# Persistence of marine populations under climate and fishing

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#### 1 Abstract

When the climate changes, so does the location of habitats suitable for an organism's survival and reproduction. This change does not occur in isolation but rather appears on a background of other disturbances, making the study of interactions between stressors important. In order to understand how two disturbances, range shift and harvesting, interact and affect population persistence, we analyzed an integrodifference model that explicitly included the mechanisms of dispersal and reproduction. We found how the critical rates of 16 harvesting and climate velocity that suffice to drive the population extinct depend on the 17 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 19 synergy only at the greatest harvest rates and climate velocity that almost drive the 20 population extinct. We also introduced two conservation techniques into simulations of the 21 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.

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

#### 27 2 Introduction

Many stressors can disturb an ecosystem, and ecologists have quantified the consequences of many of these of perturbations [Wilcove et al., 1998, Crain et al., 2008, Darling and Côté, 2008]. Less work, however, has been done to measure the effects of multiple stressors and the interactions between them. If disturbances interact synergistically, a perturbation that has

- little effect when it occurs individually may amplify the disturbance caused by a coincident perturbation [Crain et al., 2008, Darling and Côté, 2008, Nye et al., 2013, Gurevitch et al., 2000. In the most extreme (and worrying) cases, synergistic interactions between multiple 34 stressors will drive a population extinct even though it could persist in the face of any single 35 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 30 and Morris, 2010, Fordham et al., 2013, Folt et al., 1999]. 40 Climate change and fishing, two of the largest human impacts on the ocean [Halpern et al., 2008, provide an important case study of how disturbances interact in their effects on biological populations. Marine fish are already moving in response to climate change [Perry et al., 2005, Hiddink and ter Hofstede, 2008, Rijnsdorp et al., 2009, Dulvy et al., 2008, Simpson et al., 2011 and are projected to continue in the future [Kell et al., 2005, Mackenzie 45 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 synergistic interactions between warming temperatures, harvesting and 51 connectivity have been identified in microcosm experiments [Mora et al., 2007]. This empirical work underscores the importance of understanding how range shifts and harvesting interact.
- A common approach to predicting future population distributions has been to use

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bioclimatic-envelope models (also known as species distribution models – SDMs). These
   statistical models typically correlate presence-absence data with biophysical characteristics
   such as mean or maximum temperature, rainfall, or salinity, to predict how species ranges'
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   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,
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   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,
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   disturbances, and interactions difficult (but see Nye et al. [2013] for an approach using
   ecosystem-level models to discern relative importance of disturbances).
   Here we extended a previously studied model of a fish population subject to climate-driven
   range shift by also considering harvesting pressure. The model explicitly included
   reproduction and dispersal, two mechanistic processes central to species' responses to
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climate and fishing. Previous work has highlighted the importance of these two processes and their vulnerability to climate change [Fordham et al., 2013, Hastings et al., 2005]. We found the critical harvesting rate and climate velocity that drive the population extinct and how these critical rates depend on one another. We also found that climate-driven range shifts and fishing interact nearly additively, with low positive synergy at more extreme levels of the stressors. We also examined the efficacy of two different types of management strategies: threshold harvesting rules and marine protected areas (MPAs). MPAs are frequently recommended for conservation of biodiversity and improved fisheries yield [Gaines et al., 2010a], and we evaluate whether MPAs established for those purposes could improve species persistence when habitat shifts rapidly. Previous work has suggested protected areas can be a key form of climate insurance and can provide stepping stones to help species keep up with a changing environment [Thomas et al., 2012, Hannah et al., 2007]. We found that threshold harvesting rules remove the interaction between harvesting rates and climate velocity and that MPAs can help a species persist with higher harvesting pressure and slightly increase the maximum climate velocity with which a species can keep up.

#### 3 Methods

We studied a model of the dynamics of a fish population constrained to a single,
one-dimensional habitat patch by their inability to reproduce outside of that area, as
introduced by 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 harvesting rate climate velocity that would drive the

population extinct (hereafter the critical harvesting rate and critical climate velocity), and
then measured synergy by calculating the drop in biomass caused by each stressor both
individually and together. We finally added threshold harvesting rules and marine protected
areas (MPAs) in numerical simulations of the model to determine how these management
strategies affect population persistence.

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

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

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

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

Analyzing this kind of model becomes easier if the dispersal kernel is separable into its
dependence on the source of larvae and its dependence on the destination of the larvae, i.e. if
there are functions  $a_i$ ,  $b_i$  such that  $k(x-y) = \sum_{i=1}^{\infty} a_i(x)b_i(y)$ . In our analyses, as in 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 Appendix A.3.

Analytical results for a separable sinusoidal kernel are also described in Appendix A.4. We

used simulations to analyze a Laplace dispersal kernel that is not amenable to this method,

as described below.

At equilibrium, the population will move in a traveling wave, where the density of fish at a

given point in space will change but the density of fish at a location relative to the shifting

patch will not. The traveling wave  $n^*$  must satisfy

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

where  $\bar{x} \in \left[-\frac{L}{2}, \frac{L}{2}\right]$  describes the position within the patch [Zhou and Kot, 2011]. For a separable kernel, the equilibrium traveling pulse  $n^*(x)$  must satisfy

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

where the  $m_i$  satisfy the recursive equations

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

135 [Latore et al., 1998].

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velocity is slow enough, the population will be able to persist. There are threshold values of 137 the harvesting rate h and the climate velocity c such that if we increase the parameters 138 beyond these values, the population will be driven extinct. When the population is extinct, 139 the system is in equilibrium, i.e. there is a 'trivial' traveling pulse,  $n^*(\bar{x}) = 0$  for all 140  $x \in \left[-\frac{L}{2}, \frac{L}{2}\right]$ , which satisfies Equation (1). If a population persists, it must be able to avoid 141 extinction and grow even when small. If the trivial pulse is stable, the system will return to 142 extinction even after the introduction of a small population. If the trivial pulse is unstable, a 143 small population may increase and form a persistent population. Population persistence is 144 therefore equivalent to the trivial traveling pulse being an unstable equilibrium. We found 145 the critical parameters,  $h^*$  and  $c^*$ , by finding the parameters that make the trivial pulse 146 unstable. See Appendix A.1 for details. 147 Regardless of the exact functional form of the recruitment function, the critical parameter in 148 determining population persistence is how quickly recruitment increases when the population 149 size is near (but above) 0, which is equivalent to the intrinsic growth rate  $R_0 = f'(0)$ . For 150 each kernel, the population's ability to persist depends on properties of the population itself— 151 the expected distance a larva disperses  $\langle d \rangle$  and the intrinsic growth rate  $R_0$ ; properties of the 152 environment— the length of the viable patch L and how quickly the environment shifts c; and 153 the harvesting rate h. For a Gaussian kernel, the critical rates  $c^*$  and  $h^*$  are those values of c 154 and h such that 155

**Persistence** If the population is harvested at low enough levels and the climate

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

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

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

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

3.3 Calculating synergy Zhou and Kot [2011] only considered whether a shifting environment will drive a population extinct. In order to quantify whether the two stressors 159 interact additively, synergistically, or antagonistically, we found the total biomass of the 160 population when it reached an equilibrium traveling pulse and compared this equilibrium 161 biomass in the presence and absence of each stressor individually or the two stressors 162 together. Equations (3) and (2) allowed us to numerically find the total biomass in the 163 equilibrium traveling pulse. 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, 169

$$E_{\rm s} = B_0 - B_{\rm s}.$$

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

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

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

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

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

a commonly used model of larval dispersal [Pinsky, 2011]. Second, we implemented two management strategies, threshold rules and MPAs, to understand their effect on population 181 persistence and on the synergistic interactions between stressors. For every simulation, in 182 the first generation, we seeded the world with 50 individuals at a single point, as in Zhou 183 and Kot [2011]. We first ran through 150 generations in order for the population to reach 184 equilibrium without harvesting or climate shift. We then added harvesting pressure, allowed 185 the population to again reach equilibrium (150 generations), and finally added climate 186 change by moving the viable patch. We calculated equilibrium biomass as the mean biomass 187 of 300 time steps once the difference in biomass between successive generations was no 188 greater than 0.1. 189

Under the two management strategies, harvesting pressure was implemented differently. With a threshold rule, we evaluated the population at each point in space to determine how 191 much harvesting should occur. If the population abundance was below the designated 192 threshold, no harvesting occurred. If the population exceeded the threshold, then we 193 harvested all the 'surplus' individuals. 194 We introduce networks of MPAs into our simulations by designating segments of space where 195 the harvesting rate was equal to 0. MPAs are typically designed to meet either fishery 196 management or conservation goals [Agardy, 1994, Holland and Brazee, 1996, Gaines et al., 197 2010b]. Fisheries-oriented MPAs are often designed such that they maximize adult spillover 198 into fishable areas by creating many small reserves closely spaced [Hastings and Botsford, 199 2003, Gaylord et al., 2005, Gaines et al., 2010b. To mimic this management scheme, we 200 implemented MPAs with a length of  $\frac{1}{3}$  of the average dispersal distance and a distance of  $\frac{2}{3}$ 201 of the average dispersal distance between them. Conservation-oriented MPAs seek to reduce 202 adult spillover by creating fewer larger protected areas [Hastings and Botsford, 2006, Gaines 203 et al., 2010b. To mimic this scheme, we implemented MPAs with a length of 4 times the 204 average dispersal distance and a distance of 8 times the average dispersal distance between 205 them [Lockwood et al., 2002]. 206

#### $_{\scriptscriptstyle 07}$ 4 Results

4.1 Interactions Between Stressors The critical climate velocity and harvest rate are inversely related. As the climate velocity shift c increases, the critical harvesting rate  $h^*$  decreases (Figure 1). This means that a harvesting rate that is sustainable in the absence of environmental shift may no longer be sustainable if the environment starts changing.

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Conversely, as the harvesting rate h increases, the critical climate velocity c^* decreases
    (Figure 1). This means that as harvesting pressure increases, it becomes increasingly easy
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   for a shifting environment to drive the population extinct.
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   When the climate velocity or harvesting pressure exceed their critical rates (c^*, h^*)
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   respectively), the biomass of the population at equilibrium will be equal to 0. Before the
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   stressors reaches those thresholds, the equilibrium biomass of the population decreases as
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   either the harvesting pressure increases or the environmental shifts more quickly (Figure 1).
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   Our simulations confirm the analytical results with the critical speed c^* declining as the
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   critical harvest rate h^* increases and vice versa (Figure 3a).
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   It is always the case that increasing the intrinsic growth rate, R_0, increases the critical
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   climate velocity c^* and the critical harvesting rate h^*, since a population that grows more
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   quickly can recover more quickly from losses caused by these disturbances. However,
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    whether or not dispersing farther is better depends on how quickly the environment is
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   shifting (Figure 1). When the environment is shifting slowly, dispersing farther is
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   detrimental since many larvae will disperse too far away from the viable patch. When the
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   environment is shifting quickly, on the other hand, dispersing farther can help the
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   population persist because some larvae will disperse into the space that will become viable
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   shortly in the future. This affects the critical harvesting rate: at a low climate velocity, we
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   can more severely harvest populations that have a shorter dispersal distance than those that
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   disperse farther, whereas at a high climate velocity, we can more aggressively harvest
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   populations that disperse farther.
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    We found low levels of positive synergy between the two stressors in our analysis of the
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   Gaussian kernel (Figure 2). Where positive synergy exists, a doubly stressed population
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   loses more biomass than we would predict from either stressor individually. The stressors
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interact most strongly at high values, shortly before they drive the population extinct.

However, the excess loss in biomass is very low, meaning the stressors interact more or less
additively. We found similar analytical results for a sinusoidal dispersal kernel, which
indicates that this result is robust to changes in the dispersal kernel.

Management strategies Without any management strategies, we found that the 240 more severely we harvest the population, a slower climate velocity will suffice to drive the 24 population extinct. However, when we put thresholds in place, a small population can 242 always escape harvesting pressure and the critical climate velocity  $c^*$  no longer depends on 243 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 climate velocity that only 245 depends on the growth rate, length of the viable patch, and average dispersal distance. 246 With either type of MPA strategies examined (many small versus few large), the population 247 withstood combinations of higher climate velocities and harvesting rates (Figure 3). At 248 lower climate velocities, MPAs spaced more than one average dispersal distance apart 249 resulted in larger fluctuations of population biomass relative to small, closely spaced, MPAs. 250 As climate velocities increase, for both MPA strategies, the mean population abundance 251 declines but the population experiences less extreme oscillations in abundance. Since 252 minimum population biomass is increased, the population would be more buffered from 253 possible extinction in a stochastic environment.

#### 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 studied a general model that incorporates 259 dispersal and reproduction to examine how climate and harvesting interact in their effects on 260 species persistence and biomass. 261 For each kernel we studied, we found that the higher the growth rate and the better the 262 mean dispersal distance matches the climate velocity, the better a population can adjust to 263 harvest and climate change. Further, we found a negative relationship between the critical 264 harvesting rate and the climate velocity. That is, the more quickly the environment shifts 265 the less harvesting it takes to drive the population extinct. This is evidence that the 266 stressors interact since each stressor's ability to drive the population extinct depends on the 267 severity of the other stressor. 268 To quantify the interaction between the stressors, we measured the synergy between their 269 effects on population biomass. We found positive synergy between the stressors and that the 270 synergy is greatest in the region of parameter space where the equilibrium biomass is 271 smallest. We chose to measure the effect of each stressor by the absolute drop in biomass 272 caused by the stressor, and we used the sum of the individual effects for our null prediction 273 of the effect of both stressors, as in Crain et al. [2008], Darling and Côté [2008], Nye et al. 274 [2013]. In general, measuring synergy against an additive null prediction is more 275 conservative than measuring synergy multiplicatively: the presence of additive synergy 276 implies multiplicative synergy, but not vice versa [Crain et al., 2008, Folt et al., 1999]. Since we found small levels of positive additive synergy between the two stressors, other measures 278 of synergy might show even higher levels of interaction. 279 Worryingly, we find the highest synergy in those populations whose persistence is most 280 tenuous. This means that harvesting levels or climate velocity that are sustainable 281

individually together can drive a population to extinction. However the drop in biomass caused by both stressors was never much higher than the null prediction, i.e. synergistic 283 effects were quite small. Synergy between harvesting and the effects of climate change has 284 been identified in experimental populations [Mora et al., 2007], in specific populations 285 [Planque et al., 2010a], and at the ecosystem level [Kirby et al., 2009, Planque et al., 2010a]. 286 In the experimental populations, synergy was identified between warming and harvesting but 287 not between habitat fragmentation [Mora et al., 2007]. While we did find (very) low levels of 288 positive synergy, we did not find as much as predicted from these empirical studies. 289 However, these previous results are not directly comparable to ours because they focus on 290 different aspects of climate change, e.g. warming temperature [Mora et al., 2007, Kirby 291 et al., 2009] or a more variable climate [Planque et al., 2010a]. Additionally, while we can 292 isolate the affects of climate shift and harvesting in our simple analytical model, there are 293 other forces acting on real populations that may produce the observed synergistic effects. 294 Our results suggest that particular combinations of harvesting and climate velocity will 295 affect some species more than others. Species with a higher reproductive rate and a longer 296 average dispersal distance will better track a high climate velocity relative to a species that 297 has a low reproductive rate and short dispersal distance (Figure 1). The finding that a 298 higher reproductive rate can sustain higher climate velocities and harvesting rates is 299 intuitive, especially because harvesting rate and reproductive rate cancel each other out. 300 However it is worth pointing out that a higher reproductive rate can be generated either by 301 shorter generation times or higher fecundity. Finding that species with shorter generation 302 times can better keep up with shifts in climate is in agreement with empirical work which 303 has found that fish which shifted in response to warming in North Sea had faster life 304 histories than non shifting species [Perry et al., 2005]. While higher reproductive rates 305

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improved a population's ability to persist, increasing dispersal distances did not necessarily.
   At low speeds, we found that a short dispersal dispersal distance improved the maximum
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   harvesting rate a population could sustain while at higher speeds a longer dispersal distance
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   improved the maximum climate velocity in which the population could persist (Figure 1).
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   This is because when climate is shifting slowly, a large dispersal distance sends most
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   offspring ahead of the patch, while with faster climate velocities a long dispersal distance
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   allows the population to make it to the new patch (Figure 1). Thus climate velocity will
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   selectively favor species with dispersal distances best matched to the rate of shift.
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    We also examined whether frequently recommended management approaches, MPAs and
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   harvest control rules, ensure species persistence. With these management strategies we
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   found increases in the population's biomass at equilibrium and an improved ability to
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   persist. We found that a threshold harvesting rule alleviates interactions between the two
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   stressors. Thresholds have this effect as the management approach effectively prevents
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   harvesting of the leading edge, which allows colonization to occur as if these individuals were
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   moving into un-fished areas. It's interesting to note that novel, low abundance species are
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   commonly unregulated in fisheries systems; so in order to decouple the additive effects of
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   harvest and climate change, management would have to reverse this paradigm by allowing
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   no harvest of new species until they had become established.
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   Unlike thresholds, MPAs are explicitly spatial. Previous work has advanced protected areas
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   as a way to help organisms keep pace with range shifts, as well as to ameliorate
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   anthropogenic disturbances like harvesting and habitat fragmentation [Lawler et al., 2010,
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   Hannah et al., 2007, Botsford et al., 2001, Gaylord et al., 2005, Hastings and Botsford, 2003,
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   Thomas et al., 2012. Our results show that both threshold and MPAs increase the
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   equilibrium biomass at a given climate velocity, which support their use as a tool to
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ameliorate the effect of climate velocity. However, for MPAs, the details mater: few, large MPAs caused increased variability at low climate velocities while many smaller MPAs 331 maintained a population bounded farther from extinction. Finally, with sufficiently high 332 harvesting pressure, few, large MPAs rescued populations at intermediate speeds. With 333 intermediate speeds, the population was able to reach a protected area fast enough to avoid 334 extinction, and the protected area was large enough to allow a partial rebuilding of the 335 population before it moved out the other side. However this effect disappears as speed 336 continues to increase, suggesting that understanding the relationship between climate 337 velocity, dispersal distance and reproductive rate are important parameters in designing 338 management strategies effective under both climate change and harvesting pressure. 339 While the management strategies only change harvesting practices and do not directly 340 address the effects of climate change, understanding how they ameliorate synergistic affects 341 between harvesting and range shifts will help to better implement harvesting rules and place 342 protected areas. This is encouraging evidence that a single set of of management practices 343 may help to protect marine populations from both harvesting and climate change. 344 The advantage of a simple model like ours is that it is general enough to be applied to a 345 number of systems. However, this simplistic approach requires that we ignore complexities 346 known to be present in marine fisheries. For example, we do not include Allee effects, so that 347 even if the population shrank to low levels it was possible for it to persist over time. 348 However, with Alee effects we expect qualitatively similar results. An Allee effect would 349 make it harder for populations to colonize new areas and add a threshold below which 350 fishing drives the population to extinction. Thus an Allee effect would change lower the 351 critical harvest rates and climate velocity, but we do not expect the additive nature of the 352 interaction between climate and harvesting to change. We also did not include age structure 353

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 355 resonance [Botsford et al., 2011, Planque et al., 2010b]; and we leave this additional 356 complexity for future work. Similarly, we did not include any mechanisms aside from larval 357 dispersal by which the population could keep up with a shifting climate. Besides these 358 species-specific extensions, this modeling framework could be extended to consider species 350 interactions, especially predator-prey pairs. By introducing a predatory species, we would be 360 imposing yet another stressor on the focus species [Ling et al., 2009, Gurevitch et al., 2000] 361 and we are interested in measuring the interaction between the effects of this stressor and 362 the two we consider here. 363 Using a simple mechanistic model like the one we present here provides a useful framework 364 for incorporating additional ecological complexities which can mediate species persistence 365 under multiple disturbances. Using this modeling framework as a starting point, we believe 366 exploring how species interactions, age structure, and additional disturbances (e.g. 367 physiological response to temperature) affect population viability will improve our 368 predictions and help us to understand whether species will persist under predicted climate 369 and harvesting regimes. Finally, this work can help make general predictions as to whether 370 specific life histories offer selective advantages over others as harvesting and range shifts 371 increase and highlights the importance of considering stressors in combination as outcomes 372 can deviate from what we would predict in isolation. This is especially true for management 373 strategies which may result in unanticipated effects such as large fluctuations associated with 374 big, distant MPAs shown here. 375

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#### 599 Figure Legends

**Figure 1**: (a) The critical harvesting rate on the y-axis as a function of the climate velocity 600 on the x-axis. Black lines correspond to a growth rate of  $R_0 = 3$ , red to  $R_0 = 7$ , and blue to 601  $R_0 = 10$ . Solid lines correspond to an average dispersal distance  $\langle d \rangle = 0.1$  and dashed lines 602 correspond to an average dispersal distance  $\langle d \rangle = 0.25$ . These results are from an approxi-603 mated Gaussian dispersal kernel with L=1. (b) The equilibrium biomass of the population 604 as a function of the climate velocity on the x-axis and the harvesting rate on the y-axis. These 605 results are from a Gaussian dispersal kernel with parameters  $L=1, R_0=5, \langle d \rangle=0.399.$ 606 607 **Figure 2**: Positive synergy between the two stressors. The x-axis shows the climate velocity, 608 the y-axis shows the harvesting rate, and the color indicates the loss in biomass in the dou-609 bly stressed population in excess of the sum of the losses caused by each stressor individually, 610  $E_{\rm hc} - E_{\rm h} - E_{\rm c}$ . This excess loss, on the order of .001, is small in comparison to the total biomass, 611 which can be as large as 20. These results are from an approximated Gaussian dispersal kernel 612 with parameters L = 1,  $R_0 = 5$ ,  $\langle d \rangle = 0.399$ . 613 **Figure 3**: The equilibrium biomass of the population as a function of the climate velocity 614 on the x-axis and the harvesting rate on the y-axis with and without management strategies. 615 (a) No management. (b) Threshold harvesting levels. (c) MPAs. These results are from a 616 simulation with a Laplacian dispersal kernel with parameters L = 1,  $R_0 = 5$ , K = 100, and 617  $\langle d \rangle = 2.$ 618

# 619 6 Figures

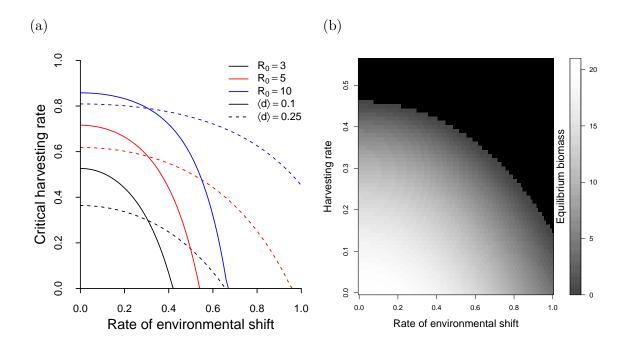


Figure 1

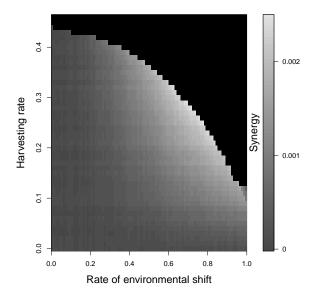
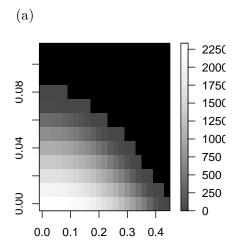


Figure 2



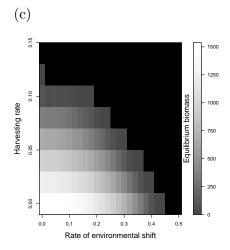
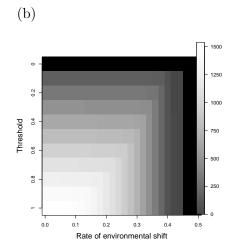


Figure 3



## 7 Tables

Table 1: Table of variables used in the text

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