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Modeling coupled dynamics of an empirical predator-prey system to predict top predator recovery

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ABSTRACT

Limited data, time, and funding lead conservation managers to make difficult choices in managing species recovery. Coupled dynamical models are relied upon for decision support, but their application to empirical predator-prey systems has generally been restricted to small, tractable species. To broaden their use in conservation decision-making, we developed a model suitable for predicting the population dynamics of a larger apex carnivore and its prey. We selected southern sea otters (*Enhydra lutris nereis*) and their primary estuarine prey as our case study and parameterized the dynamical model with data on sea otter, clam, and crab abundances; predator-prey interactions; and sea otter bioenergetics collected from Elkhorn Slough, CA. Our model, having integrated all these salient factors, was able to successfully reproduce trends in taxa abundance as well as shifts in sea otter diet composition and energy intake rates. Rich data inputs allow the model to predict population dynamics over realistic temporal scales not only for the site of data collection, but also for similar estuaries uncolonized by sea otters. Based on model projections parameterized with prey survey data from two such estuaries, Tomales Bay and Drakes Estero, we predict the sites could support over 160 sea otters and may hold potential to further species recovery. In systems with good data availability, the model has high predictive power and can provide multi-taxa projections useful for making informed management decisions.

1. Introduction

Common dilemmas faced by conservation managers include ecological and socioeconomic tradeoffs, resource constraints, and data shortages (Bower et al., 2018). These challenges complicate decisionmaking in resource management and necessitate making difficult choices under high uncertainty (Villero et al., 2017). A suite of tools has been developed to provide decision support, including influence diagrams (Marcot, 2006), decision tables and trees (Regan et al., 2005), and population models (Converse et al., 2013). Population models are particularly valuable to conservation managers because they allow different scenarios to be tested and can help identify key information gaps contributing to model uncertainty.

Some like coupled dynamical models, however, have had limited use in conservation decision-making. The model, which draws on coupled ordinary differential equations (ODE) to link the dynamics of a predator and its prey, has been extensively described in the theoretical literature (Abrams, 2006; Mougi, 2010; Oaten and Murdoch, 1975; Yamauchi and Yamamura, 2005) but narrowly applied on empirical systems. Thus far, the model has been used almost strictly on small, tractable species (dos Anjos et al., 2023). The inherent challenges of collecting data needed to parameterize the model for larger predators have prevented its broader

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application. A model capable of predicting the population dynamics of such predator-prey systems would allow managers to make better informed decisions for species of interest, including apex carnivores like sea otters (*Enhydra lutris*).

Here, we develop such a dynamical model for a case study on southern sea otter (E. lutris nereis) recovery in estuarine systems. This threatened subspecies was once on the brink of extinction but is now in slow recovery (Tinker and Hatfield, 2017). U.S. federal and state protections enacted in the 1900s have allowed it to extend its range, and today, populations occur along the California coast between San Mateo and Santa Barbara Counties (Hatfield et al., 2019). Continued range expansion is possible but has ceased in the last decade likely due to predation by white sharks (Carcharodon carcharias) on the north and south end of their range (Tinker et al., 2016). Because of this, conservation managers are turning their attention to estuaries as potential areas for sea otter recolonization and range expansion (Hughes et al., 2019). Estuarine habitats contain plentiful prey and accessible haul-out areas for pup rearing (Eby et al., 2017). They also serve as important refuges from white shark predation (Silliman et al., 2018). These benefits have led managers to seriously consider San Francisco Bay (SFB)the largest estuary in California-for future range expansion (Hughes et al., 2019), but inhabiting a large urban estuary comes with a host of risks for the subspecies like boat traffic and exposure to environmental contaminants (Rudebusch et al., 2020). Immediately to the north are relatively smaller estuaries, Tomales Bay and Drakes Estero, which offer less risk to sea otters as they are situated in relatively pristine watersheds in two protected areas: Point Reyes National Seashore (PRNS) and Greater Farallones National Marine Sanctuary (GFNMS).

There are important knowledge gaps to fill before conservation managers can include Tomales Bay and Drakes Estero in sea otter recovery plans. Questions remain about the capacity of estuaries to support sea otters and the cascading effects of recolonization on estuarine ecosystems (Zwartjes et al., 2022). Laidre et al. (2006) began filling these gaps by using a GIS-based strategy to measure habitat availability and estimate the number of sea otters that could be sustained along the California coast. Hughes et al. (2019) built on these efforts by developing a sea otter population growth model to create an equilibrium abundance projection for SFB. A more recent contribution was made by Tinker et al. (2021b), who used a hierarchical Bayesian model to incorporate an expanded set of habitat characteristics. However, these approaches are imperfect: they rely solely on habitat-specific parameters and exclude salient considerations like predator-prey dynamics. This is especially true when population potential is evaluated for estuaries, where the paucity of available prey data has encouraged total dependence on habitat information (Hughes et al., 2019; Rudebusch et al., 2020). An updated model that takes such data into account can help bridge persistent gaps and provide more robust carrying capacity estimates in estuaries. It could also make accurate predictions on prey resource impacts following predator recolonization, which are rarely produced by population models.

This paper presents a mechanistic model that projects the coupled dynamics of sea otters and their primary estuarine prey, crabs and clams, based on empirically measured prey densities, predator-prey trophic interactions, and sea otter bioenergetics. We develop and calibrate our model by fitting it to multiple datasets collected in Elkhorn Slough—an estuary where sea otters have successfully recolonized and likely reached carrying capacity (Silliman et al., 2018). These datasets include predator and prey survey data as well as observational data on sea otter foraging behavior and diet composition. We then apply the model to Tomales Bay and Drakes Estero, accounting for habitat-specific prey densities measured from the two estuaries to initialize it with local conditions, and use the results to estimate the potential equilibrium abundance of sea otters that could be supported by these sites.

2. Methods

2.1. Study site

Tomales Bay and Drakes Estero (Fig. 1) are two relatively large California estuaries with minimal human development and some federal and state protections. Tomales Bay is 27.4 km² and the second largest California estuary, while Drakes Estero is the state's eighth largest, covering 10.1 km² (Hughes et al., 2014). Both have extensive seagrass meadows (*Zostera marina*)—a known sea otter habitat—and are suspected to have adequate prey availability to support sea otter populations (Hughes et al., 2019). Archaeological evidence indicates that sea otters were once present in PRNS, possibly within Drakes Estero (PRNS Museum, 2016), and recent observations suggest sea otter presence there has increased (Figs. 2, A1). These estuaries could provide important habitat for sea otter range expansion given their size, existing resources, and historical occupation by sea otters.

2.2. Sea otter habitat mapping

We produced GIS layers of seagrass coverage at Drakes Estero based on composite summer aerial surveys conducted in 2017, 2018, and 2019. Aerial imagery was collected at 100-m altitude using a DJI (2016) Phantom 4 Pro drone during successive low-tide days from May–August. Flights took place over all areas of the Estero except the mouth, which was restricted due to sensitive wildlife activity. The resulting imagery had a resolution of approximately 3 cm, lateral uncertainty of 0.5–3.0 m, and spatial overlap of 80–90 %. Images were post-processed to remove water-surface glint using a blue-band mask in MATLAB R2019a; (Cavanaugh et al., 2021; MathWorks, 2019). Orthomosaics were constructed using Agisoft Metashape Pro 1.5.2 (Agisoft LLC, 2019), and georeferencing was validated using contemporary 0.5-m resolution satellite imagery in Google Earth Pro 7.3 (Google, 2019).

We manually annotated seagrass distributions using QGIS 3.14



Fig. 1. Map of study sites (light blue) and relevant water bodies, including San Francisco Bay and Elkhorn Slough (dark blue), in northern California, USA (credit: California State Parks; Esri; Garmin; Food and Agricultural Organization; Ministry of Economy, Trade, and Industry/National Aeronautics and Space Administration; U.S. Geological Survey; Bureau of Land Management; Environmental Protection Agency; National Park Service; U.S. Fish and Wildlife Service). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)



Fig. 2. Sea otters occupying estuarine habitats around Point Reyes National Seashore (PRNS), California, USA. Sea otters spotted in Tomales Bay on (A) April 12, 2015 (credit: Sarah Allen) and (B) July 21, 2018 (credit: Catie Clune). (C) Sea otter approaching a kayaker in Drakes Estero, March 2008 (credit: Sarah Allen). (D) Sea otter in giant kelp bed at the mouth of Drakes Estero, March 2008 (credit: Sarah Allen). (E) Sea otter foraging on European green crab in Drakes Estero on December 05, 2017 (credit: Pete Smith). (F) Sea otter with a group of river otters in Drakes Estero on May 13, 2018 (credit: Harry McGrath). Photographs from the PRNS Museum Collections.

(QGIS Development Team, 2020). We created separate layers for dense seagrass (70–100 % cover), moderate seagrass (30–70 % cover), sparse seagrass (1–30 % cover), and no seagrass (0 % cover). Because we were unable to image all sections of the Estero in all years due to weather, we produced a composite of the three-year survey period that represents our best estimate of all seagrass within the Estero.

Habitat data for Tomales Bay were sourced from seagrass survey data produced by Merkel and Associates and published by NOAA in August 2017 (Merkel and Associates, Inc., and GFNMS, 2017). The survey was carried out using vessel-mounted interferometric side scan sonar in deep subtidal and low intertidal regions during high tide, while unmanned aerial vehicles were used above shallow subtidal and intertidal areas during low tide. Data collected by both instruments give a complete seagrass inventory within the estuary.

2.3. Sea otter prey sampling

2.3.1. Subtidal benthic infauna and crab sampling

From June–August 2016, we sampled the benthos for key infaunal prey species at five sites spaced evenly along the main channel of

Elkhorn Slough, ordered by increasing distance from the ocean. We established three 10-m transects parallel to the channel at each site: one at the deepest point mid-channel, one toward the north bank, and one toward the south bank. The two bank transects were placed where the bottom slope was not too steep (<30 degrees), and the depth at working tide was >4 m for dredge work.

At three of the sites, sampling was achieved using a suction dredge. At the other two sites, only visual sampling was conducted. Ten 0.25-m^2 quadrats were placed haphazardly along three unmarked transects. As with the dredged sites, numbers of burrows and siphons in each quadrat were recorded. No size data were recorded from these sites because clams were not removed from the benthos.

In October 2021, we sampled five sites in Drakes Estero with two in Schooner Bay and three in the main Estero. At each site, three 10-m transects were laid out on the benthos, radiating out from a central point at predetermined random compass bearings. The transects defined three 2-m by 10-m belt transects for crab sampling and determined the placement of ten 0.25-m^2 quadrats on each transect for infauna sampling. All crabs observed along each 2-m belt transect were captured by hand and transported to the surface, where they were separated by species and their carapace width measured before release. Crabs that escaped capture on each transect were noted by species. Each of the 30 quadrats per site was classified as seagrass or bare habitat, and the numbers of burrows and siphons were recorded. Visual inspection of siphons enabled determination of clam species, and in some cases, inspection of burrows allowed determination that they were the residence of fat innkeeper worms (*Urechis caupo*).

2.3.2. Crab trapping surveys

We also sampled crabs using baited crab traps in three regions of Drakes Estero and Tomales Bay: outer (i.e., close to the mouth), mid, and inner (Kimbro et al., 2009; Smith and Hollibaugh, 1997). In each of these regions, we sampled two habitat types, seagrass beds and channels. GPS points for the channel sites were chosen using a random number generator while using upper and lower bounds to separate the different estuary regions. We used capture mechanisms consisting of three trap types tied together in a string (>1 m spacing between each)trap): Fukui traps, shrimp pots, and minnow traps. Each trap was baited with frozen anchovy and left to soak for about 24 h. After the string of traps was collected, we recorded the species, sex, and longest carapace length of each crab caught. Crabs were binned into edible size classes based on observational data on the sizes of crabs consumed by sea otters (Tinker et al., 2019), with crabs <35 mm considered too small. After edible crabs were tallied, we calculated the catch per unit effort (CPUE) standardized to 24-hour soak times.

2.4. Predator-prey model of sea otter population dynamics in estuaries

2.4.1. Process model

To describe the interactions between sea otters and their two primary prey taxa in Elkhorn Slough, we used a well-studied analytical framework describing the coupled dynamics of a single predator and multiple prey species (Oaten and Murdoch, 1975). We built upon a previously described formulation of the one-predator, two-prey model framework (Abrams, 2006; Mougi, 2010; Yamauchi and Yamamura, 2005) that assumes each individual predator has probability p_i of attacking prev type *i* when encountered. It also assumes that prey types are characterized by several key attributes including: per-capita encounter rate by a foraging predator (a_i , units = encounters \cdot predator⁻¹ \cdot prey⁻¹ \cdot minute⁻¹), handling time (h_i , units = minutes prey⁻¹), net energy content (g_i , units = kcal · prey⁻¹), and the intrinsic rate of population increase (r_i) and equilibrium abundance (K_i) that determine the dynamics of each prey population in the absence of sea otter predation. The dynamics of the predator (Y) and the primary prey populations (crabs = X_1 and clams = X_2) are then described by a series of coupled nonlinear differential equations:

$$\frac{dX_1}{dt} = \left\{ r_1 \cdot \left(1 - \frac{X_1}{K_1} \right) - \frac{p_1 \cdot a_1 \cdot Y \cdot \xi}{1 + p_1 \cdot h_1 \cdot a_1 \cdot X_1 + p_2 \cdot h_2 \cdot a_2 \cdot X_2 + p_3 \cdot h_3 \cdot a_3} \right\} \cdot X_1$$

$$\tag{1}$$

$$\frac{dX_2}{dt} = \left\{ r_2 \cdot \left(1 - \frac{X_2}{K_2} \right) - \frac{p_2 \cdot a_2 \cdot Y \cdot \xi}{1 + p_1 \cdot h_1 \cdot a_1 \cdot X_1 + p_2 \cdot h_2 \cdot a_2 \cdot X_2 + p_3 \cdot h_3 \cdot a_3} \right\} \cdot X_2$$
(2)

$$\frac{dY}{dt} = \{z_1 \cdot (E - z_2)\} \cdot Y, \text{ where } E$$

$$= \frac{p_1 \cdot a_1 \cdot X_1 \cdot g_1 + p_2 \cdot a_2 \cdot X_2 \cdot g_2 + p_3 \cdot a_3 \cdot g_3}{1 + p_1 \cdot h_1 \cdot a_1 \cdot X_1 + p_2 \cdot h_2 \cdot a_2 \cdot X_2 + p_3 \cdot h_3 \cdot a_3}$$
(3)

In Eqs. (1)–(3), ξ is a rescaling constant used to translate between the spatial and temporal scales of prev density and dynamics (Eqs. (1), (2)) and sea otter density and foraging dynamics (Eq. (3), see Methods in Supplementary Materials for details). The parameters z_1 and z_2 together determine the relationship between the predator population growth rate $(r_{\rm v})$ and the net rate of energy gain while foraging (E, units = kcal \cdot \min^{-1}). We calculate *E* according to the basic type-II functional response for multiple prev species (Oaten and Murdoch, 1975), and we calculate r_{y} as $z_{1}(E-z_{2})$, where z_{1} determines the slope of the relationship between energy gain and population growth rate, and z_2 represents the base energy intake rate required for sea otters to maintain metabolic demands and low levels of reproductive output sufficient to cancel out losses from mortality (Thometz et al., 2014; Yeates et al., 2009). This formulation reflects the approximately linear relationship that has been shown in previous studies between sea otter population growth rates and local rates of energy gain while foraging (Tinker et al., 2019), with growth rates approaching 0 as the rate of energy gain declines to a base level (z_2) .

An ODE solver was used to calculate the annual abundance dynamics of predator and prey species described by Eqs. (1)–(3). We note that these equations include attributes for a third prey type (i = 3) that represents all invertebrate prey taxa other than crabs and clams. Since these other taxa comprise a small portion of sea otter diets in Elkhorn Slough, their abundance is assumed to be effectively decoupled from sea otter abundance and thus not tracked by the model. Based on the estimated annual abundance of Y, X_1 and X_2 , we calculated other derived parameters for comparison with observed data, including (1) the annual proportion of foraging effort allotted to each prey type and (2) the rate of energy gain from each prey type (see Methods in Supplementary Materials for details).

2.4.2. Observation model

We made use of several available datasets, both for parameterizing model constants and for fitting the process model (Section 2.4.3). We used previously published data on sea otter diets and foraging behavior in California (Hughes et al., 2013; Tinker et al., 2008, 2012, 2019) to calculate the average handling times (h_i) for crabs, clams, and other prey types. We also used bioenergetic and morphometric data for sea otter prey species (Oftedal et al., 2007) to estimate prey-specific energy content (gi) and standardize prey counts (Table A1, see Methods in Supplementary Materials for details). All remaining model parameters (Table A2) were estimated as part of model fitting. We used five data series for model fitting: (1) annual U.S. Geological Survey counts of sea otters in the Slough (Hatfield et al., 2019); (2) crab trapping CPUE data from the 1970s (Hughes et al., 2013) and 2011-2017 period (Grimes et al., 2020; Hughes et al., 2013); (3) benthic sampling data on clam density for 1986 (Kvitek et al., 1998) and 2016 (Table A3); and observational data on sea otter foraging behavior for three time periods (2005-2011, 2013-2014, and 2015-2016) that provided empirical estimates of (4) prey-specific foraging effort (i.e., proportion of feeding dives allocated to each prey type) and (5) estimated rate of energy gain by prey type (Table A1). Observed counts of otters, crabs, and clams were modeled using negative binomial distributions, while proportional

allocations of feeding dives among prey types were modeled by a Dirichlet distribution and prey-specific energy intake rates by gamma distributions (see Methods in Supplementary Materials for details).

2.4.3. Model fitting

Model fitting consisted of relating the data observations probabilistically to the expected values calculated from the process model and using Markov Chain Monte Carlo methods to find the parameter values that maximized the joint likelihood of all five observed datasets (Eqs. (6)-(10), see Methods in Supplementary Materials for details). We set uninformative priors on all estimated parameters (Table A2) except z_2 , which was set based on published estimates of energy intake rates in populations near K (Tinker et al., 2019, 2021a; see Methods in Supplementary Materials for details). We used R (R Core Team, 2014), RStudio (RStudio Team, 2020), and Stan software (Carpenter et al., 2017) to code and fit the model, saving N = 10,000 Monte Carlo samples after a burn-in of 1000 samples. We evaluated model convergence and goodness of fit using a variety of standard diagnostics and graphical posterior predictive checks (see Methods in Supplementary Materials for details) and created plots of observed vs. model-predicted dynamics. To estimate prev-determined carrying capacity for otters in Elkhorn Slough, we drew from the joint posteriors of all parameters and reinitialized and solved Eqs. (1)–(3) over a 100-year period using the ode45 solver in R.

We next used crab CPUE data and clam siphon counts from Drakes Estero and Tomales Bay to reinitialize and run the model for these different prey densities, starting with an initial population of two sea otters. Since siphon counts were not available for Tomales Bay, we used the siphon count surveys from Drakes Estero to parameterize clam densities at both estuaries. We note that this prospective analysis is based on several key assumptions: (1) invertebrate populations in Drakes Estero and Tomales Bay were at or near their maximum potential densities (K) at the time of sampling and (2) all other parameters (e.g., prey population productivity, sea otter diet preferences) would be equivalent to Elkhorn Slough. Based on a recognition that invertebrate productivity in Elkhorn Slough may be unusually high due to its location at the head of Monterey Bay Canyon and significant agricultural loads in the watershed (Hughes et al., 2013), we ran the prospective analyses for Drakes Estero and Tomales Bay under two scenarios. They include a baseline scenario in which the intrinsic rates of population increase for crabs and clams were identical to the values estimated for Elkhorn Slough, and a "reduced productivity" scenario in which the intrinsic growth rates of the prey populations were reduced by 50 % to simulate the possibility of lower recruitment or growth rates in Drakes Estero and Tomales Bay.

3. Results

3.1. Habitat and prey availability in Tomales Bay and Drakes Estero

Mapping efforts of estuarine habitats in Drakes Estero and Tomales Bay revealed extensive seagrass and unvegetated habitats (Table 1). Drakes Estero and Tomales Bay had 3.51 and 6.18 km² of seagrass habitat, respectively, and 2.47 and 19.02 km² of unvegetated habitat, respectively. In comparison, Elkhorn Slough had 0.15 km² of seagrass habitat during this period (Beheshti et al., 2022; Hughes et al., 2013) and 3.30 km² of unvegetated habitat. When combined, the total sea otter habitat for Tomales Bay and Drakes Estero used for sea otter population modeling was 31.18 km².

Both Tomales Bay and Drakes Estero have a wide array of sea otter prey availability based on our 2019–2021 surveys (Table A4). The most common species found in these surveys were rough piddock clam (*Zirfaea pilsbryi*) and red rock crab (*Cancer productus*). For subtidal infaunal surveys, we were able to count few Washington clams (*Saxidomus nuttalli*), rough piddock clams, and littleneck clams (*Leukoma* spp.) and fat innkeeper worms in Drakes Estero. Poor visibility prevented us from sampling Tomales Bay. Therefore, we used siphon counts from Elkhorn Table 1

Mean estimates and 95 % credible intervals (CI) of sea otter equilibrium densities for Elkhorn Slough, Drakes Estero, and Tomales Bay, California, USA.

Location	Area (km²)	Mean density	Mean carrying capacity	CI ₉₅ _low	CI ₉₅ _high
Elkhorn Slough	3.45	25.80	89	54	131
Drakes Estero,					
baseline					
scenario					
Seagrass areas	3.51	9.38	33	22	46
Non-seagrass	2.47	4.13	10	0	45
areas	F 00	7.01	40	05	(F
Total Drokos Fotoro, FO	5.98	7.21	43	25	65
Drakes Estero, 50					
scenario					
Seagrass areas	3.51	4.73	17	10	24
Non-seagrass			-,		
areas	2.47	2.11	5	0	22
Total	5.98	3.64	22	12	33
Tomales Bay,					
baseline					
scenario					
Seagrass areas	6.18	8.71	54	36	75
Non-seagrass areas	19.02	3.60	68	0	302
Total	25.2	4.85	122	36	254
Tomales Bay, 50					
% reduced					
scenario	6.10	4.40	07	15	10
Seagrass areas	6.18	4.40	27	17	40
areas	19.02	1.85	35	0	150
Total	25.2	2.48	62	17	131

Slough for parameterizing infaunal prey in the model and assumed infaunal prey densities to be similar for Drakes Estero and Tomales Bay. Our 20-m² swath surveys of crab in Drakes Estero revealed abundant crab populations in the size range (mean \pm SD) considered to be suitable sea otter prey: Pacific rock crab (*Romaleon antennarium*) (81.3 \pm 25.7 mm), graceful crab (*Metacarcinus gracilis*) (60.1 \pm 10.7 mm), red rock crab (*Cancer productus*) (75.4 \pm 32.2 mm), and the invasive European green crab (*Carcinus maenas*) (53.4 \pm 13.7 mm). When considering both habitat types, there was a mean density of 0.2 \pm 0.27 edible crab/m² (*N* = 13 transects), and seagrass habitats had a greater density of edible crab compared to bare habitats (Fig. A2).

Crab trapping efforts in Drakes Estero (Fig. A3) reflected patterns we observed in subtidal swath surveys, with the most frequently captured crab being Pacific rock crab, red rock crab, and European green crab. In Drakes Estero, crab CPUE peaked around the mid-estuary, and most crabs caught were in seagrass compared to bare channel habitats. A similar pattern of peak crab CPUE occurred in the mid-estuary of Tomales Bay, and overall crab CPUE was greater in seagrass than bare channel habitats. However, crab CPUE appeared lower in Tomales Bay compared to Drakes Estero, and the European green crab dominated the mid- to inner estuary of Tomales Bay, whereas in Drakes Estero it was only caught in inner seagrass habitats. In general, crab sizes decreased moving up the estuary for both Drakes Estero and Tomales Bay.

3.2. Predator-prey model of sea otter population dynamics in estuaries

The Bayesian predator-prey model fit to data from Elkhorn Slough provided excellent convergence and goodness of fit, with well-mixed chains (r-hat values <1.01) and high effective sample sizes for all estimated parameters (Table A5). Posterior predictive checks indicated excellent fit of the model to observed datasets (Figs. A4, A5), and posterior distributions were distinct from prior distributions for all parameters (Fig. A6). The model provided a good approximation to observed temporal dynamics of the abundance of prey populations (Fig. A7), sea otters (Fig. A8), and rates of energy gain and allocation of foraging effort over time (Figs. A9, A10). The estimated equilibrium density for clams was higher than that of crabs, although both taxa had similar estimated intrinsic growth rates (Figs. A6a, A6b). Despite the greater overall abundance of clams, the per-capita encounter rate for crabs was more than double that for clams (Fig. A6c). This is likely because epi-benthic crabs are easier to detect and capture by otters than are infaunal clams (Kvitek and Oliver, 1988), and this higher capture rate resulted in more rapid and dramatic depletion of crab populations (Fig. A7). When both prey taxa were abundant, the rate of energy return for an otter feeding on crabs was slightly higher than for clams. But as prey became depleted, the overall rate of energy intake declined

(Fig. A9). Because depletion occurred more quickly for crabs than clams, the relative profitability of the two prey taxa eventually reversed. The model captured the dynamics of prey abundance well along with the resulting behavioral response by foraging sea otters. Specifically, the proportional allocation of feeding effort to crabs decreased while the allocation of feeding effort to clams increased over time, as did allocation of effort to alternative species (Fig. A10).

When we solved the parameterized predator-prey model over a 100year period, it projected a stable equilibrium for all three taxa (Fig. 3a). After accounting for parameter estimation uncertainty, the predicted equilibrium abundance of sea otters in Elkhorn Slough was 89 (95 % credible interval (CI₉₅) = 54–131; Table 1). Solving the same model for



Fig. 3. Line plots showing model-projected trends in abundance for sea otters (per 1 km²), crabs (catch per unit effort), and clams (per 25 m²) in three estuaries: (A) Elkhorn Slough, (B) Drakes Estero, and (C) Tomales Bay in California, USA. Trends were calculated by solving a series of differential equations describing predatorprey interactions over a 100-year period. Projections for Drakes Estero and Tomales Bay are based on eelgrass habitat, while estimated equilibrium densities of sea otters for non-eelgrass areas, as well as their credible intervals, can be found in Table 1.

Drakes Estero and Tomales Bay based on local conditions produced similar dynamics under the baseline scenario (Fig. 3b, 3c). We note that the differing equilibrium densities reflect the differing initial prey population densities. Drakes Estero and Tomales Bay's lower prey densities explain the lower potential sea otter densities projected by the model, especially for non-seagrass areas, despite the two estuaries having larger subtidal areas than Elkhorn Slough. The mean estimated equilibrium abundance at Drakes Estero was approximately half that at Elkhorn Slough, while the estimated equilibrium abundance at Tomales Bay was approximately 37 % higher than Elkhorn Slough despite the total subtidal area of Tomales Bay being more than seven times greater (Table 1).

If we instead assumed lower productivity at Drakes Estero and Tomales Bay, as modeled by a 50 % reduction in the intrinsic population growth rate of crabs and clams relative to Elkhorn Slough, then the potential equilibrium abundance of sea otters at Drakes Estero would be reduced from 43 to 22 individuals and at Tomales Bay from 122 to 62 sea otters (Table 1, Fig. 4).

4. Discussion

Our results suggest Tomales Bay and Drakes Estero could be important locations for sea otter recovery in northern California. Our model predicts that together these estuaries can support a mean expected total of 84 to 165 sea otters, depending on prey productivity. Further research is needed to determine whether the baseline or "reduced productivity" scenario is more accurate. Field studies measuring growth rates and recruitment dynamics of invertebrates at both estuaries could resolve this uncertainty, but the range provided remains informative given its conservative nature. It is based on a founder population consisting of a single male and female pair and does not account for some sea otter habitats like salt marshes and unvege-tated intertidal mudflats. These precluded areas, when combined, could add an extra 8 km² of estuarine habitat to the 31 km² assessed for this study. The conservative range is also shaped by unexpectedly low clam density estimates in Tomales Bay and Drakes Estero. Future efforts considering excluded habitats and involving more thorough benthic surveys would likely show that the estuaries can accommodate more sea otters than predicted here.

Few sites are as promising as Tomales Bay and Drakes Estero for sea otter recolonization. These estuaries have a small human footprint and carry minimal risks compared to other prospective systems. Alternatives like outer coast habitats are problematic because of regional kelp forest declines (McPherson et al., 2021; Rogers-Bennett and Catton, 2019) and potential shark predation (Anderson et al., 2008), and SFB has significant anthropogenic stressors (Hughes et al., 2019; Rudebusch et al., 2020). Our predictions indicate that permanent reestablishment of Tomales Bay and Drakes Estero alone could advance sea otter recovery. The southern sea otter range would expand by 100 km, and the current California population would increase by as much as 8 %, increasing subspecies resilience to oil spills and disease. Human intervention may be needed to successfully repopulate the two estuaries, but natural recolonization is feasible. Simultaneous migration of at least one male and female seems possible given the increased number of sea otters detected in PRNS (Figs. 2, A1). The recent sighting of a tagged female in Drakes Estero (J. Fujii, Monterey Bay Aquarium, written comm., 2021)



Fig. 4. Violin plots showing the posterior distributions of model-estimated values for the equilibrium densities of sea otters in three California estuaries: Elkhorn Slough, Drakes Estero, and Tomales Bay. Estimates for Drakes Estero and Tomales Bay are shown for two scenarios: a baseline scenario that assumes similar prey productivity rates (r), and an alternative scenario (r/2) that assumes prey productivity rates for Drakes Estero and Tomales Bay are reduced by 50 % relative to Elkhorn Slough.

is especially encouraging.

If sea otters successfully recolonize Tomales Bay and Drakes Estero, significant ecosystem changes can be expected. Sea otters are an apex predator capable of generating trophic cascades that benefit ecosystems in kelp forests (Estes and Palmisano, 1974) and estuaries (Hughes et al., 2013, 2024). It has been demonstrated that their presence stabilizes estuarine ecosystems through two mechanisms. First, the consumption of crabs may cause a trophic cascade that increases abundance of small grazers, decreases the abundance of epiphytic algae, and increases light availability for seagrass (Hughes et al., 2013, 2016). However, nutrient enrichment and eutrophication effects on Drakes Estero seagrass do not appear to be an issue affecting the seagrass stability or health as in other eutrophic systems. Second, the removal of benthic infaunal prey enhances seagrass genetic diversity by triggering flowering and sexual reproduction (Foster et al., 2021), and greater genetic diversity in seagrass has been shown to increase its productivity and restoration success (Williams, 2001). It has also been found that removal of benthic infauna frees up belowground space for seagrass rhizomes, which in the presence of sea otters leads to belowground growth and productivity of seagrass (Saavedra, 2021). Additionally, sea otter predation in Elkhorn Slough has recently been shown to be instrumental for reducing the impacts of burrowing crabs on eroding salt marshes (Hughes et al., 2024), and sea otters have been observed consuming the invasive European green crab abundant in both Tomales Bay and Drakes Estero (Fig. A3). This species has been found to have negative effects on estuarine community dynamics by competing with native species and damaging seagrass (Grosholz and Ruiz, 1995) and thus far, eradication attempts have failed (Grosholz et al., 2021). The benefits sea otters confer on estuaries could even spill over to nearby outer rocky reefs and help recover overgrazed kelp forests (Estes and Palmisano, 1974).

While sea otters help maintain balance in the ecosystems they inhabit, they can also create conflict where humans depend on prey items for sustenance or livelihood (Kone et al., 2021). In California estuaries, sea otters mainly prey on crabs and clam-both of which are harvested commercially or recreationally. Crabs can be caught in Tomales Bay and Drakes Estero, but prime crabbing locations are found outside the estuaries in deeper water beyond most sea otters' diving limits (avg. 62 m; Bodkin et al., 2004; Tinker et al., 2019). Although the southern sea otter can affect crab size and abundance in estuaries (Hughes et al., 2013), there is no evidence of them impacting commercially valuable crab fisheries (Grimes et al., 2020). It is uncertain if this would hold true following sea otter recovery in Tomales Bay and Drakes Estero, which is projected to reduce crab populations by half (Fig. 3). We also predict that benthic infauna abundance will decrease by a similar percentage (Fig. 3). Neither estuary supports commercial clam harvests, but sea otters could depress yields for recreational harvesting communities in Tomales Bay and Drakes Estero. It should also be noted that while oysters (family Ostreidae) are not a known prey item (Oftedal et al., 2007), captive sea otters have been shown to successfully open and consume them (Oregon Zoo, 2021). Commercial oyster mariculture ended in Drakes Estero in 2014, but Tomales Bay has several oyster farming operations that may need to prepare for potential sea otter recolonization to limit possible impacts from predation.

Our model gives conservation managers realistic estimates of the two estuaries' potential to support sea otter recovery. Among those expected to apply this information are the U.S. Fish and Wildlife Service (USFWS), who is tasked with ensuring the recovery of threatened southern sea otters listed under the U.S. Endangered Species Act. At present, they are evaluating the biological feasibility of sea otter reintroduction in northern California and considering a variety of open-coast and estuarine habitats (Zwartjes et al., 2022). However, narrowing their focus to specific sites would allow more targeted use of resources. Predictions made on the number of sea otters that could be sustained by Tomales Bay and Drakes Estero, as well as the cascading effects on prey species, can help inform the agency's selection of reintroduction sites. Without these data, USFWS risks making decisions that may fail to maximize conservation benefit to the species and its ecosystem (Zwartjes et al., 2022).

Previous efforts estimating sea otter population growth rates and equilibrium abundances in estuaries (Hughes et al., 2019; Tinker et al., 2021b), while statistically sound, did not incorporate predator-prey dynamics and resulted in large variance around predictions. In contrast, the model reported here accounts for the mechanistic interactions between abundance and dynamics of key prey species, bioenergetic requirements of sea otters, and the resulting emergent dynamics of sea otter populations. The development of this mechanistic model was possible given the spatially constrained habitats and relatively simple food web of California estuaries, as well as the large quantity of data collected over decades of extensive monitoring of sea otters and invertebrates in Elkhorn Slough (Hughes et al., 2013; Jackson et al., 2001; Tinker et al., 2008). Fitting our model to these datasets enabled us to generate process-based predictions of sea otter carrying capacity in estuaries that are more robust than those provided by earlier models.

This study focuses on the southern sea otter, but the recovery of other top predators can be better understood using the model as well. Reliable estimates about the capacity of habitats to support predator populations could help conservation managers make better informed choices. Managers should note that the model demands extensive data on predatorprey dynamics to produce meaningful results (Fig. A11) and thus may be impractical to use for data-poor systems. Improved technology such as environmental DNA could be used in some cases to acquire difficultto-collect data, but at present such solutions are often cost prohibitive. Despite this limitation, we consider our dynamical population model—one of the first to explicitly account for the process-based interactions between a larger predator and its prey—to be a powerful tool with significant utility for conservation decision-making.

CRediT authorship contribution statement

Samantha N.M. Hamilton: Visualization, Writing - original draft, Writing - review & editing. M. Tim Tinker: Conceptualization, Data curation, Formal analysis, Methodology, Validation, Visualization, Writing – original draft, Writing – review & editing. Joseph Jackson: Data curation, Funding acquisition. Joseph A. Tomoleoni: Writing original draft, Writing - review & editing, Data curation, Methodology, Resources, Validation. Michael C. Kenner: Data curation, Methodology, Resources, Validation, Writing - review & editing. Julie L. Yee: Validation, Writing - review & editing. Tom W. Bell: Data curation, Funding acquisition, Methodology, Resources, Visualization, Writing original draft, Writing - review & editing. Max C.N. Castorani: Data curation, Funding acquisition, Methodology, Resources, Visualization, Writing - original draft, Writing - review & editing. Benjamin H. Becker: Funding acquisition, Resources, Visualization, Writing - original draft, Writing - review & editing, Data curation. Brent B. Hughes: Conceptualization, Funding acquisition, Methodology, Project administration, Resources, Supervision, Visualization, Writing - original draft, Writing - review & editing.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper. Views and conclusions expressed in this paper are those of the authors and do not necessarily represent those of the funders or the U.S. Department of the Interior. All work in Drakes Estero was conducted under National Park Service Wilderness Permits, Research Permits, and Uncrewed Aerial System Authorizations.

Data availability

The full code and data utilized in this study are publicly available

from https://github.com/mttinker/Predprey_estuary. Queries should be directed to the corresponding author.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.biocon.2024.110623.

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