Dear Dr. Trexler,

## 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 it is much improved from the previous submission. We would like to thank the reviewers and editor for thorough and constructive reviews. We have made substantive responses to the manuscript which we outline here. We provide detailed responses to specific critiques below.

## The major change we have made to the manuscript is to revisit and rewrite the sections connecting kelp dynamics to climate variables. Our work is unfortunately limited by available information about abiotic variables at a spatial scale appropriate to understand site-to-site differences in temperature, upwelling, or other factors. We have added a new set of analyses to illustrate that the spatial scale of correlation among sites has changed in recent decades (new Figure 5 and associated description). We have also added some analyses of major oceanographic indices to show that the large-scale climate regimes did not differ between our early and late study periods. Finally, we have rewritten the language about climate linkages in the discussion to improve clarity and avoid vague claims. We believe these changes, along with the edits described below, greatly improve the manuscript.

Sincerely,

AO Shelton for the co-authors

Specific responses to the Editor and reviewers. Responses are in red.

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.

Response: In the revised ms, we include a new figure and analysis to examine how aspects of the physical environment changed over the study period. This analysis shows that patterns of kelp have changed between the early and late study periods (Fig. 5, lines starting 386 and 456), and we have included additional Discussion of large scale oceanographic drivers (lines 274 and 347), and rephrased our description of climate variables in the Discussion (see line 456). We agree that we cannot definitively evaluate the dominant factor controlling kelp abundance once herbivores are rare, but rather we can claim that the probabilities that herbivores or large-scale oceanographic factors are dominant are quite low.

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?  
Response: We agree that it is possible that sea urchins control kelps when kelps are rare but not when they are common, and indeed this is a potential mechanism for creating hysteresis in shifts between kelp- and urchin-dominated states in the study system. In the revised ms we have added a citation of the Ling paper (line 448) and added text noting that it is possible that non-linear functional responses play a role in the dynamics.

We note here that it is entirely possible to get the patterns outlined in the Ling et al. paper with time-invariant linear functional responses between kelp and urchins and a small amount of stochasticity. It is not possible to determine whether there is a complex non-linear interaction between urchins and kelp by plotting the relationship as Ling et al. do: bounding one axis between 0 and 1 guarantees a non-linear relationship between variables. Stronger inferences could be made based on plots of estimated interaction strengths (in per capita units rather than proportion cover units) and/or via the application of a dynamical model. Unfortunately, such an exercise is beyond the scope of our data and this paper.

Specific points of the Editor  
L120-123, the point of the information about sea urchin fisheries is unclear.  I assume you say this to indicate that changes in sea urchin abundance do not likely reflect harvesting (because harvest only occurred early in the survey when urchins were more numerous and at certain sites).  You need to be clear about the point of this information.    
Response: We have added a sentence to make it explicit that harvest is unlikely to be the driver of urchin populations (line 122).

L145-146, “developed a one dimensional coastline” is unclear, do you mean you just examined abundance as a function of latitude?  What are the units on the one dimensional coastline?

Response: The kernel smoothed distribution of otters is in units of kilometers. We used a simplified or one-dimensional shoreline because the nearshore bathymetry off the Olympic coast is not high enough resolution to generate an accurate two-dimensional region (see lines starting at 155). In addition, a one dimensional coastline is a reasonable approximation owing to the high rugosity of the shoreline (i.e., otters likely follow a straight line across fined grained embayments rather than hugging the exact shoreline). We provide references to other papers that have constructed linear shorelines for these waters as well.

L134, I’m unclear how you accounted for sampling effort in your estimate of otter abundance.  Presumably the sampling effort varied among years or surveys (or did it?).

Response: The sea otter surveys are considered a complete census of the population. We have added a line to emphasize this point and provide references to the full survey methodologies. (line 148)

L170, was kelp coverage estimated by digitizing aerial images or by visual estimates made in the field?    
Response: The methods are derived from digitized aerial images. We note this briefly and cite provide the references for the kelp surveys (line 190).

L223-225 needs a reference to support it.

Response: We have added references for this assertion (line 262)  
L230, “regressed exponential trends” is unclear, do you mean you regressed sea otter abundance against kelp cover?

Response: We have rephrased this section for clarity (line 268)  
L236, temporal or spatial variability?  (I assume temporal but you should say so).    
Response: Yes. We mean temporal variability (line 280)

L334-336 is material for Discussion, Results just describe the data.  Same with L350-352 and L354-356.  
Response: We have removed these sentences.

**Reviewer 1:**

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: Of all of the variables, we only included wind as it is the only variable that varies in space relative to the scale of our study domain. All of the other variables the reviewer mentions are spatially invariant among sites and therefore do not have the ability to explain the variation among sites even if we included them. We would love to be able to include additional local variables for each site, but they simply do not exist. We have added this point to the Methods, added an investigation of two broad scale oceanographic variables (lines 135-141), and modified the discussion of environmental variables to reflect questions of spatial scale (starting at line 456). In addition, we provide a citation for the Pfister et al. paper that investigates various climate drivers on coastal kelp at the aggregate, regional level (and includes PDO, SST, etc.). We do not wish to revisit previously published analyses so we do not address variation at the regional scale in our manuscript or construct detailed dynamic models for each site. While more sophisticated time-series models can be constructed for these populations, they will have to wait for a later manuscript.

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.

Response: Unfortunately, there are no areas outside of the WADNR survey region on the outer coast. The amount of hard substrate south of Destruction Island in Washington is trivial and not conducive to supporting significant kelp forests. There are other areas of hard substrate to the east along the Strait of Juan de Fuca, but these sites are considered biogeographically distinct from than outer coast areas and have substantially different invertebrate and algal communities. The Pfister et al. (2018) manuscript present some comparisons between different regions in Washington state.

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.  
Response: This is an interesting idea that deserves to be investigated more fully than we can here. We have added several plots to the online supplement to show that, in general, there is no obvious evidence of successional dynamics between *Nereocystis* and *Macrocystis* and that the patterns are virtually identical for individual species as they are for both species combined (Fig. S3, S4, S5). Across all sites, there is generally a positive relationship between *Nereocystis* and *Macrocystis* – as found in the Pfister et al. (2018) paper we cite. At the local scale, Fig. S4 suggests that years of low abundance of *Nereocystis* are years of low abundance for *Macrocystis* but beyond that there appears to be minimal relationship between these two species. This is not the pattern one would expect from a successional dynamic between the species, suggesting something different and interesting is going on. Additionally, we have added a final figure to illustrate how the relationship between sea otter population growth and *Macrocystis* population growth are the same as for both species combined (Fig. S5). We do not present parallel plots for *Nereocystis* alone because there are a few sites where area estimates go to zero in some years, complicating the log-linear analysis for those sites.

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.  
Response: This is also of interest to us, but detailed information about kelp succession is not really available for the historical period examined here. As the canopy kelp surveys are done from planes, understory information is not available on an annual basis. Indeed, we have found data on understory kelp density from only three sites in 1987, 1995, and 1999; there is not a continuous time series to be examined for all 10 sites we examine in the other analyses. We have collected information about understory algae during more recent surveys (2015-present) and hope to analyze that information in later analyses. We note this is of interest in the Discussion (line 502) but we have not added further discussion of the understory algal community.

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.  
Response: We appreciate the critique, but would argue that our data supports the interpretation that there are interesting dynamics occurring beyond the well-known and well-studied urchin-sea otter interaction. We broadly agree with the simple story outlined by the reviewer – without sea otters urchins would likely return and kelp would decline. However, the variability in the kelp abundance among sites and across time and the gradual changes in other invertebrate species indicates there is more to this story than indicated by the reviewer. One only has to look at Fig. 1 to note that 2014 had less kelp than 1990 when sea otters were ~15% of their current abundance to recognize that while sea otters and urchins are an important component, they are not the whole story. We have made some substantial edits to the discussion to tighten up the language noted by the reviewer (deleting the reference to equilibrium dynamics mentioned by the reviewer and eliminating the reference to climate) but we believe it is important to avoid the impression that this is a wholly solved puzzle that only involves sea otters and urchins. In addition, we have added an analysis of kelp synchrony and spatial correlation to bolster our discussion of spatial dynamics of kelp (Fig. 5, Discussion paragraph starting about line 444).

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.  
Response: The survey of sea otters is considered a census. We have added a sentence to the methods to emphasize this (line 148) and changed our language to eliminate the impression that there are discrete survey locations for the sea otter data.

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.

Response: As the survey of sea otters is a census, the amount of area surveyed is constant among years (see response to the editor and the previous comment). We like this figure as it provides a visualization of the relative distribution of otters and the center of mass through time. We think it complements Figures 1 and 2 but are open to moving it to the Supplement if the editor requests.

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).  
Response: The three historical surveys by Kvitek et al. and our surveys do vary in their methods (summarized briefly in Table S1). The Kvitek surveys in 1987 were an epic, all underwater ordeal. The 1995 and 1999 surveys were conducted using video and post-processing of the video (and included both quadrats and transects). Our surveys in 2015 were exclusively underwater and while we only reported transect results, we did conduct both transect- and quadrat-based surveys. We only report the transect information because it was focused on surveying other things and the methods in this paper were getting overwhelming, but the quadrats did identify sea urchins and quadrat-level and transect-level information do not suggest notably different values for urchins or other invertebrates. Our analyses are based on the knowledge that our surveys were carefully done and the good faith – supported by discussions with earlier researchers - that previous surveys were carefully done. We cannot do much more that that.

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….  
Response: To make comparisons among sites we need to convert all of the sites into comparable units. In the absence of information about the area of habitat available at each site for kelp or sea otters - not all areas have similar topography or have similar amount of shallow habitat, but we have no direct measure of available habitat – we cannot calculate a defensible absolute density measure for sea otters or kelp. However, measures of growth rate are comparable among sites and among times because the amount of area at each site scales out of this calculation. We agree that sea otter density might be a reasonable driver of change in kelp, but over long-periods, changes in sea otter and kelp populations are best described by their growth rates.

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))  
Response: As mentioned above, we analyze variability in kelp for precisely the reason that it is not well explained by classical sea otter-urchin-kelp dynamics. However, the broader point about regressing something against itself is well taken. We have re-analyzed this section using raw CV values for each time period which avoid the self-referencing problem (line 280). The main point result of the analysis has not changed – CV declines between period but locations with relatively high variability remain highly variable (lines 374-385).

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.)  
Response: We have not added anything to the figures to distinguish them. We feel like the current labeling should be sufficient. However, we are open to the possibility of adding drawings if the editor requests it.

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.  
Response: We have added this point to the map in Figure 1.

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.

Response: See response above.