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Interactive effects of predator and prey harvest on ecological resilience of rocky reefs

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Abstract. A major goal of ecosystem-based fisheries management is to prevent fishery-induced shifts in community states. This requires an understanding of ecological resilience: the ability of an ecosystem to return to the same state following a perturbation, which can strongly depend on species interactions across trophic levels. We use a structured model of a temperate rocky reef to explore how multi-trophic level fisheries impact ecological resilience. Increasing fishing mortality of prey (urchins) has a minor effect on equilibrium biomass of kelp, urchins, and spiny lobster predators, but increases resilience by reducing the range of predator harvest rates at which alternative stable states are possible. Size-structured predation on urchins acts as the feedback maintaining each state. Our results demonstrate that the resilience of ecosystems strongly depends on the interactive effects of predator and prey harvest in multi-trophic level fisheries, which are common in marine ecosystems but are unaccounted for by traditional management.

Key words: alternative stable states; ecological resilience; ecosystem-based fisheries management; global sensitivity analysis; Macrocystis pyrifera; Mesocentrotus franciscanus; *multi-trophic level harvest;* Panulirus interruptus; Strongylocentrotus purpuratus.

Introduction

Ecosystem-based fisheries management (EBFM) is an inherently multi-species approach, which recognizes the fact that targeted species are components of complex, diverse, ecological communities in which the harvest of one species can affect other interacting species (Larkin 1996, Pikitch et al. 2004). For example, reductions in predator production due to prey harvest may reduce the total fisheries yield beyond that expected under single-species management (May et al. 1979, Collie and DeLong 1999, Walters et al. 2005). Consideration of species interactions and altered ecosystem function are key differences between EBFM and the traditional fishery management focus on single-species population dynamics. Despite some encouraging advances in EBFM (McClanahan et al. 2011), numerous challenges remain regarding its implementation and operation due to the inherent complexity of accounting for multiple species and ecological processes within a dynamic environment. Impacts to ecosystems such as fishery harvest are important drivers of ecosystem change in marine and estuarine environments (Halpern et al. 2008, Smith et al. 2011, Altieri et al. 2012), but the impacts of simultaneous harvest at multiple trophic levels within the same system remain poorly understood (Essington et al. 2006, Kellner et al. 2010, Garcia et al. 2012).

One goal of EBFM is that of ecologically sustainable yield, which aims to maximize multi-species fishery harvest while avoiding ecosystem shifts from productive to less productive states (Zabel et al. 2003). The ability of a state to persist following a perturbation is ecological resilience (Levin and Lubchenco 2008), drawing from the original definition of Holling (1973). This concept assumes alternative stable states, wherein an ecosystem can be found with multiple, distinct species assemblages under identical environmental conditions (Lewontin 1969, Holling 1973). The forward and reverse shifts between alternative stable states exhibit hysteresis, in that they occur at different levels of forcing (Scheffer et al. 2001, Scheffer and Carpenter 2003), which can make a return to the alternative state difficult once a shift has occurred. While the existence of alternative stable states can be difficult to demonstrate empirically because of the long time scales required (Petraitis and Dudgeon 2004, Schröder et al. 2005), mathematical models can reveal the potential for hysteretic behavior, provide evidence of mechanistic drivers of community shifts, and estimate threshold values of important ecosystem state variables and/or parameters (Scheffer and Carpenter 2003, Mumby et al. 2007, Baskett and Salomon 2010, Bozec et al. 2016). Systems that exhibit alternative stable states often have strong feedbacks both within and across trophic levels that act to maintain a given state, including recruitment facilitation (Mumby et al. 2007, Baskett and Salomon 2010) and predator–prey role reversals (Barkai and McQuaid 1988, Walters and Kitchell 2001). Previous modeling efforts demonstrate that multi-trophic level harvest and concomitant alterations in trophic interactions have the potential to affect community composition (Kellner et al. 2010) and

drive the provision of ecosystem services such as fishery yield (McClanahan 1995, Houle et al. 2013). The effects of multi-trophic level harvest on ecological resilience remain unexplored, despite the importance of trophic-related feedbacks to alternative stable states.

Temperate, subtidal rocky reefs are a common near-shore habitat in marine ecosystems in which strong trophic interactions occur among macroalgae, herbivorous sea urchins, and urchin predators (e.g., fishes, crustaceans, and mammals; Steneck et al. 2002, Ling et al. 2015). Many rocky reefs exhibit multiple community states in which they are either covered by dense understory and canopy forming macroalgae, or are denuded of algae by extremely high densities of sea urchins (Filbee-Dexter and Scheibling 2014, Ling et al. 2015). The kelp forest state supports a highly diverse community of fishes, benthic invertebrates, epifauna, and marine mammals (Foster and Schiel 1985, Graham et al. 2008) as well as numerous important fisheries (Bertocci et al. 2015). Conversely, the urchin barren state is dominated by sea urchins and crustose coralline algae, has low macroalgal biomass, and is characterized by reduced species diversity and ecosystem productivity (Graham 2004). Whether these communities are true alternative stable states or phase shifts under different environmental conditions remains unresolved empirically.

Sea urchins and many of their predators support major fisheries in nearshore regions worldwide (Tegner and Dayton 2000, Andrew et al. 2002, Steneck et al. 2002), but the effects of simultaneously harvesting these species on rocky reef communities, and on ecological resilience, may be difficult to predict. Fishery removal of herbivores may increase resilience and promote diversity via reduced grazing pressure on the basal resource, favoring the kelp forest state. Alternatively, herbivore harvest could reduce resilience via the removal of biomass available to predators, which may lower predator abundance and allow remaining herbivores to increase per capita grazing pressure on kelp through, for example, changes in prey size structure (Stevenson et al. 2016) or reductions in non-consumptive fear effects (Babcock et al. 2010). These contrasting potential outcomes illustrate the complexity of multi-trophic level harvest when accounting for species interactions. Here, we use a dynamical model of a rocky reef community in southern California to resolve the contrasting potential outcomes of simultaneous fishery harvest of a predator and an herbivore. Because alternative stable states are inherent to the question of how harvest affects ecological resilience, our model includes multiple ecological processes that could contribute to the presence of alternative stable states, including recruitment facilitation, size-structured predation, and size-selective fishery harvest. We aim to determine (1) how harvest of species at each trophic level affects the biomass of other community members, (2) whether alternative stable states can occur under different levels of fishery harvest for each trophic level, and (3) how harvest at different trophic levels affects ecological resilience.

Methods

Model system

Rocky reefs in southern California are a useful model system to examine the complexities of multi-trophic level harvest because this system is well studied, macroalgal habitats provide multiple ecosystem services, and because fishers harvest multiple ecologically important, strongly interacting predator and prey species. In the kelp forest state, foundational giant kelp (*Macrocystis pyrifera*) and several species of understory macroalgae are consumed by red (*Mesocentrotus franciscanus*) and purple (*Strongylocentrotus purpuratus*) sea urchins. Large red urchins also provide important recruitment habitat for juvenile red and purple urchins underneath their spine canopy (Tegner and Dayton 1977). Sea urchins are consumed by a variety of predators, but California sheephead (*Semicossyphus pulcher*) and California spiny lobsters (*Panulirus interruptus*) became dominant predators of urchins following the eradication of sea otters from mainland southern California in the late 19th Century (Cowen 1983, Tegner and Levin 1983, Hamilton and Caselle 2015, Selden et al. 2017). Both of these predators are the focus of fisheries in this region, as are herbivorous red sea urchins (Tegner and Dayton 2000). Purple urchins do not provide the same recruitment refuge as large red urchins and are not harvested in the urchin fishery. In the urchin barren state, rocky reefs become covered in high densities of (mostly purple) sea urchins that consume all available macroalgae and prevent recruitment of juvenile kelps (Steneck et al. 2002). Urchin barrens have lower productivity and diversity than the kelp forest state (Graham 2004), and once established can persist for long periods due to a variety of possible feedback mechanisms (Ling et al. 2015) including recruitment facilitation (Baskett and Salomon 2010).

Model overview

We construct the simplest model that effectively captures the dynamics relevant to the effect of multi-trophic level harvest on ecological resilience (Fig. 1). We vary fishery harvest of lobsters and urchins, as well as the degree of recruitment facilitation provided by large red urchins, to determine the interactive effects of these factors on the dynamics of spiny lobsters, sea urchins, and algae, and on ecological resilience. We include size structure for urchins because predation, recruitment facilitation, and harvest (and therefore their interactive effects on community state) all depend on urchin size. Our model focuses on one size class of a single predator species, California spiny lobster, to avoid multiple predator compartments and because empirical data on this size of lobsters are available to parameterize the model. We also provide a first approximation of system dynamics using California sheephead as the sole predator (Appendix S1).
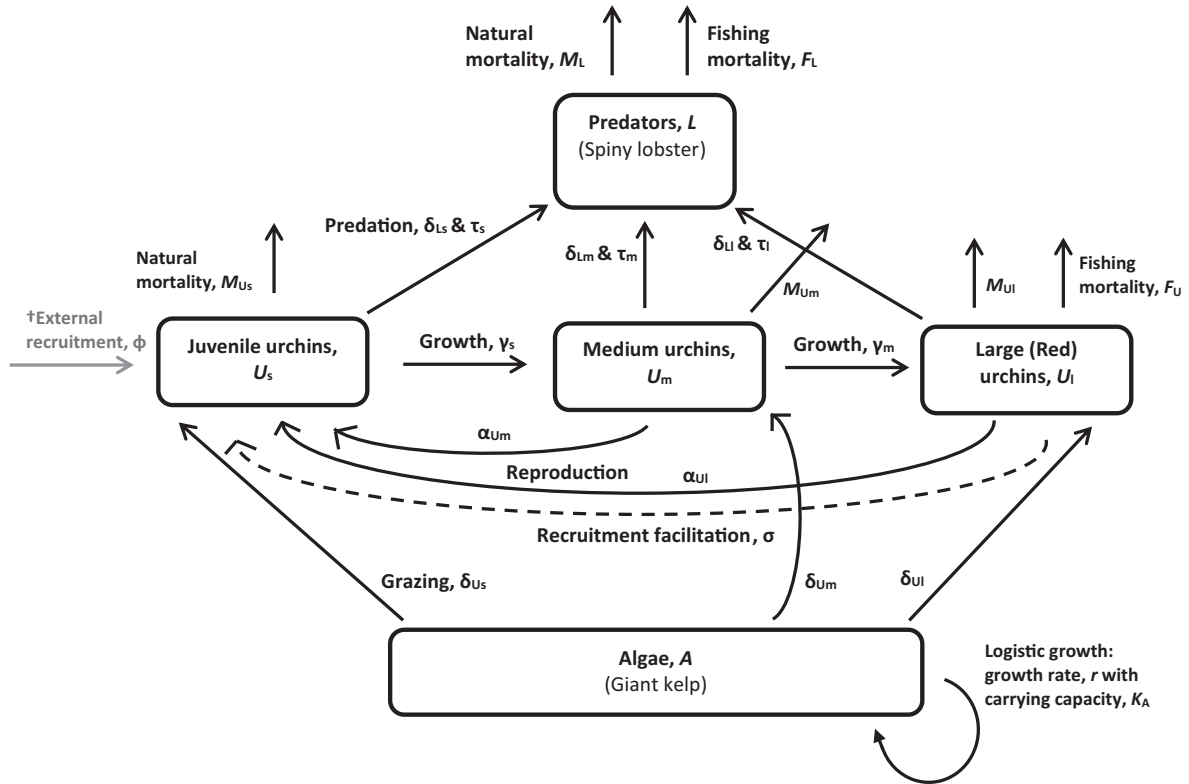
Fig. 1. Outline of the rocky reef community dynamics model. Boxes indicate state variables, arrows indicate dynamics and are labeled with the associated parameters. Urchins graze on algae with a type I (linear) functional response while predators consume urchins with a type II (saturating) response, both informed by empirical feeding assays. Urchin fishing only removes large urchins, and recruitment facilitation is only provided by large urchins. Reproduction, but not urchin growth, is dependent on biomass of algae. See Appendix S1: Table S1 for baseline parameter values and full range of values explored. †External recruitment, φ, is not included in our baseline model; see Appendix S1 for a description of the model with this dynamic.

Model details

The model follows the biomass of predatory spiny lobsters L, three size classes of herbivorous sea urchins U_i (where $i \in \{s,m,l\}$ for small, medium, and large urchins, respectively), and macroalgae A (also referred to as kelp). Algae grows logistically with growth rate r and has carrying capacity K_A, and is consumed by urchins at an urchin size class-specific linear rate, δ_{U_i} (type I functional response). Urchin grazing is modeled as a type I functional response because urchin feeding assays did not reveal a particular functional response shape (R. P. Dunn, *unpublished manuscript*), to maintain mathematical simplicity, and to match previous models of urchin grazing (Baskett and Salomon 2010). Medium U_m and large U_l urchins convert algae into reproduction with efficiencies α_{U_m} and α_{U_l}, which depend on the abundance of algae. For simplicity, we do not include exogenous recruitment of urchins in our baseline model, though we explore this assumption with an alternate model formulation that includes constant background recruitment of urchins (Appendix S1). To model recruitment facilitation of juvenile urchins U_s by large red urchins, we define σ as the proportional strength of recruitment

facilitation, ranging from 0 to 1, where 0 indicates no recruitment facilitation (i.e., recruitment is independent of large urchin biomass) and 1 indicates complete dependence on adult urchin spine canopy for successful recruitment. Specifically, when $\sigma = 0$, there is no relationship between large urchin abundance and small urchin recruitment beyond conversion of grazing into urchin recruits, and small urchins can recruit regardless of the presence of a large urchin spine canopy. When $\sigma = 1$, realized recruitment is completely dependent on the presence of large urchins to protect recruits. For $0 < \sigma < 1$, some level of baseline recruitment occurs $(1 - \sigma)$ in proportion to total recruit production by medium and large urchins, with additional recruitment occurring with increasing urchin abundance relative to its maximum biomass K_{U_l} (Baskett and Salomon 2010). Urchins grow from each size class i to the next size class at rate γ_i, and natural mortality of urchins occurs at rate M_{U_i}. To maintain the simplest model possible while still addressing our objectives, urchin reproduction is food dependent while urchin growth is not food dependent. Urchin gonad indices from barren grounds are generally significantly lower than those from kelp-dominated areas (Konar and Estes 2003, Eurich et al. 2014) and

while we acknowledge that urchin growth is also affected by food availability, we assume that the magnitude of any effect of food dependence will be equally or more important for reproduction than for growth. Predators consume urchins at rate δ_{L_i}, which declines monotonically with urchin size, and predation saturates due to handling time τ_i (type II functional response chosen based on laboratory feeding assays; R. P. Dunn, *unpublished manuscript*). Predatory spiny lobsters convert urchin prey into population growth with conversion efficiency β and experience natural mortality at a rate M_L. Spiny lobsters and large urchins are harvested at rates F_L and F_U, respectively. Given these terms, the model dynamics are

$$\frac{dA}{dt} = \left[r\left(1 - \frac{A}{K_A}\right) - \left(\sum_i \delta_{U_i} U_i\right) \right] A$$

$$\frac{dU_s}{dt} = A(\alpha_{U_m}\delta_{U_m} U_m + \alpha_{U_l}\delta_{U_l} U_l)\left(1 - \sigma + \sigma\frac{U_l}{K_{U_l}}\right)$$
$$- \left[\gamma_s + L\left(\frac{\delta_{L_s}}{1 + \sum_i \tau_i \delta_{L_i} U_i}\right) + M_{U_s}\right] U_s$$

$$\frac{dU_m}{dt} = \gamma_s U_s - \left[\gamma_m + L\left(\frac{\delta_{L_m}}{1 + \sum_i \tau_i \delta_{L_i} U_i}\right) + M_{U_m}\right] U_m$$

$$\frac{dU_l}{dt} = \gamma_m U_m - \left[L\left(\frac{\delta_{L_l}}{1 + \sum_i \tau_i \delta_{L_i} U_i}\right) + M_{U_l} + F_U\right] U_l$$

$$\frac{dL}{dt} = \left[\left(\frac{\beta \sum_i \delta_{L_i} U_i}{1 + \sum_i \tau_i \delta_{L_i} U_i} - (M_L + F_L)\right)\right] L$$

We do not include exogenous recruitment of spiny lobsters because recruitment of this species to the Southern California Bight is highly variable (Pringle 1986) and few empirical data exist to permit parameterization. In addition, we do not include size structure for lobsters in order to maintain mathematical tractability as a moderate-complexity strategic model (Collie et al. 2016; see Appendix S1 for more discussion of the model structure).

Model analysis

To parameterize the model for numerical simulation, we use a combination of published parameter values from peer-reviewed literature and stock assessments, empirically derived estimates, and assumptions for biological realism (Appendix S1, Appendix S1: Table S1). Baseline parameter values had empirical support, or for parameters with less empirical evidence available, we estimated baseline values such that we obtained biologically reasonable equilibrium biomass values during model exploration. We run numerical simulations using the differential equation solver package deSolve (Soetaert et al.

2010) in R v.3.1.2 (R Development Core Team 2014). All simulations run for 200 time steps, which is sufficient to achieve equilibrium abundances (Appendix S1: Fig. S1).

We test for the existence of alternative stable states with hysteresis using path-dependency analysis in which we incrementally increase and then decrease values of F_U, F_L, and σ, recording the equilibrium biomass at the end of each simulation, which determines the initial conditions for the next simulation (see Appendix S1: Table S1 for baseline parameter values and ranges explored). For rocky reef communities, hysteresis indicates that moving from a kelp forest to an urchin barren follows a different trajectory than the path of recovery from an urchin barren to kelp forest (Baskett and Salomon 2010, Ling et al. 2015). To ensure that we capture all possible outcomes, we conduct two path analyses for each focal parameter using different initial conditions for the first run on the forward path: one starting in the kelp forest state and one in the urchin barren state (kelp-dominated state, kelp biomass = 1,000 kg, all urchin size classes biomass = 70 kg, and spiny lobster biomass = 20 kg; urchin-dominated state, kelp biomass = 1 kg, all urchin size classes biomass = 100 kg, and spiny lobster biomass = 5 kg). Initial conditions in subsequent model runs are values adjusted by <2% away from the equilibrium biomass from the previous simulation to avoid starting exactly at a potentially unstable equilibrium. For the first run on the reverse path, initial conditions are values adjusted away from the equilibrium biomasses of the final forward simulation. To test for an interactive effect of harvest at different trophic levels, we analyze path dependence for one harvest rate at three values of the other harvest rate. We also explore the effect of changing recruitment facilitation strength because of its potential importance to alternative stable states. We confirmed that this analysis of hysteresis captures all locally stable equilibria by numerically solving for all equilibria and determining their stability using Mathematica version 9.0 (Wolfram Research, Champaign, Illinois, USA). Finally, in addition to quantifying changes in resilience (as indicated by the range of path-dependent bistable regions), we examine changes in equilibrium biomass when starting from a kelp-dominated state due to the interactive effects of varying lobster harvest, urchin harvest, and recruitment facilitation strength.

To determine which ecological processes (individual parameters and interactions among parameters) have the greatest effect on equilibrium biomass, we conduct a global sensitivity analysis (GSA) following the method of Harper et al. (2011) (full methodology in Appendix S1). We use a random forest analysis to calculate the importance of individual parameters to model output when all parameters are perturbed simultaneously. Briefly, we create 4,000 different combinations of parameter values, which are drawn at random from a range of potential values for each parameter. We use these 4,000 parameter sets to simulate the model beginning at each of two initial conditions: one beginning in the kelp forest state and one

in the urchin barren state. Random forest uses multiple classification and regression trees (CART) to quantify how informative each parameter is in predicting model output; based on these trees, an importance value is assigned to each parameter. In our case, importance values are a measure of how informative each parameter is in predicting mean trophic level (mTL) at equilibrium, excluding kelp. Mean trophic level is a common ecosystem indicator used to estimate the effects of fishery harvest on energy flow within an ecosystem (see Appendix S1 for calculation of mTL). We normalize importance values to sum to 1 because relative, not absolute, importance values are informative. Parameters with large importance values have strong impacts on community structure at equilibrium, given the model's assumptions, but do not necessarily reflect a parameter's ability to drive alternative stable states. We also use classification and regression trees to reveal break points in specific parameter values at which community structure diverges. For parameters with the highest importance values,

whether or not the parameter is above or below these break points will generally determine equilibrium community structure, regardless of the values of less important parameters.

RESULTS

Equilibrium biomass with multi-trophic level harvest

Increasing lobster fishing mortality (F_L) increases urchin biomass and drives a decline in kelp and lobster biomass (Figs. 2, 3, Appendix S1: Fig. S2). In comparison, changes in urchin fishing mortality (F_U) have little impact on equilibrium biomasses unless F_L is high (Fig. 4, Appendix S1: Fig. S2). When we simultaneously vary lobster harvest and recruitment facilitation (σ), most compartments demonstrate similar patterns as described above for simulations varying F_L and F_U (Appendix S1: Fig. S2). Namely, increases in F_L drive declines in kelp and lobster biomass and increases in urchin biomass
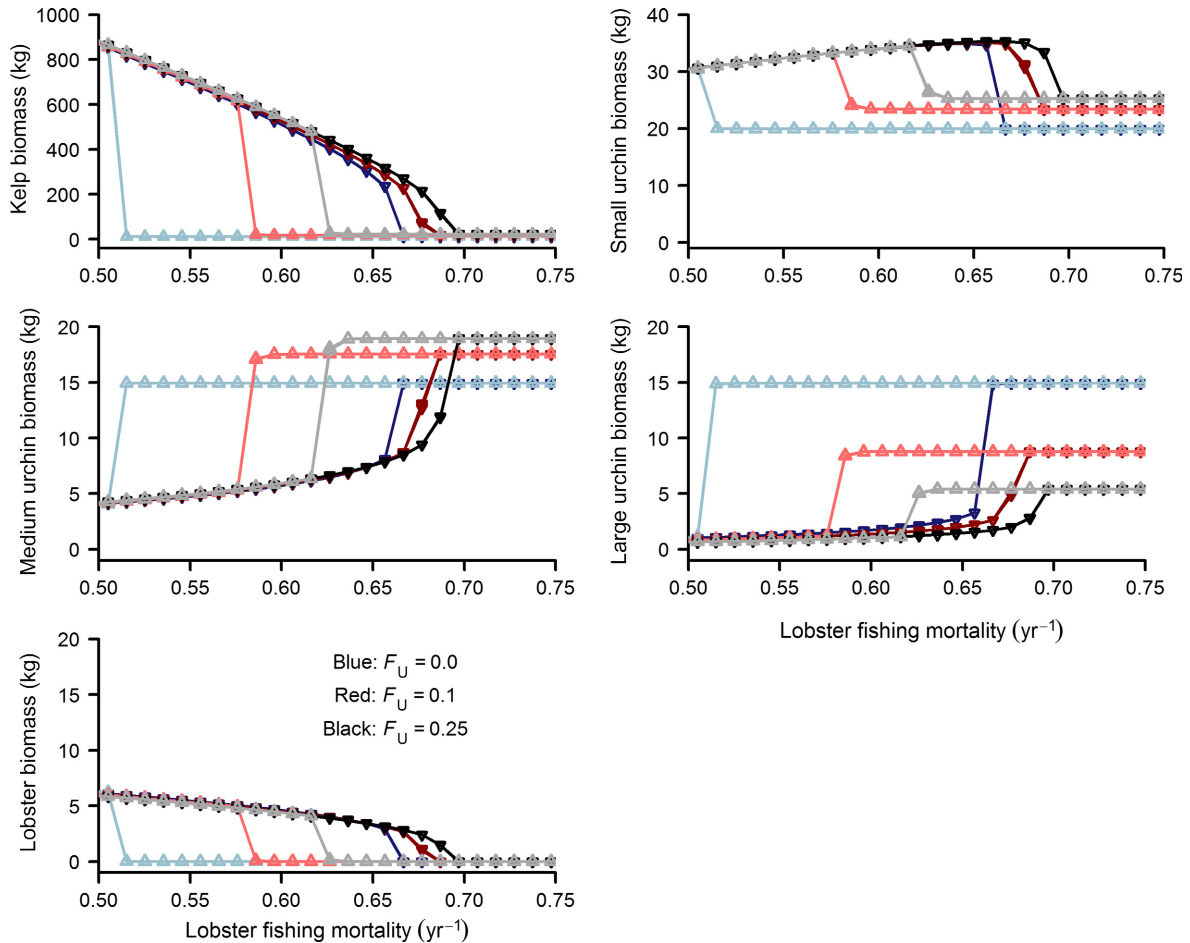

FIG. 2. Path-dependency analysis for lobster fishing mortality at three values of urchin fishing mortality. All panels show biomass (kg), and we have zoomed in on the region in which bistability occurs. Within each color (i.e., for a given level of F_U), the upside-down triangles and darker shaded line represent the forward path as F_L is increased, and the vertical triangles and lighter shaded line show the reverse path as F_L is decreased. Equilibria are represented by triangles, and lines connecting the equilibria as we increase and then decrease F_L indicate hysteresis. [Color figure can be viewed at wileyonlinelibrary.com]
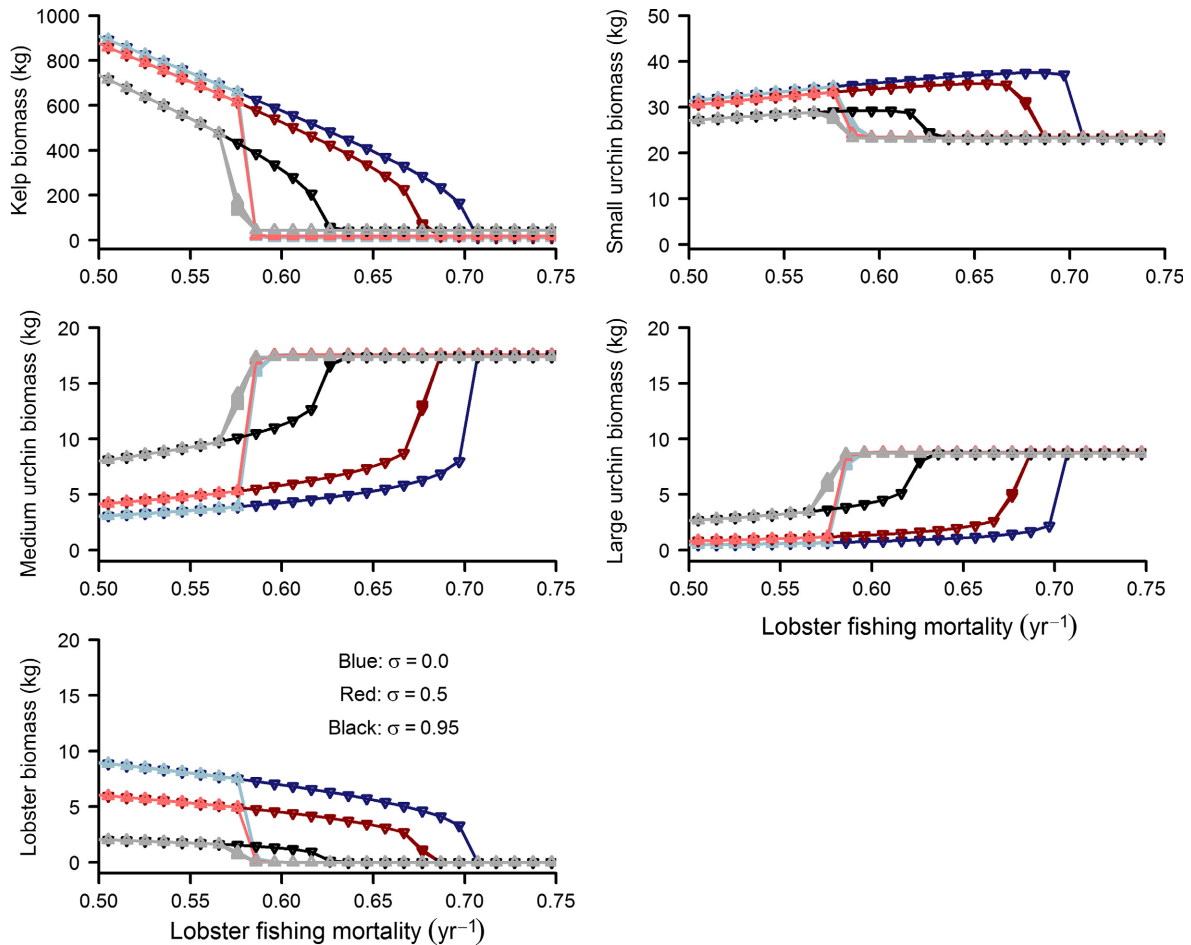
FIG. 3.   Path-dependency analysis for lobster fishing mortality at three values of recruitment facilitation. All panels show biomass (kg), and we have zoomed in on the region in which bistability occurs. Within each color (i.e., for a given level of σ), the upside-down triangles and darker shaded line represent the forward path as F_L is increased, and the vertical triangles and lighter shaded line show the reverse path as F_L is decreased. Equilibria are represented by triangles, and lines connecting the equilibria as we increase and then decrease F_L indicate hysteresis. [Color figure can be viewed at wileyonlinelibrary.com]

across all six levels of σ that we simulate. The similarities between varying the rate of urchin fishing mortality and varying the strength of recruitment facilitation occur because changes to equilibrium biomass arising from changes to F_U or σ are both expressed in the dynamics of the largest and smallest urchin size classes. In particular, when urchin fishing mortality is high, large urchins do not contribute to production of juvenile urchins directly via reproduction, and if recruitment facilitation strength is high, large urchins are necessary for adequate recruitment to maintain urchin populations.

Alternative stable states and ecological resilience

Whether or not alternative stable states occur depends strongly on lobster harvest, while urchin harvest mortality and recruitment facilitation strength affect the range of lobster harvest in which alternative stable states occur (Figs. 2, 3). Specifically, alternative stable states are present at high values of lobster fishing mortality. The kelp forest state is the only stable state at low lobster harvest values, and the urchin barren state is the only stable state at the highest lobster harvest values (Figs. 2, 3). At higher values of urchin fishing mortality, the return path as we ramp down F_L moves to the right, such that the threshold to return to the kelp forest state moves closer to the threshold leading into the urchin barren as fishing ramps up. Increasing the return threshold acts to shrink the range of parameter space with alternative stable states and reduces the strength of hysteresis (Fig. 2). Thus, increasing the level of urchin harvest increases ecological resilience by reducing the parameter space in which an external perturbation could shift the system from one alternative stable state to another. Increasing F_U also shifts the forward threshold leading to the urchin barren to the right, making alternative stable states less likely without high lobster harvest mortality (Fig. 2). Increasing recruitment facilitation strength acts in a
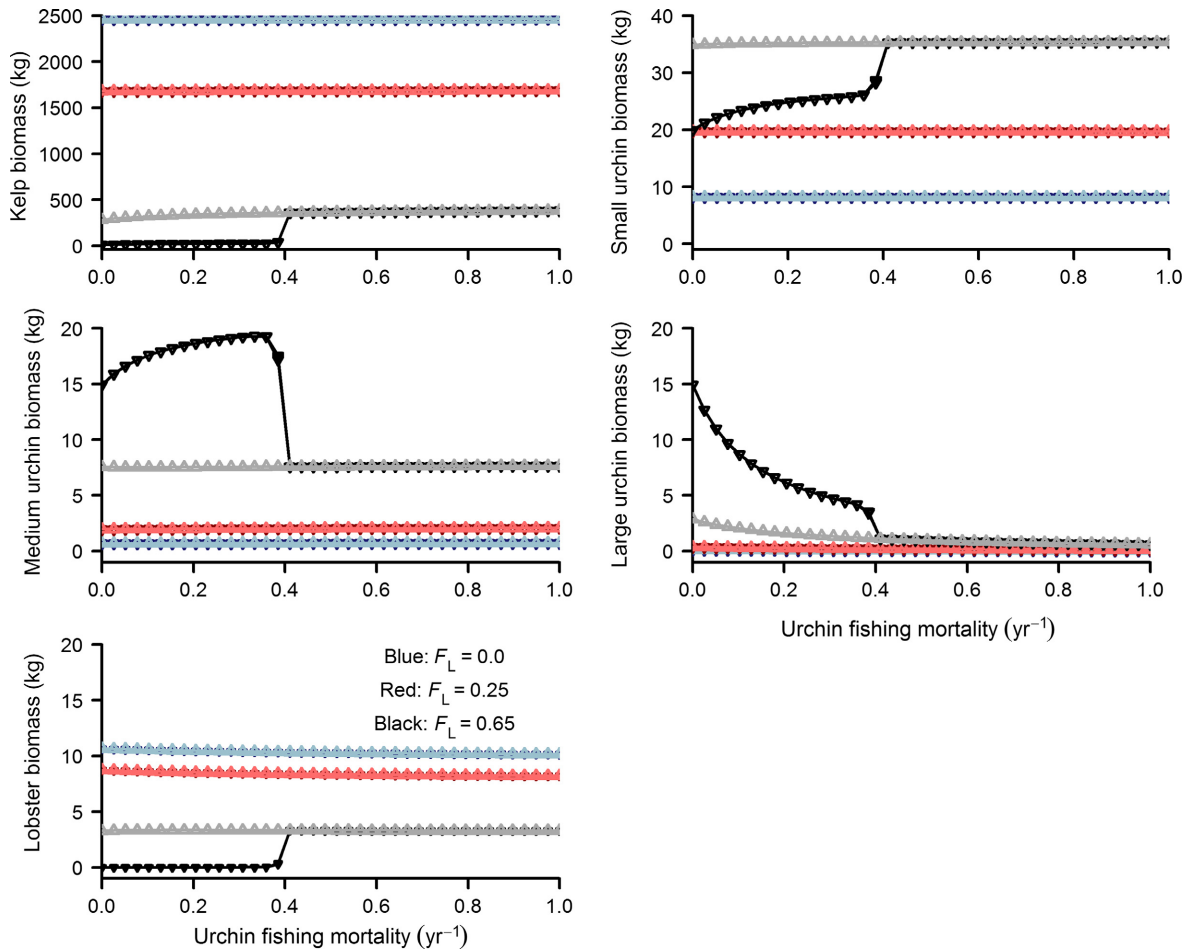
FIG. 4.   Path-dependency analysis for urchin fishing mortality at three values of lobster fishing mortality. Within each color (i.e., for a given level of F_L), the upside-down triangles and darker shaded line represent the forward path as F_U is increased, and the vertical triangles and lighter shaded line show the reverse path as F_U is decreased. Equilibria are represented by triangles, and lines connecting the equilibria as we increase and then decrease F_U indicate hysteresis. [Color figure can be viewed at wileyonlinelibrary.com]

similar fashion to urchin fishing mortality, shrinking the parameter space with alternative stable states as σ increases (Fig. 3). Interestingly, alternative stable states can exist without any recruitment facilitation if lobsters are overfished (σ = 0, F_L > 0.55; Fig. 3), despite recruitment facilitation being a feedback that allows for the existence of alternative stable states (Baskett and Salomon 2010). Alternative stable states only exist at low levels of urchin harvest (F_U < 0.4), and only when lobsters are heavily overfished (i.e., F_L = 0.65; Fig. 4).

The same relationships are evident when examining the entire parameter space for both fishing mortality rates. The region of lobster harvest rates with bistability shrinks with increased urchin harvest and for higher values of recruitment facilitation strength (Fig. 5, center column). To compare the region of bistability in our model to harvest rates that lobsters may actually experience, we use the lobster harvest rate at maximum sustainable yield (F_{MSY}) from the California spiny lobster

stock assessment (≈0.25/yr), estimated using a different modeling framework (Neilson 2011). In our baseline model, alternative stable states only occur when predators are fished at a rate above this estimate of F_{MSY}, regardless of the urchin harvest rate (Fig. 5, center column). Note that F_{MSY} for spiny lobsters in our model is = 0.5/yr (Appendix S1, Appendix S1: Fig. S3) approximately double that of Neilson (2011). The discrepancy in these estimates likely arises from differences in model structure (dependence on kelp and urchin production in our model, size structure and explicit growth function for lobsters in the stock assessment). Our estimate of F_{MSY} is just below the critical transition into the urchin barren when urchins are not harvested (Figs. 2, 5), demonstrating the potential benefits of a well-managed urchin fishery to ecological resilience. This increased resilience occurs because lobsters can be harvested at F_{MSY} with a lower risk of shifting into the urchin barren state.
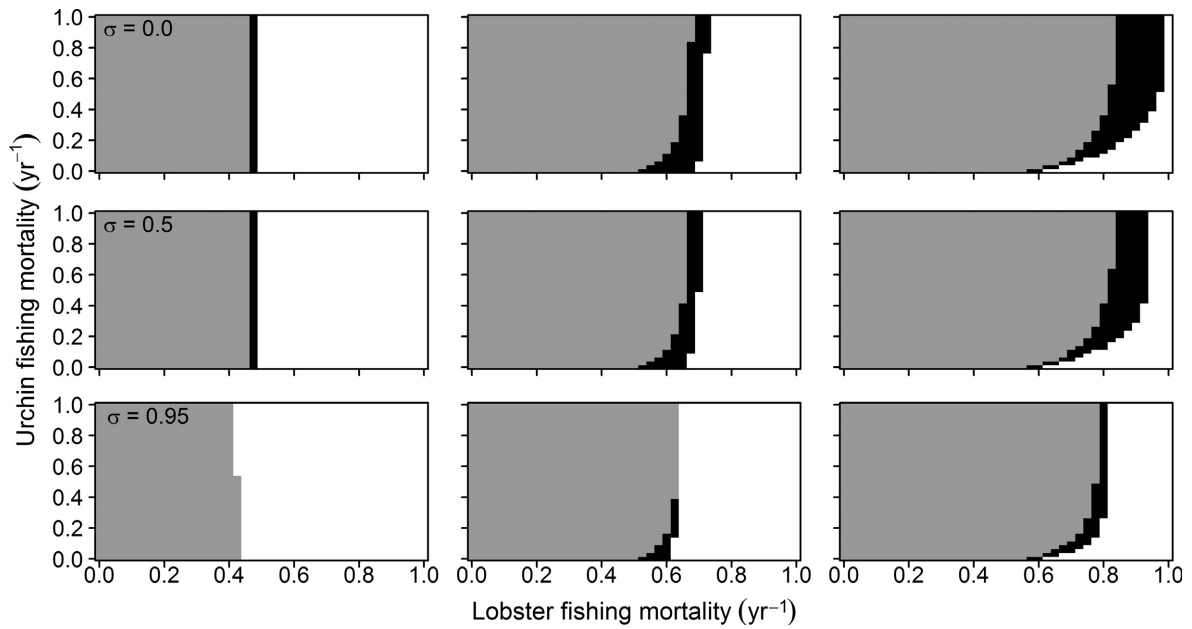
FIG. 5. Parameter space with bistability across all simulated values of F_L and F_U, with recruitment facilitation, $\sigma = 0.0$ (top row), 0.5 (middle row), and 0.95 (bottom row) for three alternative predation scenarios: no size-structured predation ($\delta_{L_i} = 0.133$, left column), baseline model ($\delta_{L_s} = 0.2$, $\delta_{L_m} = 0.15$, $\delta_{L_l} = 0.05$; center column), enhanced size-structured predation ($\delta_{L_s} = 0.3$, $\delta_{L_m} = 0.1$, $\delta_{L_l} = 0.005$; right column). Black regions have two locally stable equilibria, gray regions are stable in the kelp-dominated state, and white regions are stable in the urchin barren state.
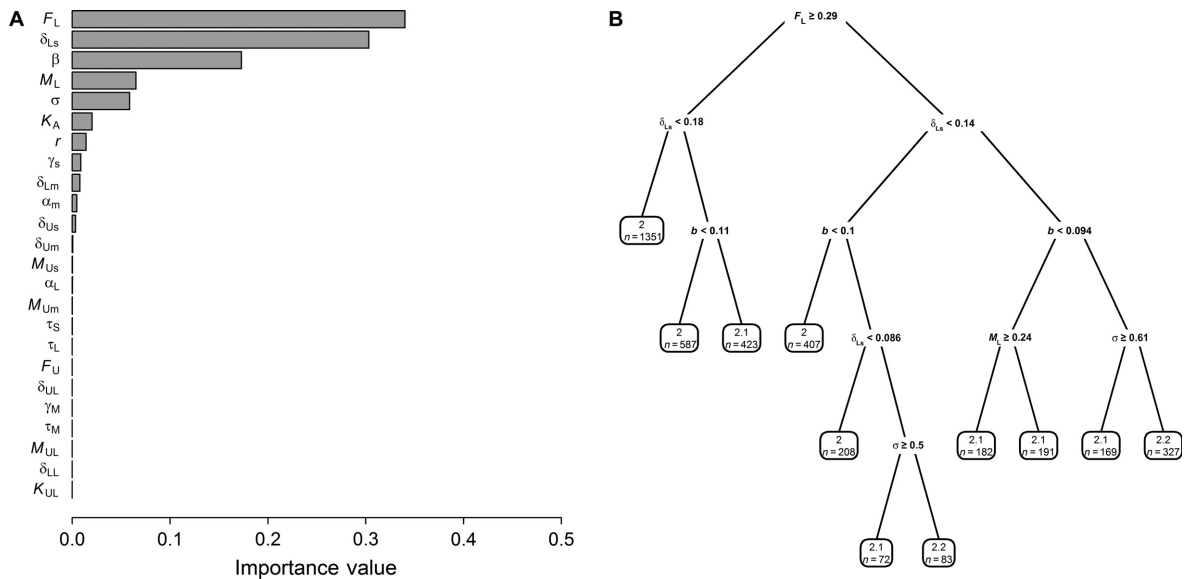

FIG. 6. Results from global sensitivity analysis with mean trophic level (mTL) at equilibrium as the model output and initial conditions in the kelp-dominated state. (A) Normalized importance values from Random Forest. (B) Classification and regression tree (CART). "Yes" is the left branch coming from a particular break point, "No" is the right branch. See Fig. 1 and Appendix S1: Table S1 for parameter names.

Global sensitivity analysis

Lobster fishing mortality, F_L and the attack rate of lobsters on small urchins, δ_{L_s}, are the two most important parameters to mean trophic level and together account for ~65% of the normalized importance value. Conversion rate of urchins to lobsters, β, is the third most important parameter (Fig. 6). Attack rates on medium and large urchins, δ_{L_m} and δ_{L_l}, respectively, are unimportant parameters, together accounting for <1%

of the normalized importance value. Results of the global sensitivity analysis are nearly identical regardless of initial conditions (kelp dominated or urchin barren; Fig. 6 and Appendix S1: Fig. S4).

The pruned classification tree contains exclusively the five parameters with the highest normalized importance values from the random forest analysis (F_L, δ_{L_s}, β, M_L, and σ; Fig. 6), and these five parameters interact to determine mTL at equilibrium. For example, when the rate of lobster fishing is high ($F_L > = 0.29$) and the attack rate of lobsters on small urchins is low ($\delta_{L_s} < 0.18$), the community is found in the urchin barren state (left-most branch of the tree, mTL = 2.0) regardless of other parameter values. This makes intuitive sense: if fishing removes many lobsters and the remaining lobsters do not consume many of the most vulnerable urchins, the results will be an urchin barren. In contrast, when lobsters are fished at or below the stock assessment estimation for F_{MSY} ($F_L < 0.25$) and have a relatively high rate of attack on small urchins ($\delta_{L_s} > 0.14$), the community is generally dominated by kelp and lobsters (mTL $>= 2.1$). Again, this result is intuitive: if lobsters are not overfished and they consume many small urchins, urchins will be unable to grow into the invulnerable size class.

Discussion

The resilience of many marine ecosystems has declined due to a variety of exogenous threats including global climate change, overfishing, eutrophication, and coastal development (Levin and Lubchenco 2008), and many habitats are approaching or have crossed tipping points into new community states (Selkoe et al. 2015). Ecosystem-based management therefore requires an understanding of the factors that interactively drive ecosystem shifts into alternative states and ecological resilience to perturbations. We demonstrate that while the interactive effects of fishing for predators and fishing for prey may only minimally impact biomass, these changes can mask the significantly larger alterations to ecological resilience wrought by multi-trophic level harvest (Figs. 2–4). We also show that moderate fishery harvest of mid-trophic level species has the potential to increase ecological resilience even absent a compensatory mechanism (Fig. 2). This property has previously been overlooked because the focus has been on harvesting predators rather than incorporating multiple trophic levels when assessing ecological resilience (Ling et al. 2009, Britten et al. 2014, Hamilton and Caselle 2015). Size-selective harvest of the largest urchin stage is the mechanism underlying these dynamics. Large urchins are vital to maintaining the urchin barren state via a feedback loop in which large urchins obtain a partial size refuge from predation. At first glance, the importance of urchin harvest to ecological resilience (Fig. 2) is surprising given its small effects on equilibrium biomass of individual community members across values of spiny lobster fishing mortality and recruitment facilitation (Appendix S1: Fig. S2). However, urchin harvest has a weak impact on

biomass at equilibrium for the same reason it strongly affects resilience: large urchins achieve a partial size refuge from predation and thus directly contribute very little to the production of lobsters. It is only by accounting for these size-structured species interactions that we can see the full effect of multi-trophic level harvest.

In contrast to herbivore harvest, fishing for the predator strongly affects equilibrium biomasses and reduces resilience (Ling et al. 2009, Britten et al. 2014, Marzloff et al. 2016). In our case, increasing lobster harvest drives a trophic cascade with reduced top-down control on urchins leading to alternative community states, as has been documented empirically for rocky reefs in the California Channel Islands (Lafferty 2004) and New Zealand (Babcock et al. 1999), and both empirically and through modeling for Tasmanian reefs (Ling et al. 2009, Marzloff et al. 2016). More generally, we provide another example that removal of a key node in a food web allows for a shift between community states, similar to results from terrestrial, freshwater, and pelagic marine systems (Scheffer et al. 2001). Our conclusion regarding the importance of predator harvest agrees with other rocky reef models (using different modeling frameworks) in which lobster harvest is a main driver of ecosystem structure (Eddy et al. 2015, Marzloff et al. 2016). However, unlike our result of a positive relationship between urchin harvest and resilience, an ecosystem model of rocky reefs in New Zealand suggests that urchin harvest negatively impacts both pelagic biomass and full community biomass despite allowing for increased primary production (Eddy et al. 2015). Thus, the direction and magnitude of the effect of herbivore harvest likely depend on species identity, the particular dynamics being modeled, and the community metric being analyzed.

Which ecological processes act as drivers of rocky reef communities?

We include recruitment facilitation as a feedback that can drive alternative stable states (Baskett and Salomon 2010), but our results indicate that size-structured predation, and not recruitment facilitation, is the primary driver of rocky reef alternative stable states in our model. The strengthened feedback created by increasing recruitment facilitation shifts the range of urchin domination but has a minimal effect on the threshold between the kelp dominated state and the bistable region (Fig. 5), effectively shrinking the parameter space in which alternative stable states can occur. Conversely, size-structured predation acts as a straightforward feedback maintaining alternative states because small urchins are under intense consumer pressure relative to larger stages, and predators prevent them from reaching larger sizes. When fishing for lobsters is sufficiently strong, consumer pressure on small urchins relaxes and they are able to grow to larger stages. Because of the lower predation rate on larger stages, large urchins can persist even if lobster fishing mortality is subsequently reduced. We verify the

importance of size-structured predation by demonstrating highly reduced hysteresis in a model with equal predation on all urchin sizes (Appendix S1: Fig. S5) and a corresponding shrinkage in the parameter space with bistability (Fig. 5, left column). Conversely, increasing the degree of size-structured predation, such that small urchins are even more vulnerable to predators and large urchins even less so (relative to our baseline model), acts to expand the parameter space in which bistability occurs (Fig. 5, right column). Size-structured predation has been implicated as a driver of multiple ecological phenomena, including alternative stable states, persistence of competing predators, and collapse of predator populations via an emergent Allee effect (Walters and Kitchell 2001, De Roos and Persson 2002, De Roos et al. 2008). This study adds to recent research incorporating size-structured predation into tests of another emergent property: ecological resilience (see Ling et al. 2009, Barnett and Baskett 2015, Marzloff et al. 2016, Selden et al. 2017 for other examples).

Predation mortality need not decline monotonically while still being size-structured. For instance, hump-shaped distributions of search rates across predator–prey body mass ratios can arise due to smaller predators searching a smaller domain and larger predators' relative difficulty handling small prey (Vucic-Pestic et al. 2010). Because we do not include size-structure at the predator trophic level and large lobsters do not have difficulty consuming small urchins (and in fact generally consume small urchins most readily, R. P. Dunn, *unpublished manuscript*), we use monotonically decreasing attack rates on urchins. However, in an initial exploration of hump-shaped attack rates, we find minimal qualitative change in the effects of lobster and urchin fishing on the hysteretic nature of the system (Appendix S1: Fig. S6), though the location of the bistable region is sensitive to the specific values of lobster attack rates. We are currently working to construct a fully size-structured predator–prey model for spiny lobsters and urchins, which will provide insight on the how the shape of the size-structured predation function alters ecological resilience, including the relative roles of size-structured predation and recruitment facilitation in driving alternative stable states. This modeling framework will also allow exploration of how the degree of concentration of these feedback mechanisms within a size range affect bistability, as well as the potential for an interaction between a feedback mechanism and fishery harvest if those processes are concentrated on a similar size range.

In addition to driving the existence of alternative stable states, size-structured predation is crucial to the biomass of kelp, urchins, and lobsters at equilibrium: in the GSA, the attack rate of predators on the smallest stage of urchins (δ_{L_s}) is one of the two most important parameters to mean trophic level in the model, while the attack rate on the largest urchins has an importance value close to zero (Fig. 6). Predation mortality of sea urchins is highly size dependent (Tegner and Dayton

1981, Tegner and Levin 1983, Ling et al. 2009, Selden et al. 2017), though predation rates on juvenile urchins (<25 mm test diameter) under subtidal field conditions remain poorly known. Determining the influence of predators on survival of recently settled urchins will be an important contribution to the ongoing debate regarding the relative importance of top down vs. bottom up forces on rocky reef community structure.

Model assumptions

As with any model, for simplicity we ignore a number of dynamics that occur in reality. For example, stochastic environmental drivers such as wave energy, climatic regimes, and temperature (Jackson 1977, Seymour et al. 1989, Tegner and Dayton 1991, Young et al. 2016) could drive switches between alternative stable states through, for example, pulses of recruitment or kelp mortality (Tegner and Dayton 1981, 1991). The potential for alternative stable states themselves would depend on additional feedbacks within and between the species modeled. By strengthening feedback loops, spiny lobster preference for urchins from forested habitats over barrens (Eurich et al. 2014) and fisher behavior to avoid low-gonad-quality urchins in barrens (Claisse et al. 2013) could increase the likelihood of alternative stable states. Weakened feedbacks via kelp canopy-dependent larval settlement (Tegner and Dayton 1981, Gaines and Roughgarden 1987) and density-dependent disease spread in urchins (Lafferty 2004) could decrease the likelihood of alternative stable states. Similarly, urchin fishers may preferentially harvest in high density barrens (Selkoe et al. 2015), although this practice is unsustainable without active management (Miller and Nolan 2008) and likely occurs more during transitions than after a state shift has occurred. Another factor that can increase resilience and buffer trophic cascades is increased diversity (Polis et al. 2000, Levin and Lubchenco 2008), which our sub-web model ignores at all three trophic levels. One potentially key missing species from our model is California sheephead, which prey on both urchins (Cowen 1983) and lobsters (Loflen and Hovel 2010). While sheephead and other fish predators likely have lower handling times and higher attack rates on urchin prey (R. P. Dunn, *personal observation*), these parameter changes do not qualitatively alter the baseline dynamics produced (Appendix S1: Fig. S7). Given that increasing the urchin attack rate would increase the strength of top-down control, modeling lobsters (rather than sheephead) may provide conservative estimates of the importance of predators on rocky reefs. Note that increases in the attack rate of lobsters on urchins with increasing water temperature (sensu Pianka 1981; R. P. Dunn, *personal observation* in this system) would have a similar effect. Finally, we do not model food-dependent growth for urchins, but because of the strong effects of food-limitation on reproduction, urchins in our model are unable to persist in the absence of algae in the long term. Thus, this

choice likely affects the time scale of the transient dynamics our model exhibits rather than the equilibrium outcome that is the focus of our analysis.

Finally, our model is a closed system in which external recruitment of urchins and lobsters is non-existent. Given the pelagic larval duration of these species (Johnson 1960, Strathmann 1978), this is unrealistic for the approximate spatial scale of our model (one kelp forest, thousands of square meters). To explore the effects of this assumption, we conduct simulations that include an additional constant external recruitment term for urchins (Appendix S1). We find that medium levels of external recruitment do not affect the qualitative outcome of alternative stable state dynamics (Appendix S1: Figs. S8–S10). A deeper exploration of how both system openness and recruitment stochasticity affect alternative stable state dynamics on rocky reefs is the focus of ongoing investigation (V. Karatayev and M. L. Baskett, *in preparation*).

Management implications

This is an empirically motivated model with which we aim to determine the potential effects of multi-trophic level fishery harvest on rocky reef community structure and dynamics. It is not intended to provide prescriptive estimates of appropriate levels of fishing mortality for either predators or herbivores. Rather, we aim to understand potential drivers of this community from both an ecological and a management perspective. While the parameter space in which alternative stable states occurs is relatively small under our baseline scenario (Fig. 5, center column), alternative stable state dynamics can play a prominent role under relevant harvest values and our independently determined default parameter values for biological processes. The critical transition and hysteresis that we show across values of lobster fishing would require managers to make significant reductions in lobster harvest to escape the urchin barren state (Fig. 2; Marzloff et al. 2016). This condition becomes even more urgent when considering our estimate of F_{MSY} using model simulations ($F_{MSY} = 0.5/yr$; Appendix S1: Fig. S3), which is just below the critical transition into the urchin barren when urchins are not harvested (Figs. 2, 5). Standard practice for fisheries managed in line with the precautionary principle is to set management benchmarks below F_{MSY} to account for multiple sources of uncertainty (Mace 2001, Shertzer et al. 2010). As with other social and ecological systems in which hysteresis can occur, the potentially large costs of passing a critical threshold (in this case, collapse to the urchin barren state and required reductions in lobster harvest) warrant a precautionary management approach that explicitly recognizes and actively avoids thresholds (Selkoe et al. 2015).

Although maintenance of kelp forests appears to depend most strongly on effective management of the lobster fishery, the fishery for sea urchins also plays an important role in determining the strength of hysteresis the system exhibits. Thus, maintaining ecologically sustainable yield will require collaborative management across trophic levels when setting harvest quotas and mortality reference points. The classification and regression tree analysis we use here could contribute to that management need by deriving specific break points in parameter space that drive model outcomes. For management parameters such as F_L and F_U, this type of analysis could be used to inform fishing mortality reference points within a more data-driven tactical model.

Ecosystem-based fisheries management inherently requires trade-offs (Link 2010), generally in species-specific yield, so as to avoid ecological overfishing (sensu Zabel et al. 2003). We demonstrate that despite this trade-off, harvest of herbivores can actually increase resilience of the macroalgal-dominated state when predators are fished above their single-species F_{MSY}. Generally, these results highlight the need for improvement of moderate-complexity, multi-species tactical models (Collie et al. 2016), which build on the insights of strategic models already developed and which specifically incorporate the components shown to drive system outcomes (e.g., a focus on size-structured interactions rather than recruitment facilitation for the system modeled here). Explicit measurement of ecological resilience and the incorporation of resilience thresholds into strategic models can improve management of systems potentially susceptible to alternative stable states while allowing well-managed fisheries to continue to operate. In this case, while harvest of herbivores can modulate resilience if predators are overfished, decreasing fishing mortality of the predator is the more effective management strategy to maximize resilience of kelp forests.

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SUPPORTING INFORMATION

Additional supporting information may be found online at: http://onlinelibrary.wiley.com/doi/10.1002/eap.1581/full

DATA AVAILABILITY

Data available from the Dryad Digital Repository: https://doi.org/10.5061/dryad.m62ms