

Persistence of marine populations under climate and fishing

Emma Fuller¹, Eleanor Brush¹, Malin Pinsky^{1,2}

(1): Department of Ecology and Evolutionary Biology, Princeton University, Princeton, New Jersey 08544 USA

(2): Department of Ecology, Evolution and Natural Resources, Rutgers University, New Brunswick, New Jersey 08901 USA

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

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

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

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

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

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

117 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

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

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

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

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

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

161 where the m_i satisfy the recursive equations

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

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

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

$$E_s = B_0 - B_s.$$

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

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

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

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

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

181 a commonly used model of larval dispersal [Pinsky, 2011]. Second, we examined harvesting
 182 rules more complex than harvesting a constant proportion of the population. Whereas
 183 population persistence in the analytical model does not depend on the functional form of
 184 recruitment f , to perform simulations we must specify a recruitment function. Again, we
 185 chose to use a Beverton-Holt function. In the first generation, we seeded the world with 50

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

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

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

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

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

225 4 Results

226 **4.1 Interactions Between Stressors** We find the critical climate velocity and harvest
 227 rate to be inversely related: as the harvesting rate h increases, the critical climate velocity c^*
 228 decreases, as the environment must move more slowly to accommodate the population
 229 growing more slowly (Figure 1). Conversely, as the rate of environmental shift c increases,
 230 the critical harvesting rate h^* decreases (Figure 1). This means that a harvesting rate that is
 231 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. We also 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. 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

301 of both stressors, as in Crain et al. [2008], Darling and Côté [2008], Nye et al. [2013]. We
302 could also have measured the effect by the percentage drop caused by the stressor(s) and
303 used a multiplicative null prediction for the effect of both stressors. In general, measuring
304 synergy against an additive null prediction is more conservative than measuring synergy
305 multiplicatively: the presence of additive synergy implies multiplicative synergy, but not vice
306 versa [Crain et al., 2008, Folt et al., 1999]. Since we found small levels of positive additive
307 synergy between the two stressors, other measures of synergy might show even higher levels
308 of interaction.

309 Worryingly, we find the highest synergy in those populations whose persistence is most
310 tenuous. This means that harvesting levels or climate velocity that are sustainable
311 individually together can drive a population to extinction. However the drop in biomass
312 caused by both stressors was never much higher than the null prediction, i.e. synergistic
313 effects were quite small. Experimental work has identified synergy between harvesting and
314 climate changes [Mora et al., 2007], in specific populations [Planque et al., 2010a], and at the
315 ecosystem level [Kirby et al., 2009, Planque et al., 2010a]. Additionally, experimental
316 populations have identified synergy between warming and harvesting but not between
317 habitat fragmentation [Mora et al., 2007]. While we did find (very) low levels of positive
318 synergy, we did not find as much as predicted from these empirical studies. However, these
319 previous results are not directly comparable to ours because they focus on different aspects
320 of climate change, e.g. warming temperature [Mora et al., 2007, Kirby et al., 2009] or a more
321 variable climate [Planque et al., 2010a]. Additionally, while we can isolate the affects of
322 climate shift and harvesting in our simple analytical model, there are other forces acting on
323 real populations that may produce the observed synergistic effects.

324 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 reproductive rate and a longer average dispersal distance will better track a high rate of environmental shift relative to a species that has a low reproductive rate and short dispersal 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. Previous work has advanced protected areas as a way to help organisms keep pace

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

364 Unlike MPAs, thresholds are not explicitly spatial, and we found that this harvest control
365 rule alleviates interactions between the two stressors. Thresholds have this effect as the
366 management approach effectively prevents harvesting of the leading edge, which allows
367 colonization to occur as if these individuals were moving into un-fished areas. It's interesting
368 to note that novel, low abundance species are commonly unregulated in fisheries systems; so
369 in order to decouple the additive effects of harvest and climate change, management would
370 have to reverse this paradigm by allowing no harvest of new species until they had become
371 established. These results highlight that while management strategies only change
372 harvesting practices, they can effect the way stressors interact and so understanding these

interacts help to better design harvesting rules and place protected areas.

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, Planque et al., 2010b]; 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.

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

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408 **References**

- 409 M. Tundi Agardy. Advances in marine conservation: the role of marine protected areas. *Trends*
410 *in Ecology & Evolution*, 9(7):267–270, 1994. ISSN 0169-5347.
- 411 C. H. . H. Ainsworth, J. F. . F. Samhuri, D. S. . S. Busch, W. W. L. Cheung, J. Dunne, and
412 T. A. . A. Okey. Potential impacts of climate change on northeast pacific marine foodwebs
413 and fisheries. *ICES Journal of Marine Science*, 68(6):1217–1229, 7 2011. ISSN 1054-3139.
414 doi: 10.1093/icesjms/fsr043.
- 415 Edward H. Allison, Allison L. Perry, Marie-Caroline . C. Badjeck, W. Neil Adger, Katrina
416 Brown, Declan Conway, Ashley S. Halls, Graham M. Pilling, John D. Reynolds, Neil L.

417 Andrew, and Nicholas K. Dulvy. Vulnerability of national economies to the impacts of
 418 climate change on fisheries. *Fish and Fisheries*, 10(2):173–196, 6 2009. ISSN 14672960. doi:
 419 10.1111/j.1467-2979.2008.00310.x.

420 Millennium Ecosystem Assessment. *Ecosystems and human well-being*, volume 5. Island Press
 421 Washington, DC, 2005.

422 Manuel Barange, Icarus Allen, Eddie Allison, Marie-Caroline Badjeck, Juila Blanchard, Ben-
 423 jamin Drakeford, Nicholas K. Dulvy, James Harle, Robert Holmes, Jason Holt, Simon
 424 Jennings, Jason Lowe, Gorka Merino, Christian Mullon, Graham Pilling, Lynda Rod-
 425 well, Emma Tompkins, Francisco Werner, and KL Cochrane. *Response of ocean ecosys-*
 426 *tems to climate warming*, volume 18, page 440. Wiley-Blackwell, New Jersey, 2011. doi:
 427 10.1029/2003GB002134.

428 J. P. Barry, C. H. Baxter, and S. E. Gilman. Climate-related, long-term faunal changes in a
 429 california rocky intertidal community. *Science*, 267(5198):672–675, 1995.

430 H. Berestycki, O. Diekmann, C. J. Nagelkerke, and P. A. Zegeling. Can a species keep pace
 431 with a shifting climate? *Bull Math Biol*, 71(2):399–429, 2 2009. ISSN 1522-9602. doi:
 432 10.1007/s11538-008-9367-5.

433 Louis W. Botsford, Alan Hastings, and Steven D. Gaines. Dependence of sustainability on the
 434 configuration of marine reserves and larval dispersal distance. *Ecology Letters*, 4:144–150,
 435 2001. ISSN 1461-0248.

436 Louis W. Botsford, Matthew D. Holland, Jameal F. Samhouri, J. Wilson White, and Alan
 437 Hastings. Importance of age structure in models of the response of upper trophic levels to

438 fishing and climate change. *ICES Journal of Marine Science: Journal du Conseil*, 68(6):
439 1270–1283, 2011.

440 C. J. Brown, E. A. Fulton, A. J. Hobday, R. J. Matear, H. P. Possingham, C. Bulman,
441 V. Christensen, R. E. Forrest, P. C. Gehrke, N. A. Gribble, S. P. Griffiths, H. Lozano-
442 Montes, J. M. Martin, S. Metcalf, T. A. Okey, R. Watson, and A. J. Richardson. Effects of
443 climate-driven primary production change on marine food webs: implications for fisheries
444 and conservation. *Global Change Biology*, 16(4):1194–1212, 4 2010. ISSN 13541013. doi:
445 10.1111/j.1365-2486.2009.02046.x.

446 William WL Cheung, Vicky WY Lam, Jorge L. Sarmiento, Kelly Kearney, R. E. G. Watson,
447 Dirk Zeller, and Daniel Pauly. Large-scale redistribution of maximum fisheries catch poten-
448 tial in the global ocean under climate change. *Global Change Biology*, 16(1):24–35, 2010.
449 ISSN 1354-1013.

450 Caitlin Mullan Crain, Kristy Kroeker, and Benjamin S. Halpern. Interactive and cumulative
451 effects of multiple human stressors in marine systems. *Ecol Lett*, 11(12):1304–15, 12 2008.
452 ISSN 1461-0248. doi: 10.1111/j.1461-0248.2008.01253.x.

453 Emily S. Darling and Isabelle M. Côté. Quantifying the evidence for ecological synergies. *Ecol*
454 *Lett*, 11(12):1278–86, 12 2008. ISSN 1461-0248. doi: 10.1111/j.1461-0248.2008.01243.x.

455 Daniel F. Doak and William F. Morris. Demographic compensation and tipping points in
456 climate-induced range shifts. *Nature*, 467(7318):959–62, 10 2010. ISSN 1476-4687. doi:
457 10.1038/nature09439.

458 Nicholas K. Dulvy, Stuart I. Rogers, Simon Jennings, Vanessa Stelzenmiller, Stephen R. Dye,
459 and Hein R. Skjoldal. Climate change and deepening of the north sea fish assemblage: a

460 biotic indicator of warming seas. *Journal of Applied Ecology*, 45(4):1029–1039, 8 2008. ISSN
461 00218901. doi: 10.1111/j.1365-2664.2008.01488.x.

462 Jane Elith, Catherine H. Graham, Robert P Anderson, Miroslav Dudík, Simon Ferrier, Antoine
463 Guisan, Robert J Hijmans, Falk Huettmann, John R Leathwick, Anthony Lehmann, Jin Li,
464 and Lucia G Lohmann. Novel methods improve prediction of species?’ distributions from
465 occurrence data. *Ecography*, 29(2):129–151, 2006.

466 C. L. Folt, C. Y. Chen, M. V. Moore, and J. Burnaford. Synergism and antagonism among
467 multiple stressors. *Limnology and Oceanography*, 44(3):864–877, 1999.

468 D. A. . A. Fordham, C. Mellin, B. D. . D. Russell, H. R. . R. Akçakaya, C. J. A. Bradshaw,
469 M. E. . E. Aiello-Lammens, MJ J. Caley, S. D. . D. Connell, S. Mayfield, S. A. . A. Shepherd,
470 and B. W. . W. Brook. Population dynamics can be more important than physiological limits
471 for determining range shifts under climate change. *Global Change Biology*, page n/a, 6 2013.
472 doi: 10.1111/gcb.12289.

473 Steven D. Gaines, Sarah E. Lester, Kirsten Grorud-Colvert, Christopher Costello, and Richard
474 Pollnac. Evolving science of marine reserves: new developments and emerging research
475 frontiers. *Proc Natl Acad Sci U S A*, 107(43):18251–5, 10 2010a. ISSN 1091-6490. doi:
476 10.1073/pnas.1002098107.

477 Steven D. Gaines, Crow White, Mark H. Carr, and Stephen R. Palumbi. Designing marine
478 reserve networks for both conservation and fisheries management. *Proc Natl Acad Sci U S*
479 *A*, 107(43):18286–93, 10 2010b. ISSN 1091-6490. doi: 10.1073/pnas.0906473107.

480 Brian Gaylord, Steven D. Gaines, David A. Siegel, and Mark H. Carr. Marine reserves exploit

481 population structure and life history in potentially improving fisheries yields. *Ecological*
482 *Applications*, 15(6):2180–2191, 2005.

483 Antoine Guisan and Wilfried Thuiller. Predicting species distribution: offering more than
484 simple habitat models. *Ecology Letters*, 8(9):993–1009, 9 2005. ISSN 1461-023X. doi:
485 10.1111/j.1461-0248.2005.00792.x.

486 Antoine Guisan and Niklaus E. Zimmermann. Predictive habitat distribution models in ecol-
487 ogy. *Ecological modelling*, 135(2):147–186, 2000.

488 Jessica Gurevitch, Janet A. Morrison, and Larry V. Hedges. The interaction between compe-
489 tition and predation: A metaanalysis of field experiments. *The American Naturalist*, 155
490 (4):435–453, 4 2000. ISSN 0003-0147. doi: 10.1086/303337.

491 Benjamin S. Halpern, Shaun Walbridge, Kimberly A. Selkoe, Carrie V. Kappel, Fiorenza
492 Micheli, Caterina D’Agrosa, John F. Bruno, Kenneth S. Casey, Colin Ebert, Helen E. Fox,
493 Rod Fujita, Dennis Heinemann, Hunter S. Lenihan, Elizabeth M. P. Madin, Matthew T.
494 Perry, Elizabeth R. Selig, Mark Spalding, Robert Steneck, and Reg Watson. A global map of
495 human impact on marine ecosystems. *Science*, 319(5865):948–52, 2 2008. ISSN 1095-9203.
496 doi: 10.1126/science.1149345.

497 Lee Hannah, Guy Midgley, Sandy Andelman, Miguel Araújo, Greg Hughes, Enrique Martinez-
498 Meyer, Richard Pearson, and Paul Williams. Protected area needs in a changing climate.
499 *Frontiers in Ecology and the Environment*, 5(3):131–138, 2007.

500 Alan Hastings and Louis W. Botsford. Comparing designs of marine reserves for fisheries and
501 for biodiversity. *Ecological Applications*, 13(sp1):65–70, 2003.

502 Alan Hastings and Louis W. Botsford. Persistence of spatial populations depends on returning
503 home. *Proceedings of the National Academy of Sciences*, 103(15):6067–6072, 2006.

504 Alan Hastings, Kim Cuddington, Kendi F. Davies, Christopher J. Dugaw, Sarah Elmendorf,
505 Amy Freestone, Susan Harrison, Matthew Holland, John Lambrinos, Urmila Malvadkar,
506 Brett A. Melbourne, Kara Moore, Caz Taylor, and Diane Thomson. The spatial spread of
507 invasions: new developments in theory and evidence. *Ecology Letters*, 8(1):91–101, 2005.
508 ISSN 14610248. doi: 10.1111/j.1461-0248.2004.00687.x.

509 J. G. Hiddink and R. ter Hofstede. Climate induced increases in species richness of marine
510 fishes. *Global Change Biology*, 14(3):453–460, 3 2008. ISSN 1354-1013. doi: 10.1111/j.
511 1365-2486.2007.01518.x.

512 Daniel S. Holland and Richard J. Brazee. Marine reserves for fisheries management. *Marine*
513 *Resource Economics*, 11:157–172, 1996.

514 Jennifer Howard, Eleanora Babij, Roger Griffis, Brian Helmuth, Stewart Allen, Guillermo
515 Auad, Russell Beard, Mary Boatman, Nicholas Bond, Timothy Boyer, David Brown,
516 Patricia Clay, Katherine Crane, Scott Cross, Michael Dalton, Jordan Diamond, Robert
517 Diaz, Quay Dortch, Emmett Duffy, Deborah Fauquier, William Fisher, Michael Graham,
518 Benjamin Halpern, Lara Hansen, Bryan Hayum, Samuel Herrick, Anne Hollowed, David
519 Hutchins, Elizabeth Jewett, Di Jin, Nancy Knowlton, Dawn Kotowicz, Trond Kristiansen,
520 Peter Little, Cary Lopez, Philip Loring, Rick Lumpkin, Amber Mace, Katheryn Mengerink,
521 J. Ru Moorison, Jason Murray, Karma Norman, James O’Donnell, James Overland, Rost
522 Parsons, Neal Pettigrew, Lisa Pfeiffer, Emily Pidgeon, Mark Plummer, Jeffrey Polovina,
523 Josie Quintrell, Teresa Rowles, Jeffrey Runge, Michael Rust, Eric Sanford, Ewe Send, Mer-
524 rill Singer, Cameron Speir, Diane Stanitski, Carol Thornber, Cara Wilson, and Yan Xue.

525 Oceans and marine resources in a changing climate. Technical report, Oceanography and
 526 Marine Biology: An Annual Review, 2013.

527 Michael Kearney and Warren Porter. Mechanistic niche modelling: combining physiological
 528 and spatial data to predict species' ranges. *Ecol Lett*, 12(4):334–50, 4 2009. ISSN 1461-0248.
 529 doi: 10.1111/j.1461-0248.2008.01277.x.

530 L. Kell, G. Pilling, and C. O'Brien. Implications of climate change for the management of
 531 north sea cod (*gadus morhua*). *ICES Journal of Marine Science*, 62(7):1483–1491, 10 2005.
 532 ISSN 10543139. doi: 10.1016/j.icesjms.2005.05.006.

533 J. R. King and G. A. McFarlane. A framework for incorporating climate regime shifts into the
 534 management of marine resources. *Fisheries Management and Ecology*, 13(2):93–102, 2006.

535 Richard R. Kirby, Gregory Beaugrand, and John A. Lindley. Synergistic effects of climate and
 536 fishing in a marine ecosystem. *Ecosystems*, 12:548–556, 2009.

537 J. Latore, P. Gould, and A. M. Mortimer. Spatial dynamics and critical patch size of annual
 538 plant populations. *Journal of Theoretical Biology*, 190(3):277–285, 1998.

539 Joshua J. Lawler, Timothy H. Tear, Chris Pyke, M. Rebecca Shaw, Patrick Gonzalez, Peter
 540 Kareiva, Lara Hansen, Lee Hannah, Kirk Klausmeyer, Allison Aldous, Craig Bienz, and
 541 Sam Pearsall. Resource management in a changing and uncertain climate. *Frontiers in*
 542 *Ecology and the Environment*, 8(1):35–43, 2 2010. ISSN 1540-9295. doi: 10.1890/070146.

543 Martin Lindegren, Christian Möllmann, Anders Nielsen, Keith Brander, Brian R. MacKenzie,
 544 and Nils Chr Stenseth. Ecological forecasting under climate change: the case of baltic cod.
 545 *Proc Biol Sci*, 277(1691):2121–30, 7 2010. ISSN 1471-2954. doi: 10.1098/rspb.2010.0353.

546 S. D. Ling, C. R. Johnson, S. D. Frusher, and K. R. Ridgway. Overfishing reduces resilience of
 547 kelp beds to climate-driven catastrophic phase shift. *Proceedings of the National Academy
 548 of Sciences*, 106(52):22341–22345, 2009.

549 Dale R. Lockwood, Alan Hastings, and Louis W. Botsford. The effects of dispersal patterns
 550 on marine reserves: does the tail wag the dog? *Theor Popul Biol*, 61(3):297–309, 5 2002.
 551 ISSN 0040-5809. doi: 10.1006/tpbi.2002.1572.

552 Brian R. Mackenzie, Henrik Gislason, Christian Möllmann, and Friedrich W. Köster. Impact
 553 of 21st century climate change on the baltic sea fish community and fisheries. *Global Change
 554 Biology*, 13(7):1348–1367, 7 2007. ISSN 1354-1013. doi: 10.1111/j.1365-2486.2007.01369.x.

555 Gorka Merino, Manuel Barange, and Christian Mullon. Climate variability and change scenar-
 556 ios for a marine commodity: Modelling small pelagic fish, fisheries and fishmeal in a glob-
 557 alized market. *Journal of Marine Systems*, 81(1–2):196 – 205, 2010a. ISSN 0924-7963. doi:
 558 10.1016/j.jmarsys.2009.12.010. URL [http://www.sciencedirect.com/science/article/
 559 pii/S0924796309003480](http://www.sciencedirect.com/science/article/pii/S0924796309003480).

560 Gorka Merino, Manuel Barange, Christian Mullon, and Lynda Rodwell. Impacts of global en-
 561 vironmental change and aquaculture expansion on marine ecosystems. *Global Environmental
 562 Change*, 20(4):586–596, 10 2010b. ISSN 09593780. doi: 10.1016/j.gloenvcha.2010.07.008.

563 Camilo Mora, Rebekka Metzger, Audrey Rollo, and Ransom A. Myers. Experimental simula-
 564 tions about the effects of overexploitation and habitat fragmentation on populations facing
 565 environmental warming. *Proc Biol Sci*, 274(1613):1023–8, 4 2007. ISSN 0962-8452. doi:
 566 10.1098/rspb.2006.0338.

567 Janet A. Nye, Jason S. Link, Jonathan A. Hare, and William J. Overholtz. Changing spatial

distribution of fish stocks in relation to climate and population size on the northeast united states continental shelf. *Marine Ecology Progress Series*, 393:111–129, 10 2009. ISSN 0171-8630. doi: 10.3354/meps08220.

Janet A. Nye, Robert J. Gamble, and Jason S. Link. The relative impact of warming and removing top predators on the northeast us large marine biotic community. *Ecological Modelling*, 264:157–168, 8 2013. ISSN 03043800. doi: 10.1016/j.ecolmodel.2012.08.019.

E. Pelletier, P. Sargian, J. Payet, and S. Demers. Ecotoxicological effects of combined uvb and organic contaminants in coastal waters: a review. *Photochemistry and photobiology*, 82(4):981–993, 2006. ISSN 0031-8655.

Allison L. Perry, Paula J. Low, Jim R. Ellis, and John D. Reynolds. Climate change and distribution shifts in marine fishes. *Science*, 308:1912–1915, 2005.

Malin Pinsky. *Dispersal, Fishing, and the Conservation of Marine Species*. PhD thesis, Stanford University, Stanford University, 6 2011.

Malin L. Pinsky, Boris Worm, Michael J. Fogarty, Jorge L. Sarmiento, and Simon A. Levin. Marine taxa track local climate velocities. *Science*, 341(6151):1239–42, 9 2013. ISSN 1095-9203. doi: 10.1126/science.1239352.

E. E. . E. Plaganyi, S. J. . J. Weeks, T. D. . D. Skewes, M. T. . T. Gibbs, E. S. . S. Poloczanska, A. Norman-Lopez, L. K. . K. Blamey, M. Soares, and W. M. L. Robinson. Assessing the adequacy of current fisheries management under changing climate: a southern synopsis. *ICES Journal of Marine Science*, 68(6):1305–1317, 7 2011. ISSN 1054-3139. doi: 10.1093/icesjms/fsr049.

Benjamin Planque, Jean-Marc Fromentin, Philippe Cury, Kenneth F. Drinkwater, Simon Jennings, R. Ian Perry, and Souad Kifani. How does fishing alter marine populations and ecosystems sensitivity to climate? *Journal of Marine Systems*, 79:403–417, 2010a.

Benjamin Planque, Jean-Marc . M. Fromentin, Philippe Cury, Kenneth F. Drinkwater, Simon Jennings, R. Ian Perry, and Souad Kifani. How does fishing alter marine populations and ecosystems sensitivity to climate? *Journal of Marine Systems*, 79(3):403–417, 2010b.

A. D. . D. Rijnsdorp, M. A. . A. Peck, G. H. . H. Engelhard, C. Mollmann, and J. K. . K. Pinnegar. Resolving the effect of climate change on fish populations. *ICES Journal of Marine Science*, 66(7):1570–1583, 8 2009. ISSN 1054-3139. doi: 10.1093/icesjms/fsp056.

L. M. . M. Robinson, J. Elith, A. J. . J. Hobday, R. G. . G. Pearson, B. E. . E. Kendall, H. P. . P. Possingham, and A. J. . J. Richardson. Pushing the limits in marine species distribution modelling: lessons from the land present challenges and opportunities. *Global Ecology and Biogeography*, 20(6):789–802, 11 2011. doi: 10.1111/j.1466-8238.2010.00636.x.

O. E. . E. Sala. Global biodiversity scenarios for the year 2100. *Science*, 287(5459):1770–1774, 3 2000. ISSN 00368075. doi: 10.1126/science.287.5459.1770.

Stephen D. Simpson, Simon Jennings, Mark P. Johnson, Julia L. Blanchard, Pieter-Jan J. Schön, David W. Sims, and Martin J. Genner. Continental shelf-wide response of a fish assemblage to rapid warming of the sea. *Curr Biol*, 21(18):1565–70, 9 2011. ISSN 1879-0445. doi: 10.1016/j.cub.2011.08.016.

Chris D. Thomas, Phillipa K. Gillingham, Richard B. Bradbury, David B. Roy, Barbara J. Anderson, John M. Baxter, Nigel A. D. Bourn, Humphrey Q. P. Crick, Richard A. Findon, Richard Fox, Jenny A. Hodgson, Alison R. Holt, Mike D. Morecroft, Nina J. O’Hanlon,

611 Tom H. Oliver, James W. Pearce-Higgins, Deborah A. Procter, Jeremy A. Thomas, Kevin J.
 612 Walker, Clive A. Walmsley, Robert J. Wilson, and Jane K. Hill. Protected areas facilitate
 613 species' range expansions. *Proc Natl Acad Sci U S A*, 109(35):14063–8, 8 2012. ISSN
 614 1091-6490. doi: 10.1073/pnas.1210251109.

615 Carl Walters and Ana M. Parma. Fixed exploitation rate strategies for coping with effects of
 616 climate change. *Canadian Journal of Fisheries and Aquatic Sciences*, 53(1):148–158, 1996.
 617 URL 2.

618 David S. Wilcove, David Rothstein, Jason Dubow, Ali Phillips, and Elizabeth Losos. Quan-
 619 tifying threats to imperiled species in the united states. *BioScience*, 48(8):607–615, 1998.

620 Phoebe L. Zarnetske, David K. Skelly, and Mark C. Urban. Ecology. biotic multipliers of
 621 climate change. *Science*, 336(6088):1516–8, 6 2012. ISSN 1095-9203. doi: 10.1126/science.
 622 1222732.

623 C. I. . I. Zhang, A. B. . B. Hollowed, J-B . B. Lee, and D-H . H. Kim. An iframe approach
 624 for assessing impacts of climate change on fisheries. *ICES Journal of Marine Science*, 68
 625 (6):1318–1328, 7 2011. ISSN 1054-3139. doi: 10.1093/icesjms/fsr073.

626 Ying Zhou and Mark Kot. Discrete-time growth-dispersal models with shifting species ranges.
 627 *Theoretical Ecology*, 4(1):13–25, 2 2011. ISSN 1874-1738. doi: 10.1007/s12080-010-0071-3.

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 $\langle d \rangle = 2$.

649 **6 Figures**

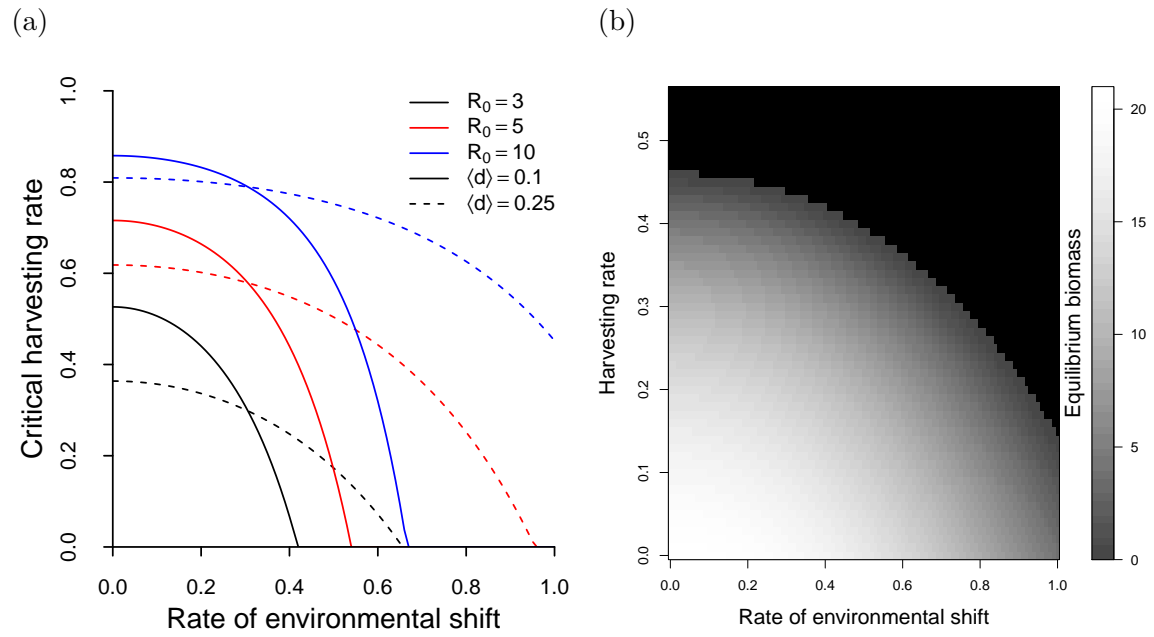


Figure 1

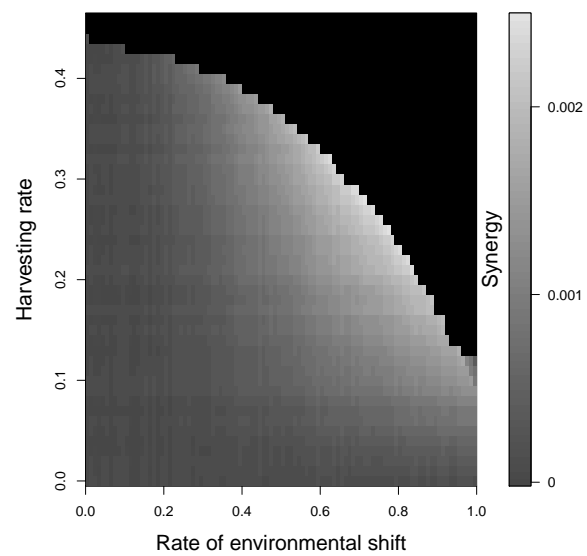


Figure 2

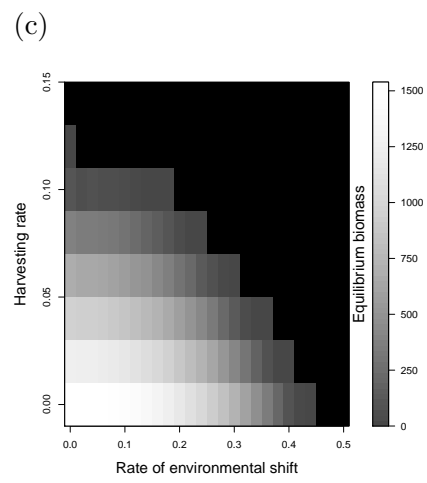
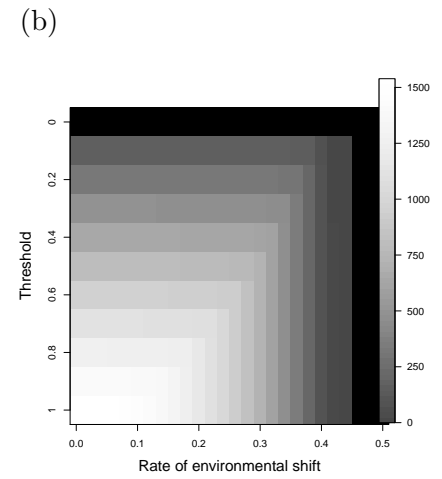
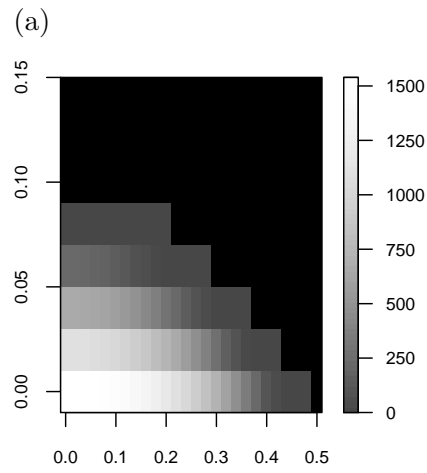


Figure 3

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