Sea otters are recolonizing southern California in fits and starts

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Abstract.   After near extinction as a result of the fur trade in the 1700s and 1800s, the southern sea otter slowly reoccupied the core of its range in central California. Range expansion beyond central California is seen as key to full recovery of otters, but the rate of expansion has been sporadic, raising concerns about habitat quality in southern California. To describe the range expansion of sea otters from central into southern California, we used skiff surveys, aerial surveys, and archival time-depth recorders from 2004 to 2013. These observations show that range expansion began when male otters swam southeast of Point Conception (Cojo Anchorage), perhaps to seek refuge from bad weather and to feed on unexploited resources. After several years of seasonal use by male groups, females began to use the area, leading to reproduction and a secondary increase in abundance. In contrast, a second male group that moved farther down the coast to Coal Oil Point stalled and retreated. Such range expansion and contraction can be explained by the social nature of sea otters, which acts to slow dispersal away from groups. Otter densities at Cojo Anchorage are now approaching equilibrium levels reported for central California. As in central California, otters rested in and near kelp forest habitat, but used deeper water for foraging. Together, these observations suggest habitat in the Santa Barbara Channel can still support sea otters, but range expansion of otters into southern California will be episodic due to social dynamics.

Key words: Allee effect; conservation; endangered species; *Enhydra lutris nereis*; keystone species; southern California; spread.

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INTRODUCTION

Range expansions require pioneers. But pioneering is a lonely endeavor, and this might constrain how social species colonize new locations. Although diffusion models (e.g., Lensink 1997) can account for physical barriers and variation in habitat, they don't capture how dispersal differs with age, sex, or social structure. A case in point is the California sea otter (*Enhydra lutris nereis*). Southern sea otters numbered between 15,000–20,000 in California before the 18th century north Pacific fur harvest (Kenyon 1969, Laidre et al. 2001). But by the 1900s, only a few dozen sea otters remained in California. California sea otters were listed as "Threatened" in 1977 and have recolonized the central part of their former range (Kenyon 1969), where they now number around 2,900 (www.werc.usgs.gov/seaottercount). Although mathematical models have predicted a continuous, linear rate of range expansion into southern California (Lubina and

Levin 1988, Tinker et al. 2008b), expansion has been sporadic and population growth has stalled just shy of the 3,090 threshold abundance required for delisting (USFWS 2012).

Sea otter abundance in central California now appears to be limited by food and shelter (Tinker et al. 2006a, Tinker et al. 2008a). Almost all California sea otters feed and rest in and around central California's productive kelp forests (Riedman and Estes 1990). Kelp forests form over rocky habitat where otters dive for abalone, rock crabs, sea urchins, kelp crabs, clams, turban snails, mussels, octopus, barnacles, scallops, sea stars, and chitons (Tinker et al. 2008a). Although foraging otters can dive to 100 m (Bodkin et al. 2004), most dives in California go to depths of 40 m or less (Riedman and Estes 1990, Ralls et al. 1995, Tinker et al. 2006b), limiting available foraging habitat to the nearshore. In addition to containing food for otters, kelp forests shelter otters from wind, currents, and predators like great white sharks (Ames and Morejohn 1980).

Because competition for resources limits sea otter abundance within the current central California range, it is clear that recovery of the southern sea otter will require range expansion to the north or south or both. Re-colonization into southern California could allow otter numbers to reach 16,000 individuals if the new habitat supports densities as high as central California (Laidre et al. 2001). There are some reasons to expect that habitat in southern California might be poorer than central California; human densities are higher in southern California, which corresponds to more disturbance and pollution, and depleted prey resources. Furthermore, southern California has warmer water, different and novel prey types, and lower oceanic productivity compared to central California. Nonetheless, range expansion remains a critical requirement for population recovery. Despite its importance, several aspects of range expansion in California sea otters have not been described, including the population growth rate in frontal areas, habitat-use patterns, and the shift from population dynamics driven by immigration to that driven by local reproduction and survival.

For several years, the US Fish and Wildlife Service (USFWS) hoped to direct the southern expansion of sea otters in a way that would lead to recovery while minimizing competition be-

tween sea otters and commercial and recreational fisheries. The USFWS translocated otters to distant San Nicolas Island in 1987, and, as mitigation, created a no-otter" management zone south of Point Conception (USFWS 2003). Point Conception divides central from southern California and forms a bend in the coastline from west facing to south facing (Fig. 1). South of Point Conception, the coastline has reduced wave energy, increased giant kelp persistence, and represents a shift from the cold Oregonian marine province to the warmer San Diego marine province (Reed et al. 2011). For many years, the few otters that swam south of Point Conception into the "no-otter" management zone were removed and transported back to central California. But in 1998, before our study, a raft of 93 male sea otters was seen in the Cojo Anchorage just south of Point Conception (USFWS 2003). This raft was too large to remove, and most otters swam back to central California in the summers. In subsequent years, otters were sometimes seen south of Point Conception, but their appearances were episodic, and the small groups were males that might be seeking temporary refuge behind the headland from strong winds.

We used repeated surveys to find and count sea otters in the Cojo Anchorage area, to describe the patterns of population re-colonization, and to define their habitat associations in this new biogeographic region. Specifically, we asked whether the otter population was persistent, expanding in abundance, expanding in distribution, and whether seasonal or inter-annual variation explained variation in numbers. We also asked whether otters were associated with depth, kelp canopy, bottom type, and bottom topography. We used archival data from time-depth recorders implanted in tagged sea otters to compare dive depths with resting depths. As we report below, sea otters increased in the study area and had habitat associations, diving patterns, and local densities similar to that observed in central California.

Methods

Beginning in April 2004, we surveyed sea otter abundance and distribution from a 17' open hull skiff at intervals from one to several months. Survey frequency depended on boat access and weather. A one-year gap in skiff surveys began in
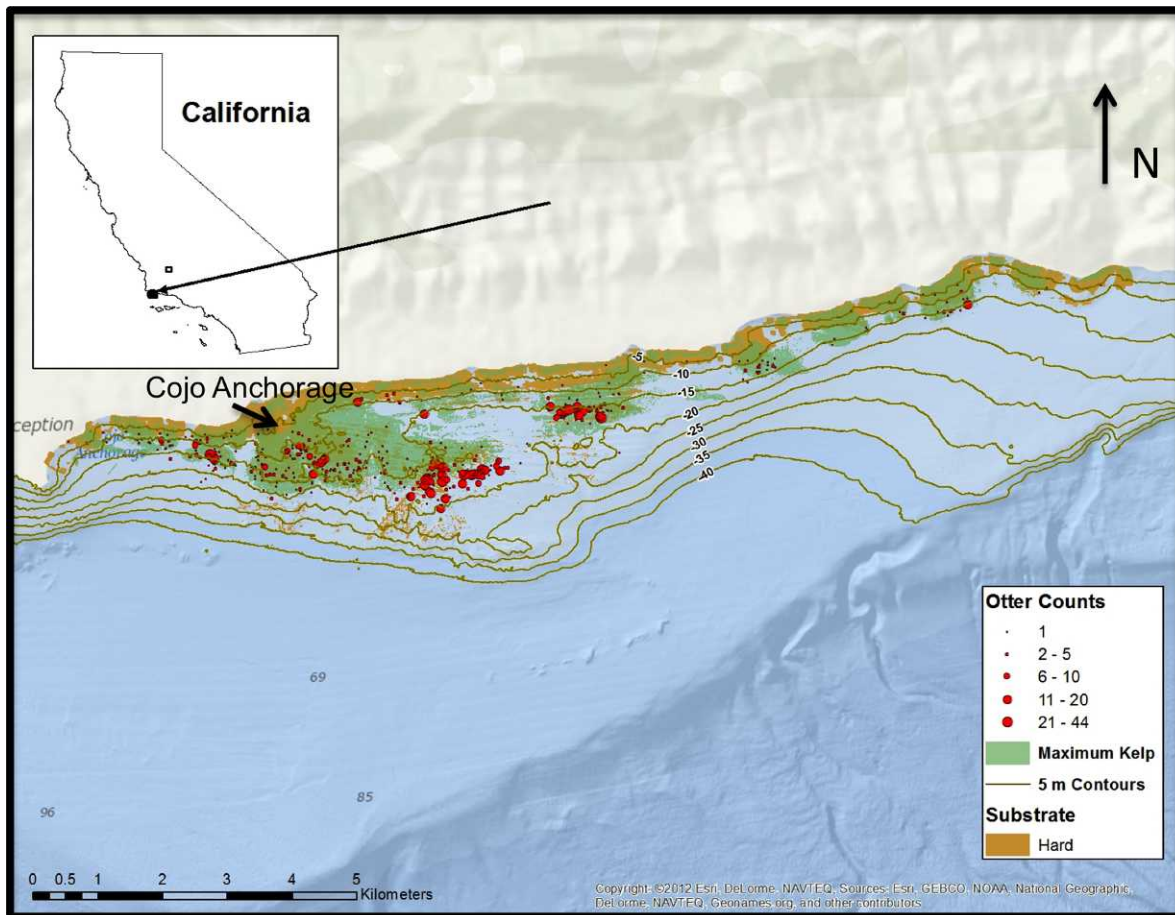
Fig. 1. Map of the study area, showing the coastline just to the southeast of Point Conception, California (which lies 1 km east of the map boundary). The combined locations of sea otter observations are plotted (dark/red circles, scaled to group size), along with the maximum coverage of kelp canopy (light/green shading), bathymetric contours (dark/brown lines), the distribution of hard benthic substrates (dark/brown shading), and the perimeter of the study area for resting otters (thick/yellow line).

September 2005 due to the loss of the survey vessel. Otters were counted by skiff between noon and 15:00, when otters are least likely to be under water (Tinker et al. 2006b). Starting at Government Point (just east of Point Conception), the survey crew cruised (<5 knots) around the kelp-bed edge while trending east toward Gaviota Pier, scanning the beds with binoculars. The observer was always the same person, while the skiff driver and usually a scribe recorded observations and GPS coordinates. Starting in June 2008, we counted other marine mammals and birds using the survey area. The observer's position was determined with a GPS when we sighted an otter or otter group. The observer then estimated the distances in m along the cardinal axes to the point that the otter was first seen. The goal was to map otters with at least 30-m accuracy. Sea otters were often in groups ("rafts") within a 15-m radius. In such cases, we assigned all otters in the group to a central point.

There were three potential count errors: double counts, missed otters, or a pinniped mistaken for an otter. We could have double counted when otters moved from one course of the boat to another, but we knew this was possible and did not count otters that seemed likely to have moved from a previously surveyed spot. Otters are easy to see and spend a lot of time resting at the surface. Because we might have missed some

otters if they were underwater or inside large kelp beds, and therefore far from counting routes, we carefully scanned open water areas and large kelp beds. From a distance, harbor seals wrapped in kelp can appear like sea otters, however careful examination by an experienced observer using binoculars reduced mistaken identities. Back-to-back counts in 2011 found 63 otters on 12 July and 62 otters on 14 July, suggesting that our methods were consistent.

We surveyed by skiff only in good weather, and this could mean that we missed temporary weather-related shifts in otter movements. A second data set on trends in sea otter abundance within the study area was available from the twice-annual aerial counts flown by the U.S. Geological Survey and the California Department of Fish and Wildlife (www.werc.usgs.gov/seaottercount). These data, although much less frequent than the skiff counts, were not as dependent on weather, and were used to compare with the skiff count data. A third independent data set on periodic sea otter sightings in select kelp beds between Pt. Conception and Santa Barbara was available from the Santa Barbara Coastal Long Term Ecological Research (LTER) Program (Reed et al. 2012). For these data we report the proportion of dates that otters were observed at eight index LTER sampling sites, and the mean number of otters observed on those dates when otters were present.

To test for long-term trends in sea otter abundance within the study area, counts were first averaged by month (to smooth out the sampling error), and we fit an exponential growth model $\log(N_t) = \log(N_0) + r*(t/12)$ to the data using maximum likelihood methods. Although the time steps in the fitted model were months, by convention we express the parameter of interest, r (the instantaneous rate of growth), in years. To test for cyclical trends in abundance, the spectral density of the time series was also analyzed and plotted as a periodogram of the absolute value of the Fast Fourier Transform (scaled such that variance equals the mean of the transform). Peaks in spectral density with value >2 were identified from the periodogram.

To analyze the habitat variables associated with observed sea otters, we constructed polygons bounded by the western- and eastern-most

sea otters and ranging from the shore on the north to the 30-m depth contours on the south (representing 1488 sea otter observations within 3125 ha, long axis = 17 km, short axis = 2.3 km) (Fig. 1). Bottom habitat within this area was around 25% rock. Water depth in the polygon was 11% 0–5 m, 56% 6–20 m, and 33% 20–30 m. Within the polygon, we chose 450 random points to represent a random sample of the habitat variables. From each point (observation or random), we took several habitat measures. We did similar exercises at the 40-m contour to compare densities with Central California and with the 60-m contour to compare with diving depths.

To chart the water depth below the observation point, we used 2-m resolution bathymetry data from the California Seafloor Mapping Project at California State University at Monterey Bay (CSUMB). This dataset goes close enough to the shoreline to cover almost all the otter observations, but there were some gaps near shore that we filled using a second dataset from NOAA (with a 10-m resolution). Because we observed a hump-shaped relationship between otter locations and water depth, we used a knotted spline when analyzing depth.

We also described bottom topography underneath each observation. Maximum bottom slope (in degrees) for each cell was taken from the bathymetry layer using the Slope tool in ArcGIS 10.1 (ESRI, Redlands, CA). Variation in bottom topography was measured by the standard deviation in depth of a 30 m by 30 m square centered on the observation. Habitat type (soft or hard) was taken from two different data sources. The first was 2-m resolution habitat data from the Sea Floor Mapping Project at CSUMB. However, like the bathymetry dataset from the same project, the data do not go all the way to shore. To fill in that gap, we used the *Predicted SubstrateSouth* dataset from the California Department of Fish and Wildlife. Kelp data for the California coastline were derived from aerial surveys flown by California Department of Fish and Wildlife in 1989, 1999, 2002–2006, and 2008–2009. The dataset represents a merge of all nine years of kelp data into one feature to display the maximum extent of kelp in California. Note that an otter observed in an area listed as kelp in the merged kelp layer does not mean that the otter

was in a kelp bed, only that it was over a location that had kelp canopy at one or more of the aerial surveys. In addition to the habitat at an otter's position, we calculated the nearest distance between an otter and the kelp habitat edge (from inside or out).

We used a nominal logistic regression to compare the habitat between otter observations and random points. For observed otter rafts, the point was weighted by how many otters were in the raft.

Our habitat assessment for resting otters does not show where otters forage. Knowing where otters forage is, therefore, needed to understand habitat use. An independent data set on otter feeding depths at Cojo Anchorage was available from seven male sea otters that were captured in May 2001 and April 2002, radio-tagged and equipped with time-depth recorders (TDRs; Wildlife Computers, Redmond, WA), monitored in the wild for 1–2 years, and then re-captured between April 2003 and June 2005 to retrieve the TDRs (for details on capture methods and monitoring radio tagged sea otters, refer to Tinker et al. [2006a]). Although most tagged otters moved between Cojo Anchorage and areas farther north, regular monitoring by radio telemetry showed when they were present at Cojo Anchorage. The TDR recorded depth readings at 2-s intervals, and these were analyzed to compile individual depth records into dives that were classified as feeding or non-feeding dives (following methods described by Bodkin et al. [2004]), and feeding dives were then grouped into contiguous dives called feeding bouts. To normalize sample sizes for each otter and reduce sampling error, we used bootstrap re-sampling, selecting (with replacement) 50 bouts from each otter, calculating average dive depth for each bout, and then iterating this procedure 10,000 times to obtain bootstrap estimates for the mean and 10–90% quantiles of foraging dive depths.

RESULTS

Apart from counting 35 otters in April 2005, counts were low (3.6 otters on average) between May 2004 and September 2005. When surveys resumed in August 2006, the otter population had increased tenfold (42 otters, SD = 19) (Fig. 2). A noticeable demographic change happened in 2010; we began seeing pups, indicating a shift from a migrating front to a breeding population. Note that although sea otter sex was not recorded, when sex could be determined, most (if not all) otters observed in the study area before 2007 were male.

The sea otter distribution south of Pt. Conception remained relatively consistent over the study period, with almost all sightings occurring within 10 km of the Cojo Anchorage kelp bed complex (Fig. 1). Independent observations from the Santa Barbara Coastal LTER (Reed et al. 2012) help put this into context: between 5/2007 and 12/2013 otters were seen to the southeast of our Point Conception study site on just 50 of 949 mainland kelp forest surveys and zero out of 119 Channel Islands surveys. At the eight regularly sampled LTER sites (ordered from northwest to southeast), otters were sighted occasionally at Arroyo Hondo (5/28 dates, mean = 1.6 otter), Arroyo Quemado (11/150 dates, mean = 7.3 otters), Naples Reef (3/128 dates, mean = 1.3 otters), Coal Oil Point (16/79 dates, mean = 7.3 otters), Goleta Beach (0/49 dates), Arroyo Burro (0/118 dates), Mohawk Reef (1/277 dates, mean = 1 otter) and Carpinteria (2/112 dates, mean = 1 otter). Most years, the LTER saw otters on 1–5% of their mainland surveys southeast of our study site. These sightings appeared to represent the transient exploratory movements of single animals or small groups. However, in 2008, otters were present in 16% of LTER surveys. The most significant of the 2008 range expansions was at Coal Oil Point (more than 40 km down coast of Cojo Anchorage): between 28 January and 24 March 2008, there were, on average, 3.1 (SD = 2.4) otters observed around Coal Oil Point (observations were made by the NMFS gray whale monitoring program). That count jumped to 25.6 (SD = 9.2) otters in April–June, and it appeared as if the otters might establish a new southern range extent, but soon thereafter the raft dispersed (presumably back up the coast towards Cojo Anchorage). Since June 2008, there have been few otter sightings at Coal Oil Point.

Unlike the sporadic otter sightings made to the southeast, sea otters were consistently present at Cojo Anchorage. An exponential growth model fit to the skiff count time series in Fig. 2 shows a significant increase in population abundance over time, with a 0.23 (95% CL = 0.119–0.334)
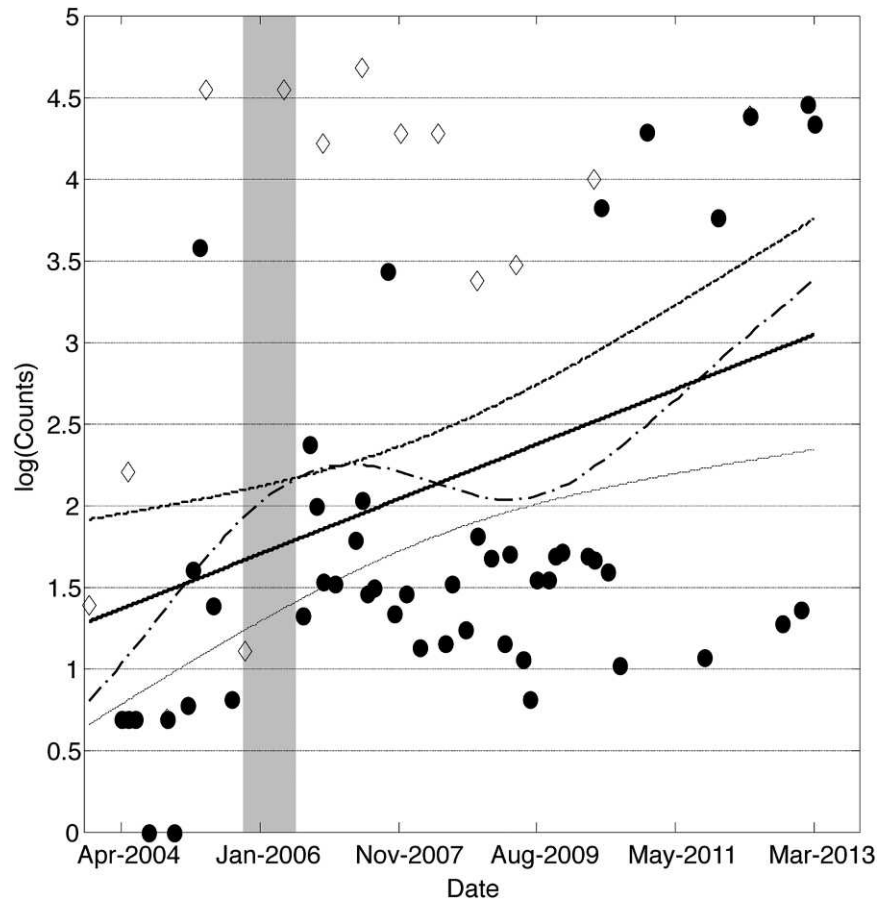
Fig. 2. Log-transformed data on sea otter abundance at Cojo Anchorage based on monthly skiff surveys (filled circles) and twice-annual aerial surveys (open diamonds) between April 2004 and March 2013. The solid line represents an exponential growth model of the form $\log(N_t) = \log(N_0) + r \times (t/12)$, fit to the data using maximum likelihood methods (see text for details). Dashed lines indicate the 95% prediction interval for the best-fit function ($r = 0.19$, 95% CL = 0.063–0.314). A smoothing spline is also fit to the data (alternating short and long dashes) to illustrate the multi-year cyclical trend detected by spectral analysis (see Fig. 3). The grey shaded bar indicates the 1-year period during which we could not survey.

instantaneous growth rate (r). A similar, though less-precise, estimate was obtained using the twice-annual aerial counts (estimated $r = 0.33$, 95% CL = 0.026–0.631), and combining the two data sets led to a growth rate of $r = 0.19$ (95% CL = 0.063–0.314). Some variation in the monthly skiff counts was probably due to otters moving into and out of the study area. Spectral density analysis of both the skiff counts and the less-frequent aerial counts exhibited two significant peaks in cyclical trends: one with a 3- to 8-year period, and the second with an annual period (Fig. 3). The annual period corresponded to a tendency for higher counts in winter/spring months (January–June). Indeed, an analysis of the residuals from the fitted exponential growth model showed that de-trended counts in winter/spring were 1.7 times greater than de-trended counts from summer months ($t = 2.024$, df = 50, $P = 0.0485$).

Sea otter density within the study area varied by habitat type, with an average of 3.8 otters/km^2 of kelp habitat and 0.4 otters/km^2 in non-kelp habitat. Kelp forest habitat and depth were the primary determinants of sea otter distribution. Inside kelp forest habitat, otter observations
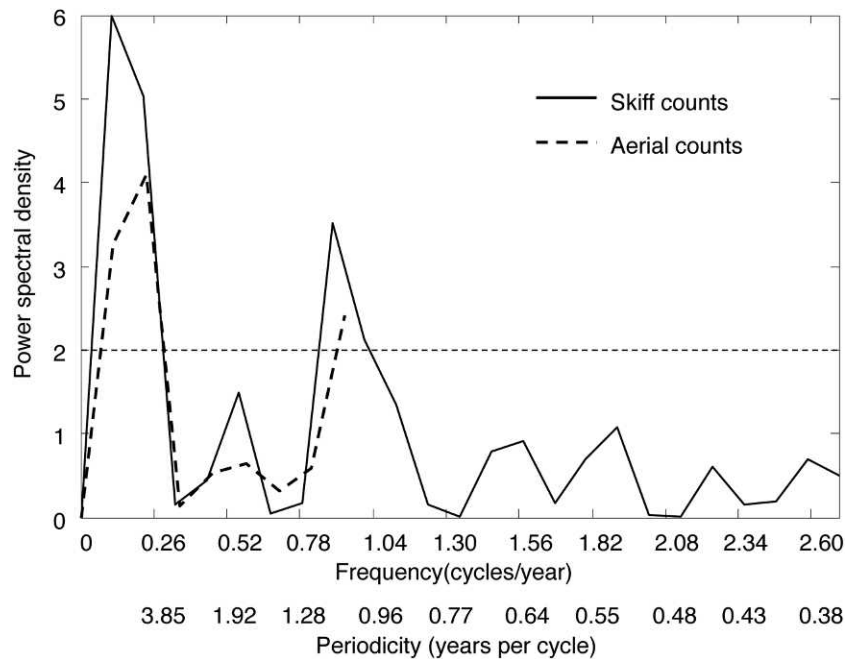
Fig. 3. Spectral density analysis of the time series of survey data shown in Fig. 2, plotted as a periodogram of the absolute value of the Fast Fourier Transform (power spectral density was scaled such that variance equals the mean of the transform). Peaks in spectral density with value >2 represent significant cycles in sea otter abundance, with frequency (number of cycles per year) and periodicity (number of years required to complete a cycle) as indicated along the x-axis. Both skiff survey (solid line) and aerial survey (dashed line) time series show two distinct cyclical patterns, one with a period of 1 year (seasonal fluctuations) and one with a period of 3–8 years.

peaked in 12.6 m deep water (half the otters were between 10.5 m and 14.4 m), which was just deeper than the median water depth of kelp habitat (10.9 m) (Fig. 4). Once we controlled for habitat depth distribution, otter locations were not associated with physical factors like bottom slope, bottom complexity, or bottom type within kelp forests. Outside kelp forest habitat, otters were most common in deeper water habitats (on average over 15.5 m depths, with half between 15.8 m and 18.6 m). For a given depth, otter counts declined with distance from the kelp habitat edge (estimate = −0.007 ± 0.0008, χ^2 = 38.2, $P < 0.0001$), indicating that otters outside kelp forest habitat still did not stray far. Otters outside kelp forest habitat were more abundant over complex than simple topography (estimate = 3.7 ± 1.3, χ^2 = 8.3, $P = 0.004$) and soft than hard substrate (estimate = 0.26 ± 0.11, χ^2 = 5.1, $P = 0.023$).

We compiled 1,187 feeding bouts from 58,450 feeding dives recorded at Cojo Anchorage. The depths used for feeding were twice as deep as where otters rested (Fig. 4): the median dive depth during feeding bouts was 23.1 m (10–90% quantiles = 10.54–37.5 m), and there were a few dives to >75-m depth (Fig. 4). Casual observations found that sea otters in the Cojo Anchorage fed on crabs, urchins, large marine snails, and octopus.

Sea otters shared the kelp forest with other birds and mammals (Table 1). Because such species are often not considered in studies on kelp forest ecology and can interact with sea otters indirectly through the kelp forest food web, we include a brief summary of our observations. On average, we counted 26 (SD = 22) harbor seals, 11 (SD = 12) California sea lions, three (SD = 3) Pacific bottlenose dolphins, and 0.4 (SD = 0.9) California gray whales. We also recorded 33 bird species using the habitat, of which we saw, on average, 13 species per survey.
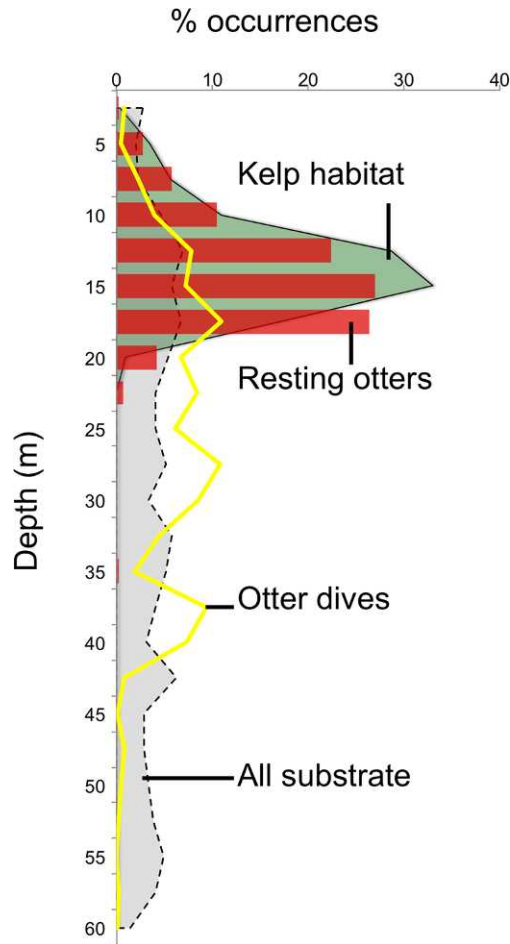
% occurrences

Fig. 4. Depth-use histograms for sea otters at Cojo Anchorage showing the frequency of use of different depths by resting otters (dark/red bars) and otter dives (thick solid/yellow line). For reference, the depth distributions are also shown for kelp canopy (dark/green shaded area with solid line) and the depth of all substrate (light/gray shaded area with dotted line) within the study area.

DISCUSSION

Our time-series data show that sea otters numbers increased south of Point Conception at the theoretical maximum for this species ($r_{max} = 0.20$; Estes 1990), though here the observed growth represents immigration and births. This fast growth rate stands in stark contrast to the sluggish growth rate ($r = 0.02$) seen north of Pt. Conception over the same time (Estes et al. 2003, Tinker et al. 2006a; USGS-WERC, *unpublished*

Table 1. Birds observed in the study area in order of frequency.

Species	Proportion dates seen
Brown Pelican	1.00
Double-crested cormorant	1.00
Brandt's Cormorant	0.96
Western Gull	0.96
Heermann's Gull	0.88
Surf Scoter	0.84
Western/Clark's Grebe	0.84
Common Loon	0.76
Great Egret	0.52
Royal Tern	0.52
Eared Grebe	0.48
California Gull	0.40
Ring-billed Gull	0.40
Pigeon Guillemot	0.36
Pelagic Cormorant	0.24
Caspian Tern	0.16
Common Murre	0.16
Elegant Tern	0.16
Brant	0.12
Great-blue Heron	0.12
Pacific Loon	0.12
Snowy Egret	0.12
Black-vented Shearwater	0.08
Mew Gull	0.08
Rhinoceros Auklet	0.08
Red-necked phalarope	0.08
Bald Eagle	0.04
Cinnamon Teal	0.04
Northern Fulmar	0.04
Pied-billed Grebe	0.04
Red-breasted Merganser	0.04
Red-throated Loon	0.04

data) and suggests ample resources. Spectral analysis found a strong seasonal cycle in abundance, with higher counts in winter/spring months (December–June). This seasonal pattern is consistent with reports that some male sea otters from resource-limited areas in the range center travel to peripheral areas to search for more abundant food during the winter-spring (Jameson 1989, Tinker et al. 2006b, Tinker et al. 2008b) then return to the range center after females wean their pups and come into estrous (Jameson and Johnson 1993). The increase in females with pups after 2010 shows that intrinsic demographic processes are now contributing to population growth at Cojo Anchorage. Unlike males, adult female sea otters do not regularly move far (Tinker et al. 2008b), so we expect strong seasonal trends in abundance to dampen over time.

Spectral analysis also showed a longer-term cyclic trend in the time series data, with a 3- to 8-year period. The multi-year sinusoidal pattern is

perhaps best explained as (1) a rapid colonization by males (2004–2006), followed by (2) a plateau with continued seasonal changes (2007–2010), and then (3) a secondary increase in growth (2010–2013), likely reflecting increased female recruitment and intrinsic growth driven by reproduction. This cyclical pattern provides new insights into the episodic nature of sea otter range expansion (Lubina and Levin 1988). Our findings and other published data (Wild and Ames 1974, Jameson 1989, Tinker et al. 2006b) are consistent with the following hypothesis for sea otter range expansion: groups of transient or non-territorial males at the range margins colonize adjacent "open habitat" to exploit abundant prey resources, often in response to increasing competition for prey in the neighboring occupied habitat. The makeup of these male groups is fluid, as many males move between the peripheral male groups and other male-dominated habitat areas within the established range, and some territorial males join the peripheral groups in winter months to take advantage of more abundant prey (Jameson 1989, Tinker et al. 2006b). However, female otters are much more sedentary than males, particularly while they care for dependent pups. For this reason, males that depart a group of breeding females give up mating opportunities (Jameson 1989). Furthermore, sea otters group together for safety from predators and to maintain breeding territories. Otters also aggregate at larger spatial scales because kelp forest habitat is patchy, potentially constraining dispersal among kelp beds. Additional range expansion slows or stops as local densities build up, reflecting the social nature (and thus positive feedback) of sea otters. If males don't abandon the area after 5–10 years, females begin to arrive from neighboring areas, initiating a demographic change from seasonally abundant male groups to resident, mixed-sex groups that include adult females with pups. As females begin to wean pups and come into estrous, a few males will establish reproductive territories, from which all other males are excluded. This final stage triggers another range-expansion into unoccupied habitat by groups of non-territorial males, and thus the cycle starts again. This combination of aggregation and sedentary female behavior can help explain why sea otter range expansion has been slow and intermittent (Wendell et al. 1986, Lubina and Levin 1988), and shows how it might continue to spread south in future decades. Similar range expansions have also been reported for northern sea otter populations, including British Columbia (Gregr et al. 2008), southeast Alaska (Esslinger and Bodkin 2009), Prince William Sound (Garshelis and Garshelis 1984), and Russia (Bodkin et al. 2000), however the sparser temporal resolution of survey data from those areas precludes the comprehensive, longer-term analysis that was possible here.

Our study shows that habitat use just south of Pt. Conception is similar to that reported for central California. Sea otters favored kelp habitat for resting and pup rearing. The ratio of sea otter densities in kelp vs. open areas was almost identical to that reported for central California, and the absolute densities within kelp beds at Cojo Anchorage (3.8 otters/km^2), while still increasing, are already approaching densities reported for kelp forests in central California that are thought to be at or near equilibrium (4.7–5.6 otters/km^2; Laidre et al. 2001).

The archival time-depth data from tagged otters showed that otters foraged in deeper water than where they rested. These data expand our view of habitat use by otters in southern California. Although we only had data from seven male otters for a part of the study period, their feeding patterns were similar to central California (Tinker et al. 2007), suggesting that food resources are also similar in central California and the Cojo Anchorage, underscoring our hypothesis that southern California has suitable habitat for sea otters.

Although the Cojo Anchorage has suitable habitat for sea otters, it is not representative of the southern California mainland. At present, the Bixby Ranch adjacent to Cojo Anchorage has no housing or public access, and most visitors boat in to surf. Furthermore, in 2013, the State of California designated the area around Point Conception a no-take marine reserve. In comparison, with the exception of the California Channel Islands and Camp Pendleton Marine Corps Base, most of southern California is heavily populated. This variation in human presence could add to the episodic nature of sea otter range expansion.

Our study was not designed to record dietary data. However, our observations are consistent

with sea otter diets reported for the translocated otter population at San Nicolas Island, the only other southern California site occupied by sea otters (Tinker et al. 2008a).

Sea otters share the kelp forest with several marine mammals and birds. But, except for gulls that sometimes shadowed feeding otters in hope of scraps, these other species did not interact with otters. However, because of their intense predation on benthic herbivores like urchins, sea otters might increase kelp-forest persistence at this site, and this could improve habitat for several birds and mammals.

In December 2012, the US Fish and Wildlife Service determined the California sea otter translocation program a failure and ended it, halting enforcement of the "no-otter" management zone. Sea otters are now legally free to expand into their former range. As shown by our study, sea otters can colonize and persist in southern California habitats at densities comparable to central California, and their affinity for specific habitat features makes it possible to predict their future distribution. We predict that otters will continue to expand their range into southern California, aided by adequate habitat and a lower great white shark density. But patchy kelp-forest habitat and their strong social structure mean that this expansion will come in fits and starts.

ACKNOWLEDGMENTS

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