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RESEARCH ARTICLE

Revealing the extent of sea otter impacts on bivalve prey through multi-trophic monitoring and mechanistic models

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Abstract

1. Sea otters are apex predators that can exert considerable influence over the nearshore communities they occupy. Since facing near extinction in the early 1900s, sea otters are making a remarkable recovery in Southeast Alaska, particularly in Glacier Bay, the largest protected tidewater glacier fjord in the world. The expansion of sea otters across Glacier Bay offers both a challenge to monitoring and stewardship and an unprecedented opportunity to study the top-down effect of a novel apex predator across a diverse and productive ecosystem.
2. Our goal was to integrate monitoring data across trophic levels, space, and time to quantify and map the predator–prey interaction between sea otters and butter clams *Saxidomus gigantea*, one of the dominant large bivalves in Glacier Bay and a favoured prey of sea otters.
3. We developed a spatially-referenced mechanistic differential equation model of butter clam dynamics that combined both environmental drivers of local population growth and estimates of otter abundance from aerial survey data. We embedded this model in a Bayesian statistical framework and fit it to clam survey data from 43 intertidal and subtidal sites across Glacier Bay.
4. Prior to substantial sea otter expansion, we found that butter clam density was structured by an environmental gradient driven by distance from glacier (represented by latitude) and a quadratic effect of current speed. Estimates of sea otter attack rate revealed spatial heterogeneity in sea otter impacts and a negative relationship with local shoreline complexity.
5. Sea otter exploitation of productive butter clam habitat substantially reduced the abundance and altered the distribution of butter clams across Glacier Bay, with potential cascading consequences for nearshore community structure and

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function. Spatial variation in estimated sea otter predation processes further suggests that community context and local environmental conditions mediate the top-down influence of sea otters on a given prey. Overall, our framework provides high-resolution insights about the interaction among components of this food web and could be applied to a variety of other systems involving invasive species, epidemiology or migration.

KEYWORDS
apex predator, Bayesian hierarchical modelling, colonization dynamics, mechanistic modelling, predator–prey interactions, sea otters

1 | INTRODUCTION

Apex predators can exert considerable influence over the ecosystems they inhabit, with effects that cascade beyond their target prey (Estes et al., 2011; Ripple et al., 2014). Sea otters *Enhydra lutris* in rocky nearshore habitats provide a classic example of this top-down influence, where otter predation of sea urchins releases kelp from urchin grazing and facilitates maintenance of diverse kelp forest systems (as opposed to urchin barrens that form in the absence of sea otters; Estes & Duggins, 1995; Estes & Palmisano, 1974). In addition to this well-documented trophic cascade from otters to urchins to kelp, sea otters have a diverse diet (Tinker et al., 2012) and a metabolism that requires they consume roughly 25% of their body weight daily (Morrison et al., 1974). Sea otters thus have considerable potential to affect nearshore communities across habitat types and food web structures, though the strength and generality of those effects may vary (Kvitek et al., 1992). In unconsolidated and soft-sediment communities, large burrowing clams like the butter clam *Saxidomus gigantea* account for a large portion of otter diet (Doroff & DeGange, 1994; Kvitek et al., 1993), in addition to epifauna like urchins and crabs. In these systems, the long-term impacts of otters may be blunted by the relative difficulty of digging for infaunal prey, and subsequent cascades from depletion of filter-feeding clams may be slower to develop and may propagate more diffusely through the food web than in the tightly coupled food chains of rocky habitats (Kvitek et al., 1992; Kvitek & Oliver, 1992; Weitzman, 2013). Given this slower and more diffuse influence, the effect of sea otters in soft-sediment communities may also be more spatially variable and dependent on local community structure.

Intense exploitation by fur traders in the 18th and 19th centuries led to the extirpation of sea otters across much of their range in the North Pacific (Bodkin, 2015; Kenyon, 1969). Legislative protections, combined with translocations from remnant populations (Jameson et al., 1982), have permitted sea otters to recover and reoccupy much of their former range (Bodkin, 2015), with cascading consequences for nearshore community structure (Estes & Duggins, 1995). The recovery and expansion put sea otters at the mouth of Glacier Bay, Alaska by the late 1980s (Williams et al., 2019).

Glacier Bay is a tidewater glacier fjord that was covered in ice 270 years ago (Field, 1947; Hall et al., 1995). The subsequent rapid deglaciation (Avdievitch & Coe, 2022) and the recruitment of marine organisms, absent the influence of sea otters, allowed the largely soft-sediment nearshore ecosystem of Glacier Bay to develop a diverse and abundant invertebrate community, including urchins, crabs, sea stars and a diverse assemblage of infaunal clams (Weitzman, 2013). Continued glacial inputs of cold fresh water (Etherington et al., 2007) and sediment in the upper arms of Glacier Bay generate a physical gradient in the nearshore environment (from sites nearer to existing glaciers to sites farther away) that, in turn, structures the nearshore invertebrate community (Sharman, 1990). In particular, nearshore invertebrates are generally more diverse and abundant near the mouth of the bay and less diverse and abundant in the upper bay, nearer the remaining glaciers (Hale, 1979; Sharman, 1990), providing a gradient of prey communities for colonizing sea otters to exploit.

Glacier Bay, a marine protected area with limited commercial fishing (Nielsen & Seitz, 2017) and no sea otter harvest, is unique in Southeast Alaska (Eisaguirre et al., 2021). Moreover, it is geographically well-defined, and the subject of extensive long-term monitoring and stewardship efforts (e.g. Gabriele et al., 2022; Whitlock et al., 2020; Womble et al., 2021; Womble, Ver Hoef, et al., 2020). The arrival of sea otters in Glacier Bay presented an excellent opportunity to study sea otter colonization in the absence of substantial human activities and to document the effects of sea otters on soft-sediment nearshore communities. As such, programs to monitor sea otters have been ongoing since 1993 (Bodkin & Udevitz, 1999; Womble, Williams, et al., 2020) and surveys of their invertebrate prey at sites across Glacier Bay were established in 1998 (Bodkin & Kloecker, 1999). From their arrival in the late 1980s, sea otter abundance and distribution have expanded greatly within Glacier Bay, reaching an estimated total population of 8000 and presence throughout the bay by 2018 (Lu et al., 2019). Concurrently, prey surveys have documented changes in the nearshore community (Weitzman, 2013).

Understanding the role of sea otters in driving those system changes is crucial for informed stewardship, but this presents unique challenges even in the well-studied natural laboratory of Glacier Bay. In particular, linking sea otters and the nearshore community requires integrating multiple sources of monitoring data collected across multiple trophic levels (e.g. sea otter aerial surveys and benthic invertebrate surveys). These monitoring data may be sparse and are often not easily aligned in space or time. Due to these limitations, previous studies of soft-sediment habitats have relied on space-for-time substitutions that compared infaunal populations across categorical levels of otter occupancy (Kvitek et al., 1992; Kvitek & Oliver, 1992). Alternatively, process-based models (Ellner et al., 1998; Wikle & Hooten, 2010) offer a framework for linking different sources of data to a shared, dynamic, ecologically meaningful structure. Taking this approach, Lu et al. (2019) developed and fit a dynamic ecological diffusion model to multiple sources of sea otter aerial survey data collected over 26 years, providing high-resolution estimates of sea otter abundance across Glacier Bay. We built on this work and developed a mechanistic consumer-resource model, embedded in a Bayesian hierarchical framework (Berliner, 1996), that allowed us to couple the estimates of sea otter abundance produced by Lu et al. (2019) with subtidal and intertidal surveys of bivalve prey, focusing specifically on the butter clam *S. gigantea*, a common and favoured prey of sea otters in southeast Alaska (Bodkin, Ballachey, et al., 2007; Kvitek et al., 1993; Weitzman, 2013). This framework allowed us to make inference on the effect of sea otter colonization on butter clam populations across Glacier Bay and to quantify the spatiotemporal response of butter clams to sea otter colonization.

2 | MATERIALS AND METHODS

2.1 | Data

Surveys of invertebrate communities at intertidal and subtidal sites were conducted between 1998 and 2011. The intertidal data contain samples from 47 randomly selected sites along the Glacier Bay shoreline, and 9 "preferred clam habitat" (PCH) sites (Figure 1), chosen based on presence of clam siphons and shell litter at low tide (Bodkin et al., 2001). These sites were each sampled once initially between 1998 and 2000. Of the 56 intertidal sites, 12 were not resampled. The remaining sites were sampled again in 2010 or 2011, with some sites opportunistically sampled during the interim as well (Figure 2). At each sampling event at each site, 10 0.25 m^2 quadrats were sampled 20 m apart along a 200 m transect positioned at 0 mean lower low water (Bodkin & Kloecker, 1999). Each quadrat was excavated to a depth of 25 cm, and all bivalves of at least 14 mm in width (the mesh size used to sift sediment) were identified to the species level, counted and measured (Bodkin & Kloecker, 1999).

The subtidal data contain samples from 13 sites (Figure 1) selected based on presence of abundant visible clam siphons and proximity to areas occupied by sea otters (Bodkin et al., 2002). These

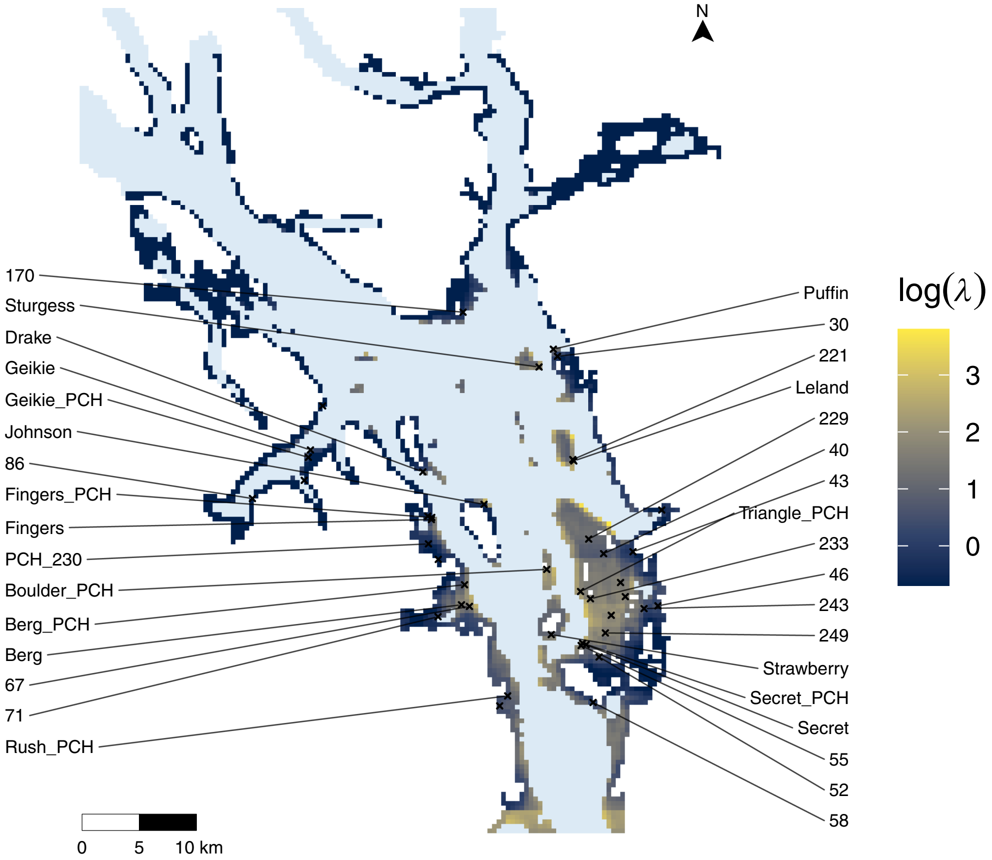

FIGURE 1 Map of invertebrate sampling sites in Glacier Bay. Sites are indicated with a black 'x'. Only sites with observed *Saxidomus gigantea* are labelled. Sites with 'PCH' in their name are intertidal preferred clam habitat sites, numbered sites are randomly selected intertidal sites, and other named sites are subtidal sites. White indicates land, and light blue indicates water deeper than 40 m. The colour gradient shows the log posterior mean sea otter abundance across the nearshore habitat in 2012 (Lu et al., 2019).

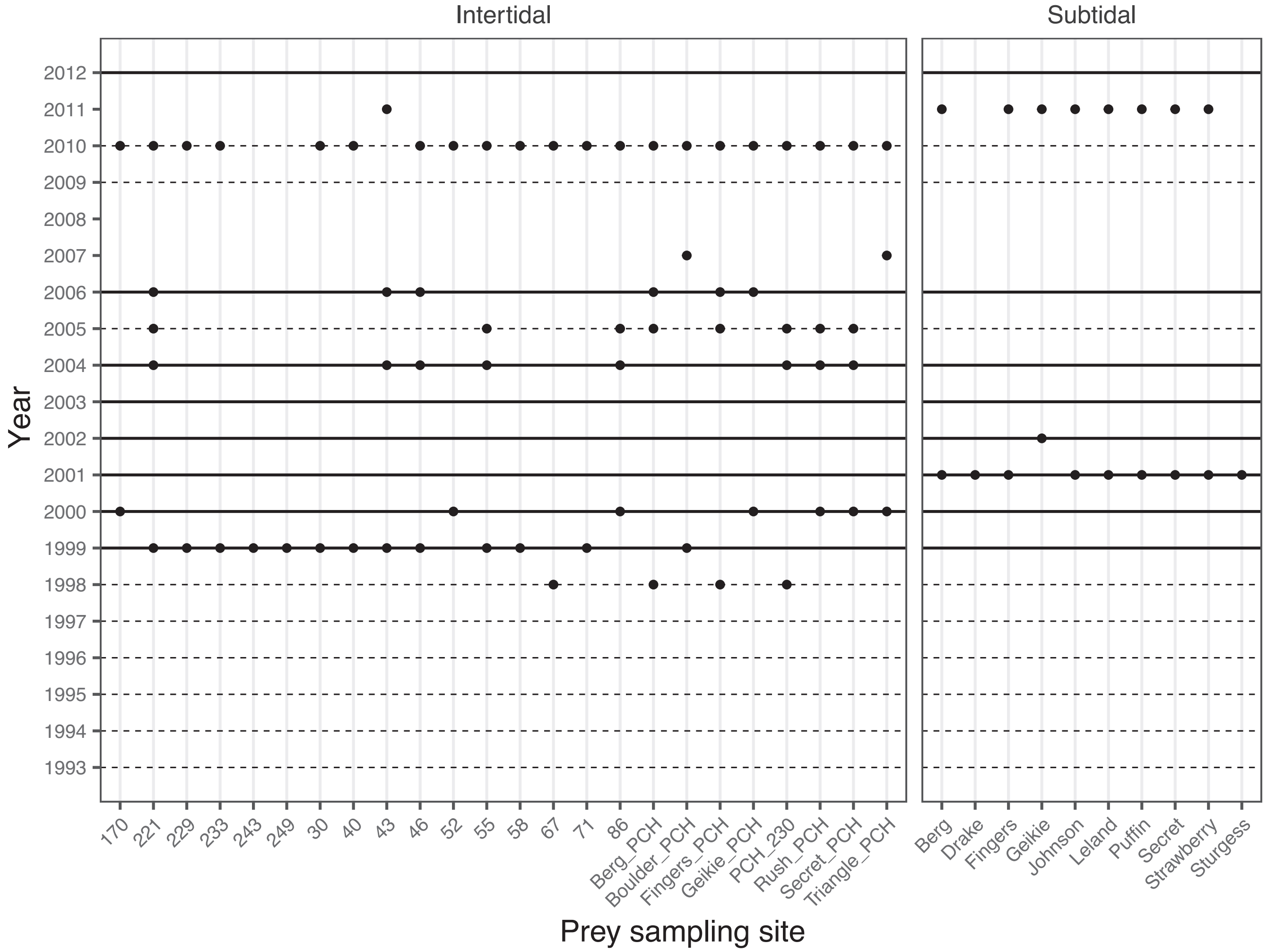

FIGURE 2 Timing of Glacier Bay intertidal and subtidal invertebrate surveys and sea otter aerial surveys. Points indicate the years in which each intertidal or subtidal site was sampled (only sites with observed *Saxidomus gigantea* are shown). Dashed lines across a given year indicate that a sea otter distribution survey was conducted in that year, while solid lines indicate that a design-based otter abundance survey was conducted. See Figure S1 for maps of the transects flown in design-based survey years.

sites were sampled initially in either 2001 or 2002, and 11 sites were sampled again in 2011 (Figure 2). At each sampling event at each site, 20 0.25 m^2 randomly located quadrats were sampled within a 20 m × 20 m grid (Bodkin et al., 2002). Each quadrat was excavated to a depth of 25 cm with a suction dredge, and all bivalves of at least 14 mm in width were identified to the species level, counted and measured (Bodkin et al., 2002). *S. gigantea* was almost entirely absent from intertidal and subtidal sites in the upper arms of Glacier Bay, and as such, we focused our analysis on only the 43 intertidal and subtidal sites in the main channel (Figure 1).

Sea otter abundance and distribution observations were collected in aerial surveys conducted from 1993 to 2019. Initially, two types of observer-based aerial surveys were conducted: broad scale distribution surveys (flown throughout occupied and adjacent habitats and conducted in 1993–1998, 2004–2005, 2009–2010) and design-based abundance surveys (flown along pre-defined 400 m wide transects and conducted in 1999–2004, 2006 and 2012, and supplemented with intensive survey units used to estimate sea otter detectability; Bodkin & Udevitz, 1999; Esslinger, 2019; Williams et al., 2019). More recently, surveys were conducted from 2017 to 2019 using aerial photographic methods (Womble et al., 2018; Womble, Williams, et al., 2020) that were scaled to match the observer-based surveys (Lu et al., 2019). These sea otter aerial survey data provide snapshots of the growing sea otter presence in Glacier Bay, but do not always align spatially or temporally with the invertebrate surveys (Figure 2, Figure S1). To aid in monitoring of sea otters in Glacier Bay, Lu et al. (2019) developed a Bayesian hierarchical framework that integrates the sea otter aerial survey data with a mechanistic diffusion model (specified as a partial differential equation, or PDE), while accounting for environmental drivers of sea otter diffusion rate and detection error in the otter observations (details in Lu et al., 2019 and Supporting Information). This model, via posterior realizations of the solution to the diffusion PDE, produces spatially and temporally complete posterior estimates of sea otter abundance across Glacier Bay, including at sites of the nearshore invertebrate surveys. The results of the analysis by Lu et al. (2019) thus enable us to align observed *S. gigantea* dynamics with estimates of local sea otter dynamics.

This study did not require ethical approval.

2.2 | *Saxidomus gigantea* prey model

We denote z_{jit} as the observed total count of *S. gigantea* individuals in quadrat j (generally $j = 1, \ldots, 10$ at intertidal sites and $j = 1, \ldots, 20$ at subtidal sites, although some sampling events recorded fewer quadrats) at site i ($i = 1, \ldots, 43$) in year t ($t \in \tau_i$, the vector of years in which site i was sampled). To allow for over-dispersion in the quadrat counts (e.g. due to spatial clustering of clams across a transect), we specified a negative binomial data model for the observed counts, such that

$$z_{jit} \sim \text{NegativeBinomial}\left(n_i(t), \phi_i\right), \tag{1}$$

where the negative binomial is parameterized to have mean $n_i(t)$, the latent true density (abundance per quadrat) of *S. gigantea* at site i in year t, and ϕ_i is a parameter that controls how the variance of the observations scales with the mean at site i.

At a particular site, clam dynamics are governed by an ordinary differential equation (ODE) capturing local recruitment (r_i, integrating broadcast spawning, settlement, and recruitment to observable sizes larger than 14 mm) and losses due to background mortality and interactions with sea otters:

$$\frac{dn_i(t)}{dt} = r_i - \nu n_i(t) - a_i \hat{\lambda}_i(t) n_i(t), \tag{2}$$

where $\hat{\lambda}_i(t)$ is the posterior mean sea otter density within 1000 m of site i (from Lu et al., 2019, with the 1000 m radius derived from findings from the Washington coast that sea otters generally rest and forage within 1000 m of shore, Laidre et al., 2009). The negative effect of sea otters on clams (from both direct predation and any potential indirect effects) is governed by a type I functional response with a spatially variable interaction coefficient a_i (henceforth referred to more narrowly as the attack rate). We assume that the background adult mortality rate of *S. gigantea* is constant across Glacier Bay. Hence, we modelled mortality using a spatially homogeneous term ν. We completed the specification of the differential equation by assuming that the initial clam density at each site is equal to the long-term equilibrium density in the absence of sea otters, given by $n_i(0) = r_i / \nu$. This leads to a useful alternative parameterization of Equation 2 in terms of $n_i(0)$, rather than r_i, yielding

$$\frac{dn_i(t)}{dt} = \nu\left(n_i(0) - n_i(t)\right) - a_i \hat{\lambda}_i(t) n_i(t). \tag{3}$$

This parameterization enables us to link the initial pre-otter densities of *S. gigantea* (the $n_i(0)$) to spatially-varying environmental factors, including latitude (as a proxy for factors like temperature, salinity, and sedimentation that broadly vary with distance from glacier Herter & Eckert, 2008; Sharman, 1990), current speed (Roegner, 2000; Wells, 1957), and shoreline complexity (the length of shoreline within 1000 m of the site). The initial density is restricted to be non-negative, so we modelled the vector of initial site densities, $\mathbf{n}_0$ as a log-linear Gaussian process, such that

$$\log\left(\mathbf{n}_0\right) \sim \text{MVN}\left(\mathbf{X}_n \beta_{n_0}, \mathbf{\Sigma}_n\right). \tag{4}$$

The matrix $\mathbf{X}_n$ contains an intercept and the environmental covariates latitude, the root mean square estimate of current speed (derived from a tidal circulation model of Glacier Bay; Drew et al., 2013; Hill et al., 2009), the square of current speed, and shoreline complexity. The spatial covariance matrix, $\mathbf{\Sigma}_n$, was defined such that the covariance between the initial density at sites i and j is

$$\Sigma_{n,ij} = \sigma_n^2 \exp\left(-\frac{1}{2}\frac{d_{ij}}{\rho_n}\right), \tag{5}$$

where d_{ij} is the Euclidean distance (in meters) between sites i and j, σ_n^2 is a variance parameter, and ρ_n is a range parameter. We fixed the hyperparameter $\rho_n = 100$ m to allow clam abundance to vary over relatively short spatial scales (Dethier, Kobelt, et al., 2019), and set $\sigma_n = 1.0$ to allow initial abundance to vary over roughly 2 orders of magnitude (expecting abundances to vary from < 1 to a maximum of approximately 60; Kvitek et al., 1992).

Similarly, we assume that the sea otter attack rate, a_i, may vary from site to site as a result of local environmental characteristics that influence sea otter foraging efficiency or differences in the nearshore community that influence the targeting of *S. gigantea*. Similar to $\mathbf{n}_0$, we modelled spatial variation in the sea otter attack rate as a log-linear Gaussian process, such that

$$\log(\mathbf{a}) \sim \text{MVN}\left(\mathbf{X}_a \beta_a, \mathbf{\Sigma}_a\right). \tag{6}$$

The matrix $\mathbf{X}_a$ contains an intercept, current speed (an important driver of foraging effort in diving sea birds; Drew et al., 2013; Heath & Gilchrist, 2010), and shoreline complexity, and $\mathbf{\Sigma}_a$ is a spatial covariance matrix defined as in (Equation 5), with variance parameter σ_a^2 and range parameter ρ_a. We fixed the hyperparameters $\sigma_a = 1$ and $\rho_a = 100$ m in our analysis to allow sea otter behaviour to vary over small spatial scales, and to permit attack rate to vary over a range that produces realistic simulated clam dynamics (e.g. ranging from no effect of otters to steep declines within only a few years).

We completed the model specification with prior distributions for β_{n_0}, β_a, ν, and ϕ_i. Where possible, we specified informative priors for these quantities based either on the literature or simulations of the prey model (Equation 2) that result in reasonable behaviour of the simulated ecological process (Supporting Information). We sampled from the posterior distributions of the above parameters using Markov chain Monte Carlo (MCMC) with Metropolis-Hastings updates (Supporting Information). To summarize changes in clam distribution across Glacier Bay, we also specified a derived quantity

($\boldsymbol{\beta}_{n_T}$) representing the coefficients of a log-linear regression analogous to Equation 4 on the estimated clam abundances from 2012 (i.e. $\log(\mathbf{n}_T) \sim \text{MVN}(\mathbf{X}_n \boldsymbol{\beta}_{n_T}, \boldsymbol{\Sigma}_n)$, where $\mathbf{n}_T$ is the vector of solutions to Equation 3 in 2012). We sampled these regression coefficients from their posterior predictive distribution (Supporting Information). To facilitate mixing and stability, we integrated $\boldsymbol{\beta}_a$ and $\boldsymbol{\beta}_{n_0}$ out of the spatial regressions (Hooten & Hefley, 2019). We implemented the MCMC algorithm in the Julia language (Bezanson et al., 2017), and solved the prey differential equation (Equation 3) using the DifferentialEquations package (Rackauckas & Nie, 2017).

3 | RESULTS

The fitted model captured the observed patterns of *S. gigantea* density across the invertebrate sampling sites, producing posterior predictions of the mean and variance of clam counts per quadrat that align well with observations (Figure S2, Supporting Information). Moreover, Bayesian model checking using the deviance as a discrepancy function (Conn et al., 2018) suggests that our model provides an adequate representation of the data (i.e. the computed Bayesian *p*-value of 0.82 is not extreme enough to suggest substantial lack-of-fit, Supporting Information). In particular, the mechanistic model captures the variation in initial *S. gigantea* density across Glacier Bay, and the diversity of *S. gigantea* responses to local sea otter population growth (Figure 3). Posterior estimates of $\boldsymbol{\beta}_{n_0}$ suggest that the initial (1993) abundance distribution of *S. gigantea* was driven in part by a positive effect of latitude (a proxy for distance to glacier) and a quadratic effect of current speed, with clam abundance initially increasing with increased current speed, then declining at the highest current speeds (Figure 4, Table 1). The initial *S. gigantea* distribution was unrelated to shoreline complexity (i.e. the length of the shoreline within 1000 m, Table 1).

Across many of the productive clam sites in central Glacier Bay, large increases in local sea otter density aligned with substantial declines in *S. gigantea* density (Figure 3). We estimated the largest declines at the highly productive island sites Strawberry (which dropped from a posterior median of 25 clams per quadrat in 1993 to just 2 in 2012) and Boulder_PCH (from 30 clams per quadrat to 4). In contrast, *S. gigantea* populations at a number of sites (e.g. Berg, 67) remained constant despite increases in local otter density (Figure 3). This variability in response was captured through estimated variability in sea otter attack rate, a_i, across sites (Figure 5). Sea otter attack rate was unrelated to current speed, but negatively related to shoreline complexity (Figure 5, Table 2).

The observed declines in *S. gigantea* at sites with large estimated a_i substantially altered the structure of its distribution across Glacier Bay. We summarized this shift by comparing the regression coefficients for the estimated initial clam densities (in 1993, $\boldsymbol{\beta}_{n_0}$) with analogous coefficients for the estimated final clam densities (in 2012, $\boldsymbol{\beta}_{n_T}$). We found that the regression intercept decreased substantially from 1993 to 2012 (Table 1), indicating an overall downward shift in *S. gigantea* density. The strength of the quadratic relationship between current and abundance also weakened from 1993 to 2012, with the estimated coefficients for both the linear and quadratic terms nearer to zero in 2012 than in 1993 (Table 1). Compared to the concave relationship estimated for 1993, the relationship between *S. gigantea* density and current speed in 2012 was nearly monotonic, with an overall shallower increase in expected density with increasing current speed and a much weaker decline in expected density at high current speeds (Figure 4). In contrast, the estimated relationship between latitude and *S. gigantea* density was steeper in 2012, than in 1993 (Figure 4, Table 1). Lastly, *S. gigantea* abundance remained unrelated to shoreline complexity in 2012, though the posterior distribution of the coefficient shifted toward more positive values (Table 1).

4 | DISCUSSION

The arrival of sea otters in Glacier Bay—a diverse and productive nearshore community that developed in the absence of sea otter predation—created both a unique natural experiment and a challenge for monitoring. Understanding the interaction between otters and their infaunal prey across the soft-sediment nearshore of Glacier Bay requires both a diverse collection of monitoring data, and a robust and flexible framework to link those data together across mismatched spatial and temporal sampling domains (Figure 2, Figure S1). Similar to integrated population modelling (Schaub & Abadi, 2010), our framework integrates multiple data sets and provides an example of the powerful role that mechanistic models can play in extending that integration across multiple trophic levels. In particular, the mechanistic diffusion model of Lu et al. (2019) assimilates sea otter aerial survey data from two sources and produces spatiotemporally complete estimates of sea otter abundance across Glacier Bay that are consistent with the fundamental ecological processes of diffusion and local logistic growth. Coupled with the otter abundance estimates produced by Lu et al. (2019), the differential equation model we specified for *S. gigantea* dynamics provides a natural framework for integrating the effects of sea otters through time and over the irregular sampling intervals of the invertebrate surveys (Figure 2). Moreover, the mechanistic framework enables us to initialize *S. gigantea* abundance in 1993 and integrate over any sea otter impacts that occurred prior to the initial invertebrate surveys in 1998–2002. Lastly, the mechanistic framework provides more detailed ecological inference than comparing otter-occupied and unoccupied sites, enabling us to estimate both the strength of the predator–prey interaction between sea otters and *S. gigantea*, as well as the bottom-up environmental drivers of *S. gigantea* productivity.

The waters nearer existing glaciers (i.e. at higher latitude in the arms of the upper bay) are generally colder, fresher, and contain more suspended sediment than the waters nearer the bay mouth (Arimitsu et al., 2016; Etherington et al., 2007; Sharman, 1990). Due to this gradient in habitat suitability, we expected a negative latitudinal gradient in initial *S. gigantea* density. However, with our analysis restricted to the main channel of Glacier Bay, we estimated a

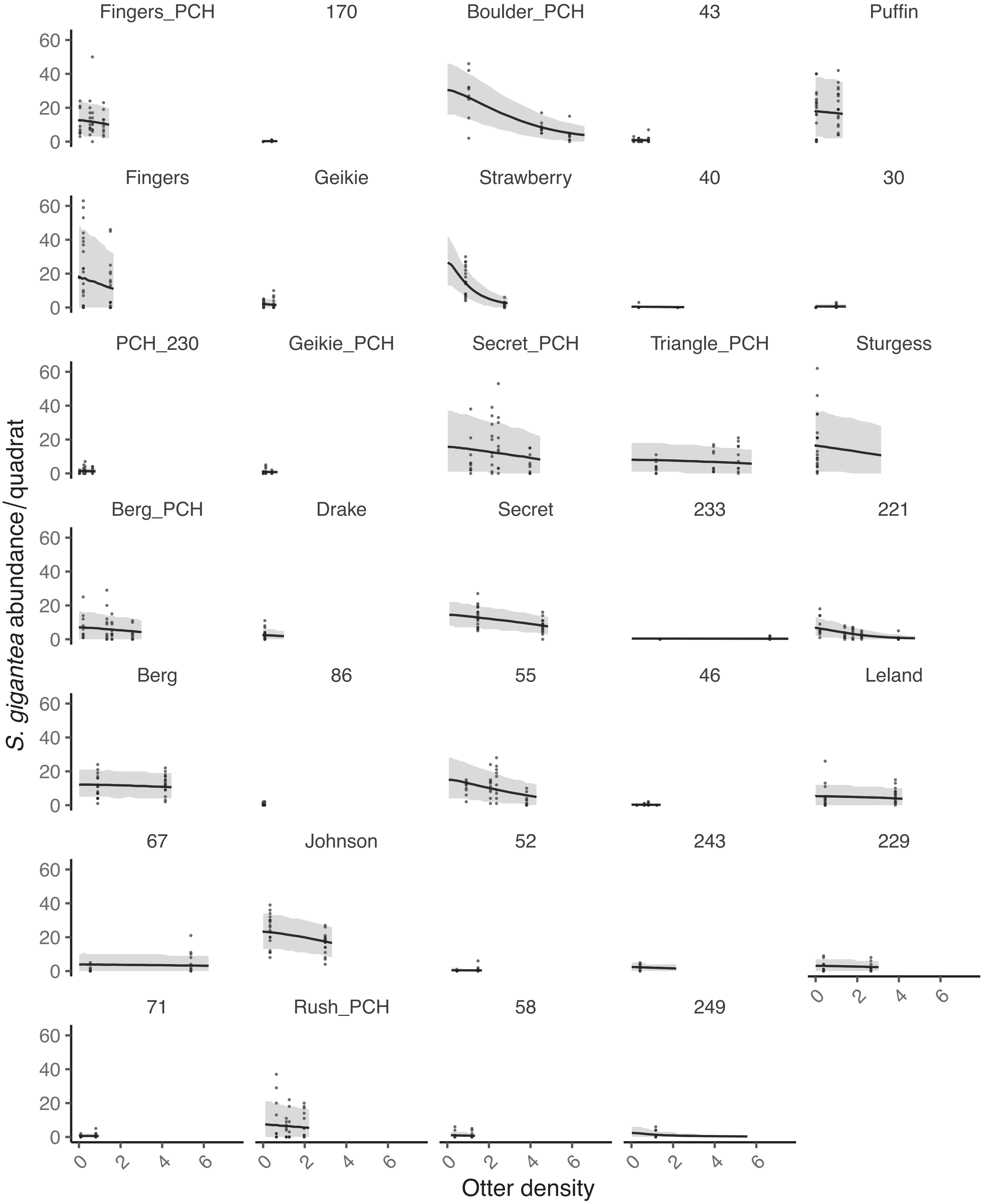

FIGURE 3 Estimated *Saxidomus gigantea* density and observations as a function of estimated local sea otter density. Each panel shows the estimated state-space trajectory at each site, advancing through time from left (corresponding to the pre-otter state in 1993) to right (corresponding to the local system state in 2012). Only sites with observed *S. gigantea* are shown. The black points represent the observed counts per quadrat. The black lines indicate the mean posterior predicted abundance per quadrat and the grey ribbon indicates the 80% credible interval. Sites are ordered by latitude from bottom to top.

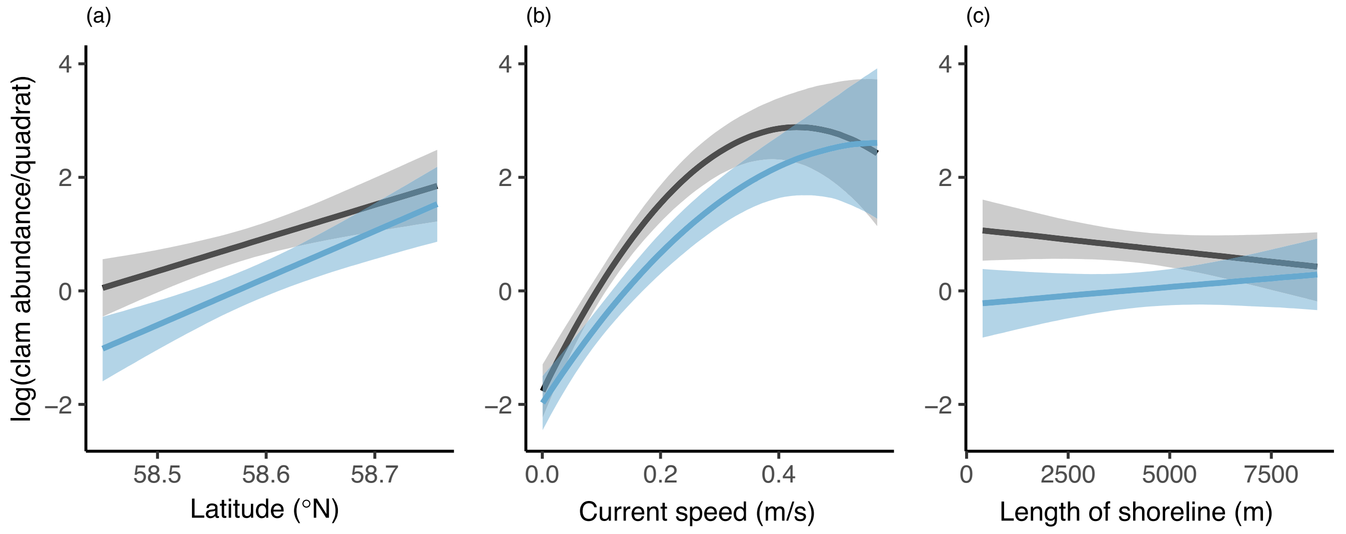

FIGURE 4 Predicted main effects of (a) latitude, (b) current speed, and (c) length of local shoreline (i.e., shoreline complexity) on local clam density in 1993 (prior to otter impacts, in grey) and 2012 (after otter impacts, in blue). Solid lines show the posterior median main effect of the given covariate, with all other covariates held fixed at their mean. Shaded ribbons show the 80% posterior credible interval.

TABLE 1 Posterior means and 95% credible intervals (in brackets) of coefficients for log-linear regressions of clam abundance. The β_{n_0} correspond to the abundance distribution in 1993 and the β_{n_T} correspond to the abundance distribution in 2012. $P(|\beta_{n_T}| < |\beta_{n_0}|)$ gives the posterior probability that the regression coefficient for 2012 is nearer to zero (i.e. has a shallower slope) than the coefficient for 1993.

Covariate	β_{n_0}	β_{n_T}	$P(\|\beta_{n_T}\| < \|\beta_{n_0}\|)$
Intercept	0.8 [0.4, 1.1]	0.01 [−0.4, 0.4]	0.99
Latitude	0.4 [0.1, 0.8]	0.6 [0.3, 1.0]	0.25
Current	1.8 [1.4, 2.2]	1.5 [1.1, 1.9]	0.82
Current^2	−0.4 [−0.6, −0.2]	−0.2 [−0.4, 0.0]	0.85
Shoreline	−0.2 [−0.5, 0.2]	0.1 [−0.2, 0.4]	0.52

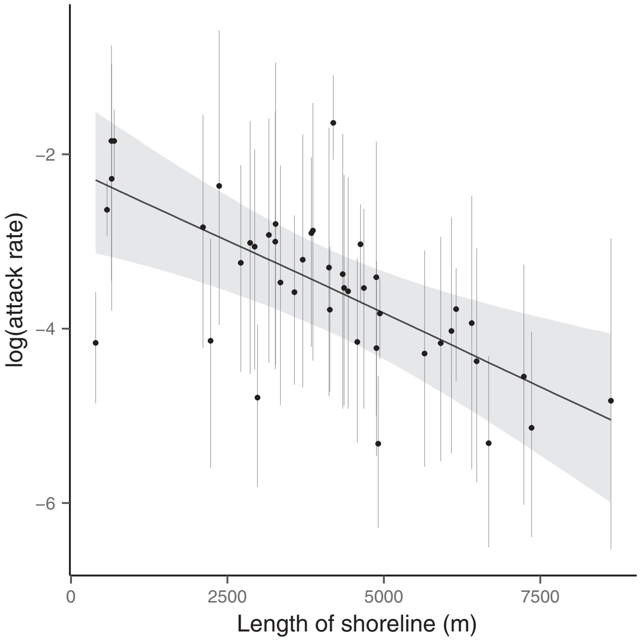

FIGURE 5 Estimated log sea otter attack rates ($\log(a_i)$) as a function of the length of shoreline (m) within 1000 m of each site (as a measure of shoreline complexity). The thick line gives the posterior median main effect of shoreline length, and the grey ribbon gives the 80% credible interval. Points give the posterior median $\log(a_i)$ for each site and vertical lines give the 80% credible intervals.

positive relationship between latitude and initial *S. gigantea* density (Table 1, Figure 4a). The near absence of *S. gigantea* from the invertebrate sampling sites in the upper arms of the bay suggests that glacial inputs create a categorical distinction between the bay arms and the main channel, but do not generate a monotonic bay-wide gradient in habitat suitability for *S. gigantea*. As such, physical factors that decay very quickly (i.e. nonlinearly) with distance from a glacier and the associated freshwater inputs (e.g. suspended sediment, turbidity, and grounded bergs; Etherington et al., 2007; Sharman, 1990) may be the main drivers of the absence of *S. gigantea* from the bay arms, perhaps together with limited transport of larvae, as Herter and Eckert (2008) found for Dungeness crab.

Temperature and salinity both change more slowly (i.e. linearly) with distance from glacier (Etherington et al., 2007; Sharman, 1990) and may be responsible for the estimated positive relationship between latitude and initial *S. gigantea* abundance within the main-channel. In particular, the salinities in the northern main channel of Glacier Bay are not likely low enough to affect clam survival (as in Marsden, 2004; Wells, 1957), but instead may facilitate increased availability of high quality particulate organic matter (Lowe et al., 2016), an important food source that may help maintain larger clam densities further up the bay. In addition to documenting the latitudinal gradient, by connecting the prey model to a tidal circulation model (Drew et al., 2013; Hill et al., 2009), we were also

TABLE 2 Posterior means and 95% credible intervals of sea otter attack rate regression coefficients.

Parameter	Posterior mean	Posterior CI
$\beta_{a,\text{intercept}}$	−3.5	[−4.3, −2.8]
$\beta_{a,\text{current}}$	−0.2	[−0.8, 0.4]
$\beta_{a,\text{shoreline}}$	−0.6	[−1.2, −0.1]

able to confirm the expected positive effect of current speed on clam density at relatively low current speeds (Figure 4b; Grizzle et al., 1992; Wells, 1957). The negative effect of the square of current speed (Table 1) suggests that clam density declines at high current speeds (Figure 4b; Vincenzi et al., 2011), consistent with studies of growth in non-siphon-feeding bivalves (Grizzle et al., 1992) and the potential inhibition of larval settlement at high water velocities (Roegner, 2000).

Beyond latitude and current, a number of other environmental factors are also likely important in driving spatial variation in *S. gigantea* productivity, though quantifying them for use in modelling is challenging. Local hydrodynamics, beyond the effects of current speed, can influence the retention, import and settlement of larvae (Herter & Eckert, 2008; Roegner, 2000), as well as clam growth (Dethier, Kobelt, et al., 2019). Patchily distributed predators like crabs (Dethier, Dobkowski, et al., 2019), or interactions between temperature, salinity and food availability, can further influence the survival of young clams (Dethier, Kobelt, et al., 2019).

Our dynamic model assumes that local clam recruitment to observable classes (14mm and larger) is variable in space, but constant in time. We were thus unable to account for short-term fluctuations in *S. gigantea* that have been documented elsewhere (Barber et al., 2019). These temporal fluctuations may be driven by factors such as local temperature extremes (Dethier, Kobelt, et al., 2019), year-to-year variation in the timing of larval settlement relative to the phytoplankton bloom and predator dynamics (Philippart et al., 2003), large scale oceanographic processes (e.g. the North Pacific Gyre Oscillation; Barber et al., 2019; Menge et al., 2009) and environmental perturbations such as the North Pacific marine heatwave (Di Lorenzo & Mantua, 2016). Detecting the effects of any of the above drivers would likely require higher resolution temporal sampling of nearshore infauna, and even so would potentially be swamped by the strong top-down influence of sea otters across much of Glacier Bay.

Across many of the invertebrate sampling sites, especially in the central bay, distinct declines in *S. gigantea* abundance aligned with substantial increases in local sea otter density (Figure 3). The dynamics at these sites are suggestive of a net negative effect of sea otters on clams, but our assumption of temporally constant recruitment and background mortality prevents us from attributing declines in *S. gigantea* to sources other than sea otters, such as recruitment failure. However, the observed size distributions at sites with distinct *S. gigantea* declines reveal that the most dramatic declines occurred in large clams, while small clams were relatively stable (Figure S3), consistent with otter size-selective predation (Kvitek et al., 1992; Kvitek & Oliver, 1992). Further parsing the effects of predation and recruitment would be aided by the development of a size-structured model of *S. gigantea* dynamics, but observations of extensive sea otter foraging on *S. gigantea* in Glacier Bay (Weitzman, 2013) and elsewhere in Alaska (Doroff & DeGange, 1994; Kvitek et al., 1993), together with the observed changes in size structure, suggest that the observed *S. gigantea* declines in Glacier Bay from 1998 to 2012 were likely driven by otter predation.

However, there remains considerable variation in the magnitude of the estimated sea otter attack rate on *S. gigantea* (a_i), and at some sites (e.g. Berg and 67), *S. gigantea* density remained constant and relatively high despite local increases in otter density. The estimated variability in the relationship between sea otters and *S. gigantea* may reflect mechanistic variability in sea otter foraging behaviour, driven by either differences in the physical environment or the available prey community. We found that the estimated attack rates were unrelated to current speed (Table 2), in contrast to the results of Drew et al. (2013), who found that bottom-foraging seabirds used predominantly low-current habitats in Glacier Bay. Although the increased energetic costs of foraging in high current habitat (Heath & Gilchrist, 2010, studying common eiders) may deter sea otters temporarily (Kvitek et al., 1992), current may not be an important constraint on sea otter foraging in the long term, especially for high-energy prey in productive environments (Kvitek et al., 2001). We also found that the estimated attack rates were negatively related to shoreline complexity (the length of shoreline within 1000m of a site; Table 2; Figure 5), consistent with the findings of Lu et al. (2019) and Williams et al. (2019) that sea otter residence time in Glacier Bay was higher in areas with less complex shorelines. These findings may reflect the distribution of attractive sea otter habitat in Glacier Bay (where kelp beds tend to be located along relatively straight stretches of coast), or differences in physical environment that make clam beds near more complex shorelines more likely to escape or withstand otter predation (e.g. due to reduced discoverability of clam beds or better conditions for clam recruitment or growth).

The remaining unexplained variability in sea otter use of *S. gigantea* prey (Figure 5) may be related to other physical features of the environment that may modulate the ability of sea otters to find and exploit clam beds like depth (Bodkin et al., 2004) or substrate (Stewart et al., 2014). Variability in the estimated attack rate could also arise due to changes in *S. gigantea* recruitment or survival (e.g. due to the dynamics of other predators, changing temperatures, freshwater inputs, or oceanographic processes) that could alter the intrinsic dynamics of local *S. gigantea* populations and their response to sea otter predation. Lastly, site-to-site differences in nearshore community structure may contribute to the estimated variation in attack rate. In particular, low attack rates on *S. gigantea* may reflect high relative abundance of other preferred sea otter prey like urchins or crabs (Laidre & Jameson, 2006; Ostfeld, 1982). Although sea otters can quickly deplete such easily-captured epifaunal prey (Kvitek et al., 1993; Kvitek & Oliver, 1992), episodic recruitment pulses of those prey (Estes & Duggins, 1995; Menge et al., 2009) may periodically make them available to sea otters and generate recurrent, if temporary, refuges for infaunal clams. Lastly, declines in the relative abundance of other predators, for example, the loss of sea stars due to wasting disease (Smith et al., 2021), may also increase the availability of epifauna and shield infauna from sea otter predation.

Although sea otters do not uniformly deplete *S. gigantea*, their influence restructured the distribution of *S. gigantea* across Glacier Bay. In particular, the targeting of productive *S. gigantea* habitat, especially at sites with intermediate current speeds in the lower bay, shifted the relationship between *S. gigantea* and the environmental drivers of its distribution (Table 1; Figure 4). We estimated that the positive latitudinal gradient in *S. gigantea* density became steeper from 1993 to 2012 (Figure 4a), reflecting the northward spread of sea otters and the longer occupation history in the lower bay. Further, we found that the apparent relationship between *S. gigantea* and current speed eroded from 1993 to 2012, such that sites with intermediate current speed are no longer predicted to have the highest abundance (Figure 4b).

As sea otters continue to establish in Glacier Bay, the distribution of *S. gigantea* is likely to shift further. We found that shoreline complexity was not a major driver of *S. gigantea* abundance in either 1993 or 2012, but there was some evidence of a shift in the coefficient for this effect from negative to positive (Table 1). This shift, and the negative estimated relationship between sea otter attack rate and shoreline complexity (Figure 5), suggests that locations with high shoreline complexity (e.g. narrow coves) may serve as refuges for *S. gigantea* in Glacier Bay. Other predators (e.g. sea stars, sea ducks and crabs) may have played a role in structuring *S. gigantea* density historically. However, our findings suggest that the magnitude of otter predation pressure has shifted the relative importance of bottom-up and top-down drivers of clam dynamics and distribution. In fact, with *S. gigantea* densities greatly reduced across much of Glacier Bay (Figure 3), *S. gigantea* may now be regulated more strongly by predation than growth or intraspecific competition, consistent with studies of other bivalves (Beal, 2006; Beal et al., 2001).

The escape of some *S. gigantea* populations from sea otter impacts in Glacier Bay fits with the prediction that the influence of otters in soft-sediment habitats may be more variable and diffuse than in rocky habitats, blunted by the increased foraging effort for infaunal prey and a more weakly connected food web (Kvitek et al., 1992). However, prior to the arrival of sea otters, *S. gigantea* was the dominant large infauna in Glacier Bay (Weitzman, 2013) and its decline at impacted sites is still likely to have substantial consequences for the rest of the nearshore community. The reduction of *S. gigantea* (particularly the loss of large individuals; Bodkin, Ballachey, et al., 2007; Weitzman, 2013) may lead to competitive release for smaller bivalve species not targeted by otters (Kvitek & Oliver, 1988; e.g., *Macoma spp.*) although sea otter excavation may also expose those bivalves to sea star predation (Kvitek et al., 1992). In addition, the dominant top-down pressure exerted by sea otters is likely to cascade through to affect other bivalve predators like octopus, sea stars and sea ducks (Bodkin, 2003), as well as commercially important species like Dungeness crab (Barber et al., 2019). Glacier Bay is an ideal laboratory to identify these cascading effects, but such efforts will require the development of an expanded and flexible modelling framework that integrates across other species of surveyed infauna, and potentially additional monitoring data sets for a variety of prey and predator species.

Saxidomus gigantea represents a major component of, and exerts considerable influence on, the physical structure of the soft-sediment nearshore community. As in other systems where predators target so-called ecosystem engineers (e.g. wolves and beavers, Gable et al., 2020), sea otter predation of *S. gigantea* may have important consequences for ecosystem function. In particular, removal of a large quantity of filter-feeding bivalves may influence sediment and nutrient transport processes in Glacier Bay (Newell et al., 2005; Prins et al., 1998; Thrush et al., 2006). These processes may be further altered by plumes of sediment and turbid water produced when sea otters excavate clams (Kvitek et al., 1992). Moreover, shell litter produced by sea otter predation of *S. gigantea* may provide hard substrate anchors for algae (Kvitek et al., 1992), possibly paving the way for the development of new kelp forests. Given the tight coupling and linkages across the ice and ocean interface in the northeastern Gulf of Alaska (O'Neel et al., 2015), and the important role of glacial inputs to the Glacier Bay system (Arimitsu et al., 2016; Etherington et al., 2007), otter-induced changes to the function of the nearshore could have profound consequences for the rest of the marine ecosystem.

The consequences of *S. gigantea* depletion will not only affect nearshore community structure and function, but are also likely to feedback into sea otter diet and dynamics. The energetic costs of foraging for infauna will likely prevent otters from locally extirpating *S. gigantea*, even at heavily impacted sites. Thus, *S. gigantea* is likely to remain an important component of sea otter diet in Glacier Bay, as is the case at long-occupied sites elsewhere in Alaska (Doroff & DeGange, 1994; Kvitek et al., 1992). However, the reduced availability of *S. gigantea* across Glacier Bay, and the smaller average size of the remaining individuals (Bodkin, Monson, et al., 2007; Weitzman, 2013), may force sea otters to spend more time foraging (Bodkin, Monson, et al., 2007; Esslinger et al., 2014; Tinker et al., 2008), and/or switch to a more varied diet that incorporates less energy dense or smaller prey (Newsome et al., 2015; Ostfeld, 1982; Weitzman, 2013). In particular, sea otter foraging observations from the Kodiak Archipelago found that smaller *Leukoma* and *Macoma* clams became increasingly important at long-occupied sites (Kvitek et al., 1992). The shift in diet away from favoured prey has already lead to reduced energy intake rates for sea otters in Glacier Bay (based on unpublished foraging observations; Weitzman, 2013) and is consistent with observations from other long-occupied sea otter populations (Coletti et al., 2016; Tinker et al., 2021), and the broad negative correlation between population growth rate at a location and the number of years occupied (Tinker et al., 2019). This reduced energy intake signals that, in the absence of abundant, large *S. gigantea*, sea otters are becoming food limited in Glacier Bay and may be approaching carrying capacity.

Glacier Bay is one of the largest marine protected areas in the northern hemisphere and serves as a living laboratory, fostering unique opportunities for the study of marine and nearshore ecology in tidewater glacier landscapes and the associated natural successional processes. Through all the above pathways, sea otter colonization of Glacier Bay is likely to alter the structure and function of its nearshore ecosystem. Effective stewardship requires understanding these changes so that anthropogenic changes can be better detected and managed. Moreover, understanding the role of otters in Glacier Bay is crucial for understanding the impacts of colonizing sea otters elsewhere in Alaska, especially in areas where conflicts with commercial shellfisheries are more likely. The high-resolution, mechanistic insights offered by our framework provide both a first step in understanding the effects of sea otters on soft-sediment habitats, and a method for combining mechanistic structure and monitoring data that could be applied to sea otters elsewhere or more broadly in studies of invasive species, epidemiology, or migration.

AUTHOR CONTRIBUTIONS

All authors contributed to the conceptualization and investigation; Jamie N. Womble and Mevin B. Hooten acquired funding and identified objectives; Benjamin P. Weitzman, James L. Bodkin, Daniel Esler, George G. Esslinger, Kimberly A. Kloecker, and Daniel H. Monson curated the data; Clinton B. Leach and Mevin B. Hooten developed the methodology; Clinton B. Leach wrote the code and performed the analysis; Clinton B. Leach led the writing of the manuscript. All authors contributed critically to the review and editing of the drafts and gave final approval for publication.

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CONFLICT OF INTEREST STATEMENT

The authors have no conflicts of interest.

DATA AVAILABILITY STATEMENT

The intertidal and subtidal sea otter prey survey data are available at https://doi.org/10.5066/P9LODH0Z (Esslinger et al., 2022). The outputs of the sea otter ecological diffusion model (Lu et al., 2019) and the tidal circulation model (Drew et al., 2013) are available from the Dryad Digital Repository https://doi.org/10.5061/dryad.vt4b8gtx6 (Leach et al., 2023). Model code is archived at https://doi.org/10.5281/zenodo.7782112 (Leach, 2023).

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

Figure S1. Locations of Glacier Bay intertidal and subtidal invertebrate surveys and design-based sea otter aerial transect surveys. Blue 'x' indicate intertidal and subtidal invertebrate survey sites that were sampled in each year. Gray lines indicate sea otter aerial survey transect lines that were own in each year.

Figure S2. Posterior predictive checks of goodness of fit. (a) Posterior predicted mean clam count per quadrat against the observed mean clam count per quadrat. (b) Posterior predicted variance of clam count per quadrat against the observed variance of clam count per quadrat. Each point represents a single sampling event (i.e., the sampling of 10 or 20 quadrats at a site in a given year), and corresponds to the posterior predicted mean of the quantity. The vertical lines give the 95% posterior predictive credible interval. The diagonal black line represents the 1:1 line.

Figure S3. Empirical size distributions of *S. gigantea* across sampling sites. Only resampled sites with nonzero counts are shown. Each point shows the mean count/quadrat for the corresponding 1 cm size bin. Colour indicates the year of the sample.

Figure S4. Posterior distribution of ν, the background mortality rate of the *S. giantea* dynamic model. The blue line indicates the posterior median.

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