Species persistence under climate and fishing

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1 Abstract

When the climate changes, the area in which organisms can survive and reproduce moves through space. This change does not occur in isolation but rather appears on a background of other disturbances. We used an integrodifference model explicitly accounting for dispersal, reproduction, a shifting environment, and harvesting to examine how two disturbances, range shift and harvesting, interact and govern population persistence. We found threshold rates of harvesting and of environmental shift that are needed to allow the population to persist, studied how these critical parameters depend on the growth rate and dispersal behavior of the population, and measured the interactions between the stressors. In particular, we found low but positive synergy between the two stressors: harvesting aggravates the population's sensitivity to a shifting range. Finally, we introduced two conservation techniques into simulations of the population model – threshold harvest rules and marine protected areas (MPAs) – and found that these approaches could mitigate the negative interaction of the two stressors.

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

2 Introduction

There are many stressors that can disturb an ecosystem. Ecologists have quantified the effects of a number of stressors individually [Wilcove et al., 1998, Crain et al., 2008, Darling and Côté, 2008]. However, disturbances rarely occur in isolation and it is therefore important to understand how a system is affected by multiple disturbances together [Doak and Morris, 2010, Fordham et al., 2013, Folt et al., 1999]. A perturbation that has little effect when it occurs individually may still amplify the disturbance caused by a coincident perturbation [Crain et al., 2008, Darling and Côté, 2008]. Synergistic interactions between stressors can be especially problematic if an animal population can persist in the face of a single stressor but the combination of multiple stressors suffices to drive the population extinct (i.e. Pelletier et al. [2006]). However it remains difficult to predict when disturbances are likely to interact in ways not anticipated when perturbations are measured individually.

Climate change is a prime example of multiple, possibly interacting, disturbances. Species that are likely to undergo (or already undergoing) shifts in range and phenology are subject to many other disturbances including pollution, habitat fragmentation, over-exploitation, and invasive species [Wilcove et al., 1998, Sala, 2000, Assessment, 2005]. A common approach to predicting future population distrubtions under climate change has been to use bioclimatic-envelope models (also known as species distribution models – SDMs). These statistical models typically correlate presence-absence data with biophysical characteristics such as mean or maximum temperatures, rainfall, or salinity, to explain and predict how species ranges' will differ under climate change [Elith et al., 2006, Guisan and Thuiller, 2005, Guisan and Zimmermann, 2000]. Despite these models' widespread

adoption, SDMs have frequently been criticized as oversimplified as they lack species interactions, dispersal and reproductive processes [Kearney and Porter, 2009, Zarnetske et al., 2012, Robinson et al., 2011]. Recent work on range shifts has addressed some of these gaps by explicitly including dispersal and reproduction [Berestycki et al., 2009, Zhou and Kot, 2011]. However these models only address one disturbance: that of climate-driven range shifts. Not only does climate change disturb ecological systems via range shifts (for example), but these range shifts may interact with anthropogenetic stressors already present. Marine fish, for example, are already moving [Perry et al., 2005, Hiddink and ter Hofstede, 2008, Rijnsdorp et al., 2009, Dulvy et al., 2008, Simpson et al., 2011] and projected to move more [Kell et al., 2005, Mackenzie et al., 2007]. These organisms not only are faced with ocean acidification and temperature driven range shifts [Pinsky et al., 2013, Barry et al., 1995, Nye et al., 2009], but are often harvested commercially. Climate change and fishing have been identified as the two largest human impacts on the ocean [Halpern et al., 2008] so there is a need to understand whether and how these disturbances will interact in the future. Predictions for how climate change will drive shifts in marine systems have focused on how physiological limitations [Pörtner and Knust, 2007] and global fish distributions [Cheung et al., 2008, 2009, Hare et al., 2010, Lenoir et al., 2011] may change. Work considering the joint impacts of climate and fishing often consider climate fluctuations (large anomalies around the mean) rather than directional changes in climate [Walters and Parma, 1996, King and McFarlane, 2006]. Work that does consider the effects of climate-driven range shifts on fishing typically are 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

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important for management and conservation planning [Allison et al., 2009], however these models are so complex that understanding the relative importance of particular drivers, disturbances, and interactions is difficult (but see Nye et al. [2013] for an approach using ecosystem-level models to discern relative importance of disturbances). Here we develop models of intermediate complexity [sensu Gaylord et al., 2005] that can help clarify the importance of two interacting disturbances: temperature-driven range shifts and harvest. Empirical case studies have identified interactions between overfishing and temperature-driven range shifts that suggest synergy in the magnitude of the disturbance [Ling et al., 2009] and have demonstrated synergistic effects in micosm experiments between warming temperatures, harvesting and connectivity [Mora et al., 2007]. This empirical work underscores the importance of understanding how range shifts and harvesting interact and, to our knowledge, there has been limited work examining interactions between harvesting and range shifts.

Here we construct an analytical model of a fish population subject to both harvesting and climate change-induced range-shift. We explicitly include two mechanistic processes central to species' responses to climate and fishing: reproduction and dispersal. 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 focus on determining how climate-driven range shifts and fishing interact to affect population persistence. We find that these disturbances interact additively, not multiplicatively which is often the default assumption when considering mortality.

We also examine the effect of marine protected areas (MPAs) on species persistence. Protected areas have been suggested as a key form of climate insurance and stepping stones to help species keep up with a changing environment [Thomas et al., 2012, Hannah

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et al., 2007]. MPAs are frequently recommended for conservation of biodiversity and improved fisheries yield [Gaines et al., 2010], and we evaluate whether MPAs established for those purposes could improve species persistence when habitat is shifting rapidly. We find that MPAs can help a species persist with higher harvesting pressure, but does not change the maximum climate velocity with which a species can keep up.

3 Methods

We studied the dynamics of a fish population constrained to a single, one-dimensional habitat patch by their inability to reproduce outside of the patch. This viable habitat patch (here after 'patch') is shifting at a fixed velocity and fish at each point in space can be harvested. Given the reproductive rate and average dispersal distance, first we determined the climate velocity and harvesting rate that would drive the population extinct. We then implemented marine protected areas (MPAs) and threshold harvesting rules in numerical simulations of the model to determine how these management strategies affect population persistence.

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

given by

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

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. As we explain below,

the functional form of the recruitment function only affects persistence through how quickly

recruitment increases when the population size is near (but above) 0, which is equivalent to

the intrinsic growth rate, $R_0 = f'(0)$. We therefore do not specify a recruitment function

here. Similarly, the population's ability to persist only depends on how quickly harvesting

increases when a small number of fish are introduced where they were previously absent,

$h'(0)$. We therefore only considered a proportional harvesting function initially.

If a population of fish is going to persist in the face of a shifting environment, it must move

along with the patch in which it can reproduce. At equilibrium, the population will be

described by 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. We

therefore seek to describe how the population is distributed over the viable patch as it

shifts through the world. We write this as $n^*(\bar{x})$, the density of fish at each point $\bar{x}$ in the

shifting frame $\left[-\frac{L}{2}, \frac{L}{2}\right]$ As in Zhou and Kot [2011], the traveling wave n^* must satisfy

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

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One solution to Equation 2 is the 'trivial' traveling pulse, $n^*(\bar{x}) = 0$ for all $x \in \left[-\frac{L}{2}, \frac{L}{2}\right]$, i.e. a patch with no fish in it. If a population becomes very small (or if we introduce a small population), one of two things can happen. First, the population may crash and the trivial traveling pulse without any fish may appear again. Second, those small numbers may increase and form a stable population. In this sense, a small population can be thought of as a perturbation to the trivial traveling pulse. If the trivial pulse is stable, the system will return to the trivial pulse even after a perturbation in the form of the introduction of a small population. If a population is to persist, even when it is small it must be able to avoid extinction and grow. For this to be the case, the trivial pulse must be unstable to small perturbations.

We would like to know the rate of environmental shift and the harvesting rate such that as long as the environment moves more slowly or we harvest less severely than those parameters, then the population will be able to persist. We call these, respectively, the critical rate of environmental shift, c^*, and the critical harvesting rate, h^*. We found these rates by finding the parameters that make the trivial pulse unstable. Evaluating stability in this kind of model is in general difficult to do analytically. It 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, we used one such separable kernel, the Gaussian kernel given by

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

To make stability easier to analyze, we approximated this kernel, as described in the

153 Appendix. Analytical results for a separable sinusoidal kernel are also described in the

154 Appendix. We used simulations to analyze a Laplace dispersal kernel that is not amenable

155 to this method, as described below.

For each kernel, the population's ability to persist depends on properties of the population

itself: the expected distance a larva disperses ($\langle d \rangle$) and the intrinsic growth rate (R_0);

properties of the environment: the length of the viable patch (L) and how quickly the

environment is shifting (c); and the harvesting rate (h). If the environment shifts more

quickly than the critical rate c^* or the population is harvested at more than the critical

rate h^* then the population will not be able to persist, as described in the Appendix. For a

Gaussian kernel, the critical rates c^* and h^* are those values of c and h such that

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

156 A similar expression for a sinusoidal kernel is derived in the appendix. For both kernels,

157 the critical harvesting proportion can be approximated by a function that looks like

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

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

159 growth rate.

160 Zhou and Kot [2011] only consider whether a shifting environment will drive a population

161 extinct or not. To quantify the effects of both a shifting environment and harvesting

162 pressure, we found the total biomass in the equilibrium traveling wave. As in Latore et al.

163 [1998], for a separable kernel, the equilibrium traveling pulse $n^*(x)$ must satisfy

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$$n^*(x) = \sum_{i=1}^{\infty} a_i(x) \int_{-\frac{L}{2}}^{\frac{L}{2}} b_i(y-c)f((1-H(n^*(y)))n^*(y))dy = \sum_{i=1}^{\infty} m_i a_i(x), \qquad (4)$$

where the m_i satisfy the recursive equations

$$m_i = \int_{-\frac{L}{2}}^{\frac{L}{2}} b_i(y-c)f\left((1-h)\sum_{j=1}^{\infty} m_j a_j(x)\right) dy. \qquad (5)$$

Equation 5 allowed us to find the values of m_i numerically. We then found the total

biomass in the equilibrium traveling pulse by using these m_i and integrating Equation 4.

Whereas population persistence does not depend on the functional form of recruitment, f,

equilibrium biomass does depend on what recruitment function we use. We chose to use a

Beverton-Holt recruitment function,

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

3.2 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,

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

Second, we examined harvesting rules more complex than harvesting a constant proportion

of the population. Whereas population persistence in the analytical model does not depend

on the functional form of recruitment f, we must specify a recruitment function to perform

simulations. We chose to use a Beverton-Holt function,

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

177 where R_0 is the intrinsic growth rate and K is the carrying capacity. In the first generation,

178 we seeded the world with 50 individuals at a single point, as in [Zhou and Kot, 2011]. We

179 first ran through 150 generations in order for the population to reach equilibrium without

180 harvesting or climate shift. We then added harvesting pressure, allowed the population to

181 again reach equilibrium, and finally added climate change by moving the viable patch.

182 We added harvesting pressure by harvesting a constant proportion of the population, in

183 order to confirm our analytical results. We extended our work by evaluating the effect of a

184 threshold harvest rule and marine protected areas (MPAs). With a threshold rule, we

185 evaluated the population at each point in space to determine how much harvesting should

186 occur. If the population abundance was below the designated threshold, no harvesting

187 occurred. If the population exceeded the threshold, then a proportion of the 'surplus'

188 individuals were harvested. To implement an MPA management strategy, we used two

189 commonly advocated approaches: MPAs designed to improve fisheries yields and MPAs

190 designed for primarily for conservation [REFS]. These networks of MPAs were introduced

191 into our simulations by designating segments of space in which harvesting was forbidden

192 (i.e. harvesting rates were equal to 0). The conservation MPAs had a length of 4 times the

193 average dispersal distance and had a distance of 8 times the average dispersal distance

194 between them. Fisheries MPAs had a length of 1/3 of the average dispersal distance and

195 had a distance of 2/3 of the average dispersal distance between them. These distances were

196 chosen for the following reasons: the goal of conservation-oriented MPAs is to protect

197 source populations, ideally that are self sustaining under a static climate. Fisheries MPAs

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198 are focused on maximizing spillover of fish populations into fishable waters, thus many

199 MPAs, each of which are smaller than the average dispersal distance, replicates this high

200 spillover effect.

201 Equilibrium is calculated as the mean of 300 time steps once the difference in biomass

202 between time step t and $t + 1$ was no greater than 0.1. Equilibrium biomass and catch are

203 defined as the total amount of fish present and harvested, respectively, at equilibrium.

204 **3.3 Calculating Synergy** We wanted to understand whether the two stressors interact

205 additively, synergistically, or antagonistically [Crain et al., 2008] for both our analytical

206 model and simulations. In order to quantify the effect of the stressors, we found the total

207 biomass of the population when it reached an equilibrium traveling pulse and compared

208 this equilibrium biomass in the presence and absence of each stressor individually or the

209 two stressors together.

210 We measured the effects of the stressors by comparing the equilibrium biomass of the

211 stressed population to the equilibrium biomass of the unstressed population. We use B_0 to

212 denote the equilibrium biomass without either stressor, B_h the equilibrium biomass with

213 harvesting but a constant environment, B_c the equilibrium biomass with a shifting

214 environment but no harvesting, and B_{hc} the equilibrium biomass with both stressors. For

215 each stressor or combination of stressors, we found the drop in biomass caused by stressor s,

$$E_s = B_0 - B_s.$$

216 If the stressors do not interact, the drop caused by both stressors would be the sum of the

217 drops caused by either individually. The synergy is therefore defined as

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

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

4   Results

4.1   Interactions Between Stressors The equilibrium biomass of the population decreases as either the harvesting pressure increases or the environmental shifts more quickly (Figure 1). If the equilibrium biomass is 0, this indicates that the harvesting pressure has exceeded the critical harvesting rate h^* and the environmental is shifting more quickly than the critical rate of environmental shift c^*. As the harvesting rate h increases, the critical rate of environmental shift c^* decreases: the environment must move more slowly to accommodate the population growing more slowly (Figure 1). Conversely, as the rate of environmental shift c increases, the critical harvesting rate h^* decreases (Figure 1). This means that a harvesting rate that is sustainable in the absence of environmental shift may no longer be sustainable if the environment starts shifting. The simulations replicate the analytical results with the critical speed c^* declining as the critical harvest rate h^* increases and vice versa.

It is always the case that increasing the intrinsic growth rate, R_0, of the population

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increases the critical speed c^* and the critical harvesting rate h^*, since a population that grows more quickly can recover more quickly from losses caused by these disturbances. However, whether or not dispersing farther is better depends on how quickly the environment is shifting (Figure 1). When the environment is shifting slowly, dispersing farther is detrimental since many larvae will disperse too far away from the viable patch. When the environment is shifting quickly, on the other hand, dispersing farther can help the population persist because some larvae will disperse into the space that will become viable shortly in the future. This affects the critical harvesting rate: at a low rate of environmental shift, populations that disperse less can be harvested more severely than those that disperse further, whereas at a high rate of environmental shift, populations that disperse further can be harvested more severely.

We found positive synergy between the two stressors in our analysis of the Gaussian kernel (Figure 2). In other words, a doubly stressed population loses more biomass than would be predicted from either stressor individually. The stressors interact most strongly when they are both high, shortly before they drive the population extinct. We found similar analytical results for a sinusoidal dispersal kernel and our simulations with a Laplace kernel produce similar results.

4.2 Management Strategies We found that thresholds of any amount alleviate the effects of harvesting, and the ability of the population to persist is recovered (Figure 3). Thus when thresholds are in place, the harvesting rate no longer determines the critical rate of environmental shift c^*. 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. With

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261 MPAs in place, the population had a slightly higher abundance along the edges of the

262 patch where the population is limited by harvesting, which translated into a slightly

263 increased critical harvest rate (Figure 3). Additionally MPAs increased overall catch at the

264 highest harvest rates under which the population could survive (Figure 3).

5   Discussion

266 We extended a spatial to study a fish population subject to both the climate-driven range

267 shifts and harvesting. Previous work has highlighted the importance of reproduction and

268 dispersal to the vulnerability of fish populations to climate change [Hastings et al., 2005,

269 Fordham et al. [2013]] and our model explicitly includes these processes. In particular, we

270 derived expressions for critical harvesting rates and critical rates of environmental shift for

271 a separable Gaussian kernel and found these critical rates using numerical simulations of a

272 Laplace kernel. For each kernel we studied, we found that the higher the growth rate and

273 the better the mean dispersal distance matches the rate of environmental shift, the better a

274 population can adjust to harvest and climate change. More interestingly, we found a

275 negative relationship between the critical harvesting rate and the rate of environmental

276 shift. That is, the more quickly the environment shifts the less harvesting it takes to drive

277 the population extinct. The curved line separating parameters that will allow the

278 population to persist from those that won't is on indication of an interaction between the

279 stressors.

280 To quantify the interaction between the stressors, we measured the synergy between their

281 effects on population biomass. We found positive synergy between the stressors and that

282 the synergy is greatest in the region of parameter space where the equilibrium biomass is

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smallest. We found similar results from the analytically derived biomass and the simulation derived biomass. This indicates that this result is robust to changes in the dispersal kernel. We chose to measure the effect of each stressor by the absolute drop in biomass caused by the stressor, and we used the sum of the individual effects for our null prediction of the effect of both stressors, as in [Crain et al., 2008, Darling and Côté, 2008, Nye et al., 2013]. We could also have measured the effect by the percentage drop caused by the stressor(s) and used a multiplicative null prediction for the effect of both stressors. In general, measuring synergy against an additive null prediction is more conservative than measuring synergy multiplicatively: the presence of additive synergy implies multiplicative synergy, but not vice versa [Crain et al., 2008, Folt et al., 1999]. Since we found small levels of positive additive synergy between the two stressors, other measures of synergy might show even higher levels of interaction.

While we did find synergy between the stressors, the drop in biomass caused by both stressors was never very much higher than the null prediction, i.e. synergistic effects were quite small. However, the fact that synergy is highest in those populations whose persistence is most tenuous is worrisome from a conservation perspective. Additionally, the fact that we found additive synergy means that harvesting levels or rate of environment shift that are sustainable individually together can drive a population to extinction. Synergy between harvesting and climate changes, e.g. warming temperature or a more variable climate, has been identified in experiments [Mora et al., 2007], in the demography and size of specific populations [Planque et al., 2010], and at the ecosystem level [Kirby et al., 2009]. Our results agree with these empirical findings and it is therefore important to take the effects of both stressors into consideration when designing conservation and management strategies.

The two management strategies we modeled – harvesting thresholds and MPAs – both increased the population's biomass at equilibrium and improved its ability to persist. Protected areas have been advanced as a way to help organisms keep pace with range shifts, as well as to ameliorate anthropogenic disturbances like harvesting and habitat fragmentation[Lawler et al., 2010, Hannah et al., 2007, Botsford et al., 2001, Gaylord et al., 2005, Hastings and Botsford, 2003, Thomas et al., 2012]. Our results, that spatial management increased the maximum harvesting rate at which the population could survive, corroborate these previous findings. The management strategies also affect how the two stressors interact with each other. Specifically, harvesting thresholds can alleviate interactions between the two stressors. While the management strategies only change harvesting practices and do not directly address affect climate change, understanding how they ameliorate synergistic affects between harvesting and range shifts will help to better implement 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, it ignores many of the complexities present in marine fisheries. We do not include Allee effects, so that even if the population shrank to very low levels it was possible for it to persist over time. However, we found that qualitatively similar results about the interaction between climate and harvesting would hold for a model with a recruitment function with Allee effect. 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; including this level of complexity is left for future work. Additionally, we did not include any mechanisms aside from larval dispersal by which the population could keep up with a shifting climate. In addition to these species-specific extensions, this modeling framework could be extended to consider species interactions, especially predator-prey

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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. Finally, our results suggest that particular combinations of harvesting and rate of environmental shift will affect some species more than others. Indeed, Perry et al. [2005] found that fish that shifted in response to warming in North Sea had faster life histories than non shifting species (smaller body sizes, faster maturation, smaller sizes at maturity). Using a simple mechanistic model like the one we presented can incorporate these species interactions and multiple disturbances to understand whether specific life histories are likely to be selected over others as harvesting and/or range shifts increase.

6   Acknowledgements

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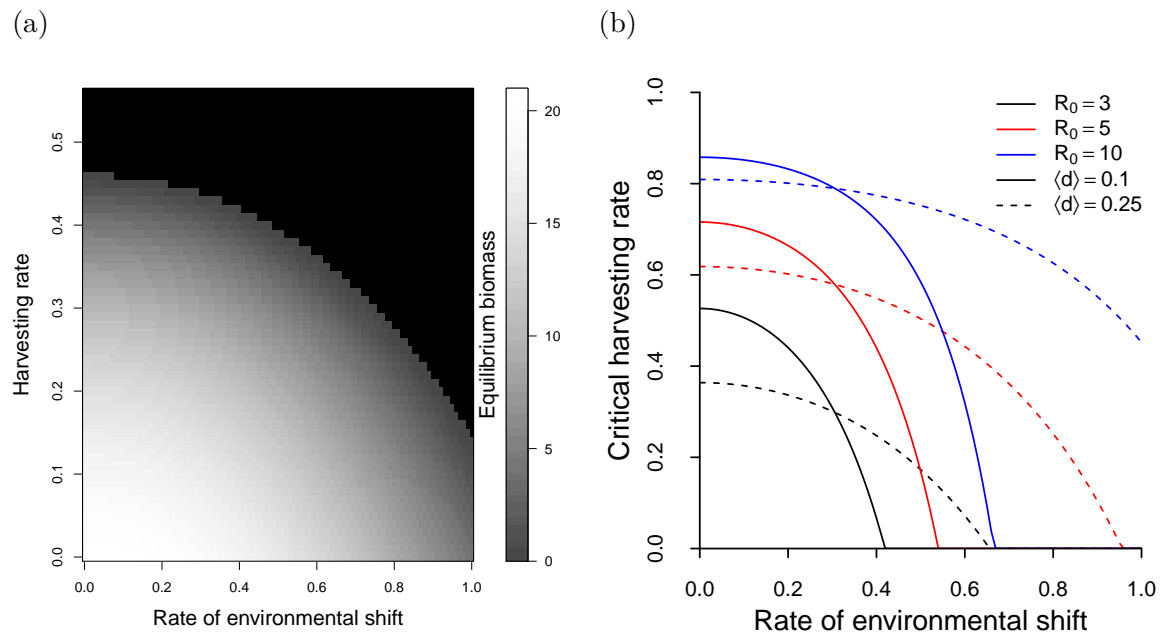
7   Figures

(a)

(b)

Figure 1

570 Figure 1: (a) The equilibrium biomass of the population as a function of the rate of

571 environmental shift on the x-axis and the harvesting rate on the y-axis. These results are

572 from a Gaussian dispersal kernel with parameters $L = 1$, $R_0 = 5$, $\langle d \rangle = 0.399$. (b) The

573 critical harvesting rate on the y-axis as a function of the rate of environmental shift on the

574 x-axis. Black lines correspond to a growth rate of $R_0 = 3$, red to $R_0 = 7$, and blue to

575 $R_0 = 10$. Solid lines correspond to an average dispersal distance $\langle d \rangle = 0.1$ and dashed lines

576 correspond to an average dispersal distance $\langle d \rangle = 0.25$. These results are from an

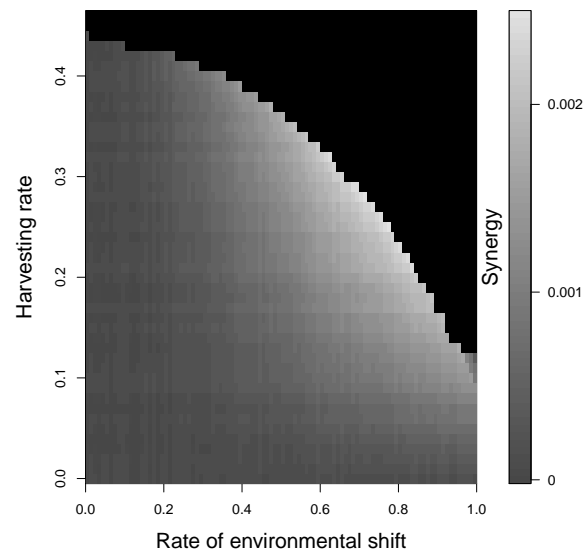577 approximated Gaussian dispersal kernel with $L = 1$.

Figure 2

578 Figure 2: Positive synergy between the two stressors. The x-axis shows the rate of

579 environmental shift, the y-axis shows the harvesting rate, and the color indicates the loss in

580 biomass in the doubly stressed population in excess of the sum of the losses caused by each

581 stressor individually, $E_{\mathrm{hc}} - E_{\mathrm{h}} - E_{\mathrm{c}}$. These results are from an approximated Gaussian

582 dispersal kernel with parameters $L = 1$, $R_0 = 5$, $\langle d \rangle = 0.399$.
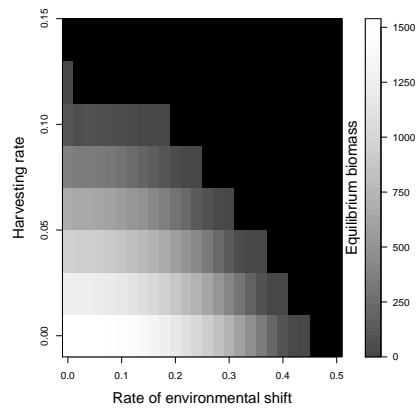
(a)

(b)

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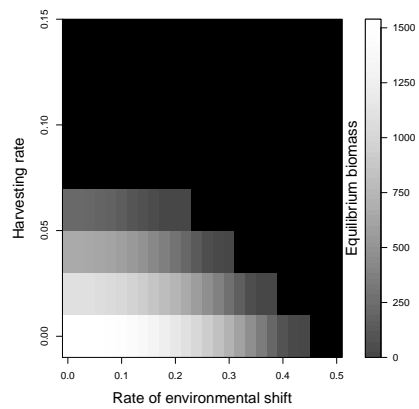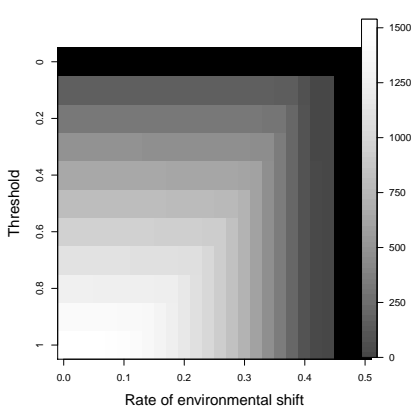
Figure 3

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 $\langle d \rangle = 2$.

8 Appendix

As in Zhou et al. [Zhou and Kot, 2011], let $k(x - y)$ be a dispersal kernel and let $f(y)$ be a recruitment function. The integrodifference model describing the population over time is given by

$$n_{t+1}(x) = \int_{-L/2+ct}^{L/2+ct} k(x - y) f(n_t(y)) dy. \tag{6}$$

To find a traveling pulse, we are only interested in the population density as a function of the location within the patch rather than absolute position, $\overline{x} \equiv x - ct$.

$$n^*(\overline{x}) \equiv n^*(x - ct) = n_t(x). \tag{7}$$

Then (6) giveas s us an expression for n^*:

$$n^*(\overline{x} - c) = \int_{-L/2}^{L/2} k(\overline{x} - \overline{y}) f(n^*(\overline{y})) d\overline{y}$$

$$\Rightarrow n^*(\overline{x}) = \int_{-L/2}^{L/2} k(\overline{x} + c - \overline{y}) f(n^*(\overline{y})) d\overline{y} \tag{*}$$

If $f(0) = 0$, $n^*(\overline{x}) \equiv 0$ for all $\overline{x} \in [-L/2, L/2]$ is a trivial solution to this problem, i.e. if there are no fish anywhere there won't be at any time in the future. The population can be said to be persistent if the trivial traveling pulse is unstable since even when there are very small population levels, the population won't crash to 0. To evaluate stability (i.e. persistence), we will introduce a small perturbation to the traveling pulse $n^*(\overline{x})$,

$$n_t(x) = n^*(\overline{x}) + \xi_t(x)$$

$$\Rightarrow \xi_{t+1}(x) = \int_{-L/2+ct}^{L/2+ct} k(x-y)f'(n^*(\overline{y}))\xi_t(y)dy \text{ by linearizing around the traveling pulse and using } (*)$$

$$\Rightarrow \xi_{t+1}(x) = \int_{-L/2+ct}^{L/2+ct} k(x-y)f'(0)\xi_t(y)dy \text{ if we're interested in the stability of the trivial traveling pulse}$$

If we assume $\xi_t(x) = \lambda^t u(x-ct)$ for some $\lambda \in \mathbb{R}$ and $u : [-L/2, L/2] \to \mathbb{R}$, then

$$\lambda u(x-ct-c) = f'(0) \int_{-L/2+ct}^{L/2+ct} k(x-y)u(y-ct)dy$$

$$\lambda u(\overline{x}) = f'(0) \int_{-L/2}^{L/2} k(\overline{x}+c-\overline{y})u(\overline{y})dy$$

Define the integral operator

$$\psi_f(g)(x) = \int_{-L/2}^{L/2} f'(0)k(x+c-y)g(y)dy.$$

600 so that the perturbation to the traveling pulse will satisfy

$$\psi_f(u)(x) = \lambda u(x) \tag{8}$$

601 Then the trivial traveling pulse is unstable when the dominant eigenvalue of ψ_f is greater

602 than 1.

603 Let f denote the recruitment function, let h denote a harvesting function and let

604 $m(y) = f(y - h(y))$, i.e. m denotes the number of offspring after the adults have been

605 harvested. Note that $m'(0) = f'(0)(1 - h'(0))$, assuming $h(0) = 0$ (which must be the case).

Suppose u is an eigenfunction of ψ_f with eigenvalue λ. Then

$$\psi_m(u)(x) = \int_{-L/2}^{L/2} m'(0)k(x + c - y)u(y)dy$$

$$= (1 - h'(0)) \int_{-L/2}^{L/2} f'(0)k(x + c - y)u(y)dy$$

$$= (1 - h'(0))\psi_f(u)(x)$$

$$= (1 - h'(0))\lambda u(x)$$

606   so that u is also an eigenfuction of ψ_m, now with eigenvalue $(1 - h'(0))\lambda$.

8.1   Separable dispersal kernels Jentzsch's theorem shows that there is an

eigenfunction u, provided that the kernel k satisfy some properties. Finding the

eigenfunction is in general a hard problem to solve. It becomes easier if the kernel k is

separable, i.e. there are functions a_n, b_n such that $k(x - y) = \sum_{n=1}^{\infty} a_n(x)b_n(y)$. In that

case, (8) becomes

$$\lambda u(x) = f'(0) \sum_{n=1}^{\infty} \left(a_n(x) \int_{-L/2}^{L/2} b_n(y - c)u(y)dy \right)$$

$$\Rightarrow \lambda \int_{-L/2}^{L/2} b_k(x - c)u(x)dx = f'(0) \sum_{n=1}^{\infty} \left(\int_{-L/2}^{L/2} b_n(x - c)u(x)dx \right) \left(\int_{-L/2}^{L/2} a_n(y)b_k(y - c)dy \right)$$

$$\Rightarrow \lambda d_k = f'(0) \sum_{n=1}^{\infty} A_{nk}d_n \tag{**}$$

where

$$A_{nk} = \int_{-L/2}^{L/2} a_n(x)b_k(x - c)dx \text{ and } d_k = \int_{-L/2}^{L/2} b_k(x - c)u(x)dx$$

8.2 Gaussian dispersal kernel The Gaussian dispersal kernel is given by

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

As in [Latore et al., 1998], this separable kernel can be written as

$$k(|x-y|) = \sum_{n=0}^{\infty} a_n(x)b_n(y)$$

where

$$a_n(x) = b_n(x) = \frac{1}{\sqrt{2n!\sqrt{D\pi}}} e^{-x^2/4D} \left(\frac{x}{\sqrt{2D}}\right)^n.$$

As a first approximation to k we ignore all but the 0th terms for a_n and b_n so that Equation ** becomes

$$\lambda d_0(c) = f'(0)A_{00}(c)d_0(c)$$

$$\Rightarrow \lambda = R_0(1-h)A_{00}(c)$$

$$\text{where } A_{00}(c) = 2\sqrt{2}\exp\left(\frac{-c^2}{8D}\right)\left[\text{erf}\left(\frac{L-c}{2\sqrt{2D}}\right) - \text{erf}\left(\frac{-L-c}{2\sqrt{2D}}\right)\right]$$

607   where erf is the error function. The critical rate of environmental shift c^* and the critical

608   harvesting rate h^* are those values of c and h, respectively, that make $\lambda = 1$.

8.3 Sinusoidal dispersal kernel A sinusoidal dispersal kernel is given by

$$k(x-y) = \begin{cases} \frac{w}{2}\cos(w(x-y)) & , \quad |x-y| \leq \frac{\pi}{2w} \\ 0 & , \quad |x-y| > \frac{\pi}{2w} \end{cases}$$

where L is the length of the patch and we assume $\frac{\pi}{2w} > L, c < \frac{\pi}{2w} - L$.

In this case, $k(x - y) = \frac{w}{2}\cos(wx)\cos(w(y - c)) + \frac{w}{2}\sin(wx)\sin(w(y - c))$ so that A_{ij} and d_i can be found for $i, j = 1, 2$ and (**) reduces to

$$\lambda^2 - \left(\frac{R_0(1 - h)wL}{2} \cos(wc) \right) \lambda + \frac{R_0^2(1 - h)^2}{16} \left(w^2 L^2 - \sin^2(wL) \right) = 0.$$

If we solve for λ, we find

$$\lambda = R_0(1 - h) \left[\frac{wL \cos(wc)}{4} + \frac{1}{4} \sqrt{\sin^2(wL) - w^2 L^2 \sin^2(wc)} \right]. \tag{9}$$

Zhou et al. [Zhou and Kot, 2011] solve for the critical speed, c^*, at the population will be driven extinct:

$$c^* = c^*(R_0) = \frac{1}{w} \cos^{-1} \left[\frac{16 + R_0^2(1 - h)^2(w^2 L^2 - \sin^2(wL))}{8R_0(1 - h)wL} \right].$$

Similarly, we can solve for the critical harvesting rate, h^*, at which the population will be driven extinct:

$$h^* = 1 - \frac{1}{R_0} \cdot \frac{4wL}{w^2 L^2 - \sin^2(wL)} \left[\cos(wc) - \sqrt{\cos^2(wc) - 1 + \frac{\sin^2(wL)}{w^2 L^2}} \right]$$

8.4 Approximate Critical Harvesting Proportions

We will use the following Taylor series to make approximations of the critical harvesting

38

proportions under the two dispersal kernels:

$$\cos(x) = 1 - \frac{x^2}{2}$$

$$\cos^2(x) = 1 - x^2$$

$$\sin^2(x) = x^2 - \frac{x^4}{3}$$

$$erf(x) = \frac{2}{\sqrt{\pi}}(x - \frac{x^3}{3})$$

$$\exp(x) = 1 + x + \frac{x^2}{2}$$

612 For the sinusoidal kernel we found

$$h^* = 1 - \frac{1}{R_0} \cdot \frac{4wL}{w^2L^2 - \sin^2(wL)} \left[\cos(wc) - \sqrt{\cos^2(wc) - 1 + \frac{\sin^2(wL)}{w^2L^2}} \right] \tag{10}$$

Using the Taylor series and the fact that $w = \frac{\sqrt{\frac{\pi^2}{4} - 2}}{\sigma}$ where σ^2 is the variance of the

sinusoidal kernel,

$$h^* \sim 1 - \frac{1}{R_0} \cdot \frac{12wL}{w^4L^4} \left[1 - \frac{w^2c^2}{2} - \sqrt{1 - w^2c^2 - \frac{w^2L^2}{3}} \right]$$

$$= 1 - \frac{1}{R_0} \cdot \frac{4\sqrt{3}}{L^3(\pi^2 - 8)^{3/2}} \cdot \sigma \left[8\sqrt{3}\sigma^2 - (\pi^2 - 8)\sqrt{3}c^2 - 4\sigma\sqrt{12\sigma^2 - (\pi^2 - 8)(3c^2 + L^2)} \right]$$

613 For the Gaussian kernel we found

$$h^* = 1 - \frac{2\sqrt{2}\exp\left(\frac{c^2}{8D}\right)}{R_0 \left[erf\left(\frac{L-c}{2\sqrt{2D}}\right) - erf\left(\frac{-L-c}{2\sqrt{2D}}\right) \right]} \tag{11}$$

Using the Taylor series and the fact that $D = \frac{\sigma^2}{2}$ where σ^2 is the variance of the

39

exponential kernel,

$$h^* \sim 1 - \frac{\sqrt{2\pi}(1 + \frac{c^2}{8D} + \frac{c^4}{128D^2})}{R_0\sqrt{\pi}\left[\frac{L-c}{2\sqrt{2D}} - \frac{(L-c)^3}{3(2\sqrt{2D})^3} - \frac{-L-c}{2\sqrt{2D}} + \frac{(-L-c)^3}{3(2\sqrt{2D})^3)}\right]}$$

$$= 1 - \frac{1}{R_0} \cdot \frac{3\sqrt{2\pi}}{8L} \frac{(32\sigma^4 + 8c^2\sigma^2 + c^4)}{\sigma\left(12\sigma^2 - (L^2 + 3c^2)\right)}$$

614 In the case of both kernels, the critical harvesting proportion can be approximated by a

615 function that looks like

$$h^* \sim 1 - \frac{1}{R_0} \cdot C(L)f(\sigma^2, c^2, L^2 + 3c^2) \tag{12}$$

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

617 growth rate.