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Transient dynamics during kelp forest recovery from fishing across multiple trophic levels

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Abstract. Outcomes of management efforts to recover or restore populations of harvested species can be highly dependent on environmental and community context. Predator–prey interactions can alter recovery trajectories, and the timing of management actions within multi-trophic level harvest scenarios may influence the dynamics of recovery and lead to management trade-offs. Recent work using a generalist predator–prey model suggests that management promoting synchronized recovery of predators and prey leads to faster and less variable recovery trajectories than sequential recovery (predator or prey first). However, more complex communities may require different management actions to minimize recovery time and variability. Here, we use a tri-trophic level rocky reef community dynamics model with size-structure and fisheries at multiple trophic levels to investigate the importance of three ecological processes to recovery of fished communities: (1) size-structured predation, (2) non-consumptive effects of predators on prey behavior, and (3) varying levels of recruitment. We also test the effects of initiating recovery from community states associated with varying degrees of fishery-induced degradation and develop a simulation in which the basal resource (kelp) is harvested. In this system, a predator-first closure generally leads to the least volatile and quickest recovery, whether from a kelp forest, urchin barren, or intermediate community state. The benefits gained by selecting this strategy are magnified when recovering from the degraded community, the urchin barren, because initial conditions in the degraded state lead to lengthy recovery times. However, the shape of the size-structured predation relationship can strongly affect recovery volatility, where the differences between alternate management strategies are negated with size-independent predation. External recruitment reduces return times by bolstering the predatory lobster population. These results show that in a tightly linked tri-trophic level food web with top-down control, a predator-first fishery closure can be the most effective strategy to reduce volatility and shorten recovery, particularly when the system is starting from the degraded community state. Given the ubiquity of top predator loss across many ecosystems, we highlight the value of incorporating insights from community ecology into ecosystem management.

Key words: ecosystem-based management; fishery closure; non-consumptive effects; recruitment facilitation; size-structured predation.

INTRODUCTION

Restoration often involves reversing human impacts that have affected multiple species in a community, with ecosystem-level goals of restoring system structure and function (Bradshaw 1996). However, many restoration and recovery interventions, such as harvest moratoria or species reintroductions, target one species at a time. How interventions targeted at single species interact to drive the rate and success of overall system recovery, up to and including top predators, inevitably will depend on species interactions, as increasingly recognized across ecosystems [marshes (Silliman et al. 2015), corals (Ladd et al. 2018), grasslands (Young et al. 2017)]. Nevertheless, examples of jointly recovering species offer relatively few generalities for managers beyond the need to recognize trade-offs as predator populations recover. For example, a growing population of bald eagles hindered population growth of ospreys and herons via

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reduced nesting success (Cruz et al. 2019), and protected white sharks may be contributing to slowed recovery of sea otters due to naïve juvenile sharks mis-targeting sea otters as a prey item (Moxley et al. 2019). Similarly, accounting for species interactions is integral to an ecosystem-based approach to fisheries management (EBFM; Larkin 1996). For example, in the case of Baltic Sea cod and their forage fish prey, modeling suggests that incorporating environmental conditions and trophic interactions into adaptive management decisions would lead to improved biological and economic outcomes compared with traditional management (Lindegren et al. 2009). In some cases, where declines in fished species have occurred, protection from fishing alone does not ensure recovery due to fishery-induced alterations in predator–prey or competitive interactions (Mangel and Levin 2005, Baskett et al. 2006). Thus, biotic interactions among recovering species can play key roles in the trajectory and likelihood of success of system rehabilitation (Perring et al. 2015, Marshall et al. 2016, Stier et al. 2016).

The importance of accounting for these community interactions is well illustrated by marine ecosystems, where serial depletion of living marine resources (e.g., harvested fish and invertebrates) has led to calls for rebuilding harvested stocks (NOAA 1996), often without guidance on how rebuilding should be implemented. Closing a fishery or heavily restricting harvest rates are species-specific management measures aimed at recovery of the target population. An alternative is the establishment of a spatial closure, or no-take marine reserve (hereafter, "reserve"), in which harvest of all species is prohibited within a defined geographic area. Establishing reserves and closing single-species fisheries thus lead to inherently different recovery scenarios, as entire communities (and potentially multiple fished species) are protected inside reserves while fishery closures typically act on a single species. While many species increase following reserve establishment (Lester et al. 2009), recovery is not a given and there are notable cases of both single species closures (Hutchings 2000) and reserves (Micheli et al. 2004) in which population increases do not immediately occur. Trophic interactions are one mechanism that can drive these population responses. For example, predator–prey role reversals, in which small pelagic fish feed on the eggs of their predators, can maintain low levels of predator recruitment even following fishery closure (Minto and Worm 2012). The potential for delayed or impeded recovery due to species interactions raises the question of whether managing fishery closures sequentially (vs. independently or simultaneously) might more effectively achieve community-level recovery goals.

The path that a population or community follows through time after harvest stops, or its recovery trajectory, can be fundamentally different from its long-term, equilibrium outcome (White et al. 2013, Hastings et al. 2018). Understanding system behavior during the transient period following a perturbation (in this case, cessation of harvest) is necessary to inform monitoring expectations for adaptive management (White et al. 2011) and to determine what management strategies lead to the most rapid recovery. To this end, recent work focused on the transient period following fishery closure (or reserve establishment) has demonstrated that intensity of harvest mortality relative to natural mortality can determine the distance from the unharvested equilibrium and therefore sets the time scale for the lag in reaching that equilibrium (White et al. 2013). In addition, oscillatory behavior can occur as part of the deterministic return to equilibrium, and can depend on a species' life history, in particular the age at maturity (White et al. 2013). Meanwhile, fishery benefits via enhanced larval export from reserves may take decades to be achieved as a result of the time lag between reserve establishment and biomass build-up of adult individuals (Hopf et al. 2016). Thus, recognizing that protected populations might not immediately increase and that initial trends may not be indicative of long-term outcomes due to the transient period following fishery closure can help to inform the time-scale for judging the efficacy of management actions (Hastings 2016).

In addition to monitoring time frames, transient dynamics inherent to species interactions might alter optimal management approaches to community recovery. Analysis of a simple model of a generalist predator and one dynamical prey shows the importance of the timing of management actions within multi-trophic level harvest scenarios, with "synchronous" closure of predator and prey fisheries (as opposed to predator-first or prey-first closures, hereafter "sequential") producing a faster return to the unexploited equilibrium and reduced volatility during the transient period (Samhouri et al. 2017). However, numerous additional ecological processes could affect the transient behavior of multispecies communities. For example, within marine reserves where predators are larger and more abundant than in fished areas, herbivores typically alter their behavior to be more cryptic (Spyksma et al. 2017). Predators thereby non-consumptively reduce prey interaction strengths with basal resources, in some cases driving a behaviorally mediated trophic cascade (Peckarsky et al. 2008), the strength of which can depend on prey size (Freeman 2006). Similarly, recruitment facilitation of juveniles by conspecific adults is a positive feedback that can affect recovery through size-structured, depensatory cultivation effects (Walters and Kitchell 2001). Thus, the sequence of recovery for predators and prey, respectively, could determine the outcome of management actions in a multi-trophic level context (Stier et al. 2016). Nonetheless, resolving the context-dependence and relative efficacy of stock recovery trajectories following sequential vs. simultaneous fishery closures will require consideration of an array of under-explored species interactions.

Our primary aim in this study is to quantify the effect of sequential vs. simultaneous fisheries closures on the recovery of exploited species that are linked through trophic interactions. Secondarily, we explore the dependency of that management outcome on an array of ecological dynamics occurring within the recovering community. These include size-structured interactions between predators and prey, non-consumptive effects of predators on prey behavior, and various recruitment scenarios (e.g., recruitment facilitation, open vs. closed populations). We also investigate the effect of initiating recovery from community states at varying degrees of degradation. In most cases we examine recovering from simultaneous harvest of predators and prey, but in one case we also explore the effect of an additional fishery for the basal resource, thereby creating a tri-trophic level harvest scenario. To achieve these aims, we analyze the recovery from fishing of a rocky reef community using a size-structured, tri-trophic level model (Fig. 1), with fisheries for predators, prey, and the basal resource. Finally, we provide a case-study of potential recovery expectations using the predator-first closure strategy while incorporating uncertainty in parameter values. Quantifying the transient response of complex communities to various recovery strategies, as we do here, can help to set expectations for the time scale and trajectory of recovery in an ecosystem-based management framework.

Methods

Model system

Rocky reefs are a common habitat on temperate coasts globally and can be observed in a range of community states, from kelp forests dominated by foundational macroalgae to urchin barrens with high densities of sea urchins and covered in crustose coralline algae with low kelp cover (Filbee-Dexter and Scheibling 2014). Predators may control the abundance and distribution of the kelp forest state by consuming urchins (Shears and Babcock 2002, Ling et al. 2009, Hamilton and Caselle 2015), although physical factors can also determine the distribution of macroalgae (Schiel and Foster 2015), and predators do not provide top-down control in all contexts (Dunn and Hovel 2019). In southern California, red sea urchins (*Mesocentrotus franciscanus*) and one of their predators, the California spiny lobster (*Panulirus interruptus*), are subject to simultaneous harvest from rocky reefs. Our model tracks the dynamics of macroalgae (also referred to as kelp) on these reefs, as well as three size compartments of herbivorous sea urchins (encompassing purple sea urchins *Strongylocentrotus purpuratus* as well as red urchins), and predatory spiny lobsters (Fig. 1). Within the model, kelp grows logistically and is eaten by urchins at size-specific rates. Small urchins are produced by medium and large urchins, and large urchins also facilitate recruitment of small urchins via protection under their spine canopy. Urchins grow into subsequent size classes and die at a background mortality rate. Predatory lobsters consume urchins at size-specific rates with a saturating, type II functional response. Lobsters then convert urchins into population growth and die at a background mortality rate. Large urchins, lobsters, and the basal resource, kelp, can be harvested in individual fisheries. We include size-structure for urchins because predation, recruitment facilitation, and harvest (and therefore their interactive effects on the rocky reef community) all depend on urchin size. For complete model details, including equations and parameter values, see Appendix S1 and Dunn et al. (2017).

Previous analysis of this model, focusing on of the interactive effects of harvesting predators (lobsters) and prey (urchins) showed that fishing for predators drove a trophic cascade, while fishing for prey altered the likelihood of shifting from one alternative community state to another. Specifically, increasing harvest of urchins increases the resilience of the system by reducing the range of predator fishery mortality rates at which alternative stable states are possible; size-structured predation on sea urchins is the feedback maintaining the kelp forest or urchin barren state, respectively. Global sensitivity analysis demonstrated that the harvest rate of lobsters and the predatory attack rate on the smallest size-class of urchins are the two most important parameters driving long-term equilibrium community structure. Without any harvest, the kelp forest is the only locally stable state, such that cessation of all harvest will, eventually, lead to recovery of the kelp-dominated state regardless of initial conditions (Dunn et al. 2017). In comparison to that equilibrium analysis, we focus here on the dynamics of the system during the transient period following cessation of fishing to better understand the effect of sequential vs. synchronous protection on the time-scale and path to long-term equilibria and how these depend on ecological processes.

Simulation and analysis

We simulated the recovery of this community from harvest under synchronous and sequential recovery scenarios, given five different assumptions about ecological processes or fishery dynamics occurring within it. To characterize the degree of variability and duration of the transient period following fishery closure, we quantified the community volatility and return time of the fished compartments in the rocky reef model (Fig. 1B). These two metrics measure the time scale of recovery (return time) and the degree of variability in the recovery path (volatility), where increased return time and increased volatility indicate longer times to and larger departures from the target ecosystem structure (Samhouri et al. 2017). These two metrics are roughly analogous to the metrics of transient duration and amplitude of oscillations in single-species models of recovery from fishing (White et al. 2013). We focused on the previously fished compartments (generally, lobsters and large urchins, but in one case kelp as well) because of their importance to managers and resource users. Other unharvested compartments tended to

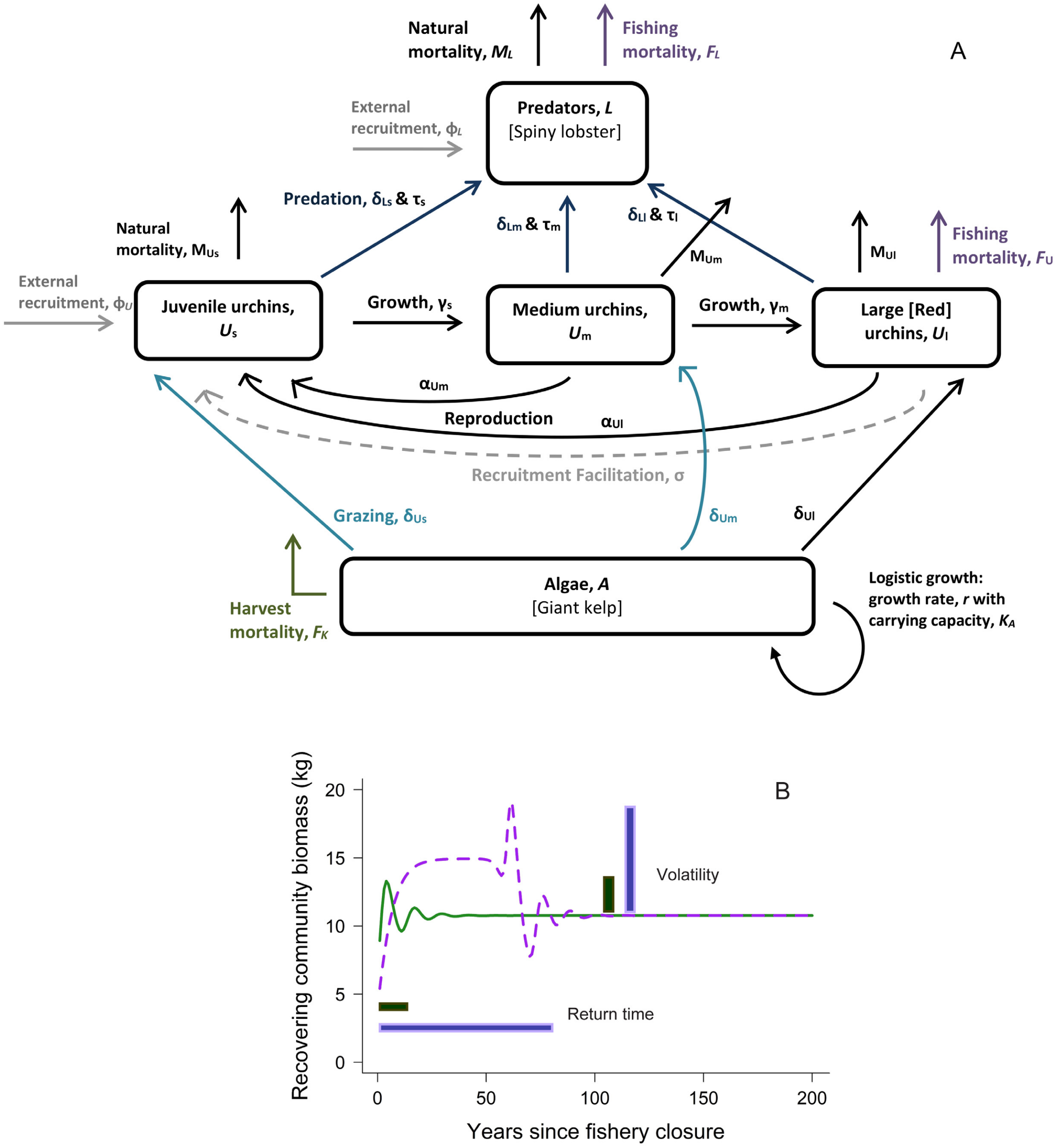

FIG. 1. Outline of the updated rocky reef community dynamics model (originally published in Dunn et al. 2017) is shown in Panel A. Boxes indicate state variables; arrows indicate biomass flows affecting dynamics and are labelled with the associated parameter names. Colored arrows and labels represent each of the five ecological processes we simulate: size-structured predation (dark blue), non-consumptive effects of predators (light blue), recruitment dynamics (gray), alternative stable states (purple), and kelp harvest (green). Within the model, predators consume urchins at size-specific rates, δ_{L_i}, which were manipulated to create various shapes of size-structured predation. Similarly, urchins graze on kelp at size-specific rates, δ_{U_i}, which we reduced for small and medium urchins when simulating the behavioral change exhibited by urchins following the closure of the lobster fishery. To create open populations of urchins and lobsters, we added a constant source of exogenous recruitment, where φ_i is a biomass of either small urchins or lobsters that recruits at each time step. To investigate the effects of fishery-induced degradation on recovery, we varied the fishery harvest rates F_U and F_L, for urchins and lobsters, respectively, which led to population recovery beginning from either the kelp forest (sustainable harvest), the urchin barren (collapsed), or the moderately degraded region between these two alternative communities (on the verge of collapse). Finally, we added an additional kelp fishery with harvest rate F_K. In Panel B, we show example time-series of recovering biomass (lobsters + large urchins) for synchronous fishery closures with initial conditions in the kelp forest (solid green line) and urchin barren (dashed purple line). Horizontal and vertical boxes denote the return time and volatility metrics, respectively.

have large responses to management actions that were not ultimately reflected in the fished compartments, and thus in some cases obscured the effects of interest. In addition, recovery of red urchins is a specific fisheries management goal. Most urchins within high density barrens are smaller purple urchins, which are not harvested, thus, rebuilding populations of large red urchins (which are harvested and long lived), does not necessarily lead to the degraded urchin barren community state.

For each community ecology scenario, we first ran the model to harvested equilibrium (specifically, we simulated for 200 yr to ensure that equilibrium was always reached) to determine the initial conditions at which to begin recovery. Next, we initiated recovery by setting fishing mortality (F_U, F_L, F_K or multiple, where U, L, K: urchins, lobsters, kelp) equal to zero, depending on the focal recovery scenario, and allowed that simulation to run to equilibrium (again simulating to 200 yr to ensure equilibrium was reached and then determining the actual time to reach equilibration within that period). For synchronous recovery, that was the end of model simulations. For sequential recovery, we used these partial-recovery equilibrium values as initial conditions when closing the next fishery (setting F_U, F_L, or F_K, whichever was not already manipulated, equal to zero), and we again ran the system to equilibrium (see Appendix S1: Fig. S1), continuing until all fisheries were closed.

We used this analytical framework to assess recovery trajectories for simultaneous, predator-first, and prey-first closures, focusing on fished species volatility and return time. Following Samhouri et al. (2017), we calculated fished species volatility as the proportional difference (i.e., the ratio) between the maximum summed biomass of previously harvested species that was achieved during the transient phase following fishery closure and their summed unexploited equilibrium biomass. For return time, we measured the length of time (yr) from when recovery began (i.e., when fishing mortality was set to zero for at least one trophic level) to when summed biomass for all previously harvested species remained within 10% of its long-term equilibrium. We calculated return time under the assumption that a manager implements the next step in sequential recovery as soon as the system equilibrates following the previous management action. That is, although we ran each simulation for 200 yr, we determined the time point when summed harvested species biomass remained within 10% of its long-term equilibrium, disregarding the remaining years. We also report the time point at which the maximum fished community volatility occurred as well as the portion of the return time attributed to predator and prey recovery, respectively, for sequential closure scenarios. Because simulations are deterministic, once harvest is stopped the system always returns to the unexploited state (upon reaching equilibrium), but with different levels of volatility and return times.

Size-structured predation

We used four alternate parameterizations of the size-specific lobster attack rate on urchins (δ_{L_i}) to represent varying shapes of size-structured predation (Appendix S1: Table S1), simulating synchronous and sequential fishery closures for each type of predation. Our baseline parameterization is a decreasing monotonic function whereby small urchins are the most vulnerable to predation and become less susceptible as they grow. Next, we set all lobster attack rates equal across urchin sizes to remove any size-structure. Third, we enhanced the degree of size-structured predation above the baseline by increasing susceptibility of small urchins and reducing susceptibility of large urchins even further, making the slope of the monotonic predation function steeper. Finally, we created a hump-shaped predation function by making medium urchins the most susceptible size class. While the baseline parameterization most accurately represents the predation function exhibited by California spiny lobsters (Dunn and Hovel 2019), we manipulate this function here to evaluate the importance of size-structured predation during recovery.

Non-consumptive effects of predators

Next, we tested the importance of including a non-consumptive effect (sensu Blaustein 1997) of predators on prey behavior following the closure of the fishery for predators. We modeled this behavior by reducing the attack rates of small and medium urchins on kelp (δ_{U_s} and δ_{U_m}) following the closure of the lobster fishery (see Appendix S1: Table S1 for parameter values). We chose this implicit approach rather than explicitly modeling behavioral feedbacks in order to maintain the same base model structure across the different scenarios. Nevertheless, indirect effects of marine reserves, such as the behavioral shifts described above, on average appear after 13 yr (Babcock et al. 2010), and we accounted for this delay in behavioral changes by altering the parameter values associated with urchin grazing after a 10-yr "build-up" period following the closure of the spiny lobsters fishery (knife-edge change in grazing rates after 10 yr). However, we also provide the results of simulations in which we forced reduced urchin grazing to occur simultaneously with setting predator harvest equal to zero, creating an instantaneous non-consumptive effect (Appendix S1).

Recruitment patterns

We provide an exploration of how various recruitment processes affect recovery trajectories, including incorporating exogenous recruitment of small urchins and spiny lobsters and, separately, facilitation of juvenile urchins by adult urchins. Our baseline model structure does not include any exogenous recruitment (i.e., all three trophic levels are closed populations). To simulate an open population and remove the complete dependence of urchins on kelp and lobsters on urchins, we added an exogenous recruitment term, φ_i, to the dynamics for small urchins and lobsters, which represents a set amount of biomass recruiting at each time step (see Appendix S1).

Large urchins can facilitate the survival of small urchins by providing protection underneath their spine canopy (Tegner and Dayton 1977). To describe the strength of this recruitment facilitation, we use the term σ, which can range from 0 to 1. When $\sigma = 0$, recruitment is independent of large urchin biomass, while at $\sigma = 1$ recruitment is completely dependent on the protection provided by the spine canopy of large urchins and is scaled by the ratio of the current large urchin biomass to its carrying capacity. For simulations presented in this study, our baseline parameterization sets $\sigma = 0.5$. We then set $\sigma = 0$ to test the effect of removing urchin recruitment facilitation on recovery trajectories. A deeper investigation of modeling recruitment facilitation of small urchins by adult urchins is available in Baskett and Salomon (2010) and Dunn et al. (2017).

Community degradation due to fishing

To investigate the effects of degradation due to fishing on recovery from harvest, we tracked recovery after harvesting predators and prey at three different intensities that led to recovery beginning from either the kelp-dominated community (sustainable lobster harvest), the urchin barren (lobsters overfished/collapsed), or the moderately degraded region between these two alternative communities (on the verge of collapse). Parameter combinations for each are in Appendix S1: Table S1.

Three-tiered fishery (including kelp harvest)

Currently, nearly 80% of California's kelp beds are open to commercial harvest in one form or another (CDFW 2014). We modeled kelp harvest by adding an additional removal parameter to the equation describing the dynamics of giant kelp (*Macrocystis pyrifera*; Appendix S1). We define F_K as the harvest rate of kelp and incorporate this new fishery into our recovery trajectory analyses just as described for the two-tiered fishery. However, given that there are now three trophic levels being harvested, sequential recovery can be either completely sequential (e.g., close predator then prey then basal) or partially sequential (e.g., close predator then synchronously close prey and basal), and the order of closures may influence the recovery trajectories. We calculate volatility and return time just as above, but now also include the harvested biomass of kelp in addition to the harvested biomass of lobsters and large urchins.

Sensitivity analysis

Each of the above scenarios could be considered a local sensitivity analysis. To understand the importance of all individual parameters in driving transient volatility of the fished community, and to quantify the range of possible recovery trajectories given uncertainty in parameter values (due to spatiotemporal variability in carrying capacity, growth rates, and predation parameters, among others), we conducted global sensitivity analyses. For both analyses, we used a single set of 4,000 parameter combinations drawn at random from a range of potential values (parameter ranges provided in Appendix S1: Table S1). First, to understand the importance of individual parameters in driving fished species volatility during the transient period, we conducted random forest analyses (Harper et al. 2011). We used all 4,000 model runs to calculate normalized importance values for each parameter under each of the three management scenarios (synchronous, predator-first, or prey-first closure), initiating the model from both the kelp forest and the urchin barren community (8,000 total model runs). Modeled conditions when initiating fishery closures and starting the recovery phase were thus caused by a combination of our initial community states, either kelp forest or urchin barren, as well as the fishing mortality rates introduced within the global sensitivity analysis. Thus, for "kelp forest" simulations within the global sensitivity analysis, randomly selected fishing rates could still have been high enough to drive the system to a degraded state prior to initiating fishery closures. Analogously, for the "urchin barren" simulations with low fishing harvest rates during the initial harvesting period, recovery could have begun from a less degraded state. Parameter importance values are a measure of how informative each parameter is in predicting fished species volatility, and we normalize values to sum to 1 to aid their interpretability. Parameters with high importance values have strong impacts on volatility during the transient period, given the model's assumptions. Second, to provide an example of how our results could be applied on prespecified management time scales while incorporating parameter uncertainty, we simulated the model for all 4,000 parameter combinations using the predator-first closure management strategy, which we implemented by first closing the lobster fishery ($F_L = 0$) and running the model for 2 yr, and then closing the urchin fishery ($F_U = 0$) and running for an additional 15 yr. From these simulations, we examined the biomass response of the recovering fished community through time. For each of the 4,000 model simulations under both sets of initial conditions, we present the range of recovery trajectories (recovering biomass time series) and plot the distributions of fished species biomass (lobsters + large urchins) at 5, 10, and 15 yr after the closure of both fisheries (8,000 total model runs). We base this time horizon on the ~5-yr recurring monitoring events used for management of marine protected areas in California, USA.

RESULTS

In contrast to previous results suggesting synchronous management of predators and prey to be more efficient than either sequential closure strategy (Samhouri et al.

2017), our model demonstrated that predator-first closures provided the least volatile and most rapid recovery in nearly all simulated scenarios in our model system. The prey-first strategy generally led to the least effective recovery outcomes (Figs. 2–4), in agreement with previous findings (Samhouri et al. 2017). When recovery began in the kelp-dominated or moderately degraded state, synchronous closure of predator and prey fisheries demonstrated a similar trajectory to predator-first management (differences in fished community volatility were <13%, volatility peaked at the same point, and return times were within 1 yr using the baseline parameterization; Fig. 2). Conversely, when the system was already severely degraded due to high fishing mortality rates (i.e., initial conditions were in the urchin barren), a predator-first closure outperformed synchronous and prey-first management in both fished species volatility and return time, and peak volatility occurred earlier (Fig. 2). A prey-first closure is particularly suboptimal in this case (return time = 161 yr vs. 61 yr for the predator-first case) because low predation rates on the largest urchins, when combined with the closure of the urchin fishery, allow them to persist for generations (red urchin age at maturity ~5 yr [Ebert et al. 1999]; purple urchin age at maturity ~2 yr [Kenner and Lares 1991]) in the low-kelp, low-lobster state.

The shape of the size-structured predation function did not alter our finding that a predator-first closure was generally least volatile and fastest, although when we removed size-structure so that all prey were equally likely to be consumed, all three management scenarios provided virtually equivalent results (Fig. 3). The mechanism for this pattern is that with the assumption of size-independent predation, there is an increased probability of predation mortality for large urchins during the recovery of predatory lobsters, accelerating the return to the kelp state. When the predation function was hump-shaped, return time in the predator-first case was reduced by more than 50% (Fig. 3). The mechanism is again that the assumption of hump-shaped, size-

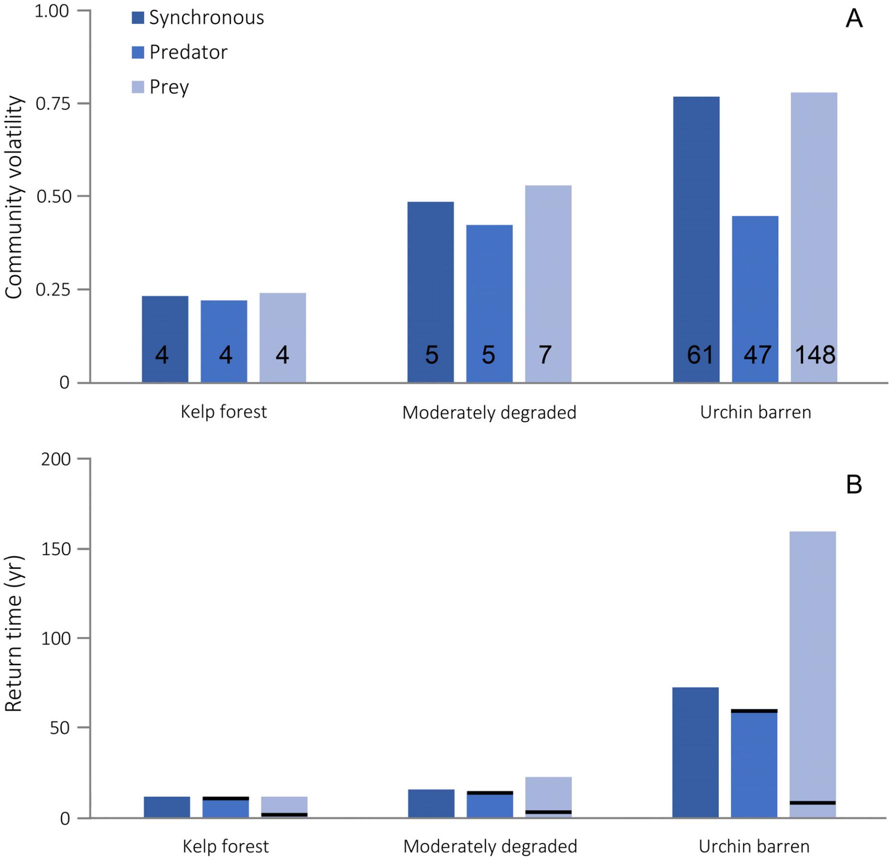

Fig. 2. (A) Fished community volatility and (B) return time for baseline model scenarios with initial conditions either in the kelp forest, moderately degraded, or urchin barren states, established by varying fishing mortality. For both volatility and return time, we show the combined biomass of lobsters and large urchins, the two compartments affected by fishery closure. In panel A, numbers on each bar provide the number of years following fishery closure(s) until community volatility peaks. In panel B, black lines on bars for predator- and prey-first management designate the portion of the return time associated with each fishery closure. For example, for prey-first closure from the urchin barren, intermediate recovery to equilibrium following closure of the urchin fishery took 10 yr, while complete recovery following secondary closure of the lobster fishery took an additional 150 yr.

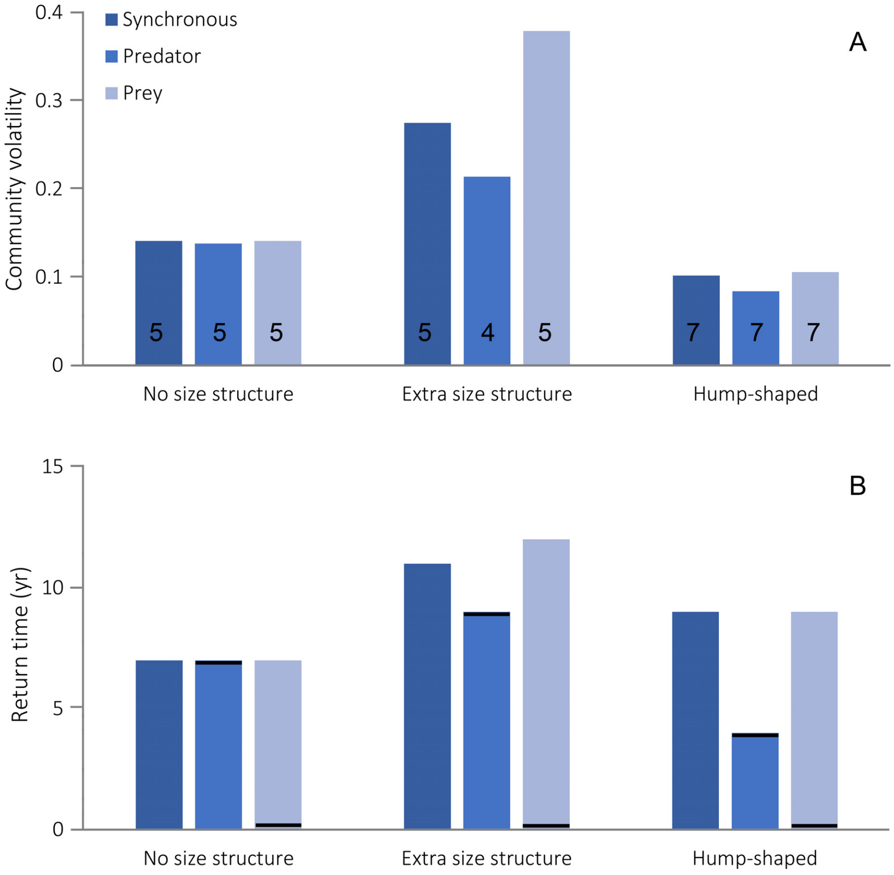

FIG. 3. (A) Fished community volatility and (B) return time for model simulations with alternate shapes of the size-structured predation function, initiated from the kelp forest. Predator-first recovery remains the least volatile and fastest return time (or tied, in the no size structure case).

structured predation reduced the likelihood of urchins reaching the large size-class due to high predation on medium sized individuals, speeding up recovery to the kelp state. Interestingly, the shape of the size-structured predation function had differing effects on the timing of peak volatility, which was later by at least 2 yr for all three management scenarios under the hump-shaped parameterization (Fig. 3A), even though return times were reduced or similar to the other size-structure cases (Fig. 3B). All of the transient behavior occurred following the lobster fishery closure, while the closure of the urchin fishery contributed very little to the return time (Fig. 3B).

Non-consumptive effects of predators on prey behavior increased both volatility and return time relative to the baseline scenario without non-consumptive effects, although differences among management strategies were minimal and volatility peaked at approximately the same time for each (Appendix S1: Fig. S2). The lengthening of return times at first appears surprising because we include non-consumptive effects that reduce kelp consumption and should ostensibly lead to a more rapid return to the unexploited equilibrium, characterized by high kelp abundance. However, recovering to this state ultimately requires lobsters to consume urchins, and by reducing urchin grazing, non-consumptive effects actually lowered lobster abundance due to the dependence of lobster population growth on urchins. As in the size-structured cases, all of the transient behavior occurred following the lobster fishery closure (Appendix S1: Fig. S2B). As would be expected, delayed initiation of a behavioral shift in grazing rate led to higher fished species volatility and longer return times than when non-consumptive effects were initiated immediately at the closure of the lobster fishery (Appendix S1: Fig. S2). This occurs because in the delayed non-consumptive effects case, urchins can continue to consume kelp at high rates until predator biomass is sufficient to alter their grazing behavior, lengthening recovery time.

Simulations testing various recruitment scenarios demonstrated that exogenous recruitment (i.e., open populations supported from outside) led to reduced volatility (though the timing of peak volatility was similar) and shorter return times than the corresponding "closed population" scenarios. This was the case whether starting conditions were in the kelp forest or urchin

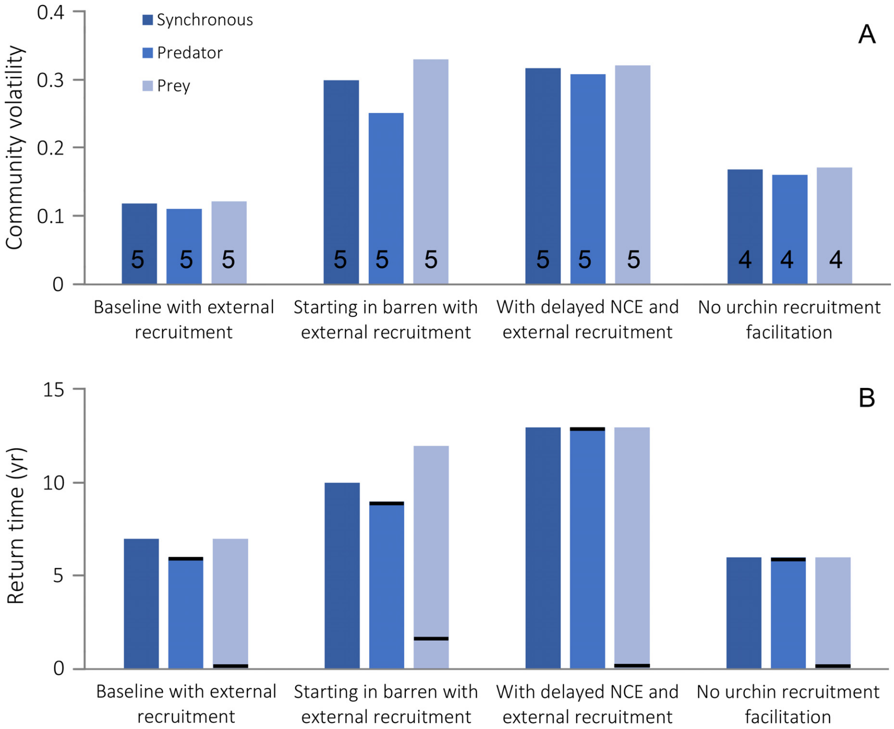

FIG. 4. Fished community (large urchin, lobster) (A) volatility and (B) return time for various recruitment scenarios. With constant exogenous recruitment of lobsters and urchins, predator-first recovery remains the least volatile. Non-consumptive effects (NCE) of predators (with exogenous recruitment) show a similar result. When removing the possibility for recruitment facilitation of small urchins by large red urchins (setting $\sigma = 0$), volatility and return time are reduced for all recovery scenarios.

barren, or if non-consumptive effects of predators were included (Fig. 4). The mechanism behind this result is that with open population dynamics there is no time lag in recruitment during the transient period following fishery closure. The impact of exogenous recruitment was most evident when comparing simulations with initial conditions in the urchin barren: recovery from the barren state to the unexploited equilibrium using the predator-first closure strategy was shortened by 85% and volatility was reduced by 44% when populations were open compared with our initial simulations of a closed population (Figs. 2, 4). These gains were even greater when focusing on the least effective management strategy based on our metrics (prey-first): volatility was more than halved and return times were shortened by an order of magnitude (160 yr vs. 12 y; Figs. 2, 4). In contrast to external recruitment, removing recruitment facilitation by adult urchins reduced volatility relatively little compared to the baseline scenario, though return times were halved (6 yr vs. 12 yr for all three management scenarios; Figs. 2, 4). In all simulations altering recruitment processes, predator-first closure was again typically the least volatile and fastest (Fig. 4), though the gains achieved by choosing predator-first closure were substantially reduced when exogenous recruitment occurred (we show a similar result when removing recruitment facilitation; Figs. 2B, 4B). As with other scenarios, closing the lobster fishery contributed to the majority of the transient behavior during recovery (Fig. 4B).

Incorporating harvest of the basal resource, thereby creating a tri-trophic level fishery, did not alter our general finding that predator-first closure was typically the least volatile management strategy, while return times were identical and relatively short (4 yr and 12 yr, when including vs. excluding kelp biomass, respectively) for each of the 10 tri-trophic level management scenarios. In the tri-trophic level fishery case, differences in recovering species volatility among closure scenarios were minimal compared with differences observed when investigating other ecological dynamics or community scenarios (Appendix S1: Fig. S3). Of note, however, volatility was reduced when we include the harvest of kelp in calculating the community biomass (Appendix S1: Fig. S3B) compared with only including lobster and urchin biomass (Appendix S1: Fig. S3A), as we did for the two-trophic level harvest scenarios.

Global sensitivity analysis using random forests demonstrated that regardless of the recovery strategy or initial community structure, community volatility during recovery is largely driven by the initial fishing mortality rate for lobsters (F_L) or the attack rate of lobsters on small urchins (δ_{L_s}). Together, these two parameters account for over 50% of the normalized importance value in each recovery scenario (Appendix S1: Figs. S4 and S5). Interestingly, urchin fishing mortality (F_U) was moderately important only in the predator-first closure cases (~5% of normalized importance value vs. <1% for prey-first and synchronous closures; Appendix S1: Figs. S4, S5).

In our case study using a predator-first closure, recovery trajectories demonstrate a similar result: when initial conditions were in the macroalgal-dominated kelp forest (a proxy for low lobster harvest rate), recovery toward higher fished biomass was initiated 2–3 yr earlier than when initial conditions were urchin dominated (Appendix S1: Fig. S6). Similarly, 5 yr after the closure of both fisheries, the distribution of recovering biomass when starting from the kelp forest was right skewed compared with initial conditions in the urchin barren (Fig. 5), suggesting a more rapid rebuilding of the population across size classes. However, in both cases, parameter variability could drive the system to low recovering biomass at 10 and 15 yr post-fishery closure (Fig. 5, Appendix S1: Fig. S6).

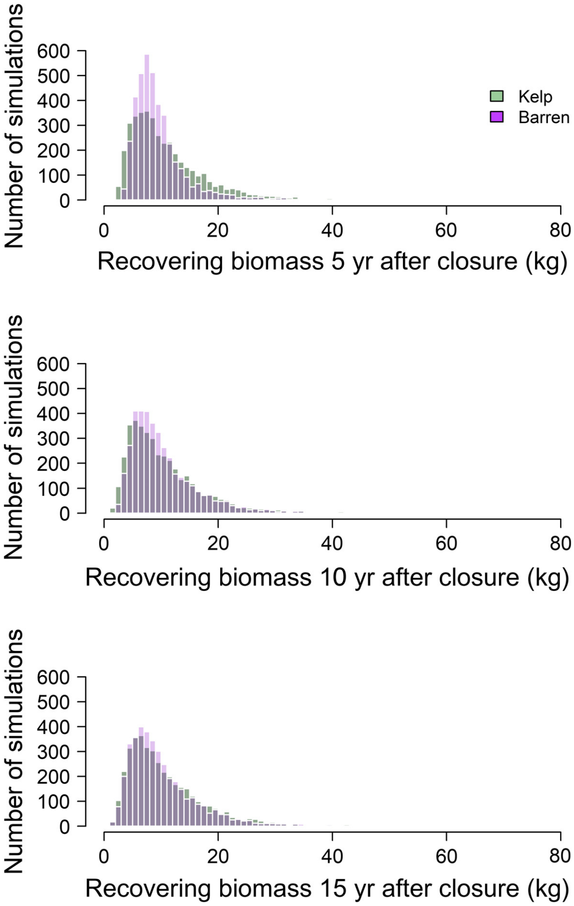

FIG. 5. Histograms representing the number of simulations that end with lobster + urchin biomass at varying amounts, 5, 10, and 15 yr after the closure of both predator and prey fisheries. These simulations use a predator-first closure management strategy and include parameter uncertainty, leading to variation in biomass at each time point. Green bars represent simulations with initial conditions (prior to closure of the lobster fishery) in the kelp forest community, purple bars are for initial conditions the urchin barren.

DISCUSSION

Population depletion in many fisheries has led to calls for rebuilding of exploited species (NOAA 1996, Safina et al. 2005), and prompted a concerted effort to understand the “how” (Wakeford et al. 2009, Neubauer et al. 2013) and “why” (Sumaila et al. 2012) of rebuilding harvested stocks. Importantly, connecting rebuilding mandates to rebuilding strategies is now feasible and typically includes consideration of ecological processes (Link 2002, Mangel and Levin 2005). For our modeled kelp forest, predator-first closures generally provide the fastest and least volatile recovery strategy. This is the case for most of the ecological processes we examined, but is particularly evident when initiating recovery from the degraded urchin barren community. Size-structured predation and recruitment facilitation are two modeled feedbacks that can lead to alternative stable states under certain parameter combinations with this model (Dunn et al. 2017), but alternative stable state dynamics only occur when fishery harvest is occurring and therefore do not apply in the case of zero fishing mortality that is the end state here. Nevertheless, these feedbacks can make recovery from the barren state particularly slow (for all three management scenarios) and volatile (for prey-first and synchronous closures), magnifying the gains from selecting the predator-first closure strategy.

For a given community, the management strategy that is least volatile and has the quickest return time will likely depend heavily on the biotic interactions occurring among harvested species. In the case of our kelp forest model, lack of size-structured predation decreases the volatility and recovery time of fished species by ~2× and 1.5×, respectively, compared to the enhanced size-structure case, and negates the differences between alternate management strategies (Fig. 3). Our results differ from previous theoretical work, which demonstrated that synchronous closures of predator and prey fisheries provided a rapid and low volatility means to return to the unharvested community state (Samhouri et al. 2017). The mechanism for this discrepancy likely lies in the requirement, in the model presented here, for predators to consume herbivores to drive shifts between community states. In previous recovery trajectory models, predators and prey were dynamically linked but their dependence was reduced by including an alternative prey species (Samhouri et al. 2017). Here, top-down control by predators is required for the persistence of the kelp forest because when lobster fishing mortality is moderate to high, the urchin barren is the only stable state (Dunn et al. 2017). With a predator-first fishery closure, removing urchins via fishing while they also experience predation from a recovering population of specialist lobsters provides the strongest degree of top-down control, and thus offers the quickest and least volatile recovery trajectory. With a prey-first closure, the recovery process is slowed because of time lags required for lobster biomass to build-up to the point at which top-down control is strong enough to drive the system back to the kelp-dominated state (Fig. 2B). We speculate that synchronous management could be more effective for diffuse food webs with generalist predation [a common feature among predatory species (Fryxell and Lundberg 1994)], while sequential closures would be more effective for food webs with specialist consumption or a few key interacting species, as exhibited here.

Modeling drivers of community structure on rocky reefs

There have been multiple previous efforts to model kelp forest communities on rocky reefs around the world, utilizing a variety of modeling structures and analytical frameworks. Time and again these models demonstrate the primacy of predator mortality rates (fishing and natural mortality) in driving community structure (Marzloff et al. 2013, Blamey et al. 2014, Eddy et al. 2014, 2015, Dunn et al. 2017) as well as recovery times on the scale of decades or more (Blamey et al. 2013, Marzloff et al. 2016, Johnson et al. 2017, Steyn 2019). For example, a model of Tasmanian rocky reefs exhibits similar results to our simulations: reduced lobster fishing and implementing urchin culling can limit the likelihood of barrens formation, but hysteresis in the system requires drastic management action in order to reverse the system from an urchin barren to an algal-dominated state (Marzloff et al. 2016). Interestingly, this model, which includes size-structure for lobsters, demonstrates that a maximum size limit for lobsters (i.e., a slot-limit regulation) could be a useful management tool, but only when lobster fishing mortality is high. At modest harvest rates, sufficient lobsters reach large size classes so that a slot-limit does not substantially reduce the risk of barren formation (Marzloff et al. 2016). We suspect that this finding could affect recovery trajectories of our kelp forest system because when lobsters are initially harvested in a slot-limit fishery, return times should be much more rapid than when only a minimum size is enforced. This is because large lobsters provide both strong predation pressure on urchins (Ling et al. 2009, Eddy et al. 2014, Eisaguirre et al. 2020), as well as enhanced egg production relative to smaller lobsters (R. Dunn, *unpublished data*), potentially speeding recovery through stronger top-down pressure (Fig. 3B) and enhanced recruitment (Fig. 4B), respectively. Interestingly, an ecosystem model for coastal New Zealand is parameterized to indicate increased herbivory for recovering lobsters due to reduced prey abundance (Eddy et al. 2014). This has not been demonstrated empirically in our model system to date, but could have important implications for lobster–urchin predation rates, and by extension, transient dynamics during the recovery period.

Transient dynamics and recovery in multi-trophic level systems

Understanding ecological processes through time is at the heart of many important questions in ecology, and the short-term response of a system to a perturbation (its transient behavior) can differ drastically from its long-term equilibria (Hastings et al. 2018). Our simulations demonstrate the transient nature of species responses following fishery closure, as observed empirically for rocky reef communities (Babcock et al. 2010). All compartments exhibit damped oscillations for tens to hundreds of years, depending on the ecological architecture and fishery closure scenario, though some of our estimated return times are shorter than empirical data suggest is generally the case (Hutchings 2000). The duration of the transient period (return time) is strongly dependent on the initial state of the system (Fig. 2), which in our case is a direct result of the fishery mortality rates of predators and prey prior to fishery closure (Dunn et al. 2017). The importance of harvest mortality prior to reserve establishment on recovery time (White et al. 2013, Kaplan et al. 2019) and abundance or biomass responses to reserves (Micheli et al. 2004, Jaco and Steele 2020) are well documented. We show that this is also true for recovery volatility, where initial lobster fishing rate (F_L) was typically the main driver of volatility when starting from the kelp forest state (Appendix S1: Fig. S4). Importantly, we also demonstrate that predatory attack rates can determine recovery volatility, particularly when initial conditions are in the overfished state (Appendix S1: Fig. S5).

We intend our model for strategic use to qualitatively compare different management approaches rather than tactical use to make precise predictions (Collie et al. 2016). Nevertheless, analysis of system behavior during the transient period can provide important insights into ecological systems, predator–prey dynamics (Hastings 2004) and management applications (Hastings 2016) in particular. We utilize two general measures of transient behavior that may be particularly useful in a management context. First, the time lag between when a management action is taken and when the maximum volatility of the system occurs can inform the timeline for evaluation of management efficacy in monitoring and adaptive management. Second, the duration of recovery within asynchronous management scenarios (predator- or prey-first closures) could provide managers with information regarding the social-ecological trade-offs required when planning for recovery from multi-trophic level harvest (discussed further below). Finally, quantifying the drivers of transient dynamics can provide insight into which species and associated life histories provide higher or lower reliability for monitoring (White et al. 2011, 2013, Kaplan et al. 2019).

Theoretical context

Our model includes several simplifying assumptions that have the potential to alter recovery planning for harvested species. First, we did not include any sources of environmental stochasticity, which can drive rocky reef community structure via kelp loss during storms and temperature-dependent nutrient availability (Jackson 1977, Seymour et al. 1989, Cavanaugh et al. 2011). In addition, stochastic recruitment pulses may be particularly important in the case of recovery dynamics by determining the likelihood of return to the unexploited equilibrium (Nickols et al. 2019). Sea urchins and spiny lobsters can exhibit episodic recruitment (Pringle 1986, Shears et al. 2012), which can cascade to kelp abundance and determine the community state under feedbacks that lead to alternative stable states (Karatayev and Baskett 2019). Second, we describe only a sub-module of the diverse kelp forest food web, and the alternative predators and prey not included could strongly influence recovery trajectories. For example, California sheephead (*Semicossyphus pulcher*) is a large-bodied fish that consumes both sea urchins (Cowen 1983, Dunn and Hovel 2019) and juvenile spiny lobsters (Loflen and Hovel 2010) and is recovering from a harvest-induced population decline (Hamilton and Caselle 2015). The local abundance of sheephead could strongly influence population dynamics of both spiny lobsters and sea urchins through intra-guild predation (Polis and Holt 1992). In addition, predator specialization can lead to delayed recovery for both biomass and mean body size (Aalto and Baskett 2017), and our sub-web model does not include all potential prey for a generalist predator. Third, our size-structured model assumes that growth, mortality, and fecundity rates are deterministic and not influenced by environmental conditions or conspecific density. A result of this framework is potential misestimation of the time spent in each stage due to a fluctuating environment or density-dependence affecting demographic rates (De Roos et al. 1992).

Our choice to model the behavioral feedbacks between urchin grazing and predator recovery implicitly (rather than an explicit, density-dependent formulation) is based on the fact that the spatial scale at which predators can induce changes in prey behavior within marine ecosystems remains poorly defined, though an area of active research (Dunn et al. 2018, DiFiore et al. 2019). Thus, we used a simpler implementation to model the effect of predators on prey grazing behavior, implicitly changing urchin grazing rates based on a delay following management action. Importantly, when urchin grazing behavior was changed simultaneously with closing the predator fishery, results were similar (Appendix S1: Fig. S2); an explicitly modeled, density-dependent parameterization is expected to be very similar to the delayed non-consumptive effect case based on the return time associated with the lobster compartment (~12 yr; Fig. 2B) and the 10-yr delay we implemented, established from empirical data (Babcock et al. 2010). Finally, predators in our model are not size-structured despite evidence that larger lobsters exhibit increased top-down control on sea urchins (Ling et al. 2009, Ling and Johnson 2012, Eisaguirre et al. 2020). Generally, our aim was to develop a moderate-complexity, "sweet-spot" model with both flexibility and specificity (Collie et al. 2016), so simplifying assumptions were required for analytical tractability. Exploration of the effects of stochastic events on recovery would be a valuable future development, as would the derivation of transient metrics for multispecies models using the Jacobian of the system, analogous to the population-level, discrete-time metrics introduced by White et al. (2013).

Integrating community ecology into environmental management

Predator-first, prey-first, and synchronous fishery closures are approximately equally likely to be implemented for a given multi-trophic level fisheries management situation, though predator-first management is typically least observed historically (Samhouri et al. 2017). However, recovering top predators, particularly marine mammals, appear to strongly affect their prey (Swain et al. 2019), with pinnipeds, for example, potentially removing enough fish biomass to cause conflicts with fisheries (Chasco et al. 2017). Managers have the difficult task of balancing competing interests when attempting to grow populations of interacting species, suggesting that an ecosystem-based management approach that explicitly accounts for biotic relationships could help to optimize ecosystem services in a multispecies context (Kellner et al. 2011).

To more fully explore the social and ecological tradeoffs of different management strategies, future analyses of multispecies recovery trajectories could incorporate the ex-vessel values of harvested predator and prey and use optimal control analysis to explore more nuanced pathways to recovery over time (e.g., Essington et al. 2018). Future investigations could also include reduced exploitation rather than outright bans on harvest, or varying the length of the initial closure period under sequential management. Varying degrees of exploitation reduction within a network of marine reserves strongly impacts community abundance, biomass, and size distribution (Rife et al. 2013), and long-term differences in the level of fishery exploitation can set the stage for different patterns of recovery across space (Collie et al. 2013). However, the degree to which varying levels of exploitation reduction (vs. an outright harvest ban) leads to differences in recovery outcomes within a multi-trophic level fishery context has, to our knowledge, not been explored comprehensively (Oken and Essington 2016). Similarly, varying time lags between sequential fishery closures is an additional dimension that could be explored, but to date has not received attention from researchers. In particular, varying the time lags between sequential fishery closures while accounting for species generation times across trophic levels could inform recovery strategies more broadly. In our model system, predators and prey reach sexual maturity on similar time-scales (<5 yr), but that need not always be the case. For example, predatory lingcod reproduce at <5 yr (Haltuch et al. 2018) while their rockfish prey can take 20 yr or more to reach sexual maturity (Conrath 2017). Finally, future work focused explicitly on conservation goals could also examine the recovery of non-fished components of this model community (or others) in further detail.

Ultimately, confronting models with data will be required to gauge the efficacy of synchronous conservation tools such as marine protected areas (White et al. 2011). Comparing our simulations against data from future in situ sampling of predator and prey abundance within the recently established protected area network in southern California (California Department of Fish and Game 2008) will provide an empirical estimate of synchronous management. There is also potential to compare synchronous vs. sequential management between reserves (synchronous closure) and historically fished areas in northern California following the recent closure of the recreational abalone fishery (sequential closure) due to widespread kelp loss (Rogers-Bennett and Catton 2019). As marine reserves are increasingly implemented and populations of overharvested species grow, empirical explorations of recovery trajectories will boost the capacity to test theoretical predictions.

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SUPPORTING INFORMATION

Additional supporting information may be found online at: http://onlinelibrary.wiley.com/doi/10.1002/eap.2367/full

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Code (Dunn et al. 2021) associated with these analyses is available from Zenodo: https://doi.org/10.5281/zenodo.4521227.