

Dear Dr. Debra Peters,

We are submitting our article (MS#ES14-00533) to Ecosphere based on your invitation to re-submit with major revisions following the reviews we received from Ecological Applications. We are grateful for this opportunity to submit a much-improved manuscript.

We have made revisions in response to the concerns of the reviewers, which we discuss in detail below. The three most substantial suggestions were to expand our discussion of (1) multi-species systems and invasion theory, (2) MPA spacing and heterogeneous harvesting pressure, and (3) introduce and apply our model to a case study. Any significant revision is highlighted in blue in the manuscript.

We believe that our revisions have fully addressed the concerns of the reviewers. We appreciate your time and look forward to your response.

Sincerely,

Emma Fuller
Eleanor Brush
Malin Pinsky

Reviewer 1

This paper was extremely well written, certainly one of the best drafts I have read in the past few years. The analyses were thorough and their application was well-identified.

However, there is a little too much repetition. For example, we receive the results in the abstract, intro, results and discussion with almost the same language. Thus, consider removing some of this repetition.

>>> We have removed the details of the results from the Introduction accordingly (lines 82-91).

The majority of these suggestions are comments for the discussion section:

1. Discussion points could use some more broadening, many of the points made were a recap of the results and their relation to references cited earlier. For example, some commentary on multi species systems might be helpful (see perhaps Travers-Trolet et al. 2014 in PLOS One).

>>> We agree and have expanded our discussion of multispecies systems by incorporating the reference the reviewer suggested, as well as a broader discussion of the merits of multispecies models and why both single- and multispecies are needed (lines 471-482).

2. More discussion about the relation of findings to invasion studies would also be

helpful. While there is some brief info in the discussion, more should be included. For example, Shigesada 1997 includes information and analytical solutions that would be helpful here for the MPA analysis on invasion in heterogeneous habitats that relates to the MPA spacing examined here. Along these lines, also helpful would be more discussion about lessons learned from invasion control, as much of the invasion literature has also focused on the leading edge and would provide some insights here.

>>> We have expanded our discussion of the similarities between an invading population at initially low abundance, as usually modeled in invasion theory, and a population tracking a shifting climate, as in our model (lines 398-409). We have also added a reference to studies of invasion into a patchy environment and a discussion of the similarity between that model and ours (lines 427-430).

3. Additionally, there has been much discussion on MPA spacing from Kaplan (multiple papers), Neubert (chattering paper), and the squeezing from others (starting with Halpern). The impacts of spacing and reallocation can depend on whether the fishery is optimally or over harvested, thus, there needs to be some discussion of this in the paper. Does this matter here when the leading edge is potentially most important? A one sentence acknowledgement that harvesting may be spatially explicit and not uniformly redistributed before or after MPA establishment should also be included as this would have important implications as well. Also, in relation to the paragraph above about invasion control, why would we expect harvesters to harvest the leading edge when the density is lower there? Again, this points out how the reallocation of effort can matter more than the threshold harvesting scenario covers.

>>> We incorporated a number of new references that showed the diversity of existing opinions about what type of MPAs are optimal and added a discussion of how our results compared to previous models (lines 438-456). We also added a discussion of how increased harvesting pressure at the boundary of protected and unprotected areas would affect our results (lines 462-470).

Minor comments:

1. There is a disconnect of the analytical methods and the simulation methods, for example, a Laplace dispersal kernel is used for the simulations. A little more discussion about the connection between these two sections and their results would be helpful and should be added to the methods and results sections.

>>> We have renamed the section previously entitled “Simulations” so that it is now entitled “Management strategies” to emphasize that simulations allow us to implement management strategies that are analytically intractable. We have added a few lines of clarification there to explain more fully the purposes of the two types of analysis (lines 206-210). We also added a sentence emphasizing that we chose to analyze a different dispersal kernel with each method to ensure that our results were robust to this choice (lines 286-290).

2. Page 17, Line 311 and Page 19, Line 19. These are example sentences where caution should be taken about the words interact and interaction. The authors clearly laid out earlier when impacts could be synergistic, additive, etc... However, the terms interact or interaction might imply something more than additive, so perhaps being clearer when using the words interact or interaction throughout the manuscript would be helpful.

>>> To help clarify our discussion of interactions, we have made a distinction between an interaction between the critical rates of the two stressors and the interaction between their effects on population biomass (lines 174-178) and we have tried to be more explicit about which type of interaction we are referring to throughout the paper.

Reviewer 2

This manuscript presents a novel framework to understand the combined effects of harvesting and climate velocity on population persistence through time. Integrating the integrodifference modeling approach proposed by Zhou and Kot 2011 for climate-induced range shifts, the Authors identified the critical rates of harvesting and climate velocity beyond which populations decline. They found that the effect of both stressors is approximately additive: positive synergies can, indeed, be evidenced only when rates of harvest and climate velocity are close to their critical values. Moreover the Authors investigated the effects on population persistence of both different conservation strategies (Harvest-oriented vs Conservation-oriented protected areas) and different reallocation of the harvesting effort (no reallocation vs full reallocation). They found that, with respect to Conservation-oriented protected areas, Harvest-oriented protected areas decrease population fluctuations at low climate velocities, if harvesting effort was not reallocated outside the protected area. On the contrary, a reallocation of the effort should involve a reduction of the critical climate velocity and harvesting rate, increasing the extinction risk for the population.

The manuscript is original and quite clearly written. However some clarifications are needed:

- the Authors state their model was built originally for marine species, but it could be applied also to some terrestrial ones (lines 83-85). In my opinion the manuscript could benefit from a clear example (e.g., an application case study): the application of some real parameters (i.e., d , R_0 , K , h = proportion of the population harvested) to a well known case study could allow the readers to more easily understand the manuscript. Moreover, the example could facilitate the researchers intending to apply their approach to different biological models or datasets.

*>>> We acknowledge that adding a case study would help to validate our results and show how they could be applied to empirical systems. We have added new results from our model parameterized to black rockfish (*Sebastes melanops*) in the California Current, using marine protected areas parameterized to represent the California Marine*

Life Protection Act MPAs and using realistic climate velocity values from Burrows et al. 2011 (lines 247-258, 267-268, 321-324.

- at lines 234 - 239 the Authors explain their simulation scheme. They use 2000 generations to reach equilibrium without perturbations (neither harvesting nor climate velocity). Subsequently, they add harvesting pressure (2000 generations) and, finally, a changing climate. They run the model for 6000 generations and finally, calculate the equilibrium biomass as the mean biomass of 2000 additional generations. If we imagine a univoltine or bivoltine species, the Authors exposed their population to 2000/1000 years of continuous harvesting (with a constant rate?) and, subsequently to 6000/3000 years of changing climate (with a constant velocity?). Did they suppose that the spatial configuration of protected areas remained constant for thousands years?

>>> We did not mean to suggest that we were modeling a population dealing with harvesting and climate change for 6000 years. The population reaches equilibrium after a short number of iterations, but we used a large number of iterations to ensure consistent numerical results. We have now added some text to the Model section to clarify this issue (lines 143-147 and 243-245).

Also in this case, the absence of an example could not allow the reader to easily understand the manuscript. What does it happen when the Authors shorten these times to simulate the effect of harvesting and climate change on a real biological model? Could I obtain the same results if I expose my species (e.g., a fish with an annual generation time) to 200 or 300 generations of harvesting at a constant rate (after 2000 generations to reach equilibrium with no perturbation) and subsequently to 100 or 200 additional generations of climate change?

>>> To address this point, we added a sentence in the text stating that our results are qualitatively robust to the choice of these parameters (lines 256-258).

Specific comments: - lines 83 and 417: Which is the difference between plants and trees? What the Authors mean for "plants": only herbaceous ones or the kingdom Plantae? In the latter case, the kingdom includes also trees.

>>> We thank the reviewer for noticing the ambiguity in our language here and fixed the sentences to remedy the issue.

- In the final portion of the Introduction section (lines: 85 - 87 and 93 - 100), the Authors explained their findings. Probably these paragraphs are more suitable for a discussion rather than for an introduction.

>>> We have removed the details of the results from the Introduction accordingly (lines 81-93).

- The parameters used for setting the model are specified only in the figure legends (cf. Figure 2 and Figure 3, lines 632 and 651 respectively), probably the insertion in the main

text could help the readers.

>>> *We added a paragraph in the Methods section about our selection of parameters for our general results, as well as the parameters we used to apply the model to black rockfish (lines 247-258).*

Literature cited: - The Authors should use always the same style to write journal titles (italic or not: Literature cited section in the Instruction for Authors (available at <http://esapubs.org/esapubs/preparation.htm#Lit>) does not provide information about this point).

>>> *We thank the reviewer for noticing these mistakes and have remedied them.*

- line 456: Tundi Agardi, M and not "Agardy, M. Tundi" - line 460: full stop after Chunco - line 491: add "Novel" to Elith et al., 2006 - line 503: remove "D. C.," after "Smith,"

>>> *We thank the reviewer for noticing these mistakes and have remedied them.*

- line 611: replace "&" with "and"

>>> *We thank the reviewer for noticing these mistakes and have remedied them.*