UNITED STATES DEPARTMENT OF COMMERCE
National Oceanic and Atmospheric Administration
National Marine Fisheries Service
Northwest Fisheries Science Center
Conservation Biology Division
2725 Montlake Blvd East
Seattle WA 98112-2097
nick.tolimieri@noaa.gov
Ph: (206)-302-2444

18 October 2022

To the editor:

Please find submitted our revised copy of the manuscript. The Reviewers' comments we valuable in improving the manuscript and we believe that we have addressed them full in the revisions and below. We appreciate the opportunity to review the manuscript and hope that it is now suitable for publication.

Sincerely,

Nick Tolimieri

Our responses to the reviewers follow. Line numbers refer to the Track-changes version of the MS unless otherwise noted. Bold text marks the original Reviewers' comments. Normal text indicates our response.

Reviewer 1 report:

Suggest change analysis for urchin and kelp

added. See below.

Dear authors,
I greatly enjoyed your manuscript describing the dynamics of kelp forests on the outer coast of Washington in the past half decade. It's been an interesting time for west coast subtidal ecology with the blob and heat wave alongside sea star wasting disease. This manuscript

adds another piece to the puzzle in our search for generality that is crucial - an area that, seemingly, initially puzzlingly, is rather unaffected.

I say initially as your discussion lays out a beautiful case as to why your region is different. The combination of otters (!!), more rugose wall-like habitats in some places (see recent work from Randell et al. 2022), potential adaptation due to a preceeding warm water event - these all set up a perfect storm, if you will, of reasons why we would suspect the patterns oberved here. Very little of this is in the introduction and framing, however, but instead is all discussion.

The manuscript as is is great as a piece of description and natural history. Patterns observed are patterns observed. However, I think if you and the editors at MEPS would like this paper to have a greater impact - that this paper is part of a larger tapestry, rather than a one-off examination of a single region that is so far underrepresented in the literature (which it is - and why I'm so glad to see this paper). As such, I would suggest the following modifications to improve this manuscript. I do not think they are onerous, and might even allow for some focus and trimming.

1. Given otters, benthic morphology, previous warming, and more - what is the a priori expectation about the response of the open coast system to the heat wave and sea star die off? Is there an a priori expectation one way or another? How does that a priori expectation arise from our current knowledge of kelp forest ecosystems - both West Coast US and Global? (There is a lack of global perspective in this piece). Setting up expectations, and looking at whether they are or are not met, and then in the discussion being able to reference back to an introduction to see how this region teaches us about the larger world of kelp forest ecology would really extend the impact and relevance of this piece, and should not be a big lift to change.

The introduction has been largely re-written to introduce a more global perspective and provide some potential a priori hypotheses or expectations. For example, we have added information on MHW effects on kelp in other areas (New Zealand, Australia, North Atlantic). The earlier draft did cover many of the topics (differences in kelp loss among regions, references to differences in predator redundancy among regions, effects of trophic cascades, effects of climate drivers, etc), but was not specific as to regional differences. In the current version we have added in more region-specific information, such as regional differences in urchin predators. Due to the extent of revisions, we do not cover specific changes here and direct the editor/reviewers to the track-changes version of the MS.

We have added some simple hypotheses to the end of the introduction (Line 333). However, given that we don't know, a priori, the thermal regime at the sites, it is difficult to make specific hypotheses regarding how Washington kelp forests would respond to the MWH. We have added the following:

"We predict fewer strong impacts from the 2014-2016 MHW and SSWS on Washington kelp forests because both *Macrosystis* and *Nereocystis* are in the central portion of their range (Smale 2020) and absolute temperature extremes are less likely to exceed species tolerances at these latitudes (Hamilton et al. 2020). Moreover, top-down pressure from sea otters, which are present along the

Washington Coast (Shelton et al. 2018, Gregr et al. 2020), may help to prevent a shift to urchin barren habitats in the event of substantial, initial kelp loss."

2. To further deepen the context, how does what is presented here contrast to recent results from the Puget Sound? I'm thinking of work from Helen Berry, Tom Mumford, and others. It's right next door! How do the patterns seen here compare and contrast to what is being seen on the open coast?

The following was added to the Discussion at line 888:

"In nearby Puget Sound, where *Nereocystis* is the sole canopy forming kelp, the effects of the MHW on kelp are somewhat hard to assess. Waters from the 2014-2016 MHW did penetrate Puget Sound leading to a 2.3°C increase in water temperatures (Khangaonkar et al. 2021). However, in the eastern Strait of St. Juan de Fuca, *Nereocystis* declined from 2007 onwards and did not show obvious MHW impacts, such as an abrupt change in canopy cover (Pfister et al. 2018). In South Puget Sound there have been long-term declines (Berry et al. 2021), but *Nereocystis* cover was lower in 2017 and 2018 than in 2013 (Berry et al. 2019). Purple and green urchins to increase in various basins within Puget Sound, potentially due to a lack of top-down control by predators as the predatory sea stars *Pisaster brevispinnus* and *Pycnopodia* both began to decline in 2014,(Montecino-Latorre et al. 2016). Pycnopodia was highly abundant in Puget Sound and the Salish Sea in general prior to SSWS (Montecino-Latorre et al. 2016), and may be the only major urchin predator in the area (Duggins 1983, Schultz et al. 2016); otters are not present as they are on the coast (Gregr et al. 2020)."

For that matter, I see very little discussion of wave exposure and how it might also play a role (e.g., thinking about Siddon and Witman's work on this). As with point #1, this will again allow the manuscript to be much broader in its reach and better advance the field of kelp forest ecology.

Wave action is clearly important for kelps. However, we have not focused on wave action because exposure does not seem to be particularly important at our sites (especially recently) based on prior analyses (Shelton et al 2018). We have added the following to the Study sites 2.1 description:

Line 359. "Previous work suggests that wave exposure was not important in explaining variability in kelp cover among these sites (Shelton et al. 2018), likely because these sites were initially selected to be somewhat protected from wave action to allow for dive surveys (Kvitek et al. 1989)."

3. The correlations between kelps and urchins are really interesting. However, I worry about the hidden spectre of omitted variable bias in terms of asking about whether one is driving another. If you're unfamiliar with econometric techniques for looking at panel data, John Antonakis has a nice 2019 paper couched in mixed models as does Andrew Bell (also couched in fixed versus random effects) that I'd recommend. There's also an excellent chapter in Wooldridge's book on cross sectional and panel data. Regardless, the simples solution is, instead of looking at correlation, to look at change in kelp and change in urchins.

I believe there is enough data here for this analysis, and looking at the relationship between change should be highly illuminating and greatly strengthen any arguments made here.

We appreciate the suggestion for a panel analysis, aka. Random-effects-within-between (REWB) model as outlined in Bell's work. The approach is an interesting one.

We have added a REWB analysis to the MS . However, we have limited this analysis to the Tatoosh Island site for data reasons—Tatoosh was the only location in which urchins were really present and showed large fluctuations in biomass (see figures in the Supplement). We have also made some changes to the basic REWB described by Bell based on our sampling design. In particular, transects were haphazardly sampled, and there is variability among years in sampling effort. As a result, it is difficult or impossible to follow one transect through time.

Description of the REWB begins at line 518 in the Methods.

Results are at line 721. There are also tables and a figure in the supplement.

The results are limited to Tatoosh Island but suggest some confounding of time (year) and the effects of urchin density on kelp stipe density and do not show strong evidence for top-down effects.

4. While I understand the presentation of regional timeseries alone and then the multivariate analysis using Site, I think something is lost by not looking at differences in site-level timeseries of at least kelp and urchins (if not other species as deemed necessary).

The figures are in the supplement and are referenced throughout the main text.

I do not think any of these changes are big lifts. It will reconfigure mostly the introduction and discussion (and perhaps a new figure or so). I'll call this a suggestion for major revision, but I think it is very achievable.

Good luck with revisions, and I'm happy to review any future drafts. Note, I sign all of my reviews as research has shown that interactions between reviewers and authors can improve manuscript quality. I am happy to answer any questions or engage in any further dialogue with the authors.

-Jarrett Byrnes

Minor comments

Line 62 (original) - Cite better reviews here - i.e., the Ling et al review

Ling et al 2015 and Smale 2020 have been added throughout.

Line 80 (original) - define heat wave

Done, with added reference to Hobday et al 2016, including a complete MHW analysis.

Line 493(original) - adaptation - were they primed? Bring this into intro - why is Washington unique?

We have not specifically addressed this comment. However, text was added noting that both *Macrocystis* and *Nereocystis* are in the central portion of their range.

Line 529 (original) - see recent work on rugosity and barren formation from Randell et al 2022

Randell et al 2022 is now cited in the introduction Line 208. Note Randell et al 2022 was already cited in the Discussion several lines earlier at line 524 (now line 844) and there are additional citations following.

Line 860 - did you expect to see effects of star die off given otters?

We removed the 'expectation' language. The sentence now reads:

'We did not see shared temporal variation in the invertebrate assemblages caused by a response to the die-off of sea stars".

The potential impact of otters is discussed in paragraph.

We have also done some additional editing to this paragraph to improve on its clarity.

Smith and Fox 2021 is missing key bibliographic information

updated

Reviewer 2 report:

Overall:
This manuscript provides an interesting and important insight into temporal shifts in kelp forests and associated fauna off the Washington coast, USA. Overall, I like the work and find it well written and an important contribution. However, the authors are attempting to link the patterns in community assemblages to MHWs (specifically, the blob) and SSWS in the area, without actually analysing these two factors or including any element of them in models. In particular, they link shifts to the unprecedented 2014-2016 MHW, but without any evidence of local events. I would urge the authors to either drastically tone down their language and links to MHWs, or examine data for defined MHWs. The most common definition follows Hobday et al. 2016 (referenced in the manuscript), and annual characteristics can easily be gathered using the heatwaveR package (in R) to interpret MHW signatures at their local sites. If they run this, characteristics such as total MHW days, or cumulative intensity for a year could be included in their models which may provide important insight. However, I'm aware this is a lot of work and so the authors might prefer to reduce the MHW language. That said, given how hot the topic is, if the authors are willing to complete the work I suspect the article will be much more highly cited.

Abstract:
I can't help but feel the abstract jumps in without including a couple of lines of background, as is typical in abstracts.

We have added the following to the Abstract to better introduce the topic:

"Canopy-forming kelps are foundation species in many coastal ecosystems, but kelp-forest communities are subject to abrupt state changes caused by environmental drivers and trophic dynamics."

We also made additional edits to meet the 250 word limit.

Introduction:
Line 128: Kelp-dominated and urchin-dominated should be hyphened.

Updated as suggested

Line 299: When roughly was the northern sea otter restored?

This is a bit of a complex question. Initial efforts started in 1969-1970. Populations began to really increase in the mid-1990s and have increased through at least 2010. See Shelton et al (2018). We have added the following:

"...with otter populations initially reintroduced in 1969-1979 and then increasing rapidly between the 1980s and 2010s."

Methods:

Lines 368: 'We targeted completing' doesn't make sense.

We have modified the text to read, "Our goal was to complete six replicate transects at each year-site-depth combination, but actual sampling effort varied." to clarify.

Line 184-196 (original): Did you consider individual plant health when counting stipes? Ie if a proportion of the plant had been consumed by urchins was it still counted? What was you cut-off for deciding whether or not to include stipes when considering urchin activity? Were all species of kelp counted in the same manner or was Macrocystis counted by number of stipes coming off an individual thallus?

No. In the initial sampling, we counted stipes of a specific length regardless of health. We have since begun to record whether the frond was missing (presumably consumed). However, we cannot provide those data for this manuscript.

Lines 205-212 (original): It seems strange to be discussing MHWs without actually assessing data for MHWs? This can quite easily be done using the R package heatwaveR (or the comparable Python package) which follows the widely-used Hobday et al. 2016 definitions.

This will enable the authors to compare their data to metrics such as MHW days, cumulative intensity etc.

To clarify, we are not analyzing MHWs in general but changes in WA kelp forests during THE 2014-2016 MHW. We feel that the (new) title and introduction are clear in this respect. The 2014-2016 event is well documented in various literature had large impacts on other areas of the California Current Ecosystem. However, we agree that temperature data are important for providing context for WA coast nearshore environments, specifically our sites.

Here, we focus (and focused) on mean monthly SST because this metric has been shown to be biologically and ecologically relevant for kelps in multiple studies, whereas MHW-type anomalies have not correlated as well with kelp canopy cover, at least for the 2014-2016 MHW. For example, Hamilton et al 2020 did not find differences in various MHW metrics for Oregon (no obvious effects on kelp) and Northern California (severe kelp loss), but the absolute SST was 1.5C warmer in NCA than in Oregon. Similarly Cavanaugh et al 2019 found absolute SST was a better predictor of kelp canopy loss than were MHW indicators.

We have added some text to Section 2.3 to clarify our choice of maximum monthly mean SST as a predictor. We have also include a 15C cut off because there is some evidence that growth of both kelps can decrease above 15C (based on a different comment).

However, we appreciate the Reviewer's suggestion to include more explicit MHW analyses, and we have also added a full, more formal MHW analysis including text in the Methods (section 2.3) and Results (section 3.1) and information in the supplement (Table S6, Fig. S4) to more completely describe the temperature regime on the WA coast and the prevalence of MHW. This added MHW analysis was valuable in that it showed that the timing of MHWs varied between 2013 and 2014-2016. While there were fewer MHW days etc in 2013, they occurred during the warmest time of year, leading to the higher monthly maximum temperatures. Those in 2014-2016 occurred during early summer or early fall, resulting in cooler overall mean temperatures. Thus, the timing of MHWs matters.

Thus while MHW activity was higher in the 2014-2016 period, as we might expect given other published literature on the 2014-2016 MHW, the absolute maximum temperatures were actually higher in 2013, which is more relevant to the kelp.

Line 225 (original): how do you distinguish 'anomalously warm SST?'

The entire sentence was deleted in revision.

Lines 224-231 (original): This section seems out of place and should be incorporated with the end of the intro.

We have moved a portion of this paragraph to the previous section on the area of the canopy kelp (section 2.4). We feel it fits better in the description of these data and should remain in the Methods section.

Repetitive use of the word 'focus'.

Second instance changed to 'examine'

Results
Lines 317-318 (original). The authors have not actually assessed local MHW signatures (which can be done using the aforementioned heatwaveR package). Would be good to do this to determine when this area was actually impacted by MHWs. It could be that the blob didn't impact this particular part of the coast? Without actually analysing the local data it is difficult to say how the blob impacted the area. Also, models can include annual MHW metrics quite simply.

Temperature data were included in the main MS and supplement, although they were not specifically used to quantify MHW statistics. We have added a full MHW analysis using heatwaveR to the Supplement, with some text in the results (Section 31.). The MHW signature is evident in the 2014-2016 period.

Line 320-321 (original): MHWs are defined as periods of 5 or more days with anomalously warm water. Averaging by month may not pick up these discrete periods.

See above.

Typo- 's'

Fixed

Lines 344-354 (original): I don't think the latin names of urchins have been linked to common names before this paragraph? It would be good include the latin and common together in first instance.

True. Added.

Line 616: Is the drop to 2.2m at 5m depth or 10 m depth?

To clarify we have altered the text from:

"This trend was largely driven by Tatoosh Island where the density of purple urchins increased from near zero to 4.4 m^{-2} in the 5-m depth zone in 2021 and to 9.5 m^{-2} in the 10-m depth zone in 2019 before dropping to 2.2 m^{-2} in 2021 (Fig. S7)."

To:

"This trend was largely driven by Tatoosh Island where the density of purple urchins increased from near zero to 4.4 m^{-2} in the 5-m depth zone in 2021. In the 10-m depth zone, urchins increased to 9.5 m^{-2} in 2019 before dropping to 2.2 m^{-2} in 2021 (Fig. S7)."

Line 351 (original): what year/period of time is 'earlier levels' referring to? Pre 2015?

Deleted "earlier levels".

Line 622: consider changing the word cryptic since this is usually linked to cryptic species where as in this instance I believe you are talking about hidden individuals.

Changed to "hidden"

Discussion
I think the authors are pinning too much of their explanation of changes in kelp and associated faunal densities onto events that have happened in the area (MHWs, SSWS). At no point have the authors made an attempt to quantitatively link the events with algal/invertebrate/fish shifts. The shifts over time are interesting in themselves and although events occurring in the area can be discussed as potential contributing factors, without including evidence, and without following standard definitions of MHWs, it is impossible to link x directly with y.

We agree with the reviewer that the data and analyses we have presented do not lend themselves to attribution of MHW and SSWS impacts on kelp forest community components. Rather, we wish to describe shifts in the Washington kelp forest communities we observed over a time period that has been widely studied due to a massive MHW and SSWS. Admittedly, this coincidence of our sample frame and these major perturbations makes walking the line difficult. In the revised MS, we focus on how Washington communities changed (or didn't) during the 2014-2016 MHW and SSWS period. We do not purport to attribute individual MHWs as causal (or not) to these community changes, however we do note that while there were substantial effects in other areas of the coast (esp Northern California) during this time period we did not see substantial changes in kelp off Washington. We feel that the title and introduction are clear on this approach.

Prior analyses (eg, Pfister et al 2018, cited in the MS) have examined longer-term time series and investigated the potential role of temperature and other environmental drivers on kelp abundance. So, we do not repeat these analyses here (they are the same data for SST and the canopy data). Additionally our subtidal dive data are too short a time series for any major attribution analysis. However, we did add the more formal MHW analysis to the MS, as noted above. For example, we changed the title to:

"Changes in kelp forest communities along the coast of Washington, USA during and after the 2014-2016 marine heatwave and sea star wasting syndrome"

Lines 483-486 (original): I agree – this is an important piece worthy of publication simply because it expands our knowledge on kelp communities in the local area.

Thanks.

Lines 487-502 (original): Again, I do not believe temperature patterns can be linked to MHWs unless they follow some specific criteria of what a MHW is.

See above. We are not analyzing MHW but the regional response to THE 2014-2016 MWH. However, a formal MHW analysis has been added to the MS to better document impacts on the WA coast.

Line 799 (original): Where has this data come from?

This is a reference to the kelp canopy data. These data are fully described in the methods and presented in Figure 1 and in the Supplement.

There is a reference for Oregon but not for California?

The reference is to Hamilton et al 2020 who first discuss the difference in SST between Oregon and California and provide the summarized data in their Table 1. We have shifted the reference to remove the confusion.

Have you considered a) local temperatures in relation to species thermal range? Or location within the species range? Typically, declines in abundance during a MHW event are more common towards a species warm-range edge as here they are more likely to experience temperatures outside the species thermal range (see work by Michael Burrows from the Scottish Association of Marine Sciences).

Both taxa are in the central portions of their range in WA (see Smale 2020). This has been noted in the text at lines 332 and 784.

We are not aware of a lot of information on thermal tolerances for these species. However, Camus & Buschmann 2017 and Supratya et al. 2020 (included in Section 2.3) suggest that growth for both species may decline above 15C with temperatures above 18C resulting in failed sporophyte production for Nereocystis. We have added a calculation of the number of 15C days to the MS in Table S6 and text in the Methods (Section 2.3) and Results (Section 3.1).

Added a reference to Burrows et al 2020 at line 784, Now reads:

"Our study region is far from the range margins for *Macrocystis* and *Nereocystis* (Smale 2020), so we might expect them to be well within their thermal thresholds at our sites (Burrows et al. 2020) resulting in a somewhat ephemeral and muted response to the MHW.."

Line ~850: What time of year do they reproduce? What was the temperature relative to other years at this time of year?

We are unaware of information on the timing of reproduction and settlement of urchins off the Washington Coast. Most of the information comes from California. The gonadal index for purple urchins in southern California is highest in October and November following feeding in the summer (Basch & Tegner 2007). So we might expect spawning to occur sometime in the winter or early spring. In Central through Baja California, the annual reproductive cycle seems to be the same (as noted in Basch & Tenger 2007), probably due to the need to feed during the summer/early fall when kelp, and drift kelp, are abundant. So we might expect similar patterns in WA.

Recruitment is less clear. Larvae can spends weeks to months in the plankton where they feed on phytoplankton, and the timing of settlement appears related to the spring phytoplankton bloom (Okamoto 2020). In California settlement occurs in ca. May in many areas in the south. However, in

the north, settlement occurs in both March and July (Okamoto 2020). This latitudinal variation makes extrapolating to the WA coast somewhat difficult.

There does appear to be an upper limit to gametogenesis around 17C, but temperatures did not approach that threshold on the WA coast, rarely passing 15C.

We have added the following to at least direct the reader to relevant literature line 853:

"In southern California, gonadal indices for purple urchins tend to peak in October and November following summer feeding, so warm waters in the fall might impact gamete production (Basch & Tegner 2007). However, temperatures in Washington did not approach 17°C where gamete storage appears to be reduced (Basch & Tegner 2007)."

'did full crash' is not correct English

Should be 'did not fully crash'. Changed.

Line 554-558: see comment above about position in range.

See response above.

Line 965: consider changing 'shocks' to 'stressors' or similar.

done