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How far to build it before they come? Analyzing the use of the Field of Dreams hypothesis in bull kelp restoration

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Abstract

In restoration ecology, the Field of Dreams hypothesis posits that restoration efforts that create a suitable environment could lead to the eventual recovery of the remaining aspects of the ecosystem through natural processes. Natural processes following partial restoration has led to ecosystem recovery in both terrestrial and aquatic systems. However, understanding the efficacy of a "Field of Dreams" approach requires a comparison of different approaches to partial restoration in terms of spatial, temporal, and ecological scale with what would happen given more comprehensive restoration efforts. We explore the relative effect of partial restoration and ongoing recovery on restoration efficacy with a dynamical model based on temperate rocky reefs in Northern California. We analyze our model for both the ability and rate of bull kelp forest recovery under different restoration strategies. We compare the efficacy of a partial restoration approach with a more comprehensive restoration effort by exploring how kelp recovery likelihood and rate change with varying intensities of urchin removal and kelp outplanting over different time periods and spatial scales. We find that, in the case of bull kelp forests, setting more favorable initial conditions for kelp recovery by implementing both urchin harvesting and kelp outplanting at the start of the restoration project has a bigger impact on the kelp recovery rate than applying restoration efforts through a longer period of time. Therefore, partial restoration efforts, in terms of spatial and temporal scale, can be significantly more effective when applied across multiple ecological scales in terms of both the capacity and rate for achieving the target outcomes.

KEYWORDS
ecological scale, Fields of Dreams, *Nereocystis luetkeana*, partial restoration, recovery rate, *Strongylocentrotus purpuratus*

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INTRODUCTION

One of the main challenges in restoration ecology is understanding the intensity and extent of the efforts required to achieve restoration goals (Bradshaw, 1996). The idea that partial restoration, that is, a restoration focused on restoring a portion of the ecosystem components and then relying on natural processes for ecosystem recovery, might be effective is embodied in the Field of Dreams hypothesis (Palmer et al., 1997), which posits that setting up favorable conditions for restoration at the beginning of a project can be enough to promote the natural processes that will lead to a successful restoration effort. Partial restoration has been successful in such cases as short-term habitat enhancement through a one-time coral reef transplantation, which then enhanced a longer-term natural recovery of coral (Maya et al., 2016), or the reintroduction of former native species in degraded systems, which led to increases in species richness in the community (Richardson et al., 2010). However, partial restoration may not always be effective at achieving management goals. In some cases, the resulting community may not be desirable due to a lower diversity than the target community (Wodika & Baer, 2015), or stochasticity may bring similar ecosystems to completely different states, making further restoration efforts necessary if one of the states is undesirable (Trowbridge, 2007).

These examples raise the question of the conditions under which engaging in partial restoration efforts can achieve restoration goals. This question can be explored in terms of partial restoration efforts occurring on three different scales: spatial, temporal, and ecological (Acosta et al., 2018; Wiens, 1992). First, considering the spatial scale, partial restoration depends on the extent of the restoration effort that will then lead to natural recovery of the rest of the region through dispersal. Second, considering the temporal scale, partial restoration arises from performing restoration efforts on a short time frame and longer-term recovery following from natural dynamics. Third, considering the ecological scale, partial restoration arises from targeting a species or component of the community (e.g., reintroducing a foundational or early successional species, removing a pest species), and then recovery of additional species in the community occurs naturally (e.g., through succession). Existing evaluations of partial restoration have explored different scales. For example, Stoddard et al. (2019) tested the ecological scale of restoration in terms of whether restoring dune vegetation could lead to the natural recovery of beach mice. They found that beach mice occupied restored habitats almost as frequently as natural habitats. In addition, a meta-analysis by Katwijk et al. (2016) of seagrass restoration found that as the spatial scale increased, the likelihood of restoration success increased as well. Therefore, the relative efficacy of different aspects of partial restoration in determining the restoration success might vary, and a next step in understanding the efficacy of a Field of Dreams approach is to comprehensively evaluate the interaction between all three types of scale of partial restoration: spatial, temporal, and ecological.

Resolving the effect of these different types of scale on restoration success is particularly relevant to systems with the potential for alternative stable states and threshold dynamics. If an ecological system exhibits multiple stable states for a single set of environmental conditions, disturbance can lead to a shift in the system to an undesirable state or ecosystem function with impeded recovery (Beisner et al., 2003). In this case, the unstable threshold represents a target restoration must cross for recovery to occur (Suding & Hobbs, 2009). In the context of the Field of Dreams hypothesis, such a threshold can provide specific partial restoration goals that must be fulfilled before natural recovery is possible. While the potential for alternative stable states has been identified across terrestrial (James et al., 2013; Ratajczak et al., 2014) and marine (Connell et al., 2013; Mumby et al., 2013; Selkoe et al., 2015) systems (further reviewed in Folke et al., 2004), establishing whether such states represent prohibited versus slowed recovery is difficult to resolve empirically given challenges over resolving community outcomes at large temporal and spatial scales (Petraitis & Dudgeon, 2004).

A system that exemplifies the potential for threshold dynamics to affect restoration decisions is the temperate rocky reefs system. Temperate rocky reefs have experienced kelp declines and associated increases in kelp-grazing urchins in several parts of the world (Ling et al., 2015), including southern Australia (Layton et al., 2020) and Northern California (Rogers-Bennett & Catton, 2019), motivating novel restoration initiatives such as those proposed for other reefs in Morris et al. (2020). In addition, temperate rocky reefs can exist in kelp forests or urchin barren states, which might represent alternative stable states depending on an array of nonlinear feedbacks (Ling et al., 2015). For example, urchins typically subsist on kelp blades that detach from extant kelp and drift to the seafloor ("drift kelp"), such that grazing does not cause kelp mortality, especially when predator presence induces cryptic urchin behavior (Harrold & Reed, 1985). However, at low kelp densities, which might result from environmental disturbances such as heat stress, low nutrient content, or storms (Bell et al., 2015), urchin starvation can lead to more active kelp grazing, especially if it is compounded by low predator density, which can further increase kelp mortality (Harrold & Reed, 1985).

These interacting environment-dependent and predator-dependent factors indicate that outcomes in kelp forests

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likely arise from a mix of bottom-up and top-down processes (Graham et al., 1997; Karatayev et al., 2021; McPherson et al., 2021). Urchins in high-density, urchin-dominated barrens can go dormant for prolonged periods and quickly become active in the presence of kelp, which can limit the capacity for kelp to settle (Dolinar & Edwards, 2021). This has led restoration efforts to focus on urchin removal (Leinaas & Christie, 1996; Watanuki et al., 2010). However, the spatial and temporal extent of urchin removal necessary for kelp recovery have only recently been studied (Miller & Shears, 2022), and several strategies that extend the ecological scale of restoration, such as kelp reseeding (introducing kelp seeds or juvenile stipes) and outplanting (planting mature kelp stipes), are under exploration (Eger et al., 2020; Morris et al., 2020).

As an example of a temperate rocky reef with ongoing restoration efforts, the Sonoma County and Mendocino County coastlines of Northern California experienced a 95% decline in bull kelp (*Nereocystis luetkeana*) forest coverage (McPherson et al., 2021). These declines occurred due to multiple factors, including anomalously warm seawater temperatures between 2014 and 2016 and nutrient-poor water, that stressed kelp and increased purple urchin (*Strongylocentrotus purpuratus*) recruitment (McPherson et al., 2021; Rogers-Bennett & Catton, 2019). The increased grazing from purple sea urchins was exacerbated by the local functional extinction of the sunflower sea star (*Pycnopodia helianthoides*), the main natural predator of urchins in this region, due to the sea star wasting disease outbreak in 2013 (Harvell et al., 2019). This decline in kelp coverage has led to the starvation of other herbivores, which has resulted in the closure of the recreational red abalone (*Haliotis rufescens*) fishery and the decline of the commercial red sea urchin (*Mesocentrotus franciscanus*) fishery (Rogers-Bennett & Catton, 2019). This economic impact has accentuated the demand to restore the kelp forest ecosystems in this region. Proposed restoration strategies include urchin removal, kelp reseeding, and outplanting (Hohman et al., 2019). However, these restoration efforts, especially kelp reseeding and outplanting, are new to California's northern coast, with associated uncertainty concerning the extent necessary for effective restoration outcomes.

In this paper, we use a dynamical population model to explore how the spatial, temporal, and ecological scales of restoration extent influence restoration efficacy in the context of bull kelp restoration in the Northern California temperate rocky reefs. To do this, we analyze two metrics for restoration efficacy: the threshold urchin density for natural kelp recovery and, when recovery occurs, rate of kelp spread into new space. We evaluate the spatial scale by exploring how varying the portion of the intervened coastline by restoration influences these metrics. We explore the temporal scale by applying the intervention either just at the beginning of the restoration project or through continuous efforts. Finally, we explore the ecological scale by analyzing the role of reintroducing kelp or reducing urchin density, separately and in combination in restoration outcomes.

METHODS

Model overview

In this subsection, we will present an overview of the model we use to describe the spread dynamics of kelp, and in the following subsection, we will provide a mathematical formulation of the model. This model follows the distribution of kelp and urchin populations through survival, reproduction, and dispersal over a one-dimensional coastline (Figure 1). First, the adults of each population survive with a given probability. We assume that urchin survival is density independent (Levitan et al., 2014). Kelp survival depends on the overall grazing intensity by urchins, which depends on both urchin and kelp density. Direct grazing intensity is unimodal with kelp, initially increasing with resource availability and then decreasing at high kelp densities, as might occur due to a switch from active grazing to passive subsistence on drift kelp (Harrold & Reed, 1985). Adult kelp produce spores at a constant per-capita amount, whereas urchin larvae production depends on kelp grazing and drift kelp consumption. Spores and larvae then disperse through the coastline, and a fraction of them settle and become adults. We assume that this fraction is density independent for urchins (Levitan et al., 2014) and depends on local kelp and urchin densities for kelp. In line with observations that urchin adult movement occurs on the order of a few meters (Dumont et al., 2006), kelp seed and zoospore dispersal on the order of magnitude of tens of meters (Dobkowski et al., 2019), and urchin larval dispersal on the order of magnitude of kilometers (Largier, 2003), we assume that adult urchin movement is significantly smaller than the dispersal of kelp and urchin juvenile stages and, thus, neglect any adult urchin movement.

We vary the amount of urchin removal, kelp reseeding, and kelp reintroduction over a range of spatial and temporal extents. We focus on these interventions and do not include predator reintroduction as well, for two reasons. First, research into the feasibility of sea star reintroduction as a restoration intervention for our focal system of the northern coast of California is still in development and at the stage of lab tests (J. Hodin, personal communication, July 6, 2021), whereas urchin removal is

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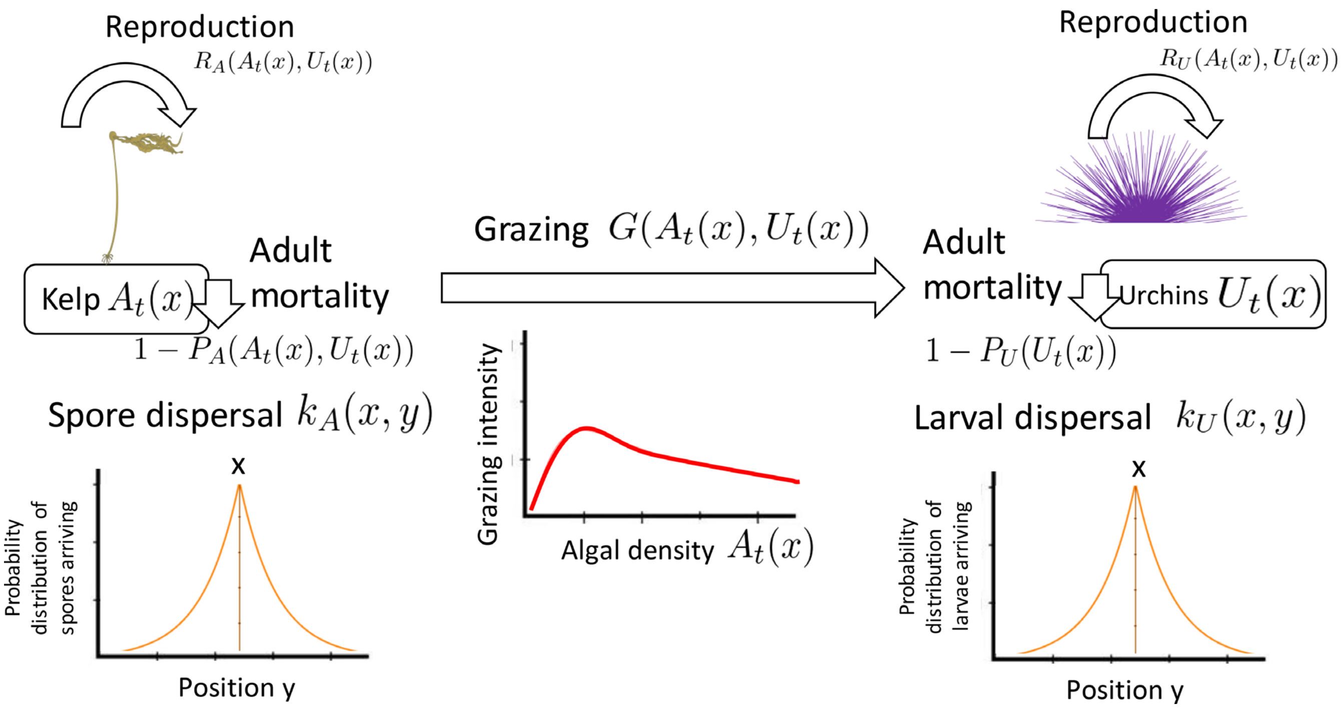

FIGURE 1 Overview of dynamics of model with respective functional forms of spore dispersal and grazing intensity. At each time step, a proportion of adults of each species dies off and recruits are produced and dispersed. The grazing interaction affects the spore production of urchins and kelp mortality. Diagram images thanks to Janes Thomas, Integration and Application Network (IAN) Image Library (https://ian.umces.edu/imagelibrary/).

under way (Ward et al., 2022) and kelp reseeding and reintroduction are undergoing field tests (B. Hughes, personal communication, July 6, 2021). Second, an ongoing question for the role and timing of predator reintroduction is whether and, if so, how much predators will seek out and gain energy from nonbarren urchins (i.e., urchins in recovered kelp stands with enough kelp consumption to support gonad production), such that predator reintroduction might be more effective if it occurs after interventions that increase kelp density. Given these considerations, current restoration efforts, which we seek to inform, are focused on urchin removal, kelp reseeding, and kelp introduction (Hohman et al., 2019).

Model

Our model combines the ecological dynamics of Karatayev et al. (2021) with the spatial dynamics of Kanary et al. (2014). We consider populations of kelp and urchins that cohabit in a one-dimensional coastline, Ω. Our model follows kelp, $A_t(x)$, and urchins, $U_t(x)$, through time, t, and space, x. At each time step and for each species i ($i = A$ for kelp and $i = U$ for urchins), the adults survive to the next step following the function $P_i(A_t(x), U_t(x))$ and adults produce recruits according to a function $R_i(A_t(x), U_t(x))$. The recruits survive to the next step following a function $S_i(A_t(x), U_t(x))$ and disperse from their source following a kernel k_i in an integrodifference equation framework, which is a discrete-time, continuous space modeling framework for population densities (Lutscher, 2019). Combining these dynamics, the populations for algae and kelp at the next time step follow:

$$\begin{aligned}
A_{t+1}(x) &= P_A(A_t(x), U_t(x)) + S_A(A_t(x), U_t(x)) \\
&\quad \times \int_\Omega k_A(x,y) R_A(A_t(y), U_t(y))\,dy, \\
U_{t+1}(x) &= P_U(A_t(x), U_t(x)) + S_U(A_t(x), U_t(x)) \\
&\quad \times \int_\Omega k_U(x,y) R_U(A_t(y), U_t(y))\,dy.
\end{aligned} \tag{1}$$

Adult kelp has a natural survival probability in the absence of urchin grazing given by δ_A, which implies a mean lifespan of $1/(1\text{-}\delta_A)$. [Correction added on 18 May 2023 after first online publication: Notation of mean lifespan has been corrected to $1/(1\text{-}\delta_A)$ in this version.] In addition, kelp survival depends on urchin grazing, which we model as a Holling's Type IV functional response $G(A_t(x), U_t(x))$. This functional response phenomenologically represents a behavioral shift from active to passive grazing with increasing kelp and can lead to two alternate stable states: a kelp-dominated state (kelp forest) and an urchin-dominated state (urchin barren) (Karatayev et al., 2021), which occurs under our parameterization (Appendix S1). Urchins graze kelp holdfast with

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a base attack intensity γ_A. Given a maximum grazing consumption at $A_t(x) = \frac{1}{\sqrt{\sigma_A}}$, adult kelp survival is

$$P_A(A_t(x), U_t(x)) = \delta_A A_t(x) \max(1 - \gamma_A G(A_t(x), U_t(x)),\ 0), \tag{2}$$

$$G(A_t(x), U_t(x)) = \frac{U_t(x) A_t(x)}{1 + \sigma_A A_t(x)^2}. \tag{3}$$

We assume that kelp produces a constant per-capita number of spores, R, which gives $R_A(A_t(y), U_t(y)) = RA_t(y)$. Kelp spore survival and recruitment depend on two factors: the probability of spore settlement and urchin predation. Settlement is density-dependent with a saturating, Beverton–Holt-type function given the maximum kelp population at a given location, x, of $1/\beta$. In addition, we assume that urchins graze recently settled kelp stipes before they can grow to a mature sporophyte with a per-capita probability γ_S. Then the survival of kelp spores is

$$S_A(A_t(x), U_t(x)) = \frac{\max(1 - \gamma_S U_t(x),\ 0)}{1 + \beta A_t(x)}. \tag{4}$$

Urchin survival occurs with a constant probability δ_U, which gives us $P_U(A_t(x), U_t(x)) = \delta_U U_t(x)$. Urchin larval production arises from two sources. First, urchins gain energy through direct grazing, proportional to Equation (3), with a proportion constant γ_U (Neubert et al., 1995). Second, urchins gain energy for larval production through drift kelp consumption at a constant proportion, ε, of the kelp available at each location, x. Both γ_U and ϵ encapsulate the conversion of energy gained from kelp consumption into larval production and survival such that $S_U(A_t(x), U_t(x)) = 1$. Combining both sources of energetic gain, the total urchin larval production is

$$R_U(A_t(y), U_t(y)) = \gamma_U G(A_t(y), U_t(y)) + \varepsilon A_t(y) U_t(y). \tag{5}$$

Finally, we model both dispersal kernels as Laplacian kernels with mean dispersal distance for each species i $1/a_i$ given by the equation (Lockwood et al., 2002)

$$k_i(x, y) = \frac{a_i}{2} \exp(-a_i |x - y|). \tag{6}$$

This shape of dispersal has been observed in several species of macroalgae (Gaylord et al., 2002), and it captures the spatial dynamics that arise from a combination of propagule diffusion with constant settlement (Lockwood et al., 2002), as is relevant to many marine organisms.

Note that, with constant and homogeneous kelp natural mortality δ_A, kelp spore production R, and urchin production γ_U and ε, we focus on kelp–urchin interactions and ignore the role of seasonal and variable environmental conditions in driving kelp and urchin dynamics. We make this simplifying assumption because of our focus on restoration decisions concerning the choice of urchin removal and kelp reintroduction interventions at different spatial extents and temporal scales. Informing the additional (and important) restoration decisions of optimal location and timing of restoration interventions, not under consideration here, would require model extensions that account for spatially heterogeneous and temporally stochastic environmental drivers such as nutrients, light, and wave disturbance that can influence kelp dynamics (Graham et al., 1997; Karatayev et al., 2021), as well as the stochasticity and seasonality of urchin reproduction (Cochran & Engelmann, 1975; Okamoto et al., 2020).

Parameter estimation

We fit the model without interventions to kelp and urchin distribution data in the Sonoma–Mendocino coast. We compile yearly kelp coverage data from the data set of McPherson et al. (2021) with the yearly urchin data of Reef Check (ReefCheck, 2020). To ensure the compatibility of these data sets with our model and between themselves, we created an evenly distributed data set by discretizing the data into a scale with a 10^{-4}-th of a degree unit. Using that scale, we connected each individual datapoint using linear interpolation, leaving us with an evenly distributed data set that works in our model. With this evenly distributed data set, we estimate all parameters except β using the 2007 and 2008 data (Figure 2). We identify two regions with available urchin data, which correspond to the coasts of Little River and Timber Cove.

To overcome the limited data on the specific parameters, combined with the complexity of our model, we estimate the parameters using the Approximate Bayesian computation (ABC) method, implemented using the EasyABC package in R (Jabot et al., 2013). To reduce estimation errors due to possible parameter correlations, we apply the ABC algorithm with Metropolis–Hastings sampling, implemented in the EasyABC package as the Marjoram method and described in Wegmann et al. (2009).

Using the ABC algorithm, we start our simulations taking the initial conditions $A_0(x), U_0(x)$ as the distribution for each of the regions at the 2007 measurement. We initialize our ABC algorithm with uniform prior distributions for each of the parameters in the range presented in Table 1. We then run the

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FIGURE 2 Kelp (green dots) and urchin (purple dots) data available for 2007–2008 in Sonoma and Mendocino counties of California. Notice the highlighted regions, circled in blue, where urchin data are available. These regions correspond to Little River (top circle) and Timber Cove (bottom circle). Note that the purple dot in the middle of the map corresponds to a single spatial point, which makes our spatial analysis unfeasible.

model for a sampled combination of parameters for a year (where each time step t corresponds to 1 month) and compare the obtained kelp distribution $A_{12}(x)$ with the distribution at the 2008 measurement. We compare these distributions using root mean square error (RMSE) as our summary function. In other words, if $A_{12}(x)$ is the 2008 distribution in the given region, we find combinations of parameters that minimize

$$\mathrm{RMSE} = \left(\int_{\Omega} (A(x) - A_{12}(x))^2 dx\right)^{1/2}.$$

While this approach ignores the seasonal nature of kelp and urchin recruitment as well as kelp mortality from winter storms (Ebert et al., 1994; Springer et al., 2010), in the absence of monthly data that would allow model fitting to seasonal processes, it does capture the year-to-year dynamics that match the time scale of the data.

To estimate the β parameter that inversely determines the kelp recruitment saturation level, we perform a linear regression at each point in space in the kelp distributions from 2004 to 2009 and fit it to a Beverton–Holt model (Beverton & Holt, 1993). This procedure allows us to make use of the higher availability of kelp data and reduce the number of parameters our ABC procedure must estimate. We then use the distribution of maximum densities as our distribution for $1/\beta$.

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TABLE 1 Description of each model parameter.

Parameter	Description	Range of possible values explored	Best-fit value
δ_A	Survival probability of adult kelp	[0, 1]	0.510
γ_A	Grazing intensity of urchins on kelp	[0, 1]	0.101 kelp m^{-2} urchins^{-1}
σ_A	Inversely determines kelp density at maximum urchin grazing	[0, 100]	15.475 kelp m^{-2}
γ_S	Probability of juvenile kelp stipes being grazed by urchin	[0, 100]	0.743 urchins^{-1}
β	Inverse of maximum kelp density	Estimated without ABC (see text)	2.42 kelp m^{-2}
a_A	Inverse of mean dispersal distance of kelp	[0, 100]	16.137 m^{-1}
R	Per-capita spores production of kelp	[0, 10]	5.500
δ_U	Survival probability of urchins	[0, 1]	0.312
γ_G	Urchin production from direct kelp consumption	[0, 10]	4.956 urchins
a_U	Inverse of mean dispersal distance of urchin	[0, 100]	93.586 m^{-1}
ε	Urchin production from kelp consumed by urchins as drift kelp	[0, 10]	9.484 kelp m^{-2}
μ_U	Intensity of urchin removal relative to natural urchin mortality	[0, 1]	
μ_S	Intensity of kelp seeding relative to per-capita spores production	[0, 1]	
μ_A	Intensity of kelp outplanting relative to natural kelp mortality	[0, 1]	
η	Length of region to apply restoration efforts around kelp oasis	[0, 100]	
A_c	Critical kelp density to identify where to apply restoration efforts	[0, 1]	
A_0	Initial kelp density at kelp oasis	[0, 5]	
U_0	Initial urchin density at coastline	[0, 100]	

Abbreviation: ABC, Approximate Bayesian computation.

Control strategies and model analysis

To explore what control strategies promote the spread of kelp, we follow the restoration focus of the Sonoma–Mendocino Bull Kelp Recovery Plan (Hohman et al., 2019). This recovery plan focuses on implementing several restoration strategies near kelp "oases," that is, patches of extant kelp, to try to enhance kelp expansion to nearby regions. We explore three restoration strategies around these oases: urchin removal, kelp reseeding, and kelp outplanting.

We initialize our simulation with initial condition of kelp $A_0(x)$ at 0 everywhere except at a starting oasis of length L, in which we start with kelp at an initial kelp density A_0; the urchin initial density is U_0 throughout the coastlines Ω. We identify target restoration locations based on kelp density (and, therefore, the location of oases) as it changes through time. At each time step t, we define the region where restoration efforts are applied as the set of all locations centered around x with length η, where the kelp density surpasses a critical density A_c. This gives us a function, $\delta_t(x)$, to indicated the presence or absence of restoration actions given by

$$\delta(x) = \begin{cases} 1 & \text{if } \int_{x-\eta/2}^{x+\eta/2} A_t(y)dy \geq A_c, \\ 0 & \text{otherwise.} \end{cases} \tag{7}$$

We multiply implementation presence $\delta_t(x)$ by the control intensity of each possible approach for ongoing restoration. First, for ongoing urchin removal, we decrease urchin survival δ_U by a proportion μ_U. Second, for kelp seeding we multiply kelp spore production R by a proportional increase μ_S. Third, for kelp outplanting, we multiply kelp adult survival δ_A by a proportional increase μ_A. The functions for urchin survival, kelp reproduction, and adult kelp survival with these ongoing restoration interventions are then

$$P_U(U_t(x)) = \delta_U(1-\mu_U\delta(x))U_t(x), \tag{8}$$

$$R_A(A_t(x)) = R(1+\mu_S\delta(x))A_t(x), \tag{9}$$

$$\begin{aligned} &P_A(A_t(x), U_t(x)) \\ &= \delta_A A_t(x)\left(1+\mu_A\delta(x) - \gamma_A U_t(x)\frac{A_t(x)}{1+\sigma_A A_t(x)^2}\right). \end{aligned} \tag{10}$$

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We explore the temporal scale of restoration through two scenarios. First, we implement a short-time-scale restoration effort by varying the initial densities A_0 and U_0 and setting long-term control $\mu_i = 0$ for function $i = U, S, A$. This corresponds to the case in which partial restoration efforts are performed at the start of the project, and then natural processes (e.g., succession) might eventually achieve restoration goals. Second, we implement a long-time-scale restoration effort where the initial kelp and urchin densities A_0 and U_0 are fixed, and we vary the restoration effort intensity μ_i. For these simulations, we set the initial kelp density $A_0 = 1/\beta$ within the oasis (and zero elsewhere) and initial urchin density U_0 to 95% of the threshold value that the system must cross for kelp recovery. Then, for ongoing restoration intervention, we explore a range of intensities in terms of (1) urchin removal modeled as a proportional decrease in urchin survival (μ_U in Equation 8), (2) seed outplanting modeled as a proportional increase in kelp recruits (μ_S in Equation 9), and (3) kelp outplanting modeled as a proportional increase in adult kelp (μ_A in Equation 10). In each case we explore weak (10%), moderate (40%), and strong (70%) intensities.

In both temporal scale scenarios, we explore the effect of different spatial scales. For the short-time-scale scenario, we explore the spatial scale of restoration by varying the length of the initial oasis L. In the long-time-scale scenario, we explore the spatial scale of restoration by varying the size of the region with a control effort η. Finally, we explore the ecological scale of restoration by comparing scenarios with only a single control strategy or a combination of strategies (urchin removal, kelp reseeding, or kelp outplanting) at varying intensities.

We evaluate these scenarios using two metrics. Our first metric is the maximum initial urchin density at which kelp can spread (hereafter the urchin threshold), which represents the restoration effort necessary for eventual recovery to take place. The second metric is the kelp recovery rate (hereafter spread rate). To calculate the spread rate, we run the system for 12 time steps (months) and, at each time step, calculate spread extent as the distance from the starting point $x = 0$ to the point x where there is a significant amount of kelp coverage, which is more than 1% of kelp coverage. We then calculate the spread rate as the slope of the linear regression of spread extent versus time. We choose months as our time scale to explore the dynamics of our system through the span of a single year, which allows us to see the short-term effect of the different restoration strategies while also accounting for the annual nature of bull kelp, where factors not modeled, such as storm disturbance, might further affect kelp survival at the end of our time horizon.

To quantify the relative effect of different processes and management levers on the urchin threshold and spread rate, we perform a global sensitivity analysis of all parameters in the model, based on the procedure by Harper et al. (2011). We first sample 2000 combinations of parameters from the posterior distributions obtained from the parameter estimations and calculate the urchin thresholds and spread rates for each combination. We then construct a random forest using the R package randomForest (Liaw & Wiener, 2002), with the parameters of our model as predictors and the urchin threshold or spread rate as the target function. The randomForest package provides an importance metric for each predictor, which indicates how frequently that predictor served a breakpoint in the random trees of the forest.

RESULTS

In our model parameterization, the ABC showed high uncertainty in all of the estimated parameters; we focus in our global sensitivity analysis on the influence of the different parameters on the model outcomes. We only show the results for the parameter estimates of the Timber Cove region, using the best-fit values presented in Table 1. We do this because the ABC of Timber Cove provided better posterior distributions than that of Little River and, thus, less uncertainty. See Appendix S2 for the posterior distributions for both regions.

Urchin threshold

We find that kelp is only capable of recovering when urchin densities are below a certain threshold. Increasing the ecological scale of restoration by including kelp outplanting (i.e., increasing initial kelp density) increases this threshold, which reduces the intensity of urchin removal efforts required to ensure kelp recovery (Figure 3). This occurs because increasing kelp density lowers the grazing intensity of urchins due to the behavioral feedback in the Type IV functional response of urchin grazing. Accordingly, an increase in σ_A (the parameter that determines the strength of the behavioral feedback) increases the threshold urchin density for kelp recovery. In the context of the Field of Dreams hypothesis, kelp natural recovery can be feasible after removing urchins below a certain threshold.

Our global sensitivity analysis (Figure 4) confirms that the main factor affecting the threshold urchin density for kelp recovery is urchin grazing activity (described by the conversion of kelp to urchins γ_A and the kelp grazing inhibition parameter σ_A). Specifically, the threshold urchin density is greater for slower urchin grazing (lower γ_A) and a reduction in the kelp density where the

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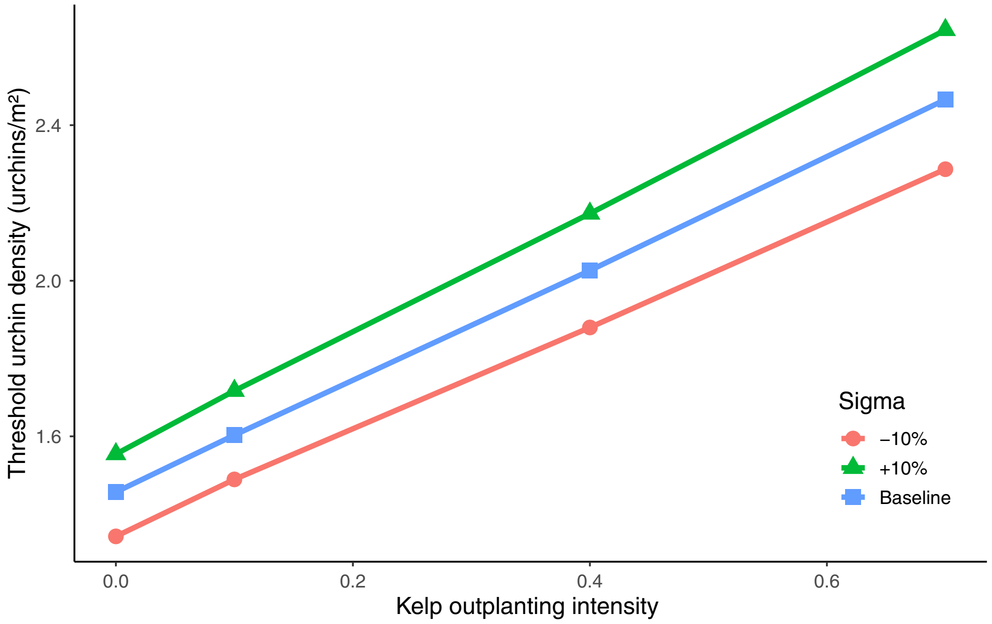

FIGURE 3 Threshold urchin density necessary for kelp recovery as a function of kelp outplanting intensity. Different lines represent different values of σ_A (inversely determines the kelp density of maximum urchin grazing in the Type IV functional response) changed by 10% from its baseline value.

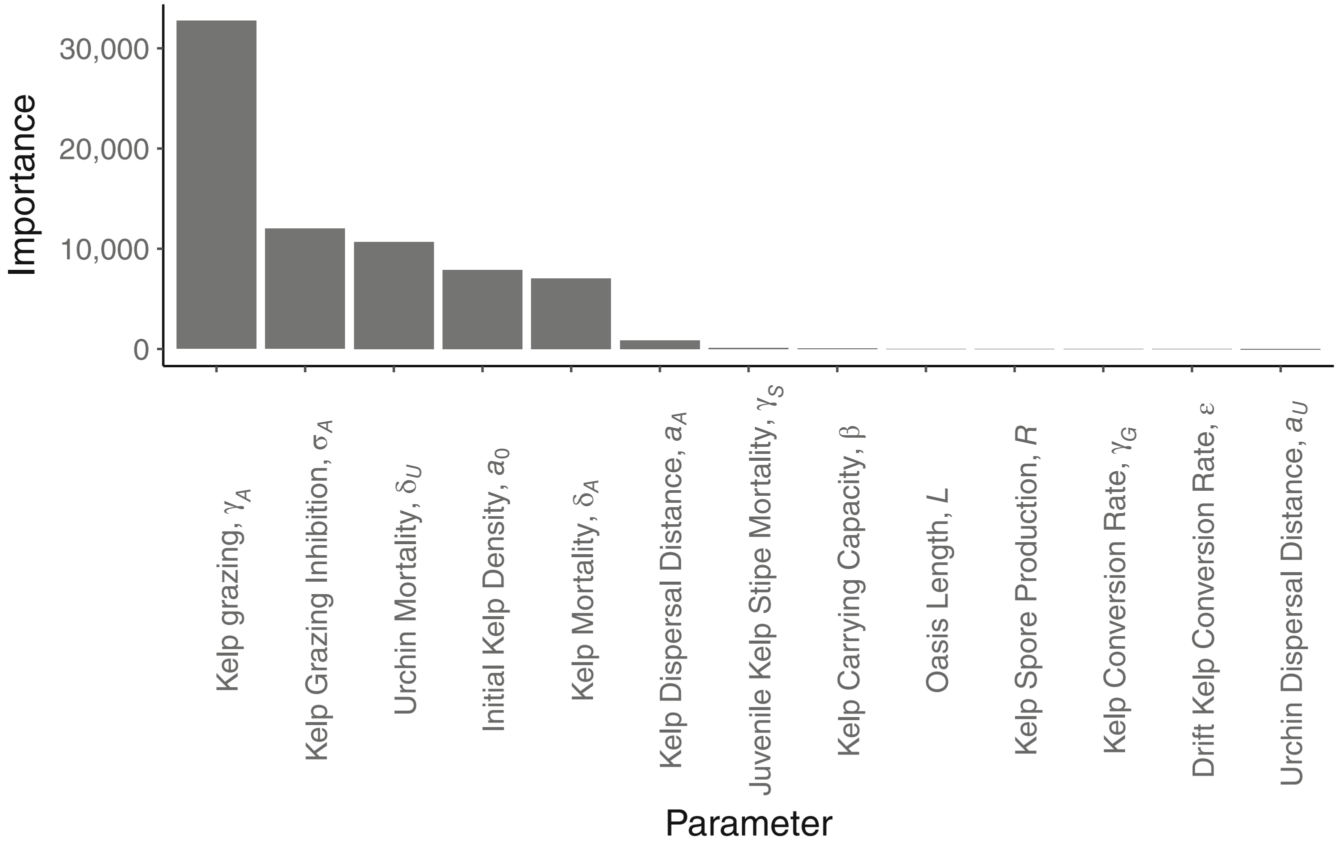

FIGURE 4 Importance ranking of parameters of Model 1 from global sensitivity analysis of threshold urchin density necessary for kelp recovery. See Table 1 for more detailed parameter definitions.

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per-capita urchin grazing reaches its maximum (lower σ_A). In addition, the threshold urchin density is higher for a higher urchin natural mortality rate (lower urchin survival probability δ_U), higher initial kelp density (A_0), and with a lower kelp natural mortality (higher kelp survival probability δ_A).

Kelp spread rate

Given initial urchin removal below the threshold value required for recovery, the kelp spread rate increases with expanding interventions across ecological scales more than over spatial or temporal scales. Under our baseline parameterization, ongoing kelp seeding enhances kelp recovery rate, while long-term, ongoing kelp outplanting or urchin removal does not (Figure 5). However, the relative effect of other strategies is sensitive to initial kelp density. With double the initial kelp density, further kelp outplanting increases the kelp recovery rate (Figure 6a), while with triple the initial kelp density, ongoing urchin removal has a greater effect on the kelp recovery rate (Figure 6b). The greater sensitivity to the initial kelp density for ongoing urchin removal and kelp outplanting, compared to kelp reseeding, is likely due to the nonlinear (Type IV) feedback between urchin grazing and extant kelp compared to the linear (Type I) feedback between urchin grazing and kelp seeds. These different dynamics lead to a different influence of the control strategies that directly affect the local kelp–urchin interaction.

For the spatial scale of restoration, increasing the extent of ongoing restoration efforts does not affect the rate of recovery of kelp (compare panels [a] and [b] of Figure 5). This suggests that kelp recovery is mainly determined by the local urchin grazing intensity, and extending restoration efforts to regions of the coastline with reduced kelp densities, where urchin grazing is stronger, will not affect the kelp recovery rate. For the temporal scale of restoration, increasing the initial kelp density and decreasing the initial urchin density through a more intense partial restoration effort at the beginning enhances kelp recovery more than ongoing restoration efforts (compare the spread rates in Figure 7 to those in Figures 5 and 6). Increasing kelp density and reducing urchin density near the kelp oasis provides better conditions for kelp survival when

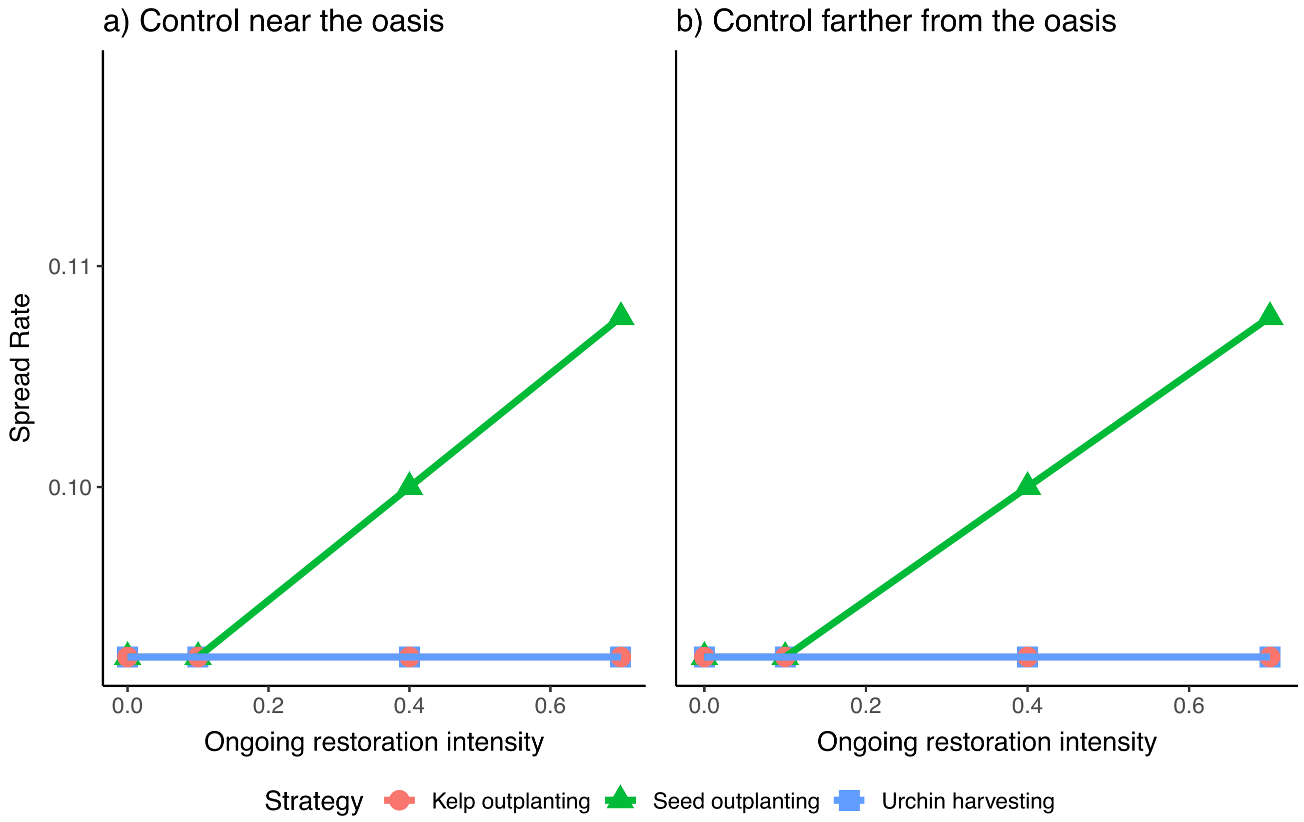

FIGURE 5 Kelp spread rate under different restoration strategies with increasing intensity following urchin removal below threshold value necessary for kelp recovery and with initial kelp density $1/\beta$. Each line represents a different strategy: kelp outplanting (μ_A) in red circles, kelp seeding (μ_S) in green triangles, and sustained urchin harvest (μ_U) in blue squares. Panel (a) shows ongoing restoration efforts near the kelp oasis ($\eta = 1$), and panel (b) shows ongoing restoration efforts across a wider region of the coastline ($\eta = 10$).

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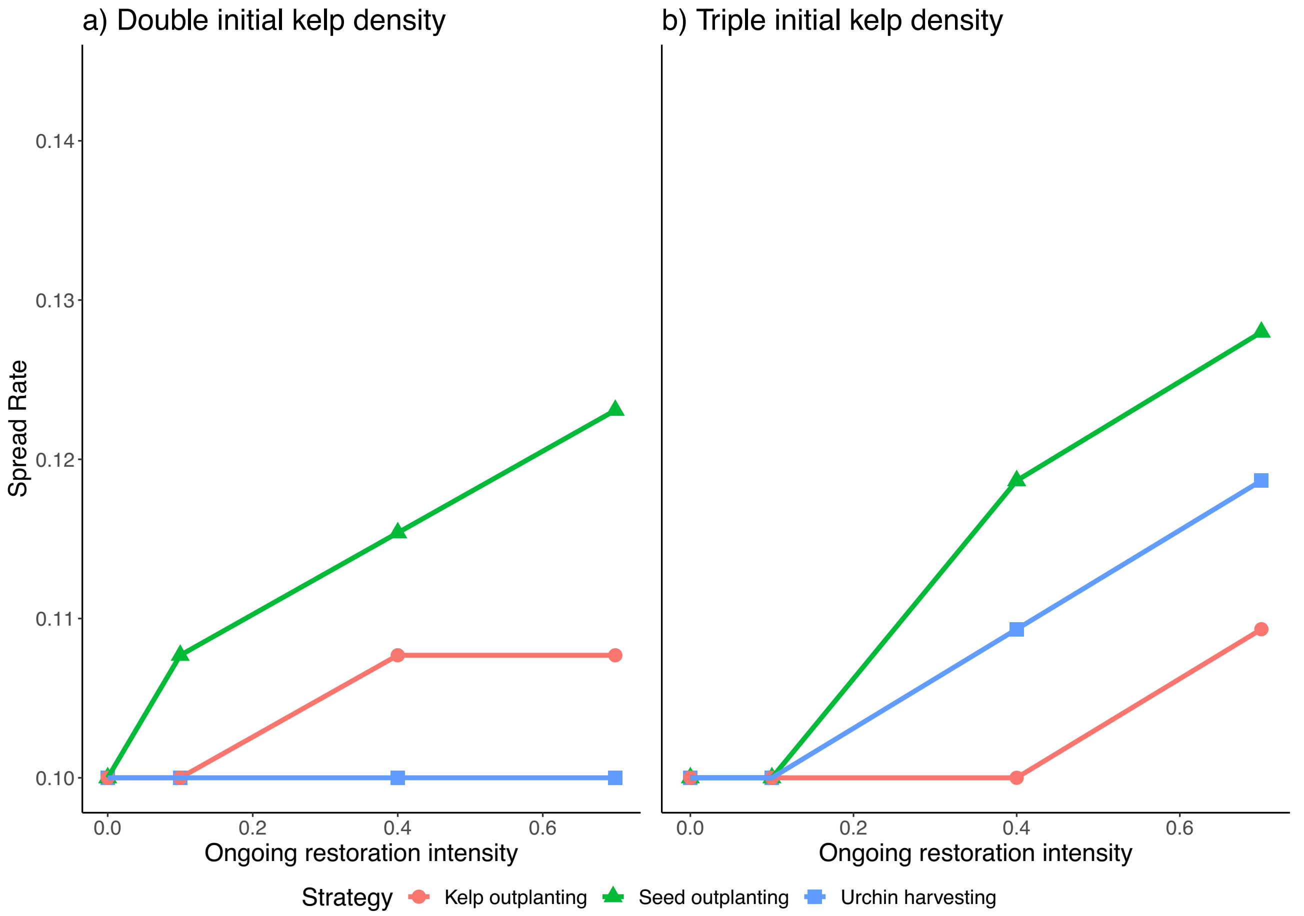

FIGURE 6 Kelp spread rate under different restoration strategies with increasing intensity following urchin removal below threshold value necessary for kelp recovery with varying initial kelp density. Each line represents a different strategy: kelp outplanting in red circles, kelp seeding in green triangles, and sustained urchin harvest in blue squares. Panel (a) shows ongoing restoration efforts with double the initial kelp density in the oasis compared to the default of 1/β, and panel (b) shows ongoing restoration efforts with triple the initial kelp density. [Correction added on 18 May 2023 after first online publication: Figure 6 has been updated in this version.]

interacting with the urchins, which further enhances the kelp recovery rate. Overall, the combination of increasing the initial kelp density, reducing the initial urchin density, and implementing an ongoing kelp seeding effort leads to the fastest kelp recovery.

The primary role of short-term restoration efforts is further evident in the global sensitivity analysis of the spread rate (Figure 8), where initial kelp and urchin densities (A_0 and U_0, respectively) have a higher impact on the spread rate than ongoing restoration efforts (μ_i for $i = U, A, S$). Therefore, both natural local conditions that lead to higher kelp coverage and lower urchin densities after a marine heatwave, as well as interventions to increase kelp density and decrease urchin density, have a strong impact on overall spread rate. When comparing the importance of the parameters for the threshold urchin density (Figure 4) and kelp recovery rate (Figure 8), we observe that parameters such as oasis size (L) and mean dispersal distance of kelp (a_A) play a role on kelp recovery once urchin density is below the threshold necessary for recovery. Intuitively, it makes sense that a higher mean dispersal distance of kelp seeds (a_A) leads to a faster spread (Figures S3–S5 in Appendix S3), especially for the strategy of seed outplanting. However, note that the relative efficacy of the different restoration strategies remains unchanged for different values of mean dispersal distances of kelp seeds. In addition, the lower importance value of kelp dispersal distance compared to parameters related to urchin grazing indicates that local kelp–urchin interactions have a greater influence on kelp spread rate than kelp dispersal. While increasing the size of the initial kelp oasis (L) through kelp outplanting enhances the kelp recovery rate, the spatial scale of ongoing restoration efforts (η) has a minimal impact on the kelp recovery rate.

DISCUSSION

In our model of kelp restoration, scaling up ecologically on restoration efforts, that is, restoring more ecological

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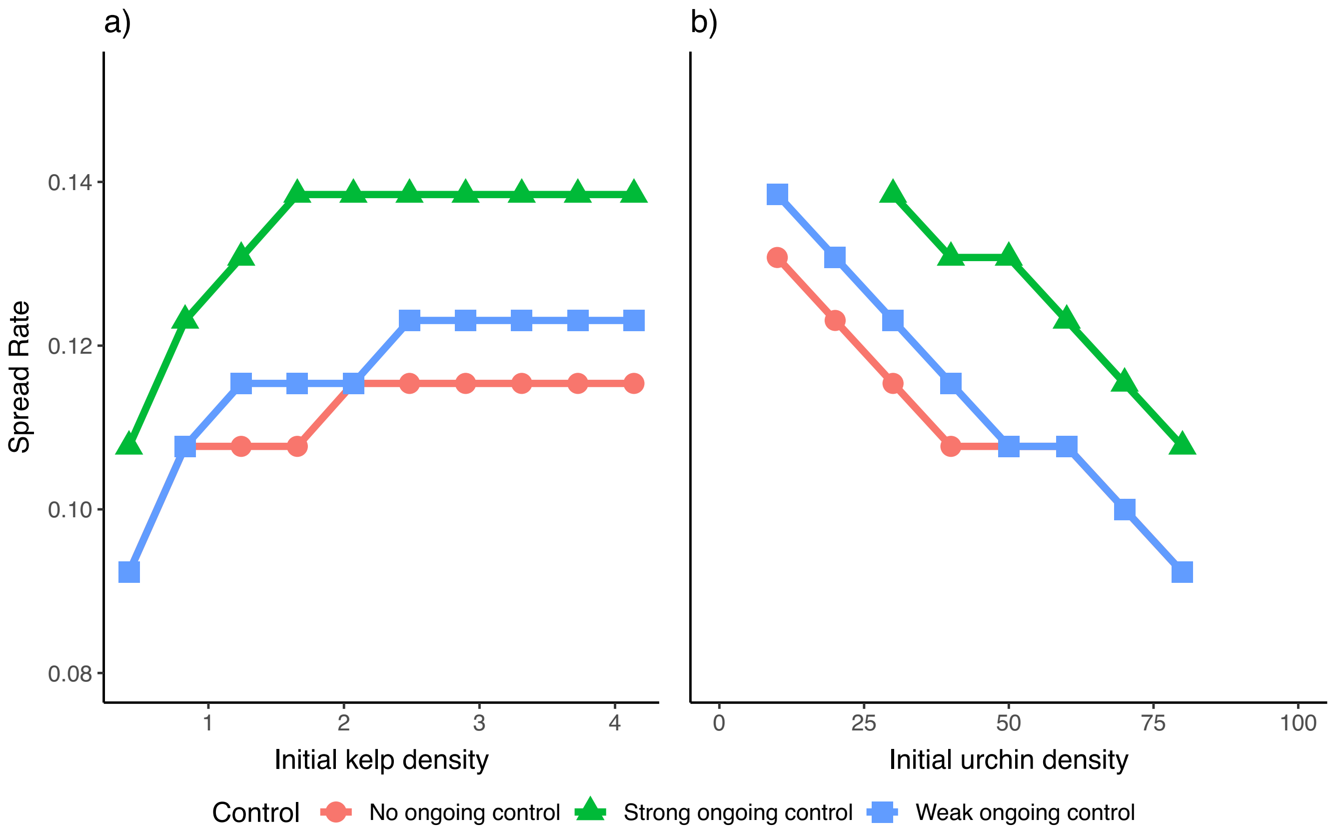

FIGURE 7 Kelp spread rate under different initial conditions for partial restoration efforts at initial (short-term) restoration stage. Each line represents a different ongoing restoration effort in terms of kelp seeding: no ongoing restoration effort in red circles, strong ongoing seeding in green triangles ($\mu_S = 0.7$), and weak ongoing seeding in blue squares ($\mu_S = 0.1$). Panel (a) shows change in spread rate as initial kelp density varies, and panel (b) shows change in spread rate as initial urchin density varies.

components of a system, can have a greater effect on restoration success than scaling up spatially or temporally. One of the key factors in determining whether kelp recovery will be possible is the threshold combination of kelp and urchin density, which our model suggests is mostly determined by local interactions. Because we incorporated kelp–urchin grazing feedbacks that can drive alternative stable states, kelp recovery does not occur in our model unless urchin density is below a certain value (Figure 3). This threshold increases as kelp density increases, that is, kelp outplanting reduces the amount of urchin removal necessary for recovery. In addition, improving the initial conditions through an increase in kelp density or decrease in urchin density at an early stage can enhance the kelp recovery rate more than ongoing restoration efforts (compare Figures 5 and 7). This suggests that a Field of Dreams approach can suitable in kelp forest restoration, as in our model enhancing the ecological conditions at a short temporal scale and small spatial scale has more impact than distributing restoration efforts over a longer period of time or to a greater spatial extent.

In the case of kelp forest restoration, however, this Field of Dreams approach may have to be complemented by maintenance urchin removals. Our simulations looked at the short-term effects of restoration, where our restoration efforts spanned over a single year. However, several previous kelp restoration projects failed due to the recovery of urchin populations in a multiyear scenario (Eger et al., 2022). One possible source of this discrepancy is that we do not account for postsettlement urchin movement, and urchins might move from barren regions into restored regions following removal efforts, with the potential to subsequently exceed the urchin threshold necessary for recovery. Therefore, in the context of our model, the long-term success of a restoration effort may require maintaining urchin densities below the urchin threshold until kelp density is high enough to promote the behavioral switch of urchins to drift kelp consumption (Kriegisch et al., 2019).

Despite this observation, our theoretical results with respect to keeping the urchin density below a certain threshold, as well as increasing the ecological scale of restoration, are consistent with a number of observations in previous kelp restoration efforts. In recent restoration efforts in our focal system of Northern California, sites

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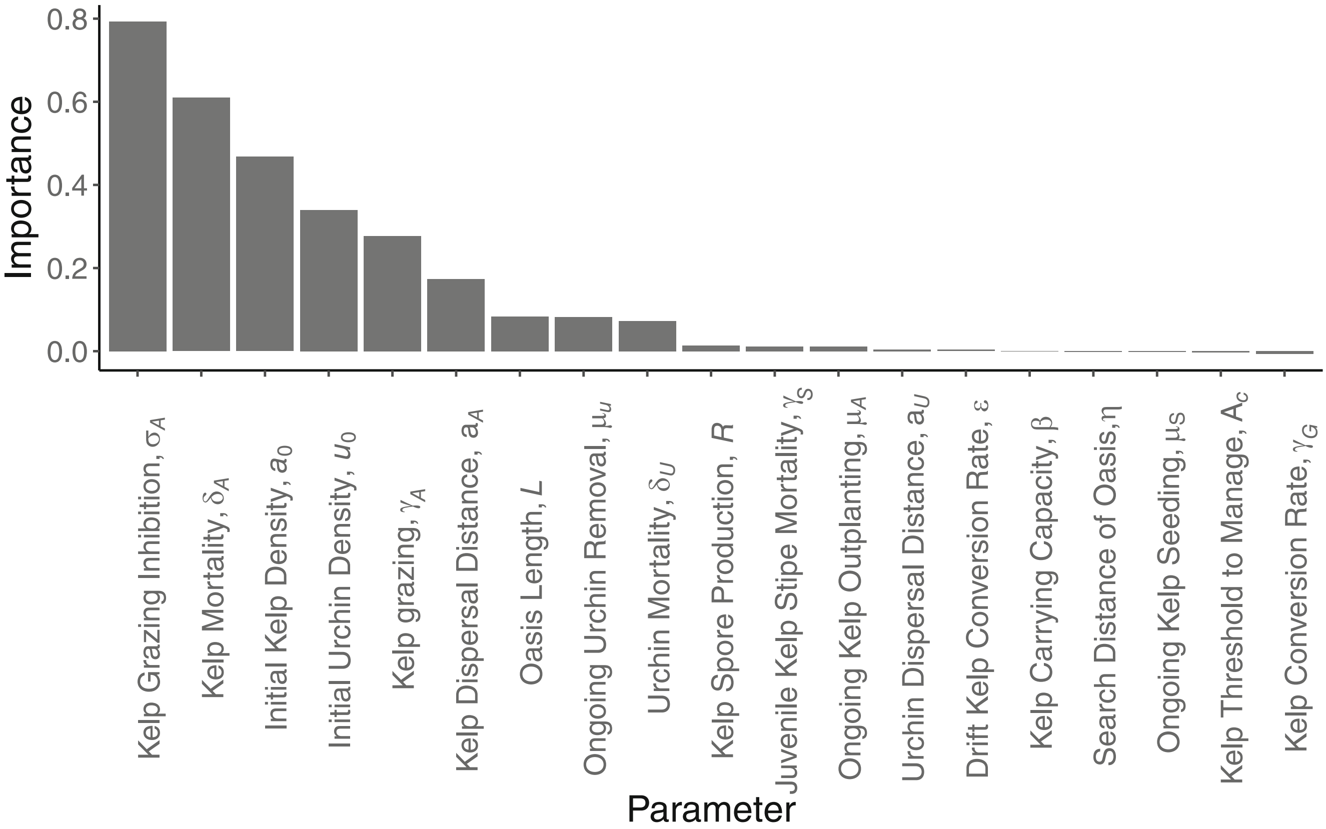

FIGURE 8 Importance ranking of parameters of Model 1 from global sensitivity analysis of kelp recovery rate. See Table 1 for more detailed parameter definitions.

where urchin removal has been implemented below a threshold density of two urchins/m^2 saw significantly higher kelp density compared to sites without urchin removal (Ward et al., 2022). While these restoration sites and regions of improved recovery cover a much smaller spatial scale compared to original loss (compare Rogers-Bennett & Catton [2019] to Ward et al. [2022]) due to resource limitation, they can facilitate kelp recovery in targeted locations of economic importance (e.g., near ports) to coastal stakeholders such as fishing and diving communities. In Southern California, sea urchin removal can increase the success of kelp reseeding (Ford and Meux 2010). Beyond California, Layton et al. (2020) found that urchin removal and kelp outplanting constituted successful restoration methods for increasing kelp density in different regions of the Australian coastline. In the case of kelp reintroduction on the coast of Tasmania, Sanderson (2003) found greater success of kelp outplants in areas with urchin removal.

The increased importance of the local grazing activity of urchins to kelp relative to more regional factors such as dispersal found in our model (Figure 8) suggests that the spatial scale of restoration near an oasis is not as important as the ecological scale. In our model, expanding restoration efforts away from the kelp oasis had little to no impact on the kelp recovery rate (Figures 5 and 6). This happens because at the low kelp densities found outside the oasis, these efforts may not decrease the local overall urchin grazing activity enough to successfully enhance kelp spread. The same local behavior of grazing activity explains why a short temporal scale of restoration led to a higher recovery rate (Figure 7). In our model, starting from a lower initial urchin density or higher kelp density and, therefore, lower grazing activity leads to faster kelp growth in the early stages after reintroduction, which allows more time for the behavioral shift of urchin grazing to occur. This produces a positive feedback loop where urchin grazing activity is further decreased and kelp recovery is further increased after an intensive initial urchin removal and/or kelp reintroduction.

This potential efficacy of partial restoration in promoting further recovery over space and time also parallels empirical findings in systems beyond that of kelp modeled here. For example, in Lee et al. (2006), restoring the habitat of anurans (wetlands) on a small spatial and temporal scale was enough to allow the eventual recovery of community composition and diversity of amphibians. In Cahall et al. (2013), thinning of the forest at an early

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stage led to an increase in the density of certain bird populations compared to unthinned forests (Figure 7).

The predominance of early restoration efforts, and greater efficacy of ecological scaling up over spatial or temporal scaling up in restoration efforts, arises, in part, because of the threshold dynamics in our model with alternative stable states. As described previously, with these threshold dynamics, once initial restoration passes the threshold, which depends on both urchin and kelp densities, then natural recovery can occur. The potential for alternative stable states arises from our Type IV (unimodal) functional response in urchin grazing to kelp density, which might occur due to an urchin grazing behavioral shift from active to passive grazing due to greater subsistence on drift kelp or cryptic behavior with higher densities of kelp and associated urchin predators (Karatayev et al., 2021). Accordingly, our global sensitivity analysis indicates that the parameters that shape urchin grazing response to kelp density constitute the main driving factors of both the possibility of recovery and its rate. If, in reality, this feedback between kelp density and urchin density is not strong enough to drive alternative stable states, we would expect a reduction in the overall role of active grazing behavior and a potential increase in the role of greater spatial and temporal scales of restoration efforts. That said, our best-fit model did find a strong enough feedback between kelp density and urchin grazing for alternative stable states to occur, and McPherson et al. (2021) provided empirical support for a significant role of urchin grazing in kelp decline on the northern coast of California, where including urchin grazing in a partial least-squares regression analysis doubled the variability in the yearly data of kelp coverage explained by the model. In further support of urchin densities and grazing (rather than abiotic environmental drivers alone) affecting kelp recovery, as noted previously, data from restoration efforts indicate that urchin removal can increase restoration success in a number of kelp systems spanning diverse parts of the oceans, such as Japan, Norway, California, and Australia (Ford & Meux, 2010; Layton et al., 2020; Norderhaug & Christie, 2009; Sanderson, 2003; Ward et al., 2022; Watanuki et al., 2010). Additional evidence for a role for urchin densities in kelp dynamics included rapid kelp recovery following urchin mass mortality in Southern California (Williams et al., 2021) and rapid kelp declines following urchin range expansions in Tasmania (Ling, 2008). In Tasmania, both theory and data suggest that alternative stable states between urchin barrens and kelp forests affect recovery success, analogous to our model (Johnson et al., 2017; Ling, 2008; Marzloff et al., 2016).

Although increasing the temporal scale of restoration has a smaller effect on the ability of kelp to recover in our deterministic simulations, an increase in the temporal scale of restoration can buffer against the potential for short-term restoration failure caused by extreme, stochastic events (Reich & Lake, 2015). In the case of kelp, an increase in the likelihood of marine heatwaves can lead to die-offs of kelp and increases in urchin recruitment, which might bring urchin density above a certain threshold and restrict kelp recovery (Rogers-Bennett & Catton, 2019). This potential for restoration failure due to environmental stochasticity has been noted in amphibian (Dodd & Seigel, 1991) and plant (Dalrymple et al., 2012) reintroductions and has been observed in coral reef restoration failure due to hurricane activity (Bowden-Kerby, 2001).

Finally, partial restoration efforts leading to longer-term, larger-scale recovery will depend on the spatial extent of dispersal and the temporal scale of generation time of the ecological components. For example, long river systems may require a timeframe on a scale of decades to reestablish their hydrological dynamics (Tockner et al., 1998). In addition, active interventions may reduce the impact of ecological traps produced by restoration efforts (Hale & Swearer, 2017). For example, Severns (2011) found that the butterfly *Lycaena xanthoides* selectively oviposited more frequently and with more eggs in seasonally flooded habitats with lower egg survival, compared to adjacent nonflooded habitats where a tall invasive grass obscured native plants. Averting this accidental cue to poor ovipositing habitat would likely require scaling up of restoration to also incorporate invasive species removal in nonflooded habitats. More generally, active management approaches to account for ecological traps may include changing the behavior of the animals by removing cues or habituating the animals to ignore the cues provided by ecological traps (Hale & Swearer, 2017).

Management implications

In our model, the most effective restoration approach for kelp forest in Northern California is a combination of reduction of purple urchin density through urchin removal and increase of bull kelp density through adult kelp outplanting at an early stage of the restoration project. The role of any ongoing restoration efforts, including further urchin removal and kelp outplanting, as well as kelp seeding, was highly sensitive to initial kelp density (Figures 5 and 6). In addition, Eger et al. (2022) found that distance to the extant kelp forest had an impact on the survival of kelp spores. These findings support targeting such efforts around extant kelp "oases." In the absence of any oases, kelp recovery might further rely on initial kelp reseeding or outplanting restoration interventions,

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depending on the potential for a germ bank, as discussed in the subsequent *Model limitations* section. Ongoing restoration efforts might play a greater role if initial removals are insufficient to pass the threshold for kelp recovery or, as noted previously, future extreme climate events disrupt restored populations.

Urchin removal is a technique that is already being applied on the northern coast of California (Hohman et al., 2019). Our results suggest that these efforts are more likely to be successful when complemented by kelp outplanting. Transplantation of *N. luetkeana* has been successfully applied further north on the coast of Washington, where transplanting of juveniles of natural populations was more successful than cultured kelp (Calloway et al., 2020; Carney et al., 2005). The effectiveness of outplanting cultured kelp or juveniles of natural populations remians an open question in the highly exposed Sonoma and Mendocino County coastlines (George et al. 2015).

In other kelp restoration projects, kelp forest restoration success has been determined by kelp introduction, removal of stressors such as active grazers, or their combination (Morris et al., 2020). Kelp introduction was a determinant for the success of *Lessonia nigrescens* restoration on the northern coast of Chile (Correa et al., 2006). In addition, previous work showed that younger kelp sporophytes are more prone to predation (Lubchenco, 1983). Thus, determining how to minimize urchin predation on younger transplants or outplants is key to ensuring successful introduction of kelp. Previous studies proposed using grazer exclusion devices (Carney et al., 2005) or choosing sites where grazers are not as highly abundant can benefit kelp introduction (Duggins et al., 2001). The sensitivity of our model to urchin grazing rate further supports the potential efficacy of such approaches.

While our model can provide qualitative management-relevant insights into the relative efficacy of different approaches (e.g., initial vs. ongoing interventions; urchin removal, kelp reseeding, and kelp outplanting separately or in combination), quantitatively precise insights, such as the exact urchin threshold and kelp densities that can enable recovery, are more challenging due to data limitations. Our best-fit model has wide-ranging posterior distributions for most parameters (Appendix S2: Figure S1), including those that strongly influence the threshold urchin and kelp densities for recovery, such as the urchin grazing rate on kelp. In addition, these parameters will inevitably vary in space and time, such as through urchin grazing dependence on water temperature and sedimentation (Traiger, 2019), such that no one target value will apply. Our sensitivity analysis can inform data collection aimed at resolving parameters (and their environmental dependencies) most likely to improve the ability to precisely estimate target values for urchin removal and kelp reintroduction. As more data become available from both kelp recovery monitoring and monitoring of potential abiotic drivers at finer spatial and temporal scales, our model (with extensions to address the assumptions described in the subsequent *Model limitations* section) provides a foundational quantitative framework for leveraging those data for more precise predictions of threshold values for achieving a target recovery likelihood or rate.

Another consideration for kelp restoration management, especially in Northern California, is the reintroduction of predators such as the sunflower sea star. A role for predator reintroduction is evident in the high sensitivity of the recovery threshold and rate in our model to parameters that likely depend on predator presence: urchin mortality (δ_A) and the potential for urchins to switch between active and passive grazing (σ_A). If the urchin grazing mode depends on a cryptic behavioral response to predator presence (Cowen, 1983; Duggins, 1983) as well as drift kelp presence (Harrold & Reed, 1985), then predator reintroduction could increase system resilience in terms of both likelihood and rate of recovery. Empirically, predator decline was one of the identified drivers of kelp forest loss in Northern California (McPherson et al., 2021; Rogers-Bennett & Catton, 2019), such that predator reintroduction is then a component of addressing the drivers of system degradation, which is a key determinant of restoration success (Morris et al., 2020; Palmer et al., 2010). As noted in the *Methods: Model overview* section, we did not explicitly include predator reintroduction because of uncertainty in its near-term feasibility and because initial restoration to a kelp-dominated system with nonbarren, nutritious urchins through the interventions modeled here might determine the potential efficacy and optimal timing of predator reintroduction. Therefore, while our model can provide insight into restoration management on the short (annual) time scales modeled here, understanding the potential long-term recovery of ecosystem structure and resilience will likely require consideration of predator dynamics and reintroduction.

Our findings provide a system-specific case study of threshold-based approaches illuminated in previous theoretical models that look at the optimal restoration strategy of partial restoration efforts. Lampert and Hastings (2014) suggested that an economically optimal approach was to engage in restoration efforts until the target population reached a certain threshold (the urchin threshold density in our case), which is consistent with what we have found in this work. Estimating threshold densities at the respective restoration sites is one of the potential challenges of restoring using this threshold approach (Suding & Hobbs, 2009). While we were data limited in making quantitatively precise estimates for our system,

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more data from ongoing restoration monitoring, fit to a model like ours, could help better resolve this threshold in the future.

In our work we find two key restoration strategies to perform at early stages of restoration: urchin removal and kelp outplanting. Lampert and Hastings (2019) further suggested that the optimal restoration strategy was to implement one strategy until a certain threshold was reached (removing urchins below the urchin threshold density) and then combine the two strategies until a certain "investment benchmark" was achieved, after which the system (e.g., kelp forest) would recover as a result of natural processes. This benchmark might be determined in terms of a minimum kelp density or a maximum urchin density in the restored kelp oasis. Budget limitations may restrict the number of target sites that can be successfully restored (Wilson et al., 2011), which makes choosing priority sites based on the likelihood of restoration success an important step when performing restoration. Finally, the three strategies explored in this work might have an optimal timing in terms of their application, and that timing likely differs for each strategy (Lampert & Liebhold, 2021). Finding the optimal timing of application of the three strategies explored in this work and other unexplored strategies remains an open question.

Model limitations

As with any model, we made a number of assumptions to construct the simplest possible model relevant to our central questions. We chose a Laplacian dispersal kernel, but the dispersal of kelp seeds is known to be highly dependent on currents, which may skew the direction of dispersal (Gaylord et al., 2004). With advection, the kelp spread rate would likely increase in favor of the direction of the current (Lou & Lutscher, 2014), depending on physical factors such as seed buoyancy and water turbulence. These physical factors could be further explored using a nonparametric kernel (Richardson et al., 2018). We also ignore adult urchin movement, where the effect will depend on urchin movement responses to kelp recovery, where urchins exhibit lower movement inside versus outside kelp forests due to differences in food availability (Mattison et al., 1977). If kelp recovery reduces urchin movement due to increased drift kelp availability, then accounting for urchin movement might decrease the amount of urchin removal and the role of ongoing restoration in restoration efficacy. Alternatively, if recovering kelp attracts high-movement barren urchins as active grazers, then accounting for urchin movement might increase the amount of urchin removal and the role of ongoing restoration in restoration efficacy.

Other physical factors not considered explicitly in this model are variations in environmental conditions such as temperature and nutrients, which are known to affect kelp productivity and growth (Bell et al., 2015). Our sensitivity analyses show that parameters highly dependent on environmental conditions in our model, such as kelp mortality (δ_A), are influential in determining both the urchin density threshold and kelp recovery rate. Thus, both urchin threshold density and kelp recovery rate might be higher at regions of the coastline with environmental conditions that further enhance kelp survival, leading to location-specific restoration intervention intensity required for success. If stable in time, local variation in environmental conditions could also help identify regions of the coastline with a higher potential to become kelp oases (Heinrichs et al., 2016).

Our model also assumes that the effects of ongoing restoration efforts occur instantaneously. In reality, restoration efforts might present lags in their impact for reasons such as long life cycles of the target population (Uezu & Metzger, 2016) or natural lags in the biogeochemical cycles (Hamilton, 2012). For kelp, a lag between seed outplanting and sporophyte establishment and maturation, during which kelp outplants might be more vulnerable to urchin grazing (Anderson et al., 1997), captured in our model with a separate grazing rate γ_S, could decrease the efficacy of seed outplanting modeled here.

In addition, we focus our model on the dynamics of kelp sporophytes and implicitly consider the dynamics of the gametophytes. Gametophytes have the potential to act as a germ bank similar to a terrestrial seed bank, with persistence in a dormant state for an extended period of time until favorable environmental conditions occur (Edwards, 2000, 2022). This could enable kelp recovery in the absence of the extant "kelp oases" modeled here and lead to the alternative stable states observed in our model to behave as long transients instead (Arroyo-Esquivel et al., 2022). In this case, management might focus on how to decrease the length of the urchin-barren transient state while also increasing the length of the kelp forest transient state, if a goal is to avoid extended periods of economic loss from kelp-associated livelihoods such as the red urchin commercial fishery, red abalone recreational fishery, and recreational diving. While analyzing the effect of different restoration interventions on transient duration given a kelp germ bank would require model modifications, given the importance of the grazing interaction between kelp and urchins found here, we suspect the qualitative results of our model would not change significantly.

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Our best-fit model also assumes that alternative stable states are relevant to the kelp–urchin dynamics observed in our system. Preliminary evidence suggests kelp is returning to some areas of the coastline, potentially due to more nutrient-rich, colder waters (B. Hughes, personal communication, July 6, 2021). This recovery could be due to a shift in environmental conditions from a range where alternative stable states were relevant to a range where the kelp-dominated state is the only relevant one. Alternatively, this recovery might indicate that the system state shifts with environmental conditions without alternative stable states. While these alternative explanations affect the relevance of our results concerning a threshold value of urchin density or kelp reintroduction that enables recovery, in either case restoration might still affect the rate of recovery, as observed in Northern California (Ward et al., 2022), especially if transients are slow, as noted earlier. Determining which case best explains this apparent recovery will require analyzing the emerging data in the coming years in comparison to model predictions with environmental drivers and different model structures with or without alternative stable states (as done for giant kelp in Southern California in Karatayev et al. [2021], where there is greater data availability than for the Northern California bull kelp system that is our focus here).

Our model considers only the interactions between sea urchins and kelp, which are central to the efficacy of current restoration interventions. In reality, an array of other species in California's temperate rocky reefs might affect recovery dynamics and restoration outcomes. For example, crustose coralline algae competing with kelp may also facilitate urchin recruitment, potentially decreasing the threshold urchin density, that is, it may increase the urchin removal necessary for kelp recovery (Baskett & Salomon, 2010). In comparison, the presence of a natural predator of sea urchins, such as the sunflower sea star (currently functionally extinct on the northern coast of California [Rogers-Bennett & Catton, 2019]), would lead to a more cryptic behavior of urchins, which would lead to an increase in threshold urchin density (Smith et al., 2021). Adding such predators and their potential reintroduction could contribute another ecological dimension to restoration, as discussed earlier in the section on *Management implications*. Therefore, adding more ecological realism could extend our model's capacity to inform restoration efforts.

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CONFLICT OF INTEREST STATEMENT

The authors declare no conflicts of interest.

DATA AVAILABILITY STATEMENT

The data used in this work are from the public data source presented in Supplementary Table S3 in the data availability section of McPherson et al. (2021). The code used to run the simulations can be found in Arroyo-Esquivel (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.

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