Persistence of populations facing climate velocity and harvest

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# Abstract

Many species are expected to shift their geographic distribution as climates change, and yet climate change is only one of a suite of stressors that species face. Species that might, in theory, be able to shift rapidly enough to keep up with climate velocity (the rate and direction that isotherms move across the landscape) may not in actuality be able to do so when facing the cumulative impacts of multiple stressors. However, despite empirical reports of substantial interactions between climate change and other stressors, we often lack a mechanistic understanding of these interactions. Here, we develop and analyze a spatial population dynamics model to explore the cumulative impacts of climate with another dominant stressor in the ocean and on land: fishing or harvest. Our results delineate the conditions under which harvesting and climate velocity can together drive populations extinct even when neither stressor would do so in isolation. We find that critical rates of harvest and climate velocity depend on the growth rate and dispersal kernel of the population, as well as the magnitude of the other stressor. We also find that, in our model, the declines in biomass caused by climate velocity and harvest are at most slightly greater than the sum of the declines caused by either stressor individually (e.g., approximately additive) and that threshold harvest rules and protected areas can be effective management tools to mitigate the interaction between the two stressors.

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

# Introduction

There are many stressors that can disturb an ecosystem, and ecologists have long quantified the consequences of individual perturbations (Wilcove et al. 1998). Less work, however, has been done to measure the effects of multiple stressors and the interactions between them (Travis 2003; Crain et al. 2008; Darling and Côté 2008). If disturbances interact synergistically, a perturbation that has little effect when occurring alone 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 worrying cases, interactions between multiple stressors could drive a population extinct even though assessments of individual impacts would suggest otherwise (e.g., Pelletier et al. 2006; Travis 2003). Because 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 harvesting, two of the largest anthropogenic impacts for both marine and terrestrial species (Milner-Gulland and Bennet 2003; Sekercioglu et al. 2008; Halpern et al. 2008), provide an important example of ecological disturbances occurring in unison. One effect of climate change is that isotherms move across a landscape with a rate and direction referred to as climate velocity (Loarie et al. 2009; Burrows et al. 2011). Marine and terrestrial population distributions shift in response to climate change (Perry et al. 2005; Chen et al. 2011), and there is evidence that climate velocities can successfully explain these shifts (Pinsky et al. 2013).

Many of these shifting species, however, are also subject to harvesting or fishing (Wilcove et al. 1998; Sala 2000; Worm et al. 2009), and there is therefore great potential for interactions between the two stressors. For example, empirical data suggest that Atlantic croaker populations move poleward with warming temperatures, but do so less when heavily fished (Hare et al. 2010). In addition, climate and fishing both appear to have influenced the distribution of North Sea cod over the past century (Engelhard et al. 2014). While not specifically addressing range shifts and harvest together, synergistic interactions between warming temperatures and harvesting have been identified in microcosm experiments (Mora et al. 2007), observations suggest that species follow warming temperatures more effectively in protected areas than in unprotected land (Thomas et al. 2012), and a number of studies conclude that harvest increases the sensitivity of populations to climate variability (Anderson et al. 2008; Botsford et al. 2011; Shelton et al. 2011; Planque et al. 2011). Taken together, this work underscores the importance of understanding in greater mechanistic detail how climate velocity and harvesting interact. Models provide a useful tool in this situation for building our intuition.

A common approach to modeling climate impacts 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 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 dispersal, reproduction, species interaction, and other processes important for population dynamics (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 in models for species distributions under climate change (Berestycki et al. 2009; Zhou and Kot 2011). In these latter models, the region in which a population can survive (e.g., the region of suitable temperatures) is shifting in space, and a population can only survive if it disperses to and grows in newly suitable habitat at a sufficient rate. Related models have been applied to study population persistence in advective environments (Byers and Pringle 2006). However, even these more mechanistic models only address one disturbance: climate-driven range shifts.

Here, we focus on a relatively simple ecological model that captures the dominant processes (reproduction, dispersal, and population growth) underlying climate-driven range shifts and population responses to harvesting pressure. We built this model originally for marine species, but because of its mathematical generality, it could also apply to any species with distinct growth and dispersal stages (e.g., plants, trees, and many insects). We derive the harvesting rate and climate velocity that drive populations extinct, and explore the combined demographic effects of these stressors. We show that the declines in biomass caused by climate-driven range shifts and harvest are at most only slightly greater than the sum of the declines caused by either stressor individually. In other words, the cumulative impacts are approximately additive. Finally, we examine the efficacy of two different types of management strategies: threshold harvesting rules and protected areas. Protected areas are often recommended for conservation of biodiversity and improved yield from harvest (Pimm et al. 2001, Gaines et al. 2010b, Watson et al. 2011), and previous work has suggested protected areas can be a key form of climate insurance that provides stepping-stones to help species keep up with a changing environment (Thomas et al. 2012; Hannah et al. 2007). We find that protected areas can help a species persist with higher harvesting pressure and can increase the maximum climate velocity a harvested species can survive. However, in our model, threshold harvesting rules have a fundamentally different effect and largely remove one of the strongest interactions between harvesting rates and climate velocity.

# Methods

We model the dynamics of populations along a one-dimensional line of longitude, similar to Zhou and Kot (2011). Individuals in the population can only reproduce within a defined segment of the environment (hereafter simply “patch”), which represents the range of thermally suitable conditions for the population. The patch shifts at a fixed rate towards the poles (i.e., at the rate of climate velocity), and offspring disperse away from their parents according to a dispersal kernel. In its basic form, harvest removes a constant fraction of the local population density from each point along the coastline.

To investigate the model, we first analytically determine the combinations of harvesting rate and climate velocity that drive the population extinct (hereafter the critical harvesting rate and critical climate velocity), and then measure their interaction by calculating the decrease in biomass caused by the stressors both individually and together. We then add threshold harvesting rules and protected areas in numerical simulations to determine how these management strategies affect population persistence and biomass.

### The Model

The above verbal description is represented well by integrodifference models, which have been used extensively for spatial population dynamics problems with discrete time (e.g., discrete growth and dispersal stages) and continuous space (Kot and Schaffer 1996; Van Kirk and Lewis 1997; Lockwood et al. 2002; Zhou and Kot 2010). More specifically, if is the number of individuals settling after dispersal at position and time , then the number of individuals in the next generation is given by

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|  | (1) |

where is a recruitment function describing the number of offspring that settle and survive in juvenile population of size , is a function describing the number of adults that remain after harvesting given local density , is the intrinsic growth rate of the population (e.g., number of offspring per adult), , is a dispersal kernel giving the probability of an offspring traveling from position to position . The model integrates over all reproduction that occurs within the suitable thermal habitat patch, where is the length of the patch and is the rate at which the patch shifts across space (the rate of climate velocity). In other words, the center of the patch at time will be at location , and so the upper and lower bounds of the patch will be found at and .

Initially, we use as our harvesting function, where *h* is the proportion of the population harvested. This model envisions that harvest removes a constant fraction from each location *x*, as could be expected from even distribution of harvesters across space.

We also used a Beverton-Holt stock-recruitment function to describe the settlement and survival of offspring after accounting for density dependent competition and mortality:

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|  | (2) |

As before, is the intrinsic growth rate, while is the carrying capacity at a given point in space, which we assume to be constant (see Table 1 for a full description of parameters and functions). As shown in Appendix A.1, the precise forms of *g(n)* and *f(n)* are not important to the persistence of the population, which instead depends only on and . The full functional forms, however, are important for equilibrium population levels.

Analyzing this kind of model becomes easier if the dispersal kernel is separable into its dependence on sources and destinations of larvae, that is if there are functions such that (see Appendix A.2 for further details). In the analyses presented below, we used a Gaussian kernel (Latore et al. 1998) given by

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To derive analytical expressions for the critical rates of harvesting and climate velocity, we approximate the kernel to its first-order terms, as described in Appendix A.3. Further, to examine the sensitivity of the model to the shape of the kernel, we also analyze a sinusoidal kernel (see Appendix A.4).

At demographic equilibrium, the population will move in a traveling wave, where the population density at a given point in space will change, but the density at a location relative to the shifting patch will not (Zhou and Kot 2011). The traveling wave must satisfy

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where describes the position within the patch. For a separable kernel, the equilibrium traveling pulse must satisfy

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|  | (5) |

where the satisfy the recursive equations

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|  | (6) |

(Latore et al. 1998). We show the derivation of these equations in Appendix A.2.

## Persistence

At low harvesting rates and low climate velocities , marine populations will persist. However, above certain critical values, populations will be driven extinct. When the population is extinct, the system is in its trivial equilibrium; for all , which satisfies Equation 4. If a population is to persist, 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, where the introduction of a small population will grow rather than return to extinction. The critical parameters and are defined as the parameters that make the trivial pulse unstable. See Appendix A.1 for further details of this analytical calculation.

Regardless of the functional form of the recruitment function , its only property that determines whether or not a population can persist is how quickly recruitment increases when the population size is near (but above) . For us, this number is , so any recruitment function with the same value will give the same results with respect to persistence. 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

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|  | (7) |

We derive a similar expression for a sinusoidal kernel in the Appendix A.4. We realize that this formula is not straightforward to understand. For both Gaussian and sinusoidal kernels, however, we can approximate the critical harvesting proportion by a function that looks like

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|  | (8) |

where is a decreasing function of the length of the viable patch and the intrinsic growth rate, and describes how *h\** increases with patch length (*L*) and varies with expected dispersal distance and climate velocity (see Appendix A.5 for details).

## Calculating the interaction of climate velocity and harvest

In order to quantify how harvesting interacts with climate velocity, we find the total biomass of the population when it reaches an equilibrium traveling pulse and compare this equilibrium biomass in the presence and absence of each stressor individually or the two stressors together. Equations 5 and 6 allow us to numerically find the total biomass in the equilibrium traveling pulse under each of these conditions.

We use 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 calculate the decline in biomass caused by stressor as

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|  | (9) |

Based upon this definition, there are three kinds of interaction types that can be defined. If the interaction is purely additive, then the cumulative response to both stressors together would be *Ehc* = *Eh* + *Ec*. If the stressors instead interact synergistically, then *Ehc* > *Eh* + *Ec*. In contrast, the stressors would interact antagonistically if *Ehc* < *Eh* + *Ec*.

We can quantify the degree of synergy as

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where positive *S* indicates synergy, negative *S* indicates antagonism, and *S* of zero indicates purely additive interactions. This is a common way to measure the interaction among stressors, though alternative approaches can use the ratio of affected to unaffected biomass as a measure of effect size (multiplicative model) or consider the effect of the single worst stressor (simple comparative effects model) (Folt et al. 2012; Crain et al. 2008). The additive model is the most conservative when quantifying negative effects, as we do here, meaning that it is less likely to identify synergistic interactions (Folt et al. 2012; Crain et al. 2008).

## Simulations

We use simulations to implement two management strategies (threshold harvesting rules and protected areas) that make our basic integrodifference model analytically intractable. Under threshold harvesting, harvesting pressure was no longer implemented as a proportional removal from the population. Instead, we evaluate the abundance at each point in space to determine how much harvesting should occur. If the population abundance is below the designated threshold, no harvesting occurrs. If the population exceeded the threshold, then we harvest all the ‘surplus’ individuals. This approach is an extreme version of the harvest control rules proposed for many existing fisheries (Froese et al. 2011).

In addition, we introduce networks of protected areas into our simulations by designating segments of space where the harvesting rate was equal to 0. Protected areas, particularly in the ocean, are typically designed to meet either harvest management or conservation goals (Agardy 1994; Holland and Brazee 1996; Gaines et al. 2010a), thus their spacing and size differ. Harvest-oriented protected areas are often designed such that they maximize adult spillover into harvestable areas by creating many small reserves closely spaced (Hastings and Botsford 2003; Gaylord et al. 2005; Gaines et al. 2010a). To mimic this management scheme, we implemented protected areas with a length of the average dispersal distance and an inter-reserve spacing of the average dispersal distance. Conservation-oriented protected areas seek to protect entire ecosystems and reduce adult spillover by creating fewer, larger protected areas (Toonen et al. 2013). To mimic this scheme, we implement protected areas with a length times the average dispersal distance and an inter-reserve spacing times the average dispersal distance between them (Lockwood et al. 2002). In both harvest-oriented and conservation-oriented protected area networks, 1/3 of the coastline is protected. With protected areas present we either assume that harvesting is proportional in areas between reserves or that harvesting pressure remains constant, and is shifted to available, unprotected habitat.

For every simulation, we seed the model with 50 individuals at a single location and iterate for 2000 generations to reach equilibrium without harvesting or climate shift (more than sufficient based on initial tests). We then add harvesting pressure, allow the population to again reach equilibrium (2000 generations), and finally add a changing climate by moving the viable patch with a certain velocity. After 6000 generations we calculate equilibrium biomass as the mean biomass of 2000 additional generations. Implementing protected areas makes the population abundance cycle, averaging over 2000 generations is sufficient to erase effects of periodicity in results. If population abundance declines below 0.001, the population is considered extinct (i.e. abundance is 0). For all simulations, we use a Laplace dispersal kernel, , which is a commonly used model of marine larval dispersal (Botsford et al. 2001) that, however, is not amenable to the analytical methods we use above.

# Results

## Persistence with Harvesting and Climate Velocity

We begin by examining the critical rates of harvesting and climate velocity, i.e., those rates sufficient to drive a population extinct. As would be expected, we find that the critical rate of each stressor is lower if a population faces higher intensities of the other stressor (downward curving lines in Fig. 1a). For example, a harvesting rate that is sustainable in the absence of environmental shift (*c* near zero) may no longer be sustainable if the environment begins to change rapidly (*c* >> zero).

We also examine the sensitivity of critical rates to growth and dispersal. In our model, it is always the case that increasing the intrinsic growth rate (), all else being equal, will increase 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 stressors (compare lines with different shading in Fig. 1a). However, whether or not dispersing farther is better depends on how quickly the environment is shifting (compare solid and dashed lines in Fig. 1a). When the environment is shifting slowly, populations with wider dispersal kernels have a lower critical harvesting rate because dispersing farther results in too many larvae dispersing off the viable patch. When the environment is shifting quickly, on the other hand, populations with wider dispersal kernels can better withstand harvesting because larvae dispersing long distances more effectively colonize the habitat patch that will be viable in the next generation.

**Interactions Between Stressors**

It is also important to ask how a population responds to moderate cumulative impacts that are insufficient to drive it extinct. Whenever climate velocity or harvesting pressure exceeds their critical rate, the biomass of the population at equilibrium will be equal to (the definition of the critical rate). Before the stressors reach those thresholds, however, the equilibrium biomass of the population decreases smoothly as either the harvesting pressure or the rate of environmental shift increases (Figure 1b).

When we compare the cumulative impacts of the stressors to the sum of each stressor individually we find low levels of positive synergy between the two stressors (Fig. 2). The stressors display a synergistic interaction most strongly at high harvest and climate velocity rates, close to where they would drive the population extinct. As a note, positive synergy indicates that cumulative impacts cause the population to lose more biomass than we would predict from either stressor individually. However, the degree of synergy is low and concentrated in a limited part of parameter space. Throughout much of the range of harvest rates and climate velocities, the interaction between the stressors is quite close to an additive model. Results are robust to changes from a Gaussian to a sinusoidal dispersal kernel.

## Alternative management strategies

Under a constant harvest rate, we find that harvest rate and climate velocity interact such that more heavily harvested populations go extinct with slower climate velocities. However, with harvest thresholds in place, a small population can always escape harvesting and the critical climate velocity no longer depends on the harvesting rate (Figure 3b). In other words, as long as there is some threshold population density below which harvesting is not allowed, critical climate velocity in our model only depends on the growth rate, length of the viable patch, and average dispersal distance. In this case, the interaction follows a simple comparative model, such that the cumulative impacts of the two stressors are equal to the individual effect of the worst stressor.

With either type of protected area strategies in effect (many small versus few large), the population withstands combinations of higher climate velocities and higher harvesting rates than without the protected areas (compare Figures 3c and d to Figure 3a). However, there are also some differences between the large and the small protected area strategies. At lower climate velocities, protected areas spaced more than one average dispersal distance apart result in larger fluctuations of population biomass relative to small, closely spaced protected areas (Appendix A.6, Figure S1). Minimum population biomass is higher in simulations with smaller protected areas, potentially providing a larger buffer against extinction relative to simulations with larger but more widely spaced protected areas.

# Discussion

Climate change and harvest are two of the dominant human impacts on marine species and many terrestrial species, but our understanding for their joint effects and interactions remains limited. By analyzing a general model that incorporates dispersal and reproduction, we show that climate velocity and harvesting interact strongly in their effects on species persistence and biomass. In particular, we find that the critical harvesting rate decreases as climate velocity increases. In other words, the more quickly the environment shifts, the less harvesting it takes to drive the population extinct. The interaction between climate velocity and harvesting are additive for most combinations of stressor levels, with weak synergy only appearing close to population extinction. However, harvesting rules that avoid harvest from low-density parts of the population, such as the leading edge, change the interaction substantially. In the latter case, the population only decreases by an amount equal to the effect of the single worst stressor (whether climate velocity or harvest).

Our results suggest that particular combinations of harvesting and climate velocity will affect certain species more than others. Species with a higher intrinsic population growth rate (i.e., growth rate at low abundance) and a longer average dispersal distance will better track rapid climate velocities, as compared to species with a low intrinsic population growth rate and short dispersal distances. This finding matches previous expectations: higher growth rates make a population more resistant to the removals from harvesting or the losses associated with tracking climate velocity. It is worth pointing out that a higher population growth rates can be generated either by shorter generation times or higher fecundity. Empirical work also suggests that marine fish and invertebrates with faster life histories, as well as terrestrial birds and plants with greater dispersal abilities, shifted their distributions more quickly in response to warming (Perry et al. 2005; Angert et al. 2011; Pinsky et al. 2013).

While higher reproductive rates improve a population’s ability to persist in our model, higher dispersal distances did not necessarily do so. In agreement with related results from Zhou and Kot (2011), we found that at low speeds, a short dispersal distance improved the maximum harvesting rate a population could sustain, while at higher speeds a longer dispersal distance improved the maximum climate velocity under which the population could persist. It appears that climate velocity could selectively favor species with dispersal distances best matched to the rate of shift.

One goal of our model is to examine the cumulative impacts of multiple stressors. We find that the interaction between harvest and climate velocity is effectively additive, with weak synergistic effects appearing primarily when the population is close to extinction. This result from our model would appear to contrast with other demonstrations of synergy between harvest and climate in the literature. For example, a number of modeling and empirical studies have found that fishing increases the sensitivity of populations to climate variability (including Anderson et al. 2008; Shelton et al. 2011; Botsford et al. 2011), and a recent review reaches the same conclusion (Planque et al. 2010). Positive feedback loops involving the loss of predators due to fishing have also been identified that amplify climate impacts on prey species (Kirby et al. 2009; Planque et al. 2010; Ling et al. 2009). Similarly, synergy between harvesting and temperature was detected in experimental populations of rotifers (Mora et al. 2007).

A partial explanation for the differences between our model results and the previous evidence for synergy may be that we analyze the ability of populations to keep pace with climate velocity, while many previous studies examined other aspects of changing climate. In the rotifer experiment, for example, populations were subjected to warming temperatures, but organisms were unable to relocate to thermal optima (Mora et al. 2007). In many other fishing and climate studies, the impacts of climate variability on stationary populations have been the focus, rather than cumulative climate change or shifting distributions (Walters and Parma 1996; Anderson et al. 2008; Shelton et al. 2011; Botsford et al. 2011; Planque et al. 2010). Work which does incorporate shifting species distributions typically examines regional or global scenarios for climate change, making it difficult to isolate the effect that different species interactions, climate and harvesting each play (Cheung et al. 2010).

Another explanation for the discrepancy may be that the only effect of harvesting in our model is a reduction in the size of the adult biomass. In reality, populations often contain a diversity of subpopulations, ages, and genotypes that can buffer them against climate variability and climate change (Schindler et al. 2010). Harvest tends to simplify this diversity within populations, making them more sensitive to climate variability (Mora et al. 2007; Planque et al. 2010). Our model also did not include food web dynamics or species interactions and yet some positive feedback loops and synergistic interactions identified between climate and harvesting in previous studies involved the loss of predators and the release of prey (Kirby et al. 2009; Ling et al. 2009). Our simple, single-species, non-age-structured model suggests that additive interactions between climate velocity and harvesting are a reasonable baseline or “null” expectation in the absence of more complicated mechanisms. Future work considering food web processes and genetic, spatial, and age diversity will be important to examine other possible sources of synergistic (or antagonistic) interactions between harvesting and climate velocity.

We also examine whether two frequently recommended management approaches, protected areas and harvest control rules, could help ensure species persistence in the face of multiple stressors. With either of these management strategies, we generally find increases in the population’s biomass at equilibrium and an improved ability to persist. Threshold harvesting rules in particular appear to fundamentally alter much of the interaction between the two stressors. In our model, thresholds appear to have this effect because they effectively prevent harvesting of the leading edge and allow colonization to occur as if these individuals were moving into un-harvested areas. This result matches well with invasion theory, which has shown that populations move into new territory at a rate approximately equal to , where *l* is the mean squared displacement of individuals per unit time (Hastings et al. 2005). With a constant harvest rate applied everywhere, the invasion rate drops to , whereas the invasion rate is unaffected if harvesting avoids the leading edge. It’s interesting to note that novel, low abundance stocks are commonly unregulated in fisheries systems (Beddington et al. 2007; Dowling et al. 2008). Whether fisheries and other harvesting activities rapidly exploit newly colonizing species depends in part on the interaction of social, economic, and regulatory factors (Pinsky and Fogarty 2012). Our work, however, highlights the fact that a low (or zero) harvest rate on species that have recently colonized new habitats can be important for helping them keep up with rapid climate velocities.

Unlike thresholds, protected areas are spatially explicit. 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 et al. 2001; Gaylord et al. 2005; Hastings and Botsford 2003; Thomas et al. 2012, Watson et al. 2011). Our results show that protected areas increase the equilibrium biomass of harvested populations at a given climate velocity, which supports their use as a tool to help these populations withstand the effects of climate velocity. However, the details of protected area design affect our results: few, large protected areas increase population fluctuations at low climate velocities, while many smaller protected areas maintain a population bounded farther from extinction. This effect appears because large gaps separate our large protected areas, which allows harvest to drive populations to lower levels while between protected areas. In contrast, populations were less fully exposed to harvesting while traversing the smaller gaps between small protected areas. While the discussion of many small vs. few large protected areas involves many factors (Gaines et al. 2010b; McCarthy et al. 2011), our results contribute to this body of work by showing that small gaps between protected areas, even if counter-balanced by small protected areas, may help species keep up with climate velocities in the face of harvest.

The advantage of a simple model like ours is that it is potentially general enough to apply to a wide range of species. Our discrete-time, continuous-space model captures the processes important to species with distinct growth and dispersal stages, including most marine organisms, plants, trees, and many insects. Our approach does not capture all the complexities of real populations or of harvesting dynamics, however. For example, we do not include the potential for negative per capita growth at low densities, often called Allee or depensation effects. Invasion theory suggests that Allee effects generally have two impacts: they slow initial rates of spread, and they allow predation to, in some cases, slow or stop an invasion (Hastings et al. 2005). Based on first principles, we would expect similar effects in a model like ours, suggesting that populations with Allee effects will be more sensitive to the combined effects of harvest and climate velocity than our model initially suggests. We also did not include age structure or other aspects of sub-population diversity (e.g., spatial or genetic) in our model. As described above, these forms of diversity have been important for studying the joint effects of harvesting and climate variability (Botsford et al. 2011; Planque et al. 2010), and will likely be important for understanding climate velocity impacts as well. Besides these species-specific extensions, this modeling framework could also be extended to consider species interactions, such as between predator and prey (Gilman et al. 2010). A final important extension is better capturing harvesting dynamics. We find that the distribution of harvesting pressure affects the outcomes of our simple model (i.e. thresholds, versus proportional harvesting). Harvester behavior, to the extent it has been considered in fisheries, highlights considerable uncertainty in how vessels allocate effort over space and respond to changes in environmental conditions (Fulton et al. 2011, Van Putten et al. 2011, Pinsky and Fogarty 2012). These responses are a rarely integrated into modeling efforts, and an important next step is integrated assessments of social-ecological systems.

Using a simple, mechanistic model like the one we present here helps 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. It also shows the importance of alternative management strategies, as the location of harvest greatly affects the interaction between harvesting and climate. While management strategies only change harvesting practices and do not directly address climate change, understanding how management approaches can affect interactions between harvesting and range shifts will help to improve harvesting rules and the development of protected areas. Our results are encouraging evidence 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

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| --- | --- |
| Variable | Definition |
|  | density of individuals at position at time |
|  | density of individuals at equilibrium at position relative to the patch |
|  | dispersal kernel, the probability of offspring traveling from position to position |
|  | expected distance traveled by an offspring |
|  | recruitment function, the number of offspring produced by a population of size |
|  | intrinsic growth rate of the population at low abundance |
|  | harvest function, the number of adults remaining after a population of size *n* has been harvested |
|  | proportion of adults harvested, when |
|  | patch length |
|  | climate velocity in units of distance per time |

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# Figure Legends

Figure 1: (a) Lines indicate the critical threshold for persistence as a function of harvesting rate on the y-axis and climate velocity on the x-axis. Shade of grey corresponds to the growth rate from smallest to greatest (light to dark). Line style indicates the average dispersal distance (solid: vs. dashed: ) from an approximated Gaussian dispersal kernel (Eq. 3). Patch length . (b) The equilibrium biomass of the population as a function of the climate velocity on the x-axis and the proportional harvesting rate on the y-axis. Results are from an approximated Gaussian dispersal kernel with parameters , , and .

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 excess loss, on the order of , is small in comparison to the total biomass, which can be as large as . These results are from calculations with the same parameters as Fig. 1b.

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 alternative management strategies. (a) The equilibrium biomass for simulations with constant harvest rates (compare to figure 1b). (b) Equilibrium biomass for simulations with threshold management. For threshold management, the maximum threshold is set to be the largest population size observed at a given time step before harvesting. The y-axis is the proportion of the maximum threshold that is protected from harvesting. (c) Equilibrium biomass for simulations with many small protected areas. (d) Equilibrium biomass for simulations with few large protected areas. These results are from a simulation with a Laplacian dispersal kernel with parameters , , , and .

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Figure 1

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Figure 2

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Figure 3