



Characterizing the impact of recovering sea otters on commercially important crabs in California estuaries

Tracy M. Grimes^{1,*}, M. Tim Tinker², Brent B. Hughes³, Katharyn E. Boyer⁴,
Lisa Needles⁵, Kathryn Beheshti², Rebecca L. Lewison¹

¹Department of Biology, San Diego State University, San Diego, CA 92182, USA

²Department of Ecology and Evolutionary Biology, University of California Santa Cruz, Santa Cruz, CA 95060, USA

³Department of Biology, Sonoma State University, Rohnert Park, CA 94928, USA

⁴Estuary & Ocean Science Center, San Francisco State University, Tiburon, CA 94920, USA

⁵Center for Coastal Marine Sciences, California Polytechnic State University, San Luis Obispo, CA 93407, USA

ABSTRACT: Protective legislation and management have led to an increase in California's sea otter *Enhydra lutris nereis* population. While sea otter recovery has been linked to ecosystem benefits, sea otter predation may negatively affect commercially valuable species. Understanding the potential influence of sea otters is of particular importance as their range expands into estuaries that function as nurseries for commercially valuable species like Dungeness crab *Metacarcinus magister*. We consider how sea otter predation has affected the abundance and size of juvenile Dungeness crab in Elkhorn Slough, California, USA, and analyzed cancrid crab abundance and size across 4 California estuaries with and without sea otters to understand how biotic and abiotic factors contribute to observed variation in crab size and abundance. We compared trends in southern sea otters relative to Dungeness crab landings in California to assess whether increasing sea otter abundance have negatively impacted landings. In Elkhorn Slough, juvenile Dungeness crab abundance and size have declined since 2012, coinciding with sea otter population growth. However, the impact of sea otters on juvenile Dungeness crab size was habitat-specific and only significant in unvegetated habitat. Across estuaries, we found that cancrid crab abundance and size were negatively associated with sea otter presence. While abiotic factors varied among estuaries, these factors explained little of the observed variation in crab abundance or size. Although we found evidence that sea otters can have localized effects on cancrid crab populations within estuaries, we found no evidence that southern sea otters, at recent population sizes, have negatively impacted Dungeness crab landings in California from 2000–2014.

KEY WORDS: *Enhydra lutris* · Dungeness crab · Species recovery · Predation · Foraging ecology

Resale or republication not permitted without written consent of the publisher

1. INTRODUCTION

Top predators can have profound influences on ecosystem structure and functioning, but many have been depleted globally due to anthropogenic factors (Estes et al. 2011, Ripple et al. 2014). When threats to top predators are mitigated, some populations are able to recover through natural recolonization or managed reintroductions (Magera et al. 2013). While conservation and management efforts are often nec-

essary and beneficial for protected species recovery, they can lead to unexpected effects on the environment and prey populations (Kemp et al. 2012, Ripple & Beschta 2012). In some systems, altered biotic interactions have been found to impact resources on which humans rely, such as livestock depredation effects by wolves (Muhly & Musiani 2009). Potential negative effects from the recovery of top predators on economically important resources present a management challenge, particularly when the recovering

*Corresponding author: tracy.m.grimes@gmail.com

species has protected status (Marshall et al. 2016, Guerra 2018).

In coastal systems, estuaries play an important role as nursery grounds for commercially valuable species (Beck et al. 2001). However, many top predators were extirpated from estuaries before studies documented the ecological role of the predators in these systems and the indirect cascading effects on the functioning of nursery habitats (Jackson et al. 2001, Heithaus et al. 2012). This lack of knowledge may have distorted our understanding of predator roles in nursery habitat structure and process, influencing our expectations of ecosystem function following predator recovery. In California, USA, the southern sea otter *Enhydra lutris nereis* survived near extirpation from the fur trade of the 18th and 19th centuries (Kenyon 1969), was listed as threatened in 1977 under the US Endangered Species Act (US Fish and Wildlife Service 2003), and has only recently re-occupied estuarine habitats.

Recovery of the southern sea otter occurred from a remnant group of approximately 50 individuals in the Big Sur area of central California; a recent estimate of the current population now numbers 2962 individuals (Hatfield et al. 2019). The rate of recovery has been relatively slow compared to northern populations (Estes 1990, Hatfield et al. 2019). Southern sea otters occupy just 13% of their historic range, with the majority of the population occurring in resource-limited areas (Hatfield et al. 2019). Because of this spatial constraint, further range expansion has been identified as an enabling condition for sustained and continued population growth (Tinker et al. 2008b). To augment natural range expansion, wildlife managers are considering reintroducing sea otters to additional habitats within their historic range, including estuaries (Mayer et al. 2019). Historical and archaeological evidence indicates that southern sea otters were once abundant in California estuaries (Ogden 1941, Jones et al. 2011), which can provide relatively protected habitats compared to higher-mortality coastal zones (Tinker et al. 2016, Nicholson et al. 2018). Furthermore, estuarine habitats will likely play a critical role in supporting future southern sea otter population growth and range expansion in California (Silliman et al. 2018, Hughes et al. 2019).

Estuaries provide important habitat for many coastal species including Cancridae crabs, which are also important prey for sea otters. This sets up a potential conflict between sea otter recovery in estuaries and crab fisheries, since one cancrid species in particular, Dungeness crab *Metacarcinus magister*, is a highly valued commercial species in California with a landed value up to \$86 US million annually (Cal-

ifornia Department of Fish and Wildlife 2014). The Dungeness crab fishery relies heavily on the annual recruitment of juveniles because the fishery frequently removes 80–90% of legal-sized (>159 mm) adult males each fishing season (Juhasz & Kalvass 2011). While Dungeness crab may be the most commercially valuable cancrid crab in California, other cancrid species are also harvested and share similar life histories and environmental requirements (Carroll & Winn 1989, Wing et al. 1995) with one exception; Dungeness crabs use estuarine habitats only as nursery grounds (Tasto 1983, Gunderson et al. 1990, Armstrong et al. 2003). Dungeness crabs reach sexual maturity after about 1 yr in estuaries and move towards the open coast when they are 100–110 mm, whereas other cancrid crabs can be found in estuaries as juveniles and adults. While juvenile Dungeness crabs may recruit to other nearshore environments as well as estuaries, growth rates in estuaries are faster and thought to compensate for the high predation risk during early life history stages in these habitats (Gunderson et al. 1990, Armstrong et al. 2003).

Sea otters can exert both direct (consumptive) and indirect influences on prey species such as the Dungeness crab. Complex food web interactions can lead to unanticipated indirect effects: for example, in one California estuary (Elkhorn Slough, CA, USA), sea otters have been found to indirectly increase expansion of eelgrass beds (Hughes et al. 2013) and also improve kelp habitat on the outer coast (Estes et al. 2004), which can benefit some species of finfish, crabs, and other invertebrate prey such as abalone (Reisewitz et al. 2006, Tinker et al. 2008a, Markel & Shurin 2015, Raimondi et al. 2015, Lee et al. 2016). While sea otters have been linked to positive indirect effects on some fishery species (e.g. *Sebastes* spp.; Markel & Shurin 2015), there is also evidence to suggest that direct effects of sea otter predation have led to decreased size and abundance of crab and other invertebrate fishery species (Shirley et al. 1996, Larson et al. 2013). These cases suggest that recovery of sea otters in estuaries may have both positive and negative impacts on commercially important invertebrate species. In California, there is overlap in the distribution of sea otters and the Dungeness crab fishery (Hatfield et al. 2011) but there is limited information on the interaction between them (e.g. bycatch of sea otters by the fishery or competition between them). Fishing for Dungeness crabs is most typical at depths greater than 30 m. While sea otters are capable of diving to these depths (Bodkin et al. 2004, Thometz et al. 2016), foraging dives in California average less than 9 m (Thometz et al. 2016).

We examined the effects of sea otters on cancrid crabs across 4 estuaries in California (see Section 2.1), with detailed analyses of one estuary, to evaluate how sea otter recovery could impact the Dungeness crab fishery through predation on juvenile crabs. We first examined changes in juvenile Dungeness crab abundance and size over 4 yr in an estuary with sea otters, where we expected a decline in abundance and size of juvenile Dungeness crab as a function of sea otter density. We then considered whether the relationship between juvenile Dungeness crabs and sea otter density varied between eelgrass and unvegetated habitat types within an estuary. Since juvenile Dungeness crabs are known to use eelgrass as refuge from predators, we expected to see more juvenile Dungeness crabs but fewer foraging sea otters in eelgrass habitat. Finally, we assessed variation in cancrid crab abundance and size across 4 California estuaries to examine how the presence or absence of sea otters contributed to observed variation. As part of this comparison, we compared trends in southern sea otter abundance to Dungeness crab landings in California. We predicted that in estuaries without sea otters, cancrid crabs would be higher in abundance and larger in size because of direct effects of sea otter predation. Our predictions about the impacts of sea otter consumption of juvenile crabs in estuaries on commercial fishery landings were more ambiguous: if there is a strong link between juvenile crab popu-

lations in estuaries and adult populations of the outer coast, then we would expect a negative relationship between sea otter abundance and crab landings; conversely, if the link between estuaries and adult crab populations is weaker, then we would expect no relationship. Characterizing cancrid crab abundance and size in estuaries across California with and without sea otters can provide a clearer understanding of the potential impact of future reintroductions or natural range expansion of a key predator on commercially important species and can offer critical information for wildlife and resource managers working to concurrently recover sea otters and support sustainable fisheries in California.

2. MATERIALS AND METHODS

2.1. Study estuaries

We focused on 4 estuaries along the central coast of California, USA: Drakes Estero and San Francisco Bay where sea otters were absent, and Elkhorn Slough and Morro Bay where sea otters were present (Fig. 1). At the time of this study, Elkhorn Slough was the most extensively used estuary by sea otters in California, while Morro Bay served as an intermediate-use estuary, since sea otters primarily occurred in the harbor area rather than the inland estuarine

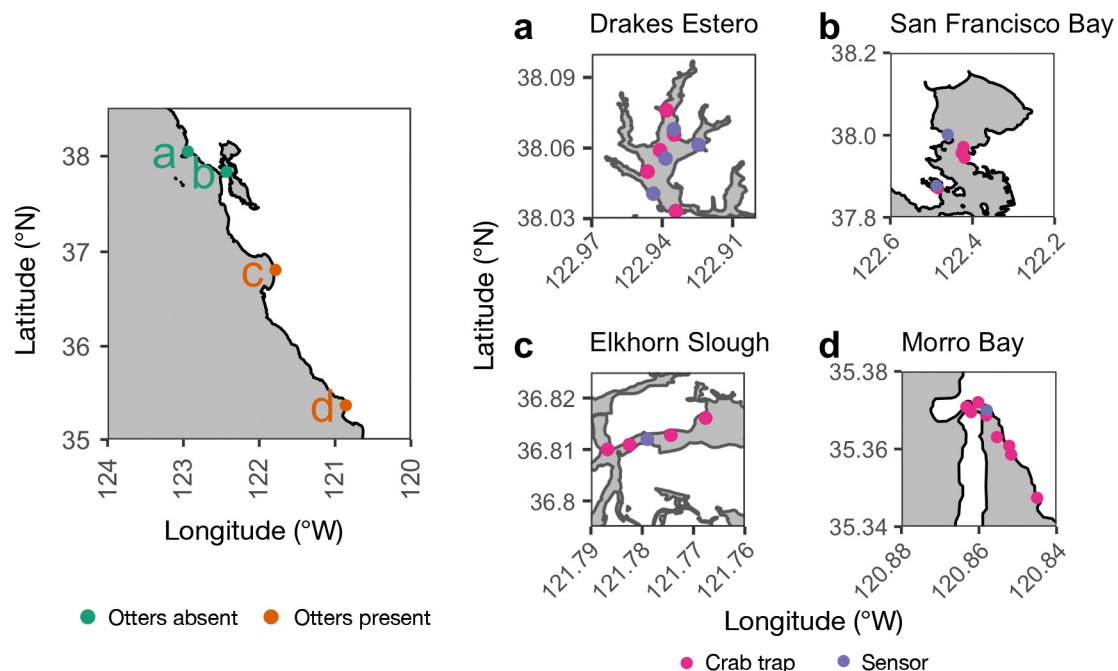


Fig. 1. Central California, USA, showing the 4 estuaries sampled for Dungeness crabs. Letters represent each estuary; colors note either the presence/absence of sea otters or the locations of crab traps and water quality samples

areas. San Francisco Bay and Drakes Estero were both north of the sea otter range in California but were likely to experience sea otter recolonization through natural expansion or managed reintroductions, given that archaeological evidence suggests that sea otters once inhabited these systems (Jones et al. 2011).

Since Elkhorn Slough was the most extensively inhabited California estuary for sea otters and has been the focus of long-term otter monitoring, we focused on this estuary to assess how juvenile Dungeness crab abundance and size changed in response to predation pressure from sea otters. In Elkhorn Slough, our study focused on a portion of the main channel dominated by soft, unvegetated sediment and eelgrass habitat where juvenile Dungeness crabs were known to occur (Hughes et al. 2013). To distribute sampling effort equally between unvegetated and eelgrass habitat, we divided the estuary into 4 strata that reflected increasing distance from the ocean and used distance from the ocean in our analyses to capture this spatial component of the study site.

2.2. Sampling crab abundance and size

We sampled crab abundance and size from 4 cancrinid species for this study — *Metacarcinus magister*, *Cancer productus*, *Romaleon antennarium*, and *Metacarcinus gracilis*—across all 4 estuaries following methods described in Hughes et al. (2013). We sampled Elkhorn Slough sites 1–4 times mo^{-1} in 2016 (May–August and October–December) and 2017 (March and May–August); Morro Bay sites 3 times in 2017 (January, July, and October); San Francisco Bay sites 4 times in 2017 (April, twice in August, and December); and Drakes Estero sites 3 times in 2017 (June, July, and August). Due to logistical constraints, we were unable to sample all 4 sites at the same time or with the same frequency. Crab traps were metal-framed modified shrimp pots ($61 \times 61 \times 23$ cm; 0.0856 m^3) with 22×22 mm mesh. The traps had a circular funnel opening approximately 120 mm in circumference to allow for crabs of all size classes to enter but prevent sea otters from becoming entrapped. A minnow trap with a 25 mm circular opening and 6×6 mm mesh was also deployed with each shrimp pot to capture crabs that were small enough to escape through the mesh of the shrimp pots. Traps were baited with anchovies and set for approximately 24 h. Captured crabs were identified to species, measured at the widest part of the carapace, and released at least 50 m from redeployed

traps as specified by a previous study (Hughes et al. 2013). Crab carapace width was used as a metric of crab size. To standardize abundance across all traps, catch per unit effort (CPUE) was calculated as the number of cancrinid crabs caught per trap per 24 h period.

In Elkhorn Slough, information on Dungeness crab size and abundance in 2012 was taken from Hughes et al. (2013). In 2016, we used comparable trapping methods, with one key difference to address questions about habitat differences; in 2012, traps were deployed in 4 main eelgrass beds, whereas traps in 2016 were deployed in both eelgrass and unvegetated habitat.

2.3. Sea otter spatial distribution within Elkhorn Slough

We obtained information on sea otter distribution from 2 data sources with different temporal scales. The first data source was an annual statewide census conducted by the US Geological Survey (USGS) with data from 2012 and 2016 (Tinker & Hatfield 2017, Hughes et al. 2019, their Supplement 2). These annual census data were used to assess the effect of sea otters on Dungeness crab in Elkhorn Slough between 2012 and 2016. The second source was a sea otter population study conducted in Elkhorn Slough from 2013–2016 and included biweekly censuses. We used the biweekly censuses from May–September 2016 to obtain finer scale distribution patterns for sea otters within Elkhorn Slough than those provided by the 2016 annual census data. During the surveys, pairs of observers located at all accessible vantage points within Elkhorn Slough used high-power (50–80 \times) Questar spotting scopes to count and mark the location of individual sea otters on a map (1:24 000), which was digitized using GIS. In addition to location, animal behavior (e.g. foraging, resting, grooming) was noted in association with each observed sea otter. We filtered observations to sea otters that were foraging and created a kernel density surface using a 200 m smoothing parameter (to account for uncertainty in recorded locations and the mobility of sea otters) using the Spatial Analyst toolbox in ArcGIS (ArcMap v.10.6; ESRI). The density of foraging sea otters, calculated as otters ha^{-1} , was used to capture the potential impacts of sea otter predation on prey species. Kernel density layers were estimated separately from the annual and biweekly censuses. The mean kernel density value for each year (for annual census) or month (for biweekly census) was extracted

by strata for both census types, and by habitat type (eelgrass vs. unvegetated) in the case of biweekly data, using the Zonal Statistics tool in ArcGIS. To account for any bias due to low sample size in the biweekly otter data, we calculated a monthly weighted moving average density for comparisons with crab survey data (June–August 2016), with the primary month receiving 3 times the weight of the preceding and subsequent months.

In addition to census data, we also used diet observations collected during the Elkhorn Slough study following methods described by Tinker et al. (2008a). Diet observations occurred in both eelgrass and unvegetated habitats. These foraging data allowed us to assess whether sea otters were consuming Dungeness crabs in significant numbers, and whether selection of crabs was size-specific. We compared the composition of prey items in the sea otter diet from 2 periods—1999–2012 (Hughes et al. 2013) and 2013–2016—to determine whether sea otter predation rates on cancrid crabs have remained constant or have changed over time.

2.4. Accounting for environmental variability

To consider how environmental variability may affect cancrid crab abundance, we compiled archived sea surface temperature (SST) and the Biologically Effective Upwelling Transport Index data (BEUTI; Jacox et al. 2018) from locations outside of each estuary. SST data came from NOAA's National Data Buoy Center (PRYC1, 46237, 46092, 46011). We selected BEUTI as the upwelling index over the historically used Bakun Index for the US West coast because it provides an estimate of vertical nitrate flux near the coast (Jacox et al. 2018). Daily measures of BEUTI were available to download at the nearest degree of latitude for each estuary. We considered data from time periods where cancrid crab recruitment would be impacted (Tasto 1983, Miller & Shanks 2004). We grouped SST and BEUTI data into 3 time periods to correspond to the peak timing for different crab larval stages based on prior studies conducted in California (Tasto 1983): early larval stage (averaging values between mid-December–mid-February), late larval stage (averaging values between mid-February–mid-March), and megalopal stage (averaging values between mid-March–mid-April).

We also compiled SST and salinity data within each estuary from periods when crab trapping occurred to consider along with variation in cancrid crab size (Fig. 1). For San Francisco Bay, Elkhorn

Slough, and Morro Bay, we used estuarine SST and salinity data from the National Estuarine Research Reserve System Centralized Data Management Office (NERRS 2012). For Drakes Estero, estuarine SST and salinity data were collected with a handheld water quality meter (ProDSS; YSI).

2.5. Dungeness crab fishery landings and sea otter population census

To compare trends between the Dungeness crab fishery and the southern sea otter population, we gathered data collected between 2000 and 2014 from the California Department of Fish and Wildlife (CDFW) statewide reports on commercial Dungeness crab landings and USGS's annual California sea otter census surveys. To account for varying levels of fishing effort across years, we multiplied the summed annual landings by the proportion of active commercial Dungeness crab fishing permits relative to the average number of active permits across all years. The annual California sea otter census survey was conducted each spring (with the exception of 2011) and included shore-based and aerial counts. Shore-based observations were used in accessible areas where otters could readily be seen via Questar spotting scopes. Aerial surveys were used in areas where otters were often located further offshore and entailed transects flown parallel to the shore out to the 60 m depth contour (Hatfield et al. 2019). The census counts used are a 3 yr running average of counts in order to reduce the influence of anomalously high or low counts from any particular year (US Fish and Wildlife Service 2003).

2.6. Data analysis

All analyses were performed in R 3.4.2 (R Core Team 2018). Due to the nature of the data, we *a priori* expected a large number of zeros in our crab abundance data. Therefore, we measured overdispersion in crab abundance using the R package 'sjstats' (Lüdtke 2019). For some models, overdispersion of data precluded use of a Poisson distribution so we instead used a negative binomial distribution. An additional zero-inflation parameter was used in both models specific to Dungeness crab abundance in Elkhorn Slough (between 2012 and 2016, and 2016 only). Our analyses included both generalized linear models (GLMs) and mixed models (GLMMs), using the R package 'glmmTMB' (Brooks et al. 2017).

When building either GLMs or GLMMs, predictor variables were dropped from subsequent models if found to have no individual significance. Candidate models were ranked using Akaike's information criterion with a correction for small sample sizes (AIC_C). We assessed the relative importance of predictor variables by summing AIC weights (AIC_w) of models that included variables of interest (Burnham & Anderson 2002).

2.6.1. Relationship between sea otters and Dungeness crabs in Elkhorn Slough

In Elkhorn Slough, we analyzed the relationship between sea otter density and Dungeness crab abundance and size as a function of habitat type (eelgrass vs. unvegetated), abundance of other competitively dominant crab species, and distance of the crab trap from the ocean. We used the quadratic function of distance from the ocean in our models because it provided a better fit than a linear effect, and because we expected that the effect of proximity to the ocean might be non-linear.

Using the annual otter census data, we built 2 sets of candidate GLMs (Tables S1 & S2 in the Supplement at www.int-res.com/articles/suppl/m655p123_supp.pdf) with Dungeness crab abundance and size as the respective response variables. Predictor variables included the average annual sea otter density in the corresponding strata of each crab trap, quadratic distance from ocean, and year. Only data from eelgrass habitat in 2012 and 2016 was used in this analysis.

With finer scale crab data across 2 habitat types and biweekly otter census data for 2016, we conducted a second set of analyses of Dungeness crab abundance and size, using biweekly sea otter census data to capture temporally and spatially explicit density estimates. We built GLMs with Dungeness crab abundance or size as response variables. Our candidate models included local sea otter density, habitat type, quadratic distance from ocean, and other cancrid crab abundance as predictor variables (Tables S3 & S4).

2.6.2. Variation in cancrid crab abundance and size across estuaries

Across all estuaries, we used GLMMs to determine the effects of offshore SST, BEUTI, and sea otter presence (fixed effects) on cancrid crab abundance, using estuary as a random effect. Since estuaries

with and without sea otters did not experience the same range of SST and BEUTI values, we considered these effects in separate GLMMs based on whether otters were present or absent. With compiled SST and BEUTI across 3 time periods (early, late, or megalopal larval stage), we fit and compared separate models for each larval stage. Offshore SST and BEUTI were correlated and therefore were not included together in the same model.

We tested for differences in crab size, estuarine temperature, and salinity across estuaries using non-parametric Kruskal-Wallis rank sum tests, as data were not normal and exhibited unequal variances among estuaries. Post hoc Wilcoxon pairwise comparisons were made to determine which estuaries differed from one another. Significance levels were assessed at $\alpha = 0.05$.

2.6.3. Trends in the California Dungeness crab fishery and sea otter population counts

To assess the trends between the sea otter population counts and the Dungeness crab fishery landings, we used Spearman correlations. Correlations were conducted on 3 time frames: (1) year-to-year comparison of sea otter counts and Dungeness crab landings to determine if sea otters have any impact on the adult population (outside of estuaries), (2) sea otter counts lagged by 3 yr, or (3) sea otter counts lagged by 4 yr to account for the time it would take juvenile Dungeness crabs in estuaries to enter the fishery. We only used landings data from Monterey and Morro Bay, since these were the only fishery regions that overlapped with the sea otter population range. The landings data were log transformed in order to meet the assumption of normality. Additionally, we compiled Dungeness crab fishery landings from each fishing region in California to assess general patterns in landings over time in areas where sea otters were present and absent.

3. RESULTS

3.1. Effects of sea otters on Dungeness crabs in Elkhorn Slough

Between 2012 and 2016, we found that increasing sea otter density negatively affected Dungeness crab abundance (Fig. 2a, Table 1). Sea otter density was the most important predictor variable ($AIC_w = 1$). Year was the most important predictor variable for

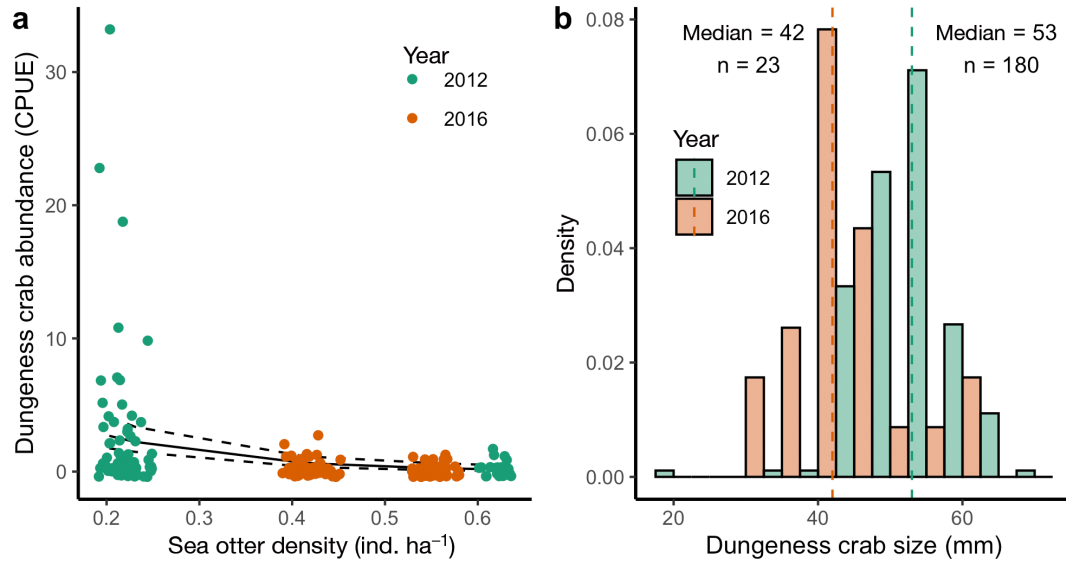


Fig. 2. (a) Model predictions for Dungeness crab abundance (catch per unit effort, CPUE) as a function of sea otter density from 2012 and 2016 in Elkhorn Slough. Solid line: predicted mean; dashed lines: $\pm 95\%$ CI. (b) Distributions of Dungeness crab size (carapace width) from 2012 and 2016 in Elkhorn Slough. Dashed lines: median values for each year

Table 1. Predictor variables ranked according to relative importance (as Akaike's information criterion weights, AIC_w) for each set of Dungeness crab abundance and size candidate models for comparisons between 2012 and 2016 in Elkhorn Slough

Response variable	Predictor variable	Relative importance (AIC_w)	Rank
Crab abundance	Sea otter density	1	1
	Year	0.81	2
Crab size	Sea otter density	0.76	2
	Year	1	1

Dungeness crab size ($AIC_w = 1$); median carapace width declined from 53 mm in 2012 to 42 mm by 2016 (Fig. 2b, Table 1). Furthermore, there was no statistically significant relationship between Dungeness crab size and sea otter density after controlling for year (Fig. 2b, Table 1).

Additionally, there was evidence of a shift in the composition of sea otter diets between study periods (Fig. S1). The composition of sea otter diets in Elkhorn Slough prior to 2012 consisted of 43% cancrid crabs and 39% clams, but in the more recent time period (2013–2016) the diet had shifted to 79% clam species and 3% cancrid crab species.

Using the higher temporal resolution (biweekly) data for 2016, we found that Dungeness crab abundance was positively associated with sea otter density, particularly in locations closer to the ocean (Fig. 3a). Both sea otter density and distance from the

ocean were found to have high relative importance for Dungeness crab abundance ($AIC_w = 0.999$ for both; Table 2). When we considered habitat type, we found that Dungeness crab sizes declined with increasing sea otter density; however, this pattern was more pronounced in unvegetated habitat (Fig. 3b, Table 2).

3.2. Abiotic and biotic drivers of cancrid crab abundance and size across estuaries

Cancrid crab abundance was significantly lower in estuaries with sea otters present ($Z = -4.749$, $p < 0.001$; Fig. 4a). In estuaries where sea otters were present, the best performing model for crab abundance included BEUTI at the early larval stage for crabs (Table 3) with positive BEUTI values associated

Table 2. Predictor variables ranked according to relative importance (as Akaike's information criterion weights, AIC_w) for each set of Dungeness crab abundance and size candidate models during 2016 only in Elkhorn Slough

Response variable	Predictor variable	Relative importance (AIC_w)	Rank
Crab abundance	Sea otter density	0.999	1
	Distance from ocean	0.999	1
	Habitat	0.429	2
Crab size	Sea otter density	1	1
	Habitat	0.79	2

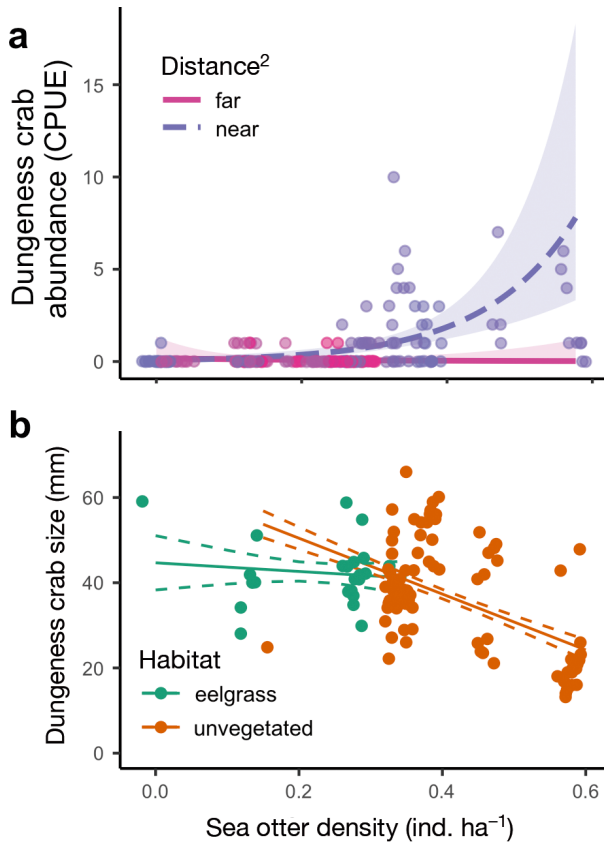


Fig. 3. Model predictions for Dungeness crab (a) abundance (catch per unit effort, CPUE) during 2016 in Elkhorn Slough as a function of sea otter density, distance of the trap from the ocean, and their interaction (shading: 95 % CI of the mean predicted values for the 2 study zones 'near' the ocean and the 2 study zones 'far' from the ocean), and (b) size (carapace width) as a function of sea otter density, habitat, and their interaction from 2016 in Elkhorn Slough (dashed lines: upper and lower limits to the 95 % CI of the predicted mean values within eelgrass and unvegetated habitats)

with higher crab abundance (Fig. 5a). For estuaries where otters were absent, there was no single model for crab abundance best supported by the data, based upon ΔAIC_C values (Table 3). We assessed the relative importance of each fixed effect variable contained in the top 4 models, each of which contained a single fixed effect predictor variable in addition to the random estuary effect. The variables in order of relative importance were SST at late larval stage ($AIC_w = 0.295$; Fig. 5b), BEUTI at both late and early larval stage ($AIC_w = 0.265$), and SST at early larval stage ($AIC_w = 0.173$).

Crab carapace width differed significantly by estuary ($H = 484.34$, $df = 3$, $p < 0.001$; Fig. 4b). A post hoc Wilcoxon pairwise comparison showed that the 2 estuaries with sea otters, Elkhorn Slough and Morro Bay, did not differ significantly from each other ($p =$

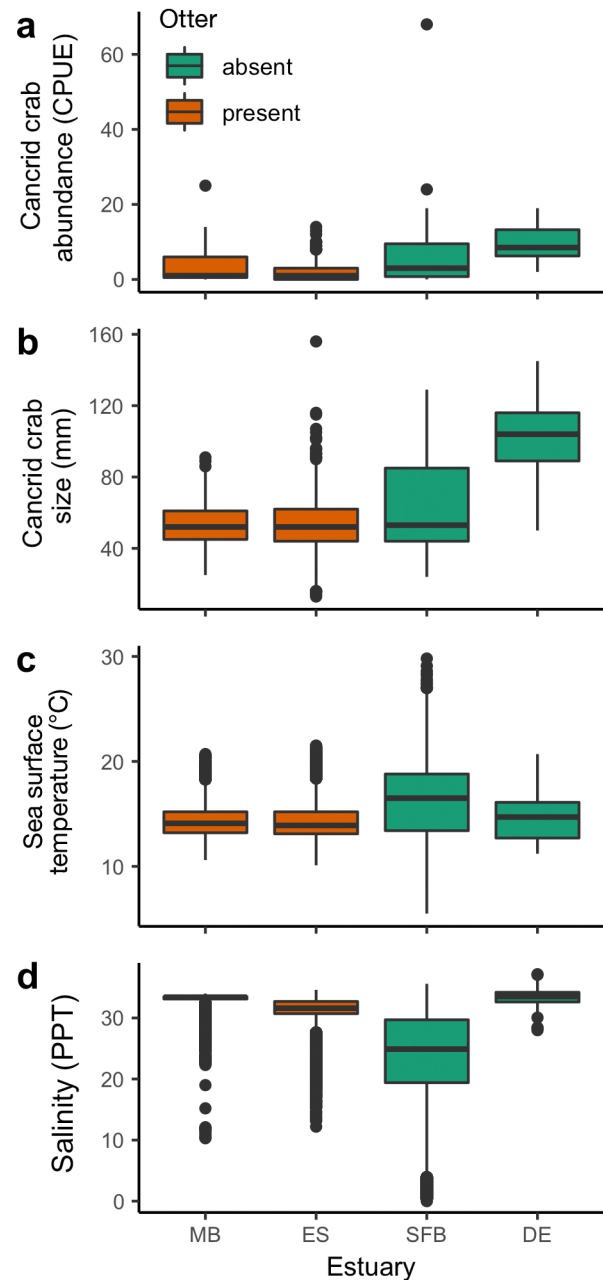


Fig. 4. Cancrid crab (a) abundance (catch per unit effort, CPUE) and (b) size (carapace width), and estuarine (c) sea surface temperature and (d) salinity at the 4 estuaries (MB: Morro Bay; ES: Elkhorn Slough; SFB: San Francisco Bay; DE: Drakes Estero). Center line: median; dots: outliers. Colors indicate presence or absence of sea otters in the estuary

0.984), but both differed significantly from San Francisco Bay ($p = 0.001$ and $p = 0.020$, respectively) and Drakes Estero ($p < 0.001$ for both). Crabs in Drakes Estero were significantly larger than crabs at any other estuary, including San Francisco Bay ($p < 0.001$). SST varied significantly among estuaries ($H =$

Table 3. Candidate models and ranking for cancrid crab abundance across estuaries. AIC_C : Akaike's information criterion with a correction for small sample sizes; ΔAIC_C : difference from the best model; AIC_w : Akaike weights. BEUTI: Biologically Effective Upwelling Transport Index; SST: sea surface temperature

Response variable	Models	AIC_C	ΔAIC_C	df	Relative importance (AIC_w)
Crab abundance in estuaries with otters present	Early BEUTI + (1 Location)	2021.6	0	4	0.8925
	Early SST + (1 Location)	2027	5.4	4	0.0591
	Late SST + (1 Location)	2028.8	7.3	4	0.0234
	Mega SST + (1 Location)	2030.2	8.7	4	0.0116
	Late BEUTI + (1 Location)	2030.5	8.9	4	0.0103
	Mega BEUTI + (1 Location)	2032.9	11.3	4	0.0031
Crab abundance in estuaries with otters absent	Late SST + (1 Location)	308	0	4	0.295
	Late BEUTI + (1 Location)	308.3	0.2	4	0.265
	Early BEUTI + (1 Location)	308.3	0.2	4	0.265
	Early SST + (1 Location)	309.1	1.1	4	0.1713
	Mega SST + (1 Location)	316.8	8.8	4	0.0037

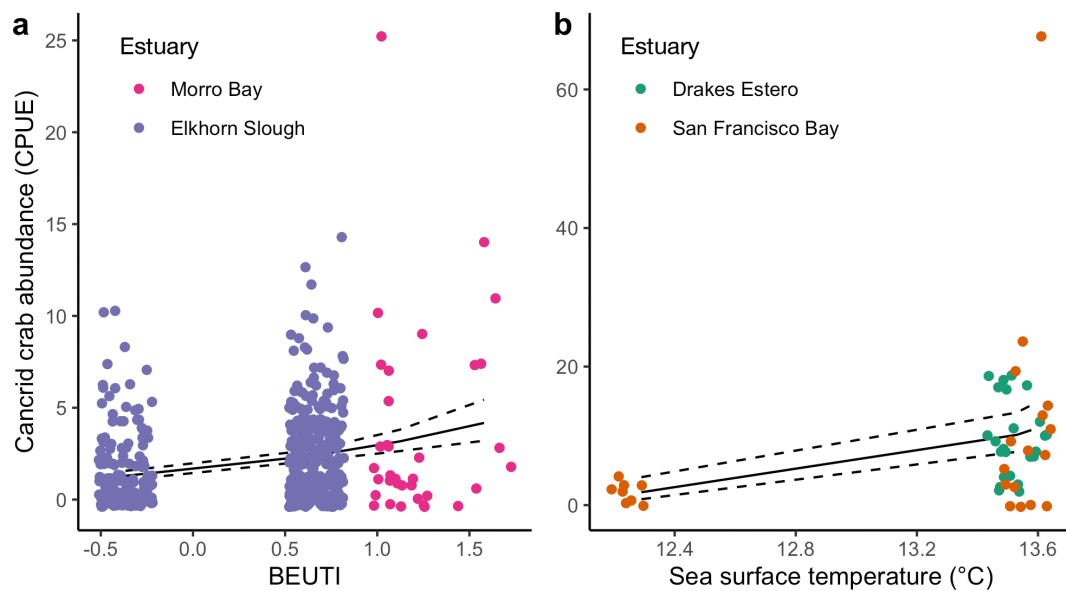


Fig. 5. Model predictions of cancrid crab abundance (catch per unit effort, CPUE) (a) in Elkhorn Slough and Morro Bay as a function of the Biologically Effective Upwelling Transport Index (BEUTI) at the early crab larval stage, and (b) in San Francisco Bay and Drakes Estero as a function of sea surface temperature at the late larval stage. Dashed lines: upper and lower bounds of the 95% CI; solid lines predicted mean values. Note the difference in scale on the y-axes

20950, $df = 3$, $p < 0.001$; Fig. 4c), with the exception of Morro Bay and Drakes Estero ($p = 0.074$). Salinity also varied significantly among all estuaries ($H = 114646$, $df = 3$, $p < 0.001$; Fig. 4d). San Francisco Bay had significantly higher temperatures and lower salinity than all other estuaries.

3.3. Dungeness crab fishery landings and sea otter population counts

Dungeness crab landings in Eureka, where the majority of Dungeness crabs have historically been

landed, exhibited a high level of variability. Comparatively, the landings in other regions were low from 2000 until 2009, at which point landings more than doubled in the San Francisco and Bodega regions (Fig. 6). Landings in Monterey and Morro Bay have continued to increase each year thereafter. It is important to note that the absolute differences in landings among the regions pre-dates the recovery of sea otters in California (Dahlstrom & Wild 1983). Despite an increasing sea otter population in California (Hatfield et al. 2019), the fishery in regions of overlap with sea otters (i.e. Monterey and Morro Bay) does not appear negatively im-

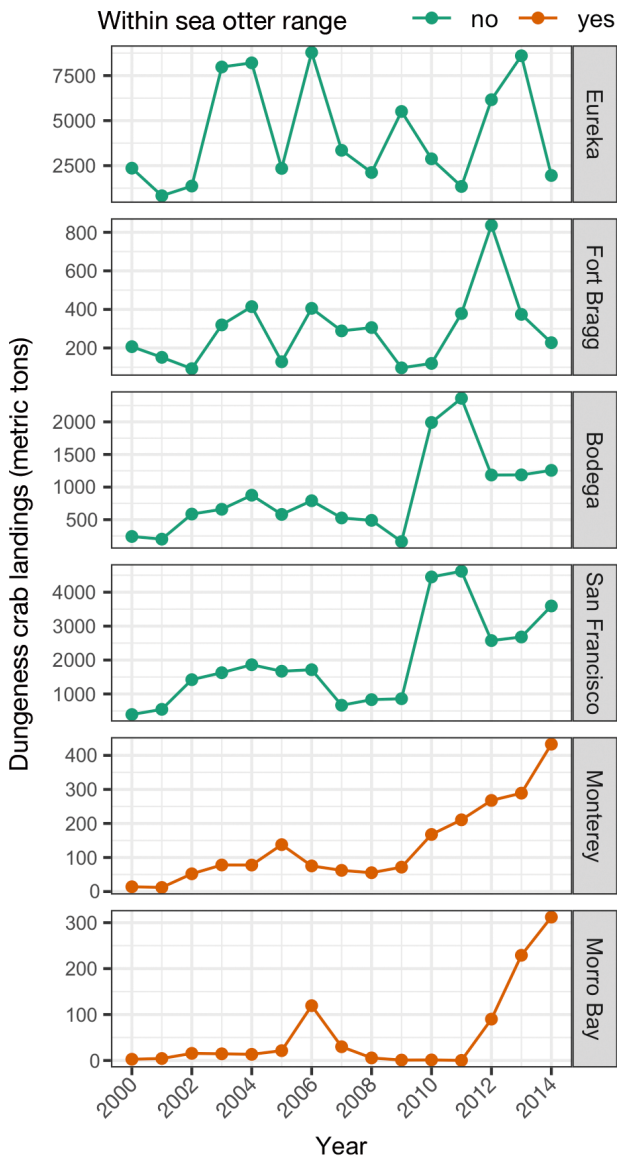


Fig. 6. Total annual landings of Dungeness crab (adjusted for fishing effort) in 6 regions of California from 2000–2014. Note difference in y-axis scales among regions

pacted by current levels of sea otter predation on either adult Dungeness crab populations outside of estuaries or juvenile Dungeness crabs within Morro Bay and Elkhorn Slough. There was a positive relationship between sea otter counts and Dungeness crab landings in the Monterey and Morro Bay regions when assessing the relationship with no time lag ($r = 0.727$; Fig. 7a). However, there was no relationship when assessing the relationship with a 3 yr ($r = 0.158$; Fig. 7b) or 4 yr ($r = 0.130$; Fig. 7c) time lag between sea otter counts and Dungeness crab landings.

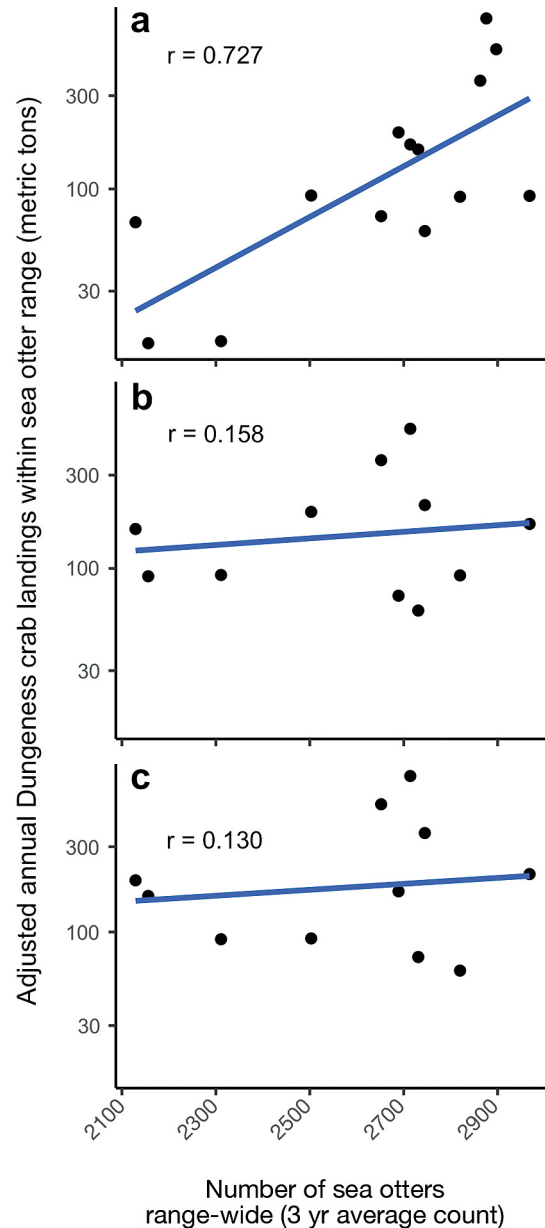


Fig. 7. Summed landings of Dungeness crab (adjusted for fishing effort) from Monterey and Morro Bay fishing regions as a function of sea otter population counts from (a) the same year as reported landings, (b) 3 yr prior to the reported landings, (c) 4 yr prior to the reported landings. Note the log scale on the y-axis

4. DISCUSSION

4.1. Sea otters reduce abundance and size of juvenile Dungeness crab in Elkhorn Slough

Sea otters have been found to deplete invertebrate prey resources and reduce the overall size distribu-

tion of invertebrate prey in soft-sediment systems throughout their range (Garshelis et al. 1986, Kvitek et al. 1989, Shirley et al. 1996, Larson et al. 2013). In Elkhorn Slough, we similarly found that an overall decrease in Dungeness crab abundance between 2012 and 2016 was associated with increasing sea otter density. Over this same time period, Dungeness crabs also experienced a decrease in size. Due to their high energetic demands, sea otters consume 20–25% of their body mass per day (Costa & Kooyman 1982). While faster growth rates of juvenile Dungeness crabs in estuaries compared to those along the open coast are thought to offset high predation rates from predators such as fish, crabs, and elasmobranchs in these environments (Gunderson et al. 1990, Armstrong et al. 1995, Fernández 1999, Hughes et al. 2014), this life history strategy likely does not protect juvenile crabs from a highly efficient predator such as a sea otter.

Results from the interannual comparisons in Elkhorn Slough suggest that the foraging activity of sea otters over time may have negatively affected the juvenile Dungeness crab population. While there are limitations to these broad-scale analyses, they nevertheless offer insight into multi-year trends in the Dungeness crab population in Elkhorn Slough. The interannual otter census data point to a shift in the distribution of sea otter density, and while there was no clear link between sea otter density and the decline of Dungeness crab size at this scale, the persistent presence of foraging sea otters in Elkhorn Slough, and the increase in sea otter abundance within the Elkhorn Slough over the last 2 decades (Estes & Tinker 2017, Hughes et al. 2019, Mayer et al. 2019) may still explain the reductions in crab abundance and size, as even low levels of sea otter foraging are likely sufficient to reduce the largest and most preferred size classes.

We found similar patterns in Elkhorn Slough, using higher resolution biweekly otter census data from 2016 when more frequent otter distribution surveys were available. The biweekly data revealed a negative relationship between Dungeness crab size and sea otter density in unvegetated habitat. Sea otters in Elkhorn Slough have been found to forage more in unvegetated habitats than in other habitat types (Lindsey 2016). Additionally, the higher resolution data from 2016 showed that Dungeness crab abundance was positively associated with higher otter density in locations closer to the ocean. While this result was counter to our expectations given the negative consumptive effects, it is worth noting that the median size of the crabs

measured (42 mm) was smaller than the median size of cancrid crabs typically selected by foraging sea otters in Elkhorn Slough (63 mm) (Tinker et al. 2008a, 2012). Moreover, while cancrid crabs comprised the majority (43%) of the otter diet in Elkhorn Slough between 1999 and 2012 (Hughes et al. 2013), the diet had shifted to primarily clams (79%) between 2013 and 2016 (Fig. S1), so the high densities of foraging sea otters were likely targeting clams in these areas rather than smaller Dungeness crabs. In addition to an observed shift in diet composition, the distribution of foraging sea otters has become more dispersed (Fig. S2), potentially indicating a functional response to the depletion of larger and more energetically profitable Dungeness and other cancrid crabs. Taken together, our results suggest that smaller juvenile crabs may benefit from a size refuge from sea otter predation; however, whether these smaller crabs are able to successfully recruit to the open ocean or have reduced viability relative to larger recruits remains a question for future research.

4.2. Sea otters and ocean conditions influence cancrid crab abundance and size across estuaries

Dungeness crab population dynamics are influenced by both biotic and abiotic conditions (Higgins et al. 1997). The presence of sea otters was negatively associated with the abundance of juvenile cancrid crabs in estuaries. Cancrid crab abundance had a positive relationship with BEUTI where sea otters were present and a positive relationship with SST where sea otters were absent. Positive upwelling indices have previously been linked to an increase in Dungeness crab recruitment (Miller & Shanks 2004), and we also found that BEUTI was an important variable at both the early and late larval stage. While warmer offshore temperatures are linked to mortality in crab larvae (Tasto 1983), we observed an increase in juvenile crab abundance with higher offshore SST. However, no offshore temperature beyond the optimal range for larvae of 10–14°C (Pauley et al. 1989) was observed in this study.

Estuaries with sea otters had smaller crabs than estuaries without otters. Estuary-reared Dungeness crabs exhibit faster growth rates due to warmer temperatures in estuaries than along the open coast (Stevens & Armstrong 1984, Wainwright & Armstrong 1993). While favorable temperatures may enhance growth rates, extremely low or high salin-

ities may negatively impact the survival of juvenile crabs in estuaries (Reed 1969, Wainwright & Armstrong 1993). Temperatures and salinities varied across estuaries, with the largest difference between San Francisco Bay and the other 3 estuaries. Juvenile Dungeness crabs have demonstrated thermal tolerance of temperatures up to 25°C, but experience lethal temperatures at 27.5°C (Pauley et al. 1989). Additionally, temperatures above 18°C negatively affect growth rates of juvenile Dungeness crabs (Sulkin et al. 1996). This may explain why San Francisco Bay had lower crab abundance and smaller crabs than Drakes Estero, since temperatures beyond these thresholds occurred during the study period. However, the similar temperatures and salinities among Morro Bay, Elkhorn Slough, and Drakes Estero suggest that the crab size differences are not solely due to the effects of salinity and temperature on growth rates, while the presence of sea otters at Morro Bay and Elkhorn Slough could explain the lower crab abundance and smaller crabs at these estuaries.

4.3. No evidence of sea otter impacts on Dungeness crab fishery landings over the short term

While there is evidence that sea otters have localized effects on juvenile crab abundance and size within estuaries, there is no evidence that the recovering sea otter population has negatively impacted Dungeness crab landings in California. Sea otters expend more energy than other marine mammals while diving (Yeates et al. 2007, Thometz et al. 2016) and therefore are relatively shallow divers. The Dungeness crab fishery sets gear at depths beyond typical sea otter foraging dives (Bodkin et al. 2004, Thometz et al. 2016). However, the apparent absence of a negative relationship between sea otter abundance and fisheries landings must be interpreted with caution. While there is no evidence that sea otter predation on Dungeness crabs in Elkhorn Slough and Morro Bay negatively affects the fishery in those regions, there is also no information about the relative importance of juvenile Dungeness crab production from those estuaries to the respective fishing regions. Elkhorn Slough and Morro Bay are relatively small estuaries, and the estuarine contributions of Dungeness crabs to the fishery in these regions are likely reflected by their size. For example, smaller estuaries in Oregon were found to have a smaller contribution to the regional Dungeness crab fishery com-

pared with the contributions of the larger estuaries of Washington (Armstrong et al. 2003). San Francisco Bay is known to be a critical nursery habitat for Dungeness crab and supplies a large fraction of annual recruits to the fishery stocks (Tasto 1979). It will become increasingly important to monitor crab recruitment as climate change continues to alter the abiotic drivers of crab recruitment, growth, and survival within estuaries.

4.4. Management implications

As sea otters naturally expand or are reintroduced beyond their current range, understanding the effects of their predation pressure on prey abundance and size in nursery habitats will be critical to inform conservation efforts while mitigating potential conflicts with fishery stakeholders. While there remains considerable uncertainty regarding the relative importance of estuaries to Dungeness crab fisheries in California, existing information suggests that the link is important (Tasto 1979, Gunderson et al. 1990, Armstrong et al. 2003). Although it is likely that adult Dungeness crab populations occupy depths outside the typical range of sea otter foraging dives (Thometz et al. 2016), sea otters could still impact fishery yield if sea otter consumption of juvenile crabs in estuaries impacts the supply to the fishery population. San Francisco Bay has already been determined and deemed a critical nursery ground for the Dungeness crab (Tasto 1979). While the majority of the California's commercial Dungeness crab landings have historically been landed in northern California (north of Sonoma–Mendocino county line), recent CDFW landings data suggest that the San Francisco fishing areas are increasingly important for the fishery. The potential recolonization of otters in San Francisco Bay could impact the region's Dungeness crab fishery, depending on the influence of Dungeness recruits in that estuary to the fishery. However, sea otters indirectly promote growth and expansion of nursery habitat (Hughes et al. 2013) for Dungeness crabs and this may result in more recruitment of juvenile Dungeness to the estuary and potentially more recruitment to the fishery if the crabs emigrate from the estuary before reaching a size class that makes them vulnerable to sea otter predation. As southern sea otters continue to inhabit estuaries within their historic range, targeted research on the direct and indirect impacts of sea otter predation on economically valuable prey populations will be needed to address key knowl-

edge gaps and provide wildlife and resource managers with the information necessary to continue to support the recovery of the species without negatively impacting fishery stakeholders.

Acknowledgements. This research was funded by the CSU COAST, American Academy of Underwater Sciences Kevin Gurr Scholarship, and Myer's Oceanographic and Marine Biology Trust to T.M.G.; B.B.H. was supported by a David H. Smith Conservation Research Fellowship. We thank R. Eby and B. Becker for the incredible logistical and field support in Elkhorn Slough and Drakes Estero. Many thanks to E. Aiello, S. Codde, L. Cullen, A. Donaldson, C. Endris, C. Harris, L. Hijikata, M. Jenkins, A. Lapidés, M. MacDonald, J. Miller, A. Pacheco, M. Patten, G. Reyes, B. Roseberry, and H. Whitehead for assistance trapping crabs in the field, F. Wilkerson for providing water quality data for Drakes Estero, and C. Juhasz for information related to the commercial Dungeness crab fishery in California. Funding for the Elkhorn Slough sea otter study was provided by the California Coastal Conservancy and US Fish and Wildlife Service with additional support from the US Geological Survey, UC Santa Cruz, Monterey Bay Aquarium, CA Department of Fish and Wildlife, and Elkhorn Slough National Estuarine Research Reserve.

LITERATURE CITED

- Armstrong D, 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
- Armstrong JL, Armstrong DA, Mathews SB (1995) Food habits of estuarine staghorn sculpin, *Leptocottus armatus*, with focus on consumption of juvenile Dungeness crab, *Cancer magister*. *Fish Bull* 93:456–470
- Beck MW, Heck KL Jr, Able KW, Childers DL and others (2001) The identification, conservation, and management of estuarine and marine nurseries for fish and invertebrates. *Bioscience* 51:633–641
- Bodkin JL, Esslinger GG, Monson DH (2004) Foraging depths of sea otters and implications to coastal marine communities. *Mar Mamm Sci* 20:305–321
- Brooks ME, Kristensen K, van Benthem KJ, Magnusson A and others (2017) Modeling zero-inflated count data with glmmTMB. *R J* 9:378–400
- Burnham KP, Anderson DR (2002) Model selection and multimodel inference: a practical information-theoretic approach, 2nd edn. Springer, New York, NY
- California Department of Fish and Wildlife (2014) Dungeness crab. In: 2014 California legislative fisheries forum. Annual marine fisheries report. California Department of Fish & Wildlife, Monterey, CA, p 23–25
- Carroll JC, Winn RN (1989) Species profiles: life histories and environmental requirements of coastal fishes and invertebrates (Pacific Southwest): brown rock crab, red rock crab, and yellow rock crab. US Fish and Wildlife Service Biological Report 82(11.1117). US Army Corps of Engineers, Washington, DC
- Costa DP, Kooyman GL (1982) Oxygen consumption, thermoregulation, and the effect of fur oiling and washing on the sea otter, *Enhydra lutris*. *Can J Zool* 60:2761–2767
- Dahlstrom WA, Wild PW (1983) A history of Dungeness crab fisheries in California. In: Wild PW, Tasto RN (eds) Life history, environment, and mariculture studies of the Dungeness crab, *Cancer magister*, with emphasis on the central California fishery. California Department of Fish and Game, Long Beach, CA, p 135–154
- Estes JA (1990) Growth and equilibrium in sea otter populations. *J Anim Ecol* 59:385–401
- Estes JA, Tinker MT (2017) Rehabilitating sea otters: feeling good versus being effective. In: Kareiva P, Marvier M, Silliman B (eds) Effective conservation science: data not dogma. Oxford University Press, Oxford, p 128–134
- Estes JA, Danner EM, Doak DF, Konar B and others (2004) Complex trophic interactions in kelp forest ecosystems. *Bull Mar Sci* 74:621–638
- Estes JA, Terborgh J, Brashares JS, Power ME and others (2011) Trophic downgrading of planet Earth. *Science* 333:301–306
- Fernández M (1999) Cannibalism in Dungeness crab *Cancer magister*: effects of predator–prey size ratio, density, and habitat type. *Mar Ecol Prog Ser* 182:221–230
- Garshelis DL, Garshelis JA, Kimker AT (1986) Sea otter time budgets and prey relationships in Alaska. *J Wildl Manag* 50:637–647
- Guerra AS (2018) Wolves of the sea: managing human–wildlife conflict in an increasingly tense ocean. *Mar Policy* 29:369–373
- Gunderson DR, Armstrong DA, Shi YB, McConnaughey RA (1990) Patterns of estuarine use by juvenile English sole (*Parophrys vetulus*) and Dungeness crab (*Cancer magister*). *Estuaries* 13:59–71
- Hatfield BB, Ames JA, Estes JA, Tinker MT, Johnson AB, Staedler MM, Harris MD (2011) Sea otter mortality in fish and shellfish traps: estimating potential impacts and exploring possible solutions. *Endang Species Res* 13: 219–229
- Hatfield BB, Yee JL, Kenner MC, Tomoleoni JA (2019) California sea otter (*Enhydra lutris nereis*) census results, spring 2019. US Geological Survey Data Series No. 1118. US Geological Survey, Reston, VA
- Heithaus MR, Wirsing AJ, Dill LM (2012) The ecological importance of intact top-predator populations: a synthesis of 15 years of research in a seagrass ecosystem. *Mar Freshw Res* 63:1039–1050
- Higgins K, Hastings A, Sarvela JN, Botsford LW (1997) Stochastic dynamics and deterministic skeletons: population behavior of Dungeness crab. *Science* 276:1431–1435
- Hughes BB, Eby R, Van Dyke E, Tinker MT, Marks CI, Johnson KS, Wasson K (2013) Recovery of a top predator mediates negative eutrophic effects on seagrass. *Proc Natl Acad Sci USA* 110:15313–15318
- Hughes BB, Levey MD, Brown JA, Fountain MC and others (2014) Nursery functions of US west coast estuaries: the state of knowledge for juveniles of focal invertebrate and fish species. The Nature Conservancy, Arlington, VA
- Hughes BB, Wasson K, Tinker MT, Williams SL and others (2019) Species recovery and recolonization of past habitats: lessons for science and conservation from sea otters in estuaries. *PeerJ* 7:e8100
- Jackson JB, Kirby M, Berger W, Bjørndal K and others (2001) Historical overfishing and the recent collapse of coastal ecosystems. *Science* 293:629–637
- Jacox MG, Edwards CA, Hazen EL, Bograd SJ (2018) Coastal upwelling revisited: Ekman, Bakun, and improved upwelling indices for the US west coast. *J Geophys Res Oceans* 123:7332–7350

- Jones TL, Culleton BJ, Larson S, Mellinger S, Porcasi JF (2011) Toward a prehistory of the southern sea otter (*Enhydra lutris nereis*). In: Braje TJ, Rick TC (eds) Human impacts on seals, sea lions, and sea otters: integrating archaeology and ecology in the Northeast Pacific. University of California Press, Berkeley, CA, p 243–271
- Juhasz C, Kalvass P (2011) Dungeness crab, *Metacarcinus magister*. In: Larinto T (ed) Status of the fisheries report: an update through 2011. California Department of Fish and Wildlife, p 2-1–2-12
- ✦ Kemp PS, Worthington TA, Langford TEL, Tree ARJ, Gaywood MJ (2012) Qualitative and quantitative effects of reintroduced beavers on stream fish. *Fish Fish* 13:158–181
- ✦ Kenyon KW (1969) The sea otter in the eastern Pacific Ocean. *N Am Fauna* 68:1–352
- ✦ Kvitek RG, Shull D, Canestro D, Bowlby EC, Troutman BL (1989) Sea otters and benthic prey communities in Washington State. *Mar Mamm Sci* 5:266–280
- ✦ Larson SD, Hoyt ZN, Eckert GL, Gill VA (2013) Impacts of sea otter (*Enhydra lutris*) predation on commercially important sea cucumbers (*Parastichopus californicus*) in southeast Alaska. *Can J Fish Aquat Sci* 70:1498–1507
- ✦ Lee LC, Watson JC, Trebilco R, Salomon AK (2016) Indirect effects and prey behavior mediate interactions between an endangered prey and recovering predator. *Ecosphere* 7:e01604
- Lindsey JK (2016) Estuarine habitat use by the California sea otter (*Enhydra lutris nereis*). MS thesis, San Jose State University, San Jose, CA
- ✦ Lüdecke D (2019) sjstats: statistical functions for regression models, version 0.17.3. <https://mrnan.microsoft.com/snapshot/2019-01-10/web/packages/sjstats/sjstats.pdf>
- ✦ Magera AM, Mills Flemming JE, Kaschner K, Christensen LB, Lotze HK (2013) Recovery trends in marine mammal populations. *PLOS ONE* 8:e77908
- ✦ Markel RW, Shurin JB (2015) Indirect effects of sea otters on rockfish (*Sebastes* spp.) in giant kelp forests. *Ecology* 96:2877–2890
- ✦ Marshall KN, Stier AC, Samhoury JF, Kelly RP, Ward EJ (2016) Conservation challenges of predator recovery. *Conserv Lett* 9:70–78
- ✦ Mayer KA, Tinker MT, Nicholson TE, Murray MJ and others (2019) Surrogate rearing a keystone species to enhance population and ecosystem restoration. *Oryx*, doi:10.1017/S0030605319000346
- ✦ Miller JA, Shanks AL (2004) Ocean–estuary coupling in the Oregon upwelling region: abundance and transport of juvenile fish and of crab megalopae. *Mar Ecol Prog Ser* 271:267–279
- ✦ Muhly TB, Musiani M (2009) Livestock depredation by wolves and the ranching economy in the Northwestern US. *Ecol Econ* 68:2439–2450
- ✦ NERRS (National Estuarine Research Reserve System) (2012) System-wide monitoring program. Data accessed from the NOAA NERRS Centralized Data Management Office. <http://cdmo.baruch.sc.edu/> (accessed 12 October 2012)
- ✦ Nicholson TE, Mayer KA, Staedler MM, Fujii JA and others (2018) Gaps in kelp cover may threaten the recovery of California sea otters. *Ecography* 41:1751–1762
- Ogden A (1941) The California sea otter trade, 1784–1848. University of California Press, Berkeley, CA
- Pauley GB, Armstrong DA, Van Citter R, Thomas GL (1989) Species profiles: life histories and environmental requirements of coastal fishes and invertebrates (Pacific Southwest): Dungeness crab. US Fish and Wildlife Service Biological Report 82(11.121). US Army Corps of Engineers, Washington, DC
- R Core Team (2018) R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna. www.r-project.org
- ✦ Raimondi P, Jurgens LJ, Tinker MT (2015) Evaluating potential conservation conflicts between two listed species: sea otters and black abalone. *Ecology* 96:3102–3108
- ✦ Reed P (1969) Culture methods and effects of temperature and salinity on survival and growth of Dungeness crab (*Cancer magister*) larvae in the laboratory. *J Fish Res Board Can* 26:389–397
- ✦ Reisewitz SE, Estes JA, Simenstad CA (2006) Indirect food web interactions: sea otters and kelp forest fishes in the Aleutian archipelago. *Oecologia* 146:623–631
- ✦ Ripple WJ, Beschta RL (2012) Trophic cascades in Yellowstone: the first 15 years after wolf reintroduction. *Biol Conserv* 145:205–213
- ✦ Ripple WJ, Estes JA, Beschta RL, Wilmers CC and others (2014) Status and ecological effects of the world's largest carnivores. *Science* 343:1241484
- Shirley TC, Bishop GH, O'Clair CE, Taggart SJ, Bodkin JL (1996) Sea otter predation on Dungeness crab in Glacier Bay, Alaska. In: High latitude crabs: biology, management and economics. Alaska Sea Grant, Anchorage, AK, p 565–575
- ✦ Silliman BR, Hughes BB, Gaskins LC, He Q and others (2018) Are the ghosts of nature's past haunting ecology today? *Curr Biol* 28:R532–R537
- Stevens B, Armstrong DA (1984) Distribution, abundance, and growth of juvenile Dungeness crabs, *Cancer magister*, in Grays Harbor estuary, Washington. *Fish Bull* 82:469–483
- Sulkin SD, Mojica E, McKeen GL (1996) Elevated summer temperature effects on megalopal and early juvenile development in the Dungeness crab, *Cancer magister*. *Can J Fish Aquat Sci* 53:2076–2079
- Tasto RN (1979) San Francisco Bay: Critical to the Dungeness crab? In: Conomos TJ (ed) San Francisco Bay: the urbanized estuary. Pacific Division of the American Association for the Advancement of Science, San Francisco, CA, p 479–490
- Tasto RN (1983) Juvenile Dungeness crab, *Cancer magister*, studies in the San Francisco Bay area. In: Wild PW, Tasto RN (eds) Life history, environment, and mariculture studies of the Dungeness crab, *Cancer magister*, with emphasis on the central California fishery. California Department of Fish and Game, Long Beach, CA, p 135–154
- ✦ Thometz NM, Staedler MM, Tomoleoni JA, Bodkin JL, Bental GB, Tinker MT (2016) Trade-offs between energy maximization and parental care in a central place forager, the sea otter. *Behav Ecol* 27:1552–1566
- Tinker MT, Hatfield BB (2017) California sea otter (*Enhydra lutris nereis*) census results, spring 2017. US Geological Survey Data Series No. 1067. US Geological Survey, Reston, VA
- ✦ Tinker MT, Bental GB, Estes JA (2008a) Food limitation leads to behavioral diversification and dietary specialization in sea otters. *Proc Natl Acad Sci USA* 105:560–565

- ✦ Tinker MT, Doak DF, Estes JA (2008b) Using demography and movement behavior to predict range expansion of the southern sea otter. *Ecol Appl* 18: 1781–1794
- ✦ Tinker MT, Guimarães PR, Novak M, Marquitti FMD and others (2012) Structure and mechanism of diet specialisation: testing models of individual variation in resource use with sea otters. *Ecol Lett* 15:475–483
- ✦ Tinker MT, Hatfield BB, Harris MD, Ames JA (2016) Dramatic increase in sea otter mortality from white sharks in California. *Mar Mamm Sci* 32:309–326
- US Fish and Wildlife Service (2003) Final revised recovery plan for the southern sea otter (*Enhydra lutris nereis*). US Fish and Wildlife Service, Portland, OR
- ✦ Wainwright TC, Armstrong DA (1993) Growth patterns in the Dungeness crab (*Cancer magister* Dana): synthesis of data and comparison of models. *J Crustac Biol* 13:36–50
- ✦ Wing SR, Botsford LW, Largier JL, Morgan LE (1995) Spatial structure of relaxation events and crab settlement in the northern California upwelling system. *Mar Ecol Prog Ser* 128:199–211
- ✦ Yeates LC, Williams TM, Fink TL (2007) Diving and foraging energetics of the smallest marine mammal, the sea otter (*Enhydra lutris*). *J Exp Biol* 210:1960–1970

Editorial responsibility: Rochelle D. Seitz,
Gloucester Point, Virginia, USA
Reviewed by: 3 anonymous referees

Submitted: October 28, 2019
Accepted: October 9, 2020
Proofs received from author(s): November 13, 2020