Biological Conservation 253 (2021) 108830

Contents lists available at ScienceDirect

Biological Conservation

journal homepage: www.elsevier.com/locate/biocon

Examining the potential conflict between sea otter recovery and Dungeness crab fisheries in California

Andre M. Boustany[a,b,1,*], David A. Hernandez[a,1], Emily A. Miller[a], Jessica A. Fujii[a], Teri E. Nicholson[a], Joseph A. Tomoleoni[c], Kyle S. Van Houtan[a,b]

[a] Monterey Bay Aquarium, 886 Cannery Row, Monterey, CA 93940, USA
[b] Nicholas School of the Environment, Duke University, Box 90328, Durham, NC 27708, USA
[c] U.S. Geological Survey, Western Ecological Research Center, 2885 Mission Street, Santa Cruz, CA 95060, USA

ARTICLE INFO

Keywords:
Reintroduction
Human-wildlife conflict
Southern sea otter
Dungeness crab
Species recovery

ABSTRACT

Human exploitation of marine mammals led to precipitous declines in many wild populations within the last three centuries. Legal protections enacted throughout the 20th century have enabled the recovery of many of these species and some recoveries have resulted in conflict with humans for shared resources. With legal protections and reintroduction programs, the southern sea otter (*Enhydra lutris nereis*) has returned to portions of its former range from which it had been extirpated for decades, causing concern that the Dungeness crab (*Cancer magister*) fishery could be negatively affected by increasing otter range and population size. The Dungeness crab fishery is one of the most valuable in California, and these crabs are a known prey item of sea otters. We examine sea otter population growth by port region in relation to Dungeness crab catch using landing receipts since the early 1980s. We find Dungeness crab landings and fishing success, as measured by landings per trip receipt, increased across all ports. In the most recent decade, we observed slower growth in fishing success in northern ports where otters were absent, relative to southern ports where sea otters exist and their populations have grown. In ports where otters were present, fishing success was positively correlated with otter population size over time. Further, an extensive dataset of 83,000 sea otter foraging dives identified Dungeness crab to be less than 2% of the total diet. Though we find no evidence that sea otter populations impact the Dungeness crab fishery in California, other potential conflicts could be considered before expanding reintroduction programs.

1. Introduction

Throughout history, humans have harvested marine mammals for meat, fur, blubber, bone, and other products (Bodkin, 2015; David and Van Sittert, 2008; Hovelsrud et al., 2008; Roman and Palumbi, 2003). Typified by a late onset of breeding, low fecundity, high parental investment, and high juvenile survival (Pearl, 1928), marine mammal populations are resilient to bottom-up environmental forcing, but sensitive to top-down harvest pressures (Halley et al., 2018). Overexploitation has led to precipitous losses in marine mammal populations globally (Lotze and Worm, 2009) with an average 71% decline in the modern era (Magera et al., 2013), as exploitation rates increased with industrialization (Lotze et al., 2006). Strict conservation measures were enacted as early as 1911 to avoid widespread extinctions (Baldwin, 2011; Birnie, 1989; Coggins, 1975; Dorsey, 1991; Houck, 1993; Magera et al., 2013; Roman et al., 2013).

The collective result of marine mammal protections and conservation efforts has been largely successful. Many populations have begun to expand in number and geographic extent (Cammen et al., 2019). Though threats to many marine mammals persist and 59% of marine mammal species remain threatened or data deficient (an established proxy for threatened status) according to the IUCN (Jenkins and Van Houtan, 2016), roughly 42% of marine mammal populations are growing globally (Magera et al., 2013), with 78% of U.S. populations also showing increases (Valdivia et al. 2019). While the conservation successes can be appreciated, these recoveries have also led to conflict with the coupled human-natural systems that developed in the interim (Marshall et al., 2016). Conflicts between recovering pinnipeds and fisheries in Denmark (Scharff-Olsen et al., 2019), California (DeMaster et al., 1985), and Chile (Goetz et al., 2008) are notable examples.

* Corresponding author at: Monterey Bay Aquarium, 886 Cannery Row, Monterey, CA 93940, USA.
E-mail address: aboustany@mbayaq.org (A.M. Boustany).
[1] These authors contributed equally.

https://doi.org/10.1016/j.biocon.2020.108830
Received 9 June 2020; Received in revised form 14 October 2020; Accepted 20 October 2020

The sea otter (*Enhydra lutris*) is another marine mammal whose recovery may present conflicts with human interests. With a historical North American distribution from Alaska to Baja California, the species was hunted to near extinction during the fur trade until the International Fur Treaty banned harvests (Kenyon, 1969). The southern subspecies (*E. lutris nereis*) was thought to be extirpated from California until a small population of 50–100 individuals was located off of Point Sur in 1915 (Bryant, 1915;Kittinger et al., 2015). Since then, the population gradually recovered to over 3000 individuals in 2018 (Hatfield et al., 2018), with reintroduction programs aiding this growth in the last quarter of the twentieth century (Mayer et al., 2019). Range expansion and population growth since 1938 has led to the reestablishment of food web interactions in ecosystems that have been without sea otters for decades. southern sea otters currently range from the Channel Islands in the south to Half Moon Bay (HMB) in the north and future efforts aim to restore sea otters to ecosystems where they have been absent for over a century (Hatfield et al., 2018; Mayer et al., 2019).

While the growth of the southern sea otter's population and expansion of its geographic range are stated conservation goals, this may impact economically important shellfish fisheries (Doroff and DeGange, 1994; Estes et al., 2003). As southern sea otter population and range expanded in the first half of the 20th century, otters came into contact with lucrative abalone populations in Southern California, with commercial fishers attributing the decline in abalone populations to the reemergent otters (Carswell et al., 2015). Whether or not this threat from otters was real (e.g., Wild and Ames, 1974) the state of California nonetheless managed otters with an aim of limiting overlap with the fishery (CDFG, 1968). This management plan was rendered moot by the passage of the U.S. Marine Mammal Protection Act and the listing of the southern sea otter as "threatened" under the U.S. Endangered Species Act in 1977, which gave priority to preservation over management. Even under a preservation-minded regime, the potential for conflict from real or perceived negative impacts can impede recovery by decreasing public support for further conservation measures (Roman et al., 2015).

One area for potential conflict in California is between increasing sea otter populations and the Dungeness crab (*Cancer magister*) fishery. Dungeness crab supports one of the most valuable fisheries in California, generating an average annual ex-vessel value of $57 million (California Department of Fish and Game, 2011; Sweetnam, 2010). There have been concerns among fishermen that the increasing presence of otters may lead to lower catch rates (Johnson, 1982; Shirley et al., 1996). While sea otters are known to feed on Dungeness crabs (Newsome et al., 2009), the relative dietary proportion is unknown, and therefore the extent to which this predation might affect Dungeness crab fisheries remains poorly understood. Here, we examine the potential resource conflict between recovering sea otter populations and human extractive use by examining trends in Dungeness crab catch and sea otter population growth since the 1980s.

2. Methods

2.1. Dungeness catch and effort

California Department of Fish and Wildlife ("CDFW") provided monthly Dungeness crab landings and receipts for nine port complexes extending from Trinidad to Morro Bay for 1980–2018. Port complexes ("ports", see Fig. 1) are statistical areas that summarize landings within their boundaries (California Department of Fish and Wildlife, 2019). In addition to catch, CDFW provided monthly port offload receipts, generated from individual vessel unloads. Catch and receipt data are both aggregated monthly to maintain fisher confidentiality. The number of receipts shows that a fishing trip took place and catch was offloaded but does not detail fishing effort (e.g., the number of traps, sets, or rebaitings). Therefore, we calculated a measure of fishing success, ψ, during each fishing year using:

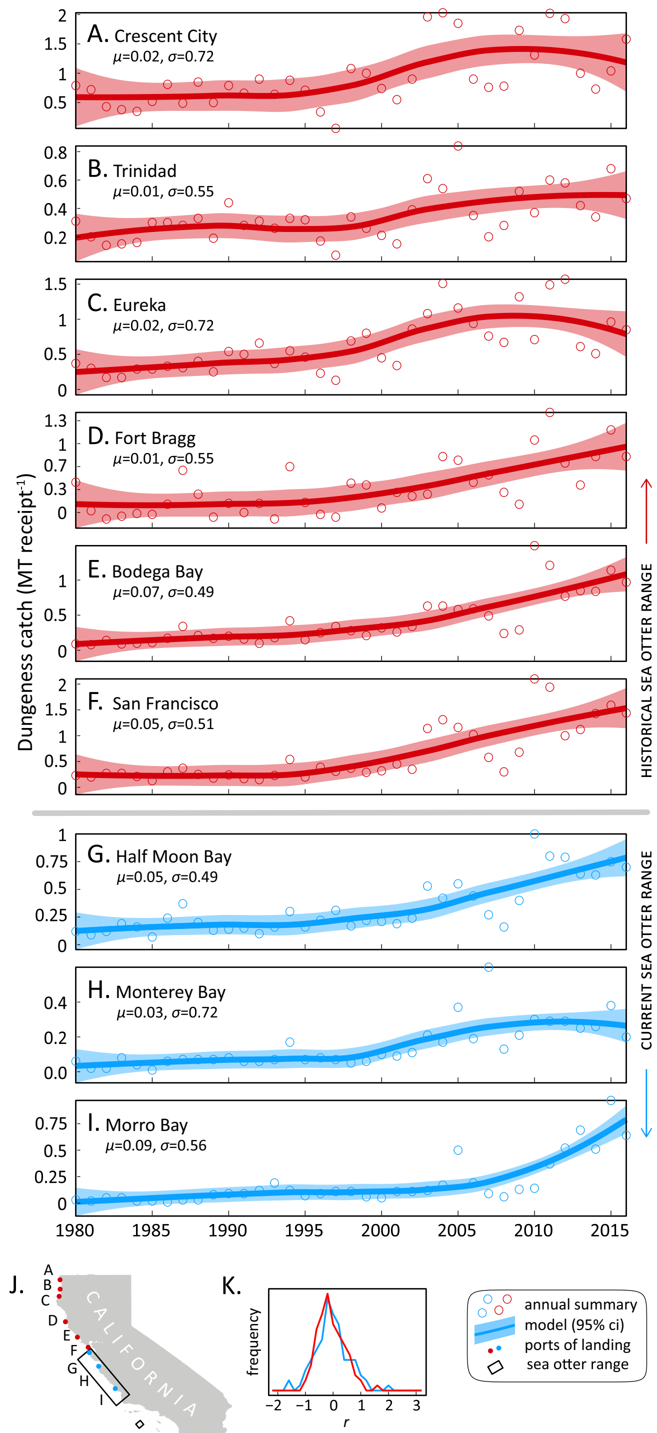

Fig. 1. California Dungeness crab catch show steady growth and no effect from southern sea otters. (A–I) Dungeness catch weighted for effort across nine statistical regions from 1980 to 2018. Solid line is a loess model, shaded area is 95% interval, derived from annual (November–October) values (hollow circles). Summary statistics for each series are labeled. Panels are sorted from north to south with series noted in red being north of the current southern sea otter range, and blue being within. (J) Inset map of the geographical position of ports in California. (K) Frequency distributions for collective summary statistics for ports within and outside the otter range. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

$$\psi = \frac{\sum_i^j \omega}{\sum_i^j \varphi} \tag{1}$$

where ω is the monthly Dungeness landing mass, and φ is the number of monthly offload receipts, reported over the fishing year November (i) through October (j). As CDFW reports (C. Juhasz, pers. comm.) the average offload size at peak season is 5.5–9 mt per vessel, we excluded values above 11 mt from our analyses as landings above this size were likely to be spurious.

From the annual values of fishing success, for each port series we calculated the annual intrinsic rate of growth among consecutive years (r), the mean over the entire time series (μ) and standard deviation (σ). To examine whether trends in fishing success differed among ports, we used a one-way analysis of variance ("ANOVA") on the annual growth rate in fishing success for each port. We also examined the distributions of annual intrinsic rates of growth for ports within the range of sea otters (Morro Bay, Monterey, Half Moon Bay) vs. those that were not within the home range of otters (San Francisco, Bodega Bay, Fort Bragg, Eureka, Trinidad, Crescent City). Although Half Moon Bay lies just outside the official range of southern sea otters, crab fishers out of this port are likely to set their gear in areas where otters are present. Since we are mainly interested in overlaps between the fishery and otters and not overlap of ports and otters, we include HMB with the other ports within the range of otters.

Next, we compared the proportion of the statewide Dungeness crab landings that occurred at ports within the range of southern sea otters vs. ports outside the range of otters. Since the Dungeness crab fishery has experienced shifts in the distribution of fishing effort over time, we also calculated the landings per offload receipt coming from ports within the range of otters compared to ports outside. This results in a relative proportion of fishing success within and outside the range of otters and partially corrects for changes in the relative proportion of fishing effort between these two areas. Yearly fishing success was calculated for the three ports within the otter range, then divided by the fishing success for ports outside the range to yield a fishing success ratio inside vs. outside the range of otters.

To examine port deviations from statewide trends in fishing success, we calculated the normalized residual fishing success for each port relative to the statewide trend. This was done by first calculating the trend in fishing success for each port. These port-level values of fishing success were then normalized to a variance of 1 with the first year of the survey, 1985, set to 0. Statewide fishing success was constructed from the normalized yearly mean fishing success across all ports. This ensures that the trend of each port is weighted equally, regardless of the total landings at a given port. Each port's deviation from the normalized statewide trend was calculated to arrive at the residual fishing success for each port.

2.2. Sea otter population densities

The California Sea Otter Annual Census monitors the abundance and distribution of the southern sea otter as part of the Southern Sea Otter Recovery Plan. This survey has been conducted every spring since 1982 with the exception of 2011. The survey area extends from San Mateo County in the North to the Santa Barbara/Ventura County line in the South (Hatfield et al., 2018). Abundance is the number of otters observed in survey cells that measure 500 m along the shore extending to the 60 m isobath (Hatfield et al., 2018). At the time of this study, complete survey data were available for the years 1985–2017. Since this survey occurs in the spring, we matched sea otter survey year data to the previous CDFW Dungeness season which includes 10 months of the subsequent calendar year.

2.3. Comparing sea otter and Dungeness data

We explored whether the size of a sea otter population near crab fishing ports influences fishing success. The otter population size at each of the three ports within the otter's range was estimated by assigning otter survey grids to their nearest port and summing all the otters within these port associated grids for a given year. This resulted in 112 km of coastline being assigned to Morro Bay, 187 km to Monterey Bay, and 75 km to Half Moon Bay. The total annual census of otters assigned to each of these ports was then compared to the annual fishing success for the same port, a linear regression was run through these points, and the slopes tested for significance. We performed a sensitivity analysis by examining how this relationship varied using a series of different buffer sizes (10, 20, 50, 150, 200 km) from each of the three ports.

2.4. Sea otter diet

To determine the prevalence of Dungeness crab in sea otter diets, we examined diet composition in an intertidal estuary (Elkhorn Slough, 2013–2016) and near-shore ocean ecosystem (Monterey Peninsula, 2007–2012 and 2016–2019) using diet data that were collected from previous projects in collaboration with MBA, USGS and University of California, Santa Cruz. Shore-based observers collected otter feeding data, following individual sea otters on continuous foraging bouts consisting of multiple dives. Observers recorded the size and taxonomic classification of prey items that they obtained during dives. Prey size and counts followed established protocols, and were converted to estimates of biomass using Monte Carlo resampling methods to account for observer bias (see Tinker et al., 2012). Total biomass consumed for each taxonomic group determined the proportional composition of diet for each geographic area. Crabs were placed in one of three taxonomic classifications: 'Dungeness crab' identified to species, '*Cancridae* crab' which includes all species of cancer crab as well as Dungeness that were not identified to species, and 'other crab', for crabs that were in a family other than *Cancridae* or could not be identified to the family level.

3. Results

From 1980 to 2018, the trend in Dungeness crab landings and fishing success increased in all statistical areas (Fig. 1A–I). The three most northern ports (Fig. 1A–C) also showed a flat or decreasing trend after 2010. The northern ports had higher average catches and fishing success than the three southern ports (Fig. 1G–I), but average rates of increase in crab landings per trip receipt did not differ significantly among ports (ANOVA, $p = 0.99$, df $= 8$). The average year-to-year increase in fishing success varied from 0.01 to 0.09 among ports, and distributions in μ between ports within the otter range and those outside did not differ (t-test, $p = 0.195$). Trends in fishing success stayed relatively stable at all ports from 1980 to 2000 and then increased. The four ports at the northern extent of the range showed the lowest mean annual rates of increase (0.01–0.02). A density function of all annual rates of growth for ports within and outside the otter range (Fig. 1K) showed a high degree of overlap, suggesting similar growth rates in fishing success between these two groups. When normalizing fishing success across ports and comparing to the statewide trend, there were no general trends over the entire time series, but there were periods when certain ports trended above or below the mean (Fig. S1). Since 2013, Bodega Bay, San Francisco, Half Moon Bay and Monterey Bay trended above the statewide mean. The five southernmost ports tended to show a positive deviation from the mean in the most recent years, but overall most ports closely followed the statewide pattern in increases of fishing success over time (Fig. S1).

While ports within the otter range had lower catch and fishing success than the more northerly ports, these ratios changed over time with the southern ports constituting an increasing proportion of the catch and showing a faster growth in fishing success over the time series (Fig. 2).

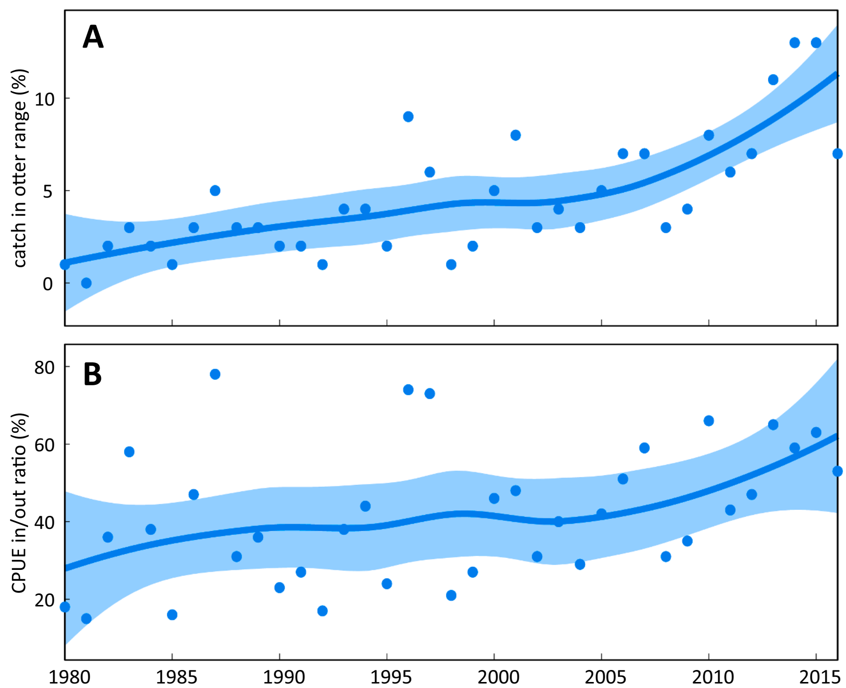

Fig. 2. The absolute and relative significance of Dungeness landings in the sea otter range increase over time. (A) Proportion of California statewide catch of Dungeness crab occurring within the southern sea otter geographic range increased from 1 to 11% during the study. (B) The ratio of Dungeness landings per offload receipt compared collectively for ports within the otter range vs. outside increased from 27 to 63% during the study. The solid line is a loess model, shaded area the 95% interval, and filled circles are annual means between groups of ports.

The annual number of receipts declined in the three northernmost ports (Crescent City, Trinidad, and Eureka), was fairly stable in Fort Bragg and Bodega Bay, and increased in the southernmost ports (San Francisco, Half Moon Bay, Monterey Bay, and Morro Bay), indicating a southern shift in overall fishing effort (results not shown). Partially as a result of southward shifts in fishing effort, the proportion of statewide landings coming from the southernmost ports, within the otter range, increased from approximately 0.7% in 1980 to over 11.4% in recent years (Fig. 2A). However, shifts in effort were not the only reason for an increasing statewide proportion of catch within the otter range, as landings per trip receipt also increased more within the otter range than outside (Fig. 2B). The three southernmost ports observed landings per receipt of 27.5% of those in the more northern ports at the beginning of the time series, and closer to 62.8% of the northern ports by the end of the time series.

At ports within the otter range, we found a positive correlation between the size of the otter population and the port's fishing success over time (Fig. 3). All three ports saw a significantly positive slope when regressing otter population size vs. landings per receipt over the entire time series. The positive correlation mostly remains when different buffer sizes (10–200 km) were used (Fig. S2), suggesting this effect is not an artifact of buffer size. The exception to the trend occurred when using a buffer radius of 10–50 km at Half Moon Bay, or 10–20 km at Morro Bay. These buffer sizes showed varying trends, but none of these slopes was significantly different from zero (Fig. S2). All significant slopes across ports and buffer size were positive.

Sea otters in Elkhorn Slough and the greater Monterey Bay area have been observed eating Dungeness crab, although this food item was a relatively minor portion of the overall diet (Fig. 4). Observers recorded prey items from a total of 26,154 dives from 1069 foraging bouts of 28 sea otters in Elkhorn Slough, and 57,186 dives from 2572 foraging bouts of 117 sea otters along the Monterey Peninsula. In Elkhorn Slough, 0.007% of the biomass consumed was Dungeness crabs and a further 15.6% of the biomass was 'Cancridae crab' or 'other crab', an umbrella category of unidentified crabs, which may contain Dungeness. In the greater Monterey Bay area, 1.6% of the biomass consumed by sea otters was identified as Dungeness crab, with total proportion of crab biomass in otter diet of 30.7% (Fig. 4).

4. Discussion

Our results suggest that southern sea otter population growth and range expansion have not had negative effect on landings in the California Dungeness crab fishery in the past 40 years. Landings of Dungeness crab have increased statewide from 1980 into the most recent decade (CDFW, 2019). Trends in fishing success (landings per offload receipt) increased at all statistical sampling areas between 1980 and 2018, with the greatest average annual increase occurring in Morro Bay ($\mu = 0.09$), and the lowest increases in Trinidad and Fort Bragg ($\mu = 0.01$; Fig. 1). While the commercial landings of Dungeness only include male crabs above 15.9 cm, and therefore do not sample the entire population, crabs in this size class are mature, sex ratios are believed to be equal, and it is estimated that more than 90% of male crabs in this age class are harvested annually, so availability to the fishery is a useful estimate for trends in adult biomass (Dunn and Shanks, 2012; Hankin et al., 1997; Taggart et al., 2004). Although a formal stock assessment has not been completed for Dungeness crab in California it is believed that landings in this fishery mirror overall abundance (Methot and Botsford, 1982; Richerson et al., 2020). We therefore believe that our calculation of fishing success is a suitable proxy for crab abundance in California waters.

Both theory and data indicate the California-wide increase in Dungeness crab landings may not be related to sea otters, but rather bottom-up oceanographic forcing (Botsford, 2001; Shanks, 2013; Shanks and Roegner, 2007). Shanks and Roegner (2007) found that timing of the spring transition, the onset of wind-driven upwelling in the California Current, explains 90% of the recruitment variability in megalopae, their final larval stage. Megalopae recruitment subsequently explains over 90% of the variability in commercial Dungeness crab landings 4 years later as larvae reach commercial size. The spring upwelling induces shoreward movement of deeper waters, where the larvae reside, and facilitates greater shoreward larval advection (Lynn et al., 2003; Shanks and Roegner, 2007). While timing of the spring transition may help explain interannual variability in Dungeness crab recruitment, decadal indices may better explain the trends we observe. Recruitment success of Dungeness megalopae is positively correlated with cold phases of the Pacific Decadal Oscillation ("PDO") resulting in

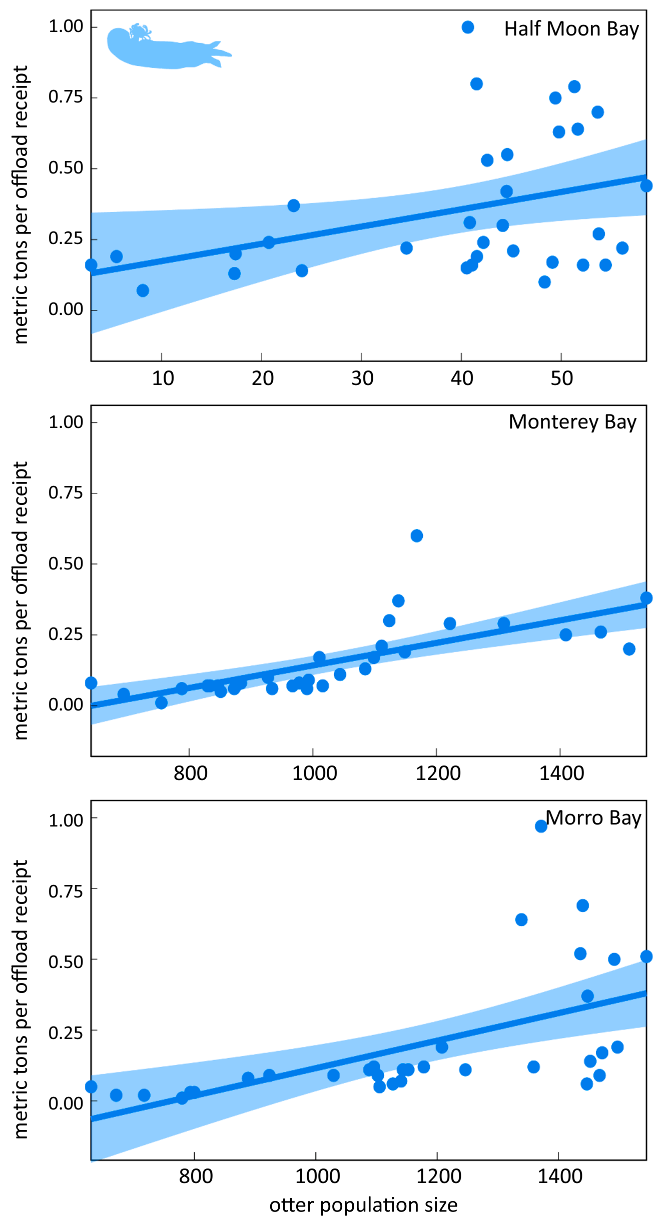

Fig. 3. Increasing otter abundance is associated with increasing Dungeness crab fishing success. Regression of southern sea otter population size for survey grid cells closest to each of the three statistical ports within the range of otters compared to fishing success (landings per offload receipt). Points represent each of the years from 1980 to 2018, and the line is a linear regression with 95% confidence interval.

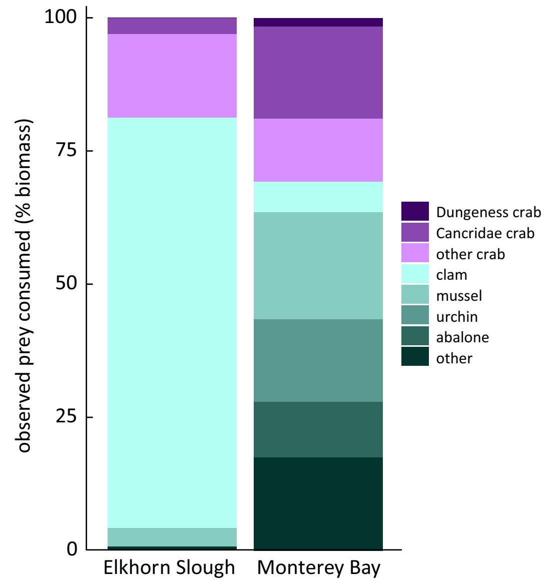

Fig. 4. Dungeness crab comprises less than 2% of the known southern sea otter diet. Relative proportion of observed sea otter diet (reflected in % total biomass) for two distinct ecosystems – the Elkhorn Slough a tidal estuary, and the greater Monterey Bay. Bivalves are the primary prey item in Elkhorn Slough while the diet in Monterey Bay is more diverse and consists of an assortment of crustaceans, mollusks, and echinoderms. In both ecosystems confirmed Dungeness crab is a negligible dietary component. Purple shades denote all crab groups (Decapoda), where all other major prey groups (clams, mussels, urchins, abalone, et al.) are green. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

increased commercial landings (Shanks, 2013). Relating to our time series, the PDO was in a largely uninterrupted warm phase from the 1970s, shifting to a cold phase around 2000 (Newman et al., 2016). The PDO patterns match our observed trends in Dungeness landings (Fig. 1) and draw significant theoretical and empirical parallels to North Pacific loggerhead sea turtles (*Carretta carretta*) dynamics. Like Dungeness crab, loggerhead sea turtles have a life history strategy of high fecundity, low parental investment, and low juvenile survival (Halley et al., 2018). This means their populations are largely regulated through bottom-up environmental forcing of juvenile recruitment (Ascani et al., 2016; Van Houtan and Halley, 2011) and not top-down forces. Though other environmental factors are influential, both California Dungeness and North Pacific loggerhead population dynamics align with the PDO.

While statewide increases in Dungeness crab landings support the idea of broad-scale, bottom-up drivers of population size, otters may still be exhibiting a detrimental effect on Dungeness crab populations if increases in crab landings and population are moderated in the presence of otters. We examined this possibility through two methods (Figs. 1 and S1). The average annual rate of growth (r) in landings was higher at ports within the range of otters (Morro Bay, Monterey, Half Moon Bay) than at other ports (average increase of 0.057 vs. 0.03, respectively). However, these differences were not significant and the distributions of the annual rate of increase between otter and non-otter ports were broadly overlapping (Fig. 1K). These results were echoed in the residual analysis, which allowed for a year-by-year examination of the deviation from the normalized statewide landings. No clear pattern emerged, although statistical areas south of Fort Bragg tended to show positive deviations from the statewide trend in the most recent decade (Fig. S1). Both these findings are supported by results from regional population estimates that found an increase in Dungeness abundance in central California (south of 38.77° latitude, the Mendocino/Sonoma county border) and relatively stable trends in population to the north (Richerson et al., 2020).

We observe evidence of a trend to a more southern distribution of Dungeness crab in the landings and fishing success data as well. The proportion of statewide catch within the range of otters has increased over the study period (Fig. 2A), and the relative fishing success (landings per trip ticket) within vs. outside the otter range has also increased (Fig. 2B). All these findings indicate a greater increase in local abundance of Dungeness crab within the otter range than outside. Since the current range of southern sea otters is at the southern extent of the range of Dungeness crab, this area may be more sensitive to changes in climate induced forcing on the larval and fishery recruitment of crab as range edges generally see greater changes in relative abundance than do population cores (Andrewartha and Birch, 1986; Bahn et al., 2006). As larval recruitment conditions improve along the entire California Current, it is also possible that these improved conditions are being hampered by other factors in the northern region. Dungeness crab larvae suffer from increased carapace, pereopod, and mechanoreceptor dissolution and decreased carapace width from decreasing pH (Bednaršek et al., 2020) and this effect has been higher north of San Francisco than to the south, which may partially explain a lower rate of crab population growth in the north (Bednaršek et al., 2014).

Increasing otter populations, coupled with increasing Dungeness crab populations, have resulted in a positive correlation between the number of otters and fishing success at ports where otters are present (Fig. 3). This pattern held across a range of buffer sizes, from 10 km to 200 km, suggesting this relationship was not an artifact of the buffer size used (Fig. S2). In other regions, where it was possible to examine the relationship between landing port and fishing area, landing port correctly predicted catch area 94.4% of the time (Richerson et al., 2020). While this positive correlation between otter and crab may be unrelated, with a climate induced increase in crab populations and an increase in otter population afforded by legal protection and captive rearing, there remains the possibility that otters could have a net positive effect on Dungeness crab populations. Sea otters are known to be ecosystem engineers, changing their local habitat, including eelgrass and rocky intertidal ecosystems, in a way that may make it more amenable to other species (Estes and Palmisano, 1974; Hughes et al., 2013; Hughes et al., 2019). Eelgrass estuaries and rocky intertidal systems with productive mollusk beds are two preferred nursery areas by young-of-the-year Dungeness crab in experimental settings (Fernandez et al., 1993) and estuary nurseries have been shown to provide important contributions to Dungeness crab populations throughout their range (Armstrong et al., 2003; Emmett and Durkin, 1985). While any ecosystem effect of otters on crab populations is currently undescribed, if the ecosystem benefit effects of otter presence outweigh the effects of direct predation by otters, the presence of otters may act to enhance local crab populations.

This study underscores the importance of using historical data exploration to examine potential outcomes of reintroduction activities. Management decisions, however, are most likely to be effective when data-driven using the best available data. Our results do not show that the recovery of the southern sea otter has detrimentally affected the Dungeness crab fishery off California.

While we know of direct predation by southern sea otters on Dungeness crabs, this is a minor component of the diet either within estuaries or outside (Fig. 4). In Elkhorn Slough and along the Monterey Peninsula, confirmed Dungeness crab were <2% of the total biomass consumed by sea otters (Fig. 4). The total biomass of all crab consumed at Elkhorn Slough and along the Monterey Peninsula was 18.7% and 30.7%, respectively. A percentage of the biomass in the '*Cancridae* crab' and 'other crab' categories were likely Dungeness crabs, but the majority of these were likely rock crab (*Cancer sp.*), as the latter were 10 times more common in scat samples from otters in the Elkhorn Slough region (Maldini et al., 2010). While otter diets may have contained a higher proportion of Dungeness crab in the past, we feel it is still unlikely otters negatively impacted the Dungeness fishery prior to this study as southern sea otter population was even smaller prior to 1980 (<1500). Additionally, crab landings in the Central Management Area have historically been low even before the sea otter population began to increase in the 1940s (287–1950 mt from 1915 to 1940; CDFW), suggesting this region has always been marginal Dungeness crab habitat.

While there is no evidence that an increasing southern sea otter population has negatively impacted Dungeness crab populations off California, it is possible that continued growth in population size and range of otters may eventually have an effect. The southern sea otter population has plateaued in recent years (Tinker and Hatfield, 2018) and natural range expansion is currently restricted by the distribution of kelp forests due to increased predation on otters in areas with low kelp cover (Moxley et al., 2019; Nicholson et al., 2018). Therefore, it seems unlikely to have an impact on Dungeness crab abundance in the near term. In the longer term, we expect otters will continue to have little impact on the Dungeness crab fishery off California since the population of otters appears to be at or close to carrying capacity within its current range, leaving range expansion as the only means for significantly increasing otter population size (Laidre et al., 2001; Mayer et al., 2019; Tinker et al., 2008). As otters expand their range northward, they will be moving from marginal Dungeness crab habitat, into the core range of Dungeness crab in Northern California to Washington state (Richerson et al., 2020). If no measurable effect of otters on crabs was observed in areas of low relative crab abundance, it seems unlikely otters would have a measurable effect in areas with much higher abundance. However, as otters move into more productive Dungeness crab habitat, their diets may shift to take advantage of the more abundant prey, resulting in a detrimental impact on the landings or spatial distribution of Dungeness crab fisheries.

The feeding habits of sea otters make broad shifts in diet choice towards Dungeness crab unlikely even as their range expands. Sea otters concentrate most foraging efforts in depths less than 25 m (Thometz et al., 2016) whereas Dungeness crabs can be found up to 250 m deep, suggesting that Dungeness crabs may find refuge from predation within their normal habitat range. Additionally, in areas of low resource abundance, sea otters show increased specialization on a subset of available prey (Tinker et al., 2008). These specializations are transmitted across matrilines, likely vertically from mother to pup (Estes et al., 2003), and require handling skills and potentially tool use specific to a prey species (Fujii et al., 2017). These learned specializations may slow the transition to alternate prey if resource abundances change. However, even in areas with abundant prey, such as San Nicolas Island, where sea otters initially foraged exclusively on preferred, abundant prey (Fujii et al., 2017; Tinker et al., 2008), as otter population increases, predation pressure on any one prey species would plateau, leading to diversification in the overall diet of sea otters and releasing pressure from any single prey species (Laidre and Jameson, 2006).

We should note that our findings only hold for impacts of southern sea otters on Dungeness crab in California and may not be representative of interactions in other regions. There is evidence that sea otters negatively affected the landings and distribution of the Dungeness fishery in Southeast Alaska (Johnson, 1982). However, crabs make up a larger portion of sea otter diet in some parts of Alaska than in California and may therefore have a greater impact per otter (Garshelis et al., 1986). In addition, the sea otter population size, density, and trajectory are all much greater in Alaska relative to California. An estimate of otter population size in Alaska was 98,780 among the three populations in 2013 (USFWS, 2013) with observed annual growth rates in some areas reaching 16–20% (Bodkin et al., 1999; Estes, 1990). In addition, densities per length of coastline are much higher in Alaska, partially due to the much more complex coastline which allows for larger otter carrying capacities per unit of alongshore coast (Tinker et al., 2019). These factors lead to areas of high-density otter populations which may more easily lead to localized depletions of prey. The historic and currently unoccupied range of sea otters in Northern California more closely approximates the coastline of the current range of southern sea otters than it does the Alaska coastline. So, it seems likely eventual carrying capacities of otters per length of coastline will more closely approximate those of Central California than Alaska. As such, we expect sea otters to have little to no impact on the west coast Dungeness crab fisheries as their population and range continues to expand northward.

Supplementary data to this article can be found online at https://doi.org/10.1016/j.biocon.2020.108830.

Data availability

Datasets analyzed for this study are included in the data repository at: https://osf.io/ub4xm/.

CRediT authorship contribution statement

KV and AB designed the study. AB, DH, EM, and KV performed the analyses. AB, EM, and KV generated the figures. DH, JF, JT, and TN collected and curated data. AB, EM, and DH wrote the manuscript with contributions from KV. All authors reviewed the manuscript.

Declaration of competing interest

The authors declare no competing interests.

Acknowledgements

M. Staedler, K. Mayer, and numerous USGS and Monterey Bay Aquarium staff and volunteers provided technical and logistical support. CDFW environmental scientists and dock observers provided Dungeness crab fishery data. L. Carswell provided advice and assisted with permits and A. Copenhaver provided programmatic support. The Moss Landing Harbor District and Elkhorn Slough National Estuarine Research Reserve provided field access. Several anonymous reviewers improved earlier versions of this manuscript.

Funding

This research was supported by generous donor contributions to the Monterey Bay Aquarium.

Ethics statement

All research activities were authorized by the U.S. Fish and Wildlife Service (permits #MA186914-2 and #MA032027-2).

References

Andrewartha, H.G., Birch, L.C., 1986. The Ecological Web: More on the Distribution and Abundance of Animals. University of Chicago Press.
Armstrong, D.P., Rooper, C., Gunderson, D., 2003. Estuarine production of juvenile Dungeness crab (Cancer magister) and contribution to the Oregon-Washington coastal fishery. Estuaries 26, 1174–1188.
Ascani, F., Van Houtan, K.S., Di Lorenzo, E., Polovina, J.J., Jones, T.T., 2016. Juvenile recruitment in loggerhead sea turtles linked to decadal changes in ocean circulation. Glob. Chang. Biol. 22, 3529–3538.
Bahn, V., O'Connor, R.J., Krohn, W.B., 2006. Effect of dispersal at range edges on the structure of species ranges. Oikos 115, 89–96.
Baldwin, E.A., 2011. Twenty-five years under the Convention of Migratory Species: migration conservation lessons from Europe. Environmental Law 41, 535.
Bednaršek, N., Feely, R., Reum, J., Peterson, B., Menkel, J., Alin, S., Hales, B., 2014. Limacina helicina shell dissolution as an indicator of declining habitat suitability owing to ocean acidification in the California Current Ecosystem. Proc. R. Soc. B Biol. Sci. 281, 20140123.
Bednaršek, N., Feely, R.A., Beck, M.W., Alin, S.R., Siedlecki, S.A., Calosi, P., Norton, E.L., Saenger, C., Štrus, J., Greeley, D., 2020. Exoskeleton dissolution with mechanoreceptor damage in larval Dungeness crab related to severity of present-day ocean acidification vertical gradients. Sci. Total Environ. 716, 136610.
Birnie, P., 1989. International legal issues in the management and protection of the whale: a review of four decades of experience. Nat. Resour. J. 29, 903.
Bodkin, J., 2015. Historic and contemporary status of sea otters in the North Pacific. In: Sea Otter Conservation. Academic Press, pp. 43–61.
Bodkin, J.L., Ballachey, B.E., Cronin, M.A., Scribner, K., 1999. Population demographics and genetic diversity in remnant and translocated populations of sea otters. Conserv. Biol. 13, 1378–1385.
Botsford, L.W., 2001. Physical influences on recruitment to California Current invertebrate populations on multiple scales. ICES J. Mar. Sci. 58, 1081–1091.
Bryant, H.C., 1915. Sea otters near Point Sur. California Department of Fish and Game Bull 134–135.
California Department of Fish and Game, 1968. Report on the Sea Otter, Abalone and Kelp Resources in San Luis Obispo and Monterey Counties and Proposals for Reducing the Conflict between the Commercial Abalone Industry and the Sea Otter. Requested by Senate Concurrent Resolution 74 in the 1967 Legislative Session. 72 pp.1 appendices.
California Department of Fish and Game, 2011. Review of selected California fisheries for 2010: coastal pelagic finfish, market squid, ocean salmon, groundfish, highly migratory species, dungeness crab, spiny lobster, spot prawn, Kellet's whelk, and white seabass. In: Sweetnam, D. (Ed.), Fisheries Review, CalCOFI Rep. California Department of Fish and Game: Marine Region, La Jolla, CA, pp. 13–35.
California Department of Fish and Wildlife, 2019. Final California Commercial Landings. California Department of Fish and Wildlife.
Cammen, K., Rasher, D., Steneck, R., 2019. Predator recovery, shifting baselines, and the adaptive management challenges they create. Ecosphere 10, e02579.
Carswell, L.P., Speckman, S.G., Gill, V.A., 2015. Shellfish fishery conflicts and perceptions of sea otters in California and Alaska. In: Sea Otter Conservation. Elsevier, pp. 333–368.
Coggins, G., 1975. Legal protection for marine mammals: an overview of innovative resource conservation legislation. Environmental Law 6.
David, J., Van Sittert, L., 2008. A reconstruction of the cape (South African) fur seal harvest 1653–1899 and a comparsion with the 20th-century harvest. S. Afr. J. Sci. 104, 107–110.
DeMaster, D., Miller, D., Henderson, J., Coe, J., 1985. Conflicts between marine mammals and fisheries off the coast of California. In: Beddington, J., Veverton, R., Lavigne, D. (Eds.), Marine Mammals and Fisheries. George Allen and Unwin, London, pp. 111–118.
Doroff, A.M., DeGange, A.R., 1994. Sea otter, Enhydra lutris, prey composition and foraging success in the northern Kodiak Archipelago. Fish. Bull. 92, 704–710.
Dorsey, K., 1991. Putting a ceiling on sealing: conservation and cooperation in the international arena, 1909–1911. Environ. Hist. Rev. 15, 27–45.
Dunn, P.H., Shanks, A.L., 2012. Mating success of female Dungeness crabs (Cancer magister) in Oregon coastal waters. J. Shellfish Res. 31, 835–839.
Emmett, R.L., Durkin, J.T., 1985. The Columbia River Estuary: an important nursery for Dungeness crabs, Cancer magister. Mar. Fish. Rev. 47, 21–25.
Estes, J.A., 1990. Growth and equilibrium in sea otter populations. J. Anim. Ecol. 385–401.
Estes, J.A., Palmisano, J.F., 1974. Sea otters: their role in structuring nearshore communities. Science 185, 1058–1060.
Estes, J.A., Riedman, M.L., Staedler, M.M., Tinker, M.T., Lyon, B.E., 2003. Individual variation in prey selection by sea otters: patterns, causes and implications. J. Anim. Ecol. 72, 144–155.
Fernandez, M., Iribarne, O., Armstrong, D., 1993. Habitat selection by young-of-the-year Dungeness crab Cancer magister and predation risk in intertidal habitats. Mar. Ecol. Prog. Ser. 92, 171–177.
Fujii, J., Ralls, K., Tinker, M.T., 2017. Food abundance, prey morphology, and diet specialization influence indivdiual sea otter tool use. Behav. Ecol. 28, 1206–1216.
Garshelis, D.L., Garshelis, J.A., Kimker, A.T., 1986. Sea otter time budgets and prey relationships in Alaska. J. Wildl. Manag. 50, 637–647.
Goetz, S., Wolff, M., Stotz, W., Villegas, M., 2008. Interactions between the South American sea lion (Otaria flavescens) and the artisanal fishery off Coquimbo, northern Chile. ICES J. Mar. Sci. 65, 1739–1746.
Halley, J.M., Van Houtan, K.S., Mantua, N., 2018. How survival curves affect populations' vulnerability to climate change. PLoS One 13 (9), e0203124.
Hankin, D.G., Butler, T.H., Wild, P.W., Xue, Q.-L., 1997. Does intense fishing on males impair mating success of female Dungeness crabs. Can. J. Fish. Aquat. Sci. 54, 655–669.
Hatfield, B.B., Yee, J.L., Kenner, M.C., Tomoleoni, J.A., 2018. California sea otter (*Enhydra lutris nereis*) census results, spring 2019. In: Data Series. U.S. Geological Survey Western Ecological Research Center, Reston, VA, p. 20.
Houck, O., 1993. The Endangered Species Act and its implementation by the US Departments of Interior and Commerce. University of Colorado Law Review 64, 277.
Hovelsrud, G., McKenna, M., Huntington, H., 2008. Marine mammal harvests and other interactions with humans. Ecol. Appl. 18, S135–S147.
Hughes, B.B., Eby, R., Van Dyke, E., Tinker, M.T., Marks, C.I., Johnson, K.S., Wasson, K., 2013. Recovery of a top predator mediates negative eutrophic effects on seagrass. Proc. Natl. Acad. Sci. U. S. A. 110, 15313–15318.
Hughes, B.B., Wasson, K., Tinker, M.T., Williams, S.L., Carswell, L.P., Boyer, K.E., Beck, M.W., Eby, R., Scoles, R., Staedler, M., 2019. Species recovery and recolonization of past habitats: lessons for science and conservation from sea otters in estuaries. PeerJ 7, e8100.
Jenkins, C.N., Van Houtan, K.S., 2016. Global and regional priorities for marine biodiversity protection. Biol. Conserv. 204, 333–339.
Johnson, A., 1982. Status of Alaska sea otter populations and developing conflicts with fisheries. In: Sabol, K. (Ed.), Transactions of the Forty-seventh North American Wildlife and Natural Resources Conference. Washington, DC, pp. 293–299.
Kenyon, K., 1969. The sea otter in the Eastern Pacific Ocean. In: North American Fauna. Bureau of Sport Fisheries and Wildlife, US Fish and Wildlife Service, Washington, DC, pp. 1–352.
Kittinger, J.N., McClenachan, L., Gedan, K.B., Blight, L.K., 2015. Marine Historical Ecology in Conservation: Applying the Past to Manage for the Future. Univ of California Press.
Laidre, K.L., Jameson, R.J., 2006. Foraging patterns and prey selection in an increasing and expanding sea otter population. J. Mammal. 87, 799–807.
Laidre, K.L., Jameson, R.J., Demaster, D.P., 2001. An estimation of carrying capacity for sea otters along the California coast. Marine Mammal Science 17, 294–309.
Lotze, H.K., Worm, B., 2009. Historical baselines for large marine mammals. Trends Ecol. Evol. 24, 254–262.
Lotze, H.K., Lenihan, H.S., Bourque, B.J., Bradbury, R.H., Cooke, R.G., Kay, M.C., Kidwell, S.M., Kirby, M.X., Peterson, C.H., Jackson, J.B., 2006. Depletion, degradation, and recovery potential of estuaries and coastal seas. Science 312, 1806–1809.
Lynn, R.J., Bograd, S.J., Chereskin, T.K., Huyer, A., 2003. Seasonal renewal of the California Current: the spring transition off California. J. Geophys. Res. Oceans 108.
Magera, A.M., Mills Flemming, J.E., Kaschner, K., Christensen, L.B., Lotze, H.K., 2013. Recovery trends in marine mammal populations. PLoS One 8, e77908.
Maldini, D., Ward, C., Cecchetti, A., Riggin, J., 2010. Southern sea otter diet in a soft sediment community. Journal of Marine Animals and Their Ecology 3, 27–36.
Marshall, K.N., Stier, A.C., Samhouri, J.F., Kelly, R.P., Ward, E.J., 2016. Conservation challenges of predator recovery. Conserv. Lett. 9, 70–78.

Mayer, K., Tinker, M., Nicholson, T., Murray, M., Johnson, A., Staedler, M., Fujii, J., Van Houtan, K., 2019. Surrogate rearing a keystone species to enhance population and ecosystem restoration. Oryx 1–11.

Methot, R.D., Botsford, L.W., 1982. Estimated preseason abundance in the California Dungeness crab (Cancer magister) fisheries. Can. J. Fish. Aquat. Sci. 39, 1077–1083.

Moxley, J.H., Nicholson, T.E., Van Houtan, K.S., Jorgensen, S.J., 2019. Non-trophic impacts from white sharks complicate population recovery for sea otters. Ecology and Evolution 9, 6378–6388.

Newman, M., Alexander, M.A., Ault, T.R., Cobb, K.M., Deser, C., Di Lorenzo, E., Mantua, N.J., Miller, A.J., Minobe, S., Nakamura, H., 2016. The Pacific decadal oscillation, revisited. J. Clim. 29, 4399–4427.

Newsome, S.D., Tinker, M.T., Monson, D.H., Oftedal, O.T., Ralls, K., Staedler, M.M., Fogel, M.L., Estes, J.A., 2009. Using stable isotopes to investigate individual diet specialization in California sea otters (Enhydra lutris nereis). Ecology 90, 961–974.

Nicholson, T.E., Mayer, K.A., Staedler, M.M., Fujii, J.A., Murray, M.J., Johnson, A.B., Tinker, M.T., Van Houtan, K.S., 2018. Gaps in kelp cover may threaten the recovery of California sea otters. Ecography 41, 1751–1762.

Pearl, R., 1928. The Rate of Living. University Press London.

Richerson, K., Punt, A.E., Holland, D.S., 2020. Nearly a half century of high but sustainable exploitation in the Dungeness crab (Cancer magister) fishery. Fish. Res. 226, 105528.

Roman, J., Palumbi, S., 2003. Whales before whaling in the North Atlantic. Science 301, 508–510.

Roman, J., Altman, I., Dunphy-Daly, M.M., Campbell, C., Jasny, M., Read, A.J., 2013. The Marine Mammal Protection Act at 40: status, recovery, and future of U.S. marine mammals. Ann. N. Y. Acad. Sci. 1286, 29–49.

Roman, J., Dunphy-Daly, M.M., Johnston, D.W., Read, A.J., 2015. Lifting baselines to address the consequences of conservation success. Trends Ecol. Evol. 30, 299–302.

Scharff-Olsen, C.H., Galatius, A., Teilmann, J., Dietz, R., Andersen, S.M., Jarnit, S., Kroner, A.-M., Botnen, A.B., Lundström, K., Møller, P.R., 2019. Diet of seals in the Baltic Sea region: a synthesis of published and new data from 1968 to 2013. ICES J. Mar. Sci. 76, 284–297.

Shanks, A., 2013. Atmospheric forcing drives recruitment variation in the Dungeness crab (Cancer magister), revisited. Fish. Oceanogr. 22, 263–272.

Shanks, A.L., Roegner, G.C., 2007. Recruitment limitation in Dungeness crab populations is driven by variation in atmospheric forcing. Ecology 88, 1726–1737.

Shirley, T.C., Bishop, G., O'Clair, C.E., Taggart, S.J., Bodkin, J.L., 1996. Sea otter predation on Dungeness crabs in Glacier Bay, Alaska. In: High Latitude Crabs: Biology, Management, and Economics. Alaska Sea Grant College Program, Alaska.

Sweetnam, D., 2010. Review of selected California fisheries for 2009: coastal pelagic finfish, market squid, red abalone, dungeness crab, pacific herring, groundfish/nearshore live-fish, highly migratory species, kelp, California halibut, and sandbasses. In: California Cooperative Oceanic Fisheries Investigations Reports. California Department of Fish and Game, Monterey, USA, pp. 14–38.

Taggart, S.J., O'Clair, C.E., Shirley, T.C., Mondragon, J., 2004. Estimating Dungeness crab (Cancer magister) abundance: crab pots and dive transects compared. Fish. Bull. 102, 488–497.

Thometz, N.M., Staedler, M.M., Tomoleoni, J.A., Bodkin, J.L., Bentall, G.B., Tinker, M.T., 2016. Trade-offs between energy maximization and parental care in a central place forager, the sea otter. Behav. Ecol. 27 (5), 1552–1566.

Tinker, M.T., Hatfield, B.B., 2018. In: U.S.G. Survey (Ed.), Annual California Sea Otter Census - 1985–2014 Spring Census Summary: U.S. Geological Survey Data Release.

Tinker, M.T., Bentall, G., Estes, J.A., 2008. Food limitation leads to behavioral diversification and dietary specialization in sea otters. PNAS 105, 560–565.

Tinker, M.T., Guimaraes Jr., P.R., Novak, M., Marquitti, F.M.D., Bodkin, J.L., Staedler, M.M., Bentall, G., Estes, J.A., 2012. Structure and mechanism of diet specialisation: testing models of individual variation in resource use with sea otters. Ecol. Lett. 15, 475–483.

Tinker, M.T., Gill, V.A., Esslinger, G.G., Bodkin, J., Monk, M., Mangel, M., Monson, D.H., Raymond, W.W., Kissling, M.L., 2019. Trends and carrying capacity of sea otters in Southeast Alaska. J. Wildl. Manag. 83, 1073–1089.

USFWS, 2013. Southwest Alaska Distinct Population Segment of the Northern Sea Otter (Enhydra lutris kenyoni) Recovery Plan. Southwest Alaska Distinct Population Segment of the Northern Sea Otter (*Enhydra lutris kenyoni*) Recovery Plan.

Valdivia, A., Wolf, S., Suckling, K., 2019. . Marine mammals and sea turtles listed under the US Endangered Species Act are recovering. PloS one 14 (1), e0210164.

Van Houtan, K.S., Halley, J.M., 2011. Long-term climate forcing in loggerhead sea turtle nesting. PLoS One 6, e19043.

Wild, P.W., Ames, J.A., 1974. A Report on the Sea Otter, *Enhydra lutris* L., in California.