucumber in the fall and winter months, which corresponded with declining energetic value.

4. Discussion

The main sea otter diet component regardless of location, sex, age, and season was clams. Sea otter intake rates at the POW regional level were comparable to studies of sea otters at or near carrying capacity , showing that locations around POW may be reaching carrying capacity. There were differences in the proportion of diet and prey composition according to time since recolonization, reproductive status, and season.

4.1 Time since recolonization

Time since recolonization affects the prey composition of sea otter diets. Although clams comprise the majority of the diet in all regions of POW, there were differences in prey items across recolonization zones.

The areas of POW that have been colonized for the least amount of time (zone 3, colonized for > 7 years) had the lowest species diversity in prey and highest energy recovery rates. In this zone, clams were overwhelmingly present in the diets of sea otters. This was similar to previous studies in mixed sediment communities in Southeast Alaska, where sea otters focus on fewer, high-quality prey species (e.g., sea urchins in rocky habitats, large clams in soft-sediment habitats) in newly occupied areas, and eventually diversify prey species as sea otter populations persist . Lipid content in sea otter diets was consistent across recolonization zones, but overall energy rate gain was slightly higher in zone 3, which may be due to the ability to obtain larger prey in newly colonized areas. Foraging records for the areas where sea otters had been present the longest (zone 1, colonized for > 30 years) had an intake rate that was comparable to previous studies where sea otters were at carrying capacity . This shows that the sea otters in this recolonization zone of POW are likely at or near carrying capacity, which is in line with modeling from aerial survey data from the region .

When considering sea otter diets and how sea otter invertebrate removal can affect the nearshore system, it is important to look at diet variation across recolonization zones as diets in the newly colonized areas were less diverse, which is similar to past studies in Alaska . In rocky habitats of Southeast Alaska and British Columbia, sea otters in newly colonized regions consumed a majority of red sea urchins . In the present study, the areas we observed where sea otters are newly colonizing were soft-sediment habitat ripe with large butter clams, which were the overwhelmingly predominant prey item.

4.2 Reproductive status

Female sea otters with pups had a more varied diet composition than females without pups and males. The difference in the diet was the largest shift among all tested metrics. Females with pups ate a higher proportion of crabs, sea cucumbers, and sea urchins than sea otters without pups. Sea cucumbers are the functional prey group with the lowest energetic content, therefore females with pups are obtaining fewer calories per gram of food consumed. This is likely due to females with pups opting for a risk-averse strategy, instead of searching for the highest quality prey and risking no success at all. One possibility could be that a female with a pup would rather come up with prey every dive instead of risking no success for a higher effort prey (such as choosing a slow-moving sea cucumber laying the ocean floor, instead of digging for a clam or a fast-moving crab). Success rates were high across the POW region, but females with pups had the highest success rate. Other studies have reported females to vary their diet according to reproductive state. In California, tagged female sea otters switched their foraging strategies and prey types consumed when they had no pup, small pups, and large pups .

There were other sex-specific differences in prey type. Males were observed to eat more snails than females, while females with pups were never observed to eat snails. In previous studies, snail specialists have been linked to poor overall body condition and higher death rates due to disease . Because we did not follow individuals in this study, we were unable to determine if there was a similar pattern in Southeast Alaska sea otters. In addition, although the prevalence of geoduck clams (*Panopea generosa*) in diets was low in our study, with only seven observations of geoduck clams consumed throughout the region, all of these were consumed by males. Geoduck clams are higher risk prey because of the increased effort needed to excavate them, thus, sea otters generally make several dives to recover one geoduck clam . We did not observe sea otters foraging for geoduck clams in the most recently colonized zones, which matches previous studies in the same region . These areas may have larger clams that reside in shallower areas (e.g., butter clams) creating a more efficient risk-reward ratio. Dietary differences between males and females are worth noting, as males are more likely to expand into new regions first . As new regions are being recolonized, knowing the diet preferences of males can help to predict invertebrate predation with relation to species that are of interest to humans.

Lipid content and energetic gain per gram were lowest for females with pups. There were no significant differences in dive or surface times for females with pups vs. other age/sex classes, which could be an artifact of eating less calorically-rich prey. However, females with pups have the highest foraging success rate when compared to females without pups and males, which could indicate that females with pups select less energy-rich prey items over the risk of no success. Previous studies of sea otter energetics showed that female sea otters with large pups operate at an energetic deficit by the time a pup reaches weaning age . In the present study, this deficit may be evidenced by the lower energetic gain per gram for females with pups. However, there are a multitude of other risks females with pups must contend with while foraging. In areas where food is limited, females with large pups may reach a maximum physical amount of time allowable for foraging . They also encounter constraints with respect to allocating energy to nursing vs. providing prey to their pup.

4.3 Seasonal diet shifts

Sea otters consume prey with higher percent lipid in the fall and winter months. This change in nutrient composition could be to compensate for colder temperatures in winter months and the need to obtain more calories to metabolize for warmth. Average sea surface temperatures (SST) for nearby Ketchikan range from a low of 6°C in the winter to a high of 14°C in the summer . Currently, to our knowledge, there are no published studies that test the density and characteristics of sea otter fur across seasons, so it is unknown if the fur is thicker and can add additional warmth in the winter months. Sea otters may need to increase the consumption of lipids to assist in thermoregulation. The low end of the water temperature range in which a sea otter can remain in a thermoneutral zone (i.e., a physiological state whereby the animal maintains its normal core body temperature without metabolic heat production or active cooling) is about 15°C . This temperature is slightly above the typical summer SST on POW, meaning that at temperatures below this critical level, sea otters must consume more energy to generate additional heat. Previous studies have shown that sea otters adjust their foraging patterns to environmental conditions, which could affect diet composition.

Based on sea otter diet estimates from LaRoche, et al (2021), clam consumption in spring and summer was lower than fall and winter. This change, which does not correlate with seasonal changes in energy or lipid content, could be due to paralytic shellfish poisoning (PSP). PSP is a toxin in algae that blooms in the spring and summer months along the Pacific coast . Studies have shown that sea otters will still eat bivalves that have PSP toxins present, but will avoid bivalves with very high amounts, as well as only consuming the foot and discarding the siphon, which usually has the highest concentration of PSP .

Sea otter consumption of sea cucumbers across seasons positively corresponded with sea cucumber total energy and lipid content. Sea cucumbers are broadcast spawners. They move into shallow waters in the late spring to begin spawning in the summer months . During the fall and winter months, they retreat to deeper water. Their highest percent lipid and caloric content were observed in the summer when they are preparing to spawn. Estimates from stable isotope analyses show the highest diet proportion in the summer, with spring slightly lower, and a drastic drop in the fall and winter months. This correlates with sea cucumber life history. The visual foraging observations show higher consumption in the summer than the spring. This correlation can be due to increased caloric content. Additionally, their shallow-water summer habitat makes them more easily obtainable for sea otters. At other times of the year, sea cucumbers inhabit depths up to 250 m, which is outside of a sea otter's diving ability .

4.4 Future Work

It is important for managers to consider the whole ecosystem and not only focus on each single species individually. Because sea otters are removing biomass similar to a fishery, their impact on invertebrate prey should be considered in management strategies. It is also important to incorporate how sea otters prioritize and change their diets; for example, this study showed that sea otters increase their sea cucumber consumption in the summer months. Currently, there is a lack of invertebrate surveys to assess current population levels. Dungeness crabs, butter clams, and other subsistence bivalves like cockles are not surveyed. Creating a complete ecosystem level management for the Alaska nearshore system with subsistence foods surveyed would account for the needs of people both local and commercial fishing, as well as the health of the ecosystem.

Within our study area only three aerial surveys were conducted over a 30-year period to estimate the sea otter abundance and geographic range . More fine-scale outcomes of sea otter diet changes were not possible because of the long gaps in population data. More frequent range-wide surveys are needed to better understand the population size and distribution. The current Southeast Alaska population movements and growth rates are currently estimated on surveys that were conducted a decade ago .

5. Conclusions

Sea otters can be used as a looking glass into the overall ecosystem due to their foraging habits. Sea otters sample benthic invertebrates at a higher rate and with better skill than people can attain with SCUBA surveys . This study provides quantitative data that can inform an ecosystem-based management approach that also considers local subsistence harvest needs and stakeholder input. However, for a more comprehensive understanding of the sea otter population in Southeast Alaska, abundance surveys of both sea otters and invertebrates need to be conducted more frequently. If used in conjunction with more comprehensive abundance surveys, the quantitative results presented here regarding sex and location-specific diet composition can be used to predict current and future sea otter ecosystem effects, thus informing co-management plans for this apex predator in addition to commercially-important and subsistence foods.

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Conflict of interest : none

Author contribution : NLL, HCP, and GLE conceived the ideas and designed methodology; NLL and SLK collected data; NLL and EF analyzed the data; NLL led the writing of the manuscript as a part of her master's thesis. All authors contributed critically to the drafts and gave final approval for publication.

Data availability statement : Visual foraging observation data used in this study are published through KNB at:*https://doi.org/10.5063/F1C53J8X*. Invertebrate biomass data are published through KNB at:*https://doi.org/10.5063/F1Q23XNG*.

References

Figures

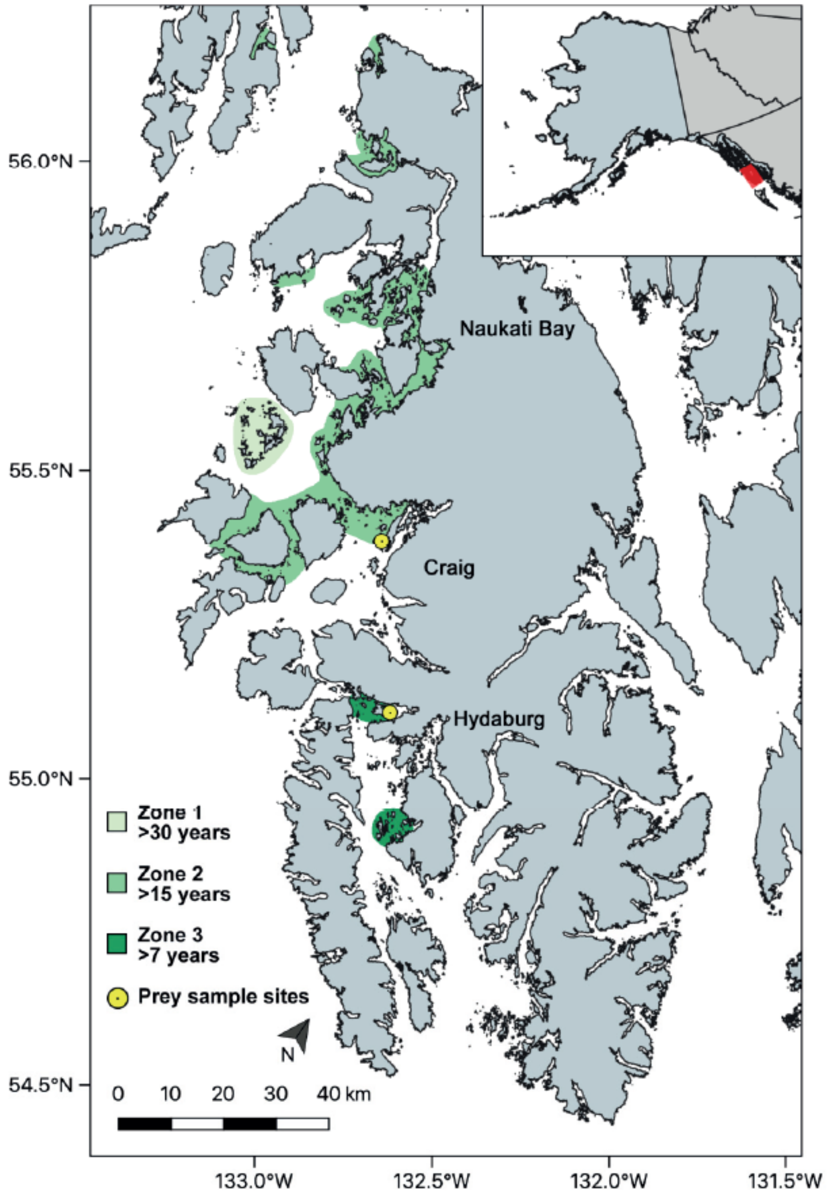

Figure 1: Sea otter visual foraging observations were made within three foraging zones (shaded areas with zone numbers listed) on Prince of Wales Island in southern Southeast Alaska. Each zone was designated by time-since-recolonization based on US Fish and Wildlife Service aerial surveys.

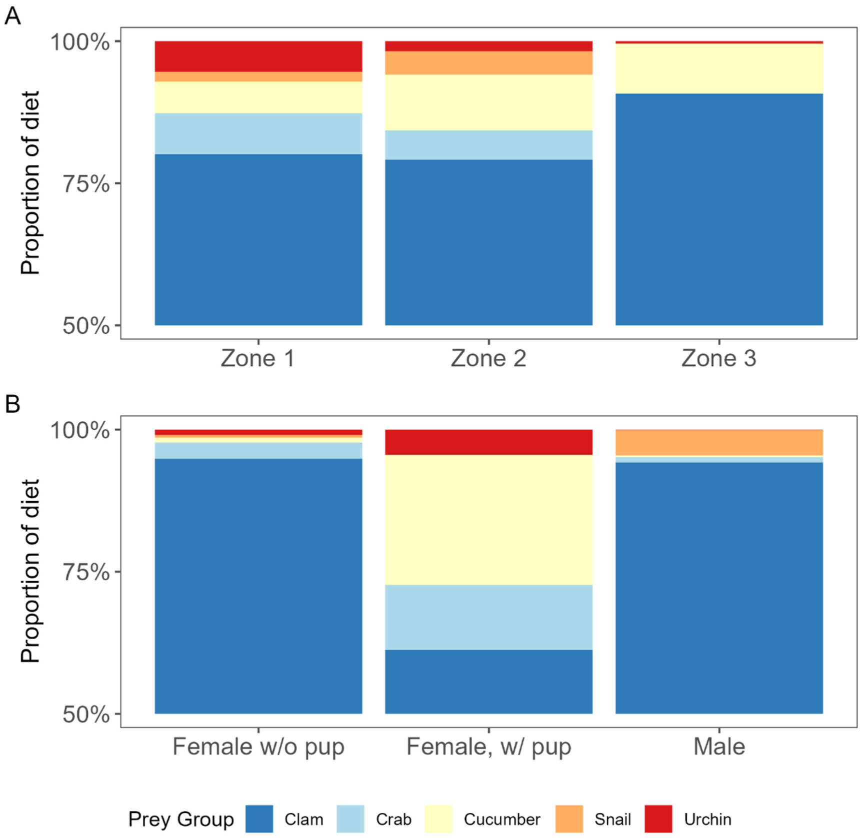

Figure 2: Proportion of diet from biomass estimates for time-since-recolonization zones (A) and sea otter reproductive status/sex (B). Zones are based on US Fish and Wildlife Service aerial surveys. Zone 1 is the area occupied for > 30 years, Zone 2 is the area occupied >15 years, and Zone 3 is the area occupied >7 years.

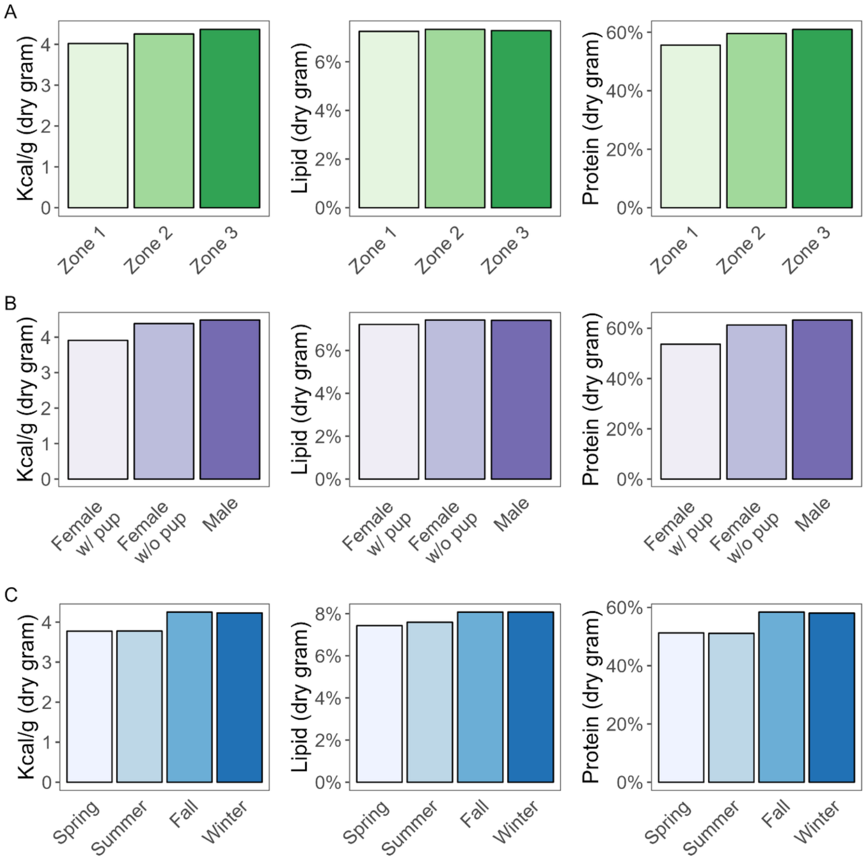

Figure 3: Comparison of the energy, lipid, and protein concentrations in population-level diets for time-since-recolonization zone (A), sea otter reproductive status/sex (B), and season (C). All calculations are made from the wet mass (as a sea otter would eat the item) and converted to dry mass for comparison. Zones are based on US Fish and Wildlife Service aerial surveys. Zone 1 is the area occupied for > 30 years, Zone 2 is the area occupied >15 years, and Zone 3 is the area occupied >7 years.

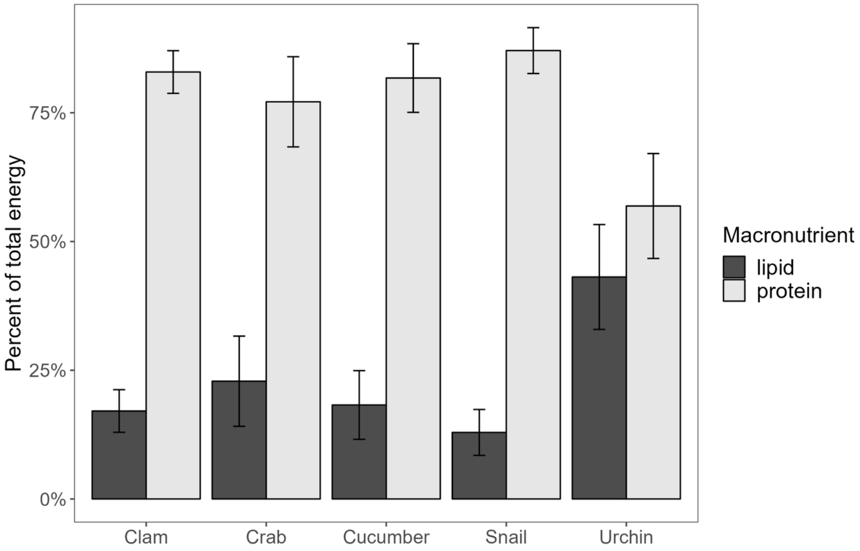

Figure 4: Proportion of energy in each functional prey group of sea otters derived from lipid and protein.

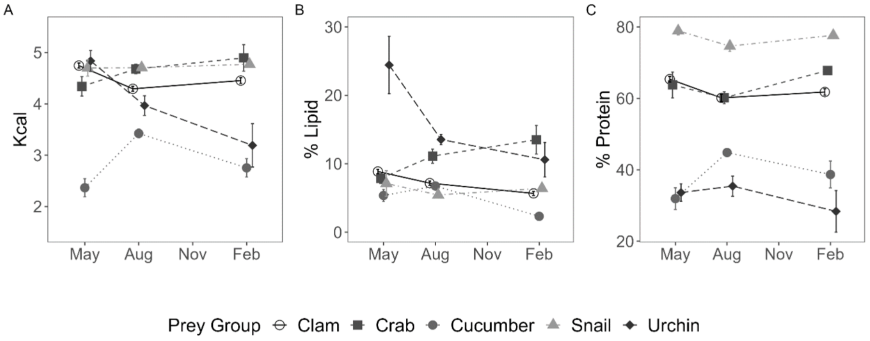

Figure 5: Seasonal whole-body nutrition of functional prey groups of sea otters in dry mass. Panel A depicts the energy content in kilocalories per dry gram (± one standard error), panel B depicts the lipid content in dry gram (± one standard error), and panel C depicts the protein content in dry grams (± one standard error).

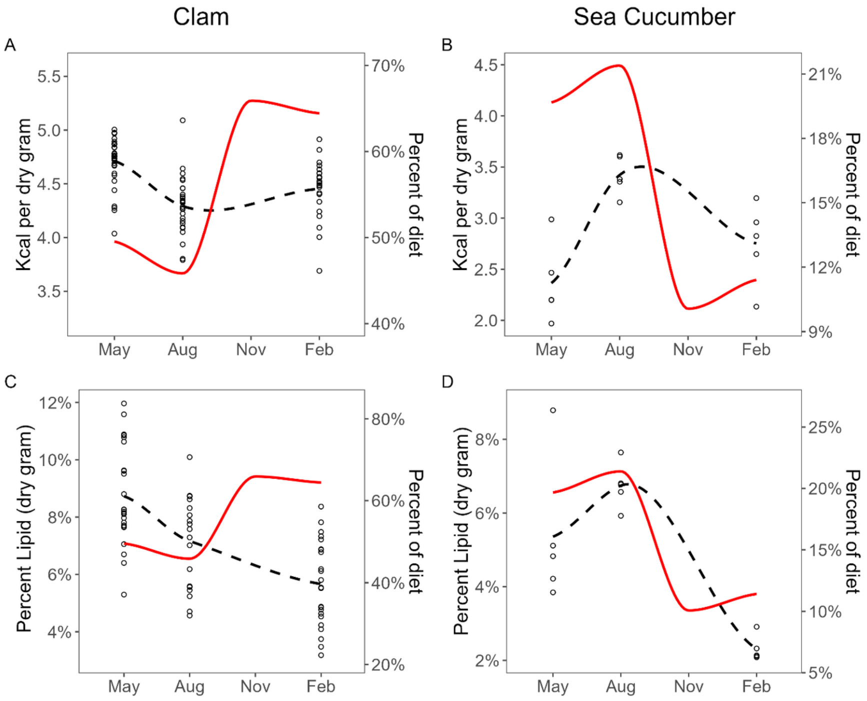

Figure 6: Seasonal variation in the nutrition of sea otter prey (A and C are clams, and B and D are sea cucumbers. Circles are individual samples and dotted lines are the mean, with percent on the left axes) and frequency of occurrence of that prey species in the diet (red solid lines, with percent on the right axes). A and B are energy density (kilocalorie per dry gram), and C and D are lipid content (percent per dry gram).

Tables

Table 1: Sea otter intake rates (in kilocalorie per minute of foraging), species diversity (H', Shannon Weiner Index), and dive statistics by recolonization zone and reproductive status/sex.

	n (bouts)	n (div
Recolonization zones (number of years occupied)	**Recolonization zones (number of years occupied)**	**Reco**
Zone 1 (> 30 years)	34	305
Zone 2 (> 15 years)	270	2864
Zone 3 (> 7 years)	58	354
Reproductive status/ sex	**Reproductive status/ sex**	**Repr**
Female no pup	37	484
Female with pup	75	849
Male	69	821

Table 2: Statistical comparison of sea otter prey groups with (A) season and (B) sex (for crabs only) as factors using analysis of similarity (ANOSIM). The R statistic ranges from near 0 (no difference between groups) and 1 (differences between groups) with bold numbers denoting significance ($p < 0.01$).

A. Season				
	Functional Prey Group	Energy R statistic	Lipid R statistic	Protein R statistic
	Clam	**0.300**	**0.213**	0.058

A. Season				
	Crab	0.077	0.024	0.133
	Sea Cucumber	**0.472**	**0.778**	0.267
	Sea Urchin	0.172	**0.404**	0.067
	Snail	-0.157	-0.158	0.096
B. Sex				
	Functional Prey Group	Energy R statistic	Lipid R statistic	Protein R statistic
	Crab	0.057	0.065	0.181

Table 3: Statistical pairwise comparisons of sea otter prey groups with season and sex (for crabs only) using analysis of similarity (ANOSIM). The R statistic ranges from near 0 (no difference between groups) and 1 (differences between groups) with bold numbers denoting significance ($p < 0.01$).

Functional Prey Group	Season	Season	Energy R statistic	Lipid R statistic	Protein R statistic
Clam	Spring	Summer	**0.470**	0.082	**0.125**
	Spring	Winter	**0.228**	**0.397**	0.034
	Summer	Winter	**0.117**	**0.117**	-0.018
Crab	Spring	Summer	0.021	0.069	0.155
	Spring	Winter	0.073	-0.102	-0.039
	Summer	Winter	0.150	-0.151	0.070
Sea Cucumber	Spring	Summer	**0.824**	0.536	0.624
	Spring	Winter	0.068	**0.672**	0.016
	Summer	Winter	0.472	**1.000**	0.156
Sea Urchin	Spring	Summer	0.133	0.426	-0.089
	Spring	Winter	0.380	0.270	0.052
	Summer	Winter	0.140	**0.410**	0.205