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

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33

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

56 down control, a predator-first fishery closure can be the most effective strategy to reduce
57 volatility and shorten recovery, particularly when the system is starting from the degraded
58 community state. Given the ubiquity of top predator loss across many ecosystems, we highlight
59 the value of incorporating insights from community ecology into ecosystem management.

60
61 **Keywords:** ecosystem-based management, fishery closure, non-consumptive effects, recruitment
62 facilitation, size-structured predation

63 64 **Introduction**

65 Restoration often involves reversing human impacts that have affected multiple species in
66 a community, with ecosystem-level goals of restoring system structure and function (Bradshaw
67 1996). However, many restoration and recovery interventions, such as harvest moratoria or
68 species reintroductions, target one species at a time. How interventions targeted at single species
69 interact to drive the rate and success of overall system recovery, up to and including top
70 predators, inevitably will depend on species interactions, as increasingly recognized across
71 ecosystems (marshes: Silliman et al., 2015; corals: Ladd et al., 2018; grasslands: Young et al.,
72 2017). Nevertheless, examples of jointly recovering species offer relatively few generalities for
73 managers beyond the need to recognize trade-offs as predator populations recover. For example,
74 a growing population of bald eagles hindered population growth of ospreys and herons via
75 reduced nesting success (Cruz et al. 2019), and protected white sharks may be contributing to
76 slowed recovery of sea otters due to naïve juvenile sharks mis-targeting sea otters as a prey item
77 (Moxley et al. 2019). Similarly, accounting for species interactions is integral to an ecosystem-
78 based approach to fisheries management (EBFM; Larkin 1996). For example, in the case of
79 Baltic Sea cod and their forage fish prey, modelling suggests that incorporating environmental
80 conditions and trophic interactions into adaptive management decisions would lead to improved
81 biological and economic outcomes compared with traditional management (Lindgren et al.
82 2009). In some cases, where declines in fished species have occurred, protection from fishing
83 alone does not ensure recovery due to fishery-induced alterations in predator-prey or competitive
84 interactions (Mangel and Levin 2005, Baskett et al. 2006). Thus, biotic interactions among

85 recovering species can play key roles in the trajectory and likelihood of success of system
86 rehabilitation (Perring et al. 2015, Marshall et al. 2016, Stier et al. 2016).

87 The importance of accounting for these community interactions is well illustrated by
88 marine ecosystems, where serial depletion of living marine resources (e.g., harvested fish and
89 invertebrates) has led to calls for rebuilding harvested stocks (NOAA 1996), often without
90 guidance on how rebuilding should be implemented. Closing a fishery or heavily restricting
91 harvest rates are species-specific management measures aimed at recovery of the target
92 population. An alternative is the establishment of a spatial closure, or no-take marine reserve
93 (hereafter, “reserve”), in which harvest of all species is prohibited within a defined geographic
94 area. Establishing reserves and closing single-species fisheries thus lead to inherently different
95 recovery scenarios, as entire communities (and potentially multiple fished species) are protected
96 inside reserves while fishery closures typically act on a single species. While many species
97 increase following reserve establishment (Lester et al. 2009), recovery is not a given and there
98 are notable cases of both single species closures (Hutchings 2000) and reserves (Micheli et al.
99 2004) in which population increases do not immediately occur. Trophic interactions are one
100 mechanism which can drive these population responses. For example, predator-prey role
101 reversals, in which small pelagic fish feed on the eggs of their predators, can maintain low levels
102 of predator recruitment even following fishery closure (Minto and Worm 2012). The potential
103 for delayed or impeded recovery due to species interactions raises the question of whether
104 managing fishery closures sequentially (versus independently or simultaneously) might more
105 effectively achieve community-level recovery goals.

106 The path that a population or community follows through time after harvest stops, or its
107 recovery trajectory, can be fundamentally different from its long-term, equilibrium outcome
108 (White et al. 2013, Hastings et al. 2018). Understanding system behavior during the transient
109 period following a perturbation (in this case, cessation of harvest) is necessary to inform
110 monitoring expectations for adaptive management (White et al. 2011) and to determine what
111 management strategies lead to the most rapid recovery. To this end, recent work focused on the
112 transient period following fishery closure (or reserve establishment) has demonstrated that
113 intensity of harvest mortality relative to natural mortality can determine the distance from the
114 unharvested equilibrium and therefore sets the time scale for the lag in reaching that equilibrium
115 (White et al. 2013). In addition, oscillatory behavior can occur as part of the deterministic return

116 to equilibrium, and can depend on a species' life history, in particular the age at maturity (White
117 et al. 2013). Meanwhile, fishery benefits via enhanced larval export from reserves may take
118 decades to be achieved as a result of the time lag between reserve establishment and biomass
119 build-up of adult individuals (Hopf et al. 2016). Thus, recognizing that protected populations
120 might not immediately increase and that initial trends may not be indicative of long-term
121 outcomes due to the transient period following fishery closure can help to inform the time-scale
122 for judging the efficacy of management actions (Hastings 2016).

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

142 Our primary aim in this study is to quantify the effect of sequential versus simultaneous
143 fisheries closures on the recovery of exploited species which are linked through trophic
144 interactions. Secondly, we explore the dependency of that management outcome on an array
145 of ecological dynamics occurring within the recovering community. These include size-
146 structured interactions between predators and prey, non-consumptive effects of predators on prey

147 behavior, and various recruitment scenarios (e.g., recruitment facilitation, open versus closed
148 populations). We also investigate the effect of initiating recovery from community states at
149 varying degrees of degradation. In most cases we examine recovering from simultaneous harvest
150 of predators and prey, but in one case we also explore the effect of an additional fishery for the
151 basal resource, thereby creating a tri-trophic level harvest scenario. To achieve these aims, we
152 analyse the recovery from fishing of a rocky reef community using a size-structured, tri-trophic
153 level model (Fig. 1), with fisheries for predators, prey, and the basal resource. Finally, we
154 provide a case-study of potential recovery expectations using the predator-first closure strategy
155 while incorporating uncertainty in parameter values. Quantifying the transient response of
156 complex communities to various recovery strategies, as we do here, can help to set expectations
157 for the time scale and trajectory of recovery in an ecosystem-based management framework.

158 **Methods**

159 *Model system*

160 Rocky reefs are a common habitat on temperate coasts globally and can be observed in a
161 range of community states, from kelp forests dominated by foundational macroalgae to urchin
162 barrens with high densities of sea urchins and covered in crustose coralline algae with low kelp
163 cover (Filbee-Dexter and Scheibling 2014). Predators may control the abundance and
164 distribution of the kelp forest state by consuming urchins (Shears and Babcock 2002, Ling et al.
165 2009, Hamilton and Caselle 2015), although physical factors can also determine the distribution
166 of macroalgae (Schiel and Foster 2015), and predators do not provide top-down control in all
167 contexts (Dunn and Hovel 2019). In southern California, red sea urchins (*Mesocentrotus*
168 *franciscanus*) and one of their predators, the California spiny lobster (*Panulirus interruptus*), are
169 subject to simultaneous harvest from rocky reefs. Our model tracks the dynamics of macroalgae
170 (also referred to as kelp) on these reefs, as well as three size compartments of herbivorous sea
171 urchins (encompassing purple sea urchins *Strongylocentrotus purpuratus* as well as red urchins),
172 and predatory spiny lobsters (Fig. 1). Within the model, kelp grows logistically and is eaten by
173 urchins at size-specific rates. Small urchins are produced by medium and large urchins, and large
174 urchins also facilitate recruitment of small urchins via protection under their spine canopy.
175 Urchins grow into subsequent size classes and die at a background mortality rate. Predatory
176 lobsters consume urchins at size-specific rates with a saturating, type II functional response.
177 Lobsters then convert urchins into population growth and die at a background mortality rate.

178 Large urchins, lobsters, and the basal resource, kelp, can be harvested in individual fisheries. We
179 include size-structure for urchins because predation, recruitment facilitation, and harvest (and
180 therefore their interactive effects on the rocky reef community) all depend on urchin size. For
181 complete model details, including equations and parameter values, see Appendix S1 and Dunn et
182 al. (2017).

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

198 *Simulation & analysis*

199 We simulated the recovery of this community from harvest under synchronous and
200 sequential recovery scenarios, given five different assumptions about ecological processes or
201 fishery dynamics occurring within it. To characterize the degree of variability and duration of the
202 transient period following fishery closure, we quantified the community volatility and return
203 time of the fished compartments in the rocky reef model (Fig. 1B). These two metrics measure
204 the time scale of recovery (return time) and the degree of variability in the recovery path
205 (volatility), where increased return time and increased volatility indicate longer times to and
206 larger departures from the target ecosystem structure (Samhuri et al. 2017). These two metrics
207 are roughly analogous to the metrics of transient duration and amplitude of oscillations in single-
208 species models of recovery from fishing (White et al. 2013). We focused on the previously

209 fished compartments (generally, lobsters and large urchins, but in one case kelp as well) because
210 of their importance to managers and resource users. Other unharvested compartments tended to
211 have large responses to management actions that were not ultimately reflected in the fished
212 compartments, and thus in some cases obscured the effects of interest. In addition, recovery of
213 red urchins is a specific fisheries management goal. Most urchins within high density barrens are
214 smaller purple urchins which are not harvested, thus, re-building populations of large red urchins
215 (which are harvested and long-lived), does not necessarily lead to the degraded urchin barren
216 community state.

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

228 We used this analytical framework to assess recovery trajectories for simultaneous,
229 predator-first, and prey-first closures, focusing on fished species volatility and return time.
230 Following Samhouri et al. (2017), we calculated fished species volatility as the proportional
231 difference (i.e., the ratio) between the maximum summed biomass of previously harvested
232 species that was achieved during the transient phase following fishery closure and their summed
233 unexploited equilibrium biomass. For return time, we measured the length of time (y) from when
234 recovery began (i.e., when fishing mortality was set to zero for at least one trophic level) to when
235 summed biomass for all previously harvested species remained within 10% of its long-term
236 equilibrium. We calculated return time under the assumption that a manager implements the next
237 step in sequential recovery as soon as the system equilibrates following the previous
238 management action. That is, although we ran each simulation for 200 y, we determined the time
239 point when summed harvested species biomass remained within 10% of its long-term

240 equilibrium, disregarding the remaining years. We also report the time point at which the
241 maximum fished community volatility occurred as well as the portion of the return time
242 attributed to predator and prey recovery, respectively, for sequential closure scenarios. Because
243 simulations are deterministic, once harvest is stopped the system always returns to the
244 unexploited state (upon reaching equilibrium), but with different levels of volatility and return
245 times.

246 Size-structured predation

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

260 Non-consumptive effects of predators

261 Next, we tested the importance of including a non-consumptive effect (*sensu* Blaustein
262 1997) of predators on prey behavior following the closure of the fishery for predators. We
263 modelled this behavior by reducing the attack rates of small and medium urchins on kelp (δ_{U_s}
264 and δ_{U_m}) following the closure of the lobster fishery (see Appendix S1: Table S1 for parameter
265 values). We chose this implicit approach rather than explicitly modeling behavioral feedbacks in
266 order to maintain the same base model structure across the different scenarios. Nevertheless,
267 indirect effects of marine reserves, such as the behavioral shifts described above, on average
268 appear after 13 y (Babcock et al. 2010), and we accounted for this delay in behavioral changes
269 by altering the parameter values associated with urchin grazing after a 10 y “build-up” period
270 following the closure of the spiny lobsters fishery (knife-edge change in grazing rates after 10 y).

271 However, we also provide the results of simulations in which we forced reduced urchin grazing
272 to occur simultaneously with setting predator harvest equal to zero, creating an instantaneous
273 non-consumptive effect (Appendix S1).

274 Recruitment patterns

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

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

293 Community degradation due to fishing

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

300 Three-tiered fishery (including kelp harvest)

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

312 Sensitivity analysis

313 Each of the above scenarios could be considered a local sensitivity analysis. To
314 understand the importance of all individual parameters in driving transient volatility of the fished
315 community, and to quantify the range of possible recovery trajectories given uncertainty in
316 parameter values (due to spatio-temporal variability in carrying capacity, growth rates, and
317 predation parameters, among others), we conducted global sensitivity analyses. For both
318 analyses, we used a single set of 4,000 parameter combinations drawn at random from a range of
319 potential values (parameter ranges provided in Appendix S1: Table S1). First, to understand the
320 importance of individual parameters in driving fished species volatility during the transient
321 period, we conducted random forest analyses (Harper et al. 2011). We used all 4,000 model runs
322 to calculate normalized importance values for each parameter under each of the three
323 management scenarios (synchronous, predator-first, or prey-first closure), initiating the model
324 from both the kelp forest and the urchin barren community (8,000 total model runs). Modelled
325 conditions when initiating fishery closures and starting the recovery phase were thus caused by a
326 combination of our initial community states, either kelp forest or urchin barren, as well as the
327 fishing mortality rates introduced within the global sensitivity analysis. Thus, for "kelp forest"
328 simulations within the global sensitivity analysis, randomly selected fishing rates could still have
329 been high enough to drive the system to a degraded state prior to initiating fishery closures.
330 Analogously, for the "urchin barren" simulations with low fishing harvest rates during the initial
331 harvesting period, recovery could have begun from a less degraded state. Parameter importance

332 values are a measure of how informative each parameter is in predicting fished species volatility,
333 and we normalize values to sum to 1 to aid their interpretability. Parameters with high
334 importance values have strong impacts on volatility during the transient period, given the
335 model's assumptions. Second, to provide an example of how our results could be applied on pre-
336 specified management time-scales while incorporating parameter uncertainty, we simulated the
337 model for all 4,000 parameter combinations using the predator-first closure management
338 strategy, which we implemented by first closing the lobster fishery ($F_L = 0$) and running the
339 model for 2 y, and then closing the urchin fishery ($F_U = 0$) and running for an additional 15 y.
340 From these simulations, we examined the biomass response of the recovering fished community
341 through time. For each of the 4,000 model simulations under both sets of initial conditions, we
342 present the range of recovery trajectories (recovering biomass time series) and plot the
343 distributions of fished species biomass (lobsters + large urchins) at 5, 10, and 15 y after the
344 closure of both fisheries (8,000 total model runs). We base this time horizon on the ~5-year
345 recurring monitoring events used for management of marine protected areas in California, U.S.A.

346 **Results**

347 In contrast to previous results suggesting synchronous management of predators and prey
348 to be more efficient than either sequential closure strategy (Samhuri et al. 2017), our model
349 demonstrated that predator-first closures provided the least volatile and most rapid recovery in
350 nearly all simulated scenarios in our model system. The prey-first strategy generally led to the
351 least effective recovery outcomes (Figs. 2-4), in agreement with previous findings (Samhuri et
352 al. 2017). When recovery began in the kelp-dominated or moderately degraded state,
353 synchronous closure of predator and prey fisheries demonstrated a similar trajectory to predator-
354 first management (differences in fished community volatility were $< 13\%$, volatility peaked at
355 the same point, and return times were within 1 y using the baseline parameterization; Fig. 2).
356 Conversely, when the system was already severely degraded due to high fishing mortality rates
357 (i.e., initial conditions were in the urchin barren), a predator-first closure outperformed
358 synchronous and prey-first management in both fished species volatility and return time, and
359 peak volatility occurred earlier (Fig. 2). A prey-first closure is particularly sub-optimal in this
360 case (return time = 161 y versus 61 y for the predator-first case) because low predation rates on
361 the largest urchins, when combined with the closure of the urchin fishery, allow them to persist

362 for generations (red urchin age-at-maturity ~ 5 y, Ebert et al. 1999; purple urchin age-at-maturity
363 ~ 2 y, Kenner and Lares 1991) in the low-kelp, low-lobster state.

364 The shape of the size-structured predation function did not alter our finding that a
365 predator-first closure was generally least volatile and fastest, although when we removed size-
366 structure so that all prey were equally likely to be consumed, all three management scenarios
367 provided virtually equivalent results (Fig. 3). The mechanism for this pattern is that with the
368 assumption of size-independent predation, there is an increased probability of predation mortality
369 for large urchins during the recovery of predatory lobsters, accelerating the return to the kelp
370 state. When the predation function was hump-shaped, return time in the predator-first case was
371 reduced by more than 50 % (Fig. 3). The mechanism is again that the assumption of hump-
372 shaped, size-structured predation reduced the likelihood of urchins reaching the large size-class
373 due to high predation on medium sized individuals, speeding up recovery to the kelp state.
374 Interestingly, the shape of the size-structured predation function had differing effects on the
375 timing of peak volatility, which was later by at least 2 years for all three management scenarios
376 under the hump-shaped parameterization (Fig. 3A), even though return times were reduced or
377 similar to the other size-structure cases (Fig. 3B). All of the transient behavior occurred
378 following the lobster fishery closure, while the closure of the urchin fishery contributed very
379 little to the return time (Fig. 3B).

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

393 the delayed non-consumptive effects case, urchins can continue to consume kelp at high rates
394 until predator biomass is sufficient to alter their grazing behavior, lengthening recovery time.

395 Simulations testing various recruitment scenarios demonstrated that exogenous
396 recruitment (i.e., open populations supported from outside) led to reduced volatility (though the
397 timing of peak volatility was similar) and shorter return times than the corresponding ‘closed
398 population’ scenarios. This was the case whether starting conditions were in the kelp forest or
399 urchin barren, or if non-consumptive effects of predators were included (Fig. 4). The mechanism
400 behind this result is that with open population dynamics there is no time lag in recruitment
401 during the transient period following fishery closure. The impact of exogenous recruitment was
402 most evident when comparing simulations with initial conditions in the urchin barren: recovery
403 from the barren state to the unexploited equilibrium using the predator-first closure strategy was
404 shortened by 85% and volatility was reduced by 44% when populations were open compared
405 with our initial simulations of a closed population (Figs. 2 & 4). These gains were even greater
406 when focusing on the least effective management strategy based on our metrics (prey-first):
407 volatility was more than halved and return times were shortened by an order of magnitude (160 y
408 versus 12 y; Figs 2 & 4). In contrast to external recruitment, removing recruitment facilitation by
409 adult urchins reduced volatility relatively little compared to the baseline scenario, though return
410 times were halved (6 y versus 12 y for all three management scenarios; Figs. 2 & 4). In all
411 simulations altering recruitment processes, predator-first closure was again typically the least
412 volatile and fastest (Fig. 4), though the gains achieved by choosing predator-first closure were
413 substantially reduced when exogenous recruitment occurred (we show a similar result when
414 removing recruitment facilitation; Figs. 2B & 4B). As with other scenarios, closing the lobster
415 fishery contributed to the majority of the transient behavior during recovery (Fig. 4B).

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

424 community biomass (Appendix S1: Fig. S3B) compared with only including lobster and urchin
425 biomass (Appendix S1: Fig. S3A), as we did for the two-trophic level harvest scenarios.

426 Global sensitivity analysis using random forests demonstrated that regardless of the
427 recovery strategy or initial community structure, community volatility during recovery is largely
428 driven by the initial fishing mortality rate for lobsters (F_L) or the attack rate of lobsters on small
429 urchins ($\delta_{L,s}$). Together, these two parameters account for over 50% of the normalized
430 importance value in each recovery scenario (Appendix S1: Fig. S4-5). Interestingly, urchin
431 fishing mortality (F_U) was moderately important only in the predator-first closure cases (~5% of
432 normalized importance value versus < 1% for prey-first and synchronous closures; Appendix S1:
433 Fig. S4-5).

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

443 **Discussion**

444 Population depletion in many fisheries has led to calls for rebuilding of exploited species
445 (NOAA 1996, Safina et al. 2005), and prompted a concerted effort to understand the “how”
446 (Wakeford et al. 2009, Neubauer et al. 2013) and “why” (Sumaila et al. 2012) of rebuilding
447 harvested stocks. Importantly, connecting rebuilding mandates to rebuilding strategies is now
448 feasible and typically includes consideration of ecological processes (Link 2002, Mangel and
449 Levin 2005). For our modelled kelp forest, predator-first closures generally provide the fastest
450 and least volatile recovery strategy. This is the case for most of the ecological processes we
451 examined, but is particularly evident when initiating recovery from the degraded urchin barren
452 community. Size-structured predation and recruitment facilitation are two modelled feedbacks
453 that can lead to alternative stable states under certain parameter combinations with this model
454 (Dunn et al. 2017), but alternative stable state dynamics only occur when fishery harvest is

455 occurring and therefore do not apply in the case of zero fishing mortality that is the end state
456 here. Nevertheless, these feedbacks can make recovery from the barren state particularly slow
457 (for all three management scenarios) and volatile (for prey-first and synchronous closures),
458 magnifying the gains from selecting the predator-first closure strategy.

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

482 *Modeling drivers of community structure on rocky reefs*

483 There have been multiple previous efforts to model kelp forest communities on rocky
484 reefs around the world, utilizing a variety of modelling structures and analytical frameworks.
485 Time and again these models demonstrate the primacy of predator mortality rates (fishing and

486 natural mortality) in driving community structure (Marzloff et al. 2013, Blamey et al. 2014, Eddy
487 et al. 2014, 2015, Dunn et al. 2017) as well as recovery times on the scale of decades or more
488 (Blamey et al. 2013, Marzloff et al. 2016, Johnson et al. 2017, Steyn 2019). For example, a
489 model of Tasmanian rocky reefs exhibits similar results to our simulations: reduced lobster
490 fishing and implementing urchin culling can limit the likelihood of barrens formation, but
491 hysteresis in the system requires drastic management action in order to reverse the system from
492 an urchin barren to an algal-dominated state (Marzloff et al. 2016). Interestingly, this model,
493 which includes size-structure for lobsters, demonstrates that a maximum size limit for lobsters
494 (i.e., a slot-limit regulation) could be a useful management tool, but only when lobster fishing
495 mortality is high. At modest harvest rates, sufficient lobsters reach large size classes so that a
496 slot-limit does not substantially reduce the risk of barren formation (Marzloff et al. 2016). We
497 suspect that this finding could affect recovery trajectories of our kelp forest system because when
498 lobsters are initially harvested in a slot-limit fishery, return times should be much more rapid
499 than when only a minimum size is enforced. This is because large lobsters provide both strong
500 predation pressure on urchins (Ling et al. 2009, Eddy et al. 2014, Eisaguirre et al. 2020), as well
501 as enhanced egg production relative to smaller lobsters (Dunn, unpublished data), potentially
502 speeding recovery through stronger top-down pressure (Fig. 3B) and enhanced recruitment (Fig.
503 4B), respectively. Interestingly, an ecosystem model for coastal New Zealand is parameterized to
504 indicate increased herbivory for recovering lobsters due to reduced prey abundance (Eddy et al.
505 2014). This has not been demonstrated empirically in our model system to date, but could have
506 important implications for lobster-urchin predation rates, and by extension, transient dynamics
507 during the recovery period.

508 *Transient dynamics and recovery in multi-trophic level systems*

509 Understanding ecological processes through time is at the heart of many important
510 questions in ecology, and the short-term response of a system to a perturbation (its transient
511 behavior) can differ drastically from its long-term equilibria (Hastings et al. 2018). Our
512 simulations demonstrate the transient nature of species responses following fishery closure, as
513 observed empirically for rocky reef communities (Babcock et al. 2010). All compartments
514 exhibit damped oscillations for tens to hundreds of years, depending on the ecological
515 architecture and fishery closure scenario, though some of our estimated return times are shorter
516 than empirical data suggest is generally the case (Hutchings 2000). The duration of the transient

517 period (return time) is strongly dependent on the initial state of the system (Fig. 2), which in our
518 case is a direct result of the fishery mortality rates of predators and prey prior to fishery closure
519 (Dunn et al. 2017). The importance of harvest mortality prior to reserve establishment on
520 recovery time (White et al. 2013, Kaplan et al. 2019) and abundance or biomass responses to
521 reserves (Micheli et al. 2004, Jaco and Steele 2020) are well documented. We show that this is
522 also true for recovery volatility, where initial lobster fishing rate (F_L) was typically the main
523 driver of volatility when starting from the kelp forest state (Appendix S1: Fig. S4). Importantly,
524 we also demonstrate that predatory attack rates can determine recovery volatility, particularly
525 when initial conditions are in the overfished state (Appendix S1: Fig. S5).

526 We intend our model for strategic use to qualitatively compare different management
527 approaches rather than tactical use to make precise predictions (Collie et al. 2016). Nevertheless,
528 analysis of system behavior during the transient period can provide important insights into
529 ecological systems, predator-prey dynamics (Hastings 2004) and management applications
530 (Hastings 2016) in particular. We utilize two general measures of transient behavior that may be
531 particularly useful in a management context. First, the time lag between when a management
532 action is taken and when the maximum volatility of the system occurs can inform the timeline for
533 evaluation of management efficacy in monitoring and adaptive management. Second, the
534 duration of recovery within asynchronous management scenarios (predator- or prey-first
535 closures) could provide managers with information regarding the social-ecological trade-offs
536 required when planning for recovery from multi-trophic level harvest (discussed further below).
537 Finally, quantifying the drivers of transient dynamics can provide insight into which species and
538 associated life histories provide higher or lower reliability for monitoring (White et al. 2011,
539 2013, Kaplan et al. 2019).

540 *Theoretical context*

541 Our model includes several simplifying assumptions that have the potential to alter
542 recovery planning for harvested species. First, we did not include any sources of environmental
543 stochasticity, which can drive rocky reef community structure via kelp loss during storms and
544 temperature-dependent nutrient availability (Jackson 1977, Seymour et al. 1989, Cavanaugh et
545 al. 2011). In addition, stochastic recruitment pulses may be particularly important in the case of
546 recovery dynamics by determining the likelihood of return to the unexploited equilibrium
547 (Nickols et al. 2019). Sea urchins and spiny lobsters can exhibit episodic recruitment (Pringle

548 1986, Shears et al. 2012), which can cascade to kelp abundance and determine the community
549 state under feedbacks that lead to alternative stable states (Karatayev and Baskett 2019). Second,
550 we describe only a sub-module of the diverse kelp forest food web, and the alternative predators
551 and prey not included could strongly influence recovery trajectories. For example, California
552 sheephead (*Semicossyphus pulcher*) are a large-bodied fish that consumes both sea urchins
553 (Cowen 1983, Dunn and Hovel 2019) and juvenile spiny lobsters (Loflen and Hovel 2010), and
554 are recovering from a harvest-induced population decline (Hamilton and Caselle 2015). The
555 local abundance of sheephead could strongly influence population dynamics of both spiny
556 lobsters and sea urchins through intra-guild predation (Polis and Holt 1992). In addition, predator
557 specialization can lead to delayed recovery for both biomass and mean body size (Aalto and
558 Baskett 2017), and our sub-web model does not include all potential prey for a generalist
559 predator. Third, our size-structured model assumes that growth, mortality, and fecundity rates are
560 deterministic and not influenced by environmental conditions or conspecific density. A result of
561 this framework is potential mis-estimation of the time spent in each stage due to a fluctuating
562 environment or density-dependence affecting demographic rates (De Roos et al. 1992).

563 Our choice to model the behavioral feedbacks between urchin grazing and predator
564 recovery implicitly (rather than an explicit, density-dependent formulation) is based on the fact
565 that the spatial scale at which predators can induce changes in prey behavior within marine
566 ecosystems remains poorly defined, though an area of active research (Dunn et al. 2018, DiFiore
567 et al. 2019). Thus, we used a simpler implementation to model the effect of predators on prey
568 grazing behavior, implicitly changing urchin grazing rates based on a delay following
569 management action. Importantly, when urchin grazing behavior was changed simultaneously
570 with closing the predator fishery, results were similar (Appendix S1: Fig S2); an explicitly
571 modelled, density-dependent parameterization is expected to be very similar to the delayed non-
572 consumptive effect case based on the return time associated with the lobster compartment (~12
573 y; Fig 2B) and the 10 y delay we implemented, established from empirical data (Babcock et al.
574 2010). Finally, predators in our model are not size-structured despite evidence that larger lobsters
575 exhibit increased top-down control on sea urchins (Ling et al. 2009, Ling and Johnson 2012,
576 Eisaguirre et al. 2020). Generally, our aim was to develop a moderate-complexity, ‘sweet-spot’
577 model with both flexibility and specificity (Collie et al. 2016), so simplifying assumptions were
578 required for analytical tractability. Exploration of the effects of stochastic events on recovery

579 would be a valuable future development, as would the derivation of transient metrics for multi-
580 species models using the Jacobian of the system, analogous to the population-level, discrete-time
581 metrics introduced by White et al. (2013).

582 *Integrating community ecology into environmental management*

583 Predator-first, prey-first, and synchronous fishery closures are approximately equally
584 likely to be implemented for a given multi-trophic level fisheries management situation, though
585 predator-first management is typically least observed historically (Samhouri et al. 2017).
586 However, recovering top predators, particularly marine mammals, appear to strongly affect their
587 prey (Swain et al. 2019), with pinnipeds, for example, potentially removing enough fish biomass
588 to cause conflicts with fisheries (Chasco et al. 2017). Managers have the difficult task of
589 balancing competing interests when attempting to grow populations of interacting species,
590 suggesting that an ecosystem-based management approach which explicitly accounts for biotic
591 relationships could help to optimize ecosystem services in a multi-species context (Kellner et al.
592 2011).

593 To more fully explore the social and ecological trade-offs of different management
594 strategies, future analyses of multi-species recovery trajectories could incorporate the ex-vessel
595 values of harvested predator and prey and use optimal control analysis to explore more nuanced
596 pathways to recovery over time (e.g., Essington et al. 2018). Future investigations could also
597 include reduced exploitation rather than outright bans on harvest, or varying the length of the
598 initial closure period under sequential management. Varying degrees of exploitation reduction
599 within a network of marine reserves strongly impacts community abundance, biomass, and size
600 distribution (Rife et al. 2013), and long-term differences in the level of fishery exploitation can
601 set the stage for different patterns of recovery across space (Collie et al. 2013). However, the
602 degree to which varying levels of exploitation reduction (versus an outright harvest ban) leads to
603 differences in recovery outcomes within a multi-trophic level fishery context has, to our
604 knowledge, not been explored comprehensively (Oken and Essington 2016). Similarly, varying
605 time lags between sequential fishery closures is an additional dimension that could be explored,
606 but to date has not received attention from researchers. In particular, varying the time lags
607 between sequential fishery closures while accounting for species generation times across trophic
608 levels could inform recovery strategies more broadly. In our model system, predators and prey
609 reach sexual maturity on similar time-scales (< 5 y), but that need not always be the case. For

610 example, predatory lingcod reproduce at < 5 y (Haltuch et al. 2018) while their rockfish prey can
611 take 20 y or more to reach sexual maturity (Conrath 2017). Finally, future work focused
612 explicitly on conservation goals could also examine the recovery of non-fished components of
613 this model community (or others) in further detail.

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

625
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634 **Supporting Information**

635 Additional supporting information may be found online at: [link to be added in production]

636 **Open Research**

637 Code (Dunn et al. 2021) associated with these analyses is available in Zenodo:
638 <https://doi.org/10.5281/zenodo.4521227>

639

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879 **Figure legends**

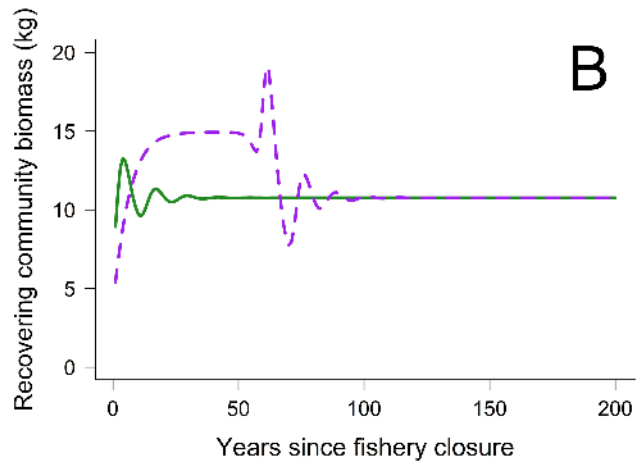
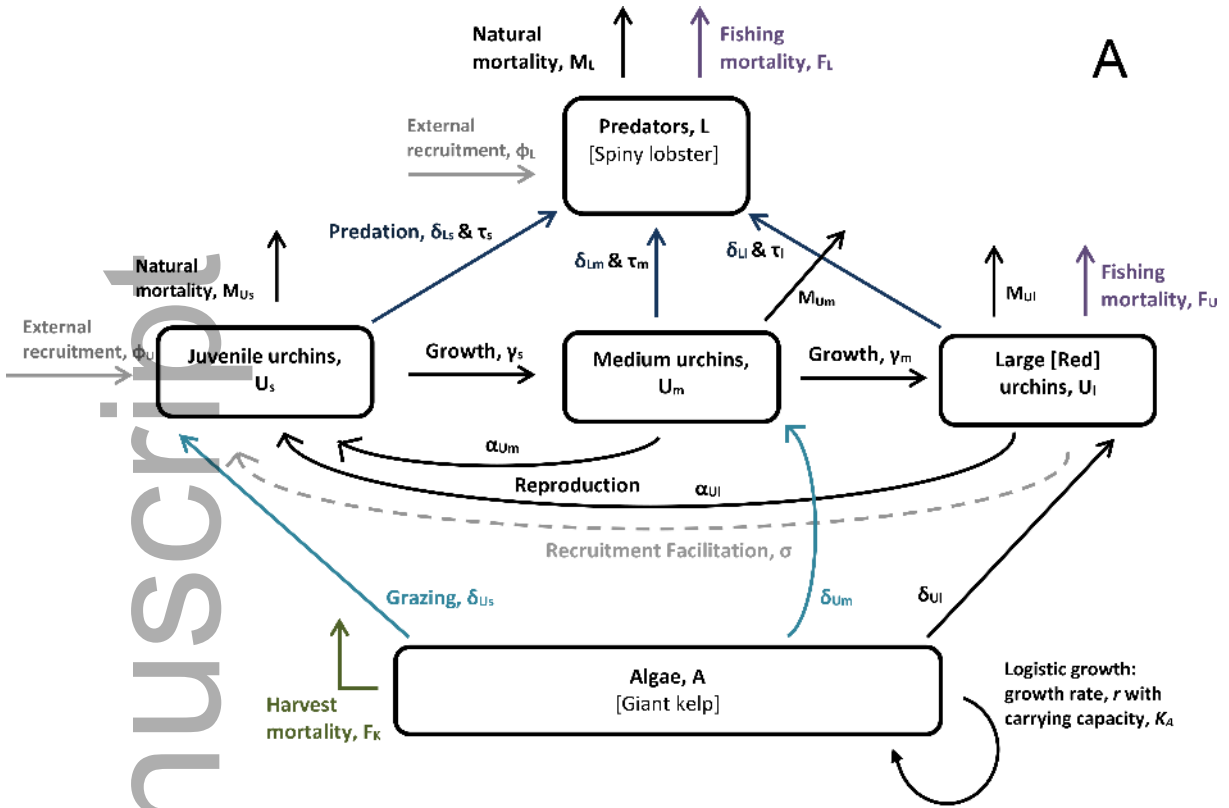
880 **Fig. 1:** Outline of the updated rocky reef community dynamics model (originally published:
881 Dunn et al. 2017) is shown in Panel A. Boxes indicate state variables; arrows indicate biomass
882 flows affecting dynamics and are labelled with the associated parameter names. Colored arrows
883 and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

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

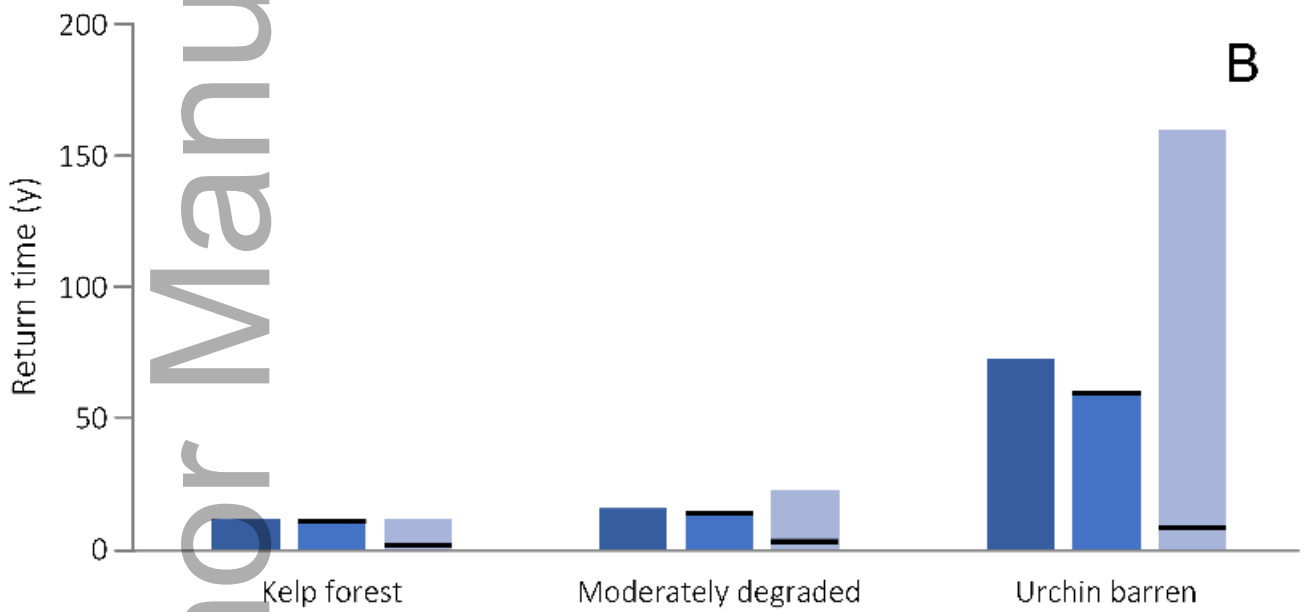
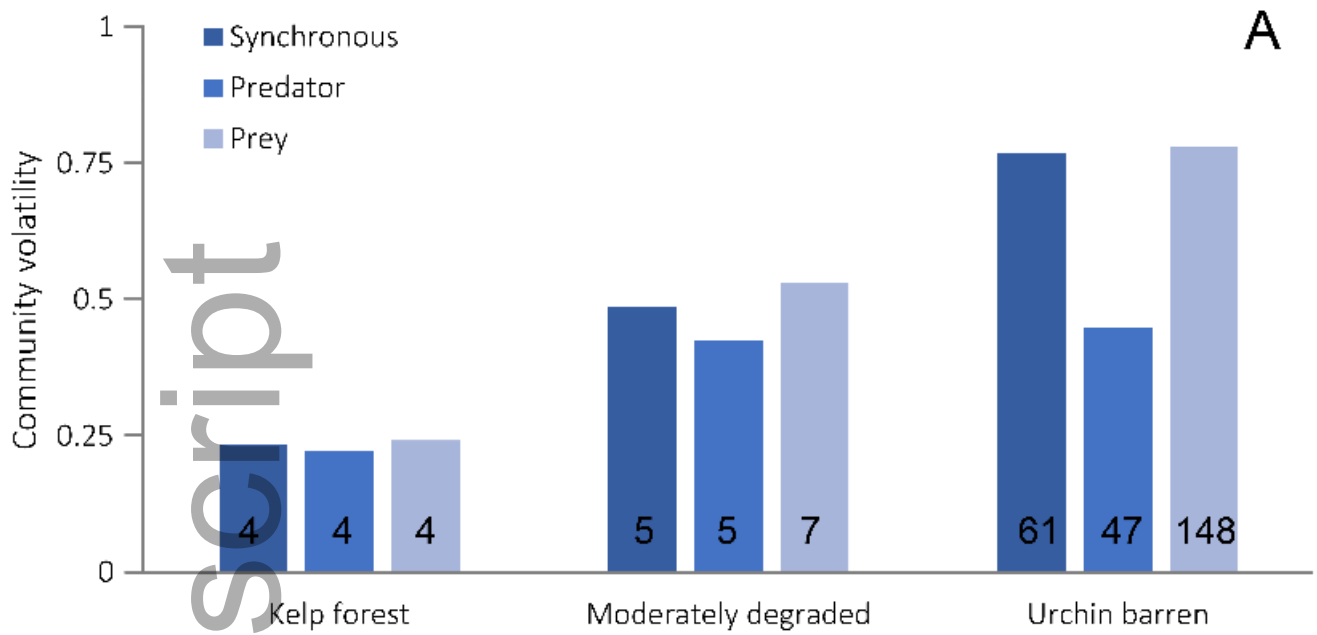
910 **Fig. 3:** Fished community volatility (A) and return time (B) for model simulations with alternate
911 shapes of the size-structured predation function, initiated from the kelp forest. Predator-first
912 recovery remains the least volatile and fastest return time (or tied, in the no size structure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

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

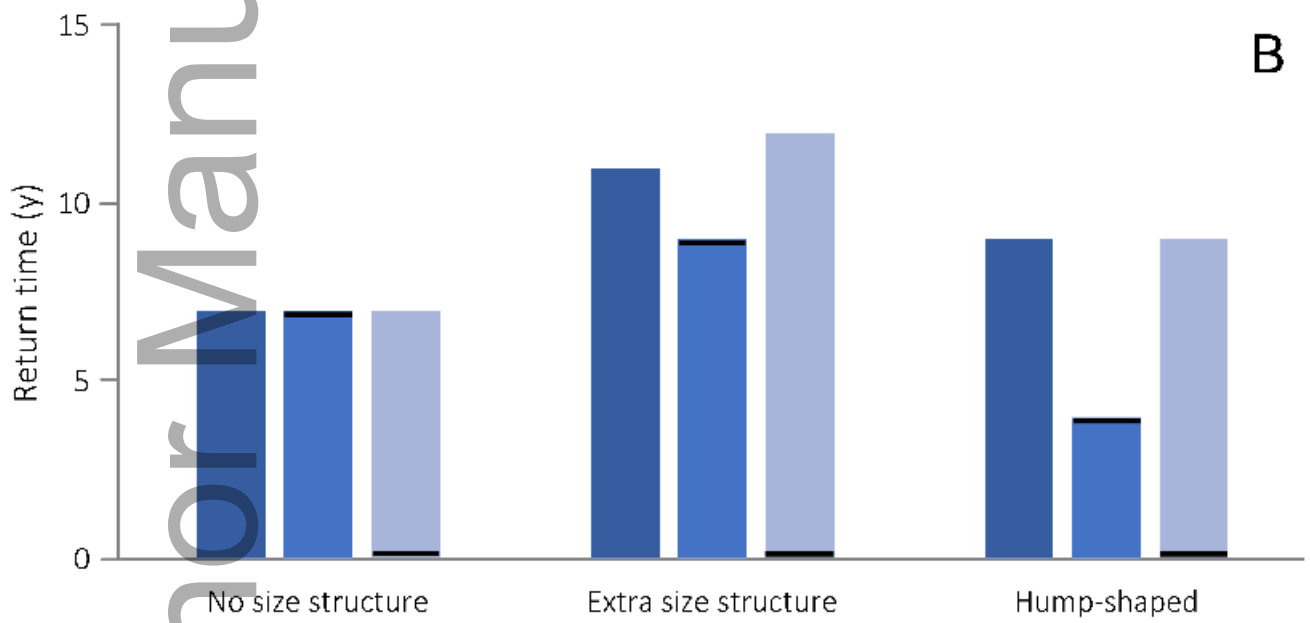
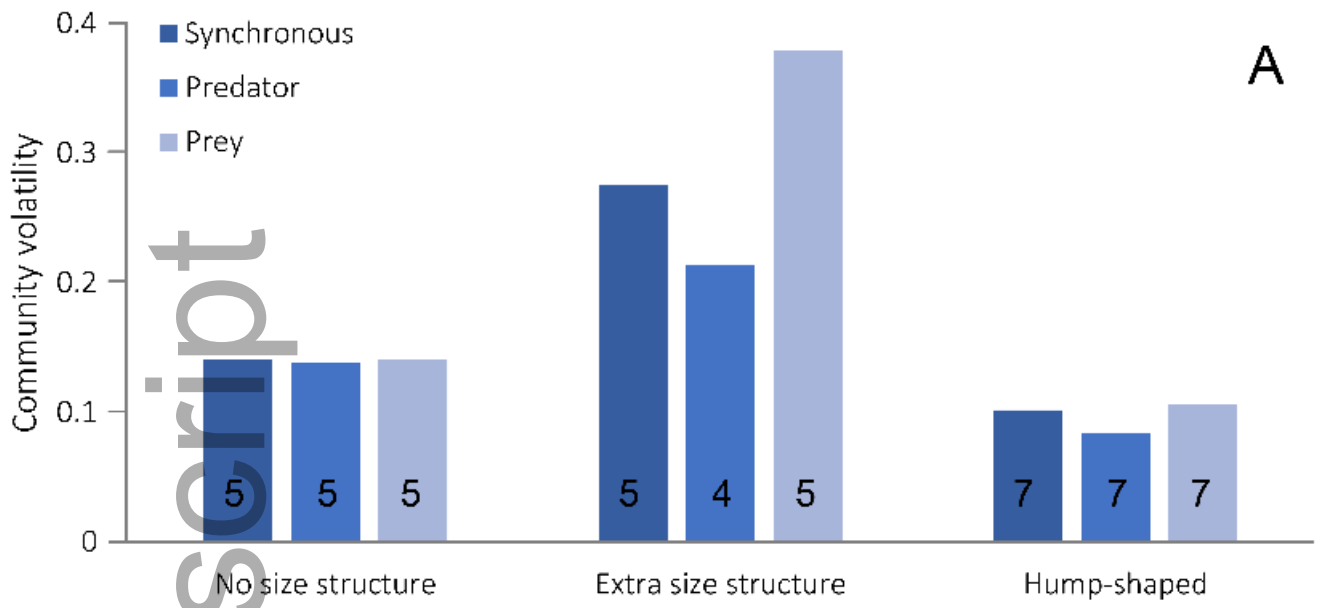
919 **Fig. 5:** Histograms representing the number of simulations that end with lobster + urchin
920 biomass at varying amounts, 5, 10, and 15 years after the closure of both predator and prey
921 fisheries. These simulations use a predator-first closure management strategy and include
922 parameter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



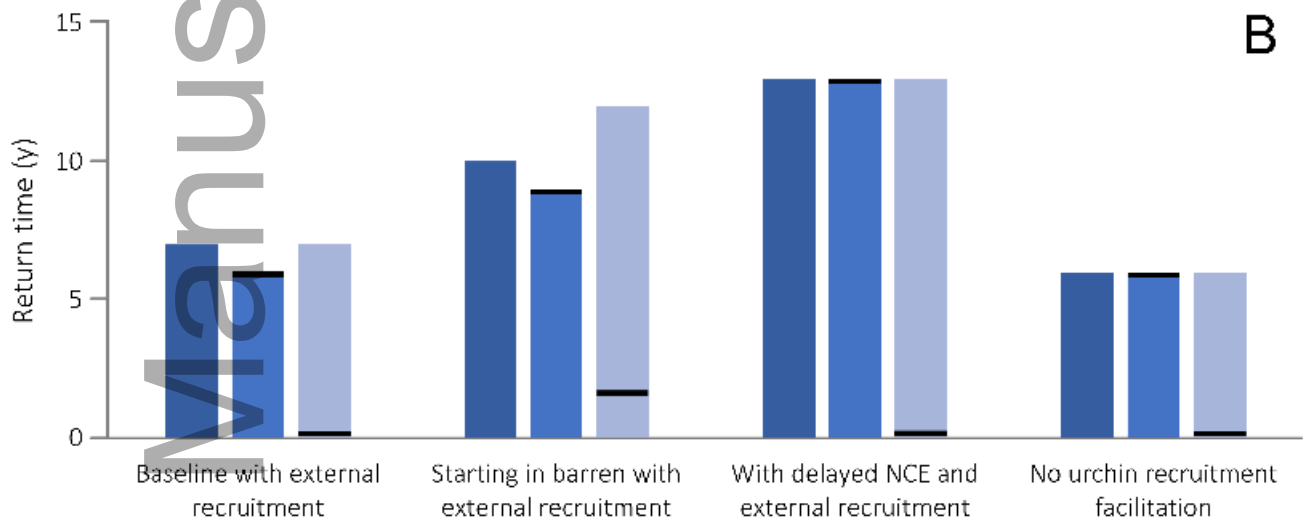
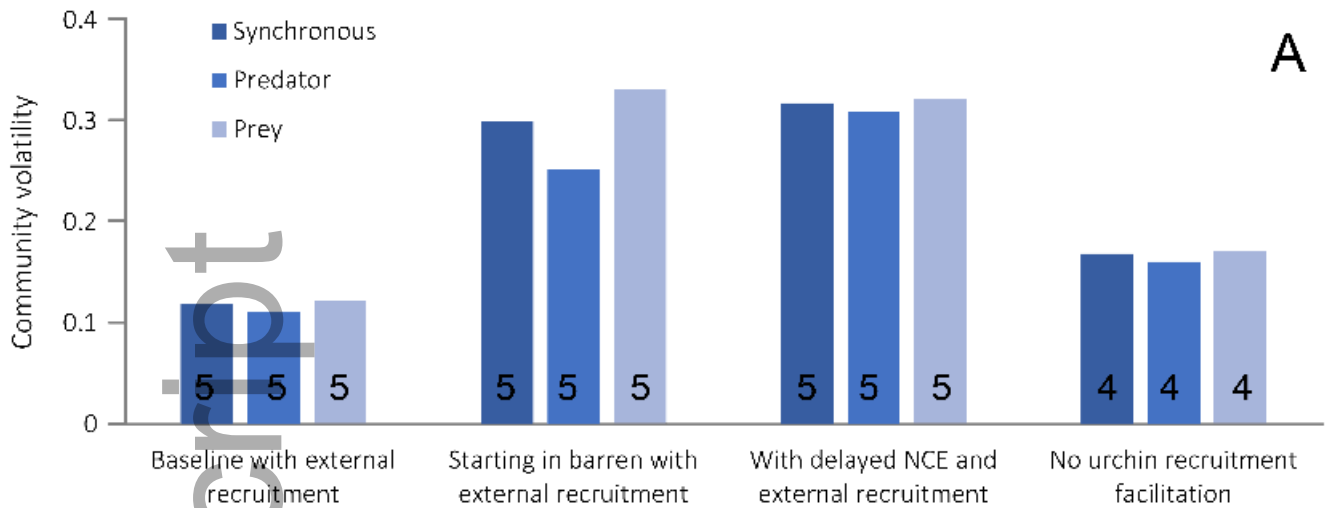
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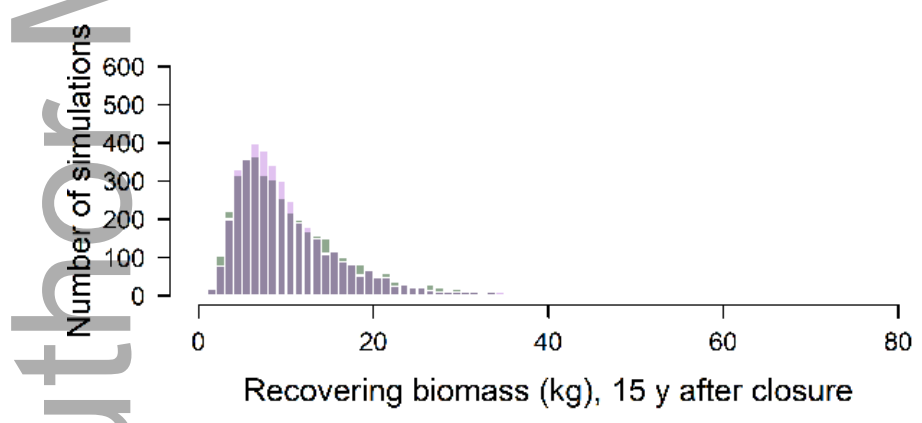
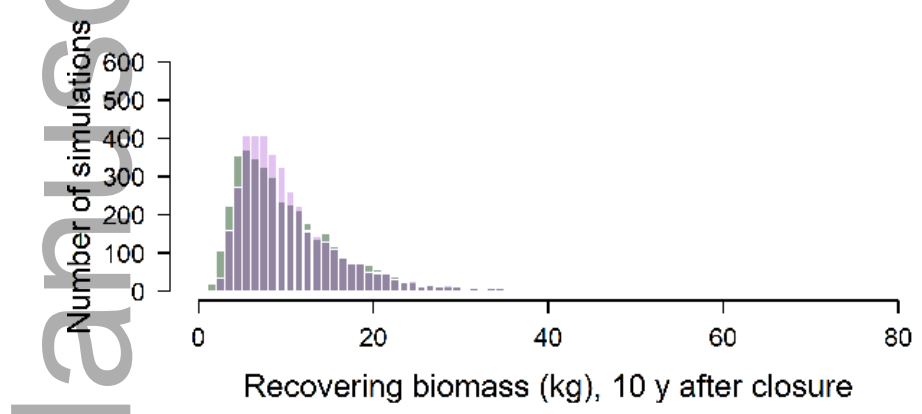
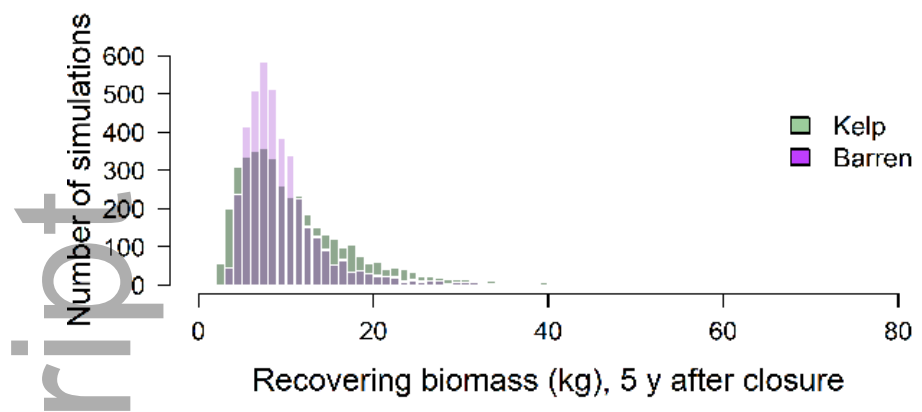
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