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Recruitment facilitation can drive alternative states on temperate reefs

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Abstract. How the combination of positive and negative species interactions acts to drive community dynamics is a fundamental question in ecology. Here we explore one aspect of this question by expanding the theory of predator-mediated coexistence to include the potential role of facilitation between the predator and inferior competitor. To motivate and illustrate our simple model, we focus on sea-urchin–algae interactions in temperate rocky reef systems and incorporate recruitment facilitation, a common characteristic of marine systems. Specifically, the model represents sea urchin grazing on macroalgae, macroalgal competition with crustose coralline algae (CCA), and facilitation of sea urchin recruitment to CCA. These interactions generate alternative stable states, one dominated by macroalgae and the other by urchins, which do not occur when recruitment facilitation of urchins to CCA is ignored. Therefore, recruitment facilitation provides a possible mechanism for alternative kelp forest and urchin barren states in temperate marine systems, where storm events or harvesting of urchins or their predators can drive switches between states that are difficult to reverse. In systems with such dynamics, spatial management such as no-take marine reserves may play a crucial role in protecting community structure by increasing the resilience to shifts between states.

Key words: alternative states; crustose coralline algae; herbivory; hysteresis; kelp forest; macroalgae; recruitment facilitation; resilience; urchin barren.

Introduction

The prevalence of positive species interactions and their potential to drive community dynamics has become increasingly apparent in both theoretical and applied ecological research (Bertness and Callaway 1994, Bruno et al. 2003, Halpern et al. 2007). In particular, understanding the way in which they interact with negative interactions (e.g., predation and competition) to structure ecological communities is a basic question in ecology. Here we explore how positive interactions can affect the coexistence of competing species and whether the feedback loops generated by positive interactions can drive alternative stable states.

Alternative states occur when a community of interacting species can exist in multiple organizational states dominated by distinct species assemblages for a given set of environmental conditions (Lewontin 1969, Holling 1973). This phenomenon is distinct from phase shifts, where the system state may shift dramatically with changing environmental conditions but only one state can exist for any given set of conditions. Theoretical studies indicate the potential for alternative states to occur in simple community models (e.g., Noy-Meir 1975, May 1977, Collie et al. 2004). While ecologists debate the empirical evidence required to demonstrate alternative states (Connell and Sousa 1983, Thrush et al. 2009), data suggestive of threshold dynamics (characteristic of both alternative states and phase shifts) exist from terrestrial (Friedel 1991, Suding and Hobbs 2009), freshwater (Carpenter et al. 1985), and marine systems (Sutherland 1974, Scheffer et al. 2001, Petraitis and Dudgeon 2004, Casini et al. 2009). For example, temperate reefs are frequently characterized as either kelp forests dominated by foliose macroalgae or barren areas dominated by urchins and crustose coralline algae (Paine and Vadas 1969, Estes and Palmisano 1974, Harrold and Pearse 1987, Witman and Dayton 2001), with each community assemblage being long lasting and difficult to reverse (Konar and Estes 2003, Shears and Babcock 2003). Storm events and changes in sea urchin grazing pressure are two major drivers triggering switches between kelp forests and urchin barrens (Dayton and Tegner 1984, Konar and Estes 2003), where changes in urchin grazing pressure may depend on variation in urchin recruitment, urchin disease, fisheries harvest of urchins and their predators, and regional oceanographic context (Tegner and Dayton 2000, Shears and Babcock 2003, Behrens and Lafferty 2004, Salomon et al. 2008).

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Although kelp and urchin-dominated reef assemblages are often used to exemplify multiple states (Hughes et al. 2005), questions remain over whether these and other communities naturally occur as alternative states and, if so, what mechanisms maintain and drive transitions between states. For example, Connell and Sousa (1983) conclude that relevant and adequate empirical examples of alternative states involve anthropogenic control of the system, and they highlight the suggestion from Paine (1977) that consumers should readily invade prey-dominated states, which calls into question whether a community without consumers can be an alternate stable state. Identifying whether alternative states exist and, if so, what mechanisms drive them can both enhance our understanding of the processes structuring communities and inform conservation and management policies designed to restore ecosystems to a desired state (Scheffer et al. 2001, Suding and Hobbs 2009, Thrush et al. 2009). For example, if a temperate reef system has shifted from a kelp forest to an urchin barren after intensive harvesting of urchin predators and only one state is stable for a given set of parameters, a moratorium on harvest should allow recovery of the predator and a return to the kelp forest state without further impediment. However, if alternative states exist, the processes maintaining those states may impede the return to the kelp forest state, even without further harvesting of urchin predators.

One possible source of the feedback loops required to maintain alternative states is the facilitation of recruitment (Petraitis and Latham 1999, Dudgeon and Petraitis 2001), the tendency, common in marine systems, for organisms such as fish and invertebrates to preferentially recruit to a habitat in the presence of specific invertebrates and/or algae (Halpern et al. 2007). For example, on temperate reefs, crustose coralline algae (CCA; e.g., *Lithothamnion* spp., *Lithophyllum* spp., and their close relatives) release chemical cues that induce the settlement and metamorphosis of invertebrate grazers such as abalone (Morse et al. 1979, Morse and Morse 1984, Strathmann 1987) and sea urchins (Pearce and Scheibling 1990). Juvenile grazers often occur at high densities in "nursery grounds" of CCA-covered rocks, and evidence suggests that CCA rely on grazers to prevent overgrowth by competitively dominant fleshy macroalgae (e.g., kelp; Paine 1980, Steneck 1982, 1983, 1986). Furthermore, kelp beds can reduce grazer recruitment by overgrowing coralline crust settlement surfaces (Paine 1980). Kelp stands can also reduce grazer post-recruitment survivorship and/or density by physical abrasion, occupying space, and providing habitat for recruit micropredators (Underwood and Jernakoff 1981, Rowley 1989, 1990, Konar and Estes 2003). These potential negative effects of kelp on grazer recruits could explain grazer-CCA recruitment facilitation despite the potential for settlement in locations with lower food (i.e., macroalgae) availability at later life history stages (many grazers feed primarily on epiphytic diatoms during early life history stages). Furthermore, by grazing macroalgae, adult grazers maintain suitable habitat for larval settlement and juvenile survival (Miner et al. 2006). Ultimately, CCA facilitation of grazer recruitment enhances future grazing and subsequently CCA survival (see Plate 1), while kelp inhibition of grazer recruitment and survivorship reduces future grazing and subsequently enhances kelp survival.

Due to these grazing- and recruitment-based feedback loops, sea urchin recruitment may depend on high CCA and low macroalgal cover, while these species also interact through CCA-macroalgal competition for space and light (Paine 1980, Steneck 1986). Therefore, a threshold sea urchin density may be necessary to suppress macroalgal densities to a level where enough CCA can exist for large-scale urchin recruitment and subsequent urchin dominance. Similarly, a reduction in urchins to a particular threshold density may be necessary to allow barren states to transition to forested states. Thus recruitment facilitation may play a role in generating alternative urchin-dominated and macroalgae-dominated states in temperate reefs.

The goal of this paper is to explore the extent to which recruitment facilitation can cause the emergence of alternative states in temperate reefs, as an illustration of how positive interactions might interact with competition and predation to drive community structure. To this end, we construct a simple model of urchin, CCA, and kelp dynamics and analyze the model under different degrees of urchin-CCA recruitment facilitation, from none to obligate. In addition, we examine how the degree of facilitation determines the effect of changing urchin mortality on the system.

MODEL AND ANALYSIS

The model follows herbivorous sea urchin (H), macroalgae (A), and crustose coralline algae (CCA; C) dynamics, where the herbivores graze on the macroalgae, the macroalgae and CCA compete, and sea urchins preferentially recruit to CCA (Fig. 1). For all of these interactions, we choose the simplest possible model structure in order to determine whether recruitment facilitation can drive alternative stable states in the most basic case. For example, we model macroalgal–CCA competition as Lotka-Volterra competition for space, where each species Y (A for macroalgae or C for CCA) has population growth rate r_Y (increase in cover due to both growth and recruitment), carrying capacity K_Y (e.g., total area of suitable habitat available), and competitive effect on species Z, α_{ZY}. We assume that macroalgae are superior competitors to CCA and thus $\alpha_{\mathrm{CA}} > K_{\mathrm{C}}/K_{\mathrm{A}}$ and $\alpha_{\mathrm{AC}} < K_{\mathrm{A}}/K_{\mathrm{C}}$ (i.e., macroalgae have a strong competitive effect on CCA while CCA have a weak competitive effect on macroalgae; Paine 1980, Steneck 1983; but see Johnson and Mann 1986, Bulleri et al. 2002).

Herbivore grazing on macroalgae occurs at a rate δ_{H}, and herbivores convert a proportion of the energy

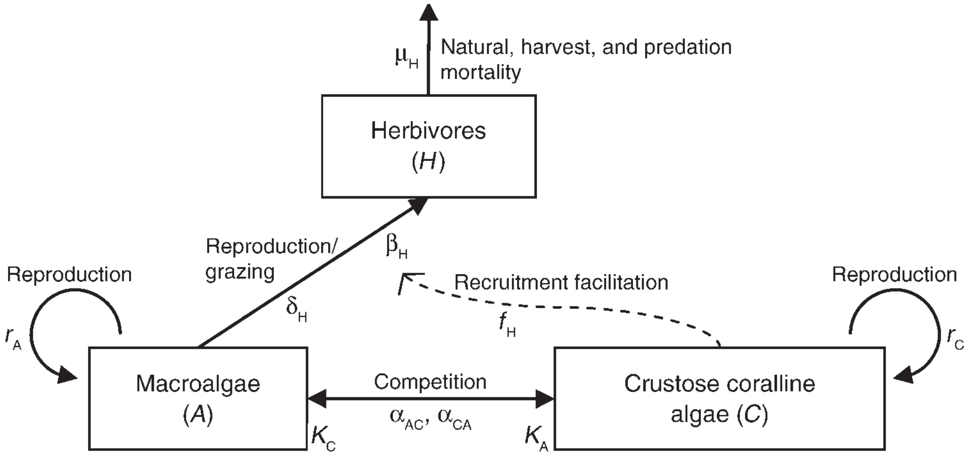

FIG. 1. Outline of the model. Boxes indicate state variables, and arrows with associated parameters indicate dynamics. The broken line indicates the influence of facilitation on the relevant dynamics when incorporated. The text in the figure describes the meaning of the adjacent parameters; see *Model and analysis* for complete definitions.

gained from grazing into population growth according to the constant β_H. In addition, herbivores experience mortality (due to predation, natural mortality, and/or harvesting) at a rate μ_H. Note that this model structure assumes that herbivores rely exclusively on the modeled macroalgae to obtain the energy necessary for reproduction, and without this food source the urchin population will decline. Urchins can eliminate entire kelp forests from large areas and then persist at high densities under food-limited conditions by reallocating body resources (Edwards and Ebert 1991) and feeding on drift algae produced elsewhere (Duggins 1981, Pearse 1981, Ebeling et al. 1985, Harrold and Reed 1985). This reality may be modeled as a very low natural mortality component to μ_H, where we assume that the reallocation of resources under food limitation includes a reduction in reproduction. Also, we assume closed herbivore dynamics for simplicity and tractability; see *Discussion* for the implications of this assumption.

Finally, to model facilitation of herbivore recruitment to CCA, we define f_H as the proportional strength of the recruitment facilitation, where $f_H = 0$ for no recruitment facilitation (i.e., no relationship between CCA density and herbivore recruitment) and $f_H = 1$ for obligate recruitment facilitation (i.e., CCA presence is necessary for herbivore recruitment to occur). For an intermediate recruitment facilitation strength ($0 < f_H < 1$), a proportion $1 - f_H$ of the total possible herbivore recruitment ($\beta_H\delta_H A$) occurs regardless of CCA density, and the proportion of the remaining possible herbivore recruitment ($f_H\beta_H\delta_H A$) that occurs increases linearly with CCA density, expressed as a fraction of its carrying capacity (C/K_C).

Given these definitions, the model dynamics are as follows (see Fig. 1):

$$\frac{dC}{dt} = C\frac{r_C}{K_C}(K_C - C - \alpha_{CA}A) \tag{1}$$

$$\frac{dA}{dt} = A\left[\frac{r_A}{K_A}(K_A - A - \alpha_{AC}C) - \delta_H H\right] \tag{2}$$

$$\frac{dH}{dt} = H\left[\beta_H\delta_H A\left(1 - f_H + f_H\frac{C}{K_C}\right) - \mu_H\right]. \tag{3}$$

In order to analyze the model presented in Eqs. 1–3, we use classic local stability analysis of calculating the leading eigenvalue (or Routh-Hurwitz criteria) of the Jacobian matrix evaluated at each equilibrium. After calculating the conditions necessary for existence and stability for each equilibrium, we rearrange the conditions to determine how they depend on both recruitment facilitation strength and herbivore mortality (see *Stability analysis*). We then graphically integrate these mathematical results to determine the potential for alternative stable states (see *Integration of model results*; Figs. 2 and 3).

Stability analysis

The model has five biologically relevant (real, nonnegative) equilibria: (1) the zero equilibrium with no species present, (2) the CCA-dominated equilibrium without herbivores or macroalgae, (3) the macroalgae-dominated equilibrium without herbivores or CCA, (4) the macroalgae–herbivore equilibrium without CCA, and (5) the "internal" equilibrium with all species present. Below we step through the conditions (relative parameter values) necessary for each of these equilibria to exist biologically and be locally stable. Note that the potential for zero densities in all but the internal equilibrium is a byproduct of our use of a closed system limited to these three species' interactions for tractability. In reality, we do not necessarily expect these species to decline to extinction, but rather consider the zero values representative of substantially reduced densities of the species considered compared to the equilibria where they dominate.

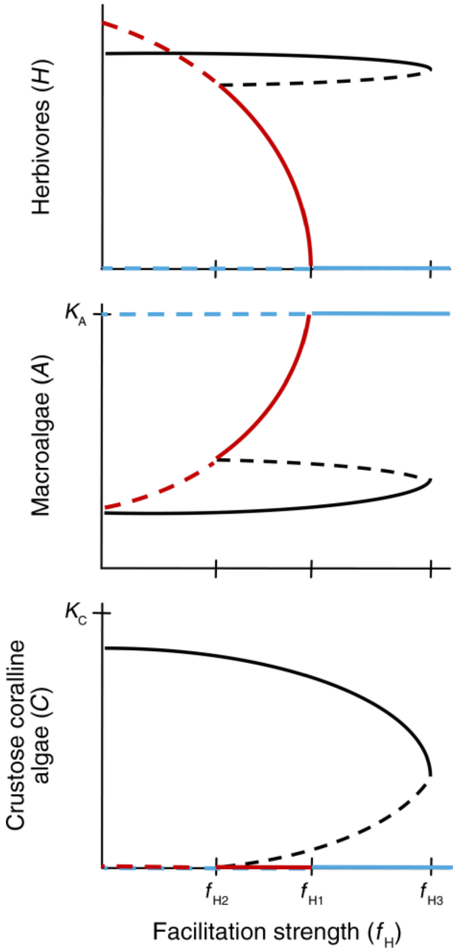

FIG. 2. Predicted equilibria values dependent on the recruitment facilitation strength. See Eqs. 4, 6, and 8 for definitions of f_{H1}, f_{H2}, and f_{H3}, respectively. K_A and K_C indicate the macroalgae and crustose coralline algae (CCA) carrying capacities. Light blue lines indicate macroalgae-dominated equilibrium, dark red lines indicate herbivore–macroalgae edge equilibrium, and black lines indicate internal herbivore–macroalgae–CCA equilibria. Solid lines indicate locally stable equilibria, and broken lines indicate locally unstable equilibria.

First, the zero equilibrium with no species present ($\bar{H} = \bar{A} = \bar{C} = 0$) is always locally unstable given biologically relevant parameters, in particular, positive population growth rates for the macroalgae and CCA (r_A, $r_C > 0$). Second, the CCA-dominated equilibrium ($\bar{C} = K_C$, $\bar{H} = \bar{A} = 0$) is always locally unstable if we assume that macroalgae are superior competitors to CCA ($\alpha_{AC} < K_A/K_C$). Third, the macroalgae-dominated equilibrium ($\bar{A} = K_A$, $\bar{H} = \bar{C} = 0$) is locally unstable if herbivore reproduction exceeds mortality ($\beta_H\delta_H K_A(1 - f_H) > \mu_H$) and locally stable otherwise, given the assumption that macroalgae are superior competitors ($\alpha_{CA} > K_C/K_A$). Rearranging this stability condition, the threshold (herbivore–CCA) recruitment facilitation strength that determines whether the macroalgae-dominated equilibrium is locally stable is

$$f_{H1} = 1 - \frac{\mu_H}{\beta_H\delta_H K_A} \qquad (4)$$

and the threshold herbivore mortality that determines whether the macroalgae-dominated equilibrium is locally stable is

$$\mu_{H1} = \beta_H\delta_H K_A(1 - f_H). \qquad (5)$$

Next, for the macroalgae-herbivore equilibrium ($\bar{C} = 0$, $\bar{A} = \mu_H/(\beta_H\delta_H(1 - f_H))$, $\bar{H} = r_A(K_A - \bar{A})/(K_A\delta_H)$) the condition for the equilibrium to exist biologically (in particular, for $\bar{H} > 0$) is the same as the condition for the macroalgae-dominated equilibrium to be locally unstable ($f_H < f_{H1}$ or $\mu_H < \mu_{H1}$). Then the macroalgae–herbivore equilibrium is locally unstable if $\alpha_{CA}\mu_H < K_A\beta_H\delta_H(1 - f_H)$ and is locally stable otherwise. Rearranging this stability condition, the threshold recruitment facilitation strength that determines whether the macroalgae–herbivore edge equilibrium is locally stable is

$$f_{H2} = 1 - \frac{\alpha_{CA}\mu_H}{\beta_H\delta_H K_A} \qquad (6)$$

and the threshold herbivore mortality that determines whether the macroalgae–herbivore edge equilibrium is locally stable is

$$\mu_{H2} = \frac{K_A\beta_H\delta_H(1 - f_H)}{\alpha_{CA}}. \qquad (7)$$

Note that there cannot be any CCA–herbivore equilibrium without macroalgae as the herbivore depends exclusively on the macroalgae for productivity. In addition, an equilibrium with just macroalgae and CCA ($\bar{H} = 0$) does not exist biologically (it is not possible to have positive values for both $\bar{A}$ and $\bar{C}$) under the assumption that macroalgae are superior competitors to CCA ($\alpha_{AC} < K_A/K_C$, $\alpha_{CA} > K_C/K_A$).

Finally, conditions for the internal equilibria (all species at nonzero densities) to exist biologically and be locally stable depend on whether recruitment facilitation occurs. When facilitation occurs ($f_H > 0$), there are two possible internal equilibria: one with greater macroalgal density and lower CCA density and one with lower macroalgal density and greater CCA density; the relative value of the herbivore density in these two equilibria depends on the parameter values. When they exist biologically, the internal equilibrium with the greater macroalgal and lower CCA density is always locally unstable and the internal equilibrium with the lower macroalgal and greater CCA density is always locally stable. Both of these equilibria exist biologically (positive real values for $\bar{A}$, $\bar{C}$, and $\bar{H}$) when $\beta_H\delta_H K_C > 4\alpha_{CA} f_H\mu_H$. Rearranging this existence condition, the upper threshold recruitment facilitation strength necessary for the existence of the internal equilibria is

$$f_{H3} = \frac{\beta_H\delta_H K_C}{4\alpha_{CA}\mu_H} \qquad (8)$$

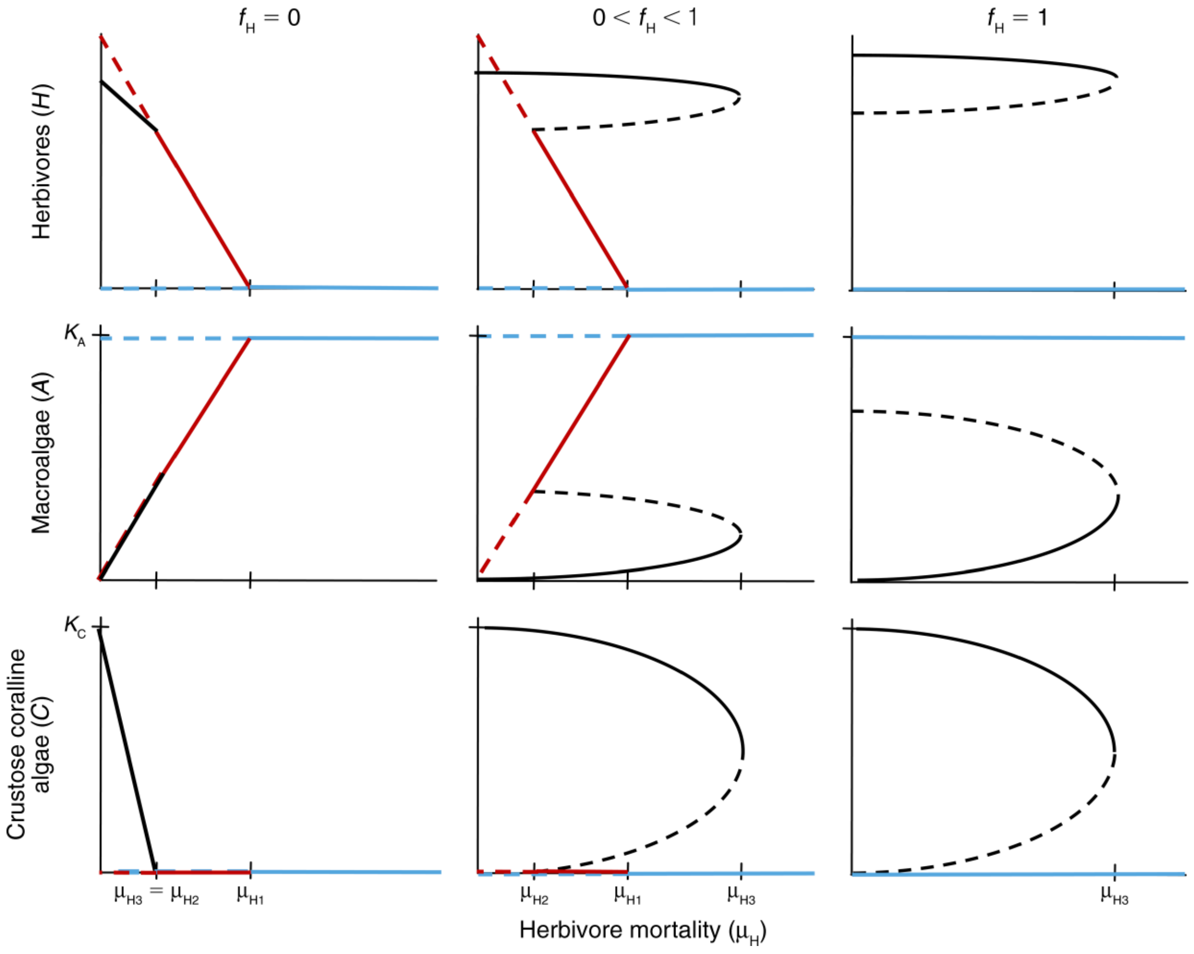

FIG. 3. Predicted equilibria values dependent on herbivore mortality for three possible recruitment facilitation strengths: no facilitation in the left column, intermediate facilitation in the middle column, and obligate facilitation in the right column. See Eqs. 5, 7, and 9 for definitions of μ_{H1}, μ_{H2}, and μ_{H3}, respectively. See Fig. 2 for an explanation of line patterns and colors.

and the upper threshold herbivore mortality necessary for the existence of the internal equilibria is

$$\mu_{H3} = \frac{\beta_H \delta_H K_C}{4\alpha_{CA} f_H}. \tag{9}$$

On the other hand, without facilitation ($f_H = 0$), only one internal equilibrium value exists; this equilibrium is biologically relevant ($\bar{C} > 0$) for $\mu_H < K_C \beta_H \delta_H / \alpha_{CA}$ and is locally stable throughout that parameter space.

Integration of model results

In Figs. 2–3, we plot the densities of each species (herbivores, macroalgae, and CCA) at the equilibria where local stability is possible (solid lines to represent conditions under which the equilibria are locally stable and broken lines for locally unstable conditions), depending on parameter values (specifically, on recruitment facilitation in Fig. 2 and on herbivore mortality in Fig. 3). Both the internal equilibrium (greater CCA, lower macroalgae) as well as the macroalgae-dominated or macroalgae–herbivore edge equilibria can simultaneously be locally stable for a subset of parameters (i.e., alternative stable states can exist) when $f_{H3} > f_{H2}$. Whether this condition holds in the general case depends on the relative parameter values (specifically, whether $\beta_H^2 \delta_H^2 K_C K_A + 4\alpha_{CA}^2 \mu_H^2 > 4\alpha_{CA} \mu_H \beta_H \delta_H K_A$). This condition always holds, and alternative stable states for a range of parameters always occur, in the specific case when the macroalgae and the CCA have the same carrying capacity ($K_A = K_C$); this case can apply if the macroalgal and CCA population sizes represent total surface area covered and they are competing for space (Paine 1980, Steneck 1983), which is biologically plausible if the macroalgae represent a broad guild of fleshy algae. Regardless, given $f_{H3} > f_{H2}$, the alternative stable states exist for intermediate recruitment facilitation strength ($f_{H2} < f_H < f_{H3}$; Fig. 2). Note that it is possible for $f_{H3} > 1$, in which case alternative stable states exist for all biologically relevant facilitation values greater than f_{H2} (i.e., $f_{H2} < f_H \leq 1$). However, without facilitation ($f_H = 0$), the internal equilibrium is always

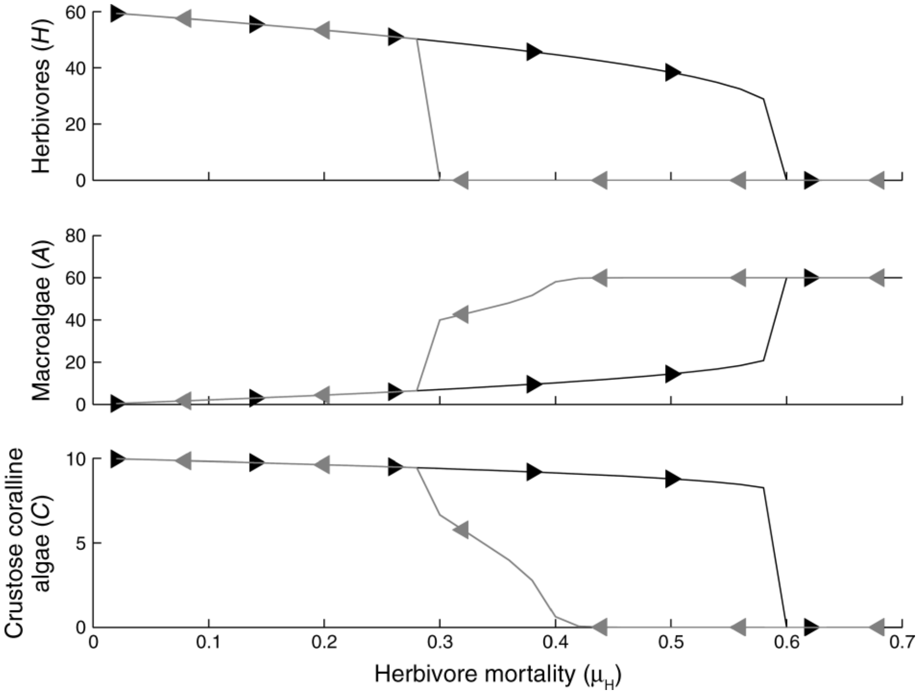

FIG. 4. Change in the system state (CCA, macroalgae, and herbivore densities), given high recruitment facilitation, as herbivore mortality (μ_H) changes. Lines with black right-facing arrows represent the change in state as μ_H increases incrementally, and lines with gray left-facing arrows represent the change in state as μ_H decreases incrementally; the different paths indicate hysteresis. Each time we change the value of μ_H, we start a simulation at the endpoint of the previous run (i.e., with the previous value of μ_H), run the simulation for 50 time steps, and plot the end point. We start the first simulation ($\mu_H = 0.02$) at the expected (only locally stable) equilibrium, and if a simulation ends in zero population densities for any of the three species guilds, we start the next run with very small nonzero densities. Parameter values are: $r_C = 50$, $r_A = 100$, $K_C = K_A = 60$, $\alpha_{CA} = 1.5$, $\alpha_{AC} = 0.5$, $\delta_H = 5$, $\beta_H = 0.01$, and $f_H = 0.85$.

the only locally stable state when it exists (i.e., no alternative stable states exist).

Therefore, without facilitation ($f_H = 0$), only one equilibrium is locally stable for a given herbivore mortality value (μ_H; Fig. 3, left column), where that state changes from the internal equilibrium to the macroalgae–herbivore edge equilibrium to the macroalgae-dominated equilibrium as herbivore mortality increases. For intermediate facilitation ($0 < f_H < 1$), alternative stable states exist for intermediate herbivore mortality values ($\mu_{H2} < \mu_H < \mu_{H3}$; Fig. 3, middle column; note that this requires $\mu_{H3} > \mu_{H2}$, identical to the $f_{H3} > f_{H2}$ condition given above necessary for alternative stable states to occur), with the macroalgae-dominated equilibrium the only locally stable state for high herbivore mortalities ($\mu_H > \mu_{H3}$) and the internal equilibrium the only locally stable state for low herbivore mortalities ($\mu_H < \mu_{H2}$). For obligate facilitation ($f_H = 1$), the herbivore–macroalgae edge equilibrium without CCA does not exist because CCA is required for herbivore recruitment. In this case, alternative stable states of the internal and macroalgae-dominated equilibria exist for all herbivore mortalities below the threshold for the existence of the internal equilibrium ($\mu_H < \mu_{H3}$, Fig. 3, right column); otherwise, the macroalgae-dominated state is the only locally stable state.

The parameter-dependent existence of alternative stable states leads to hysteresis, where the path of how the system state changes in response to incrementally changing a parameter differs depending on whether the parameter is increasing or decreasing. In the context of temperate reefs, hysteresis implies that recovery from urchin barrens to kelp forests follows a different trajectory from that observed during deforestation, from kelp forests to urchin barrens, in a changing environment. Here we illustrate this property by incrementally increasing and then decreasing the herbivore mortality, starting with the species densities from the end of the previous simulation, and running each simulation until equilibrium. For intermediate herbivore mortality, where alternative stable states exist, the predicted equilibrium outcomes follow a different path depending on the direction of change in herbivore mortality (Fig. 4).

DISCUSSION

We demonstrate that the inclusion of facilitation beyond a minimum threshold can lead to alternative stables states (Fig. 2) and thus hysteresis (Fig. 4) in a predator–prey–competitor system. As we illustrate our model with competition between crustose coralline algae (CCA) and macroalgae, grazing of macroalgae by sea urchins, and the potential for facilitation of urchin recruitment to CCA, this potential for hysteresis suggests that alternative macroalgae-dominated and urchin barren states on temperate reefs are feasible and provides a potential mechanistic explanation for them (Paine and Vadas 1969, Estes and Palmisano 1974, Konar and Estes 2003, Shears and Babcock 2003, Behrens and Lafferty 2004). More generally, given the simplicity of our model and the commonness of recruitment facilitation in marine systems (Halpern et al. 2007), our results indicate that recruitment facilitation has the potential to play a key role in structuring marine communities (Petraitis and Latham 1999).

Theoretical context and assumptions

Our model builds on the classic theory of predation-mediated coexistence (i.e., predator/grazer preference for a superior competitor has the potential to allow coexistence of competing species; Vance 1978, Chase et al. 2002) by including a positive effect of the inferior competitor (here, CCA) on predator (grazer) recruitment. The resulting increased predation on the superior competitor (macroalgae) in turn benefits the inferior competitor, leading to an indirect mutualism (sensu Boucher et al. 1982) that benefits both the inferior competitor and predator. Furthermore, this positive interaction is at the root of an emergent Allee effect (sensu de Roos et al. 2003) for the grazers, where a minimum threshold herbivore population density is necessary for them to reach a dominant state. This Allee effect emerges with greater dependence of herbivore recruitment on CCA (greater f_H; Fig. 2) because, under these conditions, a minimum herbivore density is necessary to graze down macroalgae to a level that allows great enough densities of CCA for large-scale herbivore recruitment. This trend parallels the tendency in basic mutualism models for Allee effects and alternative stable states to be particularly likely in the case of obligate mutualisms (May 1982, Dean 1983).

Therefore, existing models of mutualism can provide insight into how the potential for, and resilience (probability of avoiding shifts between alternative states; Holling 1973) of, alternative states depends on the simplifying assumptions made in formulating our model. For example, in a model with self-recruitment facilitation and interspecific competition, the potential for alternative stable states declines with spatially explicit dynamics and landscape structure (Buenau et al. 2007). Similarly, spatial dynamics can increase resilience in a model of two-species mutualism, depending on the spatial structure, dispersal dynamics, and mutualism strength (Hutson et al. 1985). Adding temporal disturbance to a spatial model with recruitment facilitation indicates that facilitation strength can determine the spatial and temporal scales of variation in community structure (Guichard et al. 2004). In addition, immigration has a stabilizing effect on modeled mutualistic communities with the potential for alternative stable states (Thompson et al. 2006). Finally, the functional response of the mutualistic interaction has a significant impact on model outcomes (Holland et al. 2002; note that we use a linear functional response for simplicity). Given these results and the ubiquity of spatial heterogeneity and open demographics in marine communities (Caley et al. 1996), as well as uncertainty about the appropriate functional response for recruitment facilitation, these processes may be particularly important to incorporate in future model extensions.

Recruitment facilitation is one of many possible mechanisms with the potential to cause alternative kelp forest-urchin barren states that could be accounted for in theoretical models. For example, Allee effects in urchin predators could delay future reduction in their sea urchin prey and thus help maintain urchin barrens. Furthermore, top predators with relatively open populations (long larval durations and subsequently dispersal) may decouple local dynamics from any areas without fisheries and therefore lead to slower local predator recovery and longer urchin barren persistence. Another mechanism that may help maintain a CCA-dominated state is CCA sloughing their epithallus, which can inhibit algal settlement and overgrowth (Johnson and Mann 1986). Such bottom-up inhibition may be as important as herbivore top-down control in terms of preventing macroalgal overgrowth (Bulleri et al. 2002). Additional processes that negatively affect post-recruitment herbivore survival or densities in kelp beds (Rowley 1989, 1990), such as physical abrasion by kelp (Konar and Estes 2003), sedimentation (Phillips and Shima 2006, Walker 2007), and predation on settling urchins by micropredators (e.g., small crabs, brittle stars), may prevent urchin invasion of kelp forests. Also, the model does not explicitly account for complexity in herbivore feeding behavior beyond direct grazing, such as aggregation that may affect grazing intensity (Vadas et al. 1986) or feeding on drift algae that may allow long-term persistence of urchin barrens (Duggins 1981, Pearse 1981, Ebeling et al. 1985, Harrold and Reed 1985) and algal–herbivore edges (Konar and Estes 2003). Many of these additional possible drivers of alternative states, such as open population dynamics and physical abrasion at kelp forest edges, may be particularly important to consider in a spatially explicit context.

These additional dynamics may act in concert with recruitment facilitation to provide complementary explanations of the feasibility of, transition dynamics between, and maintenance of alternative temperate reef states. For example, abrasion may explain why urchins do not invade kelp forests at boundaries between forests and barrens (Konar and Estes 2003) while recruitment facilitation may explain why urchins do not invade kelp forests through settlement in interior regions in large enough numbers to lead to dominance. Along with

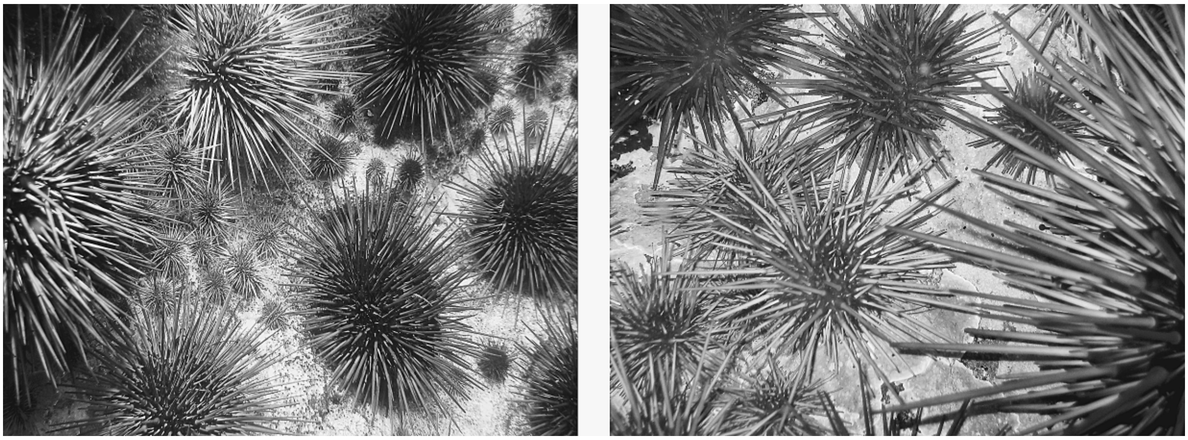

PLATE 1. Haida Gwaii, British Columbia, Canada, at 5 m depth. (Left) By grazing macroalgae on temperate rocky reefs, red sea urchins (*Strongylocentrotus franciscanus*) maintain crustose coralline algae (CCA) habitat. (Right) Coralline algal crusts (seen clearly under the urchin) release a chemical cue that induces larval settlement and metamorphosis of invertebrate grazers. CCA facilitation of grazer recruitment therefore enhances future grazing, subsequent CCA survival, and an urchin-dominated state. Photo credits: A. K. Salomon.

additional stabilizing mechanisms, our model ignores mechanisms that may destabilize a particular state. For example, density-dependent disease dynamics may destabilize urchin barrens: as urchin densities build up due to reduced predator densities, urchin populations become more susceptible to disease epidemics in crowded conditions and suffer greater mortality (Tegner and Dayton 2000, Lafferty 2004). In addition, catastrophic storm events are a key destabilization force as extreme wave energy can dislodge kelp holdfasts and destroy entire kelp forests (Dayton and Tegner 1984, Dayton et al. 1999). The model explored here provides a foundation for extensions that incorporate these additional stabilizing and destabilizing dynamics to compare the relative importance of the different mechanisms, including recruitment facilitation, in generating alternative states.

While at the sacrifice of biological realism, the simplifying assumptions described above allow analytic tractability and therefore much greater generality of results. In comparison, the inclusion of spatially explicit dynamics in Baskett's (2007) kelp forest model, with a lobster–urchin–algae trophic chain, limited the analysis to numerical simulations. In that model, the qualitatively similar equilibrium dynamics found when comparing scenarios with and without lobster-algae recruitment facilitation may have depended on the parameter values chosen. The more generic analysis here helps reveal the relative parameter values necessary for alternative stable states to exist and for recruitment facilitation to drive new dynamics (Figs. 2–3).

Management implications

The potential for nonlinear dynamics, thresholds and alternative states on temperate reefs (Figs. 3–4) have several important management implications. First, incrementally small changes in herbivore (urchin) mortality may cause a community to flip suddenly to another organizational state. Then recovery back to the previous state may require larger changes in herbivore mortality than those changes that originally triggered the switch (Fig. 4). Specifically, if intensive harvesting of herbivore predators (i.e., sea otters, spiny lobster, sheephead wrasse) leads to a decline in herbivore mortality, the system can shift from high macroalgal cover (macroalgae-dominated equilibrium or macroalgae–herbivore edge equilibrium) to low macroalgal/high CCA cover (internal equilibrium) as the only locally stable state. On the other hand, if intensive herbivore harvesting (i.e., sea urchin fishery) leads to an increase in herbivore mortality, the system can shift from low macroalgal/high CCA cover to high macroalgal cover as the only locally stable state. In both cases, if natural herbivore mortality falls within the range where alternative stable states exist (Fig. 3), release of harvesting will not necessarily mean return to the original state, depending on the relative species densities at the point of fisheries reductions or no-take reserve implementation.

Consequently, simply reducing harvest on a target species (via marine reserve establishment or a decrease in total allowable catch) may not immediately lead to the recovery of community structure (as in other multispecies fisheries models with alternative stable states; Baskett et al. 2006, 2007). Rather, active ecosystem restoration such as targeted sea urchin removals or predator additions might need to be considered if more passive management approaches fail, depending on policy trade-offs and the socioeconomically desirable ecosystem state. These community dynamics further suggests that herbivore (i.e., sea urchin) fishery policies need to be carefully tuned in accordance with predator (i.e., spiny lobster, sheephead wrasse) fishery policies given that the latter rely on productive kelp forests for both juvenile and adult habitat while both species likely benefit from kelp as a significant source of organic carbon (Duggins et al. 1989, Salomon et al. 2008). No-take marine reserves may play a critical role in the management of such multispecies fisheries with the potential for alternative states: by protecting community structure within their boundaries (Allison et al. 1998, Murray et al. 1999), reserves may enhance the resilience of populations and communities outside to shifts in organizational states (Steele and Beet 2003, Baskett et al. 2006). Finally, these dynamics suggest that an adaptive ecosystem-based management strategy could benefit from an understanding of the antecedents that precede community state shifts so that managers can anticipate and avoid undesirable state shifts.

Conclusions

In sum, this work underscores the importance of facilitation as a feedback mechanism that can drive community structure and maintain alternative states. Growing evidence from a broad range of ecosystems highlights that similar dynamics, with similar management implications, may be at work in a diversity of ecological communities (Friedel 1991, Suding and Hobbs 2009). On tropical reefs, for instance, indirect mutualism is critical for the maintenance of coral cover given that herbivorous species such as urchins (*Diadema*), parrotfish, and surgeonfish suppress algal competitors that would otherwise inhibit coral recruitment (Edmunds and Carpenter 2001, Hughes et al. 2005). In fact, Mumby et al.'s (2007) model of coral, algal turf, and macroalgal competition that includes coral recruitment to algal turf and algal susceptibility to urchin and parrotfish grazing produces similar hysteretic dynamics to those presented here. In terrestrial systems, the effects of plants on microclimate and soils can facilitate plant recolonization on the microscale, which in turn can drive a region's water cycle and response to climate change (Scheffer et al. 2005). These feedbacks between vegetation and water availability on small spatial scales may cause nonlinearity in the response of vegetation to climatic variation at regional scales and are thought to play a major role in determining the stability of plant cover (van de Koppel et al. 1997).

Complex permutations of positive and negative interactions, operating simultaneously, appear to be widespread in nature and may be responsible for the transition between and maintenance of alternative states. This potential prevalence of hysteresis suggests that short-term reductions in human impacts do not necessarily ensure recovery to a pristine state. Similarly, the lack of recovery to a pristine state following a management regulation does not automatically suggest that something else caused the original state shift. Ultimately, management action will need to consider these dynamics and respond adaptively if it is to promote resilient ecosystems that can withstand or quickly recover from human disturbances (Levin and Lubchenco 2008).

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Literature Cited

Allison, G. W., J. Lubchenco, and M. H. Carr. 1998. Marine reserves are necessary but not sufficient for marine conservation. Ecological Applications 8(Supplement):S79–S92.

Baskett, M. L. 2007. Simple fisheries and marine reserve models of interacting species: an overview and example with recruitment facilitation. California Cooperative Oceanic Fisheries Investigations Reports 48:71–81.

Baskett, M. L., F. Micheli, and S. A. Levin. 2007. Designing marine reserves for interacting species: Insights from theory. Biological Conservation 137:163–179.

Baskett, M. L., M. Yoklavich, and M. S. Love. 2006. Predation, competition and the recovery of overexploited fish stocks in marine reserves. Canadian Journal of Fisheries and Aquatic Sciences 63:1214–1229.

Behrens, M. D., and K. D. Lafferty. 2004. Effects of marine reserves and urchin disease on southern Californian rocky reef communities. Marine Ecology Progress Series 279:129–139.

Bertness, M. D., and R. Callaway. 1994. Positive interactions in communities. Trends in Ecology and Evolution 9:191–193.

Boucher, D. H., S. James, and K. H. Keeler. 1982. The ecology of mutualism. Annual Revue of Ecology and Systematics 13: 315–347.

Bruno, J. F., J. J. Stachowicz, and M. D. Bertness. 2003. Inclusion of facilitation into ecological theory. Trends in Ecology and Evolution 18:119–125.

Buenau, K. E., A. Rassweiler, and R. M. Nisbet. 2007. The effects of landscape structure on space competition and alternative stable states. Ecology 88:3022–3031.

Bulleri, F., I. Bertocci, and F. Micheli. 2002. Interplay of encrusting coralline algae and sea urchins in maintaining alternative habitats. Marine Ecology Progress Series 243: 101–109.

Caley, M. J., M. H. Carr, M. A. Hixon, T. P. Hughes, G. P. Jones, and B. A. Menge. 1996. Recruitment and the local dynamics of open marine populations. Annual Review of Ecology and Systematics 27:477–500.

Carpenter, S. R., J. F. Kitchell, and J. R. Hodgson. 1985. Cascading trophic interactions and lake productivity. BioScience 35:634–639.

Casini, M., J. Hjelm, J. C. Molinero, J. Lovgren, M. Cardinale, V. Bartolino, A. Belgrano, and G. Kornilovs. 2009. Trophic cascades promote threshold-like shifts in pelagic marine ecosystems. Proceedings of the National Academy of Sciences (USA) 106:197–202.

Chase, J. M., P. A. Abrams, J. P. Grover, S. Diehl, P. Chesson, R. D. Holt, S. A. Richards, R. M. Nisbet, and T. J. Case. 2002. The interaction between predation and competition: a review and synthesis. Ecology Letters 5:302–315.

Collie, J. S., K. Richardson, and J. H. Steele. 2004. Regime shifts: can ecological theory illuminate the mechanisms? Progress in Oceanography 60:281–302.

Connell, J. H., and W. P. Sousa. 1983. On the evidence needed to judge ecological stability or persistence. American Naturalist 121:789–824.

Dayton, P. K., and M. J. Tegner. 1984. Catastrophic storms, El Niño, and patch stability in a southern California kelp community. Science 224:283–285.

Dayton, P. K., M. J. Tegner, P. B. Edwards, and K. L. Riser. 1999. Temporal and spatial patterns of kelp demography: the role of oceanographic climate. Ecological Monographs 69: 219–250.

de Roos, A. M., L. Persson, and H. R. Thieme. 2003. Emergent Allee effects in top predators feeding on structured prey populations. Proceedings of the Royal Society B 270:611–618.

Dean, A. M. 1983. A simple-model of mutualism. American Naturalist 121:409–417.

Dudgeon, S., and P. S. Petraitis. 2001. Scale-dependent recruitment and divergence of intertidal communities. Ecology 82:991–1006.

Duggins, D. 1981. Sea urchins and kelp: the effects of short-term changes in urchin diet. Limnology and Oceanography 26:391–394.

Duggins, D. O., C. A. Simenstad, and J. A. Estes. 1989. Magnification of secondary production by kelp detritus in coastal marine ecosystems. Science 245:170–173.

Ebeling, A. W., D. R. Laur, and R. J. Rowley. 1985. Severe storm disturbances and reversal of community structure in a southern-California kelp forest. Marine Biology 84:287–294.

Edmunds, P. J., and R. C. Carpenter. 2001. Recovery of *Diadema antillarum* reduces macroalgal cover and increases abundance of juvenile corals on a Caribbean reef. Proceedings of the National Academy of Sciences (USA) 98:5067–5071.

Edwards, P. B., and T. A. Ebert. 1991. Plastic responses to limited food availability and spine damage in the sea-urchin *Stronglycentrotus purpuratus* (Stimpson). Journal of Experimental Marine Biology and Ecology 145:205–220.

Estes, J. A., and J. Palmisano. 1974. Sea otters: Their role in structuring nearshore communities. Science 185:1058–1060.

Friedel, M. H. 1991. Range condition assessment and the concept of thresholds: a viewpoint. Journal of Range Management 44:422–426.

Guichard, F., S. A. Levin, A. Hastings, and D. Siegel. 2004. Toward a dynamic metacommunity approach to marine reserve theory. BioScience 54:1003–1011.

Halpern, B. S., B. R. Silliman, J. D. Olden, J. P. Bruno, and M. D. Bertness. 2007. Incorporating positive interactions in aquatic restoration and conservation. Frontiers in Ecology and Environment 5:153–160.

Harrold, C., and J. S. Pearse. 1987. The ecological role of echinoderms in kelp forests. Pages 137–233 *in* M. Jangoux and J. M. Lawrence, editors. Echinoderm studies. Volume 2. A. A. Balkema, Rotterdam, The Netherlands.

Harrold, C., and D. C. Reed. 1985. Food availability, sea urchin grazing, and kelp forest community structure. Ecology 66:1160–1169.

Holland, J. N., D. L. DeAngelis, and J. L. Bronstein. 2002. Population dynamics and mutualism: functional responses of benefits and costs. American Naturalist 159:231–244.

Holling, C. S. 1973. Resilience and stability of ecological systems. Annual Review of Ecology and Systematics 4:1–23.

Hughes, T., D. Bellwood, C. Folke, R. Steneck, and J. Wilson. 2005. New paradigms for supporting the resilience of marine ecosystems. Trends in Ecology and Evolution 20:380–386.

Hutson, V., R. Law, and D. Lewis. 1985. Dynamics of ecologically obligate mutualisms: effects of spatial diffusion on resilience of the interacting species. American Naturalist 126:445–448.

Johnson, C. R., and K. H. Mann. 1986. The crustose coralline alga, *Phymatolithon foslie*, inhibits the overgrowth of seaweeds without relying on herbivores. Journal of Experimental Marine Biology and Ecology 96:127–146.

Konar, B., and J. A. Estes. 2003. The stability of boundary regions between kelp beds and deforested areas. Ecology 84: 174–185.

Lafferty, K. D. 2004. Fishing for lobsters indirectly increases epidemics in sea urchins. Ecological Applications 14:1566–1573.

Levin, S. A., and J. Lubchenco. 2008. Resilience, robustness, and marine ecosystem-based management. BioScience 58:27–32.

Lewontin, R. C. 1969. Meaning of stability. Brookhaven Symposia in Biology 22:13.

May, R. M. 1977. Thresholds and breakpoints in ecosystems with a multiplicity of stable states. Nature 269:471–477.

May, R. M. 1982. Mutualistic interactions among species. Nature 296:803–804.

Miner, C. M., J. M. Altstatt, P. T. Raimondi, and T. E. Minchinton. 2006. Recruitment failure and shifts in community structure following mass mortality limit recovery prospects of black abalone. Marine Ecology Progress Series 327:107–117.

Morse, A. N. C., and D. E. Morse. 1984. Recruitment and metamorphosis of *Haliotis larvae* induced by molecules uniquely available at the surfaces of crustose red algae. Journal of Experimental Marine Biology and Ecology 75: 191–215.

Morse, D. E., N. Hooker, H. Duncan, and L. Jensen. 1979. Gamma-aminobutyric acid, a neurotransmitter, induces planktonic abalone larvae to settle and begin metamorphosis. Science 204:407–410.

Mumby, P. J., A. Hastings, and H. J. Edwards. 2007. Thresholds and the resilience of Caribbean coral reefs. Nature 450:98–101.

Murray, S. N., et al. 1999. No-take reserve networks: Sustaining fishery populations and marine ecosystems. Fisheries 24:11–25.

Noy-Meir, I. 1975. Stability of grazing systems: application of predator–prey graphs. Journal of Ecology 63:459–481.

Paine, R. T. 1977. Controlled manipulations in the marine intertidal zone and their contributions to ecological theory. Pages 245–270 *in* C. E. Goulden, editor. The changing scenes in the natural sciences, 1776–1976. Volume 12 of Academy of Natural Sciences Philadelphia Special Publication. Academy of Natural Sciences, Philadelphia, Pennsylvania, USA.

Paine, R. T. 1980. Food webs: linkage, interaction strength and community infrastructure. Journal of Animal Ecology 49: 667–685.

Paine, R., and R. Vadas. 1969. The effects of grazing by sea urchins *Strongylocentrotus* spp., on benthic algal populations. Limnology and Oceanography 14:710–719.

Pearce, C. M., and R. E. Scheibling. 1990. Induction of metamorphosis of larvae of the green sea-urchin, *Strongylocentrotus droebachiensis*, by coralline red algae. Biology Bulletin 179:304–311.

Pearse, J. S. 1981. Synchronization of gametogenesis in the sea urchins *Strongylocentrotus purpuratus* and *S. franciscanus*. Pages 53–68 *in* J. W. H. Clark and T. S. Adams, editors. Advances in invertebrate reproduction. Elsevier North Holland, Amsterdam, The Netherlands.

Petraitis, P. S., and S. R. Dudgeon. 2004. Detection of alternative stable states in marine communities. Journal of Experimental Marine Biology and Ecology 300:343–371.

Petraitis, P. S., and R. E. Latham. 1999. The importance of scale in testing the origins of alternative community states. Ecology 80:429–442.

Phillips, N. E., and J. S. Shima. 2006. Differential effects of suspended sediments on larval survival and settlement of New Zealand urchins *Evechinus chloroticus* and abalone *Haliotis iris*. Marine Ecology Progress Series 314:149–158.

Rowley, R. J. 1989. Settlement and recruitment of sea-urchins (*Strongylocentrotus* spp.) in a sea-urchin barren ground and a kelp bed: are populations regulated by settlement or post-settlement processes. Marine Biology 100:485–494.

Rowley, R. J. 1990. Newly settled sea-urchins in a kelp bed and urchin barren ground: a comparison of growth and mortality. Marine Ecology Progress Series 62:229–240.

Salomon, A., N. Shears, T. Langlois, and R. Babcock. 2008. Cascading effects of fishing can alter carbon flow through a temperate coastal ecosystem. Ecological Applications 18: 1874–1887.

Scheffer, M., S. Carpenter, J. A. Foley, C. Folke, and B. Walker. 2001. Catastrophic shifts in ecosystems. Nature 413: 591–596.

Scheffer, M., M. Holmgren, V. Brovkin, and M. Claussen. 2005. Synergy between small- and large-scale feedbacks of vegetation on the water cycle. Global Change Biology 11: 1003–1012.

Shears, N. T., and R. C. Babcock. 2003. Continuing trophic cascade effects after 25 years of no-take marine reserve protection. Marine Ecology Progress Series 246:1–16.

Steele, J. H., and A. R. Beet. 2003. Marine protected areas in "nonlinear" ecosystems. Proceedings of the Royal Society B 270:S230–S233.

Steneck, R. S. 1982. A limpet-coralline alga association: adaptations and defenses between a selective herbivore and its prey. Ecology 63:507–522.

Steneck, R. S. 1983. Escalating herbivory and resulting adaptive trends in calcareous algal crusts. Paleobiology 9:44–61.

Steneck, R. S. 1986. The ecology of coralline algal crusts: convergent patterns and adaptative strategies. Annual Review of Ecology and Systematics 17:273–303.

Strathmann, M. 1987. Reproduction and development of marine invertebrates on the Northern Pacific coast: data and methods for the study of eggs, embryos, and larvae. University of Washington Press, Seattle, Washington, USA.

Suding, K. N., and R. J. Hobbs. 2009. Threshold models in restoration and conservation: a developing framework. Trends in Ecology and Evolution 24:271–279.

Sutherland, J. 1974. Multiple stable points in natural communities. American Naturalist 108:859–873.

Tegner, M. J., and P. K. Dayton. 2000. Ecosystem effects of fishing in kelp forest communities. ICES Journal of Marine Science 57:579–589.

Thompson, A. R., R. M. Nisbet, and R. J. Schmitt. 2006. Dynamics of mutualist populations that are demographically open. Journal of Animal Ecology 75:1239–1251.

Thrush, S. F., J. E. Hewitt, P. K. Dayton, G. Coco, A. M. Lohrer, A. Norkko, J. Norkko, and M. Chiantore. 2009. Forecasting the limits of resilience: integrating empirical research with theory. Proceedings of the Royal Society B 276: 3209–3217.

Underwood, A. J., and P. Jernakoff. 1981. Effects of interactions between algae and grazing gastropods on the structure of a low-shore inter-tidal algal community. Oecologia 48:221–233.

Vadas, R. L., R. W. Elner, P. E. Garwood, and I. G. Babb. 1986. Experimental evaluation of aggregation behavior in the sea urchin *Strongylocentrotus droebachiensis*. Marine Biology 90:433–448.

Vance, R. R. 1978. Predation and resource partitioning in one predator–2 prey model communities. American Naturalist 112:797–813.

van de Koppel, J., M. Rietkerk, and F. J. Weissing. 1997. Catastrophic vegetation shifts and soil degradation in terrestrial grazing systems. Trends in Ecology and Evolution 12:352–356.

Walker, J. W. 2007. Effects of fine sediments on settlement and survival of the sea urchin *Evechinus chloroticus* in northeastern New Zealand. Marine Ecology Progress Series 331:109–118.

Witman, J. D., and P. K. Dayton. 2001. Rocky subtidal communities. Pages 339–366 *in* M. D. Bertness, S. D. Gaines, and M. E. Hay, editors. Marine community ecology. Sinauer Associates, Sunderland, Massachusetts, USA.