

# Persistence of marine populations under climate and fishing

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# 1 Abstract

When the climate changes, the habitat with suitable conditions in which organisms can survive and reproduce moves. This change does not occur in isolation but rather appears on a background of other disturbances. In order to understand how two disturbances, range shift and harvesting, interact and affect population persistence, we studied an integrodifference model that explicitly included the mechanisms of dispersal and reproduction. If the viable habitat moves too quickly or harvesting pressure is too great, the population is driven extinct. We found the rates of harvesting and environmental shift required to allow the population to persist and studied how these critical parameters depend on the growth rate and dispersal behavior of the population. We then measured the interaction between the stressors. The stressors interact nearly additively: we found very low positive synergy at those levels of the stressors that almost drive the population extinct. Positive synergy suggests that harvesting may aggravate the population's sensitivity to a shifting range. Finally, we 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 mitigate the interaction between the two stressors.

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

# 2 Introduction

There are many stressors that can disturb an ecosystem. Ecologists have quantified the effects of a number of stressors individually [Wilcove et al., 1998, Crain et al., 2008, Darling and Côté, 2008], but less work 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, it is important to measure the synergy between disturbances in order to understand how a system will be affected by their presence and to understand when multiple disturbances will drive a population extinct [Doak and Morris, 2010, Fordham et al., 2013, Folt et al., 1999].

Climate change and fishing have been identified as the two largest human impacts on the ocean [Halpern et al., 2008]. They therefore provide an important case study of how disturbances interact in their effects on biological populations. Further, understanding these interactions will be crucial to managing populations subjected to both of these disturbances. 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 they are projected to continue moving in the future [Kell et al., 2005, Mackenzie et al., 2007]. Species that are likely to undergo or already undergoing shifts in range are also subject to harvesting, in addition to many 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]. Synergistic interactions between overfishing and temperature-driven range shifts have been found in empirical case

studies [Ling et al., 2009] and synergistic interactions between warming temperatures, harvesting and connectivity have been identified in microcosm experiments[Mora et al., 2007]. This empirical work underscores the importance of understanding how range shifts and harvesting interact.

A common approach to predicting how populations will be distributed in future after climate-driven range shifts 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 explain and 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, SDMs have frequently been criticized 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 the effects of climate-driven range shifts on fishing are considered, 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 understanding the relative importance of particular drivers, disturbances, and interactions is difficult (but see Nye et al. [2013] for an approach using ecosystem-level models to discern relative importance of disturbances). The degree of detail and case-specificity in these studies makes it difficult to draw general conclusions. Here we extended a previously studied model of a fish population subject to climate-driven range shift by also considering harvesting pressure. Reproduction and dispersal, two mechanistic processes central to species' responses to climate and fishing, are explicitly included. 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 rate of harvesting and the rate of environmental shift that drive the population extinct and how the threshold harvesting level depends on how quickly the range is shifting. We also found that climate-driven range shifts and fishing interact nearly additively, with very low positive synergy at more extreme levels of the stressors. We also examined the effect of threshold harvesting rules and marine protected areas (MPAs) on species persistence. Protected areas have been suggested as a key form of climate insurance and stepping stones to help species keep up with a changing environment [Thomas et al., 2012, Hannah et al., 2007]. 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 is shifting rapidly. We found that MPAs can help a species persist with higher harvesting pressure, but does not change 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 the patch. This viable habitat patch (here after ‘patch’) is shifting at a fixed velocity and the fish at each point in space can be harvested. We first determined the climate velocity and harvesting rate that would drive the population extinct. We then measured the drop in biomass caused by range shifts, harvesting, and both stressors together in order to determine whether they interact synergistically. We finally implemented marine protected areas (MPAs) and threshold harvesting rules in numerical simulations of the model to determine how these management strategies affect population persistence.

**3.1 The Model** In the model of Zhou and Kot [2011], 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

121 position  $x$ ,  $L$  is the length of the patch, and  $c$  is the rate at which it shifts across space. We  
 122 provide a list of variables and functions in Table 1. We chose to use a Beverton-Holt  
 123 recruitment function,

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

124 Regardless of the exact functional form of the recruitment function, the critical parameter in  
 125 determining population persistence is how quickly recruitment increases when the population  
 126 size is near (but above) 0, which is equivalent to the intrinsic growth rate,  $R_0 = f'(0)$ .  
 127 Analyzing this kind of model becomes easier if the dispersal kernel is separable into its  
 128 dependence on the source of larvae and its dependence on the destination of the larvae, i.e. if  
 129 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  
 130 et al., 1998], we used the separable Gaussian kernel given by

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

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

135 At equilibrium, the population will be described by a traveling wave, where the density of  
 136 fish at a given point in space will change but the density of fish at a location relative to the  
 137 shifting patch will not. We sought to describe how the population is distributed over the  
 138 viable patch as it shifts through the world in order to study the size of the population at  
 139 equilibrium and whether or not the population could persist. The traveling wave  $n^*$  must

140 satisfy

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

141 where  $\bar{x} \in \left[-\frac{L}{2}, \frac{L}{2}\right]$  describes the position within the patch [Zhou and Kot, 2011].

142 **3.2 Persistence** One possible equilibrium traveling wave that solves Equation (1) is the  
143 ‘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  
144 population is to persist, it must be able to avoid extinction and grow even when it is small.  
145 A small population can be thought of as a perturbation to the trivial traveling pulse. If the  
146 trivial pulse is stable, the system will return to the trivial pulse even after the introduction  
147 of a small population. If the trivial pulse is unstable, a small population may increase and  
148 form a stable population. Population persistence is therefore equivalent to the trivial  
149 traveling pulse being an unstable equilibrium.

150 If the population is harvested at low enough levels and the environment shifts slowly enough,  
151 the population will be able to persist. There are threshold values of the harvesting rate  $h$   
152 and the rate of environmental shift  $c$  such that if the parameters are increased beyond these  
153 values, the population will be driven extinct. We found these critical parameters,  $h^*$ , and  $c^*$ ,  
154 by finding the parameters that make the trivial pulse unstable. Details are provided in  
155 Appendix ??.

156 For each kernel, the population’s ability to persist depends on properties of the population  
157 itself– the expected distance a larva disperses ( $\langle d \rangle$ ) and the intrinsic growth rate ( $R_0$ );  
158 properties of the environment– the length of the viable patch ( $L$ ) and how quickly the  
159 environment is shifting ( $c$ ); and the harvesting rate ( $h$ ). The population biomass at  
160 equilibrium depends on the function form of recruitment, but population persistence only



161 depends on the intrinsic growth rate  $R_0$ . For a Gaussian kernel, the critical rates  $c^*$  and  $h^*$   
 162 are those values of  $c$  and  $h$  such that

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

A similar expression for a sinusoidal kernel is derived in the appendix. For both kernels, the critical harvesting proportion can be approximated by a function that looks like

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

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

165 **3.3 Calculating synergy** Zhou and Kot [2011] only considered whether a shifting  
 166 environment will drive a population extinct. In order to quantify whether the two stressors  
 167 are interacting additively, synergistically, or antagonistically, we found the total biomass of  
 168 the population when it reached an equilibrium traveling pulse and compared this equilibrium  
 169 biomass in the presence and absence of each stressor individually or the two stressors  
 170 together. For a separable kernel, the equilibrium traveling pulse  $n^*(x)$  must satisfy

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

171 where the  $m_i$  satisfy the recursive equations

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

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

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

$$E_s = B_0 - B_s.$$

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

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

If the stressors aggravate each other, the effect of both stressors is worse than would be expected from considering either stressor individually, and synergy is positive. If the stressors alleviate each other, the effect of both stressors is better than would be expected from considering either stressor individually, and synergy is negative. If the effect of both stressors is exactly as expected from considering either stressor individually, there is no interaction and no synergy.

**3.4 Simulations** We used simulations to extend the basic integrodifference model in two ways that make it analytically intractable. First, we examined the sensitivity of the model to

190 choice of dispersal kernel by using the Laplace dispersal kernel,

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

191 a commonly used model of larval dispersal [Pinsky, 2011]. Second, we examined harvesting  
192 rules more complex than harvesting a constant proportion of the population. Whereas  
193 population persistence in the analytical model does not depend on the functional form of  
194 recruitment  $f$ , to perform simulations we must specify a recruitment function. Again, we  
195 chose to use a Beverton-Holt function. In the first generation, we seeded the world with 50  
196 individuals at a single point, as in [Zhou and Kot, 2011]. We first ran through 150  
197 generations in order for the population to reach equilibrium without harvesting or climate  
198 shift. We then added harvesting pressure, allowed the population to again reach equilibrium,  
199 and finally added climate change by moving the viable patch. Equilibrium biomass is  
200 calculated as the mean biomass of 300 time steps once the difference in biomass between  
201 time step  $t$  and  $t + 1$  was no greater than 0.1.

202 We added harvesting pressure by harvesting a constant proportion of the population, in  
203 order to confirm our analytical results. We then evaluated the effect of a threshold harvest  
204 rule and marine protected areas (MPAs). With a threshold rule, we evaluated the population  
205 at each point in space to determine how much harvesting should occur. If the population  
206 abundance was below the designated threshold, no harvesting occurred. If the population  
207 exceeded the threshold, then a proportion of the ‘surplus’ individuals were harvested.

208 MPAs are a form of management designed to check the impact of fishing on targeted  
209 populations and are typically designed to meet either conservation or fishery management  
210 goals [Agardy, 1994, Holland and Brazee, 1996, Gaines et al., 2010b]. To implement an MPA  
211 management strategy in our model, we examine the effect of both of these commonly

212 advocated approaches. While both conservation and fisheries oriented MPA schemes align in  
213 their goal of maintaining a sustainable fished population, they differ in desired level of adult  
214 spillover. Fisheries-oriented MPAs are often designed such that they maximize adult  
215 spillover into fishable areas by creating many small reserves closely spaced [Hastings and  
216 Botsford, 2003]. The converse of this is the goal of conservation-oriented MPAs which seek  
217 to reduce adult spillover by minimizing the ratio between the reserve edge length relative to  
218 area protected [Gaines et al., 2010b].

219 Networks of MPAs were introduced into our simulations by designating segments of space in  
220 which harvesting was forbidden (i.e. harvesting rates were equal to 0). Conservation-oriented  
221 MPAs, are frequently large and rarely part of a larger network of reserves [Hastings and  
222 Botsford, 2003]. For solitary reserves to be successful at protecting target species, they must  
223 encompass self-sustaining fish populations [Hastings and Botsford, 2006, Gaines et al.,  
224 2010b]. As such modeling studies estimate that isolated reserves must be at least as large as  
225 the average dispersal distance for the targeted fish species [Lockwood et al., 2002, Hastings  
226 and Botsford, 2003, Botsford et al., 2001, Gaines et al., 2010a]. To implement conservation  
227 MPAs we created reserves with a length of 4 times the average dispersal distance and had a  
228 distance of 8 times the average dispersal distance between them to ensure that populations  
229 would be self sustaining and not dependent on other dispersal for other reserves [Lockwood  
230 et al., 2002].

231 Previous work has shown that if MPAs are to benefit fisheries, the reserves should be broken  
232 into a network, closely spaced to maximize adult spillover into fishable areas and export of  
233 larvae from reserve to reserve [Hastings and Botsford, 2003, Gaylord et al., 2005, Gaines  
234 et al., 2010b]. To mimic this management scheme, MPAs had a length of  $\frac{1}{3}$  of the average  
235 dispersal distance and had a distance of  $\frac{2}{3}$  of the average dispersal distance between them.

## 4 Results

**4.1 Interactions Between Stressors** We find the critical climate velocity and harvest rate to be inversely related: as the harvesting rate  $h$  increases, the critical climate velocity  $c^*$  decreases as the environment must move more slowly to accommodate the population growing more slowly (Figure 1). Conversely, as the rate of environmental shift  $c$  increases, the critical harvesting rate  $h^*$  decreases (Figure 1). 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. 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 those thresholds are reached, 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 speed  $c^*$  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, populations that disperse less can be harvested more severely than those that disperse further, whereas at a high rate of environmental shift, populations that disperse further can be harvested more severely.

We found very low levels of positive synergy between the two stressors in our analysis of the Gaussian kernel (Figure 2). Where there is positive synergy, a doubly stressed population loses more biomass than would be predicted from either stressor individually. The stressors interact most strongly when they are both high, shortly before they drive the population extinct. However, the excess loss in biomass is extremely 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 when the population is harvested more severely, slower rates of environmental shift will suffice to drive the population extinct. However, when thresholds are 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 both MPA strategies examined (many small versus few large), allowed the population was able to withstand combinations of higher climate velocities and harvesting rates. However MPAs did not increase the critical climate velocity (Figure 3). We also found that the spacing and size of the MPAs changed population dynamics. MPAs that were spaced more than 1 average

dispersal distance apart resulted in large oscillations of population biomass at low climate velocities. As climate velocities increase, the mean population abundance declines but the population experiences less extreme oscillations in abundance, which results in the population being bounded further from possible extinction in a stochastic environment.

## 5 Discussion

Knowing whether two disturbances interact in their impacts for a given population is important for management. 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. The curved line separating parameters that will allow the population to persist from those that won't 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.

305 We chose to measure the effect of each stressor by the absolute drop in biomass caused by  
306 the stressor, and we used the sum of the individual effects for our null prediction of the effect  
307 of both stressors, as in [Crain et al., 2008, Darling and Côté, 2008, Nye et al., 2013]. We  
308 could also have measured the effect by the percentage drop caused by the stressor(s) and  
309 used a multiplicative null prediction for the effect of both stressors. In general, measuring  
310 synergy against an additive null prediction is more conservative than measuring synergy  
311 multiplicatively: the presence of additive synergy implies multiplicative synergy, but not vice  
312 versa [Crain et al., 2008, Folt et al., 1999]. Since we found small levels of positive additive  
313 synergy between the two stressors, other measures of synergy might show even higher levels  
314 of interaction.

315 The fact that synergy is highest in those populations whose persistence is most tenuous is  
316 worrisome from a conservation perspective. This means that harvesting levels or rate of  
317 environment shift that are sustainable individually together can drive a population to  
318 extinction. However, the drop in biomass caused by both stressors was never very much  
319 higher than the null prediction, i.e. synergistic effects were quite small. Synergy between  
320 harvesting and climate changes has been identified in experimental populations [Mora et al.,  
321 2007], in specific populations [Planque et al., 2010a], and at the ecosystem level [Kirby et al.,  
322 2009, Planque et al., 2010a]. Additionally, in the experimental populations, synergy was  
323 identified between warming and harvesting but not between habitat fragmentation [Mora  
324 et al., 2007]. While we did find (very) low levels of positive synergy, we did not find as much  
325 as might be predicted from these empirical studies. However, these previous results are not  
326 directly comparable to ours because they focus on different aspects of climate change, e.g.  
327 warming temperature [Mora et al., 2007, Kirby et al., 2009] or a more variable climate  
328 [Planque et al., 2010a]. Additionally, while we can isolate the affects of climate shift and



329 harvesting in our simple analytical model, there are other forces acting on real populations  
 330 that may produce the observed synergistic effects.

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

352 We also examined whether frequently recommended management approaches ensure species

353 persistence. With these management strategies we found increases in the population's  
354 biomass at equilibrium and an improved ability to persist. Protected areas have been  
355 advanced as a way to help organisms keep pace with range shifts, as well as to ameliorate  
356 anthropogenic disturbances like harvesting and habitat fragmentation [Lawler et al., 2010,  
357 Hannah et al., 2007, Botsford et al., 2001, Gaylord et al., 2005, Hastings and Botsford, 2003,  
358 Thomas et al., 2012]. Our results, that spatial management increased the maximum  
359 harvesting rate at which the population could survive and improved the populations ability  
360 to persist at a slightly higher climate velocity conditional on a given harvesting rate [NEW  
361 FIGURE], support the idea that MPAs could be used to reduce the impact of harvesting and  
362 help to ameliorate the effects of climate velocity. However the spacing and size of the MPAs  
363 matter: few, large MPAs caused increased variability at low climate velocities while many  
364 smaller MPAs maintained a population that was bounded further from extinction.

365 When we applied harvesting thresholds, we found that it alleviates interactions between the  
366 two stressors. Thresholds have this effect as the management approach effectively prevents  
367 harvesting of the leading edge, which allows colonization to occur as if these individuals were  
368 moving into un-fished areas. It's interesting to note that novel, low abundance species are  
369 commonly unregulated in fisheries systems; in order to decouple the additive effects of  
370 harvest and climate change, this paradigm would have to be reversed: no new species would  
371 be allowed to harvest until they had become established. These results highlight that while  
372 management strategies only change harvesting practices, they can effect the way stressors  
373 interact and help to better implement harvesting rules and place protected areas.

374 The advantage of a simple model like ours is that it is general enough to be applied to a  
375 number of systems. However, it ignores many of the complexities present in marine fisheries.  
376 We do not include Allee effects, so that even if the population shrank to very low levels it

377 was possible for it to persist over time. However, we expect qualitatively similar results. An  
378 Allee effect would make it harder for populations to colonize new areas and add a threshold  
379 below which fishing drives the population to extinction. Thus an Allee effect would change  
380 lower the critical harvest rates and climate velocity, but we do not expect the additive  
381 nature of the interaction between climate and harvesting to change. We also did not include  
382 age structure in our model. The effects of both harvesting and climate change may be  
383 different across different age classes and may destabilize the system in complicated ways,  
384 including resonance [Botsford et al., 2011, Planque et al., 2010b]; including this level of  
385 complexity is left for future work. Similarly, we did not include any mechanisms aside from  
386 larval dispersal by which the population could keep up with a shifting climate. Besides these  
387 species-specific extensions, this modeling framework could be extended to consider species  
388 interactions, especially predator-prey pairs. By introducing a predatory species, we would be  
389 imposing yet another stressor on the focus species [Ling et al., 2009, Gurevitch et al.,  
390 2000]and we are interested in measuring the interaction between the effects of this stressor  
391 and the two we consider here.

392 Using a simple mechanistic model like the one we present here provides a useful framework  
393 for incorporating additional ecological complexities which can mediate species persistence  
394 under multiple disturbances. Exploring how species interactions, age structure, and  
395 additional disturbances (e.g. physiological response to temperature) affect population  
396 viability will improve our predictions and help us to understand whether species will persist  
397 under predicted climate and harvesting regimes. Finally, this work can help make general  
398 predictions as to whether specific life histories are likely to be selected over others as  
399 harvesting and range shifts increase and highlights the importance of considering stressors in  
400 combination as outcomes can deviate substantially from what would be predicted in

isolation. This is especially true for management strategies which may result in unanticipated effects such as large fluctuations associated with 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  $\langle d \rangle = 2$ .

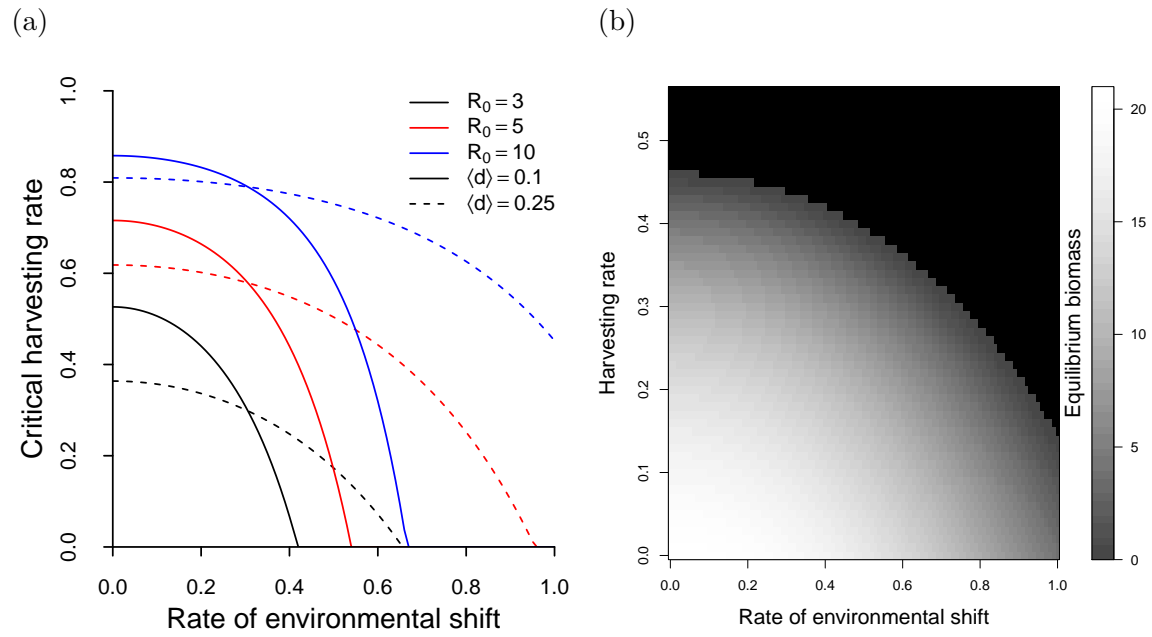


Figure 1



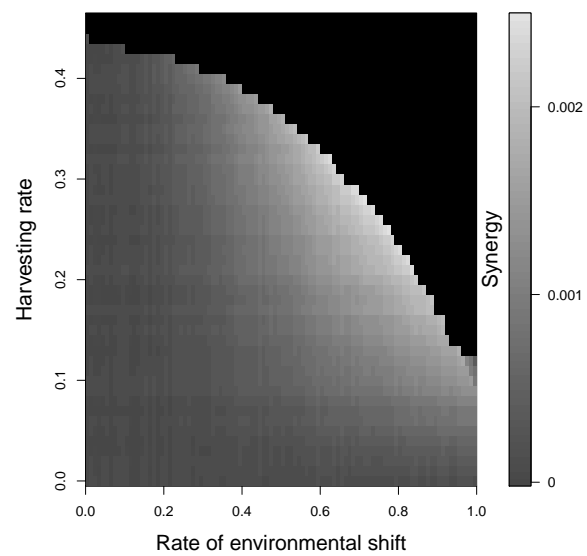
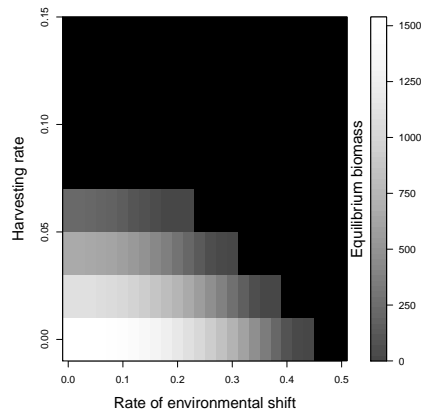
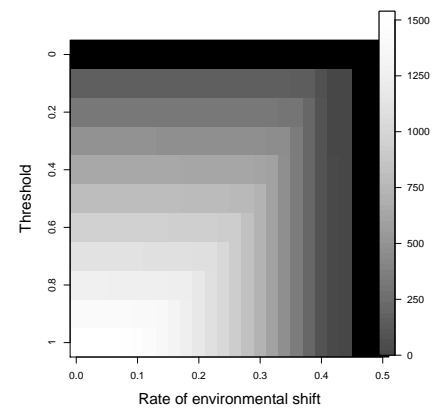


Figure 2

(a)



(b)



(c)

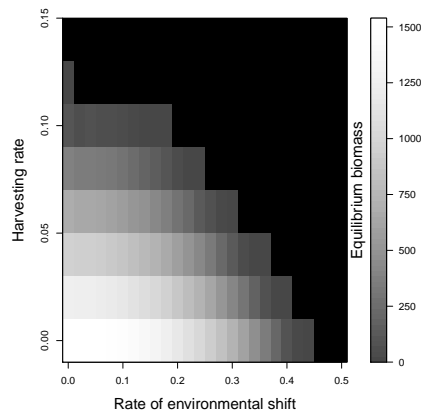


Figure 3

## 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   |
| $c$                 | rate of environmental shift  |