

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 will move through space. This change does not occur in isolation but rather appears on a background of other disturbances. We use 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 the harvesting rate and the rate 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 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 population levels below which harvesting is not allowed and marine protected areas (MPAs) – and found that the robustness of the population to the two stressors improved.

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. 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 affecting a system individually may amplify the disturbance caused by a coincident perturbation [Crain et al., 2008, Darling and Côté, 2008]. Synergistic interactions between stressors are especially worrying if an animal population can persist in the face of a single stressor but not in the presence of multiple stressors (e.g. Pelletier et al. [2006]). However, it remains hard to predict when disturbances are likely to interact in ways not predicted by the effects of individual perturbations.

Climate change is a prime example of a stressor occurring in a background of multiple other, possibly interacting, disturbances. These include pollution, habitat fragmentation, invasive species, and over-exploitation [Wilcove et al., 1998, Sala, 2000, Assessment, 2005]. It is expected that species will move their home ranges in response to climate change. Many marine fish 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 are projected to continue to move in the future [Kell et al., 2005, Mackenzie et al., 2007]. These species are faced not only with temperature-driven range shifts but also with anthropogenic stressors including ocean acidification and commercial fishing [Pinsky et al., 2013, Barry et al., 1995, Nye et al., 2009]. 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.

Many methods have been proposed to help mitigate the effects of harvesting on fish populations. Marine protected areas (MPAs), which provide stepping stones to help species keep up with a changing environment, have been suggested as a key form of climate insurance [Thomas et al., 2012, Hannah et al., 2007]. MPAs are frequently recommended for both conservation of biodiversity and improved fisheries yield [Gaines et al., 2010]. Threshold harvesting levels below which no fish may be harvested have also been proposed as a means of both optimizing yield and conserving resources [Lande et al., 1995, 1997].

A wide range of models have been used to study the effect of climate change and harvesting on fish populations. A common approach to predicting future population distributions under climate change has been to use bioclimatic-envelope models (also known as species distribution models – SDMs). These statistical models have been used to find correlations between the presence or absence of fish species and biophysical properties of the environment 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]. Similarly, projection models of future climate conditions have been used to predict where conditions will be favorable for fish populations in the future [Cheung et al., 2008, 2009]. Despite these models' widespread adoption, they have been criticized

for being oversimplified as they lack species interactions, dispersal and reproductive processes [Kearney and Porter, 2009, Zarnetske et al., 2012, Robinson et al., 2011].

Some recent work on range shifts has addressed these gaps by explicitly including dispersal and reproduction [Berestycki et al., 2009, Zhou and Kot, 2011], which have been highlighted as important factors in fish populations’ vulnerability to climate change [Fordham et al., 2013, Hastings et al., 2005]. These models only address one disturbance, climate-driven range shifts, and do not consider other anthropogenic stressors. The models of Zhou and Kot [Zhou and Kot, 2011] and Berestycki et al. [Berestycki et al., 2009] are of intermediate complexity (sensu [Gaylord et al., 2005]). Work that consider both climate-driven range shifts and fishing is often case-specific and detailed, including 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 cumulative impacts are important for management and conservation planning [Allison et al., 2009]. However, these models are so complex that understanding the relative importance of particular drivers, disturbances, and interactions is difficult (but see [Nye et al., 2013] for an approach using ecosystem-level models to discern relative importance of disturbances).

We analyzed an integrodifference model to study the effect of temperature-driven range shifts and harvesting, two important interacting disturbances, on the persistence of a marine population. In particular, we extended the model of Zhou and Kot [Zhou and Kot, 2011], which describes a fish population reproducing and dispersing while their range shifts, by additionally including harvesting pressure and introducing two different conservation measures. We found that the disturbances interact synergistically. We also found that MPAs can help a species persist with higher harvesting pressure, but they do not change the maximum speed of habitat shift 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 the patch can be harvested. Given the reproductive rate and average dispersal distance, we determined the climate velocity and harvesting rate that would drive the population extinct. We 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 our model, 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. The adults are subjected to harvesting before they produce offspring so that only a proportion of the fish survive to reproduce. We incorporated these processes—recruitment, harvesting, and dispersal—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

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

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 , $k(x-y)$ is the dispersal kernel giving the probability of the larvae 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. The functional form of the recruitment function only affects persistence through how quickly recruitment increases when the population increases from 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.

If a population of fish is going to persist in the face of a shifting environment, it must move along with the patch of environment 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 $[-\frac{L}{2}, \frac{L}{2}]$. As in Zhou and Kot [2011], the traveling wave n^* must satisfy

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

One solution to Equation 2 is the ‘trivial’ traveling pulse, $n^*(\bar{x}) = 0$ for all $x \in [-\frac{L}{2}, \frac{L}{2}]$, 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.

For the separable Gaussian kernel, the equilibrium traveling pulse $n^*(x)$ must satisfy

$$n^*(x) = \sum_{i=1}^{\infty} a_i(x) \int_{-\frac{L}{2}}^{\frac{L}{2}} b_i(y - c) f((1 - H(n^*(y)))n^*(y)) dy = \sum_{i=1}^{\infty} m_i a_i(x), \quad (3)$$

where the m_i satisfy the recursive equations

$$m_i = \int_{-\frac{L}{2}}^{\frac{L}{2}} b_i(y - c) f\left((1 - h) \sum_{i=1}^{\infty} m_i a_i(x)\right) dy. \quad (4)$$

Equation 4 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 3.

In general, we would like to know the rate of environmental shift and the harvesting rate such that if the environment moves more quickly or we harvest more severely then the population will not be able to persist. We call these, respectively, the critical rate of environmental shift, c^* , and the critical harvesting rate, h^* . We can find these rates by finding the parameters that make the trivial pulse unstable. Evaluating stability 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 $k(x - y) = \sum_{i=1}^{\infty} a_i(x)b_i(y)$. We used simulations to analyze dispersal kernels that are not amenable to this method.

In our analyses, we used a Gaussian kernel,

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

To make stability easier to analyze, we approximated this kernel, as described in the Appendix. In our simulations, we used an analytically intractable Laplace kernel,

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

For each kernel, we can find the expected distance an offspring will travel, $\langle d \rangle$, which we will use to compare the two kernels. For each kernel, the population’s ability to persist depends on properties of the population itself: how far larvae tend to disperse ($\langle d \rangle$) 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.

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 a Laplace dispersal kernel. Second, we examined harvesting rules more complex than harvesting a constant proportion of the population. Whereas the analytical results do not depend on the functional form of recruitment f , to perform simulations we must specify a recruitment function. We chose to use a Beverton-Holt model,

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

where R_0 is the intrinsic growth rate and K is the carrying capacity. In the first generation, we seeded the world with 50 individuals at a single point, as in [Zhou and Kot, 2011]. We first allowed the population to reach equilibrium

without harvesting or climate shift. We then added harvesting pressure, allowed the population to again reach equilibrium, and finally added climate change by moving the viable patch.

We added harvesting pressure by harvesting a constant proportion of the population, in order to confirm our analytical results. We also extended our analytical work by evaluating the effect of a threshold harvest rule and marine protected areas (MPAs). With a threshold rule, we evaluated the population at each point in space to determine how much harvesting should occur. If the population abundance was below the designated threshold, no harvesting occurred. If the population exceeded the threshold, then a proportion of the ‘surplus’ individuals were harvested. To implement an MPA management strategy, we used two commonly advocated approaches: MPAs designed to improve fisheries yields and MPAs designed primarily for conservation. These networks of MPAs were introduced into our simulations by designating segments of space in which harvesting was forbidden (i.e. harvesting rates were equal to 0). The conservation MPAs had a length of twice the average dispersal distance and had a distance of 4 times the average dispersal distance between them. Fisheries MPAs had a length of 1/3 of the average dispersal distance and had a distance of 2/3 of the average dispersal distance between them.

In our simulations, we defined the critical rate of environmental shift and the critical harvest rate as model runs in which the total population at equilibrium was less than 0.001. Equilibrium is calculated as the mean of 300 time steps once the difference in biomass between time step t and $t + 1$ is no greater than 0.0360515. Equilibrium biomass and catch are defined as the total amount of fish present and harvested, respectively, at equilibrium.

3.3 Calculating Synergy We wanted to understand whether the two stressors interact additively, synergistically, or antagonistically [Crain et al., 2008] for both our analytical model and simulations. In order to quantify the effect of the stressors, we found the total biomass of the population when it reached an equilibrium traveling pulse and compared this equilibrium biomass in the presence and absence of each stressor individually or the two stressors together.

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

$$E_s = B_0 - B_s.$$

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

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

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

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 environment 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 2). Conversely, as the rate of environmental shift c increases, the critical harvesting rate h^* decreases (Figure 2). 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 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 2). When the environment is shifting slowly, dispersing farther is detrimental

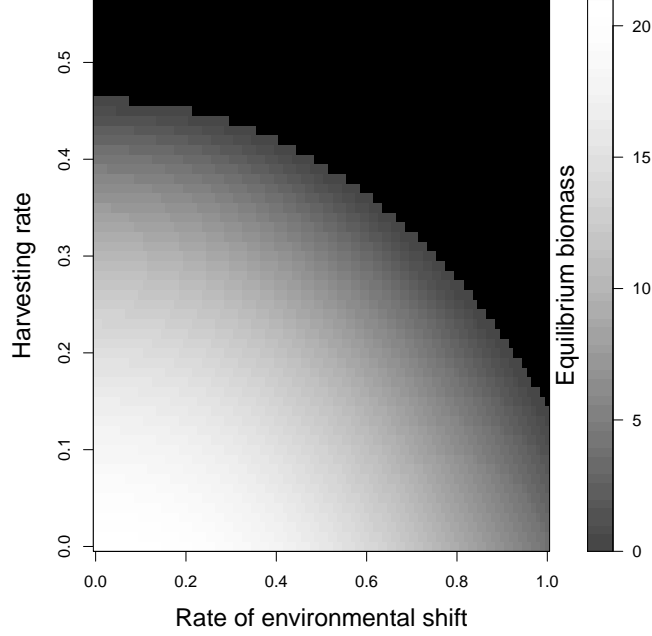


Figure 1: The equilibrium biomass of the population decreases as either the harvesting rate or rate of environmental shift increases. If either harvesting rate or rate of environmental shift are too high the population is driven to extinction. The x-axis shows the rate of environmental shift, the y-axis shows the harvesting rate, and the color indicates the equilibrium biomass. These results are from a Gaussian dispersal kernel with parameters $L = 1$, $R_0 = 5$, $\langle d \rangle = 0.399$.

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.

We found positive synergy between the two stressors in our analysis of the Gaussian kernel (Figure 3). 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. Our simulations with a Laplace kernel produce similar results. In the Appendix, we show analogous results for a sinusoidal dispersal kernel.

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 4). 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 MPAs in place, the population had a slightly higher abundance along the edges of the patch where the population is limited by harvesting, which translated into a slightly increased critical harvest rate (Figure 5). Additionally MPAs increased overall catch at the highest harvest rates under which the population could survive (Figure 5).

5 Discussion

We extended the model of Zhou and Kot [Zhou and Kot, 2011] to study a fish population subject to both the climate-driven range shifts already included and harvesting. Previous work has highlighted the importance of reproduction and dispersal to the vulnerability of fish populations to climate change [Hastings et al., 2005, Fordham et al. [2013]] and the integrodifference model explicitly includes these processes. We found that the two disturbances interact synergistically with each other in some cases. However, we also found that placing thresholds on harvesting intensity can alleviate interactions between the two stressors and that spatial management increased the maximum harvesting

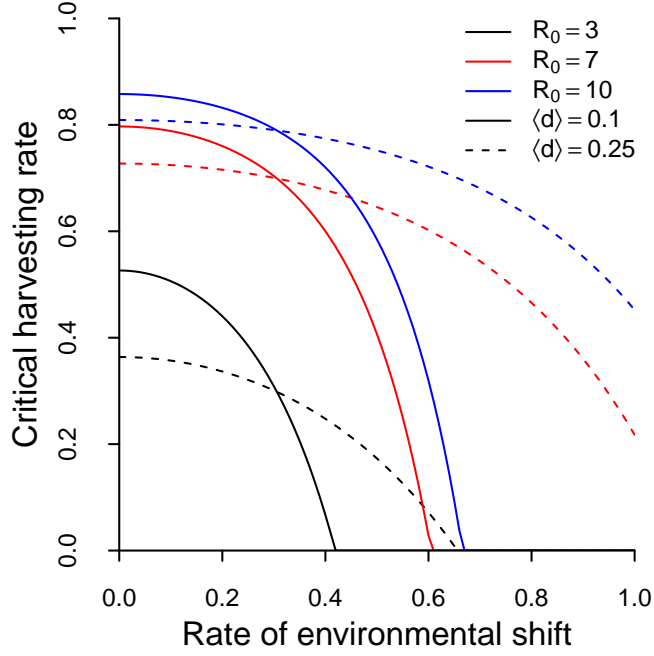


Figure 2: As the rate of environmental shift c increases, the critical harvesting rate h^* decreases. In other words, less harvesting pressure is required to drive the population extinct. Increasing the growth rate always increases the critical harvesting rate. On the other hand, increasing average dispersal distance increases the critical harvesting rate depends on how quickly the environment is shifting: it is more advantageous to disperse farther when the environment is shifting more quickly. The rate of environmental shift is plotted on the x-axis and the critical harvesting rate is plotted on the y-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 a Gaussian dispersal kernel with $L = 1$.

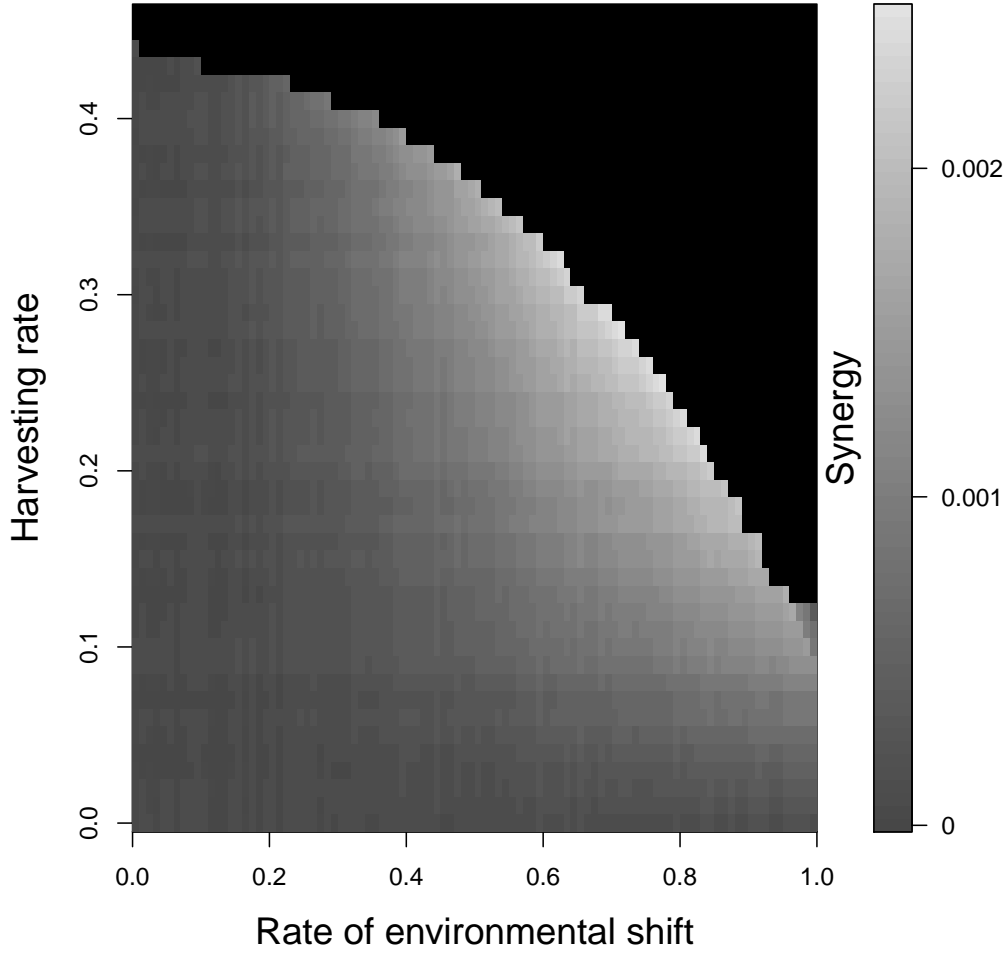


Figure 3: There is positive synergy between the two stressors: a doubly stressed population loses more biomass than would be predicted from either stressor individually. The x-axis shows the rate of environmental shift, the y-axis shows the harvesting rate, and the color indicates the loss in biomass in the doubly stressed population in excess of the sum of the losses caused by each stressor individually, $E_{hc} - E_h - E_c$. These results are from a Gaussian dispersal kernel with parameters $L = 1$, $R_0 = 5$, $\langle d \rangle = 0.399$.

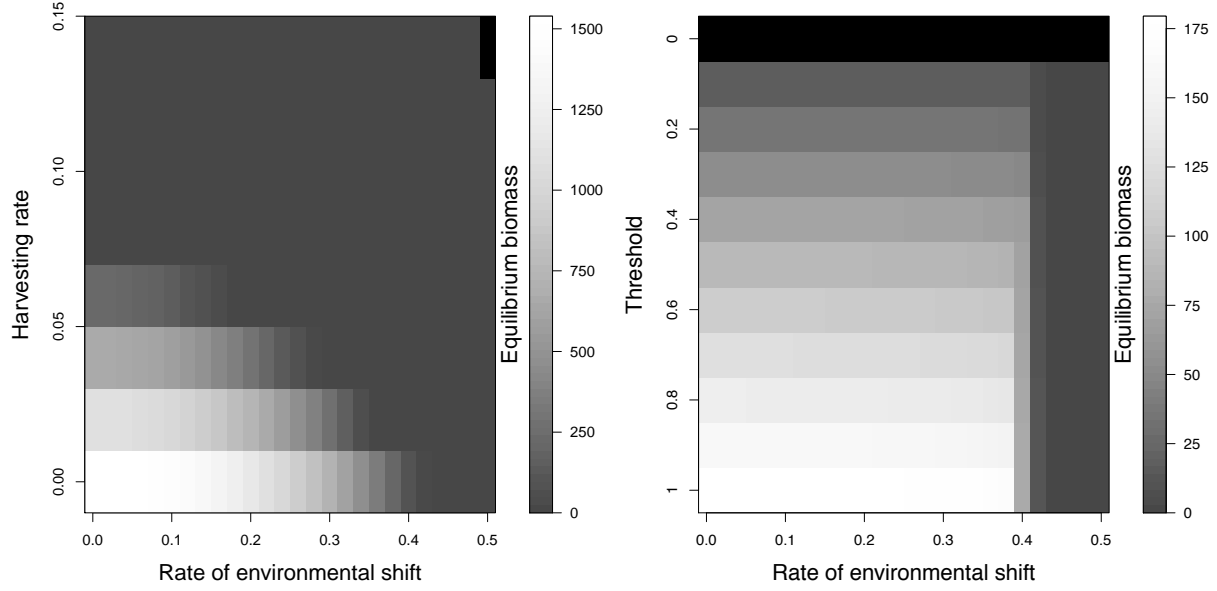


Figure 4: With threshold harvesting rules, such that all biomass above a threshold level was harvested, the population always reached an equilibrium biomass greater than 0 so that threshold harvesting rules increased biomass at equilibrium and improved the population's ability to persist. Additionally, threshold harvesting rules remove the interaction between harvesting and environmental shift: the critical rate of environmental shift no longer depends on harvesting. The figure on the left corresponds to no thresholds and the figure on the right corresponds to threshold harvesting rule. The x-axis shows the rate of environmental shift, the y-axis shows either the proportion of the population harvested or the threshold above which harvesting was allowed, and the color indicates the equilibrium biomass. These results are from a simulation with a Laplacian dispersal kernel with parameters $L = 1$, $R_0 = 5$, $K = 100$, and $\langle d \rangle = 2$.

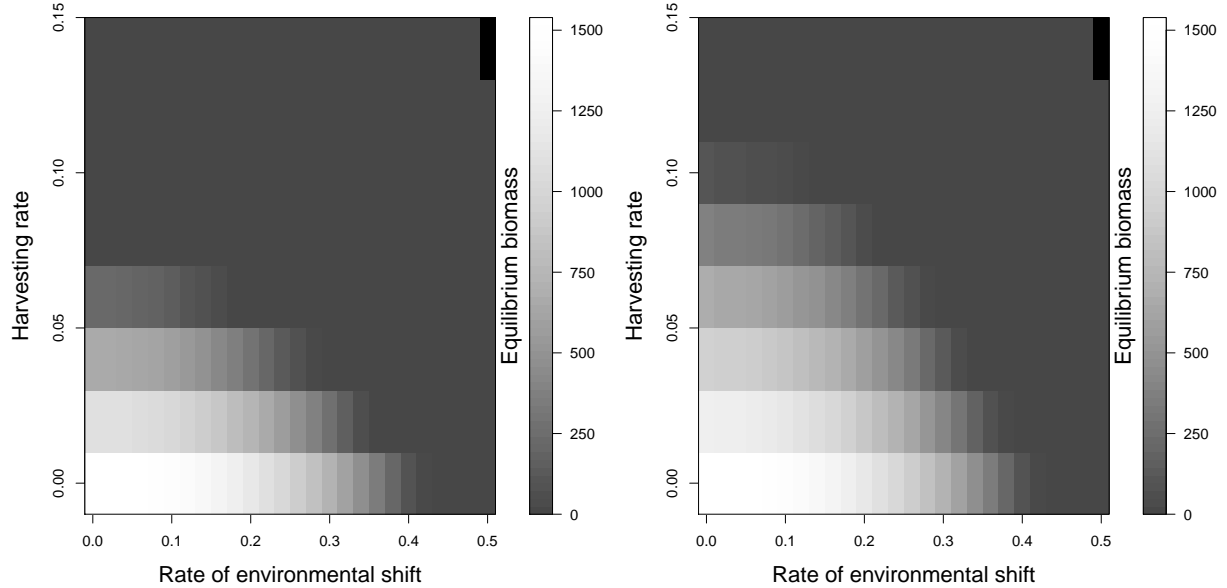


Figure 5: MPAs improved the population's ability to persist. The figure on the left corresponds to no MPAs and the figure on the right corresponds to MPAs designed to optimize fishing yields. MPAs designed to optimize conservation give similar results. The x-axis shows the rate of environmental shift, the y-axis shows the harvesting rate, and the color indicates the equilibrium biomass. These results are from a simulation with a Laplacian dispersal kernel with parameters $L = 1$, $R_0 = 5$, $K = 100$, and $\langle d \rangle = 2$.

rate at which the population could survive.

We found that the synergy between the two stressors is positive and that the synergy is greatest in the region of parameter space where the equilibrium biomass is smallest. Additionally, 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 find 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. Similarly, in experiments, Mora et al. [2007] found no interaction between harvesting and habitat fragmentation but did find an interaction between harvesting and warming temperature [Mora et al., 2007]. We chose to measure the effect of each stressor by the drop in biomass caused by the stressor, as in Crain et al. [2008]. In general, measuring synergy additively is more conservative than measuring synergy multiplicatively: stressors that have positive multiplicative synergy may have zero additive synergy [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. This synergy and the fact that it most severely affects those populations whose persistence is most tenuous is worrisome from a conservation perspective. Harvesting levels or rate of environment shift that are sustainable individually together can drive a population to extinction. 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. These management strategies also affect how the two stressors interact with each other. 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]. While MPAs 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 can easily be adjusted to consider species interactions, especially predator-prey pairs. Predatory species affect marine populations and considering a set of species that included both predators and prey would be equivalent to imposing additional stressors on the prey species whose interactions we would like to measure [Ling et al., 2009, Gurevitch et al., 2000]. Considering multiple species would not only allow us to understand the effects of multiple stressors on prey populations but would also afford us the opportunity to study how community composition would change as a result of climate change, as has been observed in some marine systems [Urban et al., 2012].

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.

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6 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

$$n_{t+1}(x) = \int_{-L/2+ct}^{L/2+ct} k(x - y)f(n_t(y))dy. \quad (5)$$

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, $\bar{x} \equiv x - ct$.

$$n^*(\bar{x}) \equiv n^*(x - ct) = n_t(x). \quad (6)$$

Then (5) gives us an expression for n^* :

$$\begin{aligned} n^*(\bar{x} - c) &= \int_{-L/2}^{L/2} k(\bar{x} - \bar{y})f(n^*(\bar{y}))d\bar{y} \\ \Rightarrow n^*(\bar{x}) &= \int_{-L/2}^{L/2} k(\bar{x} + c - \bar{y})f(n^*(\bar{y}))d\bar{y} \end{aligned} \quad (*)$$

If $f(0) = 0$, $n^*(\bar{x}) \equiv 0$ for all $\bar{x} \in [-L/2, L/2]$ 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 $n^*(\bar{x})$,

$$\begin{aligned} n_t(x) &= n^*(\bar{x}) + \xi_t(x) \\ \Rightarrow \xi_{t+1}(x) &= \int_{-L/2+ct}^{L/2+ct} k(x - y)f'(n^*(\bar{y}))\xi_t(y)dy \text{ by linearizing around the traveling pulse and using } (*) \\ \Rightarrow \xi_{t+1}(x) &= \int_{-L/2+ct}^{L/2+ct} k(x - y)f'(0)\xi_t(y)dy \text{ if we're interested in the stability of the trivial traveling pulse} \end{aligned}$$

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

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

Define the integral operator

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

so that the perturbation to the traveling pulse will satisfy

$$\psi_f(u)(x) = \lambda u(x) \quad (7)$$

Then the trivial traveling pulse is unstable when the dominant eigenvalue of ψ_f is greater than 1.

Let f denote the recruitment function, let h denote a harvesting function and let $m(y) = f(y - h(y))$, i.e. m denotes the number of offspring after the adults have been 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

$$\begin{aligned}\psi_m(u)(x) &= \int_{-L/2}^{L/2} m'(0)k(x+c-y)u(y)dy \\ &= (1 - h'(0)) \int_{-L/2}^{L/2} f'(0)k(x+c-y)u(y)dy \\ &= (1 - h'(0))\psi_f(u)(x) \\ &= (1 - h'(0))\lambda u(x)\end{aligned}$$

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

6.1 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, (7) becomes

$$\begin{aligned}\lambda u(x) &= f'(0) \sum_{n=1}^{\infty} \left(a_n(x) \int_{-L/2}^{L/2} b_n(y-c)u(y)dy \right) \\ \Rightarrow \lambda \int_{-L/2}^{L/2} b_k(x-c)u(x)dx &= f'(0) \sum_{n=1}^{\infty} \left(\int_{-L/2}^{L/2} b_n(x-c)u(x)dx \right) \left(\int_{-L/2}^{L/2} a_n(y)b_k(y-c)dy \right) \\ \Rightarrow \lambda d_k &= f'(0) \sum_{n=1}^{\infty} A_{nk}d_n\end{aligned} \quad (**)$$

where

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

6.2 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 0^{th} terms for a_n and b_n so that Equation ** becomes

$$\begin{aligned} \lambda d_0(c) &= f'(0) A_{00}(c) d_0(c) \\ \Rightarrow \lambda &= R_0(1-h) A_{00}(c) \\ \text{where } A_{00}(c) &= 2\sqrt{2} \exp\left(\frac{-c^2}{8D}\right) \left[\operatorname{erf}\left(\frac{L-c}{2\sqrt{2D}}\right) - \operatorname{erf}\left(\frac{-L-c}{2\sqrt{2D}}\right) \right] \end{aligned}$$

where erf is the error function. The critical rate of environmental shift c^* and the critical harvesting rate h^* are those values of c and h , respectively, that make $\lambda = 1$.

6.3 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

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

If we solve for λ , we find

$$\lambda = R_0(1-h) \left[\frac{wL \cos(wc)}{4} + \frac{1}{4} \sqrt{\sin^2(wL) - w^2 L^2 \sin^2(wc)} \right]. \quad (8)$$

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:

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

6.4 Approximate Critical Harvesting Proportions

We will use the following Taylor series to make approximations of the critical harvesting proportions under the two dispersal kernels:

$$\begin{aligned} \cos(x) &= 1 - \frac{x^2}{2} \\ \cos^2(x) &= 1 - x^2 \\ \sin^2(x) &= x^2 - \frac{x^4}{3} \\ \operatorname{erf}(x) &= \frac{2}{\sqrt{\pi}} \left(x - \frac{x^3}{3} \right) \\ \exp(x) &= 1 + x + \frac{x^2}{2} \end{aligned}$$

For the sinusoidal kernel we found

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

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

$$\begin{aligned} h^* &\sim 1 - \frac{1}{R_0} \cdot \frac{12wL}{w^4L^4} \left[1 - \frac{w^2c^2}{2} - \sqrt{1 - w^2c^2 - \frac{w^2L^2}{3}} \right] \\ &= 1 - \frac{1}{R_0} \cdot \frac{4\sqrt{3}}{L^3(\pi^2 - 8)^{3/2}} \cdot \sigma \left[8\sqrt{3}\sigma^2 - (\pi^2 - 8)\sqrt{3}c^2 - 4\sigma\sqrt{12\sigma^2 - (\pi^2 - 8)(3c^2 + L^2)} \right] \end{aligned}$$

For the Gaussian kernel we found

$$h^* = 1 - \frac{2\sqrt{2} \exp\left(\frac{c^2}{8D}\right)}{R_0 \left[\operatorname{erf}\left(\frac{L-c}{2\sqrt{2D}}\right) - \operatorname{erf}\left(\frac{-L-c}{2\sqrt{2D}}\right) \right]} \quad (10)$$

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

$$\begin{aligned} h^* &\sim 1 - \frac{\sqrt{2\pi}(1 + \frac{c^2}{8D} + \frac{c^4}{128D^2})}{R_0\sqrt{\pi} \left[\frac{L-c}{2\sqrt{2D}} - \frac{(L-c)^3}{3(2\sqrt{2D})^3} - \frac{-L-c}{2\sqrt{2D}} + \frac{(-L-c)^3}{3(2\sqrt{2D})^3} \right]} \\ &= 1 - \frac{1}{R_0} \cdot \frac{3\sqrt{2\pi}}{8L} \frac{(32\sigma^4 + 8c^2\sigma^2 + c^4)}{\sigma(12\sigma^2 - (L^2 + 3c^2))} \end{aligned}$$

In the case of both kernels, the critical harvesting proportion can be approximated by a function that looks like

$$h^* \sim 1 - \frac{1}{R_0} \cdot C(L)f(\sigma^2, c^2, L^2 + 3c^2) \quad (11)$$

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