

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 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 measured 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 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 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, 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. We explicitly include 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 drives 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). Previous work has suggested protected areas 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 shifts rapidly. We found that threshold harvesting rules erase the interaction between harvesting rates and climate velocity and 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 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 finally add marine protected areas (MPAs) and threshold harvesting rules in numerical

100 simulations of the model to determine how these management strategies affect population
 101 persistence.

102 **3.1 The Model** In the model of Zhou and Kot [2011], the adults from the current year
 103 produce offspring according to a recruitment function and these offspring disperse across the
 104 one-dimensional world according to a dispersal kernel to become the next generation's
 105 adults. We extend this model by additionally subjecting the adults to harvesting before they
 106 produce offspring so that only a proportion of the fish survive to reproduce. We incorporate
 107 these processes— recruitment, harvesting, and dispersal— into an integrodifference model to
 108 describe how the population changes over time. If $n_t(x)$ is the density of fish at position x at
 109 time t , then the density of fish at the next generation is given by

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

110 where h is the proportion of adults harvested, $f(n)$ is the recruitment function giving the
 111 number of offspring produced by a population of size n (accounting for density dependence),
 112 $k(x-y)$ is the dispersal kernel giving the probability of a larva traveling from position y to
 113 position x , L is the length of the patch, and c is the rate at which it shifts across space. We
 114 provide a list of variables and functions in Table 1. We use a Beverton-Holt recruitment
 115 function,

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

116 but regardless of the exact functional form of the recruitment function, the critical
 117 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 population persists, it must be able to avoid extinction and grow even when small. We can

136 think of a small population as a perturbation to the trivial traveling pulse. If the trivial
 137 pulse is stable, the system will return to the trivial pulse even after the introduction of a
 138 small population. If the trivial pulse is unstable, a small population may increase and form a
 139 persistent population. Population persistence is therefore equivalent to the trivial traveling
 140 pulse being an unstable equilibrium.

141 If we harvest the population at low enough levels and the climate velocity is slow enough,
 142 the population will be able to persist. There exists threshold values of the harvesting rate h
 143 and a climate velocity c such that if we increase parameters beyond these values, we drive
 144 the population extinct. We found these critical parameters, h^* , and c^* , by finding the
 145 parameters that make the trivial pulse unstable (See Appendix ??).

146 For each kernel, the population's ability to persist depends on properties of the population
 147 itself– the expected distance a larva disperses $\langle d \rangle$ and the intrinsic growth rate R_0 ; properties
 148 of the environment– the length of the viable patch L and how quickly the environment shifts
 149 c ; and the harvesting rate h . The population biomass at equilibrium depends on the function
 150 form of recruitment, but population persistence only depends on the intrinsic growth rate
 151 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

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

152 where $C(L, R_0)$ is a decreasing function of the length of the viable patch and the intrinsic

153 growth rate.

154 **3.3 Calculating synergy** Zhou and Kot [2011] only considered whether a shifting
 155 environment will drive a population extinct. In order to quantify whether the two stressors
 156 interact additively, synergistically, or antagonistically, we found the total biomass of the
 157 population when it reached an equilibrium traveling pulse and compared this equilibrium
 158 biomass in the presence and absence of each stressor individually or the two stressors
 159 together. For a separable kernel, the equilibrium traveling pulse $n^*(x)$ must satisfy

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

160 where the m_i satisfy the recursive equations

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

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

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

$$E_s = B_0 - B_s.$$

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

$$S = E_{\text{hc}} - (E_{\text{h}} + E_{\text{c}}).$$

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

177 **3.4 Simulations** We used simulations to extend the basic integrodifference model in two
 178 ways that make it analytically intractable. First, we examined the sensitivity of the model to
 179 choice of dispersal kernel by using the Laplace dispersal kernel,

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

180 a commonly used model of larval dispersal [?]. Second, we examined harvesting rules more
 181 complex than harvesting a constant proportion of the population. Whereas population
 182 persistence in the analytical model does not depend on the functional form of recruitment f ,
 183 to perform simulations we must specify a recruitment function. Again, we chose to use a
 184 Beverton-Holt function. In the first generation, we seeded the world with 50 individuals at a
 185 single point, as in Zhou and Kot [2011]. We first ran through 150 generations in order for
 186 the population to reach equilibrium without harvesting or climate shift. We then added

187 harvesting pressure, allowed the population to again reach equilibrium (150 generations),
 188 and finally added climate change by moving the viable patch. We calculate equilibrium
 189 biomass as the mean biomass of 300 time steps once the difference in biomass between time
 190 step t and $t + 1$ was no greater than 0.1.

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

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

208 We introduce networks of MPAs into our simulations by designating segments of space where
 209 the harvesting rate was equal to 0. Conservation-oriented MPAs, are frequently large and
 210 rarely part of a larger network of reserves [Hastings and Botsford, 2003]. For solitary

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

224 4 Results

225 **4.1 Interactions Between Stressors** We find the critical climate velocity and harvest
 226 rate to be inversely related: as the harvesting rate h increases, the critical climate velocity c^*
 227 decreases, as the environment must move more slowly to accommodate the population
 228 growing more slowly (Figure 1). Conversely, as the rate of environmental shift c increases,
 229 the critical harvesting rate h^* decreases (Figure 1). This means that a harvesting rate that is
 230 sustainable in the absence of environmental shift may no longer be sustainable if the
 231 environment starts changing. When the climate velocity or harvesting pressure exceed their
 232 critical rates (h^*, c^* respectively), the biomass of the population at equilibrium will be equal

233 to 0. Before the stressors reaches those thresholds, the equilibrium biomass of the population
 234 decreases as either the harvesting pressure increases or the environmental shifts more quickly
 235 (Figure 1). Our simulations confirm the analytical results with the critical speed c^* declining
 236 as the critical harvest rate h^* increases and vice versa (Figure 3a).

237 It is always the case that increasing the intrinsic growth rate, R_0 , of the population increases
 238 the critical climate velocity c^* and the critical harvesting rate h^* , since a population that
 239 grows more quickly can recover more quickly from losses caused by these disturbances.

240 However, whether or not dispersing farther is better depends on how quickly the
 241 environment is shifting (Figure 1). When the environment is shifting slowly, dispersing
 242 farther is detrimental since many larvae will disperse too far away from the viable patch.

243 When the environment is shifting quickly, on the other hand, dispersing farther can help the
 244 population persist because some larvae will disperse into the space that will become viable
 245 shortly in the future. This affects the critical harvesting rate: at a low rate of environmental
 246 shift, we can more severely harvest populations that have a shorter dispersal distance than
 247 those that disperse farther, whereas at a high rate of environmental shift, we can more
 248 aggressively harvest populations that disperse farther.

249 We found low levels of positive synergy between the two stressors in our analysis of the
 250 Gaussian kernel (Figure 2). Where positive synergy exists, a doubly stressed population
 251 loses more biomass than we would predict from either stressor individually. The stressors
 252 interact most strongly at high values, shortly before they drive the population extinct.

253 However, the excess loss in biomass is low, making it difficult to distinguish positive synergy
 254 from additive interactions. We found similar analytical results for a sinusoidal dispersal
 255 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

303 multiplicatively: the presence of additive synergy implies multiplicative synergy, but not vice
304 versa [Crain et al., 2008, Folt et al., 1999]. Since we found small levels of positive additive
305 synergy between the two stressors, other measures of synergy might show even higher levels
306 of interaction.

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

317 However, these previous results are not directly comparable to ours because they focus on
318 different aspects of climate change, e.g. warming temperature [Mora et al., 2007, Kirby
319 et al., 2009] or a more variable climate [Planque et al., 2010]. Additionally, while we can
320 isolate the affects of climate shift and harvesting in our simple analytical model, there are
321 other forces acting on real populations that may produce the observed synergistic effects.

322 Our results suggest that particular combinations of harvesting and rate of environmental
323 shift will affect some species more than others. As shown in Figure 1, species with a higher
324 reproductive rate and a longer average dispersal distance will better track a high rate of
325 environmental shift relative to a species that has a low reproductive rate and short dispersal
326 distance. The finding that a higher reproductive rate can sustain higher climate velocities

and harvesting rates is intuitive, especially because harvesting rate and reproductive rate cancel each other out. 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 [Perry et al., 2005]. While higher reproductive rates improved a population's ability to persist, there was a tradeoff in increasing dispersal distances. 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 1). This tradeoff is due to the proportion of dispersing offspring at time step t which lands within the patch at time step $t + 1$. 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 1). 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 [Lawler et al., 2010, Hannah et al., 2007, Botsford et al., 2001, Gaylord et al., 2005, Hastings and Botsford, 2003, Thomas et al., 2012]. 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 effects 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 fishing drives the population to extinction. Thus an Allee effect would change lower the critical harvest rates and climate velocity, but we do not expect the additive nature of the interaction between climate and harvesting to change. We also did not include age structure in our model. The effects of both harvesting and climate change may be different across different age classes and may destabilize the system in complicated ways, including resonance [Botsford et al., 2011, ?]; and we leave this additional complexity for future work. Similarly, we did not include any mechanisms aside from larval dispersal by which the population could keep up with a shifting climate. Besides these species-specific extensions, this modeling framework could be extended to consider species interactions, especially predator-prey pairs. By introducing a predatory species, we would be imposing yet another stressor on the focus species [Ling et al., 2009, Gurevitch et al., 2000] and we are interested in measuring the interaction between the effects of this stressor and the two we consider here. Using a simple mechanistic model like the one we present here provides a useful framework for incorporating additional ecological complexities which can mediate species persistence under multiple disturbances. Using this modeling framework as a starting point, we believe exploring how species interactions, age structure, and additional disturbances (e.g. physiological response to temperature) affect population viability will improve our predictions and help us to understand whether species will persist under predicted climate and harvesting regimes. Finally, this work can help make general predictions as to whether

specific life histories offer selective advantages over others as harvesting and range shifts increase and highlights the importance of considering stressors in combination as outcomes can deviate from what we would predict 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 $\langle d \rangle = 2$.

646 **6 Figures**

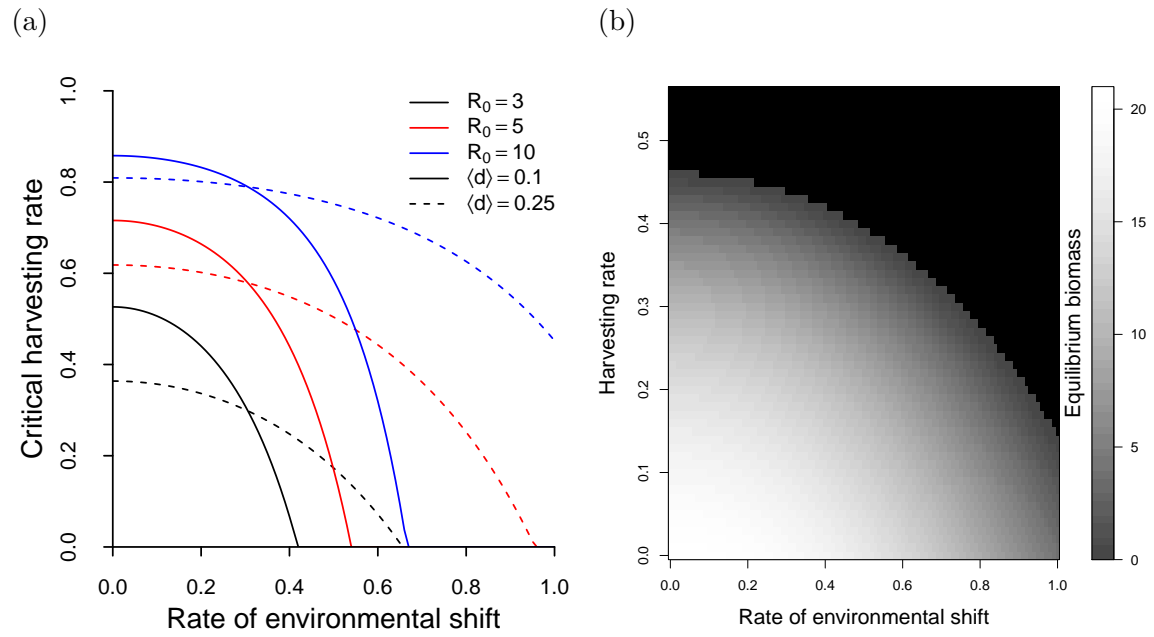


Figure 1

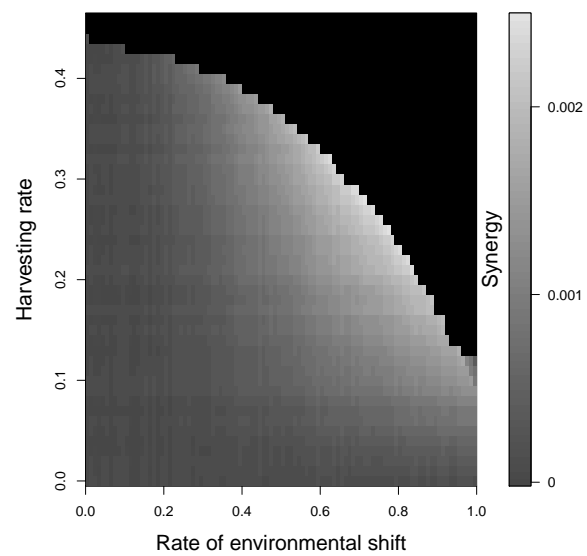


Figure 2

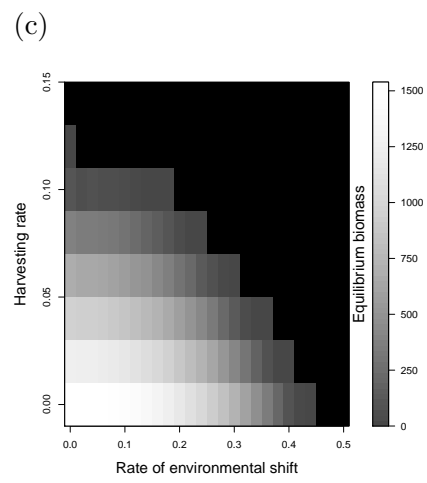
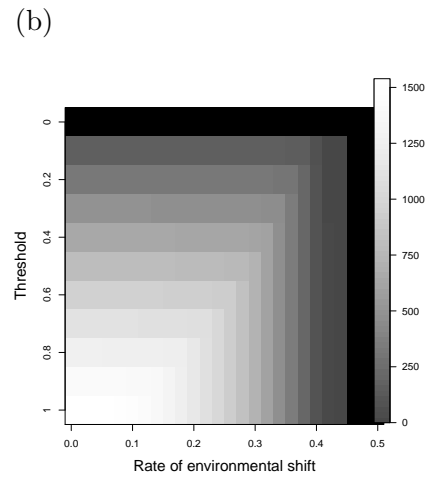
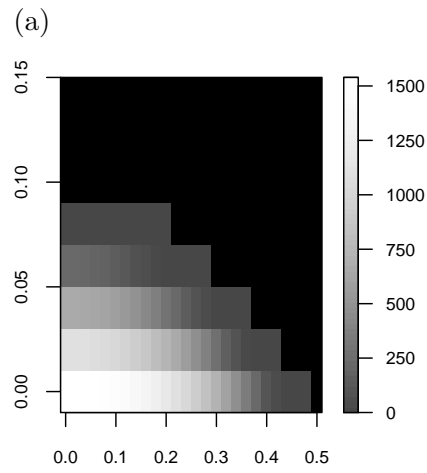


Figure 3

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