

# 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 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 a great deal of these perturbations [Wilcove et al., 1998, Crain et al., 2008, Darling and Côté, 2008]. 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 [Crain et al., 2008, Darling and Côté, 2008, Nye et al., 2013, Gurevitch et al., 2000]. 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. Pelletier et al. [2006]). 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 [Doak and Morris, 2010, Fordham et al., 2013, Folt et al., 1999]. Climate change and fishing, two of the largest human impacts on the ocean [Halpern et al., 2008], 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 [Perry et al., 2005, Hiddink and ter Hofstede, 2008, Rijnsdorp et al., 2009, Dulvy et al., 2008, Simpson et al., 2011] and are projected to continue in the future [Kell et al., 2005, Mackenzie et al., 2007]. 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 [Wilcove et al., 1998, Sala, 2000, Assessment, 2005, Pinsky et al., 2013, Barry et al., 1995, Nye et al., 2009]. Previous empirical work has found synergistic interactions between overfishing and temperature-driven range shifts [Ling et al., 2009] and microcosm experiments have identified synergistic interactions between warming temperatures, harvesting and connectivity [Mora et al., 2007]. 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 temperatures, rainfall, or salinity, to predict how species ranges' will differ under climate change [Elith et al., 2006, Guisan and Thuiller, 2005, Guisan and Zimmermann, 2000]. Despite these models' widespread adoption, many papers have criticized SDMs as oversimplified as they lack species interactions, dispersal and reproductive processes [Kearney and Porter, 2009, Zarnetske et al., 2012, Robinson et al., 2011]. Recent work on range shifts has addressed some of these gaps by explicitly including dispersal and reproduction [Berestycki et al., 2009, Zhou and Kot, 2011]. However these models only address one disturbance, climate-driven range shifts.

Work on the joint impacts of climate and fishing often considers climate fluctuations (large anomalies around the mean) rather than directional changes in climate [Walters and Parma, 1996, King and McFarlane, 2006]. When studies consider the effects of climate-driven range shifts on fishing, the models are typically case-specific and detailed, integrating multiple drivers and disturbances [Cheung et al., 2010, Lindegren et al., 2010, Brown et al., 2010, Merino et al., 2010a,b, Plaganyi et al., 2011, Ainsworth et al., 2011, Zhang et al., 2011, Barange et al., 2011, Howard et al., 2013]. These predicted impacts are important for management and conservation planning [Allison et al., 2009], however these models are so complex that it makes understanding the relative importance of particular drivers, disturbances, and interactions difficult (but see Nye et al. [2013] for an approach using ecosystem-level models to discern relative importance of disturbances).

Here we extended a previously studied model of a fish population subject to climate-driven range shift by also considering harvesting pressure. The model explicitly included reproduction and dispersal, two mechanistic processes central to species' responses to climate and fishing. Previous work has highlighted the importance of these two processes and their vulnerability to climate change [Fordham et al., 2013, Hastings et al., 2005]. We

found the critical harvesting rate and climate velocity that drive the population extinct and how these critical rates depend on one another. We also found that climate-driven range shifts and fishing interact nearly additively, with low positive synergy at more extreme levels of the stressors.

We also examined the efficacy of two different types of management strategies: threshold harvesting rules and marine protected areas (MPAs). MPAs are frequently recommended for conservation of biodiversity and improved fisheries yield [Gaines et al., 2010a], and we evaluate whether MPAs established for those purposes could improve species persistence when habitat shifts rapidly. Previous work has suggested protected areas can be a key form of climate insurance and can provide stepping stones to help species keep up with a changing environment [Thomas et al., 2012, Hannah et al., 2007]. 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 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 Zhou and Kot [2011]. 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 climate velocity and harvesting rate that would drive the population extinct (hereafter the critical harvesting rate and climate velocity), and then measured synergy by calculating the drop in biomass caused by each stressor both individually and together. We

102 finally add marine protected areas (MPAs) and threshold harvesting rules in numerical  
 103 simulations of the model to determine how these management strategies affect population  
 104 persistence.

105 **3.1 The Model** In the model of Zhou and Kot [2011], the adults from the current year  
 106 produce offspring according to a recruitment function and these offspring disperse across the  
 107 one-dimensional world according to a dispersal kernel to become the next generation's  
 108 adults. We extend this model by additionally subjecting the adults to harvesting before they  
 109 produce offspring so that only a proportion of the fish survive to reproduce. We incorporate  
 110 these processes— recruitment, harvesting, and dispersal— into an integrodifference model to  
 111 describe how the population changes over time. If  $n_t(x)$  is the density of fish at position  $x$  at  
 112 time  $t$ , then the density of fish at the next generation is given by

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

113 where  $h$  is the proportion of adults harvested,  $f(n)$  is the recruitment function giving the  
 114 number of offspring produced by a population of size  $n$  (accounting for density dependence),  
 115  $k(x-y)$  is the dispersal kernel giving the probability of a larva traveling from position  $y$  to  
 116 position  $x$ ,  $L$  is the length of the patch, and  $c$  is the rate at which it shifts across space. We  
 117 provide a list of variables and functions in Table 1. We use a Beverton-Holt recruitment  
 118 function,

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

119 but regardless of the exact functional form of the recruitment function, the critical

parameter in determining population persistence is how quickly recruitment increases when the population size is near (but above) 0, which is equivalent to the intrinsic growth rate  $R_0 = f'(0)$ . 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 Latore et al. [1998], 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 in the Appendix. Analytical results for a separable sinusoidal kernel are also described in the Appendix. We used simulations to analyze a Laplace dispersal kernel that is not amenable to this method, as described below.

At equilibrium, a traveling wave will describe the population, 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. We sought to describe the distribution of the population over the viable patch as it shifts through the world in order to study the size of the population at equilibrium and whether or not the population could persist. 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 [Zhou and Kot, 2011].

**3.2 Persistence** One possible equilibrium traveling wave that solves Equation (1) is the ‘trivial’ traveling pulse,  $n^*(\bar{x}) = 0$  for all  $x \in \left[-\frac{L}{2}, \frac{L}{2}\right]$ , i.e. a patch with no fish in it. If a

138 population persists, it must be able to avoid extinction and grow even when small. We can  
 139 think of a small population as a perturbation to the trivial traveling pulse. If the trivial  
 140 pulse is stable, the system will return to the trivial pulse even after the introduction of a  
 141 small population. If the trivial pulse is unstable, a small population may increase and form a  
 142 persistent population. Population persistence is therefore equivalent to the trivial traveling  
 143 pulse being an unstable equilibrium.  
 144 If we harvest the population at low enough levels and the climate velocity is slow enough,  
 145 the population will be able to persist. There exists threshold values of the harvesting rate  $h$   
 146 and a climate velocity  $c$  such that if we increase parameters beyond these values, we drive  
 147 the population extinct. We found these critical parameters,  $h^*$ , and  $c^*$ , by finding the  
 148 parameters that make the trivial pulse unstable (See Appendix ??).  
 149 For each kernel, the population's ability to persist depends on properties of the population  
 150 itself– the expected distance a larva disperses  $\langle d \rangle$  and the intrinsic growth rate  $R_0$ ; properties  
 151 of the environment– the length of the viable patch  $L$  and how quickly the environment shifts  
 152  $c$ ; and the harvesting rate  $h$ . The population biomass at equilibrium depends on the function  
 153 form of recruitment, but population persistence only depends on the intrinsic growth rate  
 154  $R_0$ . For a Gaussian kernel, the critical rates  $c^*$  and  $h^*$  are those values of  $c$  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 [REF?]. For both  
 kernels, we can approximate the critical harvesting proportion by a function that looks like

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



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

157 **3.3 Calculating synergy** Zhou and Kot [2011] only considered whether a shifting  
 158 environment will drive a population extinct. In order to quantify whether the two stressors  
 159 interact additively, synergistically, or antagonistically, we found the total biomass of the  
 160 population when it reached an equilibrium traveling pulse and compared this equilibrium  
 161 biomass in the presence and absence of each stressor individually or the two stressors  
 162 together. For a separable kernel, the equilibrium traveling pulse  $n^*(x)$  must satisfy

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

163 where the  $m_i$  satisfy the recursive equations

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

164 [Latore et al., 1998]. Equation (3) allowed us to find the values of  $m_i$  numerically. We then  
 165 found the total biomass in the equilibrium traveling pulse by using these  $m_i$  and integrating  
 166 Equation (2).

167 We used  $B_0$  to denote the equilibrium biomass without either stressor,  $B_h$  the equilibrium  
 168 biomass with harvesting but a constant environment,  $B_c$  the equilibrium biomass with a  
 169 shifting environment but no harvesting, and  $B_{hc}$  the equilibrium biomass with both  
 170 stressors. For each stressor or combination of stressors, we found the drop in biomass caused  
 171 by stressor  $s$ ,

$$E_s = B_0 - B_s.$$

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

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

174 If the stressors aggravate each other, synergy is positive, and the effect of both stressors is  
 175 worse than would we expect from considering either stressor individually. If the stressors  
 176 alleviate each other, the synergy is negative, and the effect of both stressors is better than  
 177 we expecte from considering either stressor individually. If the effect of both stressors is  
 178 exactly as expected from considering either stressor individually, there is no interaction and  
 179 no synergy.

180 **3.4 Simulations** We used simulations to extend the basic integrodifference model in two  
 181 ways that make it analytically intractable. First, we examined the sensitivity of the model to  
 182 choice of dispersal kernel by using the Laplace dispersal kernel,

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

183 a commonly used model of larval dispersal [?]. Second, we examined harvesting rules more  
 184 complex than harvesting a constant proportion of the population. Whereas population  
 185 persistence in the analytical model does not depend on the functional form of recruitment  $f$ ,  
 186 to perform simulations we must specify a recruitment function. Again, we chose to use a  
 187 Beverton-Holt function. In the first generation, we seeded the world with 50 individuals at a

188 single point, as in Zhou and Kot [2011]. We first ran through 150 generations in order for  
 189 the population to reach equilibrium without harvesting or climate shift. We then added  
 190 harvesting pressure, allowed the population to again reach equilibrium (150 generations),  
 191 and finally added climate change by moving the viable patch. We calculate equilibrium  
 192 biomass as the mean biomass of 300 time steps once the difference in biomass between time  
 193 step  $t$  and  $t + 1$  was no greater than 0.1.

194 n, in order to confirm our analytical results, we first added harvesting pressure by harvesting  
 195 a constant proportion of the population. We then evaluated the effect of a threshold harvest  
 196 rule and marine protected areas (MPAs). With a threshold rule, we evaluated the  
 197 population at each point in space to determine how much harvesting should occur. If the  
 198 population abundance was below the designated threshold, no harvesting occurred. If the  
 199 population exceeded the threshold, then we harvested all the ‘surplus’ individuals.

200 MPAs are a form of management designed to check the impact of fishing on targeted  
 201 populations and are typically designed to meet either conservation of fishery management  
 202 goals [Agardy, 1994, Holland and Brazee, 1996, Gaines et al., 2010b]. To implement an MPA  
 203 management strategy in our model, we examine the effect of both of these commonly  
 204 advocated approaches. While both conservation and fisheries oriented MPA schemes align in  
 205 their goal of maintaining a sustainable fished population, they differ in desired level of adult  
 206 spillover. Fisheries-oriented MPAs are often designed such that they maximize adult  
 207 spillover into fishable areas by creating many small reserves closely spaced [Hastings and  
 208 Botsford, 2003]. The converse of this is the goal of conservation-oriented MPAs which seek  
 209 to reduce adult spillover by minimizing the ratio between the reserve edge length relative to  
 210 area protected [Gaines et al., 2010b].

211 We introduce networks of MPAs into our simulations by designating segments of space where

212 the harvesting rate was equal to 0. Conservation-oriented MPAs, are frequently large and  
 213 rarely part of a larger network of reserves [Hastings and Botsford, 2003]. For solitary  
 214 reserves to be successful at protecting target species, they must encompass self-sustaining  
 215 fish populations [Hastings and Botsford, 2006, Gaines et al., 2010b]. As such modeling  
 216 studies estimate that isolated reserves must be at least as large as the average dispersal  
 217 distance for the targeted fish species [Lockwood et al., 2002, Hastings and Botsford, 2003,  
 218 Botsford et al., 2001, Gaines et al., 2010a]. To implement conservation MPAs we created  
 219 reserves with a length of 4 times the average dispersal distance and had a distance of 8 times  
 220 the average dispersal distance between them to ensure that populations would be self  
 221 sustaining and not dependent on other dispersal for other reserves [Lockwood et al., 2002].  
 222 Previous work has shown that if MPAs are to benefit fisheries, the reserves should be broken  
 223 into a network, closely spaced to maximize adult spillover into fishable areas and export of  
 224 larvae from reserve to reserve [Hastings and Botsford, 2003, Gaylord et al., 2005, Gaines  
 225 et al., 2010b]. To mimic this management scheme, MPAs had a length of  $\frac{1}{3}$  of the average  
 226 dispersal distance and had a distance of  $\frac{2}{3}$  of the average dispersal distance between them.

## 227 4 Results

228 **4.1 Interactions Between Stressors** We find the critical climate velocity and harvest  
 229 rate to be inversely related: as the harvesting rate  $h$  increases, the critical climate velocity  $c^*$   
 230 decreases, as the environment must move more slowly to accommodate the population  
 231 growing more slowly (Figure 1). Conversely, as the rate of environmental shift  $c$  increases,  
 232 the critical harvesting rate  $h^*$  decreases (Figure 1). This means that a harvesting rate that is  
 233 sustainable in the absence of environmental shift may no longer be sustainable if the

environment starts changing. When the climate velocity or harvesting pressure exceed their critical rates ( $h^*, c^*$  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 1). Our simulations confirm the analytical results with the critical speed  $c^*$  declining as the critical harvest rate  $h^*$  increases and vice versa (Figure 3a).

It is always the case that increasing the intrinsic growth rate,  $R_0$ , of the population 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 1). 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 rate of environmental shift, we can more severely harvest populations that have a shorter dispersal distance than those that disperse farther, whereas at a high rate of environmental shift, 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 2). 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 low, making it difficult to distinguish positive synergy from additive interactions. 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, the slower the rate of environmental shift 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 rate of environmental shift  $c^*$  no longer depends on the harvesting rate (Figure 3). In other words, as long as there is some threshold below which harvesting is not allowed, there is a constant critical rate of environmental shift that only depends on the growth rate, length of the viable patch, and average dispersal distance.

We also examined the effect of marine protected areas (MPAs) on the population's persistence to see whether it might extend the range of harvesting and climate change parameters where the fish population could survive. We found that with either type of MPA strategies examined (many small versus few large), the population withstood combinations of higher climate velocities and harvesting rates, although the critical climate velocity  $c^*$  was unchanged (Figure 3). We also found that the spacing and size of the MPAs changed population dynamics. MPAs spaced more than one average dispersal distance apart resulted in large oscillations of population biomass at low climate velocities relative to small, closely spaced, MPAs. For both of these MPA strategies we find that as climate velocities increase, the mean population abundance declines but the population experiences less extreme oscillations in abundance, which results in a population bounded farther from possible extinction in a stochastic environment. Additionally, large MPAs were able to increase equilibrium biomass under relatively high harvest and intermediate speeds relative to a population harvested at the same rate, but at a slower speed. This effect disappears at faster

climate velocities and is not present in the other, many-small MPA, strategy we tested.

## 5 Discussion

Understanding interactions among disturbances will help to design management for populations subjected to these disturbances. The co-occurrence of climate change-driven range shifts and fishing mean that there is the potential for synergistic interactions, which have been largely unexamined. Here we have built a general model to examine how climate and harvesting interact to affect species persistence by incorporating dispersal and reproduction.

For each kernel we studied, we found that the higher the growth rate and the better the mean dispersal distance matches the rate of environmental shift, the better a population can adjust to harvest and climate change. More interestingly, we found a negative relationship between the critical harvesting rate and the rate of environmental shift. That is, the more quickly the environment shifts the less harvesting it takes to drive the population extinct. This is an indication of an interaction between the stressors.

To quantify the interaction between the stressors, we measured the synergy between their effects on population biomass. We found positive synergy between the stressors and that the synergy is greatest in the region of parameter space where the equilibrium biomass is smallest. We found similar results from the analytically derived biomass and the simulation derived biomass. This indicates that this result is robust to changes in the dispersal kernel.

We chose to measure the effect of each stressor by the absolute drop in biomass caused by the stressor, and we used the sum of the individual effects for our null prediction of the effect of both stressors, as in Crain et al. [2008], Darling and Côté [2008], Nye et al. [2013]. We

could also have measured the effect by the percentage drop caused by the stressor(s) and used a multiplicative null prediction for the effect of both stressors. In general, measuring synergy against an additive null prediction is more conservative than measuring synergy multiplicatively: the presence of additive synergy implies multiplicative synergy, but not vice versa [Crain et al., 2008, Folt et al., 1999]. Since we found small levels of positive additive synergy between the two stressors, other measures of synergy might show even higher levels of interaction.

Worryingly, we find the highest synergy in those populations whose persistence is most tenuous. This means that harvesting levels or climate velocity that are sustainable individually together can drive a population to extinction. However the drop in biomass caused by both stressors was never much higher than the null prediction, i.e. synergistic effects were quite small. Synergy between harvesting and the effects of climate change has been identified in experimental populations [Mora et al., 2007], in specific populations [Planque et al., 2010], and at the ecosystem level [Kirby et al., 2009, Planque et al., 2010]. In the experimental populations, synergy was identified between warming and harvesting but not between habitat fragmentation [Mora et al., 2007]. While we did find (very) low levels of positive synergy, we did not find as much as predicted from these empirical studies.

However, these previous results are not directly comparable to ours because they focus on different aspects of climate change, e.g. warming temperature [Mora et al., 2007, Kirby et al., 2009] or a more variable climate [Planque et al., 2010]. Additionally, while we can isolate the affects of climate shift and harvesting in our simple analytical model, there are other forces acting on real populations that may produce the observed synergistic effects. Our results suggest that particular combinations of harvesting and rate of environmental shift will affect some species more than others. As shown in Figure 1, species with a higher



327 reproductive rate and a longer average dispersal distance will better track a high rate of  
328 environmental shift relative to a species that has a low reproductive rate and short dispersal  
329 distance. The finding that a higher reproductive rate can sustain higher climate velocities  
330 and harvesting rates is intuitive, especially because harvesting rate and reproductive rate  
331 cancel each other out. However it is worth pointing out that a higher reproductive rate can  
332 be generated either by shorter generation times or higher fecundity. Finding that species  
333 with shorter generation times can better keep up with shifts in climate is in agreement with  
334 empirical work which has found that fish which shifted in response to warming in North Sea  
335 had faster life histories than non shifting species [Perry et al., 2005]. While higher  
336 reproductive rates improved a population's ability to persist, there was a tradeoff in  
337 increasing dispersal distances. At low speeds, we found that a short dispersal dispersal  
338 distance improved the maximum harvesting rate a population could sustain while at higher  
339 speeds a longer dispersal distance improved the maximum climate velocity in which the  
340 population could persist (Figure 1). This tradeoff is due to the proportion of dispersing  
341 offspring at time step  $t$  which lands within the patch at time step  $t + 1$ . When climate is  
342 shifting slowly, a large dispersal distance sends most offspring ahead of the patch, while with  
343 faster climate velocities a long dispersal distance allows the population to make it to the new  
344 patch (Figure 1). Thus climate velocity will selectively favor species with dispersal distances  
345 best matched to the rate of shift.

346 We also examined whether frequently recommended management approaches, MPAs and  
347 harvest control rules, ensure species persistence. With these management strategies we  
348 found increases in the population's biomass at equilibrium and an improved ability to  
349 persist. We found that a threshold harvesting rule alleviates interactions between the two  
350 stressors. Thresholds have this effect as the management approach effectively prevents

351 harvesting of the leading edge, which allows colonization to occur as if these individuals were  
352 moving into un-fished areas. It's interesting to note that novel, low abundance species are  
353 commonly unregulated in fisheries systems; so in order to decouple the additive effects of  
354 harvest and climate change, management would have to reverse this paradigm by allowing  
355 no harvest of new species until they had become established.

356 Unlike thresholds, MPAs are explicitly spatial. Previous work has advanced protected areas  
357 as a way to help organisms keep pace with range shifts, as well as to ameliorate  
358 anthropogenic disturbances like harvesting and habitat fragmentation [Lawler et al., 2010,  
359 Hannah et al., 2007, Botsford et al., 2001, Gaylord et al., 2005, Hastings and Botsford, 2003,  
360 Thomas et al., 2012]. Our results show that both threshold and MPAs increase the  
361 equilibrium biomass at a given climate velocity, which support their use as a tool to  
362 ameliorate the effect of climate velocity. However, for MPAs, the details matter: few, large  
363 MPAs caused increased variability at low climate velocities while many smaller MPAs  
364 maintained a population bounded farther from extinction. Finally, with sufficiently high  
365 harvesting pressure, few, large MPAs rescued populations at intermediate speeds. With  
366 intermediate speeds, the population was able to reach a protected area fast enough to avoid  
367 extinction, and the protected area was large enough to allow a partial rebuilding of the  
368 population before it moved out the other side. However this effect disappears as speed  
369 continues to increase, suggesting that understanding the relationship between climate  
370 velocity, dispersal distance and reproductive rate are important parameters in designing  
371 management strategies effective under both climate change and harvesting pressure.

372 While the management strategies only change harvesting practices and do not directly  
373 address the effects of climate change, understanding how they ameliorate synergistic effects  
374 between harvesting and range shifts will help to better implement harvesting rules and place

375 protected areas. This is encouraging evidence that a single set of management practices  
376 may help to protect marine populations from both harvesting and climate change.

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

381 However, with Allee effects we expect qualitatively similar results. An Allee effect would  
382 make it harder for populations to colonize new areas and add a threshold below which  
383 fishing drives the population to extinction. Thus an Allee effect would change lower the  
384 critical harvest rates and climate velocity, but we do not expect the additive nature of the  
385 interaction between climate and harvesting to change. We also did not include age structure  
386 in our model. The effects of both harvesting and climate change may be different across  
387 different age classes and may destabilize the system in complicated ways, including  
388 resonance [Botsford et al., 2011, ?]; and we leave this additional complexity for future work.

389 Similarly, we did not include any mechanisms aside from larval dispersal by which the  
390 population could keep up with a shifting climate. Besides these species-specific extensions,  
391 this modeling framework could be extended to consider species interactions, especially  
392 predator-prey pairs. By introducing a predatory species, we would be imposing yet another  
393 stressor on the focus species [Ling et al., 2009, Gurevitch et al., 2000] and we are interested  
394 in measuring the interaction between the effects of this stressor and the two we consider here.

395 Using a simple mechanistic model like the one we present here provides a useful framework  
396 for incorporating additional ecological complexities which can mediate species persistence  
397 under multiple disturbances. Using this modeling framework as a starting point, we believe  
398 exploring how species interactions, age structure, and additional disturbances (e.g.

399 physiological response to temperature) affect population viability will improve our  
400 predictions and help us to understand whether species will persist under predicted climate  
401 and harvesting regimes. Finally, this work can help make general predictions as to whether  
402 specific life histories offer selective advantages over others as harvesting and range shifts  
403 increase and highlights the importance of considering stressors in combination as outcomes  
404 can deviate from what we would predict in isolation. This is especially true for management  
405 strategies which may result in unanticipated effects such as large fluctuations associated with  
406 big, distant MPAs shown here.

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## Figure Legends

**Figure 1:** (a) The critical harvesting rate on the y-axis as a function of the rate of environmental shift 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 rate of environmental shift 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 2:** Positive synergy between the two stressors. The x-axis shows the rate of environmental shift, 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 3:** The equilibrium biomass of the population as a function of the rate of environmental shift 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  $\langle d \rangle = 2$ .

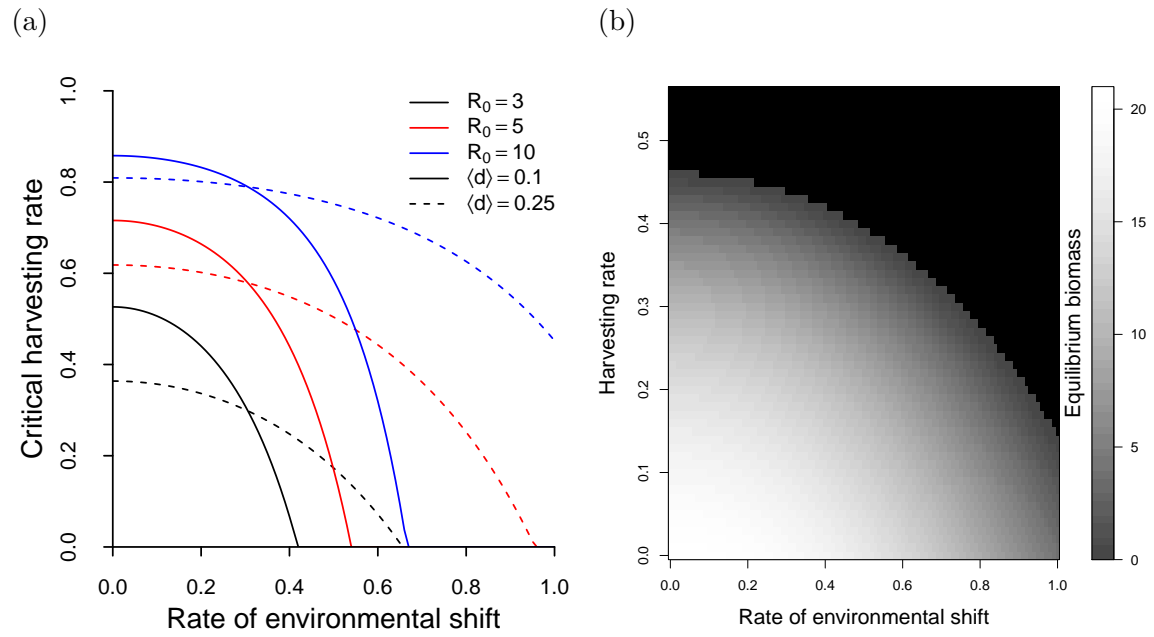


Figure 1



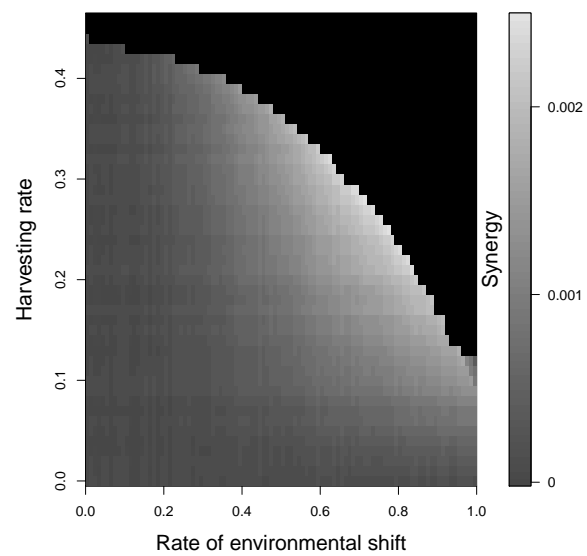


Figure 2

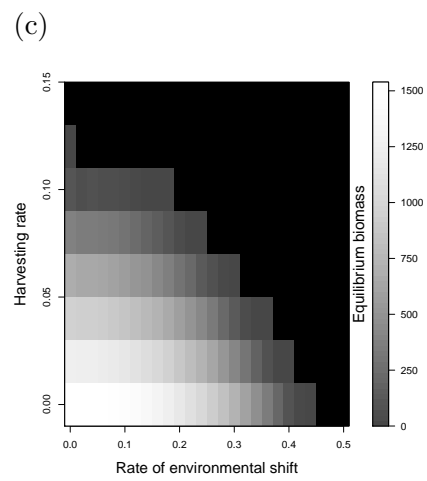
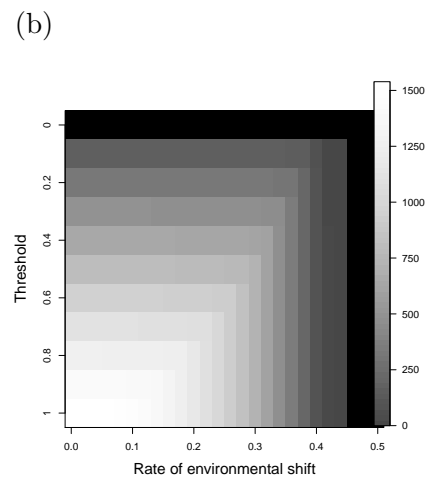
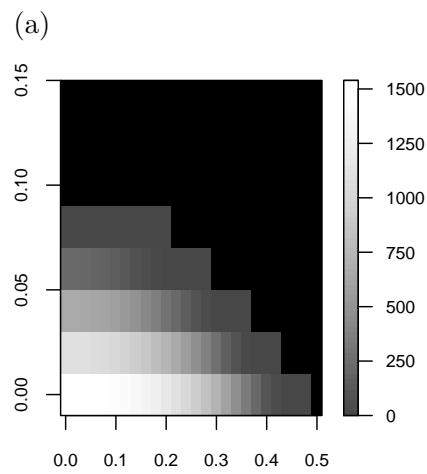


Figure 3

## 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
$c$	rate of environmental shift