**About this document:**

Reviewer comments in red.

Author responses in in black.

**REVIEWER 1**

**Q 4**

**Does the title clearly and precisely reflect the findings of the manuscript, as described in the author guidelines?**

**Reviewer 1** | 14 Sep 2017 | 01:13

Mostly, but perhaps adding "and environmental drivers" at the end would better reflect the contents of the paper.

**Author**: Albertus J Smit | 24 Oct 2017 | 10:34

We considered this suggestion. Since Reviewer 2 did not find this problematic, we decided not to change the title in favour of the current version, which we feel is 'catchier' and more concise. We think that the statement before the colon "Seaweeds in Two Oceans" provides the context within which the patterns of beta-diversity are assessed. We argue in the paper that the major effect that the two oceans have is in setting the thermal properties of the coastal seawater, which then structure beta-diversity.

**Q 6**

**Please comment on the Introduction section. Key elements to consider:  
- appropriateness of context  
- purpose of study**

**Reviewer 1** | 14 Sep 2017 | 01:13

Adding a paragraph to describe factors other than temperature that may affect beta diversity would make the study more interesting, as temperature is a well-known factor structuring the biodiversity in the study regions.

**Author**: Albertus J Smit | 24 Oct 2017 | 11:34

We agree that some factors aside from temperature may be influential. These were considered when we planned the research question. In the light of the reviewers' concerns, we again thought about such additional drivers, and considered including them in an actual expanded analysis... ***but we remain of the opinion that we should not include such an analysis here now***. We have, however, made some minor edits/additions to a few lines (lines **57** to **61** in the revised manuscript’s Introduction, and later also again in the Discussion in lines **304** to **305**, and lines **315** to **319**) to alleviate the reviewers' concern that additional possible drivers were not acknowledged; we trust this will address the same concerns raised elsewhere by this reviewer and also by Reviewer 2.

Specific points addressing the reviewers’ concerns, but which we feel are too detailed to warrant inclusion in the manuscript:

***Nutrients*** are largely correlated with temperature (we have added reference to a paper by Waldron and Probyn (1992) to back this up). I have actually used ***chl-a biomass*** in an early version of the analysis (in the sense that it should be higher where nutrients are higher, i.e. I used it as a proxy for nutrients). But it turns out that both chl-a and nutrients (again see ref to the Waldron/Probyn paper) are so strongly co-correlated with temperature, that this effect is impossible to demonstrate as having an effect on the seaweed beta-diversity. We also cited the Tittensor et al. paper of 2010 and the one by Stuart-Smith et al last year (added in line **58** in the revised manuscript) that clearly show how temperature offers the best explanation for global biogeographic patterns across 13 taxa of marine organisms. We think this holds true here for seaweeds too (as in Stuart-Smith et al. 2016). Generally the effect of nutrients is on productivity and perhaps also on standing biomass, but not on diversity.

***Salinity*** (mentioned by one reviewer) is interesting to oceanographers looking at where the different currents go. There are differences in salinity between the Benguela and Agulhas currents, but the differences are so small that they do not affect biogeographical distribution of macroalgae. People have shown salinity to be a biogeographical factor. It is in places with strong salinity gradients, such as the Baltic (Middleboe et al. 1997). Some words added about this – see line **58**.

***Turbidity***. This is also very likely to have links with nutrients (via chl-a, or lack of in the case of fresh upwelled water) and hence temperature. More nutrients (which goes with cooler water), more chl-a production, more turbidity. In SA we have no major rivers (except perhaps Orange at Section 1, but nothing anomalous w.r.t. beta-diversity emerges there); in none of the 50km sections is turbidity extensive enough to influence an entire 50km stretch of coastline. Places where turbidity affects things at a biogeographical scale are where there are big rivers (Amazon is the best example – 50km is nothing there!); in SA the estuaries are most prevalent along the east coast, but they are small, localised entities (the majority temporarily open/closed estuaries) and their effect extends perhaps a km or two m along the shore, not 50 km. A few words added to this effect too –line **58**.

***Wave action***. The SA coast is generally quite wave exposed, but in all 50km sections there are sheltered bays where we can find the (relatively few) sheltered water species, so we don't see how wave action can affect the data. The seaweeds were collected at all wave levels at each sampling event, so a sampling bias is unlikely to indicate this effect.

The reviewers are confusing community ecology with biogeography, which have different drivers (*also see further comment under Q 17)*. The reason for choosing 50km coastal sections is that we are then working on a biogeographical scale, with presence/absence data (deliberately). This means that factors that affect seaweed abundance are not important unless they also affect presence/absence at a 50km scale. All 50km coastal sections will have the full spread of wave exposed to relatively sheltered shores (in the South African context).

***Photoperiod***: More about day length is said in response to a question by Reviewer 2’s *Q 3*.

***Reference mentioned above, but not cited in the text:***

Anne Lise Middelboe, Kaj Sand-Jensen, and Klaus Brodersen (*1997*) Patterns of macroalgal distribution in the Kattegat-Baltic region. Phycologia 36, 208-219

**Q 7**

**Please comment on the Material and Methods section. Key elements to consider:  
- objective errors  
- correct choice of methods  
- comprehensive description of methods  
- accuracy of procedures  
- quality of figures and tables**

**Reviewer 1** | 14 Sep 2017 | 01:13

Mostly fine, but again I feel that the authors should not consider only temperature, although this factor will certainly have high correlation with beta diversity.

**Author**: Albertus J Smit | 24 Oct 2017 | 11:35

Please see our discussion under the previous point, which also addresses the point raised here.

**Q 12**

**Please comment on the Results section. Key elements to consider:  
- objective errors  
- correct presentation of results   
- quality of figures and tables**

**Reviewer 1** | 14 Sep 2017 | 01:13

Appropriate mostly. But please see my comments on the study design.

**Author**: Albertus J Smit | 24 Oct 2017 | 11:39

**Draft**

We have covered this earlier – the omission of additional drivers is a recurring theme here, and we have already dealt with it above. Not having considered the additional drivers (i.e. by not acknowledging their existence) cannot be called objective errors, incorrect presentation of results, or poor quality of figures and tables, so we do not need to elaborate further on this here.

**Q 13**

**For any complementary data (e.g. nucleotide/amino acid sequences, crystallographic or NMR data, RNAseq) submitted to an online repository or database, do the author(s) provide the accession number?**

**Reviewer 1** | 14 Sep 2017 | 01:13

No  
The authors should make the data available. They mentioned Appendix A for the diversity data in text, but I did not see this file. They did not mention temperature data were included as supplementary material in text.

**Author**: Albertus J Smit | 24 Oct 2017 | 11:40

The data (but not raw data i.t.o. seaweeds) have been made available online at:

<https://github.com/ajsmit/Seaweeds_in_Two_Oceans.git>

We have added a link to where the data may be found on line **145** to **146** of the revised manuscript. All the data processing scripts are also accessible there.

**Q 15**

**Please comment on the Discussion section. Key elements to consider:  
- adequate discussion of research questions or hypothesis (posed in introduction)  
- conclusions supported by data  
- exhaustive discussion of previously published material (in context to current study)**

**Reviewer 1** | 14 Sep 2017 | 01:13

please see my final comments

**Author**: Albertus J Smit | 24 Oct 2017 | 11:41

We will cover these as they arise under "Final comments" below.

**Q 17**

**Please provide your further comments and overall recommendation to the authors, including the level of revisions (minor, moderate, substantial).**

**Reviewer 1** | 14 Sep 2017 | 01:13

This project aimed to understand the mechanisms that structured seaweed communities along 2,700 km of South Africa's coastline. The authors contrasted the seaweed beta diversity patterns in relation to a thermal gradient produced by the current systems in the region. To do this, they subdivided the coastline into regions and for each region they obtained data on the seaweed diversity and thermal data. Their analyses showed that the spatial and environmental predictors explained ~98% of the total variation in Bsim and the thermal gradient explained 84% of this data. They found that Bsim was the major component of beta-diversity in the Agulhas Current region, but there was a much weaker thermal gradient in the Benguela Current region. They then suggested that the intensification of upwelling during the mid-Pliocene were likely responsible for the remarkable disjunction between the beta diversity of the Atlantic and Indian Ocean influenced sides of South Africa. Overall, I feel that the manuscript was well-written, and the results were in general supported by the analysis of a large amount of data. However, I have one major concern about the design of this study regarding the factors used. Although the authors have considered several factors (the means for the year, February mean, August mean, annual standard deviation), they are different forms of temperature. It is well-known that temperature is the structural force for setting up the diversity of the two coastal regions in South Africa. from previous studies, therefore the novelty of the results is not high to me. Other factors, such as nutrient concentration and salinity, which potentially will influence the beta diversity, have not been considered. Intuitively, I would expect that these factors might also contribute to the variability of the diversity patterns along the coast. Specifically, salinity and nutrient concentrations should be considered in the modelling as they would affect the biological interactions that determine the diversity, especially in the upwelling regions and estuarine areas. In summary, I appreciate the large dataset and modelling approach used, but the novelty of this paper is limited if only temperature data are included in the modelling.

**Author**: Albertus J Smit | 24 Oct 2017 | 11:56

Many of these concerns were raised before, and we have comprehensively dealt with them under *Q 6*, above. To this end, we have added some lines of text acknowledging the possible existence of some other drivers that might link with beta-diversity patterning, but we think we have also provided sufficient justification for omitting these influences from the current analysis. Many of these things are so strongly correlated with temperature that their influence cannot conclusively be demonstrated (unless we use an experimental approach, which is not within the scope of this present paper), or their magnitude in variation is so small that for all practical purposes they will have no measurable influence on beta-diversity. The multitude of thermal drivers is already complex enough to explain, and we think that adding more complexity will distract from the intention of the study – that is, to link properties of the two oceans (the Indian and the Atlantic, or the Agulhas and the Benguela currents) to outcomes at the seaweed composition (biogeography, and especially beta-diversity!) level.

We don't agree that this study is not novel. Granted, the effect of temperature on global and regional biodiversity gradients is well known; less well known are consequences for beta-diversity (this paper); to the best of our knowledge only a small handful of papers has considered this for ocean biota (far more numerous are terrestrial studies along moisture or elevation gradients, for instance). These few marine studies are mentioned in lines 44 to 60 of the original manuscript. A study of beta-diversity is different from simply looking at biodiversity (or old-fashioned species richness). By looking at beta-diversity, we can shed some light on the 'forces' that structure biodiversity (i.e. turnover and nestedness-resultant species assembly processes). Reviewer 1 (and maybe also Reviewer 2) missed the point of one of our aims, i.e. "We were primarily interested in establishing how ***these ocean currents may have influenced the species assembly processes*** operating along an approximately 2,900 km long coastline." Temperature is directly linked to these ocean currents, and that is how the currents' influence can be detected along the shore – in the temperature profiles and the other thermal properties of the nearshore water.

**REVIEWER 2**

**Q 17**

**Please provide your further comments and overall recommendation to the authors, including the level of revisions (minor, moderate, substantial).**

**Reviewer 2** | 12 Oct 2017 | 10:17

This paper evaluates patterns in biodiversity from the perspective of beta diversity across environmental gradients at both sides of the South African coasts. I have no doubt this is a good study on biogeography of seaweeds at transitions from cold to warm waters where two oceans interact. Overall, the paper is well structured and written and I really enjoyed the methods authors used. I have to admit, however, that the methods maybe harsh to follow due to their complexity. I have a range of comments and ideas I would like to express to authors, so they can even improve their actual draft.

1. Authors are using compositional data (presence-absence), so the term “community structure” should be replaced by “composition” through the entire ms.

**Author**: Albertus J Smit | 24 Oct 2017 | 12:03

Agreed. Corrected.

2. As the two coasts are very different in their accessibility, as far as I know, I wonder whether the sampling effort is similar between both coasts, or there is coast with a larger study effort, which could have blurred some patterns.

**Author**: Albertus J Smit | 24 Oct 2017 | 12:03

The records cover historical collections as well as our recent collections (over the past 3-4 decades). A large project in the late 1980s and early 1990s produced a detailed flora of west coast seaweeds (Stegenga et al. 1997). This was followed by detailed work from the mid-1990s to mid-2000s on the seaweeds of the east coast (Bolton et al. 2001, De Clerck et al. 2005) and since then by detailed work on the south coast in between (Anderson et al. 2005, Anderson et al. 2016) – these references are already cited in the paper. Study effort is therefore deemed similar around the coastline.

3. Authors consider differences between both coasts from the perspective of varying thermal climatologies (line 81). However, a range of factors covariate across these large-scale gradients, e.g. nutrients, day length, etc., so they should not overstate the effect of temperature relative to other covarying factors. My impression is that authors have a tendency to give temperature a large explanatory power.

**Author**: Albertus J Smit | 24 Oct 2017 | 12:03

We have already covered much of this under Reviewer 1’s *Q 6*, and some text was added to strengthen the justification for focussing on temperature only (e.g. see lines **xx** to **xx**). To further our argument, a book came out last year called ‘Seaweed Phylogeography’. Here are quotes from chapter by Straub et al (2016):

“The biogeographic boundaries of seaweeds are largely determined by temperature tolerances, physical barriers and limitations to dispersal.”

“Seaweeds are confined to the photic zone, where temperature patterns are reasonably well understood, allowing species distributions to be compared to oceanographic patterns (Adey and Steneck 2001). Distribution limits of individual seaweed species typically follow major marine isotherms (Van den Hoek 1982; Lüning 1985), giving rise to strong relationships with the temperature signatures of major ocean currents (Wernberg et al. 2013b). For seaweeds, these patterns are a product of two key types of temperature boundaries: lethal boundaries, determined by a species’ capacity to survive during their unfavourable season; and growth and reproduction boundaries, determined by a species’ ability to grow and reproduce during its favourable season (Van den Hoek 1982; Lüning 1985). Seaweeds can be abundant in areas within both boundaries that are within dispersal ranges of the species. However, as thermal windows have changed over geological time (e.g. following ice age cycles), [and so] have biogeographic boundaries and seaweed distributions (Adey and Steneck 2001).”

The above is a strong statement, and ample (further) justification for omitting some of the environmental influences that both reviewers have suggested, in favour of more of the thermal variables (e.g. the average August (austral winter) temperature would cover the lower lethal limits, while the annual or summer temperature would take care of the limits to growth and reproduction).

***About day length***: Day length does not co-vary with temperature at all in South Africa (except perhaps a little on the east coast), but differences are extremely minor. There is evidence (could give you refs if you want) that a few seaweeds have been shown to have life histories which are controlled by short or long days (8 hours versus 16 hours of light per day), but 18 minutes difference in day length per day will not have any significant effect (the latitudinal range is <10 degrees, so hence the very small latitudinal range change in day length).

**Reference**

Straub S.C., Thomsen M.S., Wernberg T. (2016) The Dynamic Biogeography of the Anthropocene: The Speed of Recent Range Shifts in Seaweeds. In: Hu ZM., Fraser C. (eds) Seaweed Phylogeography. Springer, Dordrecht. Pp. 63-96.

4. The seaweeds are intertidal and subtidal? This, and what I said in point 2, should be considered at the start of the methods section.

**Author**: Albertus J Smit | 24 Oct 2017 | 12:03

Yes, they are intertidal and subtidal. The bulk of species diversity is in the low-shore and shallow subtidal. See the added text in line **xx** of the revised manuscript.

5. Why cells are 58 x 50 km? Any reason for this dimension?

**Author**: Albertus J Smit | 24 Oct 2017 | 12:03

They are 50km because for meaningful analysis of large scale biogeographical patterns the scale needs to be large enough to include all habitats. 50km or 100km are generally the scales chosen, and on a coast with areas with rapid biogeographical changes we considered 50km to contain the required detail. There are 58 of them as used by Bolton & Stegenga (2002) to comprise the entire coastline of South Africa using GIS methods.

6. A 98% of explained variation in Bsim seems to be inflated (overfitting of the model)??? Is it my impression that the matrices of temperatures and connectivity (distances) are correlated?

**Author**: Albertus J Smit | 24 Oct 2017 | 12:03

The matrices of temperature and connectivity are definitely correlated, but they were also definitely completely independently derived. The temperature matrix results from decades of *in situ* temperature measurements (i.e. they have a physical basis). The connectivity matrix is a geographic (Euclidian) distance matrix representing the pairwise distances between the 58 sections from which a truncated distance matrix was made based on a Minimum Spanning Tree topology. All the methodology behind the derivation of the matrices is in Appendix B. The reason that distance (the spatial vars) and temperature seem so strongly correlated (Table 1) is because they ARE so strongly correlated. The gradient is strong indeed. The further sites are apart (great geographic separation) the more different the temperature will be. But note (see Table 3), that this is only so for three of the ‘bioregions,’ the B-ATZ, the AMP, and the ECTZ but not the BMP.

Overfitting generally occurs in models that incorporate too many predictors. The fit that has the very high 98% explained variation does indeed contain the full set of predictors, so I imagine there is indeed some overfitting. But the simplified models are also provided for the reader who is uncomfortable with the full model: Table 1 has fits with the temperature variables only (i.e. with augMean + febRange + febSD + augSD), and the fit there is a bit lower at a more comfortable 84%. More specific fits are in Table 3. The purpose of partitioning the variation is in fact to be able to arrive at a credible explanation for what causes the variation in beta-sim along the shore, and the conclusion is that it is temperature properties (which have a strong spatial pattern, i.e. the gradient) that drives the seaweed community composition. (*Note that the model that explains 98% of the variance has 17 spatial vars and 4 thermal vars, while the simpler model has only four vars, all of them thermal. Further, even if we get very specific about the role of individual variables, we see that augMean can explain 77% of the variation in the ECTZ – this is arguably still very high, and the model cannot get any simpler than this!*)

7. The role of currents (line 433) is hard to known, as nearshore circulation is very complex and messy with many influences (tides, exposure to swells, river outputs, etc).

**Author**: Albertus J Smit | 24 Oct 2017 | 12:03

I agree that nearshore circulation is complex, especially in upwelling dominated systems. The powerful Benguela and Agulhas currents nevertheless have an overwhelming effect on even inshore conditions along the SA coast, as comparisons between nearshore and offshore temperatures reveal: the steepness and extent of the thermal profiles mirror 1:1, but their absolute magnitude differ due to the differences in the underlying physical dynamics near the shore (as I explain in Smit et al. 2013). What the reviewer is missing is:

* The ***tidal range*** is similar throughout South Africa.
* ***Exposure to swells*** is dealt with in comments about wave action in Reviewer 1’s *Q 6*. Each ‘sample’ (seaweeds in 50km coastal section) has a wide range of wave action. Most of the coastline of South Africa which is not sheltered to some extent by coastal topography is extremely wave exposed.
* ***River inputs***. There are very few major rivers (exception, the Orange), and all 50km coastal sections have habitats which are very seldom affected directly by river runoff. Again, this was covered previously elsewhere.
* ***Turbidity***. Rothman et al. (2017) has some evidence that waters in N Cape are more turbid than southern W Coast. Nevertheless, over the whole of South Africa, there will be a correlation between temperature and turbidity – warmer water has low nutrients and is clearer.

8. Line 221. Inertia is misspelled.

**Author**: Albertus J Smit | 24 Oct 2017 | 12:03

Corrected. Thank you.