Persistence of marine populations under climate and fishing

Emma Fuller, Eleanor Brush, Malin Pinsky

1   Abstract

When the climate changes, the habitat with suitable conditions in which organisms can survive and reproduce moves. This change does not occur in isolation but rather appears on a background of other disturbances. In order to understand how two disturbances, range shift and harvesting, interact and affect population persistence, we studied an integrodifference model that explicitly included the mechanisms of dispersal and reproduction. If the viable habitat moves too quickly or harvesting pressure is too great, the population is driven extinct. We found the rates of harvesting and environmental shift required to allow the population to persist and and studied how these critical parameters depend on the growth rate and dispersal behavior of the population. We then measured the interaction between the stressors. The stressors interact nearly additively: we found very low positive synergy at those levels of the stressors that almost drive the population extinct. Positive synergy suggests that harvesting may aggravate 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 under some circumstances these approaches could mitigate the interaction between the two stressors.

1

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], but less work has been done to measure the effects of multiple

stressors and the interactions between them. If disturbances interact synergistically, a

perturbation that has little effect when it occurs individually may amplify the disturbance

caused by a coincident perturbation [Crain et al., 2008, Darling and Côté, 2008, Nye et al.,

2013, Gurevitch et al., 2000]. In the most extreme (and worrying) cases, synergistic

interactions between multiple stressors will drive a population extinct even though it could

persist in the face of any single stressor (e.g. Pelletier et al. [2006]). If disturbances interact

antagonistically, on the other hand, the effects of multiple stressors may be less than that

predicted by the individual effects of the stressors. Since disturbances rarely occur in

isolation, it is important to measure the synergy between disturbances in order to

understand how a system will be affected by their presence and to understand when

multiple disturbances will drive a population extinct [Doak and Morris, 2010, Fordham

et al., 2013, Folt et al., 1999].

Climate change and fishing have been identified as the two largest human impacts on the

ocean [Halpern et al., 2008]. They therefore provide an important case study of how

disturbances interact in their effects on biological populations. Further, understanding

2

these interactions will be crucial to managing populations subjected to both of these disturbances. Marine fish are already moving in response to climate change [Perry et al., 2005, Hiddink and ter Hofstede, 2008, Rijnsdorp et al., 2009, Dulvy et al., 2008, Simpson et al., 2011] and they are projected to continue moving in the future [Kell et al., 2005, Mackenzie et al., 2007]. Species that are likely to undergo or already undergoing shifts in range are also subject to harvesting, in addition to many other disturbances including pollution, ocean acidification, habitat fragmentation, and invasive species [Wilcove et al., 1998, Sala, 2000, Assessment, 2005, Pinsky et al., 2013, Barry et al., 1995, Nye et al., 2009]. Synergistic interactions between overfishing and temperature-driven range shifts have been found in empirical case studies [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 how populations will be distributed in future after climate-driven range shifts 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

3

67 models only address one disturbance, climate-driven range shifts.

68 Work on the joint impacts of climate and fishing often considers climate fluctuations (large

69 anomalies around the mean) rather than directional changes in climate [Walters and

70 Parma, 1996, King and McFarlane, 2006]. When the effects of climate-driven range shifts

71 on fishing are considered, the models are typically case-specific and detailed, integrating

72 multiple drivers and disturbances [Cheung et al., 2010, Lindegren et al., 2010, Brown et al.,

73 2010, Merino et al., 2010a,b, Plaganyi et al., 2011, Ainsworth et al., 2011, Zhang et al.,

74 2011, Barange et al., 2011, Howard et al., 2013]. These predicted impacts are important for

75 management and conservation planning [Allison et al., 2009], however these models are so

76 complex that understanding the relative importance of particular drivers, disturbances, and

77 interactions is difficult (but see Nye et al. [2013] for an approach using ecosystem-level

78 models to discern relative importance of disturbances). The degree of detail and

79 case-specificity in these studies makes it difficult to draw general conclusions.

80 Here we extended a previously studied model of a fish population subject to climate-driven

81 range shift by also considering harvesting pressure. Reproduction and dispersal, two

82 mechanistic processes central to species' responses to climate and fishing, are explicitly

83 included. Previous work has highlighted the importance of these two processes and their

84 vulnerability to climate change [Fordham et al., 2013, Hastings et al., 2005]. We found the

85 rate of harvesting and the rate of environmental shift that drive the population extinct and

86 how the threshold harvesting level of depends on how quickly the range is shifting. We also

87 found that climate-driven range shifts and fishing interact nearly additively, with very low

88 positive synergy at more extreme levels of the stressors.

89 We also examined the effect of threshold harvesting rules and marine protected areas

90 (MPAs) on species persistence. Protected areas have been suggested as a key form of

4

climate insurance and stepping stones to help species keep up with a changing environment [Thomas et al., 2012, Hannah et al., 2007]. MPAs are frequently recommended for conservation of biodiversity and improved fisheries yield [Gaines et al., 2010a], and we evaluate whether MPAs established for those purposes could improve species persistence when habitat is shifting rapidly. We found 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 the fish at each point in space can be harvested. We first determined the climate velocity and harvesting rate that would drive the population extinct. We then measured the drop in biomass caused by range shifts, harvesting, and both stressors together in order to determine whether they interact synergistically. We finally 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

5

processes– recruitment, harvesting, and dispersal– are incorporated into an integrodifference model to describe how the population changes over time. If $n_t(x)$ is the density of fish at position x at time t, then the density of fish at the next generation is given by

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

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

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

Regardless of the exact functional form of the recruitment function, the critical parameter in determining population persistence is how quickly recruitment increases when the population size is near (but above) 0, which is equivalent to the intrinsic growth rate, $R_0 = f'(0)$. Analyzing this kind of model becomes easier if the dispersal kernel is separable into its dependence on the source of larvae and its dependence on the destination of the larvae, i.e. if there are functions a_i, b_i such that $k(x-y) = \sum_{i=1}^{\infty} a_i(x)b_i(y)$. In our analyses, as in [Latore et al., 1998], we used the separable Gaussian kernel given by

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

To derive analytical expressions, we approximated the kernel, as described in the

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

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

to this method, as described below.

At equilibrium, 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 sought to describe how the population is distributed over the

viable patch as it shifts through the world in order to study the size of the population at

equilibrium and whether or not the population could persist. The traveling wave n^* must

satisfy

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

where $\bar{x} \in \left[-\frac{L}{2}, \frac{L}{2} \right]$ describes the position within the patch [Zhou and Kot, 2011].

3.2   Persistence One possible equilibrium traveling wave that solves Equation (1) is the

'trivial' traveling pulse, $n^*(\bar{x}) = 0$ for all $x \in \left[-\frac{L}{2}, \frac{L}{2} \right]$, i.e. a patch with no fish in it. If a

population is to persist, it must be able to avoid extinction and grow even when it is small.

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 the introduction

of a small population. If the trivial pulse is unstable, a small population may increase and

form a stable population. Population persistence is therefore equivalent to the trivial

traveling pulse being an unstable equilibrium.

If the population is harvested at low enough levels and the environment shifts slowly

enough, the population will be able to persist. There are threshold values of the harvesting

7

rate h and the rate of environmental shift c such that if the parameters are increased

beyond these values, the population will be driven extinct. We found these critical

parameters, h^*, and c^*, by finding the parameters that make the trivial pulse unstable.

Details are provided in Appendix A.1.

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). The population biomass at

equilibrium depends on the function form of recruitment, but population persistence only

depends on the intrinsic growth rate R_0. For a Gaussian kernel, the critical rates c^* and h^*

are those values of c and h such that

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

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

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

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

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

growth rate.

3.3 Calculating synergy Zhou and Kot [2011] only considered whether a shifting

environment will drive a population extinct. In order to quantify whether the two stressors

are interacting additively, synergistically, or antagonistically, we found the total biomass of

8

167 the population when it reached an equilibrium traveling pulse and compared this

168 equilibrium biomass in the presence and absence of each stressor individually or the two

169 stressors together. For a separable kernel, the equilibrium traveling pulse $n^*(x)$ must satisfy

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

170 where the m_i satisfy the recursive equations

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

171 [Latore et al., 1998]. Equation (3) allowed us to find the values of m_i numerically. We then

172 found the total biomass in the equilibrium traveling pulse by using these m_i and

173 integrating Equation (2).

174 We used B_0 to denote the equilibrium biomass without either stressor, B_h the equilibrium

175 biomass with harvesting but a constant environment, B_c the equilibrium biomass with a

176 shifting environment but no harvesting, and B_{hc} the equilibrium biomass with both

177 stressors. For each stressor or combination of stressors, we found the drop in biomass

178 caused by stressor s,

$$E_s = B_0 - B_s.$$

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

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

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

9

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.

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

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

a commonly used model of larval dispersal [**?**]. 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, to perform simulations we must specify a recruitment function. Again, we chose to use a Beverton-Holt function. In the first generation, we seeded the world with 50 individuals at a single point, as in [Zhou and Kot, 2011]. We first ran through 150 generations in order for 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. Equilibrium biomass is calculated as the mean biomass of 300 time steps once the difference in biomass between time step t and $t + 1$ was no greater than 0.1.

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

order to confirm our analytical results. We then evaluated 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.

MPAs are a form of management designed to check the impact of fishing on targeted

populations and are typically designed to meet either conservation of fishery management

goals [Agardy, 1994, Holland and Brazee, 1996, Gaines et al., 2010b]. To implement an

MPA management strategy in our model, we examine the effect of both of these commonly

advocated approaches. While both conservation and fisheries oriented MPA schemes align

in their goal of maintaining a sustainable fished population, they differ in desired level of

adult spillover. 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]. The converse of this is the goal of conservation-oriented MPAs which seek

to reduce adult spillover by minizing the ratio between the reserve edge length relative to

area protected [Gaines et al., 2010b].

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).

Conservation-oriented MPAs, are frequently large and rarely part of a larger network of

reserves [Hastings and Botsford, 2003]. For solitary reserves to be successful at protecting

target species, they must encompass self-sustaining fish populations [Hastings and

Botsford, 2006, Gaines et al., 2010b]. As such modeling studies estimate that isolated

reserves must be at least as large as the average dispersal distance for the targeted fish

11

species [Lockwood et al., 2002, Hastings and Botsford, 2003, Botsford et al., 2001, Gaines et al., 2010a]. To implement conservation MPAs we created reserves with a length of 4 times the average dispersal distance and had a distance of 8 times the average dispersal distance between them to ensure that populations would be self sustiaining and not dependent on other dispersal for other reserves [Lockwood et al., 2002]. Previous work has shown that if MPAs are to benefit fisheries, the reserves should be broken into a network, closely spaced to maximize adult spillover into fishable areas and export of larvae from reserve to reserve [Hastings and Botsford, 2003, Gaylord et al., 2005, Gaines et al., 2010b]. To mimic this management scheme, MPAs had a length of $\frac{1}{3}$ of the average dispersal distance and had a distance of $\frac{2}{3}$ of the average dispersal distance between them.

4 Results

4.1 Interactions Between Stressors We find the critical climate velocity and harvest rate to be inversely related: as the harvesting rate h increases, the critical climate velocity c^* decreases as 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 changing. When the climate velocity or harvesting pressure exceed their critical rates (h^*, c^* respectively), the biomass of the population at equilibrium will be equal to 0. Before those thresholds are reached, the equilibrium biomass of the population decreases as either the harvesting pressure increases or the environmental shifts more

248 quickly (Figure 1). Our simulations confirm the analytical results with the critical speed c^*

249 declining as the critical harvest rate h^* increases and vice versa (Figure 3a).

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

251 increases the critical speed c^* and the critical harvesting rate h^*, since a population that

252 grows more quickly can recover more quickly from losses caused by these disturbances.

253 However, whether or not dispersing farther is better depends on how quickly the

254 environment is shifting (Figure 1). When the environment is shifting slowly, dispersing

255 farther is detrimental since many larvae will disperse too far away from the viable patch.

256 When the environment is shifting quickly, on the other hand, dispersing farther can help

257 the population persist because some larvae will disperse into the space that will become

258 viable shortly in the future. This affects the critical harvesting rate: at a low rate of

259 environmental shift, populations that disperse less can be harvested more severely than

260 those that disperse further, whereas at a high rate of environmental shift, populations that

261 disperse further can be harvested more severely.

262 We found very low levels of positive synergy between the two stressors in our analysis of

263 the Gaussian kernel (Figure 2). Where there is positive synergy, a doubly stressed

264 population loses more biomass than would be predicted from either stressor individually.

265 The stressors interact most strongly when they are both high, shortly before they drive the

266 population extinct. However, the excess loss in biomass is extremely low, making it difficult

267 to distinguish positive synergy from additive interactions. We found similar analytical

268 results for a sinusoidal dispersal kernel, which indicates that this result is robust to changes

269 in the dispersal kernel.

13

4.2 Management strategies Without any management strategies, we found that when the population is harvested more severely, slower rates of environmental shift will suffice to drive the population extinct. However, when thresholds are in place, the critical rate of environmental shift c^* no longer depends on the harvesting rate (Figure 3). In other words, as long as there is some threshold below which harvesting is not allowed, there is a constant critical rate of environmental shift that only depends on the growth rate, length of the viable patch, and average dispersal distance. This is because, with thresholds in place, a small portion of the population always escapes harvesting pressure and only the size, not the growth rate, of this small population depends on the level of threshold implemented. This small population can then track the shifting environment as well as a larger one. 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 can withstand a slightly higher harvesting rate in those parts of the world where harvesting is allowed (Figure 3). More surprisingly, perhaps, implementing MPAs slightly increased the critical rate of environmental shift (Figure 3). Even though MPAs are meant to protect marine populations from harvesting pressure, by providing refuges in which their intrinsic growth rates can increase back to the normal level, MPAs allow marine populations to withstand higher rates of environmental shift.

5 Discussion

Knowing whether two disturbances interact in their impacts for a given population is important for management. The co-occurrence of climate change-driven range shifts and

14

fishing mean that there is the potential for synergistic interactions, which have been largely unexamined. Here we have built a general model to examine how climate and harvesting interact to affect species persistence by incorporating dispersal and reproduction. For each kernel we studied, we found that the higher the growth rate and the better the mean dispersal distance matches the rate of environmental shift, the better a population can adjust to harvest and climate change. More interestingly, we found a negative relationship between the critical harvesting rate and the rate of environmental shift. That is, the more quickly the environment shifts the less harvesting it takes to drive the population extinct. This is an indication of an interaction between the stressors.

To quantify the interaction between the stressors, we measured the synergy between their effects on population biomass. We found positive synergy between the stressors and that the synergy is greatest in the region of parameter space where the equilibrium biomass is smallest. We found similar results from the analytically derived biomass and the simulation derived biomass. This indicates that this result is robust to changes in the dispersal kernel. We chose to measure the effect of each stressor by the absolute drop in biomass caused by the stressor, and we used the sum of the individual effects for our null prediction of the effect 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.

15

The fact that synergy is highest in those populations whose persistence is most tenuous is worrisome from a conservation perspective. This is further evidence that harvesting levels or rate of environment shift that are sustainable individually together can drive a population to extinction. However, the drop in biomass caused by both stressors was never very much higher than the null prediction, i.e. synergistic effects were quite small. Synergy between harvesting and the effects of climate change has been identified in experimental populations [Mora et al., 2007], in specific populations [Planque et al., 2010], and at the ecosystem level [Kirby et al., 2009, Planque et al., 2010]. In the experimental populations, synergy was identified between warming and harvesting but not between habitat fragmentation [Mora et al., 2007]. While we did find (very low levels of) positive synergy, we did not find as much as might be predicted from these empirical studies. However, these previous results are not directly comparable to ours because they focus on different aspects of climate change, e.g. warming temperature [Mora et al., 2007, Kirby et al., 2009] or a more variable climate [Planque et al., 2010], rather than range shifts. Additionally, while we can isolate the affects of climate shift and harvesting in our simple analytical model, there are other forces acting on real populations that may produce the observed synergistic effects.

Our results suggest that particular combinations of harvesting and rate of environmental shift will affect some species more than others. Species with higher intrinsic growth rates will always better track a shifting environment than species with lower intrinsic growth rates. This is in agreement with empirical work which has found that fish which shifted in response to warming in North Sea had faster life histories than non-shifting species (smaller body sizes, faster maturation, smaller sizes at maturity) [Perry et al., 2005]. However, as shown in Figure 1, having a longer average dispersal distance translates into a

340 better ability to track environmental shift only if the environment is shifting quickly.

341 We also examined whether frequently recommended management approaches ensure

342 species persistence. We found increases in the population's biomass at equilibrium and an

343 improved ability to persist. Harvesting thresholds, are already implemented in fisheries

344 management, and we found that this management tactic alleviates interactions between the

345 two stressors by allowing a small portion of the population to escape harvesting pressure

346 and successfully track the shifting environment. Protected areas have been advanced as a

347 way to help organisms keep pace with range shifts, as well as to ameliorate anthropogenic

348 disturbances like harvesting and habitat fragmentation [Lawler et al., 2010, Hannah et al.,

349 2007, Botsford et al., 2001, Gaylord et al., 2005, Hastings and Botsford, 2003, Thomas

350 et al., 2012]. Our results, that spatial management increased the maximum harvesting rate

351 at which the population could survive, support the idea that MPAs could be used to reduce

352 the impact of harvesting. We also found evidence that MPAs increased the climate velocity

353 under which the population could persist. MPAs help populations to persist by providing

354 regions of space in which to grow and recover before being re-subjected to harvesting.

355 While the management strategies only change harvesting practices and do not directly

356 address the effects of climate change, understanding how they ameliorate synergistic affects

357 between harvesting and range shifts will help to better implement harvesting rules and

358 place protected areas. This is encouraging evidence that a single set of of management

359 practices may help to protect marine populations from both harvesting and climate change.

360 The advantage of a simple model like ours is that it is general enough to be applied to a

361 number of systems. However, it ignores many of the complexities present in marine

362 fisheries. First, we could consider additional disturbances, like pollution, disease,

363 physiological response to temperature. However, if the main effect of these disturbances is

17

to increase mortality rates than we would expect that they would interact with climate shift in a way similar to harvesting pressure. We did 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, which has previously been shown to affect a population's resistance to harvesting and climate change [Botsford et al., 2001]. 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. Similarly, we did not include any mechanisms aside from larval dispersal by which the population could keep up with a shifting climate. Besides these species-specific extensions, this modeling framework could be extended to consider species interactions, especially predator-prey pairs. By introducing a predatory species, we would be imposing yet another stressor on the focus species [Ling et al., 2009, Gurevitch et al., 2000] and we are interested in measuring the interaction between the effects of this stressor and the two we consider here.

Using a simple mechanistic model like the one we present here provides a useful framework for understanding when it is or is not necessary to consider the interactions between multiple disturbances and for incorporating additional ecological complexities which can mediate species persistence under those disturbances. Exploring how species interactions, age structure, and additional disturbances affect population viability will improve our predictions and help us to understand whether species will persist under predicted climate and harvesting regimes. Finally, this work can help to make general predictions as to whether specific life histories are likely to be selected over others as harvesting and range shifts increase.

18

Acknowledgements

References

M. Tundi Agardy. Advances in marine conservation: the role of marine protected areas. *Trends in Ecology & Evolution*, 9(7):267–270, 1994. ISSN 0169-5347.

C. H. . H. Ainsworth, J. F. . F. Samhouri, D. S. . S. Busch, W. W. L. Cheung, J. Dunne, and T. A. . A. Okey. Potential impacts of climate change on northeast pacific marine foodwebs and fisheries. *ICES Journal of Marine Science*, 68(6):1217–1229, 7 2011. ISSN 1054-3139. doi: 10.1093/icesjms/fsr043.

Edward H. Allison, Allison L. Perry, Marie-Caroline . C. Badjeck, W. Neil Adger, Katrina Brown, Declan Conway, Ashley S. Halls, Graham M. Pilling, John D. Reynolds, Neil L. Andrew, and Nicholas K. Dulvy. Vulnerability of national economies to the impacts of climate change on fisheries. *Fish and Fisheries*, 10(2):173–196, 6 2009. ISSN 14672960. doi: 10.1111/j.1467-2979.2008.00310.x.

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

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

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

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

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

Louis W. Botsford, Matthew D. Holland, Jameal F. Samhouri, J. Wilson White, and Alan Hastings. Importance of age structure in models of the response of upper trophic levels to fishing and climate change. *ICES Journal of Marine Science: Journal du Conseil*, 68(6): 1270–1283, 2011.

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

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

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

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

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

Nicholas K. Dulvy, Stuart I. Rogers, Simon Jennings, Vanessa Stelzenmller, Stephen R. Dye, and Hein R. Skjoldal. Climate change and deepening of the north sea fish assemblage: a biotic indicator of warming seas. *Journal of Applied Ecology*, 45(4):1029–1039, 8 2008. ISSN 00218901. doi: 10.1111/j.1365-2664.2008.01488.x.

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

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

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

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

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

Brian Gaylord, Steven D. Gaines, David A. Siegel, and Mark H. Carr. Marine reserves exploit population structure and life history in potentially improving fisheries yields. *Ecological Applications*, 15(6):2180–2191, 2005.

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

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

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

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

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

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

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

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

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

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

Jennifer Howard, Eleanora Babij, Roger Griffis, Brian Helmuth, Stewart Allen, Guillermo Auad, Russell Beard, Mary Boatman, Nicholas Bond, Timothy Boyer, David Brown, Patricia Clay, Katherine Crane, Scott Cross, Michael Dalton, Jordan Diamond, Robert Diaz, Quay Dortch, Emmett Duffy, Deborah Fauquier, William Fisher, Michael Graham, Benjamin Halpern, Lara Hansen, Bryan Hayum, Samuel Herrick, Anne Hollowed, David Hutchins, Elizabeth Jewett, Di Jin, Nancy Knowlton, Dawn Kotowicz, Trond Kristiansen, Peter Little, Cary Lopez, Philip Loring, Rick Lumpkin, Amber Mace, Katheryn Mengerink, J. Ru Moorison, Jason Murray, Karma Norman, James O'Donnell, James Overland, Rost Parsons, Neal Pettigrew, Lisa Pfeiffer, Emily Pidgeon, Mark Plummer, Jeffrey Polovina, Josie Quintrell, Teressa Rowles, Jeffrey Runge, Michael Rust, Eric Sanford, Ewe Send, Merrill Singer, Cameron Speir, Diane Stanitski, Carol Thornber, Cara Wilson, and Yan Xue. Oceans and marine resources in a changing climate. Technical report, Oceanography and Marine Biology: An Annual Review, 2013.

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

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

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

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

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

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

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

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

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

Brian R. Mackenzie, Henrik Gislason, Christian Möllmann, and Friedrich W. Köster. Impact of 21st century climate change on the baltic sea fish community and fisheries. *Global Change Biology*, 13(7):1348–1367, 7 2007. ISSN 1354-1013. doi: 10.1111/j.1365-2486. 2007.01369.x.

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

Gorka Merino, Manuel Barange, Christian Mullon, and Lynda Rodwell. Impacts of global environmental change and aquaculture expansion on marine ecosystems. *Global Environmental Change*, 20(4):586–596, 10 2010b. ISSN 09593780. doi: 10.1016/j.gloenvcha.2010. 07.008.

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

Janet A. Nye, Jason S. Link, Jonathan A. Hare, and William J. Overholtz. Changing spatial distribution of fish stocks in relation to climate and population size on the northeast united states continental shelf. *Marine Ecology Progress Series*, 393:111–129, 10 2009. ISSN 0171-8630. doi: 10.3354/meps08220.

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

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

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

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

23

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

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

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

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

Tristan Rouyer, Alexander Sadykov, Jan Ohlberger, and Nils Chr Stenseth. Does increasing mortality change the response of fish populations to environmental fluctuations? *Ecol Lett*, 15(7):658–65, 7 2012. ISSN 1461-0248. doi: 10.1111/j.1461-0248.2012.01781.x.

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

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

Chris D. Thomas, Phillipa K. Gillingham, Richard B. Bradbury, David B. Roy, Barbara J. Anderson, John M. Baxter, Nigel A. D. Bourn, Humphrey Q. P. Crick, Richard A. Findon, Richard Fox, Jenny A. Hodgson, Alison R. Holt, Mike D. Morecroft, Nina J. O'Hanlon, Tom H. Oliver, James W. Pearce-Higgins, Deborah A. Procter, Jeremy A. Thomas, Kevin J. Walker, Clive A. Walmsley, Robert J. Wilson, and Jane K. Hill. Protected areas facilitate species' range expansions. *Proc Natl Acad Sci U S A*, 109(35):14063–8, 8 2012. ISSN 1091-6490. doi: 10.1073/pnas.1210251109.

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

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

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

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

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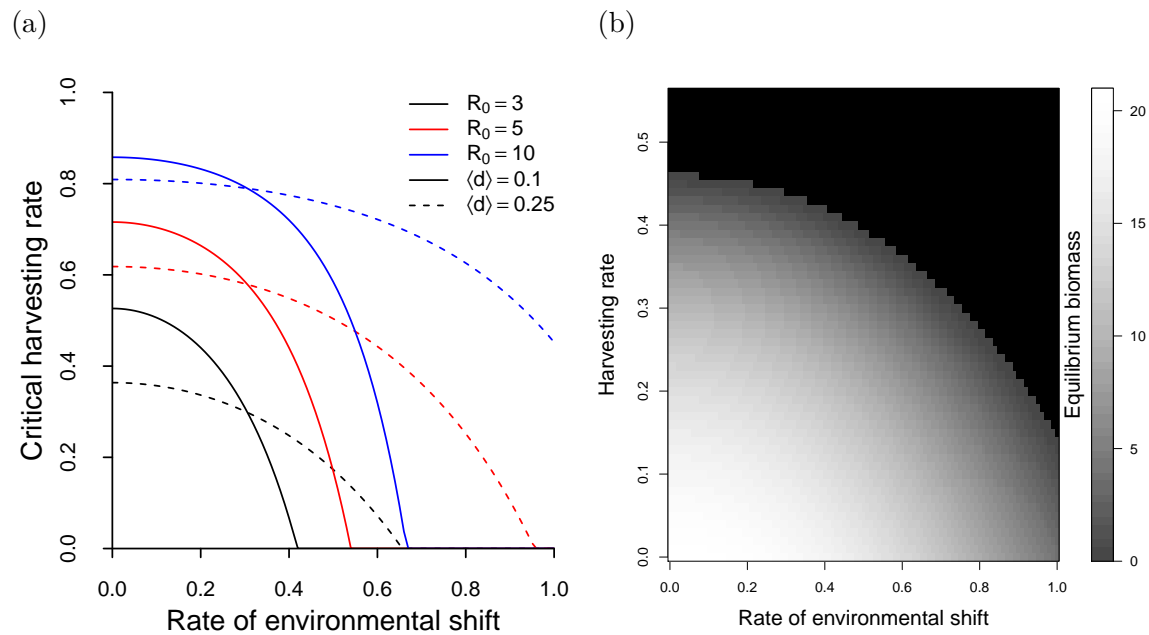
6 Figures

(a)

(b)

Figure 1

Figure 1: (a) The critical harvesting rate on the y-axis as a function of the rate of environmental shift on the x-axis. Black lines correspond to a growth rate of $R_0 = 3$, red to $R_0 = 7$, and blue to $R_0 = 10$. Solid lines correspond to an average dispersal distance $\langle d \rangle = 0.1$ and dashed lines correspond to an average dispersal distance $\langle d \rangle = 0.25$. These results are from an approximated Gaussian dispersal kernel with $L = 1$. (b) The equilibrium biomass of the population as a function of the rate of environmental shift on the x-axis and the harvesting rate on the y-axis. These results are from a Gaussian dispersal kernel with parameters $L = 1$, $R_0 = 5$, $\langle d \rangle = 0.399$.
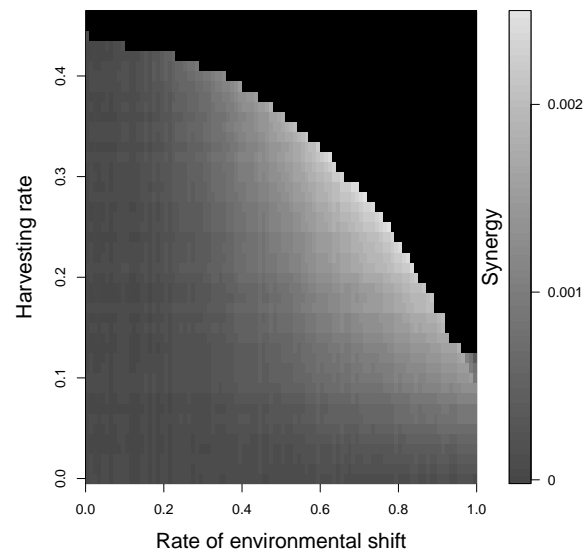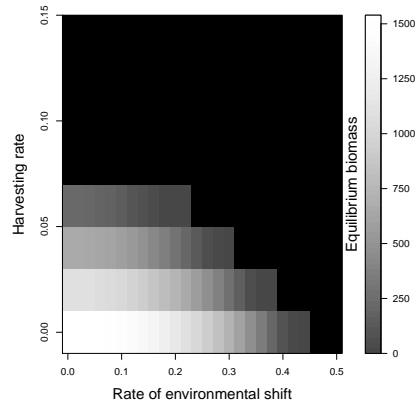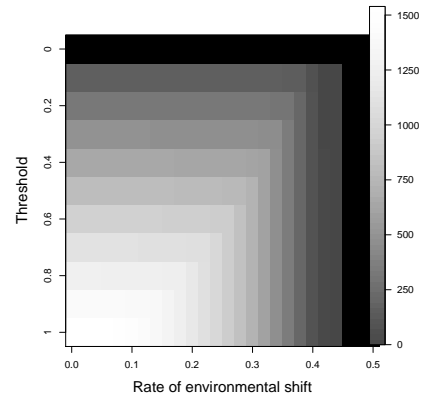
Figure 2

Figure 2: Positive synergy between the two stressors. The x-axis shows the rate of environmental shift, the y-axis shows the harvesting rate, and the color indicates the loss in biomass in the doubly stressed population in excess of the sum of the losses caused by each stressor individually, $E_{\mathrm{hc}} - E_{\mathrm{h}} - E_{\mathrm{c}}$. This excess loss, on the order of .001, is small in comparison to the total biomass, which can be as large as 20. These results are from an approximated Gaussian dispersal kernel with parameters $L = 1$, $R_0 = 5$, $\langle d \rangle = 0.399$.
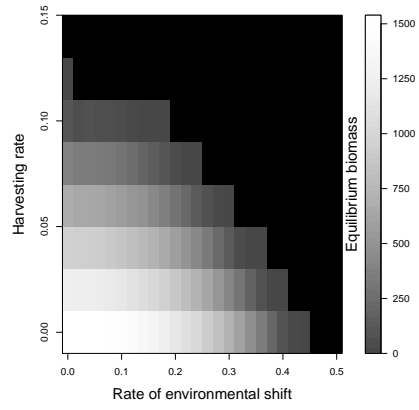
(a)

(b)

(c)

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 $\langle d \rangle = 2$.

7 Tables

Table 1: Table of variables used in the text

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

A   Appendix

In Appendix A.1, we provide the details for assessing the persistence of a population with an integrodifference model and we discuss the effect of the harvesting function on population persistence. In Appendix A.2, we provide the details for assessing population persistence with separable dispersal kernels. In Appendix A.3 and A.4, we derive expressions for the critical harvesting rate and rate of environmental shift for Gaussian and sinuosidal dispersal kernels. In Appendix A.5, we derive approximate expressions for these critical rates.

A.1   Determining stability As in Zhou et al. [Zhou and Kot, 2011], let $k(x - y)$ be a dispersal kernel, let $f(n)$ be a recruitment function, and let $g(n)$ be the harvesting function describing the number of adults harvested from a population of size n. The integrodifference model describing the population over time is given by

$$n_{t+1}(x) = \int_{-L/2+ct}^{L/2+ct} k(x - y) f(n_t(y) - g(n_t(y))) dy. \tag{4}$$

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

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

The integrodifference equation (4) gives us an expression for n^*:

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

$$\Rightarrow n^*(\overline{x}) = \int_{-L/2}^{L/2} k(\overline{x} + c - \overline{y}) f(n^*(\overline{y}) - g(n^*(\overline{y}))) d\overline{y} \tag{5}$$

As long as $f(0) = 0$, there is a trivial solution to this problem where $n^*(\overline{x}) \equiv 0$ for all $\overline{x} \in [-L/2, L/2]$, i.e. there is a trivial traveling pulse with no fish in it. If the trivial traveling pulse is unstable, even very small populations will persist or grow and avoid crashing back to the trivial pulse. To evaluate stability a traveling pulse, we introduce a small perturbation to the traveling pulse $n^*(\overline{x})$ and see if this perturbation grows or shrinks over time:

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

$$\Rightarrow \xi_{t+1}(x) = n_{t+1}(x) - n^*(\overline{x})$$

$$\Rightarrow \xi_{t+1}(x) = \int_{-L/2+ct}^{L/2+ct} k(x - y)\Big(f(n_t(y) - g(n_t(y))) - f(n^*(\overline{y}) - g(n^*(\overline{y})))\Big) dy \text{ using (5)}$$

$$\Rightarrow \xi_{t+1}(x) = \int_{-L/2+ct}^{L/2+ct} k(x - y)(1 - g'(n^*(\overline{y}))) f'(n^*(\overline{y}) - g(n^*(\overline{y}))) \xi_t(y) dy$$

by linearizing around the traveling pulse

$$\Rightarrow \xi_{t+1}(x) = \int_{-L/2+ct}^{L/2+ct} k(x - y)(1 - g'(0)) f'(0) \xi_t(y) dy \text{ if } n^*(\overline{x}) = 0 \tag{6}$$

33

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 the perturbation grows in time if and only if $\lambda > 1$. Using Equation (6), we can rewrite $\xi_t(x)$,

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

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

Define the integral operator

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

Then the perturbation to the traveling pulse will satisfy

$$\psi_f(u)(x) = \lambda u(x) \tag{7}$$

λ and u are thus an eigenvalue and eigenvector of the functional operator ψ_f. The trivial traveling pulse is unstable when the dominant eigenvalue of ψ_f is greater than 1.

The biomass in the equilibrium traveling wave depends on the specific functional form of the harvesting function $g(n)$. However, the persistence of the population only depends on $g'(0)$ so in this paper, we only considered a proportional harvesting function, i.e. the amount of fish harvested obeyed $g(n) = hn$. For this function, $g'(0) = h$.

A.2 Separable dispersal kernels Jentzsch's theorem shows that there is an eigenfunction u, provided that the kernel k satisfies some properties [Zhou and Kot, 2011]. Finding the eigenfunctions and eigenvalues 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

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

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

$$\Rightarrow \lambda d_k = f'(0) \sum_{n=1}^{\infty} A_{nk} d_n \tag{8}$$

where

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

Finding the eigenvalues of (7) then reduces to finding the eigenvalues of the matrix $(A_{nk})_{n,k=1}^{\infty}$.

A.3 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 (8) becomes

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

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

A.4 Sinusoidal dispersal kernel A sinusoidal dispersal kernel is given by

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

663 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 (8) reduces to

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

If we solve for λ, we find

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

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

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

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

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

35

A.5 Approximate critical harvesting proportions

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

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

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

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

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

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

For the sinusoidal kernel we found

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

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,

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

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

For the Gaussian kernel we found

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

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

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

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

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

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

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