

Persistence of marine populations under climate and fishing

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1 Abstract

When the climate changes, so does the location of habitats suitable for an organism's survival and reproduction. This change does not occur in isolation but rather appears on a background of other disturbances, making the study of interactions between stressors important. In order to understand how two disturbances, range shift and harvesting, interact and affect population persistence, we analyzed an integrodifference model that explicitly included the mechanisms of dispersal and reproduction. We found how the critical rates of harvesting and climate velocity that suffice to drive the population extinct depend on the growth rate and dispersal kernel of the population. We measured the interaction between the stressors and found that the disturbances interact nearly additively, with low positive synergy only at the greatest harvest rates and climate velocity that almost drive the population extinct. We also introduced two conservation techniques into simulations of the population model, threshold harvest rules and marine protected areas (MPAs), and found that under some circumstances these approaches could be effective management tools as they mitigate the interaction between the two stressors.

Keywords: Climate change, fishing, integrodifference model, synergy, multiple disturbances

2 Introduction

Many stressors can disturb an ecosystem, and ecologists have quantified the consequences of many of these perturbations (???). Less work, however, has been done to measure the effects of multiple stressors and the interactions between them. If disturbances interact synergistically, a perturbation that has little effect when it occurs individually may amplify

the disturbance caused by a coincident perturbation (????). In the most extreme (and worrying) cases, synergistic interactions between multiple stressors will drive a population extinct even though it could persist in the face of any single stressor (e.g. ?). If disturbances interact antagonistically, on the other hand, the effects of multiple stressors may be less than that predicted by the individual effects of the stressors. Since disturbances rarely occur in isolation, measuring the effects of multiple disturbances gives a better understanding of the likely impacts to the system (???)

Climate change and fishing, two of the largest human impacts on the ocean (?), provide an important case study of how disturbances interact in their effects on biological populations. Marine fish are already moving in response to climate change (?????) and are projected to continue in the future (??). These shifting species, and those likely to move in the future, are also subject to harvesting, among other disturbances including pollution, ocean acidification, habitat fragmentation, and invasive species (??????). Previous empirical work has found synergistic interactions between overfishing and temperature-driven range shifts (?) and synergistic interactions between warming temperatures, harvesting and connectivity have been identified in microcosm experiments (?). This empirical work underscores the importance of understanding how range shifts and harvesting interact.

A common approach to predicting future population distributions has been to use bioclimatic-envelope models (also known as species distribution models – SDMs). These statistical models typically correlate presence-absence data with biophysical characteristics such as mean or maximum temperature, rainfall, or salinity, to predict how species ranges’ will differ under climate change (???). Despite these models’ widespread adoption, many papers have criticized SDMs as oversimplified as they lack species interactions, dispersal and reproductive processes (???). Recent work on range shifts has addressed some of these gaps

56 by explicitly including dispersal and reproduction (??). However these models only address
 57 one disturbance, climate-driven range shifts.
 58 Work on the joint impacts of climate and fishing often considers climate fluctuations (large
 59 anomalies around the mean) rather than directional changes in climate (??). When studies
 60 consider the effects of climate-driven range shifts on fishing, the models are typically
 61 case-specific and detailed, integrating multiple drivers and disturbances (??????????).
 62 These predicted impacts are important for management and conservation planning (?),
 63 however these models are so complex that it makes understanding the relative importance of
 64 particular drivers, disturbances, and interactions difficult (but see ? for an approach using
 65 ecosystem-level models to discern relative importance of disturbances).
 66 Here we extended a previously studied model of a fish population subject to climate-driven
 67 range shift by also considering harvesting pressure. The model explicitly included
 68 reproduction and dispersal, two mechanistic processes central to species' responses to
 69 climate and fishing. Previous work has highlighted the importance of these two processes
 70 and their vulnerability to climate change (??). We found the critical harvesting rate and
 71 climate velocity that drive the population extinct and how these critical rates depend on one
 72 another. We also found that climate-driven range shifts and fishing interact nearly
 73 additively, with low positive synergy at more extreme levels of the stressors.
 74 We also examined the efficacy of two different types of management strategies: threshold
 75 harvesting rules and marine protected areas (MPAs). MPAs are frequently recommended for
 76 conservation of biodiversity and improved fisheries yield (?), and we evaluate whether MPAs
 77 established for those purposes could improve species persistence when habitat shifts rapidly.
 78 Previous work has suggested protected areas can be a key form of climate insurance and can
 79 provide stepping stones to help species keep up with a changing environment (??). We found

that threshold harvesting rules remove the interaction between harvesting rates and climate velocity and that MPAs can help a species persist with higher harvesting pressure and slightly increase the maximum climate velocity with which a species can keep up.

3 Methods

We studied a model of the dynamics of a fish population constrained to a single, one-dimensional habitat patch by their inability to reproduce outside of that area, as introduced by ?. This viable habitat patch (here after ‘patch’) shifts at a fixed velocity and harvest occurs at each point in space along the entire one-dimensional world. We first determined the harvesting rate climate velocity that would drive the population extinct (hereafter the critical harvesting rate and critical climate velocity), and then measured synergy by calculating the drop in biomass caused by each stressor both individually and together. We finally added threshold harvesting rules and marine protected areas (MPAs) in numerical simulations of the model to determine how these management strategies affect population persistence.

3.1 The Model In the model of ?, the adults from the current year produce offspring according to a recruitment function and these offspring disperse across the one-dimensional world according to a dispersal kernel to become the next generation’s adults. We extend this model by additionally subjecting the adults to harvesting before they produce offspring so that only a proportion of the fish survive to reproduce. These processes– recruitment, harvesting, and dispersal– are incorporated into an integrodifference model to describe how the population changes over time. If $n_t(x)$ is the density of fish at position x at time t , then the density of fish at the next generation is given by

$$n_{t+1}(x) = \int_{-\frac{L}{2}+ct}^{\frac{L}{2}+ct} k(x-y)f((1-h)n_t(y))dy,$$

where h is the proportion of adults harvested, $f(n)$ is the recruitment function giving the number of offspring produced by a population of size n (accounting for density dependence), $k(x-y)$ is the dispersal kernel giving the probability of a larva traveling from position y to position x , L is the length of the patch, and c is the rate at which it shifts across space. We provide a list of variables and functions in Table ?? . We used a Beverton-Holt recruitment function,

$$f(n_t) = \frac{R_0 n_t}{1 + \left(\frac{R_0-1}{K}\right) n_t}.$$

Analyzing this kind of model becomes easier if the dispersal kernel is separable into its dependence on the source of larvae and its dependence on the destination of the larvae, i.e. if there are functions a_i, b_i such that $k(x-y) = \sum_{i=1}^{\infty} a_i(x)b_i(y)$. In our analyses, as in ?, we used the separable Gaussian kernel given by

$$k(x-y) = \frac{1}{2\sqrt{D\pi}} e^{\frac{-(x-y)^2}{4D}}.$$

To derive analytical expressions, we approximated the kernel, as described Appendix A.3. Analytical results for a separable sinusoidal kernel are also described in Appendix A.4. We used simulations to analyze a Laplace dispersal kernel that is not amenable to this method, as described below.

At equilibrium, the population will move in a traveling wave, where the density of fish at a given point in space will change but the density of fish at a location relative to the shifting patch will not. The traveling wave n^* must satisfy

$$n^*(\bar{x}) = \int_{-\frac{L}{2}}^{\frac{L}{2}} k(\bar{x} + c - \bar{y}) f((1 - h)n^*(\bar{y})) d\bar{y}, \quad (1)$$

where $\bar{x} \in \left[-\frac{L}{2}, \frac{L}{2}\right]$ describes the position within the patch (?). For a separable kernel, the equilibrium traveling pulse $n^*(x)$ must satisfy

$$n^*(x) = \sum_{i=1}^{\infty} a_i(x) \int_{-\frac{L}{2}}^{\frac{L}{2}} b_i(y - c) f((1 - h)n^*(y)) dy = \sum_{i=1}^{\infty} m_i a_i(x), \quad (2)$$

where the m_i satisfy the recursive equations

$$m_i = \int_{-\frac{L}{2}}^{\frac{L}{2}} b_i(y - c) f\left((1 - h) \sum_{j=1}^{\infty} m_j a_j(x)\right) dy. \quad (3)$$

(?).

3.2 Persistence If the population is harvested at low enough levels and the climate velocity is slow enough, the population will be able to persist. There are threshold values of the harvesting rate h and the climate velocity c such that if we increase the parameters beyond these values, the population will be driven extinct. When the population is extinct, the system is in equilibrium, i.e. there is a ‘trivial’ traveling pulse, $n^*(\bar{x}) = 0$ for all $x \in \left[-\frac{L}{2}, \frac{L}{2}\right]$, which satisfies Equation (??). If a population persists, it must be able to avoid extinction and grow even when small. If the trivial pulse is stable, the system will return to extinction even after the introduction of a small population. If the trivial pulse is unstable, a small population may increase and form a persistent population. Population persistence is therefore equivalent to the trivial traveling pulse being an unstable equilibrium. We found the critical parameters, h^* and c^* , by finding the parameters that make the trivial pulse unstable. See Appendix A.1 for details.

135 Regardless of the exact functional form of the recruitment function, the critical parameter in
 136 determining population persistence is how quickly recruitment increases when the population
 137 size is near (but above) 0, which is equivalent to the intrinsic growth rate $R_0 = f'(0)$. For
 138 each kernel, the population's ability to persist depends on properties of the population itself–
 139 the expected distance a larva disperses $\langle d \rangle$ and the intrinsic growth rate R_0 ; properties of the
 140 environment– the length of the viable patch L and how quickly the environment shifts c ; and
 141 the harvesting rate h . For a Gaussian kernel, the critical rates c^* and h^* are those values of c
 142 and h such that

$$R_0(1 - h)2\sqrt{2} \exp\left(\frac{-c^2}{8D}\right) \left[\operatorname{erf}\left(\frac{L - c}{2\sqrt{2D}}\right) - \operatorname{erf}\left(\frac{-L - c}{2\sqrt{2D}}\right) \right] = 1.$$

We derive a similar expression for a sinusoidal kernel in the Appendix A.4. For both kernels,
 we can approximate the critical harvesting proportion by a function that looks like

$$h^* \sim 1 - \frac{1}{R_0} \cdot C(L, R_0) f(\langle d \rangle, c^2, L^2 + 3c^2),$$

143 where $C(L, R_0)$ is a decreasing function of the length of the viable patch and the intrinsic
 144 growth rate.

145 **3.3 Calculating synergy ?** only considered whether a shifting environment will drive a
 146 population extinct. In order to quantify whether the two stressors interact additively,
 147 synergistically, or antagonistically, we found the total biomass of the population when it
 148 reached an equilibrium traveling pulse and compared this equilibrium biomass in the
 149 presence and absence of each stressor individually or the two stressors together. Equations
 150 (??) and (??) allowed us to numerically find the total biomass in the equilibrium traveling

151 pulse.

152 We used B_0 to denote the equilibrium biomass without either stressor, B_h the equilibrium
153 biomass with harvesting but a constant environment, B_c the equilibrium biomass with a
154 shifting environment but no harvesting, and B_{hc} the equilibrium biomass with both
155 stressors. For each stressor or combination of stressors, we found the drop in biomass caused
156 by stressor s ,

$$E_s = B_0 - B_s.$$

157 If the stressors do not interact, the drop caused by both stressors would be the sum of the
158 drops caused by either individually. The synergy is therefore defined as

$$S = E_{hc} - (E_h + E_c).$$

159 If the stressors aggravate each other, the effect of both stressors is greater than we would
160 expect from considering either stressor individually and synergy is positive. If the stressors
161 alleviate each other, the effect of both stressors is less than we would expect from considering
162 either stressor individually and synergy is negative. If the effect of both stressors is exactly as
163 expected from considering either stressor individually, there is no interaction and no synergy.

164 **3.4 Simulations** We used simulations to extend the basic integrodifference model in two
165 ways that make it analytically intractable. First, we examined the sensitivity of the model to
166 choice of dispersal kernel by using the Laplace dispersal kernel,

$$k(x - y) = \frac{1}{2}be^{-b|x-y|},$$

167 a commonly used model of larval dispersal (?). Second, we implemented two management
 168 strategies, threshold rules and MPAs, to understand their effect on population persistence
 169 and on the synergistic interactions between stressors. For every simulation, in the first
 170 generation, we seeded the world with 50 individuals at a single point, as in ?. We first ran
 171 through 150 generations in order for the population to reach equilibrium without harvesting
 172 or climate shift. We then added harvesting pressure, allowed the population to again reach
 173 equilibrium (150 generations), and finally added climate change by moving the viable patch.
 174 We calculated equilibrium biomass as the mean biomass of 300 time steps once the difference
 175 in biomass between successive generations was no greater than 0.1.
 176 Under the two management strategies, harvesting pressure was implemented differently.
 177 With a threshold rule, we evaluated the population at each point in space to determine how
 178 much harvesting should occur. If the population abundance was below the designated
 179 threshold, no harvesting occurred. If the population exceeded the threshold, then we
 180 harvested all the ‘surplus’ individuals.
 181 We introduce networks of MPAs into our simulations by designating segments of space where
 182 the harvesting rate was equal to 0. MPAs are typically designed to meet either fishery
 183 management or conservation goals (???). Fisheries-oriented MPAs are often designed such
 184 that they maximize adult spillover into fishable areas by creating many small reserves closely
 185 spaced (???). To mimic this management scheme, we implemented MPAs with a length of $\frac{1}{3}$
 186 of the average dispersal distance and a distance of $\frac{2}{3}$ of the average dispersal distance
 187 between them. Conservation-oriented MPAs seek to reduce adult spillover by creating fewer
 188 larger protected areas (?). To mimic this scheme, we implemented MPAs with a length of 4
 189 times the average dispersal distance and a distance of 8 times the average dispersal distance
 190 between them (?).

4 Results

4.1 Interactions Between Stressors

The critical climate velocity and harvest rate are inversely related. As the climate velocity shift c increases, the critical harvesting rate h^* decreases (Figure ??). This means that a harvesting rate that is sustainable in the absence of environmental shift may no longer be sustainable if the environment starts changing. Conversely, as the harvesting rate h increases, the critical climate velocity c^* decreases (Figure ??). This means that as harvesting pressure increases, it becomes increasingly easy for a shifting environment to drive the population extinct.

When the climate velocity or harvesting pressure exceed their critical rates (c^*, h^* respectively), the biomass of the population at equilibrium will be equal to 0. Before the stressors reaches those thresholds, the equilibrium biomass of the population decreases as either the harvesting pressure increases or the environmental shifts more quickly (Figure ??). Our simulations confirm the analytical results with the critical speed c^* declining as the critical harvest rate h^* increases and vice versa (Figure ??).

It is always the case that increasing the intrinsic growth rate, R_0 , increases the critical climate velocity c^* and the critical harvesting rate h^* , since a population that grows more quickly can recover more quickly from losses caused by these disturbances. However, whether or not dispersing farther is better depends on how quickly the environment is shifting (Figure ??). When the environment is shifting slowly, dispersing farther is detrimental since many larvae will disperse too far away from the viable patch. When the environment is shifting quickly, on the other hand, dispersing farther can help the population persist because some larvae will disperse into the space that will become viable shortly in the future. This affects the critical harvesting rate: at a low climate velocity, we can more severely harvest populations that have a shorter dispersal distance than those that

disperse farther, whereas at a high climate velocity, we can more aggressively harvest populations that disperse farther.

We found low levels of positive synergy between the two stressors in our analysis of the Gaussian kernel (Figure ??). Where positive synergy exists, a doubly stressed population loses more biomass than we would predict from either stressor individually. The stressors interact most strongly at high values, shortly before they drive the population extinct. However, the excess loss in biomass is very low, meaning the stressors interact more or less additively. We found similar analytical results for a sinusoidal dispersal kernel, which indicates that this result is robust to changes in the dispersal kernel.

4.2 Management strategies Without any management strategies, we found that the more severely we harvest the population, a slower climate velocity will suffice to drive the population extinct. However, when we put thresholds in place, a small population can always escape harvesting pressure and the critical climate velocity c^* no longer depends on the harvesting rate (Figure ??). In other words, as long as there is some threshold below which harvesting is not allowed, there is a constant critical climate velocity that only depends on the growth rate, length of the viable patch, and average dispersal distance. With either type of MPA strategies examined (many small versus few large), the population withstood combinations of higher climate velocities and harvesting rates (Figure ??). At lower climate velocities, MPAs spaced more than one average dispersal distance apart resulted in larger fluctuations of population biomass relative to small, closely spaced, MPAs. As climate velocities increase, for both MPA strategies, the mean population abundance declines but the population experiences less extreme oscillations in abundance. Since minimum population biomass is increased, the population would be more buffered from

238 possible extinction in a stochastic environment.

239 5 Discussion

240 Understanding interactions among disturbances will help to design management for
241 populations subjected to these disturbances. The co-occurrence of climate change-driven
242 range shifts and fishing mean that there is the potential for synergistic interactions, which
243 have been largely unexamined. Here we have studied a general model that incorporates
244 dispersal and reproduction to examine how climate and harvesting interact in their effects on
245 species persistence and biomass.

246 For each kernel we studied, we found that the higher the growth rate and the better the
247 mean dispersal distance matches the climate velocity, the better a population can adjust to
248 harvest and climate change. Further, we found a negative relationship between the critical
249 harvesting rate and the climate velocity. That is, the more quickly the environment shifts
250 the less harvesting it takes to drive the population extinct. This is evidence that the
251 stressors interact since each stressor's ability to drive the population extinct depends on the
252 severity of the other stressor.

253 To quantify the interaction between the stressors, we measured the synergy between their
254 effects on population biomass. We found positive synergy between the stressors and that the
255 synergy is greatest in the region of parameter space where the equilibrium biomass is
256 smallest. We chose to measure the effect of each stressor by the absolute drop in biomass
257 caused by the stressor, and we used the sum of the individual effects for our null prediction
258 of the effect of both stressors, as in ????. In general, measuring synergy against an additive
259 null prediction is more conservative than measuring synergy multiplicatively: the presence of

260 additive synergy implies multiplicative synergy, but not vice versa (??). Since we found
 261 small levels of positive additive synergy between the two stressors, other measures of synergy
 262 might show even higher levels of interaction.

263 Worryingly, we find the highest synergy in those populations whose persistence is most
 264 tenuous. This means that harvesting levels or climate velocity that are sustainable
 265 individually together can drive a population to extinction. However the drop in biomass
 266 caused by both stressors was never much higher than the null prediction, i.e. synergistic
 267 effects were quite small. Synergy between harvesting and the effects of climate change has
 268 been identified in experimental populations (?), in specific populations (?), and at the
 269 ecosystem level (??). In the experimental populations, synergy was identified between
 270 warming and harvesting but not between habitat fragmentation (?). While we did find
 271 (very) low levels of positive synergy, we did not find as much as predicted from these
 272 empirical studies. However, these previous results are not directly comparable to ours
 273 because they focus on different aspects of climate change, e.g. warming temperature (??) or
 274 a more variable climate (?). Additionally, while we can isolate the affects of climate shift and
 275 harvesting in our simple analytical model, there are other forces acting on real populations
 276 that may produce the observed synergistic effects.

277 Our results suggest that particular combinations of harvesting and climate velocity will
 278 affect some species more than others. Species with a higher reproductive rate and a longer
 279 average dispersal distance will better track a high climate velocity relative to a species that
 280 has a low reproductive rate and short dispersal distance (Figure ??). The finding that a
 281 higher reproductive rate can sustain higher climate velocities and harvesting rates is
 282 intuitive, especially because harvesting rate and reproductive rate cancel each other out.
 283 However it is worth pointing out that a higher reproductive rate can be generated either by

shorter generation times or higher fecundity. Finding that species with shorter generation times can better keep up with shifts in climate is in agreement with empirical work which has found that fish which shifted in response to warming in North Sea had faster life histories than non shifting species (?). While higher reproductive rates improved a population's ability to persist, increasing dispersal distances did not necessarily. At low speeds, we found that a short dispersal distance improved the maximum harvesting rate a population could sustain while at higher speeds a longer dispersal distance improved the maximum climate velocity in which the population could persist (Figure ??). This is because when climate is shifting slowly, a large dispersal distance sends most offspring ahead of the patch, while with faster climate velocities a long dispersal distance allows the population to make it to the new patch (Figure ??). Thus climate velocity will selectively favor species with dispersal distances best matched to the rate of shift.

We also examined whether frequently recommended management approaches, MPAs and harvest control rules, ensure species persistence. With these management strategies we found increases in the population's biomass at equilibrium and an improved ability to persist. We found that a threshold harvesting rule alleviates interactions between the two stressors. Thresholds have this effect as the management approach effectively prevents harvesting of the leading edge, which allows colonization to occur as if these individuals were moving into un-fished areas. It's interesting to note that novel, low abundance species are commonly unregulated in fisheries systems; so in order to decouple the additive effects of harvest and climate change, management would have to reverse this paradigm by allowing no harvest of new species until they had become established.

Unlike thresholds, MPAs are explicitly spatial. Previous work has advanced protected areas as a way to help organisms keep pace with range shifts, as well as to ameliorate

anthropogenic disturbances like harvesting and habitat fragmentation (?????). Our results show that both threshold and MPAs increase the equilibrium biomass at a given climate velocity, which support their use as a tool to ameliorate the effect of climate velocity. However, for MPAs, the details matter: few, large MPAs caused increased variability at low climate velocities while many smaller MPAs maintained a population bounded farther from extinction. Finally, with sufficiently high harvesting pressure, few, large MPAs rescued populations at intermediate speeds. With intermediate speeds, the population was able to reach a protected area fast enough to avoid extinction, and the protected area was large enough to allow a partial rebuilding of the population before it moved out the other side. However this effect disappears as speed continues to increase, suggesting that understanding the relationship between climate velocity, dispersal distance and reproductive rate are important parameters in designing management strategies effective under both climate change and harvesting pressure.

While the management strategies only change harvesting practices and do not directly address the effects of climate change, understanding how they ameliorate synergistic affects between harvesting and range shifts will help to better implement harvesting rules and place protected areas. This is encouraging evidence that a single set of management practices may help to protect marine populations from both harvesting and climate change.

The advantage of a simple model like ours is that it is general enough to be applied to a number of systems. However, this simplistic approach requires that we ignore complexities known to be present in marine fisheries. For example, we do not include Allee effects, so that even if the population shrank to low levels it was possible for it to persist over time.

However, with Allee effects we expect qualitatively similar results. An Allee effect would make it harder for populations to colonize new areas and add a threshold below which

332 fishing drives the population to extinction. Thus an Allee effect would change lower the
333 critical harvest rates and climate velocity, but we do not expect the additive nature of the
334 interaction between climate and harvesting to change. We also did not include age structure
335 in our model. The effects of both harvesting and climate change may be different across
336 different age classes and may destabilize the system in complicated ways, including
337 resonance (??); and we leave this additional complexity for future work. Similarly, we did
338 not include any mechanisms aside from larval dispersal by which the population could keep
339 up with a shifting climate. Besides these species-specific extensions, this modeling
340 framework could be extended to consider species interactions, especially predator-prey pairs.
341 By introducing a predatory species, we would be imposing yet another stressor on the focus
342 species (??) and we are interested in measuring the interaction between the effects of this
343 stressor and the two we consider here.

344 Using a simple mechanistic model like the one we present here provides a useful framework
345 for incorporating additional ecological complexities which can mediate species persistence
346 under multiple disturbances. Using this modeling framework as a starting point, we believe
347 exploring how species interactions, age structure, and additional disturbances (e.g.
348 physiological response to temperature) affect population viability will improve our
349 predictions and help us to understand whether species will persist under predicted climate
350 and harvesting regimes. Finally, this work can help make general predictions as to whether
351 specific life histories offer selective advantages over others as harvesting and range shifts
352 increase and highlights the importance of considering stressors in combination as outcomes
353 can deviate from what we would predict in isolation. This is especially true for management
354 strategies which may result in unanticipated effects such as large fluctuations associated with
355 big, distant MPAs shown here.

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Figure Legends

Figure ??: (a) The critical harvesting rate on the y-axis as a function of the climate velocity on the x-axis. Black lines correspond to a growth rate of $R_0 = 3$, red to $R_0 = 7$, and blue to $R_0 = 10$. Solid lines correspond to an average dispersal distance $\langle d \rangle = 0.1$ and dashed lines correspond to an average dispersal distance $\langle d \rangle = 0.25$. These results are from an approximated Gaussian dispersal kernel with $L = 1$. (b) The equilibrium biomass of the population as a function of the climate velocity on the x-axis and the harvesting rate on the y-axis. These results are from a Gaussian dispersal kernel with parameters $L = 1$, $R_0 = 5$, $\langle d \rangle = 0.399$.

Figure ??: Positive synergy between the two stressors. The x-axis shows the climate velocity, the y-axis shows the harvesting rate, and the color indicates the loss in biomass in the doubly stressed population in excess of the sum of the losses caused by each stressor individually, $E_{hc} - E_h - E_c$. This excess loss, on the order of .001, is small in comparison to the total biomass, which can be as large as 20. These results are from an approximated Gaussian dispersal kernel with parameters $L = 1$, $R_0 = 5$, $\langle d \rangle = 0.399$.

Figure ??: The equilibrium biomass of the population as a function of the climate velocity on the x-axis and the harvesting rate on the y-axis with and without management strategies. (a) No management. (b) Threshold harvesting levels. (c) MPAs. These results are from a simulation with a Laplacian dispersal kernel with parameters $L = 1$, $R_0 = 5$, $K = 100$, and $\langle d \rangle = 2$.

6 Figures

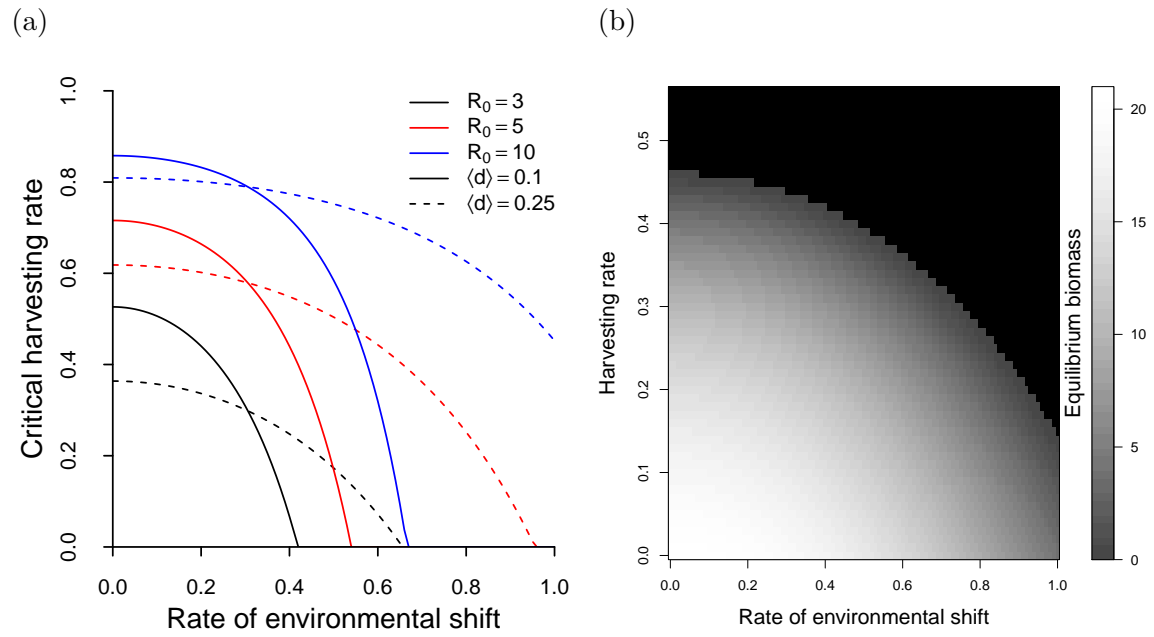


Figure 1

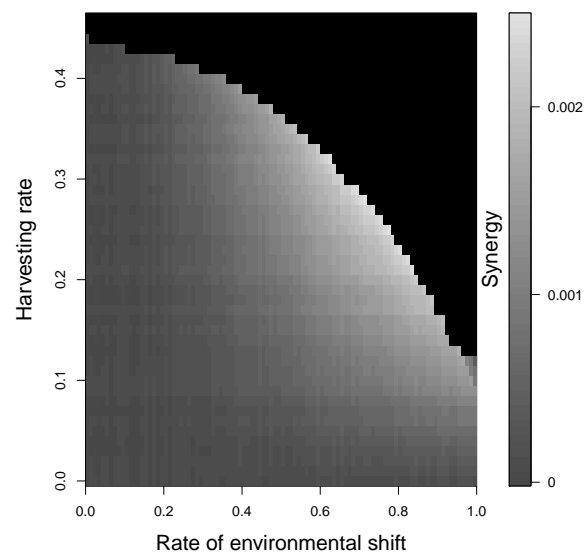
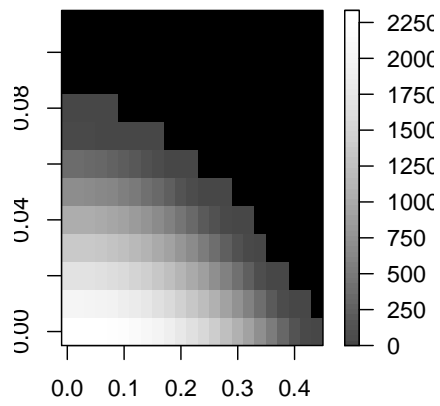
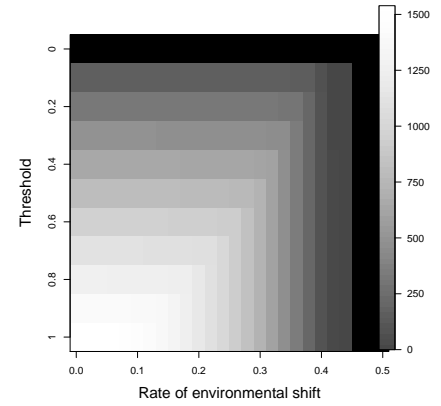


Figure 2

(a)



(b)



(c)

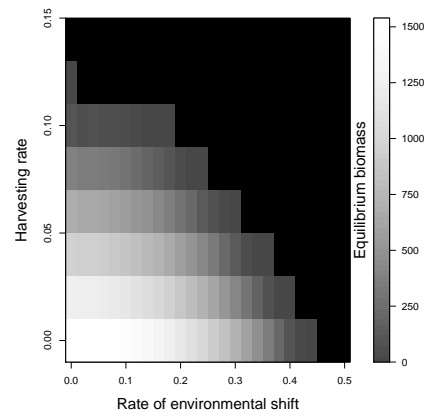


Figure 3

7 Tables

Table 1: Table of variables used in the text

Variable	Definition
$n_t(x)$	density of fish at position x at time t
$n^*(\bar{x})$	density of fish at equilibrium at position \bar{x} relative to the patch
$k(x - y)$	dispersal kernel, the probability of larva traveling from position y to position x
$\langle d \rangle$	expected distance traveled by larva
$f(n)$	recruitment function, the number of offspring produced by a population of size n
R_0	intrinsic growth rate, $R_0 = f'(0)$
h	proportion of adults harvested
L	patch length
c	climate velocity