



Foraging ecology of southern sea otters at the northern range extent informs regional population dynamics

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ABSTRACT: Sea otters *Enhydra lutris* are vital keystone predators throughout the North Pacific that were nearly extirpated during the maritime fur trade. Recovery of southern sea otters *E. l. nereis* has proceeded slowly, with much of their historical range remaining unoccupied, resulting in reduced ecosystem functioning. Numerous studies have used foraging metrics to assess the population status of southern sea otters throughout their current range, but little is known about the northern range extent, where a stall in expansion has limited recovery. Thus, we collected census and foraging data of sea otters at Año Nuevo State Park, California, from 2019 to 2021 to determine sea otter abundance, diet composition, diet diversity, and average energy intake rate at the northern range edge. We then assessed regional population status by comparing values from Año Nuevo with previously collected data from other locations in California, including high-density, range center sites and low-density, range periphery sites. We found that sea otter density at Año Nuevo was greater than surrounding areas at the northern range periphery, and the average ($\pm 95\%$ CI) energy intake (9.51 ± 0.91 kcal min⁻¹) more closely resembled values observed at high-density sites. Further, dietary diversity (using the Shannon-Wiener index, H) was intermediate between previously studied high- and low-density populations ($H = 1.81$), with crabs making up the largest proportion of the diet (~56%). Overall, this study highlights possible effects of occupation time and range stagnation, identifies unique aspects of the prey resource base at Año Nuevo, and provides insight into the ongoing lack of northern range expansion.

KEY WORDS: *Enhydra lutris nereis* · Energy intake rates · Diet composition · Diet diversity · Population recovery · Population density · Año Nuevo

1. INTRODUCTION

Terrestrial and marine predator populations across the globe are endangered and declining, resulting in considerable ecosystem-level consequences (Ripple et al. 2014). Predator losses can allow herbivore populations to rapidly expand, decimating vegetation and disrupting community structure (Estes et al. 2011). Further, ecosystems without apex predators

incur biodiversity losses and decreased resilience to natural and anthropogenic disturbance (Estes et al. 2011, Ritchie et al. 2012). Thus, facilitation of predator recovery and reintroductions have increasingly been suggested as conservation tools to enhance regional biodiversity and restore ecosystem functioning (Ritchie & Johnson 2009, Ritchie et al. 2012, Barrios-O'Neill et al. 2017, Atwood & Hammill 2018, Alston et al. 2019, Davis et al. 2019). Understanding factors that

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limit or prevent natural recovery of predator populations into previously occupied habitat can be critical for effective management efforts.

Sea otters *Enhydra lutris* are keystone predators that profoundly influence nearshore marine ecosystems by exerting top-down control on community structure (Estes & Palmisano 1974). Through a myriad of direct and indirect effects, sea otters provide stability to coastal ecosystems by preying on herbivores and mid-level consumers, in turn promoting the health and persistence of kelp forest and seagrass habitats, which leads to increased primary productivity and greater biodiversity (Estes & Palmisano 1974, Duggins 1980, Duggins et al. 1989, Hughes et al. 2013, 2016, Smith et al. 2021). Thus, ensuring the presence and long-term viability of sea otter populations throughout their historical range can have numerous beneficial effects on coastal ecosystems, including enhanced resilience.

Sea otters once occupied coastal habitats throughout the North Pacific Ocean but were hunted to near extinction during the fur trade of the 18th and 19th centuries. Following federal protections, sea otters began to recover (Nichol 2015). However, recolonization and expansion from diminished remnant groups has been incomplete, resulting in a patchy and fragmented distribution (US Fish and Wildlife Service 2015, Davis et al. 2019). Specifically, southern sea otters *E. l. nereis* remain 'threatened' under the Endangered Species Act despite nearly a century of protection (US Fish and Wildlife Service 2015).

Southern sea otters remain far below the estimated optimum sustainable population, due in large part to their continued absence from much of their historical range (Laidre et al. 2001, Tinker et al. 2021). A number of multi-year studies have revealed that southern sea otters are likely at or near carrying capacity throughout the central portion of their range (Tinker et al. 2017, 2019, 2021). In contrast, range peripheries to the north and south are considered low-density areas (Hatfield et al. 2019), and provide the greatest opportunity for population growth and range expansion into historically occupied habitat (US Fish and Wildlife Service 2015, Tinker et al. 2021). While the southern range boundary has seen some seasonal expansion, with periods of contraction (Lafferty & Tinker 2014, Tinker et al. 2017), the northern range edge has contracted and stagnated since the early 2000s, affecting population recovery in this region as well as the overall rate of sea otter recovery in California (Hatfield et al. 2019).

There are a number of subpopulation-level metrics that can be used to inform issues facing southern sea otters. Several factors affect sea otter distribution and

density at small scales (i.e. 10s of km) including prey abundance, occupation time, habitat type (e.g. rocky bottom, kelp forest, soft sediment), substrate complexity, and rates of mortality (Nicholson et al. 2018, Tinker et al. 2021). Primary sources of mortality vary across the current range and include white shark *Carcharodon carcharias* predation, infectious disease, domoic acid intoxication, and end-lactation syndrome, among others (Miller et al. 2020). Prey availability is thought to be the most fundamental environmental factor influencing sea otter population growth (Kenyon 1969, Estes & Palmisano 1974, Riedman & Estes 1990, Monson et al. 2000, Tinker et al. 2008). When sea otters are faced with limited prey availability, subpopulations spend more time foraging, with lower rates of energy gain (Bodkin et al. 2007, Tinker et al. 2008, 2019, Thometz et al. 2016). Furthermore, diet diversity is often correlated with regional sea otter density. Low-density sites exhibit low diversity indices as preferred prey types are typically abundant, whereas high-density sites exhibit higher dietary diversity due to the depletion of preferred prey and inclusion of non-preferred prey types (Tinker et al. 2008, 2012, 2019, Newsome et al. 2015). In addition, longer occupation time in a specific region can lead to the gradual depletion of prey, resulting in lower energy intake rates and higher dietary diversity (Laidre & Jameson 2006, Tinker et al. 2008, 2019, Hale et al. 2019). Therefore, energy intake rates and diet diversity are commonly used metrics to assess local population status (Dean et al. 2002, Bodkin et al. 2003, Tinker et al. 2008, 2019, Thometz et al. 2016, Hale et al. 2019, Yee et al. 2020).

To provide a greater understanding of regional population status, foraging ecology, and prey resource availability at the northern range extent, we conducted an observational study of free-ranging southern sea otters at Año Nuevo State Park, California, USA (hereinafter Año Nuevo). The aims of this study were to (1) assess abundance and distribution of sea otters at Año Nuevo, (2) determine the diet composition and foraging behavior in this region, and (3) examine how foraging metrics at Año Nuevo compare to previously collected data from both high- and low-density sites in California. We hypothesized that, as a historically low-density range periphery site, the foraging metrics of sea otters at Año Nuevo would be comparable to previously studied low-density sites in California. Overall, this study provides insight into regional population dynamics at the current northern range periphery and elucidates potential factors limiting range expansion and recovery of this threatened keystone species.

2. MATERIALS AND METHODS

2.1. Study site

Año Nuevo is located about 80 km south of San Francisco and 30 km north of Santa Cruz along the California coast (Fig. 1). As sea otters recovered from near extirpation by recolonizing historical habitats, they were first observed at Año Nuevo in the mid-1980s, and this location remains the northernmost stronghold of the southern sea otter range (Riedman & Estes 1990, Tinker & Hatfield 2018). Sea otter abundance has remained low here for decades, although annual survey counts in the area have increased in recent years (Fig. A1 in the Appendix) from 20 individuals in 2012 to 53 individuals in 2019 (Tinker & Hatfield 2018, Hatfield et al. 2019). Sea otter habitat at Año Nuevo consists of a mix of subtidal soft sediment areas and rocky reef supporting kelp beds. The varied benthic substrate provides a diverse suite of prey including urchins, bivalves, crabs, worms, gastropods, sea stars, and episodically occurring prey (Riedman & Estes 1990, Laidre et al. 2001, Oftedal et al. 2007). Our study site included the mainland portions of Año Nuevo State Park as well as Año Nuevo Island, which is situated about 900 m from shore and creates a bight

of somewhat sheltered habitat between the mainland and the island, offering protection from offshore swells. Throughout this paper we will be referring to the 6.5 km long study site as Año Nuevo or ANO, which is situated in the northernmost 30 km segment of the current southern sea otter range. This broader northern portion of the range will often be referred to in this paper as the northern range extent, the northern range edge, or the north end of the range.

2.2. Regional census data collection

We collected monthly census data throughout the study area from January 2020 to March 2021 to assess the regional abundance of sea otters and to discern potential seasonal fluctuations in subpopulation size. Spatially explicit census data were also used to identify any differences in the distribution of resting and foraging areas for sea otters at Año Nuevo. All census data were collected with ArcGIS Collector (Esri) on an iPad (Apple). Observers recorded the number of otters (including pups, if present) at each location and their behavior (e.g. resting, foraging, grooming, traveling, or interacting), as well as the date and time, ocean conditions, and habitat type (e.g. in kelp can-

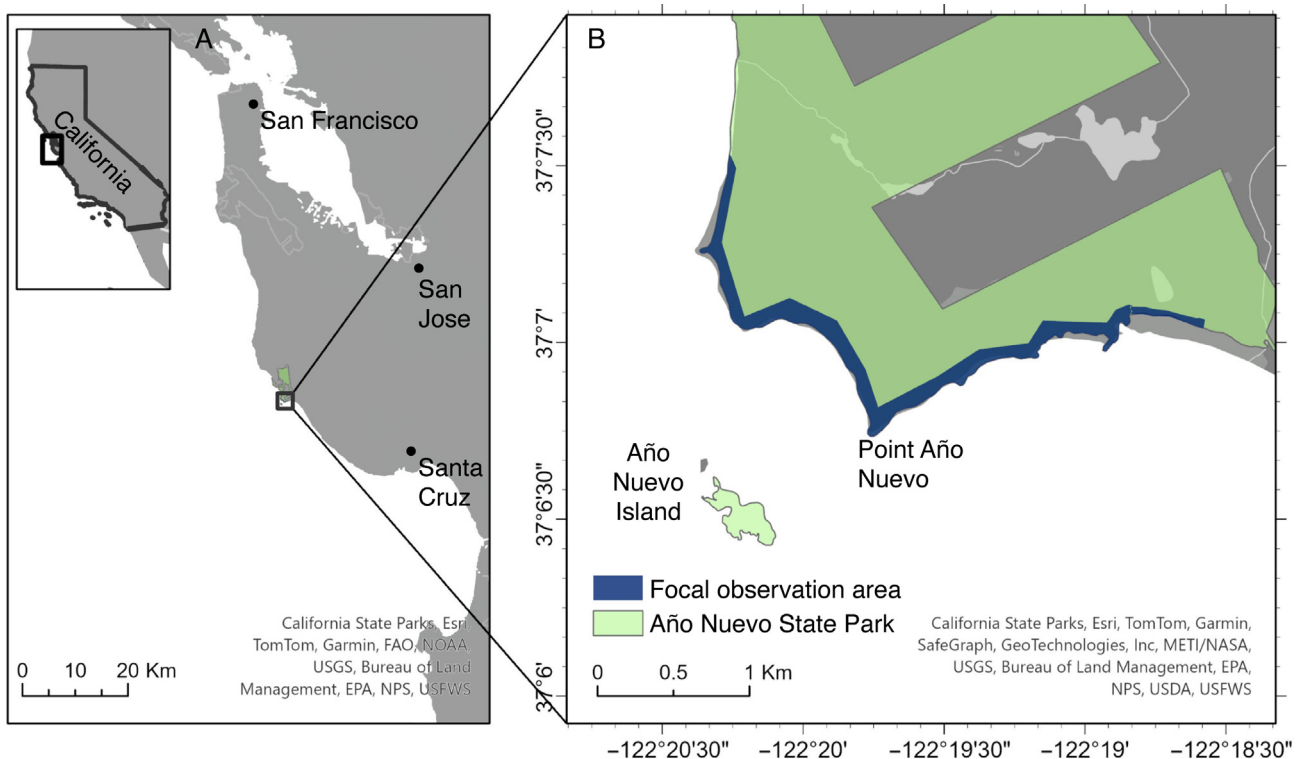


Fig. 1. (A) The study location at Año Nuevo State Park represents part of the current northern range of the southern sea otter. (B) Within the State Park, coastal areas were used for focal observations

opy, open water). Each month we selected 1 day on which to conduct a census based on the weather conditions, in which preferred days would have minimal wind and swell to maximize viewing capabilities. Surveys began at the northern end of the park at 08:00 h and concluded around 13:00 h at the southern end of the park. Survey conditions were given a rating of excellent, very good, good, fair, or poor depending on horizontal visibility, wind, swell/sea state, heat shimmer, etc. We excluded any surveys conducted during fair or poor viewing conditions from the calculation of average sea otter abundance due to reduced sea otter detectability, which would lead to an underestimate of abundance.

2.3. Density assessments

Regional sea otter density was determined for Año Nuevo as well as for 4 previously studied reference sites along the California coastline: Monterey (MON), Big Sur (BSR), Santa Barbara Channel (SBC), and San Nicolas Island (SNI). We calculated local sea otter abundance at Año Nuevo using average sea otter counts from 2020 to 2021. To calculate the regional population density of the wider north end of the range — which includes Año Nuevo plus 24 km of additional coastline — and for the 4 reference sites, we used publicly available U.S. Geological Survey (USGS) census data from annual sea otter surveys (Tinker & Hatfield 2018, Hatfield et al. 2019, Yee et al. 2020).

Given that foraging metrics are often density-dependent, census data were temporally associated with foraging data for each reference site (see Section 2.6). We determined sea otter density at each site from raw counts (Tinker & Hatfield 2018, Yee et al. 2020), then created 3 yr running averages for the number of sea otters in each 1 km section of coastline, and used a 10 km moving window to smooth the averages, similar to methods used in Hatfield et al. (2019). Sea otter density values for the north end of the range were obtained from Hatfield et al. (2019), as they were already converted to 10 km smoothed 3 yr running averages. We reported and compared the minimum and maximum values of these smoothed averages across the 4 reference sites, as well as at the north end of the range.

2.4. Geospatial data analyses

To determine local habitat use from census and foraging (see Sections 2.5 & 2.6) data, we conducted geospatial analyses in ArcGIS Pro 2.7 (Esri). In prepara-

tion for analyses, all monthly census data were merged and filtered by behavior to contain only locations where sea otters were resting, grooming, or interacting. These behavior types were selected to represent areas where sea otters rest, as grooming and interacting behaviors are often seen in or near resting rafts and are a prelude or conclusion to a resting period. In this spatial layer, we summed the total numbers of independents and pups observed at each point location across months to represent the cumulative distribution of resting locations of sea otters. For comparison, all foraging locations were similarly incorporated into a second feature layer. To provide a polygon structure for incident aggregation, we generated a tessellation layer using 5000 m² hexagons and then joined each point feature layer to the generated polygon layer. Finally, we used the Optimized Hot Spot Analysis tool, separately, for monthly census data and foraging data to examine statistically significant hot spots where sea otters were resting or foraging. The Optimized Hot Spot Analysis uses the Getis-Ord G_i^* statistic to automatically determine the scale of distance which best reveals hotspots based on analysis of incremental spatial autocorrelation (Getis & Ord 2010, ESRI 2020).

2.5. Foraging observations

We measured diet and foraging behavior of sea otters at Año Nuevo by following well-established protocols (Ralls et al. 1995, Estes et al. 2003b, Laidre & Jameson 2006, Tinker et al. 2008, 2019). Sea otters forage on benthic invertebrates in nearshore waters and bring prey to the surface to consume, allowing for direct observation (Estes & Palmisano 1974, Hughes et al. 2016). Observers opportunistically collected foraging data during daylight hours 1–3 d wk⁻¹ from October 2019 to March 2021, with a required pause in data collection from March to May 2020 due to Covid-19 restrictions at Año Nuevo. We used observation areas along the Año Nuevo coastline (Fig. 1B) to seek actively foraging sea otters. Observers collected foraging data any time a foraging sea otter was encountered within viewable range from shore (100–800 m) using a 50–80X Questar telescope.

Once observers found a foraging sea otter, they began recording its foraging bout, which is defined as a contiguous sequence of foraging dives (Tinker et al. 2019). Observers used a rangefinder (Bushnell), compass, handheld GPS (Garmin), thermo-anemometer, and stopwatch to record positional and environmental information for a foraging bout. Observers often

found an otter in the middle of a foraging bout and recorded as many dives as possible, or until the otter finished foraging or swam out of sight.

Information recorded during a bout included: date and time, precise dive location, duration of dive, duration of surface interval, dive success, prey species, number and size of prey item(s), handling time, presence or absence of tool use, proximity to kelp canopy, and the habitat where the otter was foraging. Observers also recorded any prey items that were obtained but not consumed by the focal otter, either due to pup-sharing or prey being stolen by a conspecific. Similarly, observers recorded whether the focal otter stole prey from a conspecific. Prey were identified to the lowest possible taxonomic level. Unidentifiable prey items were recorded as 'unknown'. Prey size was estimated from the maximum length or diameter of prey using its relative size compared to the sea otter's paw (average paw width is approximately 5 cm) and categorized into size classes. In addition, environmental conditions during each foraging bout were recorded.

2.6. Foraging data analysis

Sea otter foraging data were analyzed in MATLAB (MathWorks) to determine diet composition and average rates of energy intake using a Monte Carlo resampling algorithm designed to account for uncertainty and biases inherent in observation of sea otters from shore (Tinker et al. 2012). The Monte Carlo resampling algorithm estimates the mean rate of energy intake for the population using empirically derived and published taxa-specific caloric densities and functional relationships between prey size and edible biomass (Oftedal et al. 2007). Similar prey are combined and classified into 24 categories, corresponding to taxonomic groups termed 'prey types', in order to account for the inconsistencies in taxonomic resolution of different prey species (Oftedal et al. 2007, Tinker et al. 2008, 2012). Further, it uses maximum-likelihood methods to assign unidentified prey items to the most likely prey type based on its size and handling time. More information on the algorithm can be found in Tinker et al. (2012). Outcomes from the Monte Carlo procedure included diet composition as the proportion of consumed biomass of each prey type, diet diversity using prey biomass within the Shannon-Wiener index (H), and population-level mean rate of energy gain in kilocalories consumed per minute of feeding (Tinker et al. 2008, 2012).

Finally, we assessed whether diet composition at Año Nuevo differed from the diets of other previously studied subpopulations along the California coast. Comparable outcomes from the resampling algorithm were obtained from subpopulations in MON (1139 bouts from 2008–2012), BSR (439 bouts from 2008–2012), SBC (61 bouts from 2012–2014), and SNI (167 bouts from 2017–2020) (Tinker et al. 2017, 2019, Yee et al. 2020). To determine the influence of study location on diet composition, we used permutational multivariate analysis of variance (PERMANOVA) in R version 3.6.1 (R Core Team 2020) with the 'adonis' function in the 'vegan' package version 2.5-7 (Oksanen et al. 2020). The central latitude of study sites was used as the predictor variable, and we calculated assemblage dissimilarity using Bray-Curtis distances, with 119 permutations.

3. RESULTS

Sea otter abundance and distribution at Año Nuevo was determined from 10 monthly census counts conducted across the study period. We were not able to survey the entire population in some months due to a combination of poor weather conditions (August 2020) and periodic Covid-19 restrictions (March, April, and May 2020). The average (\pm SD) abundance at Año Nuevo was 69.1 ± 13.3 sea otters, including pups, and varied by season, with higher counts typically in the fall and lower in winter (Table A1). One month of data (February 2020) was excluded from this average due to substandard viewing conditions. Resting areas generally overlapped with established kelp beds (Fig. 2A). Indeed, sea otters were found resting in kelp beds 93% of the time, compared to only 7% of the time in open water. Foraging hot spots were clustered nearshore and fit closely to the shoreline (Fig. 2B). Although there may have been foraging locations farther offshore than those identified in the hot spot analysis, these would have been difficult to identify due to inherent limitations of observing untagged sea otters from shore. And even though there were distinct areas where individuals tended to rest and forage, there were also areas where both behavior types occurred.

Sea otter density estimates varied among sites, as well as between different segments of coastline within each site (Fig. 3). The comparatively small study area (along 6.5 km linear coastline) of Año Nuevo had an average density of 10.63 sea otters per km of coastline. At the broader northern end of the range (30 km) that includes Año Nuevo, the 3 yr averages smoothed to the 10 km scale exhibited densities from 0 to 4.86

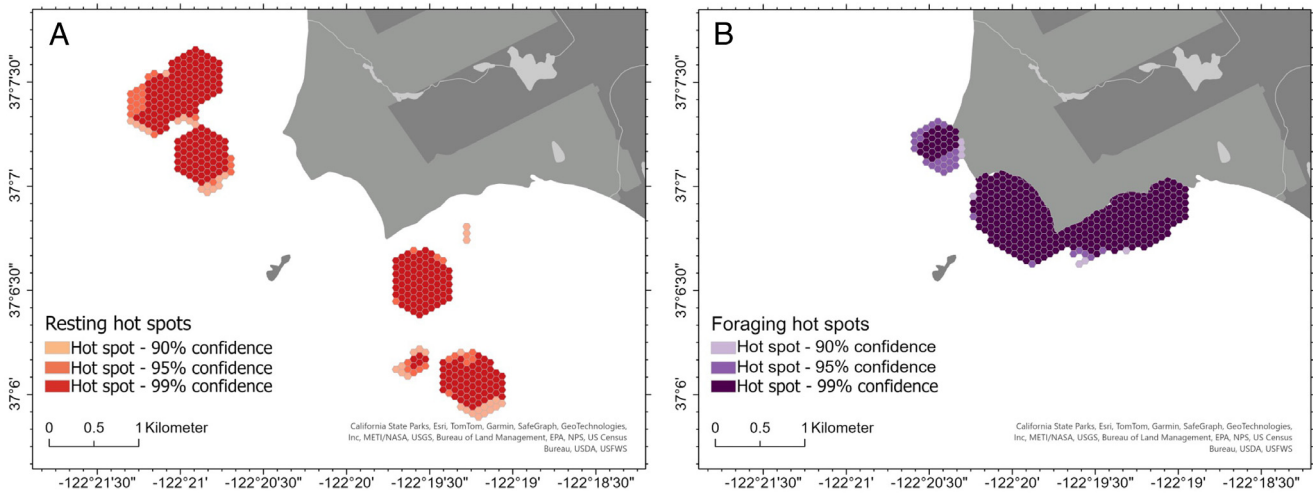


Fig. 2. Sea otter census and foraging data show behavior-specific high-use regions throughout the study area. Based on Optimized Hot Spot Analysis, sea otter preferred (A) resting and (B) foraging hot spots are highlighted with deeper colors representing higher confidence levels. Although foraging hotspots fit closely to the shoreline, potential offshore foraging hotspots may have been missed due to inherent limitations of observing untagged sea otters from shore

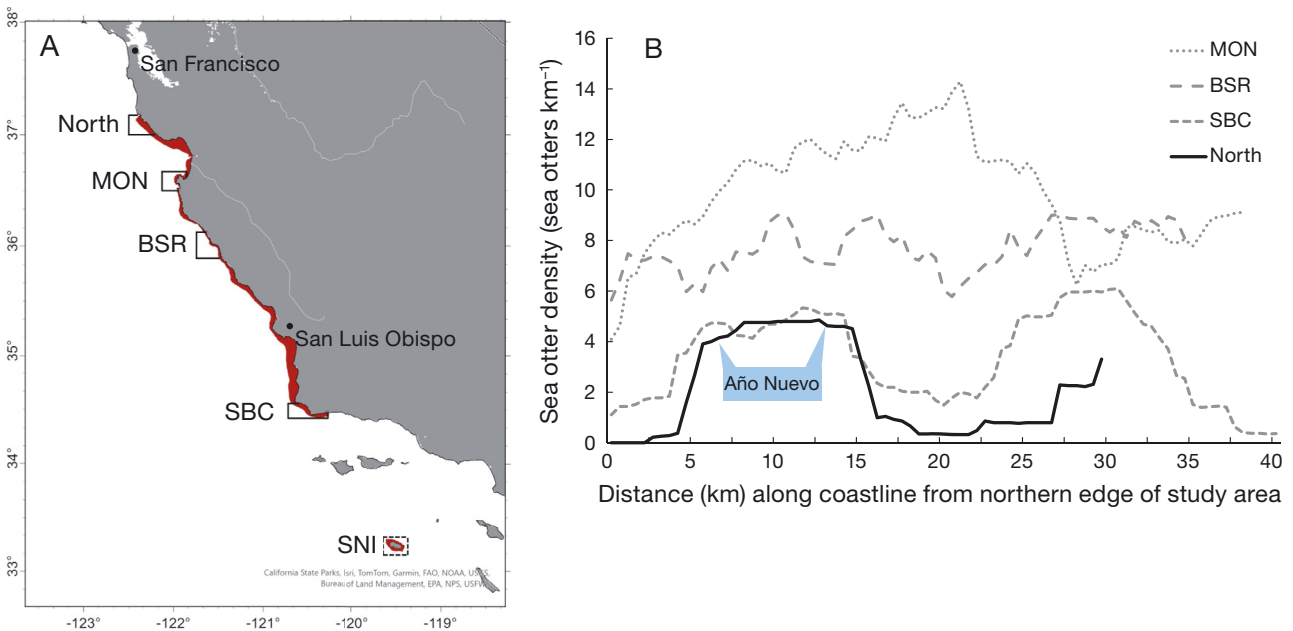


Fig. 3. Spatially explicit sea otter density along the coastline reveals that the highest density of sea otters in the north occurs at Año Nuevo; other sites are shown for comparison. (A) The current sea otter range in California is shown in red, with black boxes bounding the linear distance of the northern range edge (North) and each reference site (Monterey [MON; 2008–2012], Big Sur [BSR; 2008–2012], and Santa Barbara Channel [SBC; 2012–2014]) featured in (B). San Nicolas Island (SNI; 2017–2020; dashed box) was excluded from (B) because spatially explicit sea otter counts within 1 km segments of shoreline are not published. (B) Linear distribution of sea otter density at the northern range extent compared with 3 reference sites. Site-specific density data obtained from Tinker & Hatfield (2018) and Hatfield et al. (2019). Horizontal axis is a linear representation of the coastline of each study area, 30–40 km in length, with 0 being the northern edge. Sea otter density was spatially smoothed using 3 yr averages across a moving 10 km window. The Año Nuevo study site is marked, where local foraging and abundance data were collected for this study, within a longer 30 km stretch at the northern range edge included for comparison with the longer coastlines representing the reference sites

sea otters per km of coastline. By comparison, the 2 reference sites at the center of the sea otter range in the central coast had consistently larger smoothed densities over longer sections of coastline (Fig. 3).

MON had smoothed densities between 4.10 and 14.29 sea otters per km of coastline. BSR had smoothed densities from 5.64 to 9.05 sea otters per km of coastline. The other mainland reference site in southern

California, SBC, had lower densities and greater variation over similar distances. Here, sea otter smoothed densities ranged between 0.35 and 6.10 sea otters per km of coastline. The relatively isolated subpopulation at SNI had lower smoothed densities from 1.63 to 3.85 sea otters per km of coastline.

Foraging records at Año Nuevo consisted of 2957 foraging dives over 124 bouts. The average sea otter diet at Año Nuevo consisted of prey types from both sandy-bottom and rocky reef habitats, indicative of the mixed substrate habitat found there. Results from the resampling algorithm revealed the diet composition (% average \pm SD) of Año Nuevo sea otters included: cancer crabs (family Cancridae) ($37.5 \pm 2.8\%$), urchins ($18.0 \pm 1.3\%$), clams ($12.1 \pm 1.1\%$), kelp crabs ($11.5 \pm 0.9\%$), unidentified crabs ($7.5 \pm 0.6\%$), worms ($6.5 \pm 0.6\%$), abalone ($3.5 \pm 1.5\%$), snails ($2.0 \pm 0.3\%$), mussels ($1.4 \pm 0.3\%$), and sea stars ($0.02 \pm 0.02\%$) (Fig. 4). When combined, all groups of crabs (e.g. cancer crabs, kelp crabs, and unidentified crabs) comprised about 56% of the sea otter diet at Año Nuevo. Diet diversity, calculated using the Shannon-Wiener index, was 1.81. Over the course of the study, the average ($\pm 95\%$ CI) rate of energy intake was 9.51 ± 0.91 kcal min^{-1} . Average (\pm SD) dive and surface

interval times were 51.28 ± 24 s and 31.79 ± 37 s, respectively. Multivariate analysis further confirmed that sea otter diet composition varied among study sites (ANO, MON, BSR, SBC, SNI), as site latitude was significant in explaining the dissimilarity in sea otter diet composition (PERMANOVA pseudo- $F = 3.85$, $df = 1,3$; $p = 0.042$).

4. DISCUSSION

4.1. Foraging behavior and population dynamics

Our investigation of southern sea otters at their northern range extent provides foundational data pertaining to the regional status and foraging behavior of a previously understudied segment of the population. We found a recent increase in sea otter abundance and higher than expected sea otter density at Año Nuevo. Yet, energy intake rates indicate that prey resources may be somewhat limiting and could restrict further population growth. Overall, the foraging metrics reported for Año Nuevo sea otters generally compared more closely to high-density subpopulations than low-density subpopulations, highlighting the impact of

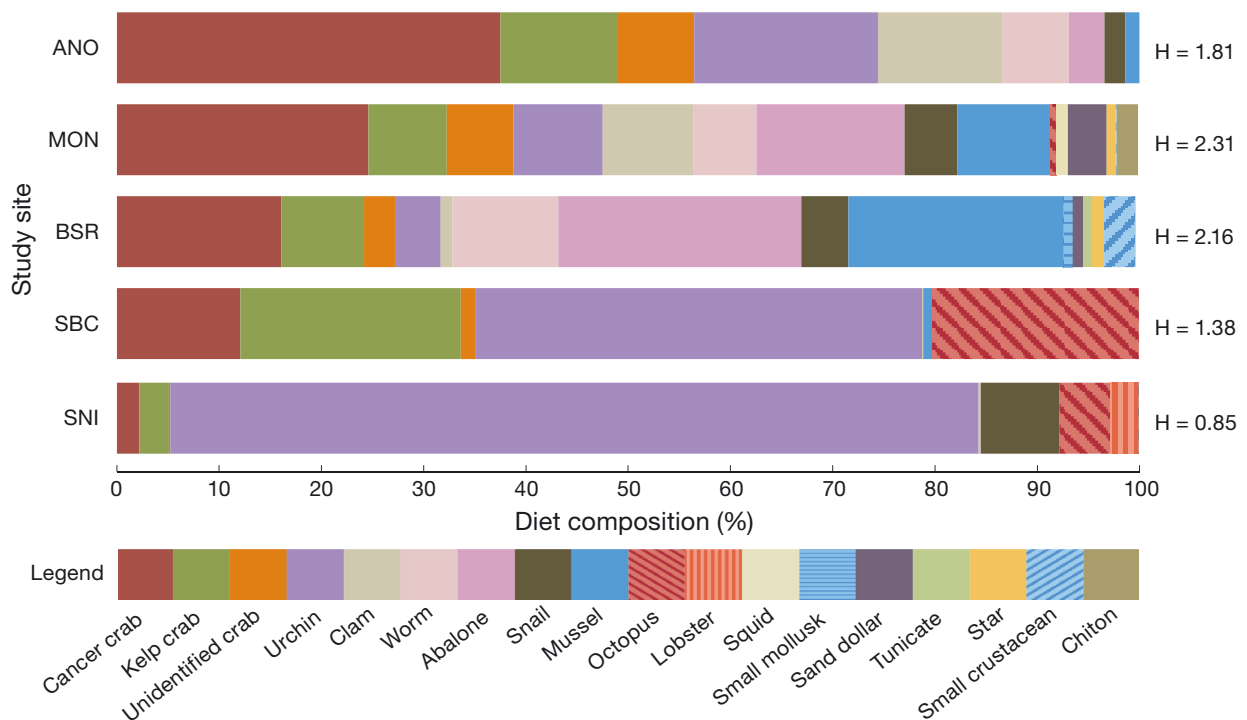


Fig. 4. Site-specific diet composition and diversity data exemplify regional differences in sea otter foraging behavior along the California coast. Sites displayed north to south: Año Nuevo (ANO; present study), MON, BSR, SBC, and SNI (see Fig. 3 for site abbreviations and study years). Site-specific diet data obtained from Tinker et al. (2017, 2019) and Yee et al. (2020). Length of each bar represents 100% of the diet at each site, with banded colors representing the relative proportion of each prey type in the diet. Shannon-Wiener index (H) values provided as a quantitative metric of diet diversity across sites

range stagnation and a lengthy occupation time at the current northern range extent.

Annual surveys conducted by USGS at Año Nuevo indicated a rise in regional abundance over the last decade (Fig. A1). The annual growth rate at Año Nuevo during our study (2019–2021) was 14.35%, which is typical of annual rates of growth observed over 10 yr at this site (mean growth: 12.9%; 95% CI: 5–22%; Fig. A1). Data from our study revealed a record high average of 69.1 individuals at Año Nuevo (Table A1). More broadly, the northern 30 km of the sea otter range had a positive 5 yr growth rate of 9.4% between 2015 and 2019 (Hatfield et al. 2019), with much of that growth driven by Año Nuevo (Fig. 3). Although some southern sea otter subpopulations have experienced growth rates up to 19% (Lafferty & Tinker 2014), California-wide sea otter growth rates have rarely exceeded 5% yr⁻¹ (Estes 1990, Estes et al. 2003a, Hatfield et al. 2019). This rapid rise in abundance at Año Nuevo could be the result of traveling sea otters seeking new resources, reaching the range end, and settling at this site, or it may be driven by intrinsic growth. The growth documented at Año Nuevo coincided with an increase in sea otter survivorship and abundance observed in the central portion of the range (Hatfield et al. 2019, Smith et al. 2021), which could have provided a source pool of migrants. Regardless of cause, the recent and relatively rapid increase at Año Nuevo may have put pressure on a small region of prey resources and likely affected the foraging metrics reported here.

Generally, recently occupied, low-density, and/or rapidly growing subpopulations with abundant resources have energy intake rates between 12 and 20 kcal min⁻¹ (Tinker et al. 2019). For example, SNI (2017–2020) sea otters had energy intake rates between 15 and 19 kcal min⁻¹, where prey were abundant and the subpopulation was well below carrying capacity (Fig. 5) (Yee et al. 2020). In comparison, long-established, high-density, and/or slowly growing subpopulations at resource-limited sites are typically characterized by energy intake rates <10 kcal min⁻¹ (Tinker et al. 2019). MON (2008–2012) and BSR (2008–2012) subpopulations had energy intake rates between 9.0–11.3 and 6.1–9.7 kcal min⁻¹, respectively, characteristic of resource-limited areas (Fig. 5) (Tinker et al. 2019). The average ($\pm 95\%$ CI) rate of energy intake observed at Año Nuevo (9.51 ± 0.91 kcal min⁻¹) falls close to the commonly recognized threshold value of 10 kcal min⁻¹ for resource-limited designation (Fig. 5). Their relatively low energy intake rate was unexpected for a range periphery site which was previously considered low-density; however, we found that sea otter density at Año Nuevo

was higher than surrounding areas in the northern segment of the sea otter range. Further, the prolonged occupation time of sea otters in this region may be contributing to observed energy intake rates.

Our work revealed that the diet diversity at Año Nuevo was intermediate to previously studied high- and low-density sites in California, with considerable differences in diet composition by location (Fig. 4). Sea otter diets in MON and BSR, both high-density sea otter sites, were similar in their diverse assemblage of prey types in the diet ($H_{\text{MON}} = 2.31$; $H_{\text{BSR}} = 2.16$) (Tinker et al. 2017, 2019). In contrast, sea otter diets at SBC and SNI, both low-density sea otter sites, were similar in that a few prey types dominated the diet composition, resulting in low diversity indices ($H_{\text{SBC}} = 1.38$; $H_{\text{SNI}} = 0.85$) (Tinker et al. 2017, Yee et al. 2020). Año Nuevo's dietary diversity ($H_{\text{ANO}} = 1.81$) was intermediate between these previously studied locations (Fig. 4). Although the typical diet at Año Nuevo was primarily composed of crabs and urchins, it also included cryptic/burrowed species such as clams, infaunal worms, and abalone as well as mussels and snails (Kvitek & Oliver 1988). This indicates that sea otters are incorporating non-preferential prey into their diet, as preferred prey may be limited (Tinker et al. 2008, 2012). Thus, our foraging data indicate that prey resources at Año Nuevo may not be as abundant as at southern range periphery sites (i.e. SBC, SNI).

The high prevalence of crabs in the sea otter diet at Año Nuevo (>56%) was unique compared to prior for-

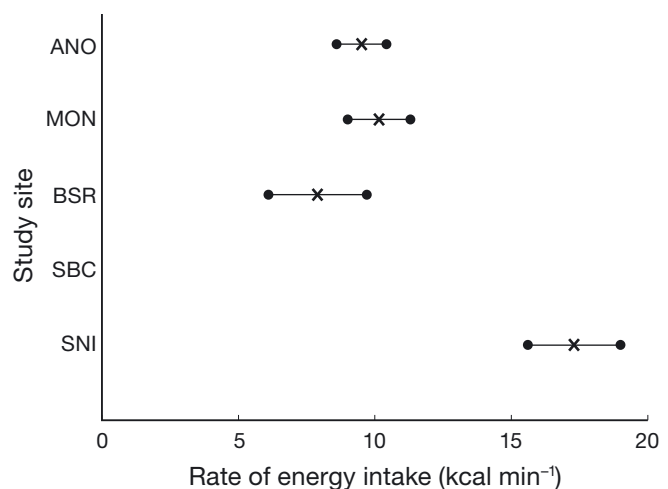


Fig. 5. Energy intake rates for sea otters at ANO relative to sea otters at previously studied high-density (MON; BSR) and low-density (SNI) sites (see Figs. 3 & 4 for site abbreviations; see Fig. 4 for references). Sites arranged north (top) to south (bottom). The range in energy intake for each site shows the 95% CI, with 'x' representing the mean. Energy intake data not available for SBC

aging studies. Between 2000 and 2011, crabs only comprised about 25% of the average sea otter diet across California subpopulations (Fujii et al. 2015). Elkhorn Slough, an estuary in Central California, is the only other subpopulation to have had a similar proportion of crabs in the diet. There, crabs comprised 43% of the average diet during a period of recolonization between 1999 and 2012 (Hughes et al. 2013). However, as the subpopulation in Elkhorn Slough stabilized between 2013 and 2016, the total proportion of crabs in the diet fell to 18.7% (Boustany et al. 2021). Similarly, soft-sediment habitats in Southeast Alaska during the early stages of sea otter recolonization experienced substantial depletion in Dungeness crab (*Metacarcinus magister*) density (Hoyt 2015). Across habitats and regions, crabs are a preferred prey source and often among the most abundant prey in the sea otter diet during recolonization. Yet, sea otters at Año Nuevo continue to recover crab species at high rates despite their relatively long occupation time. Unfortunately, we lack crab abundance and recruitment data specific to Año Nuevo that might be able to provide more insight into this issue.

4.2. Environmental considerations

In addition to prey abundance and composition, there are other environmental factors that contribute to the population trends observed at Año Nuevo, but were not directly examined in our study. Over the past decade, the leading cause of death across the southern sea otter range has been non-consumptive white shark bites, and this source of mortality has been most prevalent at the range peripheries (Tinker et al. 2016, Nicholson et al. 2018, Miller et al. 2020). Thus, white shark-related mortality is a significant factor limiting range expansion and a major obstacle for species recovery. In particular, Año Nuevo is a known white shark feeding ground with an established pinniped rookery that has experienced recent increases in white shark density (Jorgensen et al. 2019). Further, Año Nuevo is a mixed-sediment benthic habitat on the outer coast, which generally supports lower densities of sea otters than rocky habitats on the outer coast, due to the highly variable productivity of epibenthic prey communities (Tinker et al. 2021). Finally, sea otters along the outer coast of California (excluding estuaries) depend on canopy-forming kelp for resting, associated prey, and protection from predators (Ralls & Siniff 1990, Riedman & Estes 1990). Thus, formation and resilience of kelp canopies along the coast are crucial for survival, reproduction,

and consequently population growth (Nicholson et al. 2018). In particular, kelp-sparse regions correspond with increased rates of mortality from white sharks in California (Nicholson et al. 2018).

Individuals at Año Nuevo followed species-wide tendencies to aggregate in kelp-forested areas (Fig. 2). However, kelp canopy formation immediately north of Año Nuevo has remained sparse since kelp surveys began in 2002 (California Department of Fish & Wildlife — Marine Region 2016). The structure of the coastline around Año Nuevo consists of an offshore island and point (Point Año Nuevo) that protects Año Nuevo Cove from predominant northwest wind and swell, perhaps facilitating kelp canopy persistence in this area relative to exposed coastlines to the north (Fig. 1). The persistent absence of kelp north of Año Nuevo is likely playing a role in the stagnation in the current range boundary. Indeed, given the presence of white sharks in this area (Jorgensen et al. 2019) and the lack of kelp canopy to the north, pioneering sea otters attempting to travel northward in search of food or new territory may be quickly met with the reality of minimal resting habitat and increased risk of fatal interactions with white sharks (Moxley et al. 2019). Año Nuevo sea otters may be residing within a regionally 'safe' zone just inside the current range boundaries where kelp canopy may still be found.

4.3. Sea otter recovery in California

Limitations in sea otter recovery constrain the broader ecosystem benefits that sea otters provide as keystone predators (Kenyon 1969, Estes & Palmisano 1974, Estes et al. 2011, Davis et al. 2019, Moxley et al. 2019). Re-establishment of southern sea otters to their former range should facilitate increased resilience and stability of Northern California kelp forests and estuaries in the face of anthropogenic stressors and environmental change. This is an important consideration for species recovery, as these ecosystems provide habitat for many ecologically and commercially valuable species, support biodiversity, help mitigate the effects of ocean acidification, and dampen wave action, which will become increasingly beneficial as climate change intensifies (Duggins et al. 1990, Steneck et al. 2002, Hughes et al. 2019, Murie & Bourdeau 2020).

Ultimately, our study provides novel information pertaining to an important segment of the southern sea otter population. By filling key data gaps, our work can inform management efforts for an important keystone predator. It has been well documented that

fatal white shark bites on sea otters, particularly at the range peripheries, are currently a major factor limiting range expansion and population growth (Tinker et al. 2016, Nicholson et al. 2018, Moxley et al. 2019). The data presented here reveal higher than expected sea otter densities at Año Nuevo and a lower rate of energy intake than initially predicted. Across numerous foraging metrics, Año Nuevo aligned more closely with previously studied high-density sea otter subpopulations, indicating a possible effect of prolonged occupation time and range stagnation on the prey resource base in this region. More broadly, the absence of persistent kelp canopies north of Año Nuevo limits available high-quality habitat for natural, incremental expansion, exposes sea otters to a greater risk of white shark-related mortality, and limits the suite of available prey items beyond the current range. All of these factors are likely contributing to the stagnation in population growth and expansion at the northern range periphery.

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Appendix

Table A1. Monthly sea otter survey results at Año Nuevo from January 2020 to March 2021. Averages calculated using the total number of independents and pups. Viewing conditions were scored as excellent, very good, good, fair, or poor

Month year	Independents	Large pup	Small pup	Total	Viewing conditions
Jan 2020	51	1	3	55	Very good
Feb 2020	20	1	1	22	Fair
Jun 2020	62	1	1	64	Very good
Jul 2020	68	2	2	72	Good
Sep 2020	84	0	4	88	Good
Oct 2020	77	3	1	81	Good
Nov 2020	77	4	6	87	Good
Dec 2020	43	1	5	49	Good
Jan 2021	68	1	4	73	Very good
Feb 2021	57	3	1	61	Excellent
Mar 2021	54	5	2	61	Excellent
Raw average				64.8	
Average excluding fair viewing conditions \pm SD				69.1 \pm 13.3	

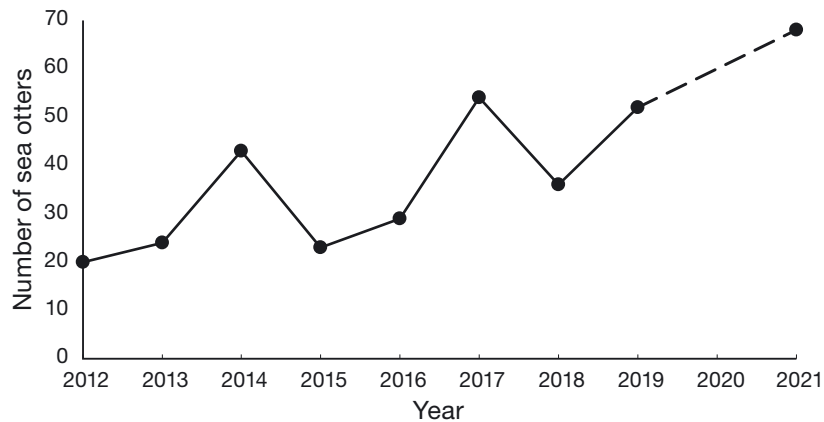


Fig. A1. Total number of sea otters (including adults and pups) counted surrounding Año Nuevo from 2012 to 2021 during the USGS annual statewide southern sea otter census (USGS unpubl. data). The count data presented here comprise a southward shifted segment of coastline (i.e. from 37.1173° N, 122.3368° W south to 37.1023° N, 122.2856° W) than was covered during our foraging study (from 37.1266° N, 122.3368° W to 37.1117° N, 122.3000° W); therefore, counts may differ slightly from our findings. Data presented here depict an overall increase in sea otter abundance in the northern part of the southern sea otter range including and adjacent to Año Nuevo. A statewide census was not conducted in 2020, thus that value is intentionally excluded and the change in abundance from 2019 to 2021 is noted by a dashed line

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