Persistence of marine populations under climate velocity and fishing

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# Abstract

The impacts of changing climates do not occur in isolation, but instead appear on a background of other disturbances and stressors. Despite empirical reports of substantial interactions between climate change and other stressors, we often lack a mechanistic understanding of these interactions. Here, we explore the cumulative impacts of the two dominant stressors in the ocean, fishing and climate change. We focus in particular on the ability of populations to shift spatially to keep up with climate velocity (the rate and direction that isotherms move across the seascape). Results suggest that harvesting and climate velocity can drive populations extinct, but that the critical thresholds depend on the growth rate and dispersal kernel of the population. We also find that climate velocity and fishing interact nearly additively, but that threshold harvest rules and marine protected areas (MPAs) can be effective management tools to mitigate the interaction between the two stressors.

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

# Introduction

A number of stressors can disturb an ecosystem, and ecologists have quantified the consequences of many of these of perturbations (Wilcove et al. 1998; Crain, Kroeker, and Halpern 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 occurring individually may amplify the disturbance caused by a coincident perturbation (Crain, Kroeker, and Halpern 2008; Darling and Côté 2008; Nye, Gamble, and Link 2013; Gurevitch, Morrison, and Hedges 2000). In the most worrying cases, interactions between multiple stressors could drive a population extinct even though assessments of impacts individually predict the population to be robust (e.g. Pelletier et al. (2006)). Since disturbances rarely occur in isolation, measuring the effects of multiple disturbances provides a better understanding of likely impacts to an ecosystem (Doak and Morris 2010; Fordham et al. 2013; Folt et al. 1999).

Climate change and harvest, two of the largest human impacts for species in ocean and for many terrestrial species (Halpern et al. 2008), provide an important example of ecological disturbances occurring in unison. Marine and terrestrial species 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; Pinsky et al. 2013) and are projected to continue in the future (Kell, Pilling, and O’Brien 2005; Mackenzie et al. 2007). Climate velocity is the rate and direction that isotherms move across the seascape (Loarie et al. 2009; Burrows et al. 2011), and observations suggest that local climate velocities successfully explain past shifts in species distributions (Pinsky et al. 2013). However, many of these shifting species are also subject to harvesting, as well as pollution, ocean acidification, habitat fragmentation, and invasive species (Wilcove et al. 1998; Sala 2000; Assessment 2005; Pinsky et al. 2013; Barry, Baxter, and Gilman 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 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 bioclimatic-envelope models (also known as species distribution models). These statistical models typically correlate presence-absence or abundance data with biophysical characteristics such as mean or maximum temperature, rainfall, or salinity, to predict how species ranges’ will differ under climate change (Elith et al. 2006; Guisan and Thuiller 2005; Guisan and Zimmermann 2000). Despite these models’ widespread adoption, many authors have criticized bioclimatic-envelope models as oversimplified because they lack species interactions, dispersal and reproductive processes (Kearney and Porter 2009; Zarnetske, Skelly, and Urban 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.

Most previous work addressing the joint impacts of climate and harvest considers climate fluctuations (large anomalies around the mean) rather than directional shifts in temperature (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 (Cheung et al. 2010; Lindegren et al. 2010; Brown et al. 2010; Merino, Barange, and Mullon 2010; Merino et al. 2010; Plaganyi et al. 2011; Ainsworth et al. 2011; Zhang et al. 2011; Barange et al. 2011; Howard et al. 2013). These predicted impacts are important for management and conservation planning (Allison et al. 2009), but the complexity of these models makes it difficult to understand the relative importance of particular drivers, disturbances, and interactions (but see Nye, Gamble, and Link (2013) for an approach using ecosystem-level models to discern relative importance of disturbances).

Here, we focus on a simpler model that is easier to diagnose. We extend a previously studied model for climate-driven range shifts (Zhou and Kot 2011) so that it includes harvesting pressure. The model explicitly includes reproduction and dispersal, two mechanistic processes central to species’ responses to climate and harvest. The model is built with marine species and fishing in mind, but also applies to terrestrial species with distinct growth and dispersal stages (e.g., plants, trees, and many insects). Previous work has suggested that these processes are important in determining species’ vulnerability to climate change (Fordham et al. 2013; Hastings et al. 2005). We find the critical harvesting rate and climate velocity that drive the population extinct and how these critical rates depend on one another. We also show that climate-driven range shifts and fishing interact nearly additively, with low positive synergy at more extreme levels of the stressors. Finally, we also examine 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, Lester, et al. 2010), 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 find 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 a species can survive.

# Methods

We studied a model of the dynamics of a 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 (hereafter ‘patch’) shifts at a fixed velocity, and harvest occurs at each point in space along the entire one-dimensional world. We first analytically determined the combinations of harvesting rate and climate velocity that drive the population extinct (hereafter the critical harvesting rate and critical climate velocity), and then measured their interaction by calculating the drop in biomass caused by the stressors both individually and together. We then added threshold harvesting rules and MPAs in numerical simulations of the model to determine how these management strategies affect population persistence and biomass.

### The Model

In our model, 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 additionally subject the adults to harvesting before they produce offspring. These processes – harvesting, recruitment, and dispersal – are incorporated into an integrodifference model. If is the number of fish at position at time , then the number of fish at the next generation is given by

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|  | (1) |

where is a function describing the number of adults harvested given local density , is a dispersal kernel giving the probability of a larva traveling from position to position , is the length of the patch, and is the rate at which the patch shifts across space (the climate velocity). In other words, the center of the patch at time *t* will be at location *ct*. As shown in Appendix A.1, the persistence of this population depends on rather than the full form of , and so we use for simplicity, where *h* is the proportion of the population harvested.

We use a Beverton-Holt stock-recruitment function for ,

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|  | (2) |

which gives the number of offspring produced by a population of size after accounting for density dependence. Here is the intrinsic growth rate and is carrying capacity (see Table 1 for a full description of parameters and functions).

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 such that (see Appendix A.2 for further details). In our analyses, as in Latore, Gould, and Mortimer (1998), we used the separable Gaussian kernel given by

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|  | (3) |

To derive analytical expressions, we approximated the kernel, as described in Appendix A.3. Analytical results for a separable sinusoidal kernel are described in Appendix A.4. We also used simulations to analyze a non-separable Laplace dispersal kernel, 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 (Zhou and Kot 2011). The traveling wave must satisfy

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|  | (4) |

where describes the position within the patch (Zhou and Kot 2011). For a separable kernel, the equilibrium traveling pulse must satisfy (see Appendix A.2)

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|  | (5) |

where the satisfy the recursive equations

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|  | (6) |

(Latore, Gould, and Mortimer 1998).

## Persistence

If the population is harvested at low enough levels and the climate velocity is slow enough, the population will be able to persist. However, there are threshold values of the harvesting rate and the climate velocity such that if we increase the parameters beyond these values, the population will be driven extinct. When the population is extinct, the system is in equilibrium, i.e., there is a ‘trivial’ traveling pulse, for all , which satisfies Equation 4. If a population persists, it must be able to avoid extinction and grow even when small (Zhou and Kot 2011). Population persistence is therefore equivalent to the trivial traveling pulse being an unstable equilibrium (the introduction of a small population will grow rather than return to extinction). We found the critical parameters, and , by finding the parameters that make the trivial pulse unstable. See Appendix A.1 for details.

Regardless of its exact functional form, the only property of the recruitment function that determines whether or not a population can persist is how quickly recruitment increases when the population size is near (but above) , which is equivalent to the intrinsic growth rate . Therefore, the population’s ability to persist depends on properties of the population itself –the intrinsic growth rate , the shape of the dispersal kernel, and the expected distance a larva disperses ; properties of the environment – the length of the viable patch and how quickly the environment shifts ; and the harvesting rate . For a Gaussian kernel, the critical rates and are those values of and such that

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

where is a decreasing function of the length of the viable patch and the intrinsic growth rate.

## Calculating the interaction of climate velocity and harvest

In order to quantify how fishing interacts with climate velocity, 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. Equations ([recursivem]) and ([separableintegrodifference]) allowed us to numerically find the total biomass in the equilibrium traveling pulse.

We used to denote the equilibrium biomass without either stressor, the equilibrium biomass with harvesting but with climate velocity equal to 0, the equilibrium biomass with climate velocity greater than 0 but no harvesting, and the equilibrium biomass with both stressors. For each stressor or combination of stressors, we found the drop in biomass caused by stressor ,

If the stressors interact additively, the drop caused by both stressors would be the sum of the drops caused by either individually. The synergy (the deviation from additive interaction) is therefore defined as

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 purely additive interaction. We focused on the additive model because it is a common hypothesis in multiple stressor research, though multiplicative and dominant stressor models are also possible (Crain et al. 2008)

## 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 alternative dispersal kernels, such as the the Laplace dispersal kernel,

a commonly used model of marine larval dispersal (Botsford et al. 2001).

Second, we implemented two management strategies (threshold harvesting rules and MPAs) to examine their effect on population persistence and on the interactions between stressors. For every simulation, we seeded the world with 50 individuals at a single point and iterated through 150 generations for the population to reach equilibrium without harvesting or climate shift. We then added harvesting pressure, allowed the population to again reach equilibrium (150 generations), and finally added climate velocity by moving the viable patch. We calculated equilibrium biomass as the mean biomass of 300 time steps once the difference in biomass between successive generations was no greater than 0.1.

Under the two alternative management strategies, harvesting pressure was no longer implemented as a proportional removal from the population. Under 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 we harvested all the ‘surplus’ individuals. This approach is a somewhat more extreme version of those proposed for many existing fisheries (Froese et al. 2011).

In addition, we introduce networks of MPAs into our simulations by designating segments of space where the harvesting rate was equal to 0. MPAs are typically designed to meet either fishery management or conservation goals (Agardy 1994; Holland and Brazee 1996; Gaines, White, et al. 2010), thus their spacing and size differ. Fisheries-oriented MPAs are often designed such that they maximize adult spillover into fishable areas by creating many small reserves closely spaced (Hastings and Botsford 2003; Gaylord et al. 2005; Gaines, White, et al. 2010). To mimic this management scheme, we implemented MPAs with a length of the average dispersal distance and an inter-reserve spacing of the average dispersal distance. Conservation-oriented MPAs seek to protect entire ecosystems and reduce adult spillover by creating fewer, larger protected areas (Toonen et al. 2013). To mimic this scheme, we implemented MPAs with a length times the average dispersal distance and an inter-reserve spacing times the average dispersal distance between them (Lockwood, Hastings, and Botsford 2002).

# Results

## Persistence with Harvesting and Climate Velocity

The climate velocity and critical harvest rate are inversely related. As the climate velocity increases, the critical harvesting rate decreases (Figure 1a). This means that a harvesting rate that is sustainable in the absence of environmental shift may no longer be sustainable if the environment begins to change. Conversely, as the harvesting rate increases, the critical climate velocity decreases (Figure 1a). Thus as harvesting pressure increases, it becomes increasingly easy for a shifting environment to drive the population extinct.

When climate velocity or harvesting pressure exceeds their critical ratesthe biomass of the population at equilibrium will be equal to . Before the stressors reach those thresholds, the equilibrium biomass of the population decreases as either the harvesting pressure increases or the environmental shifts more quickly (Figure 1b).

It is always the case that increasing the intrinsic growth rate, , increases the critical climate velocity and the critical harvesting rate , since a population that grows more quickly can recover more effectively from losses caused by these disturbances (Figure 1a). However, whether or not dispersing farther is better depends on how quickly the environment is shifting. When the environment is shifting slowly, dispersing farther is detrimental since many larvae will disperse too far away from the viable patch (compare dashed to solid lines in Figure 1a). 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 process affects the critical harvesting rate: at a low climate velocity, we can more severely harvest populations that have a shorter dispersal distance than those that disperse farther, whereas at a high climate velocity, we can more aggressively harvest populations that disperse farther.

**Interactions Between Stressors**

We found low levels of positive synergy between the two stressors in our analysis of the Gaussian kernel (Figure 2). Where positive synergy exists, a doubly stressed population loses more biomass than we would predict from either stressor individually. The stressors interact most strongly at high harvest and climate velocity rates, shortly before they drive the population extinct. However, the synergistic loss in biomass is very low, meaning that these stressors interact more or less additively. We found similar analytical results for a sinusoidal dispersal kernel, suggesting that this result is robust to changes in the dispersal kernel.

## Alternative management strategies

Under a constant harvest rate, we found that harvest rate and climate velocity interact such that more heavily harvested populations go extinct with slower climate velocities. However, when we put harvest thresholds in place, a small population can always escape fishing and the critical climate velocity no longer depends on the harvesting rate (Figure 3d). In other words, as long as there is some threshold population density below which harvesting is not allowed, critical climate velocity only depends on the growth rate, length of the viable patch, and average dispersal distance.

With either type of MPA strategies examined (many small versus few large), the population withstands combinations of higher climate velocities and higher harvesting rates than without the MPAs (compare Figures 3b and c to Figure 3a). At lower climate velocities, MPAs spaced more than one average dispersal distance apart resulted in larger fluctuations of population biomass relative to small, closely spaced, MPAs (Appendix A.6). As climate velocities increase, for both MPA strategies, the mean population abundance declines but the population experiences less extreme oscillations in abundance. Since minimum population biomass is increased, the population is a larger buffer to possible extinction in a stochastic environment.

# Discussion

Climate change and harvest are the two dominant human impacts on marine species and many terrestrial species, but our understanding for their joint effects and interactions has remained poor. By analyzing a general model that incorporates dispersal and reproduction, we showed that climate and harvesting interact strongly in their effects on species persistence and biomass. In particular, we found a negative relationship between the critical harvesting rate and climate velocity. In other words, the more quickly the environment shifts, the less harvesting it takes to drive the population extinct.

In our model, the interaction between harvest and climate was effectively additive, with weak synergistic effects appearing primarily when the population was close to extinction. This result from our model would appear to contrast with other suggestions in the literature. For example, synergy between harvesting and temperature was detected in experimental populations of rotifers (Mora et al. 2007), theory and data suggest that fishing increases the sensitivity of populations to climate (Planque, Fromentin, et al. 2010), and positive feedback loops between fishing and climate have been identified at the ecosystem level (Kirby, Beaugrand, and Lindley 2009; Planque, Fromentin, et al. 2010). However, part of this discrepancy may appear because these examples examined different aspects of changing climate than we did. In the experimental study, rotifer populations were subjected to warming temperatures, but organisms were unable to relocate to thermal optima. In that experiment, harvesting was conjectured to reduce genetic diversity, and therefore reduce populations’ adaptive capacity in the face of warming (Mora et al. 2007). In other population examples, climate variability has been the focus, not cumulative warming or shifting distributions. Fishing reduces the spatial or age diversity within populations, making them more sensitive to climate variability (Planque, Fromentin, et al. 2010). Similarly, the North Sea ecosystem study focused on warming in a single location rather than spatial processes (Kirby, Beaugrand, and Lindley 2009). Indirect food web effects mediated by warm temperatures and the loss of a top predator (cod) appeared to create a positive feedback loop favoring decapods and driving cod to even lower abundance in the North Sea. The interactive effects of climate and fishing on spatial distributions had been identified as an important area of research (Planque, Fromentin, et al. 2010), and our simple model suggests that additive effects might be the baseline expectation. However, future work considering food web processes and genetic, spatial, and age diversity will be important to examine other possible sources of synergistic impacts.

Absence of synergy, however, does not mean absence of interaction, and our results suggest that particular combinations of harvesting and climate velocity will affect some species more than others. Species with a higher reproductive rate and a longer average dispersal distance will better track rapid climate velocities, as compared to species with a low reproductive rate and short dispersal distance. The finding that a higher reproductive rate can sustain higher climate velocities and harvesting rates is intuitive, particularly because harvesting in effect reduces the maximum reproductive rate. However, it is worth pointing out that a higher reproductive rate can be generated either by shorter generation times or higher fecundity. Our finding that species with shorter generation times can better keep up with shifts in climate is in agreement with empirical work suggesting that fish that shifted in response to warming in the North Sea had faster life histories than non-shifting species (Perry et al. 2005).

While higher reproductive rates improve a population’s ability to persist, higher dispersal distances do not necessarily do so. At low speeds, we found that a short dispersal dispersal distance improved the maximum harvesting rate a population could sustain while at higher speeds a longer dispersal distance improved the maximum climate velocity in which the population could persist. This is because when climate is shifting slowly, a large dispersal distance sends most offspring ahead of the patch, while with faster climate velocities a long dispersal distance allows the population to make it to the new patch. Thus climate velocity will selectively favor species with dispersal distances best matched to the rate of shift.

We also examined whether frequently recommended management approaches, MPAs and harvest control rules, can help ensure species persistence in the face of multiple stressors. With either of these management strategies, we generally found increases in the population’s biomass at equilibrium and an improved ability to persist. Threshold harvesting rules in particular appear to alleviate much of the interaction between the two stressors. Thresholds appear to have this effect because the management approach effectively prevents harvesting of the leading edge, which allows colonization to occur as if these individuals were moving into un-fished areas. This result matches well with invasion theory, which has shown that populations move into new territory at a rate approximately equal to , where *D* is the mean squared displacement of individuals per unit time. With a constant harvest rate applied everywhere, the invasion rate drops to , whereas the invasion rate is unaffected if harvesting is prohibited at low densities (e.g., at the leading edge). It’s interesting to note that novel, low abundance stocks are commonly unregulated in fisheries systems. In order to decouple the additive effects of harvest and climate change, management would have to reverse this paradigm by preventing harvest of shifting species until they had become established in new areas.

Unlike thresholds, MPAs are explicitly spatial. Previous work has advanced protected areas as a way to help organisms keep pace with shifting climates, as well as to ameliorate anthropogenic disturbances like harvesting and habitat fragmentation (Lawler et al. 2010; Hannah et al. 2007; Botsford, Hastings, and Gaines 2001; Gaylord et al. 2005; Hastings and Botsford 2003; Thomas et al. 2012). Our results show that MPAs increase the equilibrium biomass at a given climate velocity, which support their use as a tool to ameliorate the effects of climate velocity. However, the details matter: few, large MPAs caused increased variability at low climate velocities, while many smaller MPAs maintained a population bounded farther from extinction. This effect appeared because of the large gaps (with fishing) between large MPAs. Finally, with sufficiently high harvesting pressure, few, large MPAs rescued populations at intermediate climate velocities. With intermediate speeds, the population was able to reach a protected area fast enough to avoid extinction, and the protected area was large enough to allow a partial rebuilding of the population before it moved out the other side. However this effect disappears as speed continues to increase, suggesting that understanding the relationship between climate velocity, dispersal distance and reproductive rate are important parameters in designing management strategies effective under both climate change and harvesting pressure.

The advantage of a simple model like ours is that it is general enough apply to a wide range of species. Our discrete-time, continuous-space model captures the processes important to a species with distinct growth and dispersal stages, including most marine organisms, plants, trees, and many insects. However, our approach does not capture some complexities of real populations. For example, we do not include Allee effects (negative per capita growth at low densities). However, invasion theory suggests that Allee effects have two effects: they slow initial rates of spread, and they allow predation to, in some cases, slow or stop an invasion (Hastings et al. 2005). We expect similar effects in our model, with fishing playing a similar role to predation. We also did not include age structure in our model. Age-structured models are important for studying the joint effects of fishing and climate variability (Botsford et al. 2011; Planque, Fromentin, et al. 2010), and understanding how these two processes impact the ability of species to shift their distributions would be interesting future work. Besides these species-specific extensions, this modeling framework could also be extended to consider species interactions, especially predator-prey interactions.

Using a simple mechanistic model like the one we present here help to build intuition about the conditions under which species can survive the cumulative impacts of climate and harvesting. This work highlights the importance of considering stressors in combination, as outcomes deviate from what we would predict in isolation. This is especially true for management strategies that may result in unanticipated effects such as large fluctuations associated with big, distant MPAs shown here. While management strategies only change harvesting practices and do not directly address the effects of climate change, understanding how management approaches can ameliorate interactions between harvesting and range shifts will help to better implement harvesting rules and protected areas. This is encouraging evidence, however, that management practices can help protect marine populations from the cumulative impacts of harvesting and climate change.

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# Tables

Table 1: Parameter values and functions used in the text

|  |  |
| --- | --- |
| Variable | Definition |
|  | density of fish at position at time |
|  | density of fish at equilibrium at position relative to the patch |
|  | dispersal kernel, the probability of larva traveling from position to position |
|  | expected distance traveled by a larva |
|  | recruitment function, the number of offspring produced by a population of size |
|  | intrinsic growth rate, |
| *g(n)* | harvest function, the number of adults harvested from a population of size *n* |
|  | proportion of adults harvested |
|  | patch length |
|  | climate velocity in units of distance per time |

# 

# Figure Legends

Figure 1: (a) The critical threshold for persistence as a function of harvesting rate on the y-axis and climate velocity on the x-axis. Black lines correspond to a growth rate of , red to , and blue to . Solid lines correspond to an average dispersal distance and dashed lines correspond to an average dispersal distance of . These results are from an approximated Gaussian dispersal kernel (Eq. ??) with . (b) The equilibrium biomass of the population as a function of the climate velocity on the x-axis and the harvesting rate on the y-axis. These results are from an approximated?? Gaussian dispersal kernel with parameters , , .

Figure 2: Interaction between the two stressors as a function of climate velocity and harvesting rate. Shading indicates the degree of synergistic interaction, i.e., the loss in biomass in the doubly stressed population in excess of the sum of the losses caused by each stressor individually (. Synergy of 0 indicates additive interaction of the stressors. The calculated excess loss, on the order of , is small in comparison to the total biomass, which can be as large as . These results are from an approximated Gaussian dispersal kernel with parameters , , .

Figure 3: The equilibrium biomass of the population as a function of the climate velocity on the x-axis and the harvesting rate on the y-axis under various management strategies. (a) Constant harvest rate (compare to Figure 1b). (b) Many small MPAs. (c) Few large MPAs. (d) Threshold harvesting levels, where y-axis is the proportion of the population that is protected from harvesting. These results are from a simulation with a Laplacian dispersal kernel with parameters , , , and .

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# Figures

a)  b) 

Figure 1

fig:

Figure 2

a) Macintosh HD:Users:efuller:Documents:Projects:Moving_fish:MovingFish:Writing:plots:eqbiomass_sim.pdf b) Macintosh HD:Users:efuller:Documents:Projects:Moving_fish:MovingFish:Writing:plots:eqbiomass_fishmpa.epsc) Macintosh HD:Users:efuller:Documents:Projects:Moving_fish:MovingFish:Writing:plots:eqbiomass_consmpa.epsd)Macintosh HD:Users:efuller:Documents:Projects:Moving_fish:MovingFish:Writing:plots:eqbiomass_thresh.eps

Figure 3