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Rennes, November 8th 2024

PCI Ecology
Editorial office

Manuscript #633

Object: Submission of a revised version of "Habitat structural complexity increases age-class coexistence and population growth rate in fish" authored by Eric Edeline, Yoann Bennevault and David Rozen-Rechels.

Dear Editors,

We very much appreciated the insightful and constructive comments provided by the editor, Matthew Bracken, and by the three reviewers. We sincerely thank the four of them for their valuable work.

We very carefully addressed their comments, which led us to extensively rewrite the whole manuscript so as to improve justification and description for our experimental design, and to emphasize the relevancy of our experimental results to the functioning of real-world ecosystems. In this process, we felt it was necessary to provide readers with additional data and analyses, which led us to:

- perform a 2D image analysis of the geotextile,
- provide detailed information on the structure of the five-layered geotextile mats,
- run an additional behavioural experiment to estimate the effect of the geotextile on medaka movements,
- incorporate data on filamentous algae that we collected in 2022 but omitted to incorporate in the previous manuscript version,
- generally re-emphasize the importance of cannibalism as the key underlying driver of our results.

We feel that these changes sharply improved the quality of our manuscript. As requested, we below provide a point-by-point response to the reviewers' comments.

All persons entitled to authorship have been included and all authors have read and approved the revised version of this manuscript.

On behalf of the authors,

Sincerely yours,

Eric Edeline.

##

Detailed answers to the Editor's and reviewers' comments.
Comments are in plain text, and our answers are in bold text below.

##

This manuscript has the potential to be an important contribution to our understanding of the role of habitat complexity in facilitating associated organisms. In particular, whereas it is well-known that submerged aquatic vegetation enhances the survival of juvenile fishes and other organisms (e.g., Lazzari 2012 Journal of Applied Icthyology; https://doi.org/10.1111/jai.12048), the study reported here extends that concept to highlight the role of complex submerged habitats in protecting juvenile fish (medaka, *Oryzias latipes*) from cannibalistic consumption by conspecific adults. This is an interesting wrinkle, as it merges concepts of foundation species (sensu Dayton 1972; see Bracken et al. 2007 CalCOFI Reports; https://escholarship.org/content/qt1wk4k66d/qt1wk4k66d.pdf) with those of intraguild predation (e.g., Polis & Holt 1992 Trends Ecol Evol; https://doi.org/10.1016/0169-5347(92)90208-S). The reviewers have made a number of suggestions aimed at improving the manuscript, and I look forward to a revised version of the manuscript that incorporates their suggestions. In addition, I would like to see some discussion that links your findings to real-world phenomena. Southeast Asian fish in experimental ponds in Europe that lack any other fish or predator species are interesting from a modeling perspective, but I would like to see some evidence (e.g., from the literature) that similar phenomena could be important in natural systems. Please provide a point-by-point and line-by-line accounting of your revisions.
We are grateful to Dr. Bracken and to the reviewers for their kind, sharp and constructive comments. We made our best to thoroughly address all of the comments. In doing so, we came to the conclusion that further analyses and experiments would be useful to answer the reviewer's questions. Therefore, in addition to reorganizing and rewriting multiple text sections, we further added to our study new data and analysis on pond cover by filamentous algae, which are an important food source for medaka. We also added an in-depth analysis of the structure of the geotextile, as well as an extra experiment on its effects on medaka movements (new Appendix 1). Finally, we provide the details of the analyses showing that medaka strain identity had no significant effect on the results of the 2021 experiment (new Appendix 2). We have updated accordingly the supplementary information on Zenodo, that contains all data and codes to run the analyses and reproduce the figures.

Regarding specifically the generality of our results and their applicability to more natural systems, we now more clearly emphasize throughout the manuscript the importance of cannibalism as being the main driver of our results, and highlight in the discussion that cannibalism is a very common form of interaction, that shapes life histories and population dynamics across a wide taxonomic range, such that our results are likely to be relevant to a large variety of natural systems.

We have the feeling that the revised manuscript is clearer and stronger than its previous implementation, and for this we sincerely tank Matthew Bracken, Joacim Näslund and the two anonymous reviewers.

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Review by anonymous reviewer 1, 17 Jan 2024 23:41

I enjoyed reading this manuscript and the study's objectives, results, and implications are interesting. I hope the authors find my comments helpful.

We were highly stimulated by the reviewer's sharp and constructive comments to the point that we performed an extra 2D analysis of geotextile structure, as well as an extra behavioural experiment to quantify the effects of the geotextile on medaka movements. Furthermore, we now provide extra photographs detailing the structure of the five-layered geotextile mats that we used in 2022. On top of this, we have tried to thoroughly address the reviewer's comments through deeply reorganizing the text so as to improve its clarity and accuracy, and to highlight the generality of our resulted based on the fact that cannibalism is very common in natural systems.

Summary of strengths of the ms:

- The ms is well-written and clear, and tests an important ecological concept.
- The authors effectively apply a variety of models to their experimental results to help explain mechanisms behind the results.
- The figures are nicely done and clearly display the results.

Summary of weaknesses of the ms:

- The authors say little about how relevant their experimental design is to natural ponds and naturally occurring populations of pond fish.
- The authors do not describe or justify their choices for the material used to manipulate structural complexity and for the different treatments. It is not clear how relevant the manipulation of structural complexity is to real systems, and therefore how applicable the results are to real systems.

Section-by-section comments:

Title

The title is descriptive and concise. My only small note about the title (which admittedly is a bit nitpicky) is the use of the word "fish", which implies that the authors evaluated age-class coexistence and population growth in multiple species of fish. They could consider replacing fish with "medaka" (given how common the species is in experimentation) or "a small pond fish" or "a small freshwater fish", etc.

As advised by the reviewer, we have now added "medaka" in front of "fish" in the title, where we now further point to cannibalism as being the main driver of our results.

Abstract

The abstract does a nice job of concisely describing the study's objective and primary results. The sentence on lines 20 – 25 is awkward and the authors could consider making the four results they list here into a numbered list.

We agree with the reviewer that this sentence was not optimal. As suggested, we now use a numbered lists.

Introduction

The introduction is well-written and the study's focus and objectives are articulated effectively. I agree with the authors that intraspecific interactions, and specifically the effects of habitat structural complexity on those interactions, are not as well studied as relationships among predator and prey organisms of different species. The objectives are clear and logical and flow from the introduction.

In the introduction, the authors discuss the idea that large-bodied predators may have limited mobility within structurally complex habitats, leading to lower predator-prey encounter rates and higher prey survival rates. This certainly is a primary way in which habitat structure can dictate the outcomes of predator-prey relationships. They may wish to note that encounter rates also may be reduced via the reduced detection of prey due to the obstruction of vision that structure causes for visually-oriented predators, as described nicely in (e.g.) studies by Bartholomew (such as Bartholomew et al. 2000: MEPS 206: 45-58).

We thank the reviewer for pointing to us this mechanism that we had overlooked. We have now included visual effects in the introduction (line 61) and methods (lines 198-199), and we make multiple references in the text to the very good paper of Bartholomew et al. 2000.

Materials and methods

Cannibalistic assays: this assay is a good idea, and does a nice job of establishing the bounds of cannibalism for adult medaka. But there are a few things that could use clarification for these assays. First, how were the two larvae chosen for each aquarium? Were they purposely of two different sizes/ages, or purposely the same size or age, or randomly selected? It's not clear from the description whether the idea here is to see which of the two larvae (of which one may be larger and one smaller) are selected by the adult (i.e. a prey selection experiment), or whether what is recorded is whether any predation occurred at all (this may be the case, as the authors state that they are using the mean size of the two larvae). If they were recording whether any predation occurred, was it necessary for both larvae to be consumed? If not, how did they account for the fact that the two larvae may have been of different sizes and only the smaller or larger was consumed?

To address all of these questions, we have now clarified the description of the cannibalistic assays in lines 122-136. Specifically, we now explain that (1) both larvae and adults were chosen randomly, (2) that it was not possible to follow larvae individually, and (3) that our experiment was not a prey selection experiment but rather a prey survival experiment in which we followed the changes in survival probability of an averaged-sized prey during 17.5 hours, separately in each aquarium.

I have no objection to the use of artificial structures to manipulate structural complexity, having done this myself in predation experiments. However, some discussion of the realism and relevance of the geomaterial would be helpful in the ms. Why was this material chosen, and how closely does it simulate any real natural vegetative structure? From figure 1, it is apparent that the geomaterial is a floating mat, perhaps unlike naturally occurring structure that may be much more three dimensional. If this is an accurate observation, how may restricting predation to the very top of the water (presumably where larvae are hiding) affect the relevance of the results to natural ponds? Is there a potential shading effect that may be occurring here, that interferes with visual detection of

small larvae? Without this information and insight, it is hard to relate the strong results obtained by the authors to natural systems and natural populations. Additionally, can the authors comment on how characteristics of the artificial structure relate to the mechanisms they introduce in the introduction section? In other words, how effectively does the structure inhibit movement of the adult medaka relative to the juveniles? Is it likely that inhibition of movement is the primary mechanism reducing predation risk, as opposed to impairing visual detection of juvenile prey by adults? Finally, how does their manipulation of habitat structure correspond to what is found in nature? Here what I mean is, the authors created their treatments by using different amounts of the same material, whereas in natural ponds, habitat structure can perhaps differ based on the interstitial spacing between structural elements. In nature this would refer to the spacing between (e.g.) plant shoots or roots, and in the experiment this would refer to the spacing between the strands that make up the material.
We believe that a detailed comparison of geotextile structure with the structures provided by various kinds of natural vegetation is beyond the scope of our study. However, we made our best to address these comments and to provide the readers with detailed information on the structure of the geotextile and on the way it interfered with medaka behaviour. This we did through (1) writing a new Materials & Methods section entitled “Geotextile to manipulate habitat complexity” (lines 165-218), (2) performing a new 2D image analysis of the geotextile and its complex interstice-size distribution (new Appendix 1), (3) performing a new series of behavioural assays to quantify the size-dependency of medaka ability to swim through the geotextile (new Appendix 1), and (4) providing more information on how we stacked geotextile tiles to form geotextile mats during the 2022 experiment (new Appendix 1).

In a nutshell, a floating structure is well adapted to the medaka, which is a surface-dwelling fish species, and resembles surface structures found in natural habitats such as riverbank-tree roots, dead wood, filamentous algae, or surface macrophytes (lines 174-179). We demonstrate that the geotextile selectively hampered the movements of large-sized medaka, just like natural structures selectively hamper the movements of large-bodied predators in multispecies communities (new Appendix 1). Finally, we further discuss the relevancy of floating structures relative to more 3D, maybe more natural, structures in lines 619-622.

Line 193: I was confused about how the geomaterial could have a surface area greater than that of the experimental pond, until I re-read and realized that there were 5 layers of geomaterial used in this complexity treatment. Referring to my comment above about 3 dimensional structure, this treatment seems to be fundamentally different than the others not only in terms of the amount of area covered by the material, but due to the layering which presumably resulted in a thicker layer of habitat structure, creating more of a 3 dimensional “arena” in which the fish could interact.
We re-wrote and re-organized the whole description of the methods so as to clarify this aspect of the experiments (new “Geotextile to manipulate habitat complexity” section), and we now provide a detailed presentation of five-layered geotextile mats in Appendix 1. In particular, we now make it clear that single-layered geotextile tiles had a 12-13 mm deep 3D structure, and that a five-layered mat had a 90-100 mm deep 3D structure, such that most of the water column was unstructured in both low- and high-complexity treatments.

Results

The results are summarized very nicely, and the authors effectively answer many relevant questions about the outcomes of the two experiments. The authors’ interpretations of their results seem reasonable and I am impressed by the use of different types of statistical models to sort through the potential mechanisms that cause their results (in figures 2 – 4). One thing that comes to mind, however, is (again) relevance to naturally occurring populations. While the coexistence of juvenile and adult fish within individual ponds occurs in nature (obviously, because adults reproduce), I

wonder whether there are potential roles of habitat diversity and habitat selection that are present in real ponds but not available to these experimental fish. For instance, in the pond experiment the adult fish seem to be forced to forage within the complex structures provided, whereas in real ponds, they may select to hunt plankton in less complex areas. Can the authors comment (perhaps in the discussion) on whether things like habitat diversity and selection may be an important difference between experimental and real ponds?
We now specify that medaka are omnivorous fish that prefer feeding on zooplankton in open water, but that can eat macro-algae and benthic organisms (lines 103-105 and 621-622). We also now comment on habitat selectivity in lines 622-625.

For table 1, it would be helpful to include some brief text (perhaps in the leftmost column) that reminds the reader what is being modeled, for each model 2 – 5.
Now done.

Tables and figures

The figures are very nicely done, and the captions explain them sufficiently. One small thing, it is hard to see all 8 lines in figure 3 (maybe some of them strongly overlap?).
We have now made the histograms lighter in the background of Fig. 4A, such that lines are more visible.

Discussion

On lines 466-468, the authors state (for the second time) that newly hatched larvae are very vulnerable to cannibalism in unstructured habitats. I agree that their results suggest that a wide range of fish sizes can consume newly-hatched larvae (particularly with male fish), but their assays were conducted in half-liter containers where fish were forced to exist in the same small space. I suggest making clear the distinction between vulnerability as a function of size (in the assays) vs. vulnerability that may be a function of many other things (e.g. habitat selection) in nature.
It seems that the text in lines 466-468 was referring to outdoor ponds, in which some habitat structure was provided, not to behavioural assays in the laboratory. To clarify, we have now removed the sentence referring to the behavioural assays from the discussion. We have further emphasized the importance of vulnerability (lines 598-606) and habitat selection (lines 622-625).

Lines 481-490: this is interesting speculation (that an optimal, intermediate level of habitat complexity exists for coexistence of multiple age classes), however it is based on assumptions that may or may not be true (e.g. whether complexity created in this experiment using artificial structure is lower than that found in many natural ponds). This again comes back to the relevance of the chosen artificial structures for the experiments, which is not discussed in the ms.
As stressed above, we made our best to provide a detailed description of the artificial structures that, we believe, clarifies the relevancy of the geotextile to reproduce (or not) the diversity of structures that may be found in more natural systems.

Specific comments

1. Line 113: tell the reader what CEREEP stands for and where the research was performed.
Now done.

2. Line 132: The word “then” should be “than”. It took me a minute to figure out that this function is parabolic in shape, and the authors may want to mention that.
Now done. We specify in line 410 that the relationship is bell-shaped.

3. Line 191: “in” should be “of”.
Now changed.

4. Line 468: “allow” should be “allows”.
Now changed.

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Review by anonymous reviewer 2, 02 Mar 2024 19:38

Habitat structural complexity increases age-class coexistence and population growth rate in fish
Eric Edeline, Yoann Bennevault, David Rozen-Rechels
General Comments-
Edeline et al. adapt community ecology theories about habitat structure effects on species coexistence to explain habitat structure effects on age-class coexistence within a species. They test their theories with small “medaka” fish in intra-specific predation trials and mesocosms with high or low amounts of structure. The statistical approaches used are rigorous and complex, difficult (for me) to follow, and at times seem to eclipse the eclipse the rigor of the experiments themselves. However, the approaches taken are effective in evaluating the predictions of the authors’ theories, which are upheld by their results. Importantly, increasing habitat complexity has strong positive effects on juveniles and weak negative effects on adults, such that overall population productivity and carrying capacity are increased by habitat complexity within the range tested experimentally. It is postulated that productivity might decline at very high levels of habitat structural complexity seen in the wild, but this was not seen in the experiments. The quality of the writing is excellent, and while their methods are somewhat clouded in complexity, the authors clearly explain the importance of their findings to the discipline of ecology and to global conservation endeavors. This work merits wide dissemination and should be of broad interest, though it could be improved by some revisions discussed below.

Specific comments-
Lines 51-62- Some disclaimers to the generality of habitat structure reducing predation should be included. E.g., small bodied prey may avoid macrophyte habitats where such habitats harbor ambush predators (Schultz et al. 2009, https://doi.org/10.3354/meps07779).
We have now added a reference to ambushing and to Schultz et al. 2009 in line 63.

Line 62- It might be helpful to add a brief explanation of apparent competition; negative indirect interactions between victim species that arise because they share a natural enemy. As an alternative reference to Holt’s 1987 paper you could cite the Holt and Bonsall 2017 review of apparent competition. https://www.annualreviews.org/doi/abs/10.1146/annurev-ecolsys-110316-022628
We now define apparent competition in lines 67-68.

Line 67- Citations might be needed after “age classes” to support the statement made in this sentence.
We have now added a reference to the excellent book edited by Ebenman and Persson (1988).

Line 147- Does the term “geomaterial” have a single, accepted and widely understood definition? If not, then just “material” might be more appropriate here.
We have change “geomaterial” to “geotextile” throughout the manuscript.

Line 163- It’s not made clear here why such variable numbers of fish (18-60) fish were introduced to the ponds in experiment 1, despite the later importance of these variable numbers to inferences

made about density dependent population growth rates. Was this planned or fortuitous? Why were stocking numbers not varied similarly for experiment 2?
We now clarify in lines 233-244 that the 2021 experiment was a pure-strain experiment, and medaka were available in various numbers per strains to initiate pond populations. In contrast, the 2022 experiment was the first year of a long-term experiment, which we initiated with an homogeneous strain mixture and equal fish number among ponds (lines 255-258).

Line 173- I understand that no significant effect of strain was found, but I'm not sure the statistical power to detect a strain effect was high enough to be useful. I.e., it seems like the possibility of a type II error in this test would have been pretty high.
We now provide the details of the analyses in Appendix 2 (as well as data and codes in the supplement).

Lines 199-214- The description of Model 1 is hard for this non-statistician to follow and would benefit from additional annotation. For example, a sentence or so with a less technical explanation of the purpose of the model would help.
Now done in lines 271-273.

Line 215-292- Similar issues here: some additional annotation regarding why the particular statistical methods were chosen for models 2-5 could be helpful. It would also be helpful to more fully describe the purpose of each model before describing its structure. An overview of the integrated modeling approach at the beginning of the statistical analyses section (Line 199) would also be helpful; describe the forest before describing each tree.
We have now improved the rationale for the different modelling approaches in lines 292-297 and 318-322.

Table 1- Models are identified by number (2-5) and "Response" (a mathematical term). I think it would be helpful to also have a name for each model, e.g., "Model 2- Population growth" "Model 3-Fish length" etc.
Now done in the first column of Table 1, also as an answer to a comment from reviewer #1.

Figure 4- It's unfortunate that the levels of N(t) for the 2021 experiment are not matched for the low complexity and high complexity treatments in that year. It's also interesting that N(t+1) seems higher for both complexity treatments in 2021 than 2022.
We now specify in lines 234-236 that the levels of N(t) for the 2021 experiment were not significantly different among the low- and high-complexity treatments. Please, note also that the experiment effect (2021 vs. 2022) on N(t+1) (as well as on body sizes) is accounted for in all our statistical models.

Line 396- Here an explanation of Model 2 is given, which I think would be more helpful in the methods section.
Now done, see our answer above.

Line 399- The term "production" is used in this manuscript without clarification as to how it is operationally defined. Secondary production generally refers to change in heterotrophic biomass of a population over a time interval, and therefore accounts for changes in both population numbers and body size distribution over that interval. Here perhaps the term is used to refer just to changes in numbers without incorporation of mass? That should be clarified, or a different term should be used.
We indeed used the term "production rate" to qualify the ratio between number of age-0+ fish at time *t*+1 and number of age-1+ fish introduced at time *t*. We now make this clearer in lines 320-321.

Line 474- It's odd that shallow areas are considered "absolute predation refuges." They may be absolute refuges from larger conspecifics, but they are certainly not refuges from wading birds. This could be mentioned.
We have now changed the sentence in lines 622-625 to specify that refuges are intended against cannibalism.

Line 500- Evidence should be cited at the end of the sentence that begins with "Ample evidence demonstrates…"
Now done, and sentence rephrased in lines 649-653.

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Review by Joacim Näslund, 05 Mar 2024 05:40

Title and abstract

Does the title clearly reflect the content of the article? [x] Yes, [ ] No (please explain), [ ] I don't know
Does the abstract present the main findings of the study? [x] Yes, [ ] No (please explain), [ ] I don't know

Introduction

Are the research questions/hypotheses/predictions clearly presented? [x] Yes, [ ] No (please explain), [ ] I don't know
Does the introduction build on relevant research in the field? [x] Yes, [ ] No (please explain), [ ] I don't know

Materials and methods

Are the methods and analyses sufficiently detailed to allow replication by other researchers? [x] Yes, [ ] No (please explain), [ ] I don't know
Are the methods and statistical analyses appropriate and well described? [x] Yes, [ ] No (please explain), [ ] I don't know

Results

In the case of negative results, is there a statistical power analysis (or an adequate Bayesian analysis or equivalence testing)? [x] Yes, [ ] No (please explain), [ ] I don't know
Are the results described and interpreted correctly? [x] Yes, [ ] No (please explain), [ ] I don't know

Discussion

Have the authors appropriately emphasized the strengths and limitations of their study/theory/methods/argument? [x] Yes, [ ] No (please explain), [ ] I don't know
Are the conclusions adequately supported by the results (without overstating the implications of the findings)? [x] Yes, [ ] No (please explain), [ ] I don't know

Detailed comments

The reviewed preprint is a neat study on environmental complexity, combining mesocosm and lab experiments.

The investigators find that structural complexity is important to limit cannibalism, which leads to higher population densities and a higher competition pressure (fish consequently grow slower).

I think the majority of the presentation is good, and I have only a few comments to make - none being particularly severe in nature.

In the introduction, something about rivers could be mentioned when introducing habitat simplification - rivers are important freshwater habitats and are very often heavily modified (channelized), leading to lowered complexity. Channelization could be due to hydropower (rapid removal of water downstream; relating to both modern and old hydropower systems, electricity production, mills, saw mills etc.), shipping, urban development or log-driving (N. Europe and northern N. America). A brief mention of rivers is warranted, in my opinion.
Now done in lines 49-51.

In-text references need to be polished since some initials still remain (e.g. line 52 "F. E. Smith").
This was done automatically by Zotero for some citation styles when synonymies appear among different authors (there are different Smith in our reference list). We have changed the citation style such that initials are now removed from this citation.

L 56 and forward: The essence of structural complexity effects on biota is presented as complexity facilitating predator avoidance. This is only true if the main predator itself is not benefited by the complexity, which would be the case for e.g. predatory dragonflies (drawing upon my own work, an example can be found in Mocq et al. 2021 (https://doi.org/10.1111/1365-2656.13473), but there are other examples as well. Furthermore, complexity is also likely increasing substrate area, leading to potentially higher production of primary producers and sessile animals, and in addition the niche diversity could possibly also be increased by addition of complexity (especially when previously absent). We discuss these things in our work Soukup et al. 2022 (https://doi.org/10.1002/wat2.1575). The latter paper may be interesting from the perspective of the reviewed manuscript, but I would in no way want to force the authors to cite it (and neither the previously mentioned paper). I simply relate to these papers because I know them well.
We now more clearly acknowledge that predators themselves can benefit from complexity through reduced risk of prey overexploitation at all trophic levels in lines 66-68. As suggested, we now further emphasize the effects of complexity increasing the niche space in lines 54-57. Also, we now refer to the excellent review by Soukup et al. 2022, which we were not aware of, in both the introduction and discussion. In the later, we highlight that increasing substrate area may lead to higher production of primary producers and sessile animals in lines 591-592.

Relating to Figure 4A, I would suggest to expand the axes to 0. For this panel, 0 is a relatively important location in relation to the data plotted. I'd also suggest to extend the predicted line (but not the credibility intervals) so that they reach $N(t) = 0$ - for clarity about what the regressions look like outside of the data. For panel B, 0 is irrelevant, since no fishes have a length of 0 mm - hence, no changes are suggested for this panel.
Now done. This indeed improves the figure. We preferred extending credible intervals down to zero also, because the zero constraint on stock-recruitment relationships forces credible intervals to remain realistic in the zero-to-data range.

Other than that, I do not have any issues to raise. I think this is a very good pre-print.
Thank you!

Sincerely,

Joacim Näslund, Swedish University of Agricultural Sciences

Review by Thomas Guillemaud, 09 Feb 2024 15:42

It's all perfect. The authors solved all the issues I raised in my previous comments (see attached pdf file). Consequently, every question on the checklist below has a “yes” as a reply.

1- Can we get the data and script from the links indicated in the submission form or from the article itself? ==> YES

2- Is there a readme file? ==> YES

3- Are there metadata for the data and comments for the scripts? ==> YES

4- Are the readme, and data files understandable by a normal reader? ==>YES

5- Do the scripts run on the data? ==> YES

6- Are the results the same as in the paper? ==> YES

In summary, data and scripts are available, clear, and understandable. Scripts properly run on data. The results obtained from the scripts are the same as in the article.

I thank the authors for their very clear, detailed, and precise work.