

At what spatial scales are alternative stable states relevant in highly interconnected ecosystems?

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Abstract. Whether ecosystems recover from disturbance depends on the presence of alternative stable states, which are theoretically possible in simple models of many systems. However, definitive empirical evidence for this phenomenon remains limited to demographically closed ecosystems such as lakes. In more interconnected systems such as temperate rocky reefs, the local relevance of alternative stable states might erode as immigration overwhelms local feedbacks and produces a single stable state. At larger spatial scales, dispersal might counter localized disturbance and feedbacks to synchronize states throughout a region. Here, we quantify how interconnectedness affects the relevance of alternative stable states using dynamical models of California rocky reef communities that incorporate observed environmental stochasticity and feedback loops in kelp–urchin–predator interactions. Our models demonstrate the potential for localized alternative states despite high interconnectedness likely due to feedbacks affecting dispersers as they settle into local communities. Regionally, such feedbacks affecting settlement can produce a mosaic of alternative stable states that span local (10–20 km) scales despite the synchronizing effect of long-distance dispersal. The specific spatial scale and duration of each state predominantly depend on the scales of environmental variation and on local dynamics (here, fishing). Model predictions reflect observed scales of community states in California rocky reefs and suggest how alternative states co-occur in the wide array of marine and terrestrial systems with settlement feedbacks.

Key words: *alternative stable states; dispersal; disturbance; ecological resilience; kelp forest; stochastic population dynamics; temperate rocky reefs; urchin barren.*

INTRODUCTION

When qualitatively distinct, alternatively stable ecosystem states occur under the same environmental conditions, brief (“pulse”) disturbances can lead to abrupt and persistent ecological shifts (Scheffer et al. 2001). In such cases, the persistence of a given ecological state depends on the magnitude of perturbations that ecosystems can withstand and return to the target state (“ecological resilience” hereafter; Holling 1973). Models and empirically observed feedbacks reinforcing distinct states suggest that alternative stable states could, theoretically, underlie observed shifts following environmental change in many ecosystems, including the collapse of fish stocks, declines in foundational species including corals and kelp, replacement of forests by fire-prone grasslands, and algal dominance in lakes (Scheffer et al. 2009). Alternatively, such state shifts may be readily reversed if only one state is stable under a given set of environmental

conditions, even if changes in environment lead to dramatic (nonlinear) ecological changes. Therefore, in addition to informing a basic understanding of the structure of ecological communities, resolving whether or not state shifts represent alternative stable states can affect conservation and management decisions such as the degree of restoration necessary for recovery of a target state (Suding et al. 2004). However, empirically establishing the relevance of alternative stable states requires long-term data of each state at large spatial scales under identical environmental conditions and therefore remains debated in most systems (Petraitis and Dudgeon 2004, Petraitis 2013).

One of the factors that might affect the relevancy of alternative stable states to many systems is demographic interconnectedness (Petraitis and Latham 1999, Petraitis and Dudgeon 2004). In particular, inputs of individuals from outside areas may overwhelm the feedbacks maintaining alternative stable states at small spatial scales and induce a “rescue effect” (Brown and Kodric-Brown 1977) that always allows eventual recovery of the original state after disturbance. Consequently, the best evidence for the existence of alternative stable states and their relevance to management remains limited to

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relatively small, demographically closed, shallow lake ecosystems (Scheffer et al. 1993, Schroder et al. 2005). By contrast, in most terrestrial and marine systems, manipulative studies occur on small scales (e.g., <100 m; McGill 2010) while many animal taxa disperse above the scale of kilometers (Kinlan and Gaines 2003), which can dynamically link communities across tens to hundreds of kilometers (Gouhier et al. 2010).

At the larger spatial scale of an entire ecosystem, high interconnectedness among locations raises the question of whether alternative stable states, if relevant, manifest within local communities or at system-wide scales. On the one hand, localized disturbances induce ecosystem heterogeneity that can maintain localized alternative stable states: for instance, in models with Allee effects, demographic stochasticity in a given year can reinforce population persistence in some habitat patches and promote extinction in others (Martin et al. 2015). Analogous heterogeneity in savannas, coral reefs, and predator–prey communities might maintain localized alternative stable states in spite of high external input (Durrett and Levin 1994, Mumby et al. 2007, Schertzer et al. 2015). On the other hand, dispersal at the ecosystem level can synchronize ecological states across space and produce alternative stable states at system-wide scales. In particular, spatial models emphasize that under high levels of dispersal sudden collapses to undesired ecosystem states can propagate across large scales in a domino effect (Hughes et al. 2005, 2013, van Nes and Scheffer 2005), with recovery possible only through large-scale restoration efforts (van de Leemput et al. 2015). Resolving the expected scale of alternative stable states and its drivers informs the scales at which empirical efforts could detect this phenomenon, the socioeconomic consequences of ecosystem collapses to undesired states, and which management approaches might effectively maintain desired states.

Temperate rocky reef ecosystems throughout the world exemplify systems with both extensive dispersal and a hypothesized potential for alternative stable states. Two observed ecological states of these communities are kelp forests with abundant urchin predators and barrens where urchins overgraze kelp and predators are rare (reviewed in Lawrence 1975, Steneck et al. 2002, Konar and Estes 2003, Ling et al. 2015). When fishing reduces predator densities, transitions between these states often follow localized, stochastic events such as pulses of urchin larvae and kelp loss during intense storms (Hart and Scheibling 1988, Cavanaugh et al. 2011). These community shifts typically occur on small scales (≤ 20 km of coastline) and can persist for years to decades (reviewed in Filbee-Dexter and Scheibling 2014). A number of feedbacks have the potential to drive alternative stable states on temperate reefs, such as when abundant kelp facilitate recruitment of urchin predators (Ling et al. 2015) and barrens facilitate urchin recruitment (Baskett and Salomon 2010). Alternatively, urchin barrens might instead represent a transient state as high

dispersal and connectivity allow gradual recoveries from disturbances. Specifically, urchin and predator dispersal on 50–100 km scales (Waples and Rosenblatt 1987, Edmands et al. 1996) largely decouples larval supply from local consumer densities (Okamoto 2014), and might rescue predators from local disturbance (Connell and Sousa 1983) or propagate and synchronize urchin barrens over large scales (Hughes et al. 2005). Where shifts to urchin barrens have occurred, resolving the relevance and scale of alternative stable states can inform whether reduction in predator harvest alone allows kelp forest recovery, or whether additional restoration efforts (e.g., urchin harvest; House et al. 2017) might be necessary at specific scales.

Here, we quantify whether and at what spatial scales alternative stable states and the associated concept of ecological resilience can be relevant in temperate rocky reefs given long-distance dispersal. We develop a tri-trophic community model with empirically grounded feedback mechanisms that can drive alternative forested and barren states by regulating settlement success. We first use a one-patch model to explore how the fraction of external larval supply affects the presence of alternative stable states, and then resolve their potential spatial and temporal scales using a spatially explicit model formulation that incorporates observed stochasticity. Finally, we compare the predicted scales of the alternative states from our model to long-term data. From these analyses, we find a potential for local relevance of alternative stable states in systems with high connectivity and quantify how feedbacks and local disturbance interact to determine community structure across locations and through time.

MATERIALS AND METHODS

Study system

We base our analysis on temperate rocky reefs in the northern California Channel Islands, USA, which represent a ~300 km total coastline with well-documented shifts between distinct community states (Filbee-Dexter and Scheibling 2014). Like many temperate rocky reefs around the world, strong trophic interactions characterize this system, and primarily involve kelp (*Macrocystis pyrifera*), sea urchin herbivores (*Strongylocentrotus purpuratus*), and urchin predators: sheephead (*Semicossyphus pulcher*) and spiny lobsters (*Panulirus interruptus*; Filbee-Dexter and Scheibling 2014, Hamilton and Caseille 2015). Kelp facilitate urchin predators by providing shelter that can double survival rates of settled predator larvae compared to exposed areas (Smith and Herrkind 1992, Lipcius et al. 1998; Appendix S1: Section S1). Predator recruitment facilitation by kelp via settlement cues or increased early post-settlement survival creates a strong feedback often invoked by empirical studies of temperate rocky reefs (Ling et al. 2015) that can produce alternatively stable forest and barren states under

intensive predator fishing in closed-system models (Appendix S1: Section S2, Fig. S5a; Marzloff et al. 2013). Note that predator recruitment facilitation, the focus here, is one of many possible feedbacks hypothesized to drive alternative stable states in kelp systems (Ling et al. 2015); additional possible mechanisms include recruitment facilitation of urchins to crustose coralline algae that increases in barrens (Baskett and Salomon 2010) and intensified urchin foraging behavior when kelp (Ebeling et al. 1985, Harrold and Reed 1985) or predators (Cowen 1983) are rare.

Local communities in this system are highly interconnected because dispersal distances of some key species greatly exceed the scale of predominant environmental stochasticity. Although adult consumer home ranges and kelp dispersal occur within rocky kelp habitat patches (1–5 km of coastline; Topping et al. 2005, Castorani et al. 2015), consumer larvae disperse over much longer distances (50–100 km on average; Table 1). We consider two sources of local-scale stochasticity that regulate community composition and can form persistent urchin barrens: winter storms, which annually lead to a 70% loss of kelp biomass (Dayton et al. 1999, Cavanaugh et al. 2011), and urchin larval survival, which varies temporally by an order of magnitude (Hart and Scheibling 1988, Schroeter et al. 1996). As with our focal feedback mechanism, these are not the only possible sources of environmental stochasticity, which also include extreme warm water events leading to kelp loss (Dayton et al. 1999) and disease outbreaks affecting predators (Harvell et al. 2019) and urchins (Lafferty 2004, Ling et al. 2015).

Model description

Here we describe the model of local community dynamics (Fig. 1a), and in the next subsections, we

describe the one-patch and spatially explicit formulations of the model (Fig. 1b, c). Within each patch x , our model tracks kelp biomass (algae, A_x) and densities of adult consumers (urchins, U_x , and predators, P_x). We use a semi-discrete (Mailleret and Lemesle 2009) model where kelp growth, herbivory, predation, and harvest mortality occur continuously for one year ($t \neq \tau_K$), followed by an annual discrete-time pulse (at $t = \tau_K$) with storm-induced kelp mortality and settlement of newly produced urchins and predators into local communities.

Throughout the year, kelp biomass grows logistically at a rate r_A with carrying capacity K , and urchins graze kelp at a rate δ_A . Urchins and predators experience natural mortality at rates μ_U and μ_P , and predators consume urchins at rate δ_U and experience fishing mortality at a rate F_P . Thus, the community dynamics within a year (at $t \neq \tau_K$) are

$$\frac{dA_x}{dt} = A_x \left(r_A \left(1 - \frac{A_x}{K} \right) - \delta_A U_x \right) \quad (1)$$

$$\frac{dU_x}{dt} = -U_x (\delta_U P_x + \mu_U) \quad (2)$$

$$\frac{dP_x}{dt} = -P_x (\mu_P + F_P). \quad (3)$$

Both urchins and predators experience an annual reproductive pulse at time τ_K (spring-early summer), where larvae produced within each patch disperse between patches. Larval production in each patch is proportional to grazing or predation in the local community integrated over the previous year. Urchins convert consumed kelp into larvae (accounting for larval mortality during development) given the conversion factor a . Two energetic sources contribute to predator fecundity:

TABLE 1. Definitions, base values, and sources of model parameters.

Parameter	Default value	Description	Source
r_A	12 yr ⁻¹	kelp growth rate	
K	4 kg/m ² A	kelp carrying capacity	Cavanaugh et al. (2011)
δ_A	1.1 U ⁻¹ ·yr ⁻¹	urchin grazing rate on kelp	Lauzon-Guay et al. (2009)
δ_U	11 P ⁻¹ ·yr ⁻¹	predator attack rate on urchins	Tegner and Levin (1983)
a	0.41 UA ⁻¹	kelp to urchin conversion	see Appendix S1
b	0.014 PU ⁻¹	urchin to predator conversion	see Appendix S1
f_c	0.85	predator recruitment facilitation	see Appendix S1
$s_A(\tau_K, x)$	0.305	winter kelp survival (mean)	see Appendix S1
$\sigma_U(\tau_K, x)$	1	urchin larval survival stochasticity (mean)	see Appendix S1
μ_U	0.1 yr ⁻¹	urchin natural mortality	Marzloff et al. (2013)
μ_P	0.05 yr ⁻¹	predator natural mortality	Neilson (2011), Hamilton et al. (2011)
F_P	0.19 yr ⁻¹	predator harvest rate	Neilson (2011), Hamilton et al. (2011)
β	6.7×10^{-5} ·yr ⁻¹ ·m ⁻²	non-urchin predator resources	
Δd	1.5 km	length of patch along coast	
ψ_U	80 km	mean urchin dispersal distance	Edmands et al. (1996)
ψ_P	80 km	mean predator dispersal distance	Waples and Rosenblatt (1987)
ψ_{s_A}	20.8 km	distance at 0.5 correlation in s_A	see Appendix S1
ψ_{σ_U}	12.0 km	distance at 0.5 correlation in σ_u	see Appendix S1

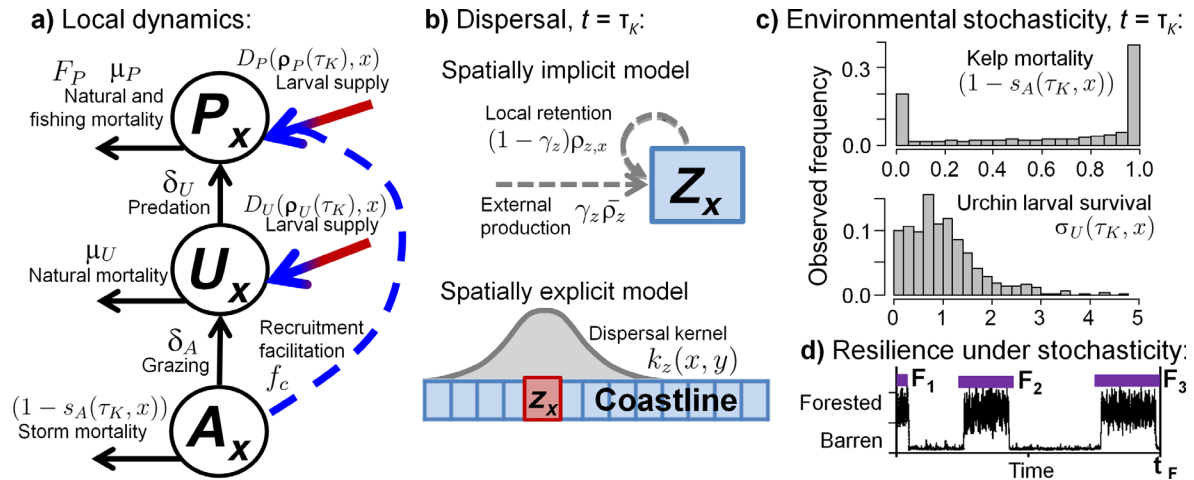


FIG. 1. (a) Model schematic of kelp (A), urchin (U), and urchin predator (P) dynamics within a local community x , denoting losses to consumption and mortality and consumer settlement dynamics at the reproductive pulse $t = \tau_K$ (time of annual reproductive pulse). Arrow colors denote pre-settlement (red), settlement (blue), and post-settlement processes (black). (b) Prior to settlement, larvae of each consumer z disperse in both one-patch and spatially explicit models. (c) Kelp mortality and urchin larval survival (relative to average conditions) implemented at the reproductive pulse are determined from empirically observed environmental stochasticity. (d) Time series illustrating two stochastic metrics of resilience used in model analysis: state frequency calculated as $t_F^{-1} \sum F_i$ and mean state duration calculated as $n^{-1} \sum F_i$. Parameters are defined in Table 1 and in *Materials and methods*.

consumption of urchins given the conversion factor b and feeding on alternative (non-urchin) prey species β , where $\beta \leq \mu_P$ to prevent unbounded predator growth. We multiply this per capita larval production by the number of individuals that live to reproduce in early spring to arrive at the larval production for species i in patch x , $\rho_{i,x}(\tau_K)$:

$$\rho_{U,x}(\tau_K) = a\delta_A U_x(\tau_K) \int_{t=\tau_{K-1}^+}^{\tau_K} A_x(t) dt \quad (4)$$

$$\rho_{P,x}(\tau_K) = P_x(\tau_K) \left(\beta + b\delta_U \int_{t=\tau_{K-1}^+}^{\tau_K} U_x(t) dt \right). \quad (5)$$

Given larval production in all n patches in the vector $\rho_i(\tau_K)$, we account for dispersal with the function $D_i(\rho_i(\tau_K), x)$, which depends on the spatial model. Urchin larvae can then experience stochasticity in the number of dispersing larvae that end up in a population $\sigma_U(\tau_K, x)$, which captures presettlement larval survival and movement by water currents (Hart and Scheibling 1988), settlement success dependent on factors such as local cues, and post-settlement survival dependent on predation on recently settled juveniles (Schroeter et al. 1996), where our distinction between “presettlement”, “settlement”, and “post-settlement” phases follows Keough and Downes (1982) and Benton and Bowler (2012). Because larval survival predominates stochasticity across these processes, from this point we refer to $\sigma_U(\tau_K, x)$ as stochasticity in larval survival. In preliminary simulations, we found that, compared to urchin larval survival, stochasticity in predator larval survival had

only weak effects on community dynamics because predators experience much lower population turnover, so we ignore it here. To account for recruitment facilitation, both the settlement of predator larvae and early post-settlement survival of predator juveniles together increase proportionally with local kelp biomass by a factor f_c , where $1 - f_c$ is the baseline predator settlement success in the absence of kelp (Baskett and Salomon 2010). Finally, kelp biomass experiences stochastic survival $s_A(\tau_K, x)$ due to storms and limited growth during winter-spring. See *Model implementation* section below for details on the distributions of $s_A(\tau_K, x)$ and $\sigma_U(\tau_K, x)$ for different model realizations. Thus, the community state just after the reproductive pulse (at $t = \tau_K^+$) is

$$A_x(\tau_K^+) = s_A(\tau_K, x) A_x(\tau_K) \quad (6)$$

$$U_x(\tau_K^+) = \sigma_U(\tau_K, x) D_U(\rho_U(\tau_K), x) + U_x(\tau_K) \quad (7)$$

$$P_x(\tau_K^+) = D_P(\rho_P(\tau_K), x) \left(1 - f_c + f_c \frac{s_A(\tau_K, x) A_x}{K} \right) + P_x(\tau_K). \quad (8)$$

Spatial dynamics

We start with a one-patch model to link to existing theory and measurement of resilience as the size of a basin of attraction (see *Model analysis*). We then extend the framework to a spatially explicit model to test the robustness of our results to greater realism and determine the spatial scale of alternative stable states where relevant. In the one-patch model (Fig. 1b), we

incorporate external larval production as the proportion γ_i of urchin and predator larvae that originate from outside communities. Thus, $\gamma_i = 0$ corresponds to demographically closed and $\gamma_i = 1$ corresponds to demographically open populations following Johnson (2005). Combining larval production in external areas for species i $\bar{\rho}_i$ with local retention, dispersal into the local community is

$$D_i(\rho_i(\tau_K)) = \gamma_i \bar{\rho}_i + (1 - \gamma_i) \rho_i(\tau_K), \quad 0 < \gamma_i \leq 1. \quad (9)$$

In the spatially explicit model (Fig. 1c), the density of species i larvae arriving in patch x depends on the dispersal kernel $k_i(x, y)$, which describes the proportion of larvae in patch y dispersing to x :

$$D_i(\rho_i(\tau_K), x) = \sum_{y=1}^n k_i(x, y) \rho_{i,y}(\tau_K). \quad (10)$$

For the discrete dispersal kernel, we integrate a continuous Gaussian distribution with mean 0 and variance $\psi_i^2 \pi/2$ (i.e., mean dispersal distance ψ_i when integrating absolute dispersal distances over all off-spring) over the length of coast Δd spanned by patch x to calculate

$$k_i(x, y) = \Phi(|y - x| + \Delta d/2, \psi_i^2 \pi/2) - \Phi(|y - x| - \Delta d/2, \psi_i^2 \pi/2) \quad (11)$$

using the Gaussian cumulative density function Φ .

Model implementation

We numerically simulate model dynamics using R 3.4.3 (R Core Team 2017; see Data S1 for model code), solving intrannual dynamics ($t \neq \tau_K^+$), and accounting for dispersal and environmental stochasticity at the end of each year ($t = \tau_K^+$). We use a spatial resolution of $\Delta d = 1.5$ km (i.e., $n = 200$ patches) to resolve the smallest-scale stochasticity, and analyze simulations over 1,000 yr following a 3,000-yr burn-in period to exclude transient dynamics (Appendix S1: Section S3). Given the presence of kelp forests outside our study area, we exclude edge effects by assuming a linear coastline with periodic boundary conditions in $k_i(x, y)$ (Gouhier et al. 2010), placing organisms that disperse beyond the limits of our system into patches on the opposite end.

We parameterize our models based on published studies (Table 1) and monitoring data (Appendix S1: Section S1). In one-patch models, we calculate external larval production $\bar{\rho}_i$ as would occur for a 75% frequency of kelp forests across all suitable habitat in the system (observed in Castorani et al. 2015; we relax this assumption in Appendix S1: Section S1, Fig. S4). Specifically, we separately determine larval production in each state for closed communities ($\rho_{i,\text{forested}}, \rho_{i,\text{barren}}$) and use the weighted average of $\bar{\rho}_i = 0.75\rho_{i,\text{forested}} + 0.25\rho_{i,\text{barren}}$. In

the stochastic case we calculate production over a transient period that precedes eventual predator declines to the long-term absorbing state of extinction (Appendix S1: Section S1) that occurs without external larval supply. In deterministic simulations we omit stochasticity in urchin larval survival ($\sigma_U(t, x) = 1$) and kelp survival ($s_A = 0.37$, the average s_A across all observations). In stochastic simulations we model $s_A(\tau_K)$ as a beta distribution fitted to remote-sensed kelp biomass in the region (31 yr; Bell et al. 2015; Fig. 1c) and $\sigma_U(\tau_K, x)$ as a beta distribution fitted to observed age-1 urchin densities (27 yr, 33 sites; Kushner et al. 2013). We then rescale $\sigma_U(\tau_K, x)$ by its mean so that stochasticity does not affect long-term larval survival (i.e., average $\sigma_U(\tau_K, x) = 1$). In the spatial model, we account for observed scales of environmental stochasticity ($\psi_{s_A}, \psi_{\sigma_U}$; Appendix S1: Section S1) using multivariate beta distributions, wherein correlations in kelp and urchin larvae survival decline with distance according to a Gaussian distribution (discretized as in Eq. 11).

Model analysis

In one-patch models, we measure resilience R of the kelp forest state, with alternative stable states present for $0 < R < 1$, and absent for $R \approx 1$ (indicating 100% forests) and $R \approx 0$ (indicating 100% barrens). In the deterministic case, we quantify R as the proportion of 1,000 uniformly spaced initial conditions that result in kelp forests. In stochastic simulations, we measure R as the proportion of time local communities spend in a forested state (Scheffer et al. 2015). For stochastic simulations, we also measure the mean duration of forest and barren states, where increasing durations signify increasing resilience of each state (Fig. 1d; Livina et al. 2010). In all stochastic simulations, we first test for multimodality in the distribution of kelp biomass using Hartigan's dip test (Hartigan and Hartigan 1985) to see if alternative stable states are present. We then identify each state by fitting mixed skewed-normal distributions to model results, and use these distributions to determine community states in every patch and year (i.e., $A_x(\tau_K), U_x(\tau_K)$). Note that, while predators are largely extinct in patches with lengthy barren states, predator densities in stochastic models generally vary over longer time scales and do not exhibit a clear bimodality.

In spatially explicit simulations, we first test for system-wide alternative stable states by investigating the initial-condition dependence of the system-wide outcome. Specifically, we measure the frequency of forest states, aggregated across space, in simulations starting from either all patches initially forested or nearly barren. In stochastic simulations where disturbances might induce localized state shifts, we quantify the mean spatial extent and duration of forests and barrens over the range of fishing intensities. To verify that our stochastic dynamics reflect the presence of alternative stable states (Scheffer et al. 2015), we run simulations with and without the

recruitment facilitation feedback (i.e., $f_c = 0.85$ and 0) and test for bimodality in kelp biomass. Bimodality with and unimodality without facilitation indicates that feedback-based alternative stable states drive community dynamics, while bimodality in both cases indicates stochasticity as the driver of observed patterns. Additionally, to evaluate whether the scale of disturbance (vs. dispersal) determines the scale of alternative stable states, we explore a range of spatial scales in urchin settlement stochasticity ψ_{σ_U} .

Comparison to observed community scales

To test the realism of our spatial model predictions, we compare the spatial scale and durations of alternative states in the model to monitoring data from 83 sites across the Channel Islands (Kushner et al. 2013, PISCO et al. 2011; see Appendix S1: Section S4 for analysis details). Monitoring sites span only kelp habitats where kelp loss arises predominantly from urchin grazing; consequently, we classify each site in every year as forested if adult plants are present (>1 individual/100 m²) or barren otherwise. Due to the limited length of time series (10–22 yr), most (76%) observations record only partially observed state durations (i.e., start and/or end years unknown). To utilize all data, we compare observations with 10,000 equivalently long subsets of model simulations, each starting at a randomly selected patch and year (omitting model transients; see Appendix S1: Section S4 for comparison of only fully observed states). Because data were recorded at individual sites, we calculate the spatial scale of states in both simulations and data as the distance at which Pearson correlation in community state κ , calculated over a 5 km window moving by 0.5 km, declines to zero (with standard error $\sqrt{(1 - \kappa^2)/(n - 2)}^{-1}$ given n comparisons).

RESULTS

Presence of alternative stable states under external larval input

We find that the occurrence of alternative stable states decreases (i.e., increasing forest resilience) with the fraction of external predator larvae but increases with the fraction of external urchin larvae in both the deterministic (Fig. 2a) and stochastic (Fig. 2b–d) implementations of our model. Intuitively, external urchin larval input increases the persistence of barren states by maintaining high settlement when kelp are overgrazed to low levels. External urchin larval input also can increase forest state persistence because greater urchin settlement increases predator consumption, which in turn increases predator production and densities to reinforce forest states. This outcome entails high urchin population turnover in forest states, as observed in reality (Kenner and Lares 1991). Overall, external urchin larval input maintains

the presence of alternative stable states and reduces forest resilience. The magnitude of annual urchin settlement, coupled with fast growth of kelp biomass, also means that pulses of high and low urchin larval survival are the primary source of environmental stochasticity that drives community shifts in our model (Appendix S1: Section S5).

In contrast to urchins, the fraction of external predator larvae increases the frequency and duration of kelp forests by increasing total settlement (which encapsulates presettlement, settlement, and early post-settlement processes that affect overall establishment) of predator larvae in urchin barrens. The feedback driving alternative stable states (recruitment facilitation) limits this outcome by controlling the number of dispersing individuals that successfully settle within a location. Taken together, external predator larval supply alone leads to loss of alternative stable states (only forests stable), while at high external larval supply in both species, effects of external urchin larval input predominate, maintaining barrens locally even in regions dominated by kelp forests. This presence of alternative stable states under high external larval input requires feedbacks that affect predator settlement, and disappears in a preliminary investigation of post-settlement feedback mechanisms that affect only established individuals (Appendix S1: Section S2, Fig. S5).

Spatial scales of alternative stable states

Consistent with the one-patch simulations, our stochastic spatially explicit model reveals forested and barren states at localized but not global scales. While the deterministic spatial model exhibits initial-condition-dependent system-wide alternative stable states at intermediate levels of fishing intensity (the predominant source of predator mortality, Fig. 3a), in the presence of stochasticity the long-term, spatially aggregate ecosystem state is independent of initial conditions (Fig. 3b; Appendix S1: Fig. S7). However, individual patches in the stochastic simulations typically occur in one of two distinct urchin- and kelp-dominated states (87% of patches with <0.02 or >1 kg/m² kelp, Fig. 4c) that span localized 10–20 km scales and can persist for decades (Fig. 5a, b). This feature reflects alternative stable state dynamics because the stochastic model without the recruitment facilitation feedback exhibits a unimodal state distribution (Fig. 4b, c).

Our spatially explicit model also illustrates how the spatial scale of alternative stable states depends on the interaction between the scale of environmental stochasticity and the amount of ecological resilience based on within patch dynamics. By reducing forest resilience, higher fishing increases the frequency and duration of barrens (and vice versa for forests; Fig. 5a, b) as pulses of urchin larvae become more likely to produce barren states. The spatial scale of barrens simultaneously increases because, for a given disturbance level, nearby

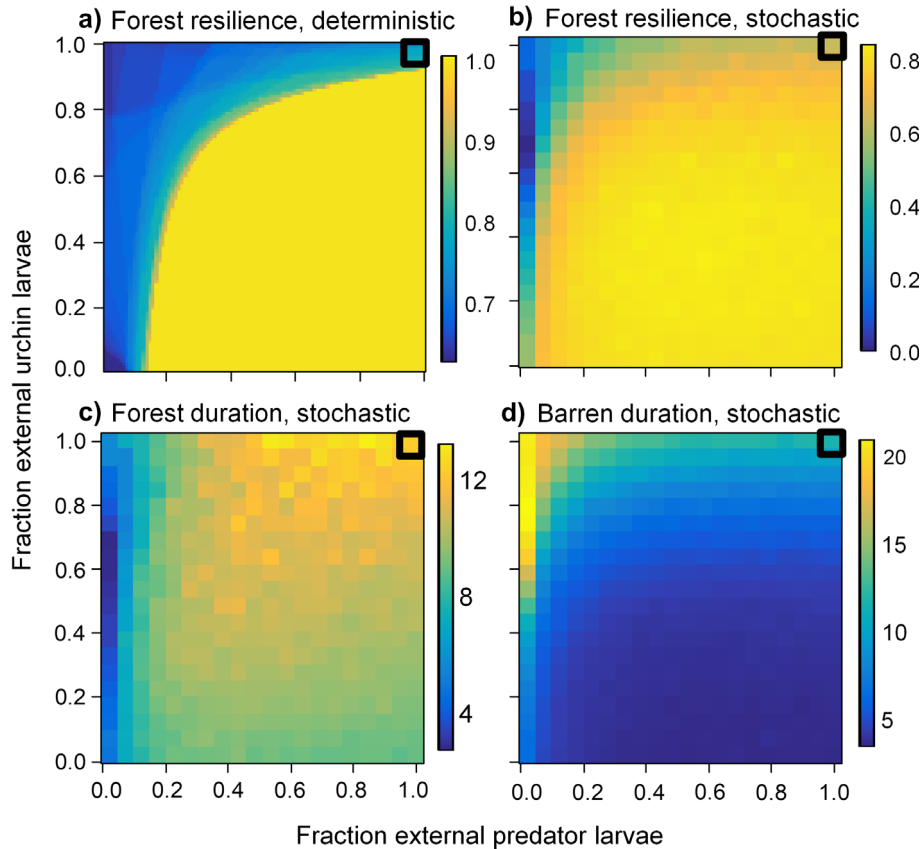


FIG. 2. Effects of external predator and urchin larval supply from a partially (75%) forested environment on the presence of alternative stable states (i.e., kelp forest resilience between 0 and 1) (a) without and (b) with environmental stochasticity, and the effects of external larval supply on mean duration of (c) forest and (d) barren states in the stochastic model. For reference, autocorrelation in community dynamics without recruitment facilitation ($f_c = 0$) declines to zero in 4–5 yr. Boxes highlighting larval supply regimes in the top-right of each panel denote the proportion of external larval supply corresponding to our spatially explicit model (dispersal distances $\psi_i = 80$ km are approximately equivalent to a fraction of external larvae $\gamma_i = 0.997$; see Appendix S1: Fig. S1 for the full relationship between γ_i and ψ_i).

locations experience greater likelihood of being in a barren state. The spatial scale of urchin barrens peaks at intermediate spatial scales of environmental stochasticity (ψ_{σ_U} ; Fig. 5c, d): initial increases in the scale of variation in larval supply increase the scale of both states by synchronizing environmental conditions among nearby communities. Eventual increases in ψ_{σ_U} reduce the capacity of urchin dispersal to mitigate stochastic population declines via larvae from areas experiencing favorable environments (i.e., the spatial storage effect). The resulting declines in overall urchin densities and settlement reduce the extent of barrens by reducing their resilience and the persistence of both states.

Comparison to observed community scales

Duration and spatial scales of alternative states in the spatial model were partially comparable to data (Fig. 6). Overall, distributions of observed forest state durations differed little from model expectations ($D = 0.07$,

$P = 0.61$, two-sample Kolmogorov-Smirnov tests here and throughout). However, distributions of barren durations differed more strongly ($D = 0.27$, $P < 0.001$), with mean barren durations shorter in simulations compared to data (2.9 vs. 4.8 yr; see *Discussion* for possible explanation). Omitting partially observed states yielded analogous results (Appendix S1: Section S4). The spatial scale of community states was on a similar magnitude in simulations compared to data, albeit substantially larger (15 vs. 30 km, distances where correlation declines to zero in Fig. 6c).

DISCUSSION

Our results show that alternative stable states can remain relevant in highly interconnected communities (Figs. 2, 4). This relevance of alternative stable states in our model most likely arises because the feedback mechanism maintaining urchin barrens (low predator facilitation) affects the settlement and early post-settlement

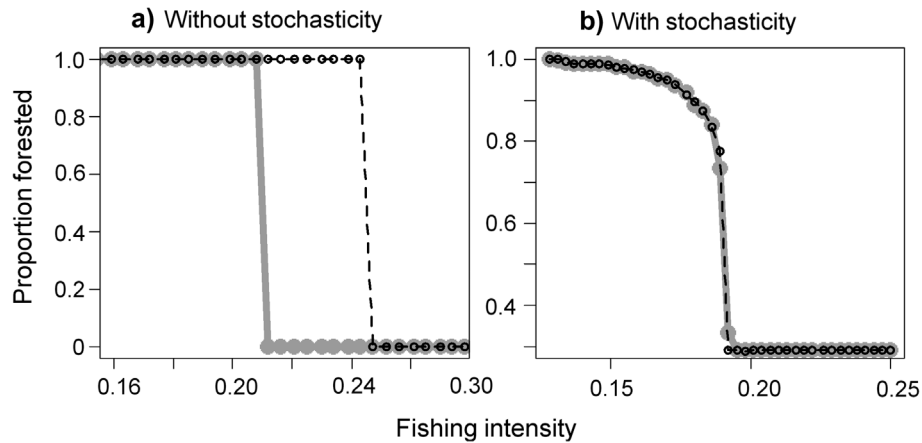


FIG. 3. System-wide alternative stable states that occur in the (a) deterministic spatially explicit model disappear in the (b) stochastic model with environmental variation. Each plot shows long-term community dynamics of simulations starting from a forested (black, dashed lines) or near-barren (gray, solid lines) state, across levels of fishing intensity, the predominant source of predator mortality.

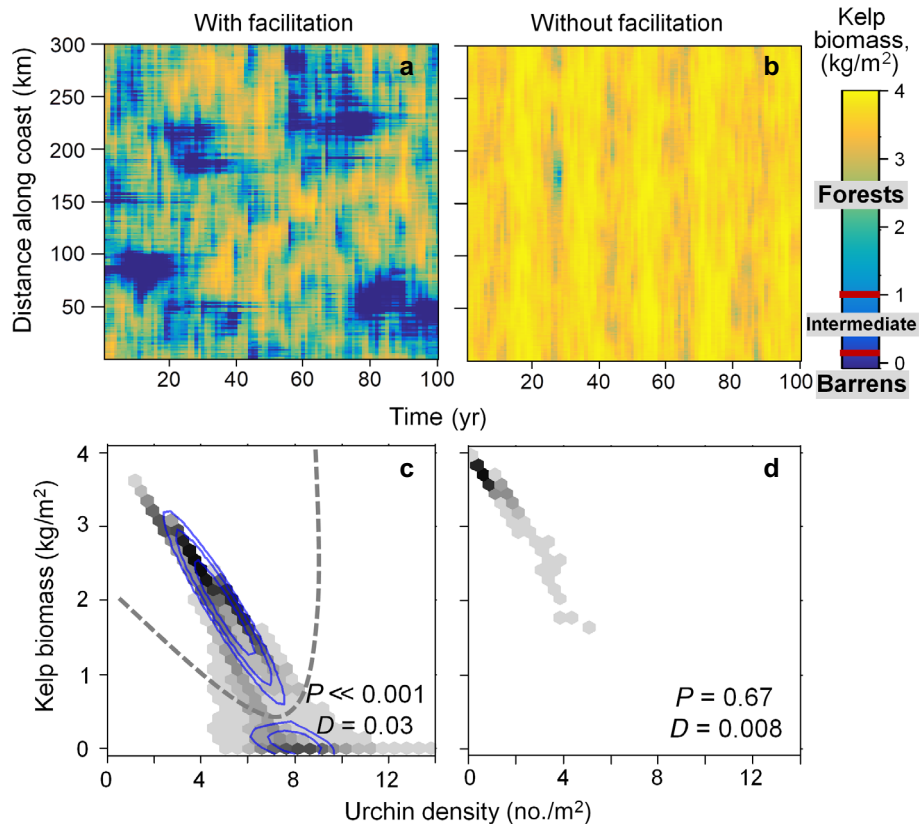


FIG. 4. Spatiotemporal kelp forest dynamics (top row) and frequency distributions of community states (bottom row) in our model with ($f_c = 0.85$, left column) and without ($f_c = 0$, right column) the recruitment facilitation feedback that produces alternative stable states. Panels a and b show kelp biomass, with forested states in green-yellow and barren states in dark blue. The time period shown is from after the 3,000-yr burn in period from a spatially homogeneous kelp forest state. P values from the dip test in panels c and d indicate whether the distributions of kelp biomass are multimodal ($P < 0.05$), indicating the presence of alternative stable states, or unimodal ($P > 0.05$), with accompanying test statistics D . In panel c, contours denote the best-fit skew-normal bivariate distributions, and dashed line denotes the fitted boundary between forest and barren states.

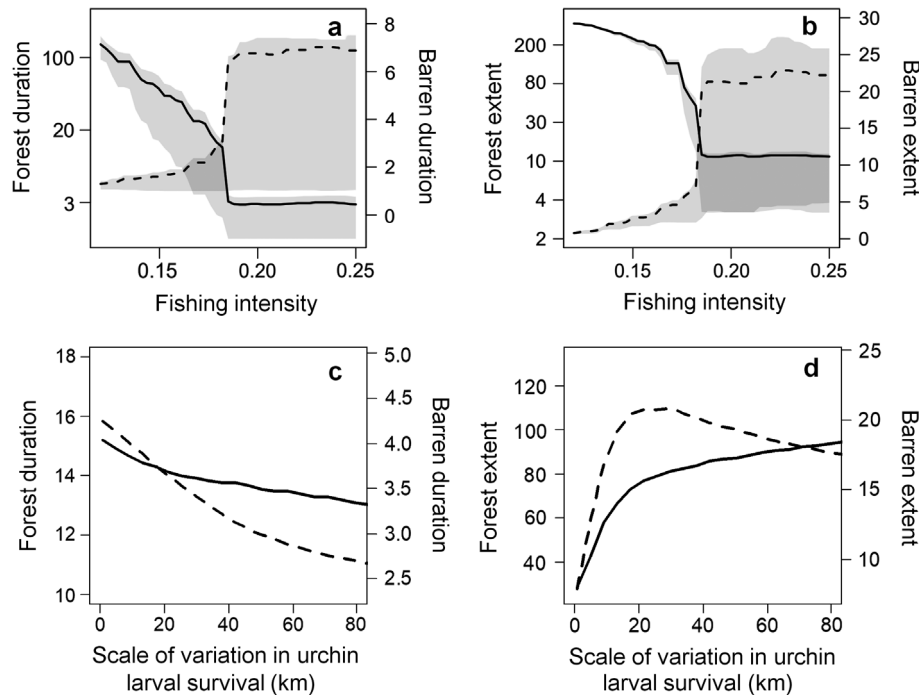


FIG. 5. (a, b) Effects of fishing intensity (which determines forest resilience) and (c, d) the spatial scale of variability in urchin larval survival (ψ_{σ_U}) on the average duration (a, c) and spatial extent (b, d) of kelp forests (solid lines) and urchin barrens (dashed lines). Shaded areas in panels a and b denote variation (25th and 75th percentiles) in state duration across patches (a) or spatial extent across years (b). Parameters not varied in each plot (i.e., F_P or ψ_{σ_U}) held at default values (Table 1).

survival of predators dispersing into local communities, but not subsequent post-settlement processes (e.g., natural predation and fishing mortality: Appendix S1: Section S2, Fig. S5). Specifically, dispersing predator larvae do not overwhelm settlement feedbacks within patches as might otherwise be intuitively expected because few dispersers successfully establish in the community. Across local communities, the settlement feedback reduces dispersal among communities in distinct states and maintains localized, alternatively stable forest and barren states (Fig. 4). In contrast, preceding spatially explicit studies that predict dispersal-induced synchrony of ecological states over large scales (van Nes and Scheffer 2005, Martin et al. 2015) have focused on post-settlement feedbacks as the drivers of alternative stable states. This suggests that the relevance of alternative stable states in highly interconnected communities might require settlement feedbacks, a hypothesis worth testing in alternate model structures.

Our results show that ecosystem heterogeneity required for alternative stable states to be relevant locally (here, spatially asynchronous stochasticity; Fig. 3) may occur below the scales of dispersal (e.g., $\psi_{\sigma_U} < \psi_U$ in our model, Fig. 5d). Conversely, in spatially explicit models with post-settlement feedbacks, alternative stable states co-occur among local communities only when stochasticity or habitat patchiness exceed the scales of dispersal (Durrett and Levin 1994, van Nes

and Scheffer 2005, Martin et al. 2015). In models with settlement feedbacks similar to ours, fine-scale (0.1–100 m, below the scales of dispersal) patterning of distinct states arises through self-organization when organisms facilitate each other locally and inhibit growth at larger scales (Rietkerk and Van de Koppel 2008). Our findings show the potential for analogous self-organization mechanisms to structure ecosystems on large (e.g., 10–20 km) spatial scales. Taken together, multiple sources of ecosystem heterogeneity can induce alternative stable states at local scales.

We also find that the spatial and temporal scales of each stable state increase with its local-scale basin of attraction and the scale of environmental variation, which outweigh the role of dispersal scale. The attraction basin size of a given state (e.g., forests) depends on localized dynamics (here, fishing intensity, Fig. 5a, b) and represents its ecological resilience. Our results integrate previous stochastic and spatially explicit models that have separately emphasized how greater resilience increases the persistence (Livina et al. 2010) and spatial scale (Bel et al. 2012) of alternative stable states. The spatial scales of alternative stable states can also increase with the spatial extent of environmental variation via environmentally induced synchrony (Fig. 5c, d; the Moran effect; Gouhier et al. 2010) when disturbances are well below the scale of dispersal. However, larger-scale disturbances can decrease the spatial extent of both

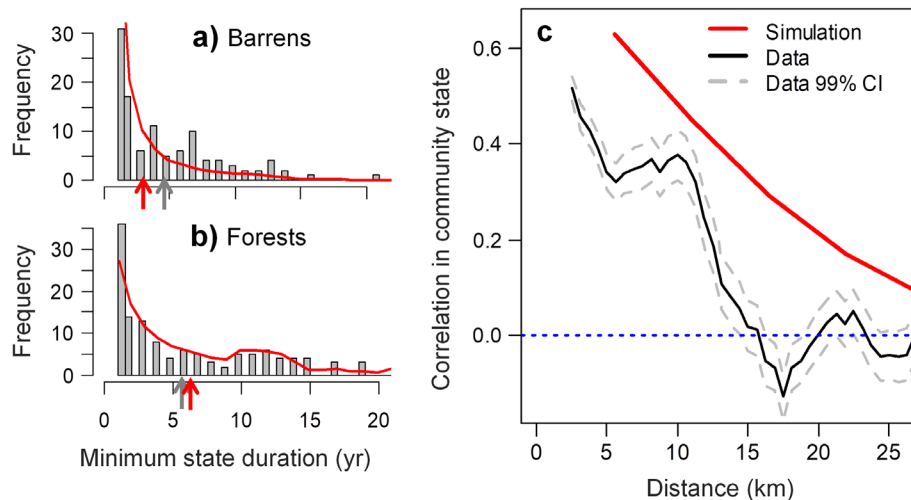


FIG. 6. (a, b) Durations and (c) spatial scales of community states in model simulations compared to field data. Minimum durations (i.e., both fully and partly observed states) of barrens (a) and forests (b) given for data (bars, frequencies) and model simulations (red). Spatial autocorrelation of community states in simulations (red) and data (black) is calculated over a 5 km window moving by 0.5 km; gray lines denote 99% confidence intervals.

states by reducing the role of dispersal and weakening dispersal-induced synchrony. Analogous dynamics occur in stochastic population models with single equilibria (Kendall et al. 2000), highlighting how extensive research on population synchrony might inform the spatial scales of alternative stable ecosystem states.

Systems where alternative stable states might be relevant locally

The settlement feedbacks expected to be necessary for the local relevance of alternative stable states in our model are likely to occur in many taxa. In general, plants and numerous marine species disperse during seed, spore, or larval stages, which often are inferior competitors compared to individuals already established in the community or rely on facilitating species for survival (reviewed in Caley et al. 1996, Bruno et al. 2003, Clobert et al. 2009). Additionally, actively moving adult animals and aquatic larvae avoid settling in areas of intense competition, high predation risk, or unfavorable conditions (Morgan et al. 1996, Benton and Bowler 2012). Thus, settlement feedbacks can arise from behavior during or high mortality immediately after settlement that prevents dispersers from establishing in the community.

Observed settlement feedbacks might in turn underlie localized alternative stable states in a variety of ecosystems beyond temperate rocky reefs. For tropical reefs where coral larvae cannot settle or survive in algae-dominated areas, alternative stable coral and macroalgal states occur in spatially explicit models on the scale of individual reefs (~500 m²) despite high levels of external larval supply (Mumby et al. 2007). Additionally, herbivorous fish that reinforce coral-dominated states

preferentially immigrate to areas of high coral cover (which offer predation refugia) when emigrating from nursery habitats (Dixon et al. 2014). Consequently, distinct states might co-occur among local reefs, especially when large-scale disturbances have reef-specific impacts due to long-term, localized environmental differences (e.g., areas with protected vs. fished herbivores; Mumby et al. 2013). In terrestrial systems where competitively inferior grasses impede tree seedling survival by amplifying fire severity, empirical studies find mounting evidence for alternative stable savanna and forest states (Staver et al. 2011). Consistent with our results, spatially explicit models predict that these states co-occur locally below (and independently of) the scale of tree dispersal (Schertzer et al. 2015) when fires propagate heterogeneously across landscapes. Numerous studies also document localized alternative stable states that arise as fine-scale patterns in systems such as mussel beds, wetlands, and arid ecosystems when established individuals deplete resources or displace growth-inhibiting factors (e.g., snow fields in alpine forests; reviewed in Rietkerk and Van de Koppel 2008). Given that both processes locally inhibit settlement of new individuals, our results imply that the scale of such patterns in general depends on the scales of resource depletion or ecosystem engineering rather than the scale of dispersal.

Empirical evidence and tests for localized alternative stable states

The localized spatial and temporal scales of alternative stable states predicted here are in line with empirical observations of temperate and tropical rocky reef systems. The duration of kelp forests in our model match observed community scales in the Channel Islands. The

greater duration of barrens observed compared to expectations might be due to lower urchin predator densities in the northern Channel Islands compared to the modeled region, which arise partly due to lower body growth or higher mortality (Caselle et al. 2011). The smaller spatial scale of community states in the data compared to expectations likely arises from spatial heterogeneity in rocky reef habitat availability not accounted for here (see *Model robustness* for details). Worldwide, studies on temperate rocky reefs often find evidence for kelp- and urchin-dominated states (analogous to Fig. 3a) even when sampling at very fine scales (5 m²; Ling et al. 2015). Among 51 transitions between these states documented worldwide, two-thirds occurred at <100 km spatial scales (Filbee-Dexter and Scheibling 2014). These scales are likely at or below the mean dispersal distance of urchins and their predators given the species' long pelagic larval duration and strong, large-scale genetic exchange (100–300 km; Waples and Rosenblatt 1987, Edmands et al. 1996). Similarly, in tropical coral reefs Ninio et al. (2000) found long-term shifts to algal-dominated regimes that were spatially localized (~10 km) and asynchronous at larger (~100 km) scales.

The spatial scales of alternative stable states found here, while local, still exceed the extent of feasible manipulative experiments and many ecological surveys, which impedes efforts to detect this phenomenon. The two most commonly used approaches to detect distinct states under the same environmental conditions involve demonstrating either (1) a lack of recovery of an original, stable state following experimental manipulations or natural disturbances or (2) a bimodality in the distribution of ecological states observed across locations in field surveys (e.g., Fig. 4c; reviewed in Mumby et al. 2013, Scheffer et al. 2015). We highlight that both features occur only when the spatial extent of experiments or surveys is greater than the spatial scale of alternative stable states; at finer scales, detection efforts might fail because dispersal or long-distance interactions rapidly reverse the effects of manipulations or disturbances, maintaining a single community state (Petraitis 2013). One approach toward resolving the presence and scale of local alternative stable states can be to pair spatially explicit dynamical models with field data (Scheffer et al. 2001). In particular, model selection given observed data can quantify the extent to which observed spatiotemporal patterns are consistent with expectations for multiple types of hypothesized feedback loops, as compared to solely the effects of environmental heterogeneity known to occur in a given system.

Model robustness

For tractability, we omitted several factors that might affect the feedback loops that drive the relevance of alternative stable states under external larval input. One factor that might erode the recruitment facilitation feedback maintaining urchin barrens in our model is strong predation on urchins by species less reliant on the

presence of kelp. Alternatively, several feedbacks omitted here might reinforce urchin barrens. First, changes in urchin foraging behavior not modeled here can lead to intensified grazing at low predator densities (Cowen 1983) or at low levels of kelp biomass and therefore reduced supply of drift kelp (Ebeling et al. 1985, Harold and Reed 1985). Second, urchins might also experience recruitment facilitation in barrens due to crustose coralline algae, which might compete with kelp (Baskett and Salomon 2010). Additionally, predators preferentially avoid consuming starving urchins in barren areas (Eurich et al. 2014). All of these mechanisms could increase urchin densities or grazing at low kelp biomass. Acting together, multiple feedbacks can produce alternative stable states even when individually each mechanism is insufficient to do so (van de Leemput et al. 2016). The strength of most feedbacks posited to drive alternative kelp and barren states, including our feedback of recruitment facilitation, is often estimated in only a few small-scale, system-specific studies (Ling et al. 2015). Nevertheless, our qualitative results are not sensitive to the level of facilitation (Appendix S1: Section S6), and this mechanism is consistent with greatly reduced predator densities in barrens vs. kelp forests in our system (Graham 2004).

Our model also makes several simplifying assumptions that might quantitatively affect the extent and duration of alternative stable states. For example, we ignore the fact that juvenile and adult predators (particularly lobsters) can potentially move over long distances and, unlike larvae, might immigrate to and survive in barren areas with low kelp cover. Our model also does not account for kelp mortality during extreme warm water events, which can span much larger spatial scales than storm-driven kelp loss (Dayton et al. 1999). Additionally, we parameterize stochasticity in urchin larval survival based on data from the Channel Islands, which experience stronger oceanographic variability compared to other California rocky reefs. Together, increased role of dispersal by adult predator movement, large-scale kelp mortality events, or lower intensity of localized stochasticity might produce larger-scale community states than predicted here. Alternatively, our model might over-estimate these scales due to limited dispersal among communities separated by areas lacking kelp habitats, particularly between islands (1–5 km; Cavanaugh et al. 2013). Other forms of local environmental heterogeneity not modeled here, such as heterogeneity in fishing intensity due to distance from ports or the presence of marine protected areas (Hamilton et al. 2011) and variation in kelp growth conditions might also make forests and barrens manifest within more localized areas of our system.

Management implications

We find that increasing stress applied to the overall ecosystem (here, fishing) can induce localized socioeconomically undesired states (here, urchin barrens) that

gradually increase in frequency, spatial extent, and duration (Fig. 5a, b). Our results suggest that while spatially synchronous state shifts expected in interconnected systems (Hughes et al. 2005, 2013) may be unlikely when settlement feedbacks reduce the role of dispersal (Fig. 3b), collapsed states could span 10–30 km of the coastline and persist for decades under intense exploitation (here, fishing). Where disturbances induce localized undesired states, local management efforts can increase the probability of recovery by increasing the attraction basin size of desired states, for example by reducing predator harvest (i.e., by implementing ecologically sustainable yield sensu Zabel et al. 2003). Alternative management approaches to restoring desired states include manipulating species densities, for example by reducing urchin densities in kelp forests (House et al. 2017). However, urchin harvest is practical only at small spatial scales such that maintenance of high potential for urchin larval supply from outside areas can limit efficacy. Furthermore, reversal of barren states may require persistent culling over long periods required for predator recovery.

The persistence of undesired barren states despite high predator larval supply from pristine, forested areas found here (Fig. 2) also suggests that settlement feedbacks can limit the role of rescue effects provided by protected areas in spatially explicit management contexts. However, the overall outcome of reserve-based management will depend both on the magnitude of rescue effects and how reserves alter the attraction basin of desired states in exploited areas. For example, Barnett and Baskett (2015) found that marine protected areas increase attraction basins of states dominated by fished predators in both harvested and protected areas compared to equivalent spatially uniform harvest in a model with well-mixed larval pools. Given the role of heterogeneity in maintaining localized alternative stable states in our spatially explicit model, the next step for understanding reserve effects on resilience in exploited areas are spatially explicit studies that account for the spatial scales of reserves, disturbance, and dispersal.

CONCLUSIONS

We expand existing resilience theory by showing that alternative stable states can occur locally below the scales of dispersal, likely due to feedbacks affecting settlement. This can explain observed community scales on temperate rocky reefs and how alternative states commonly co-occur in highly interconnected ecosystems (Scheffer and van Nes 2004, van de Leemput et al. 2015). In the wide array of marine and terrestrial systems where settlement feedbacks occur, this suggests that anthropogenic impacts such as harvest and grazing can produce increasingly large and persistent undesired states rather than sudden ecosystem-wide collapses.

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