

1 **The persistence of populations facing climate shifts and**
2 **harvest**

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10 **Abstract**

11 Many species are expected to shift their geographic distribution as climates change, and yet
12 climate change is only one of a suite of stressors that species face. Species that might, in theory,
13 be able to shift rapidly enough to keep up with climate velocity (the rate and direction that
14 isotherms move across the landscape) may not in actuality be able to do so when facing the
15 cumulative impacts of multiple stressors. Despite empirical reports of substantial interactions
16 between climate change and other stressors, we often lack a mechanistic understanding of these
17 interactions. Here, we develop and analyze a spatial population dynamics model to explore the
18 cumulative impacts of climate with another dominant stressor in the ocean and on land: harvest.
19 We find that critical rates of climate velocity and harvest depend on the growth rate and dispersal
20 kernel of the population, as well as the magnitude of the other stressor. This allows us to identify
21 conditions under which harvesting and climate velocity can together drive populations extinct
22 even when neither stressor would do so in isolation. Except in these extreme cases, we also find
23 that the interaction between the declines in biomass caused by climate velocity and harvest is
24 approximately additive. Finally, we show that threshold harvest rules can be effective
25 management tools to mitigate the interaction between the two stressors, while protected areas can
26 either help or hinder, depending on how harvesters reallocate their effort.

27 **Keywords:** Climate change, fishing, integrodifference model, synergy, multiple disturbances,
28 cumulative impacts, climate velocity

29 **Introduction**

30 There are many stressors that can disturb an ecosystem. Ecologists have been working for
31 decades to quantify the consequences of individual perturbations (Wilcove et al. 1998) and to
32 measure the effects of multiple stressors and the interactions between them (Travis 2003; Crain
33 et al. 2008; Darling and Côté 2008). If disturbances interact synergistically, a perturbation that
34 has little effect when occurring alone may amplify the disturbance caused by a coincident
35 perturbation (Crain et al. 2008; Darling and Côté 2008; Nye et al. 2013; Gurevitch et al. 2000).

36 In the most worrying cases, interactions among multiple stressors could drive a population
37 extinct, even though assessments of the individual impacts would not predict extinction (e.g.,
38 Pelletier et al. 2006; Travis 2003). Because disturbances rarely occur in isolation, measuring the
39 effects of multiple disturbances provides a better understanding of likely impacts to an
40 ecosystem (Doak and Morris 2010; Fordham et al. 2013; Folt et al. 1999).

41 Climate change and harvesting, two of the largest anthropogenic impacts for both marine and
42 terrestrial species (Milner-Gulland and Bennet 2003; Sekercioglu et al. 2008; Halpern et al.
43 2008), provide an important example of two concurrent ecological disturbances. One effect of
44 climate change is that isotherms—contour lines connecting places with the same temperature—
45 move across a landscape with a rate and direction referred to as climate velocity (Loarie et al.
46 2009; Burrows et al. 2011). Marine and terrestrial population distributions shift in response to
47 climate change (Perry et al. 2005; Chen et al. 2011), and there is evidence that climate velocities
48 can successfully explain these shifts (Pinsky et al. 2013).

49 Many of these shifting species are also subject to harvesting or fishing (Wilcove et al. 1998; Sala
50 2000; Worm et al. 2009), so interactions between the two stressors are possible. For example,

51 empirical data suggest that Atlantic croaker populations move poleward with warming
52 temperatures, but do so less when heavily fished (Hare et al. 2010); several terrestrial species
53 follow warming temperatures more effectively in protected areas than in unprotected areas
54 (Thomas et al. 2012); and a number of studies concluded that harvest increases the sensitivity of
55 populations to climate variability (Anderson et al. 2008; Botsford et al. 2011; Shelton et al. 2011;
56 Planque et al. 2011). While not specifically addressing range shifts and harvest together, there
57 have been experimental indications of synergistic interactions between warming temperatures
58 and harvesting (Mora et al. 2007). Taken together, this work underscores the importance of
59 understanding in greater mechanistic detail how climate velocity and harvesting interact. Models
60 provide a useful tool for building our intuition about this interaction.

61 A common approach to modeling climate impacts has been to use bioclimatic-envelope models
62 (also known as species distribution models). These statistical models typically correlate
63 presence-absence or abundance data with biophysical characteristics to predict how species'
64 ranges will differ under climate change (Elith et al. 2006; Guisan and Thuiller 2005; Guisan and
65 Zimmermann 2000). Despite these models' widespread adoption, many authors have criticized
66 bioclimatic-envelope models as oversimplified because they lack dispersal, reproduction, species
67 interactions, and other processes important for population dynamics (Kearney and Porter 2009;
68 Zarnetske et al. 2012; Robinson et al. 2011).

69 Recent work on range shifts has addressed some of these gaps by explicitly including dispersal
70 and reproduction in models of species distributions under climate change (Berestycki et al. 2009;
71 Zhou and Kot 2011). In these models, the region in which a population can survive (e.g., the
72 region of suitable temperatures) is shifting in space, and a population can only survive if it
73 disperses to and grows in newly suitable habitat at a sufficient rate. Related models have been

74 applied to study population persistence in advective environments (Byers and Pringle 2006).

75 However, even these more mechanistic models only address one disturbance: climate-driven
76 range shifts.

77 Here, we focus on a relatively simple ecological model that captures the dominant processes
78 (reproduction, dispersal, and population growth) underlying climate-driven range shifts and
79 population responses to harvesting pressure. We built this model originally for marine species,
80 but because of its mathematical generality, it could also apply to any species with distinct growth
81 and dispersal stages (e.g., plants, trees, and many insects). We identify the harvesting rate and
82 climate velocity that drive populations extinct, investigate how the critical rate of one stressor
83 depends on the other, and analyze the declines in biomass caused by each stressor. We also
84 examine two different types of management strategies—threshold harvesting rules and protected
85 areas—to determine how these management strategies affect population persistence and biomass.
86 We chose to model protected areas because they are often recommended for conservation of
87 biodiversity and improved yield from harvest (Pimm et al. 2001, Gaines et al. 2010b, Watson et
88 al. 2011), and previous work has suggested protected areas can be a key form of climate
89 insurance that provides stepping stones to help species keep up with a changing environment
90 (Thomas et al. 2012; Hannah et al. 2007). Finally, we demonstrate how to apply this model by
91 using parameters describing black rockfish (*Sebastodes melanops*) in California (White et al. 2010;
92 Gaines et al. 2010a).

93 **Methods**

94 **The Model**

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

102 The above verbal description is represented well by integrodifference models, which have been
103 used extensively for spatial population dynamics problems with discrete time (e.g., discrete
104 growth and dispersal stages) and continuous space (Kot and Schaffer 1996; Van Kirk and Lewis
105 1997; Lockwood et al. 2002; Zhou and Kot 2010). More specifically, if $n_t(x)$ is the number of
106 individuals settling after dispersal at position x and time t , then the number of individuals in the
107 next generation is given by

$$n_{t+1}(x) = \int_{-\frac{L}{2}+ct}^{\frac{L}{2}+ct} k(x-y)R_0g(f(n_t(y))) dy, \quad (1)$$

108 where $f(n)$ is a recruitment function describing the number of juveniles that settle and survive to
109 adulthood given that the juvenile population is of size n , $g(n)$ is a function describing the
110 number of adults that remain after harvesting given local density n , R_0 is the intrinsic growth rate
111 of the population (i.e., number of offspring per adult), and $k(x-y)$, is a dispersal kernel giving

112 the probability of an offspring traveling from position y to position x . Reproduction only occurs
113 within the suitable patch of length L , which shifts across space at a clime velocity c . In other
114 words, the center of the patch at time t will be at location ct , and the upper and lower bounds of
115 the patch will be found at $ct + L/2$ and $ct - L/2$, respectively.

116 Initially, we use $g(n) = n - hn$ as our function for those surviving harvesting, where h is the
117 proportion of the population harvested. This assumes that harvest removes a constant fraction
118 from each location x , as might be expected from an even distribution of harvesters across space.

119 We used a Beverton-Holt stock-recruitment function to describe the settlement and survival of
120 offspring $f(n)$ while accounting for density dependent competition and mortality:

$$f(n) = \frac{n}{1 + \left(\frac{R_0 - 1}{K}\right)n} \quad (2)$$

121 As before, R_0 is the intrinsic growth rate, while K is the carrying capacity at a given point in
122 space, which we assume to be constant (see Table 1 for a full description of parameters and
123 functions). Since $f(K) = \frac{K}{R_0}$, if $n = K$, there will be $\frac{K}{R_0}$ surviving offspring, and when they
124 reproduce at rate R_0 the population will remain at carrying capacity. As shown in Appendix A.1,
125 the precise forms of $g(n)$ and $f(n)$ are not important to the persistence of the population.
126 Persistence depends only on $g'(0)$ and $f'(0)$. The full functional forms do matter, however, for
127 equilibrium biomass.

128 Analyzing this kind of model becomes easier if the dispersal kernel is separable into its
129 dependence on sources and destinations of larvae, that is, if there are functions a_i, b_i such that

130 $k(x - y) = \sum_{i=1}^{\infty} a_i(x)b_i(y)$ (see Appendix A.2 for further details). In the analyses presented
 131 below, we used a Gaussian kernel (Latore et al. 1998) given by

$$k(x - y) = \frac{1}{2\sqrt{D\pi}} e^{\frac{-(x-y)^2}{4D}}. \quad (3)$$

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

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

$$n^*(\bar{x}) = \int_{-\frac{L}{2}}^{\frac{L}{2}} k(\bar{x} + c - \bar{y})R_0(1 - h)f(n^*(\bar{y}))d\bar{y}, \quad (4)$$

139 where $\bar{x}, \bar{y} \in [-\frac{L}{2}, \frac{L}{2}]$ describes the position within the patch. For a separable kernel, the
 140 equilibrium traveling pulse $n^*(x)$ must satisfy

$$n^*(x) = \sum_{i=1}^{\infty} a_i(x) \int_{-\frac{L}{2}}^{\frac{L}{2}} b_i(y - c)R_0(1 - h)f(n^*(y))dy = \sum_{i=1}^{\infty} m_i a_i(x), \quad (5)$$

141 where the m_i satisfy the equations

$$m_i = \int_{-\frac{L}{2}}^{\frac{L}{2}} b_i(y - c)R_0(1 - h)f\left(\sum_{j=1}^{\infty} m_j a_j(y)\right)dy \quad (6)$$

142 (Latore et al. 1998). We show the derivation of these equations in Appendix A.2. While there are
143 certainly interesting transient dynamics as the population reaches its equilibrium traveling wave,
144 we focus on equilibrium biomass to make results from different dispersal kernels, parameters,
145 and methods of analysis directly comparable, without the confounding effects of initial
146 conditions and rates of approach to equilibrium.

147 Calculating Persistence

148 At low harvesting rates h and low climate velocities c , populations will persist. However, above
149 certain critical values, populations will be driven extinct. When the population is extinct, the
150 system is in its trivial equilibrium: $n^*(\bar{x}) = 0$ for all $x \in \left[-\frac{L}{2}, \frac{L}{2}\right]$, which satisfies Equation 4. If a
151 population is to persist, it must be able to avoid extinction and grow even when small (Zhou and
152 Kot 2011). Population persistence is therefore equivalent to the trivial traveling pulse being an
153 unstable equilibrium, where the introduction of a small population will grow rather than return to
154 extinction. The critical parameters h^* and c^* are defined as the parameters that make the trivial
155 pulse unstable. See Appendix A.1 for further details of this analytical calculation.

156 Regardless of the functional form of the recruitment function f , the only property that
157 determines whether or not a population can persist is how quickly recruitment increases when the
158 population size is near (but above) 0. For us, this number is 1, and any recruitment function with
159 the same value will give the same results with respect to persistence. In addition to this property,
160 the population's ability to persist depends on properties of the population itself (the shape of the
161 dispersal kernel, and the expected distance a larva disperses $\langle d \rangle$), properties of the environment
162 (the length of the viable patch L and how quickly the environment shifts c), and the harvesting
163 rate h . For a Gaussian kernel, the critical rates c^* and h^* are those values of c and h such that

$$R_0(1-h)2\sqrt{2}\exp\left(\frac{-c^2}{8D}\right)\left[\operatorname{erf}\left(\frac{L-c}{2\sqrt{2D}}\right)-\operatorname{erf}\left(\frac{-L-c}{2\sqrt{2D}}\right)\right]=1. \quad (7)$$

164

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

$$h^* \sim 1 - \frac{1}{R_0} \cdot p(L, R_0)q(\langle d \rangle, c^2, L^2 + 3c^2), \quad (8)$$

168

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

172 Calculating the interaction of climate velocity and harvest

173 We identify interactions between climate velocity and harvest in two ways. The first and
 174 simplest way is to see if there is an interaction between the critical rate of one stressor and the
 175 magnitude of the other stressor. We identify such an interaction if h^* depends on c , or if c^*
 176 depends on h . If this type of interaction exists, determining the critical level of one stressor
 177 requires knowing the severity of the second. Before the stressors are extreme enough to drive the
 178 population extinct, however, they will cause it to decrease in size. The second way of identifying
 179 interactions is to compare how the two stressors affect population biomass individually and
 180 jointly. In order to do measure these effects, we find the total biomass of the population when it
 181 reaches an equilibrium traveling pulse and compare this equilibrium biomass in the presence and

182 absence of climate shift, harvesting, or both. Equations 5 and 6 allow us to numerically find the
183 total biomass in the equilibrium traveling pulse under each of these conditions.

184 We use B_0 to denote the equilibrium biomass without either stressor, B_h the equilibrium biomass
185 with harvesting but with climate velocity equal to 0, B_c the equilibrium biomass with climate
186 velocity greater than 0 but no harvesting, and B_{hc} the equilibrium biomass with both stressors.
187 For each stressor or combination of stressors, we calculate the decline in biomass caused by
188 stressor s as

$$E_s = B_0 - B_s. \quad (9)$$

189

190 Based upon this definition, there are three kinds of interaction types that can be defined. If the
191 interaction is additive, then the cumulative response to both stressors together would be $E_{hc} = E_h$
192 $+ E_c$. If the stressors instead interact synergistically, then $E_{hc} > E_h + E_c$. In contrast, if the
193 stressors interact antagonistically, then $E_{hc} < E_h + E_c$. We can therefore quantify the interaction
194 as

$$S = E_{hc} - (E_h + E_c). \quad (10)$$

195 where positive S indicates synergy, negative S indicates antagonism, and S of zero indicates an
196 additive interaction. This is a common way to measure the interaction among stressors, though
197 an alternative approaches would be to use the ratio of affected to unaffected biomass as a
198 measure of effect size (multiplicative model) or to consider the effect of the single worst stressor
199 (simple comparative effects model) (Folt et al. 1999; Crain et al. 2008). The additive model we

200 use here is the most conservative when quantifying negative effects, meaning that it is less likely
201 to identify synergistic interactions (Folt et al. 2012; Crain et al. 2008).

202 **Management strategies**

203 We use simulations to implement two management strategies (threshold harvesting rules and
204 protected areas) that make our basic integrodifference model analytically intractable. We also
205 take advantage of the increased flexibility of simulations over mathematical analysis to use the
206 Laplace dispersal kernel, $k(x - y) = \frac{1}{2}be^{-b|x-y|}$, a commonly used model of marine larval
207 dispersal (Botsford et al. 2001) that is not amenable to the analytical methods we use above. This
208 allows us to show that our results are not qualitatively dependent on our choice of dispersal
209 kernel.

210 Under threshold harvesting rules, harvesting pressure is no longer implemented as a proportional
211 removal from the population. Instead, we evaluate the abundance at each point in space to
212 determine how much harvesting should occur. If the population abundance is below the
213 designated threshold, no harvesting occurs. If the population exceeds the threshold, then all the
214 ‘surplus’ individuals are available to be harvested. This approach is an extreme version of the
215 harvest control rules proposed for many existing fisheries (Froese et al. 2011).

216 In addition, we introduce networks of protected areas into our simulations by designating
217 segments of space where the harvesting rate is equal to 0. Protected areas, particularly in the
218 ocean, are typically designed to meet either harvest management or conservation goals (Agardy
219 1994; Holland and Brazee 1996; Gaines et al. 2010a), and their spacing and size differ according
220 to which goal is being pursued. Harvest-oriented protected areas are often designed such that
221 they maximize adult spillover into harvestable areas by creating many small, closely spaced

222 reserves (Hastings and Botsford 2003; Gaylord et al. 2005; Gaines et al. 2010a). To mimic this
223 management scheme, we implemented protected areas with a length 1/3 of the average dispersal
224 distance and an inter-reserve spacing 2/3 of the average dispersal distance. Conservation-
225 oriented protected areas seek to protect entire ecosystems and reduce adult spillover by creating
226 fewer, larger protected areas (Toonen et al. 2013). To mimic this scheme, we implement
227 protected areas with a length 4 times the average dispersal distance and an inter-reserve spacing
228 8 times the average dispersal distance between them (Lockwood et al. 2002). In both harvest-
229 oriented and conservation-oriented protected area networks, 1/3 of the coastline is protected.
230 With protected areas present, we test two ways in which harvesting pressure could respond to
231 reserves: either total harvesting is reduced to 2/3 of what it would be without reserves (i.e.,
232 harvest effort in reserves is eliminated), or harvesting is shifted to available, unprotected habitat
233 such that total harvesting pressure remains constant (i.e., harvest effort is displaced).

234 For every simulation, we seed the model with 50 individuals at a single location and iterate for
235 2000 generations to reach equilibrium without harvesting or climate shift (more than sufficient
236 based on initial tests). We then add harvesting pressure, allow the population to again reach
237 equilibrium (2000 generations), and finally add a changing climate by moving the viable patch
238 with a certain velocity. After 6000 generations we calculate equilibrium biomass as the mean
239 biomass of 2000 additional generations. If population abundance declines below 0.001, the
240 population is considered extinct. Implementing protected areas makes the population abundance
241 cycle, but averaging over 2000 generations is sufficient to erase the effects of periodicity in our
242 results. For most systems, these long timespans are not biologically realistic. However, they
243 ensure that the population reaches its equilibrium traveling wave and that initial conditions do
244 not affect our results. We find qualitatively similar results with shorter simulation times.

245 **Parameters**

246 For our general model investigation, we used the following parameters: R_0 between 3 and 10,
247 $\langle d \rangle$ between 0.1 and 2, $K = 100$, $L = 1$. In this parameterization, $\langle d \rangle$ is expressed in fractions of
248 the habitable patch width, while c is expressed in fractions of the patch width per generation. In
249 addition, we used life history parameters for black rockfish (*Sebastodes melanops*) as an example
250 of how our model can be applied (White et al. 2010). We chose black rockfish because it is of
251 both conservation and commercial interest. The parameters for black rockfish in the California
252 Current were as follows: $R_0 = 2.86$, $\langle d \rangle = 73$ km, $K = 1$, and $L = 1000$ km (White et al. 2010).
253 We used marine protected areas with length and spacing representative of the reserves put in
254 place by California's Marine Life Protection Act (20km wide, spaced 76km apart, Gaines et al.
255 2010a). For the black rockfish example, we tested climate velocities from 0 to 200 km/year,
256 which was the upper limit observed globally (Burrows et al. 2011). See Appendix A.7 and Table
257 S1 for additional parameter details. While our results depend quantitatively on the parameters of
258 the model, our results are qualitatively robust and we chose a representative set of parameters to
259 analyze.

260 **Results**

261 **Persistence with Harvesting and Climate Velocity**

262 We begin by examining the critical rates of harvesting and climate velocity, i.e., those rates
263 sufficient to drive the population extinct. As one might expect, we identify an interaction
264 between the critical rate of one stressor and the magnitude of the other. Specifically, the critical
265 rate of each stressor is lower if a population faces higher intensities of the other stressor (note the

266 negative slope of the lines in Figure 1). This means that a harvesting rate that is sustainable in the
267 absence of environmental shift (c near zero) may no longer be sustainable if the environment
268 begins to change rapidly ($c >> \text{zero}$). We also found this negative relationship when we
269 parameterized the model for black rockfish (Appendix A.7, Figure S2).

270 We also examine the sensitivity of critical rates to growth and dispersal. In our model, it is
271 always the case that increasing the intrinsic growth rate (R_0), all else being equal, will increase
272 the critical climate velocity c^* and the critical harvesting rate h^* , since a population that grows
273 more quickly can recover more effectively from losses caused by these stressors (compare lines
274 with different shading in Figure 1). However, whether or not dispersing farther is better depends
275 on how quickly the environment is shifting (compare solid and dashed lines in Figure 1). When
276 the environment is shifting slowly, populations with wider dispersal kernels have a lower critical
277 harvesting rate because dispersing farther results in too many larvae dispersing off the viable
278 patch. When the environment is shifting quickly, on the other hand, populations with wider
279 dispersal kernels can better withstand harvesting because larvae dispersing long distances more
280 effectively colonize the habitat patch that will be viable in the next generation.

281 **Interactions Between Stressors**

282 We next consider how a population responds to moderate cumulative impacts that are
283 insufficient to drive it extinct. Whenever climate velocity or harvesting pressure exceeds its
284 critical rate, the biomass of the population at equilibrium will be equal to 0 (by the definition of
285 the critical rate). Before the stressors reach those thresholds, however, the equilibrium biomass
286 of the population decreases smoothly as either the harvesting pressure or the rate of
287 environmental shift increases (Figure 2a). The similarity between the shape of the equilibrium

288 biomass surface from our mathematical analysis of an approximation of a Gaussian dispersal
289 kernel (Figure 2a) and from our simulations of a Laplace dispersal kernel (Figure 3a) shows that
290 this result and the following results are robust both to changing our method of analysis and to
291 changing the dispersal kernel.

292 When we compare the cumulative impacts of the stressors to the sum of each stressor
293 individually we find low levels of positive synergy between the two stressors (Figure 2b). The
294 stressors display a synergistic interaction most strongly at high harvest and climate velocity rates,
295 close to where they would drive the population extinct. However, the degree of synergy is low
296 and concentrated in a limited part of parameter space. Throughout much of the range of harvest
297 rates and climate velocities, the interaction between the effects of the stressors is essentially
298 additive. We note that results are robust to changes from a Gaussian to a sinusoidal dispersal
299 kernel.

300 **Alternative management strategies**

301 With harvest thresholds in place, there is a threshold population density below which harvesting
302 is not allowed. Therefore, the population can only be driven extinct by harvesting alone if the
303 threshold is 0, i.e. the whole population is harvested, and otherwise a small population can
304 always escape harvesting. In addition to making it impossible for harvesting to drive a
305 population extinct, the harvest thresholds remove the interaction between the critical climate
306 velocity c^* and the harvesting rate h (notice the vertical line dividing positive and zero biomass
307 in Figure 3b). In this case, the effect of the stressors follows a simple comparative model: the
308 cumulative impacts of the two stressors are equal to the individual effect of the worst stressor.

309 If the harvesting rate in unprotected areas is not increased with implementation of the protected
310 areas (i.e., if harvest effort is eliminated instead of displaced), the population withstands
311 combinations of higher climate velocities and higher harvesting rates than without the protected
312 areas. This result applies to either strategy for implementing protected areas (many small versus
313 few large) (compare Figures 3c and d to Figure 3a). Despite these similarities, there are
314 differences between the strategies of having many small and few large protected areas. At lower
315 climate velocities, small protected areas spaced less than one average dispersal distance apart
316 result in smaller fluctuations of population biomass relative to large spaced protected areas
317 further apart (Appendix A.6, Figure S1).

318 If, on the other hand, harvesting effort is reallocated rather than eliminated by the protected
319 areas, the existence of protected areas *reduces* the critical climate velocity and harvesting rate. In
320 other words, implementation of protected areas in these cases causes extinction of the population
321 at lower climate velocities and harvesting rates than with the case of no marine protected areas
322 (compare Figures 3e and f to 3a, c and d). We find the same qualitative results in our black
323 rockfish parameterization: threshold harvesting changes the interaction between range shifts and
324 harvesting pressure to a comparative model, and displacing effort outside of MPAs can result in
325 lower population biomass than without MPAs at all (see Appendix A.7 and Figure S4 for
326 details).

327 Discussion

328 Climate change and harvest are two of the dominant human impacts on marine species and many
329 terrestrial species, but our understanding of their interaction and joint effects remains limited. By
330 analyzing a general model that incorporates dispersal and reproduction with a set of

331 representative parameters and parameters describing black rockfish, we find an interaction
332 between the critical rate of the each stressor and the magnitude of the other, such that the critical
333 harvesting rate decreases as climate velocity increases and vice versa. In other words, the more
334 quickly the environment shifts, the less harvesting it takes to drive the population extinct. We
335 then find that climate velocity and harvesting interact essentially additively in their effects on
336 biomass for most combinations of stressor levels, with weak synergy only appearing close to
337 population extinction.

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

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

354 climate velocity could selectively favor species with dispersal distances best matched to the rate
355 of shift.

356 Our finding that the interaction between harvest and climate velocity on biomass is effectively
357 additive would appear to contrast with demonstrations of synergy between harvest and climate in
358 the literature. For example, a number of modeling and empirical studies have found that fishing
359 increases the sensitivity of populations to climate variability (including Anderson et al. 2008;
360 Shelton et al. 2011; Botsford et al. 2011), and a recent review reaches the same conclusion
361 (Planque et al. 2010). Positive feedback loops involving the loss of predators due to fishing have
362 also been identified that amplify climate impacts on prey species (Kirby et al. 2009; Planque et
363 al. 2010; Ling et al. 2009). Similarly, synergy between harvesting and temperature was detected
364 in experimental populations of rotifers (Mora et al. 2007).

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

376 Another explanation for the discrepancy may be that the only effect of harvesting in our model is
377 a reduction in the amount of the adult biomass. In reality, populations often contain a diversity of
378 subpopulations, ages, and genotypes that can buffer them against climate variability and climate
379 change (Schindler et al. 2010). Harvest tends to simplify this diversity within populations,
380 making them more sensitive to climate variability (Mora et al. 2007; Planque et al. 2010). In
381 addition, some synergistic interactions between climate and harvesting identified in previous
382 studies involved the loss of predators and the release of prey (Kirby et al. 2009; Ling et al. 2009),
383 but our model did not include food web dynamics or species interactions and thus was unable to
384 capture these dynamics. Our simple, single-species, non-age-structured model suggests that
385 additive interactions between climate velocity and harvesting constitute a reasonable baseline or
386 “null” expectation in the absence of more complicated mechanisms. Future work considering
387 food web processes and genetic, spatial, and age diversity will be important to examine other
388 possible sources of synergistic (or antagonistic) interactions between harvesting and climate
389 velocity.

390 We also examine whether two frequently recommended management approaches, protected
391 areas and harvest control rules, could help ensure species persistence in the face of multiple
392 stressors, again both for a general set of parameters and for parameters describing black rockfish.
393 Threshold harvesting rules in particular appear to fundamentally alter how the two stressors
394 interact. In particular, the interaction between the critical rates is fundamentally altered: the
395 critical climate velocity no longer depends on harvesting and as long as the climate velocity is
396 below this critical rate, the population size is determined only by the magnitude of harvesting. In
397 our model, thresholds appear to have this effect because they effectively prevent harvesting of

398 the leading edge and allow colonization to occur as if these individuals were moving into un-
399 harvested areas.

400 While we framed our model as one that describes a population following a shifting climate
401 gradient, it shares many features with a population that is invading new territory. Our results
402 match well with invasion theory, which has shown that populations move into new territory at a
403 rate approximately equal to $2\sqrt{R_0 l}$, where l is the mean squared displacement of individuals per
404 unit time (Fisher 1937). With a constant harvest rate applied everywhere, the invasion rate would
405 drop to $2\sqrt{(1 - h)R_0 l}$, whereas the invasion rate would be unaffected if harvesting avoided the
406 leading edge, in accordance with our finding that protecting the low-abundance leading edge
407 from harvesting can mitigate the effect climate shift. Since this elegant early result, theoretical
408 and empirical work in invasion biology has shown that a low growth rate at the leading edge of a
409 moving population, which could, for instance result from an Allee effect caused by the low
410 population density there, can slow down or prevent an invasion (Hastings et al. 2005; Kot et al.
411 1996; Lewis et al. 1993; Veit et al. 1996). It is interesting to note that newly colonized
412 populations, which initially appear at low abundance, are commonly unregulated in fisheries
413 systems (Beddington et al. 2007; Dowling et al. 2008). Whether fisheries and other harvesting
414 activities rapidly exploit newly colonizing species depends in part on the interaction of social,
415 economic, and regulatory factors (Pinsky and Fogarty 2012). Our work highlights the fact that a
416 low (or zero) harvest rate on species that have recently colonized new habitats can be important
417 for helping them keep up with rapid climate velocities.

418 Previous work has advanced protected areas as a way to help organisms keep pace with shifting
419 climates, as well as to ameliorate anthropogenic disturbances like harvesting and habitat

420 fragmentation (Lawler et al. 2010; Hannah et al. 2007; Botsford et al. 2001; Gaylord et al. 2005;
421 Hastings and Botsford 2003; Thomas et al. 2012, Watson et al. 2011). We find that protected
422 areas can actually make the population more vulnerable to climate change and harvesting
423 pressures than a scenario in which no reserves are present if harvesting pressure is reallocated to
424 unprotected areas. If, on the other hand, harvesting pressure within reserves is removed from the
425 system, our results show that protected areas increase the critical climate velocity and harvest
426 rate of harvested populations. Since reallocation of harvesting effort has the effect of increasing
427 the harvest rate in unprotected areas, this result matches our earlier finding that high harvest
428 pressures at the leading edge of a population can make it more vulnerable to climate velocity. In
429 a theoretical model of an initially small population invading a patchy environment, decreasing
430 the growth rate in the unfavorable patches made it harder for the population to invade (Kinezaki
431 et al., 2003; Shigesada et al. 1986). This agrees with our finding that reallocating harvesting
432 pressure to unprotected areas increases sensitivity to stressors.

433 We also find that the details of protected-area design affect our results. Few, large protected
434 areas increase population fluctuations at low climate velocities as the population moves through
435 protected and unprotected areas. Many smaller protected areas, on the other hand, maintain a
436 population whose minimum biomass is higher, which could potentially provide a buffer against
437 extinction caused by stochastic events. This occurs because harvest drives the population to
438 lower levels while between protected areas. The larger those gaps are, the more diminished the
439 population will be during its transit.

440 Whether many small or fewer large protected areas is better depends on many factors and is
441 often species- or system-specific (Gaines et al. 2010b; McCarthy et al. 2011). Halpern (2003)
442 found in a meta-analysis of empirical studies of MPAs that the benefits from implementing an

443 MPA did not depend strongly on its size, though Claudet et al. (2008) found that fish density
444 increased with reserve size. Using a theoretical model, Neubert (2003) found that the optimal
445 MPA spacing to maximize harvesting yield depended on the length of the region in which the
446 population could survive: as the length increased, more and smaller MPAs became preferable.
447 Increasing the length of the viable region is equivalent to increasing the size of the habitable
448 patch in our model, so that his results are similar to our findings. On the other hand, McLeod et
449 al. (2009) argued that having fewer larger MPAs should increase an ecosystem's resilience to
450 climate change by protecting self-persistent populations. Similarly, Moffitt et al. (2011) used a
451 theoretical model to compare MPAs that were 10 km long spaced 50 km apart to MPAs that
452 were 20 km long spaced 100 km apart and found that the larger more widely spaced MPAs
453 would support the persistence of a greater number of species types. However, none of these
454 studies considered a population moving across a network of MPAs. By considering how a
455 population will track a moving isotherm, we contribute to this body of work by showing that
456 small gaps between protected areas may help species keep up with climate velocities in the face
457 of harvest and that considering a shifting climate is important for making recommendations
458 about MPA spacing.

459 The advantage of a simple model like ours is that it is potentially general enough to apply to a
460 wide range of species. Our discrete-time, continuous-space model captures the processes
461 important to species with distinct growth and dispersal stages, which includes most marine
462 organisms, plants, trees, and many insects. Our approach does not capture all the complexities of
463 real populations or of harvesting dynamics, however. For example, we do not include the
464 potential for negative per capita growth at low densities, often called Allee or depensation
465 effects. Allee effects can make it more difficult for a population to invade a new environment

466 (Hastings et al. 2005; Kot et al. 1996; Lewis et al. 1993; Veit et al. 1996). We would also expect
467 that populations with Allee effects would be more sensitive to the combined effects of harvest
468 and climate velocity than our model initially suggests. We also did not include age structure or
469 other aspects of sub-population diversity (e.g., spatial or genetic) in our model. As described
470 above, these forms of diversity have been important for studying the joint effects of harvesting
471 and climate variability (Botsford et al. 2011; Planque et al. 2010), and they will likely be
472 important for understanding climate velocity impacts as well.

473 Besides these species-specific extensions, our modeling framework could be extended to
474 consider species interactions, such as between predator and prey (Gilman et al. 2010). There are
475 some rules of thumb to predict how multiple stressors will affect multispecies systems. For
476 example, ecosystems that contain at least some species tolerant to a wide range of stressors
477 (positive species co-tolerance) can more effectively maintain functioning in the face of climate
478 change (Vinebrooke et al. 2004). End-to-end simulation models, which incorporate physical
479 environmental drivers and describe the dynamics of species at multiple trophic levels (e.g.,
480 Travers-Trolet et al. 2014), are increasingly popular as a framework for modeling multispecies
481 systems (Fulton 2008). Because our model is not specific to a particular region or set of species,
482 it can be used as a complement to these larger simulation studies. Hallowed et al. (2000)
483 recommend caution in building overly detailed models because determining model sensitivity
484 and understanding (sometimes hidden) assumptions becomes difficult.

485 A final important extension would be to represent harvesting dynamics more realistically. Our
486 results show that the success of protected areas is diminished if harvest is reallocated to
487 unprotected areas. Previous studies have also found that the details of how effort is reallocated
488 can change the predicted effects on population dynamics (Kellner 2007). Whether or not

489 harvesting pressure is reallocated, fishermen often focus their efforts at the boundaries between
490 protected and unprotected areas, where the spillover from the MPAs is likely to be highest. There
491 are circumstances under which fishing the line can lead to comparable biomass and overall catch
492 relative to uniform harvesting pressure in unprotected areas (Kellner 2007). However, in our
493 model, fishing the line would reduce the low-abundance leading edge as it moves into an
494 unprotected area and we therefore expect that it would make it more difficult for a population to
495 persist. To the extent that harvester behavior has been considered in fisheries, there is
496 considerable uncertainty in how vessels allocate effort over space and respond to changes in
497 environmental and regulatory conditions (Wilen et al. 2002, Fulton et al. 2011, Van Putten et al.
498 2011, Pinsky and Fogarty 2012). Harvest behaviors are rarely integrated into modeling efforts,
499 and an important next step will be integrated assessments of social-ecological systems.

500 Using a simple, mechanistic model like the one we present here helps to build intuition about the
501 conditions under which species can survive the cumulative impacts of climate and harvesting.
502 This work highlights the importance of considering stressors in combination, as outcomes
503 deviate from what we would predict in isolation. It also shows the importance of management
504 choices, as the location of harvest greatly affects the interaction between harvesting and climate.
505 While fisheries management strategies only change harvesting practices and do not directly
506 address climate change, understanding how regulations can affect interactions between
507 harvesting and range shifts can help to improve harvesting rules and the development of
508 protected areas. Our results offer encouraging evidence that management practices can help
509 protect marine populations from the cumulative impacts of harvesting and climate change,
510 particularly if the location of harvesting can be controlled.

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- 711

712 **Tables**

713 Table 1: Parameters and functions used in the text.

Variable	Definition
$n_t(x)$	density of individuals at position x at time t
$n^*(\bar{x})$	density of individuals at equilibrium at position \bar{x} relative to the patch
$k(x - y)$	dispersal kernel, the probability of offspring traveling from position y to position x
$\langle d \rangle$	expected distance traveled by an offspring
$f(n)$	recruitment function, the number of offspring produced by a population of size n
R_0	intrinsic growth rate of the population at low abundance
$g(n)$	harvest function, the number of adults remaining after a population of size n has been harvested
h	proportion of adults harvested, when $g(n) = (1 - h)n$
L	patch length
c	climate velocity in units of distance per time

714

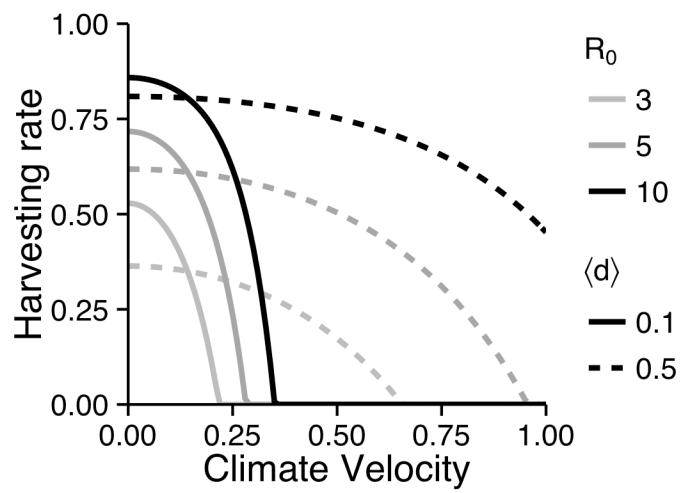
715 **Figure Legends**
716

717 Figure 1: (a) Lines indicate the critical threshold for persistence as a function of harvesting rate
718 on the y-axis and climate velocity on the x-axis. Shade of grey corresponds to the growth rate
719 from smallest to greatest (light to dark). Line style indicates the average dispersal distance (solid:
720 $\langle d \rangle = 0.1$ vs. dashed: $\langle d \rangle = 0.5$) from an approximated Gaussian dispersal kernel (Eq. 3). Patch
721 length $L = 1$.

722 Figure 2: (a) The equilibrium biomass of the population as a function of the climate velocity on
723 the x-axis and the proportional harvesting rate on the y-axis. (b) Interaction between the two
724 stressors as a function of climate velocity and harvesting rate. The heat map indicates the
725 interaction measure S , as defined in Equation (10), i.e., the loss in biomass in the doubly stressed
726 population in excess of the sum of the losses caused by each stressor individually ($E_{hc} - E_h -$
727 E_c). S of 0 indicates additive interaction of the stressors. The excess loss, on the order of 0.001,
728 is small in comparison to the total biomass, which can be as large as 20. These results are from
729 an approximated Gaussian dispersal kernel with parameters $L = 1$, $R_0 = 10$, $K = 100$, and
730 $\langle d \rangle = 0.5$.

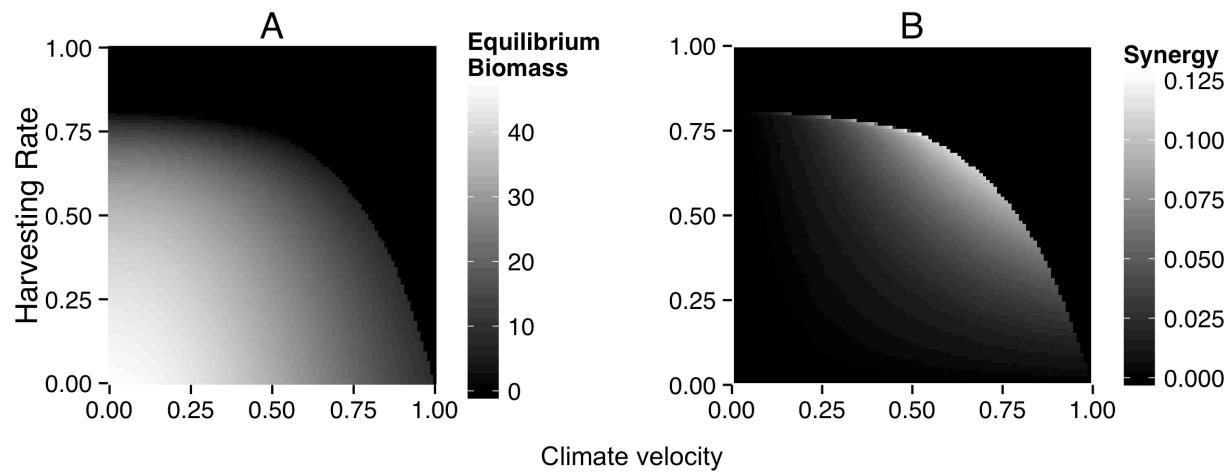
731 Figure 3: The equilibrium biomass of the population as a function of the climate velocity on the
732 x-axis and the harvesting rate on the y-axis under alternative management strategies. (a) The
733 equilibrium biomass for simulations with constant harvest rates (compare to figure 2a). (b)
734 Equilibrium biomass for simulations with threshold management. For threshold management, the
735 maximum threshold below which no harvesting is allowed is set to be the largest population size
736 observed at a given time step before harvesting. For a less severe threshold, we use a proportion
737 of this maximum threshold, so that a lower proportion gives a lower threshold and allows for
738 more harvesting. We show this proportion on the y-axis. (c) Equilibrium biomass for simulations
739 with many small protected areas with harvesting pressure outside reserves unchanged. (d)
740 Equilibrium biomass for simulations with few large protected areas with harvesting pressure
741 outside reserves unchanged. (e) Equilibrium biomass for simulations with many small protected
742 areas with harvesting pressure reallocated outside reserves. (f) Equilibrium biomass for
743 simulations with few large protected areas with harvesting pressure reallocated outside reserves.
744 These results are from a simulation with a Laplacian dispersal kernel with parameters $L = 1$,
745 $R_0 = 5$, $K = 100$, and $\langle d \rangle = 2$.

746 **Figures**



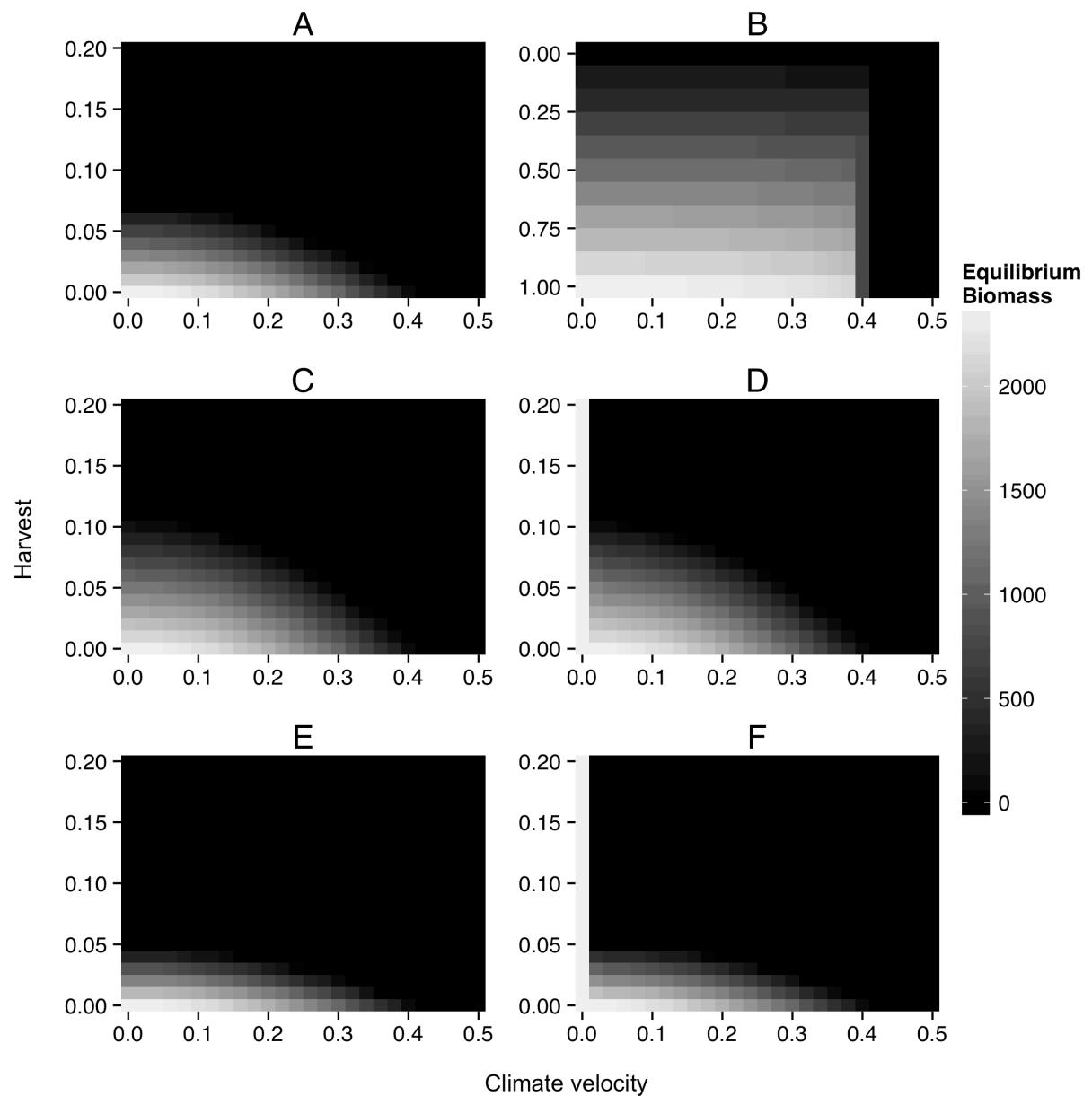
747

748 Figure 1



749

750 Figure 2



751

752 Figure 3