Dear

## Accompanying this letter is a revision to the manuscript “From the predictable to the unexpected: kelp forest and benthic invertebrate community dynamics following decades of sea otter expansion” (OECO-D-18-00256). We have revised the manuscript in response to critiques from Dr. Shurin and the two reviewers and believe

First, we would like to thank the reviewers and editors for thorough and constructive reviews. We have made several substantive responses to the manuscript which we outline here. We provide detailed responses to specific critiques below.

First, Reviewer 1 points out that you speculate that physical variables control kelp abundance once otters decimate urchins, but provide no evidence for aspects of the physical environment that may have changed during the second phase of the study period (late 1990s to present).  The second referee also points out that you provide no evidence to support the case that climate is the dominant factor controlling kelp abundance once herbivores are rare.  
  
Another possible explanation for your results may be that the interaction between kelps and their herbivores is non-linear and density dependent.  That is, urchins control kelps when kelp are rare but not when they are common.  Ling et al. (2015, Phil. Trans. R. Soc. B 370: 20130269) show that it takes a lot more urchins to reduce kelp numbers when kelp are abundant than when they are rare.  Kelp forests are a persistent state because top-down grazer effects are negatively affected by kelp density.  Might this be another explanation for why you don’t see increases in kelp even as otters continue to expand and grazers decline?  
  
If you choose to revise your paper for Oecologia, you should provide a detailed cover letter describing your point-by-point response to each of the comments of the reviewers.

Reviewer 1

Reviewer #1: The MS by Shleton et al. presents a new picture in the saga of recovering sea otters. The authors did a fantastic job of analyzing two different data sets characterizing the surface canopy kelp and benthic invert dynamics along coastal Washington state. While I think the results are solid, I had a few major issues. I think if these are addressed then this would be a nice contribution to Oecologia.

First, there was only a single physical variable, wind, that was included in the analysis. But in the discussion the authors speculate on all of the abiotic factors that could explain the slight recent downward trend. Factors such as SST, PDO, Upwelling, etc. should all be readily available for the authors to include in an analysis. Can the authors do this? I was left a bit unsatisfied with the speculative argument of kelp forest decline.

Response: This is an entirely reasonable critique. We thought long and hard about including additional covariates in our analyses and elected not to for two reasons. First, the Pfister et al. paper conducts a deep dive on kelp time series because all of the

Furthermore, are there survey areas from WADNR that are immediately outside of the sea otter range? If so, it would be nice to see those as some sort of control. Have they remained consistently low over the 30+ yr data set? Assuming that would be the expectation.   
  
My second issue, has to deal with just basic succession and the life histories of kelp. In this study, the authors did not differentiate between the two species (Nereocystis and Macrocystis), the former is an annual and the latter can be either annual (M. pyrifera type formerly known as M. intergifolia) or perennial. The annual kelps (and other short-lived algae) tend to move in first, followed by Macrocystis. It would be interesting to see how the successional dynamics of these two species plays out.  
  
Along those lines, I am also wondering about understory algae, especially kelps and other large brown algae. From Fig. 1, canopy kelp looks like it could follow a typical successional growth curve. I ask the authors what they think is covering the rocks where kelp once was? If it follows successional patterns that we have seen in southern California and Alaska then I would assume that there could be understory kelps (Laminaria, Pterygophora, etc.) or other long-lived alga (see Dayton et al. 1984 Eco Monogr, Duggins 1980 Ecology for a description of these dynamics). Are there any benthic survey data that could help resolve this? Are the kelp beds persistent, just patchier? Perhaps that is what the increase in CV was telling you.  
  
  
  
Reviewer #2:   
This is an extremely good paper with an interesting story and strong results.  I think the paper would be better with some editing.  The strong backbone story is somewhat weighed down by some weak analyses and an over-long discussion.  But none of that in any way disqualifies it from publication, and I think this would be a very good fit for Oecologia.  
  
The paper is an impressive piece of work which combines a very intensive data synthesis project with some fieldwork which has been designed to supplement historical data.  And the authors reach a very interesting conclusion. First they show that sea otters increased roughly exponentially in the region, and then document increases in kelp that occurred in the period leading up to around 2001.  All this is pretty well known already, although this may be the most comprehensive data set to address it in this region. But then the exciting part is that they show that coupling between sea otters and kelp breaks down in the subsequent decade, over which time there is really no relationship between sea otters and kelp at any spatial scale. Overall the results are very cool, they simultaneously support the dominant paradigm about otters creating trophic cascades and pushback against the overuse of that paradigm. This is important stuff and very well illustrated by their data.  
  
The authors have a lovely sentence on line 334:  
"As both primary sea otter prey and the major grazers of kelp, benthic invertebrates form the mechanistic link between sea otters and kelp."  
And it seems like the authors have shown very definitively in figure 6a that by 2000 this mechanistic link had been removed from the whole region by the presence of otters.   
  
But this simple and important story gets obscured in the discussion of alternative interpretations for the statistical decoupling of the kelp and otters.  On line 376 there is an arguments that it to do with long versus short term dynamics.  On line 396 they say kelp has "equilibrated" to the presence of the sea stars.   On line 420 they suggest "strong trophic interactions historically may change in new climate regimes." None of these thoughts are very well fleshed out, and honestly I do not understand why they are making it so complicated. Presumably the authors would agree that if you went out and shot the otters, urchins would return and the kelp would disappear. So the trophic interactions have not changed and there is no magic to the long-term dynamics, the system just has been at the zero bound of the otter-urchin relationship for more than a decade, and without urchins there is no mechanism to link otter abundance and kelp abundance. At the same time there does not  
seem to be any reason to propose that the relationship between the otters and kelp would not hold if otters were dramatically reduced.  Basically, I think the discussion could use some tightening.  
  
Now on to more specific points:  
  
They do not really tell us much about how the sea otter surveys were conducted. We do not need a lot of detail, but they should address the question of whether sampling effort varied through time or space in a way that might be important.  My impression is that sea otter surveys are typically so intensive that they end up being something like a census, so you do not have to worry about variations in sampling effort.  But I think this should be addressed in the methods in some way.  
Is particularly relevant for figure 3 which only really makes sense if either the location of every sea otters known or if sampling is consistent through space.  
  
Actually I don't love figure 3. I think it is hard to read and not very informative. I spent a bunch of time with figure 2 and figure 3 side-by-side trying to figure out how they match up. Figure 2 is fabulous but I just find figure 3 confusing. I think it is mainly because each of those kernels is standardized to have the same volume even though the overall population is going up. It seems like this data could have been presented much more clearly as a colormap where the colors represent the smoothed otter abundance.  That way the authors could show both the increase in overall abundance from left to right and the spatial changes (as color patterns from top to bottom). As it is it makes it look like otters are disappearing from some regions over time when in fact they are just continuing to increase in other regions.That said there is nothing fundamentally wrong with this figure and I do not think there is any need to remove it.   Either way I would be interested in knowing  
how many observations each of those kernels is based on. The number of observations can be written along the top of the figure  
  
I was a little concerned that transect and quadrat data have been combined in their data synthesis. Do they have samples where the same species is counted in both quads and transects to demonstrate that they get similar density estimates?  I have found that estimates from these two methods can be very different because of the amount of time the diver searches each square meter.  The authors say they avoid cryptic species which is wise, but I can say from experience that transects and quads get very different counts for sea urchins (speaking based on datasets I have used extensively) because divers in quads find urchins under ledges and in crevices that are missed on transects. If this is not true in the authors' data sets maybe they could show that in a supplement by comparing data collected in both ways from the same sites.? At the least they could check that the basic patterns they report are consistent even if you limit analysis to one data type (if so fine to just  
assert-it was not clear how much data mixing had gone on so this may be a mostly irrelevant point on my part).  
  
I do not understand why kelp growth rate is hypothesized to depend on otter growth rate (e.g. figure 4).  I guess my default assumption would have been that kelp growth rate would it depended on otter density in some way, not on the change in otter density….  
  
They spent some time analyzing changes in CV. I do not really know what the point of this is but it seems fine. My only concern is the section around line 325 where the authors seem to be regressing the CV in one period against the difference in CVs between that period and the next.  This does not seem terribly informative. You could stick any numbers into this analysis and get a significant result because you are effectively regressing one thing against itself. See this R code snippet for a toy example:  
  
rm(list=ls()); graphics.off();  
period\_1 = runif(50)  
period\_2= runif(50)  
summary(glm((period\_1-period\_2)~period\_1))  
  
Figure 1:  The plots on the right might be more readable with titles in the top left.  Or little line drawings of kelp and otters? (actually all the graphs, beyond figure 1,  would be more rapidly digestible if the otter and kelp frames were distinguished in some way.)  
  
Figure 1: can you indicate the location of point Grenville in some way?  It is in figure 3 but not indicated here.  I expect it would have to be marked on the most zoomed out map.  
  
P.S. When I read this over, it comes off awfully critical.  So I'll just close by saying that I think this is fundamentally a great paper.  And I almost clicked accept without revision, because basically none of these are actually wrong - just places it could be better.  
  
P.P.S Well, unless all the pre-1998 invert counts were quadrat-based and all the post-1998 invert counts were transect based. That would be a real problem.  But that's not my impression.