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PROCEEDINGS B

# Ecological regime shift preserved in the Anthropocene stratigraphic record

Adam Tomašových, Paolo G. Albano, Tomáš Fuksi, Ivo Gallmetzer, Alexandra Haselmair, Michał Kowalewski, Rafał Nawrot, Vedrana Nerlović, Daniele Scarponi and Martin Zuschin

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**Review timeline**

| | |
|---|---|
| Original submission: | 14 October 2019 |
| 1st revised submission: | 27 March 2020 |
| 2nd revised submission: | 22 May 2020 |
| Final acceptance: | 24 May 2020 |

Note: Reports are unedited and appear as submitted by the referee. The review history appears in chronological order.

# Review History

## RSPB-2019-2402.R0 (Original submission)

### Review form: Reviewer 1 (Steven M. Holland)

**Recommendation**
Accept with minor revision (please list in comments)

**Scientific importance: Is the manuscript an original and important contribution to its field?**
Excellent

**General interest: Is the paper of sufficient general interest?**
Excellent

**Quality of the paper: Is the overall quality of the paper suitable?**
Good

**Is the length of the paper justified?**
Yes

**Should the paper be seen by a specialist statistical reviewer?**
No

**Do you have any concerns about statistical analyses in this paper? If so, please specify them explicitly in your report.**
No

**It is a condition of publication that authors make their supporting data, code and materials available - either as supplementary material or hosted in an external repository. Please rate, if applicable, the supporting data on the following criteria.**

**Is it accessible?**
Yes

**Is it clear?**
Yes

**Is it adequate?**
Yes

**Do you have any ethical concerns with this paper?**
No

**Comments to the Author**
In this manuscript, the authors demonstrate that the most recent fossil record of the Adriatic Sea preserves decadal-scale changes in body size of the bivalve Corbula gibba. They also make a convincing case that these changes are linked to increasing frequency of hypoxia events. This is a remarkable demonstration from one of the best data sets available for the latest Pleistocene to modern shelf settings. As such, it has important implications for understanding modern biotic changes in the oceans, especially in areas where historical records are lacking.

The patterns are well-documented, and the interpretations are well-supported. I have no substantive criticisms of what the authors argue from the data. The manuscript is methodologically sound, and I have no suggested changes to the analyses. Threshold regression is appropriate, and using the adjusted R^2 and F-tests is a standard way of avoiding overfitting. Even so, the breaks implied by this approach are quite subtle. For example, looking at the time series in Figure 2A, I'm certain I would not have guessed that the breaks would exist where threshold regression placed them. Finally, the authors include all of the shell size data in the supplemental material, an admirable level of openness that I wish was standard.

My main concerns are not on the data and their interpretation, but on how the manuscript is pitched, the comparison of modern to ancient extinctions, and the writing overall. I highly recommend publication once these issues are addressed, which will require some rewriting of the beginning and ending of the manuscript. I regard these as minor revisions in that no re-analysis or re-interpretation of the data is required.

1) The manuscript is pitched towards comparing modern and deep-time biodiversity crises (lines 30–31, 41–44, 64-81, etc.). The problem in the deep-time record is only partly a matter of time resolution within beds. The second and potentially much bigger problem is the stratigraphic context of most major biotic crises (the K-Pg is perhaps the best exception). Deep-time events are consistently associated with surfaces that reflect prolonged erosion, non-deposition, or stratigraphic condensation. Just as importantly and often glossed over, these surfaces record significant changes in depositional environment and their associated communities. As a result, stratigraphic columns are rarely if ever simple time series (see 48–50), as they reflect sampling from completely different environments with nearly non-overlapping communities. Even if every bed has decadal-scale time resolution, it would not address the challenges posed by stratigraphic architecture.

What the fossil record preserves at ancient mass extinctions would be like having a record of modern ecological change up through the 1950's from a mesic forest, followed by a record beginning in the 2000's from grasslands. Time is missing from that data series, but the more severe issue is that the record is from fundamentally different communities. Even with perfect time resolution in this data set, the time points before and after the extinction cannot be compared.

As such, it is highly misleading to imply that we could now read the fine-scale record of deep-time events as an accurate chronology of that event in a single environment. I recommend dropping that pitch and focusing on what this manuscript significantly offers, that the most recent fossil record is a high-quality archive of ecological change (as the manuscript argues well beginning on line 82). That alone makes this a valuable contribution to Proceedings of the Royal Society B.

2) The manuscript makes conflicting statements about the scope of the modern biodiversity crisis relative to ancient mass extinctions. The text begins by stating that the emerging biodiversity crisis is comparable to ancient mass extinctions (47, 60–62). Shortly after this, it suggests that equivalence is an unanswered question (64–66). Near the end, the manuscript states that the modern crisis is not of the same intensity as ancient mass extinctions (355–356). I'm not aware of any fair comparison that indicates that modern rates of change are comparable to ancient ones (fair in the sense that they compare the same settings, in settings where we have a good fossil record). The data I've seen suggests we are thankfully nowhere close to the shocking calamities of the past (but give us time...). Regardless, the entire issue of how the modern compares to the ancient goes away if the authors focus on the record of relatively recent ecological changes in the youngest fossil record.

3) My main criticism with the manuscript is that the text and the figures are frequently hard to understand. For example, many sentences are too long and convoluted (e.g., 109–112, 116–123, 130–134, 135–143, 152–157, 345–350, 564–569, and many others). I found myself reading these multiple times to understand them. Splitting them would make these much easier to parse. The figures are complex, which is not a problem in itself, but the captions could do more to help the reader understand what is shown in the figures. Many of the captions describe what is to be learned from the figure, but they don't describe what is being shown. Many of the figures have numerous lines, but these are described in the captions rather than labeled directly on the figures.

It is possible that some of my comments below represent my misunderstandings. If what I suggest is incorrect, it is likely because I found the text hard to follow.

Minor comments, keyed to line numbers:

38: enemies: predators?

54: should this be highly time-averaged?

109: shifts (typo).

130–133: It would help to lay out the three main time increments in order, and with their corresponding age spans: TST, HST, and the Anthropocene (which should be described as the latest part of the HST). These are outlined on 167–172, but this should be defined the first time these terms are used.

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Figure 1A: The caption indicates that there are three types of distributions (black, gray, and white), but I see only two: dark (the lower of each pair) and light (the upper). In addition, it is unclear what the arrows under the light size distributions indicate.

Figure 1B: The caption is quite difficult for me to parse, and I'm still not sure I follow it correctly. I think the authors are trying to say this: "... separation between two groups: the first group consists of transgressive (TST), highstand (HST), and shallow-water (< 10 m) Anthropocene sites (white triangles), and the second group consists only of deeper-water (> 10 m), high-sedimentation Anthropocene sites (white circles). High-averaging Anthropocene sites bridge these two groups." Even this, though, raises the question of whether there are deep-water low-sedimentation sites. Part of the problem is that it seems like certain groups are described in different ways: for example, the caption refers to the white circles as "sites > 10 m water depth with high sedimentation rates" but the figure refers to these as "Anthropocene (ANT) (low averaging)"; a consistent set of terms should be used to connect the text, caption, and figures. The final sentence would be clearer if it stated "sites with high time averaging are based on shells that have periostracum and those that do not" (based on what is described in lines 172–176).

Figure 2: This figure is complex, and the caption should begin by stating what is being plotted, rather than doing this in the second sentence. The caption also describes the relationship of these patterns to sedimentation rates, but the sedimentation rates are not indicated on the figures, so it is hard for readers to make the connection themselves.

Figure 3: The last sentence was unclear to me, and the phrasing suggests that some of the points are based on six cores and others on the three sites with paired cores, but which is which?

Figure 4: In the last sentence, is this all the localities, or were some excluded? If so, why?

Supplemental material:

Figure S7: Was threshold regression constrained to stasis (this figure makes it appear so). For example, in the lower right, why doesn't the fitted red dash show a positive slope to match the data in the second window?

359: Anthropocene (typo)

Summary:

The authors have convincingly demonstrated that the recent fossil record in shelf settings can have excellent (decadal-scale) time resolution of modern biological changes. This is an important advance in that it shows, as have other conservation paleobiology studies, that the recent fossil record is a valuable source of time series of biotic change, especially in settings where we lack a good historical record. The authors demonstrate the strong link between this decadal-scale resolution and frequent hypoxia, and this opens the door to other similar studies in the modern and the ancient.

The authors should feel free to contact me with regard to any aspect of this review.

Steven Holland
stratum@uga.edu

# Review form: Reviewer 2

**Recommendation**
Major revision is needed (please make suggestions in comments)

**Scientific importance: Is the manuscript an original and important contribution to its field?**
Marginal

**General interest: Is the paper of sufficient general interest?**
Marginal

**Quality of the paper: Is the overall quality of the paper suitable?**
Poor

**Is the length of the paper justified?**
Yes

**Should the paper be seen by a specialist statistical reviewer?**
No

**Do you have any concerns about statistical analyses in this paper? If so, please specify them explicitly in your report.**
No

**It is a condition of publication that authors make their supporting data, code and materials available - either as supplementary material or hosted in an external repository. Please rate, if applicable, the supporting data on the following criteria.**

**Is it accessible?**
No

**Is it clear?**
No

**Is it adequate?**
No

**Do you have any ethical concerns with this paper?**
No

**Comments to the Author**
See attached review. (See Appendix A)

# Decision letter (RSPB-2019-2402.R0)

15-Nov-2019

Dear Dr Tomasovych:

I am writing to inform you that your manuscript RSPB-2019-2402 entitled "Ecological regime shift preserved in the Anthropocene stratigraphic record" has, in its current form, been rejected for publication in Proceedings B.

This action has been taken on the advice of referees, who have recommended that substantial revisions are necessary. With this in mind we would be happy to consider a resubmission, provided the comments of the referees are fully addressed. However please note that this is not a provisional acceptance.

The resubmission will be treated as a new manuscript. However, we will approach the same reviewers if they are available and it is deemed appropriate to do so by the Editor. Please note that resubmissions must be submitted within six months of the date of this email. In exceptional circumstances, extensions may be possible if agreed with the Editorial Office. Manuscripts submitted after this date will be automatically rejected.

Please find below the comments made by the referees, not including confidential reports to the Editor, which I hope you will find useful. If you do choose to resubmit your manuscript, please upload the following:

1) A 'response to referees' document including details of how you have responded to the comments, and the adjustments you have made.
2) A clean copy of the manuscript and one with 'tracked changes' indicating your 'response to referees' comments document.
3) Line numbers in your main document.

To upload a resubmitted manuscript, log into http://mc.manuscriptcentral.com/prsb and enter your Author Centre, where you will find your manuscript title listed under "Manuscripts with Decisions." Under "Actions," click on "Create a Resubmission." Please be sure to indicate in your cover letter that it is a resubmission, and supply the previous reference number.

Sincerely,
Dr Daniel Costa
mailto: proceedingsb@royalsociety.org

Associate Editor
Board Member: 1
Comments to Author:
Reviewer 1 was satisfied with the approach, analysis and goals of the ms and was overall positive about publication. However, s/he believes the paper needs substantial re-writing, particularly how the manuscript is pitched, the comparison of modern to ancient extinctions, and the writing overall. Rev 1 makes several valid points: 1) that it is misleading to imply that we can read the fine-scale record of deep-time events as an accurate chronology of that event in a single environment. The rev recommends dropping that pitch and focusing on the fact that the most recent fossil record is a high-quality archive of ecological change.; 2) drop the issue of how the modern compares to the ancient and focus on the record of relatively recent ecological changes in the youngest fossil record; and 3) clarify text and figure captions. Rev 2 was more critical, particularly with respect to the concept of regime shift. S/he was also less favourable about linking the change in body size to the change in community composition or bioturbation. S/he also found the paper difficult to evaluate due to lack of sufficient information on basic data and methods; if the paper is largely based on just two cores, then the reviewer questions the regional significance of the study. There are several issues which need further clarification before Rev 2 is happy with the publication of the paper.

Reviewer(s)' Comments to Author:
Referee: 1
Comments to the Author(s)
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convincing case that these changes are linked to increasing frequency of hypoxia events. This is a remarkable demonstration from one of the best data sets available for the latest Pleistocene to modern shelf settings. As such, it has important implications for understanding modern biotic changes in the oceans, especially in areas where historical records are lacking.

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Supplemental material:

Figure S7: Was threshold regression constrained to stasis (this figure makes it appear so). For example, in the lower right, why doesn't the fitted red dash show a positive slope to match the data in the second window?

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Summary:

The authors have convincingly demonstrated that the recent fossil record in shelf settings can have excellent (decadal-scale) time resolution of modern biological changes. This is an important advance in that it shows, as have other conservation paleobiology studies, that the recent fossil record is a valuable source of time series of biotic change, especially in settings where we lack a good historical record. The authors demonstrate the strong link between this decadal-scale resolution and frequent hypoxia, and this opens the door to other similar studies in the modern and the ancient.

The authors should feel free to contact me with regard to any aspect of this review.

Steven Holland
stratum@uga.edu

Referee: 2

Comments to the Author(s)
See attached review

## Author's Response to Decision Letter for (RSPB-2019-2402.R0)

See Appendix B.

# RSPB-2020-0695.R0

## Review form: Reviewer 1

**Recommendation**
Accept as is

**Scientific importance: Is the manuscript an original and important contribution to its field?**
Excellent

**General interest: Is the paper of sufficient general interest?**
Excellent

**Quality of the paper: Is the overall quality of the paper suitable?**
Excellent

**Is the length of the paper justified?**
Yes

**Should the paper be seen by a specialist statistical reviewer?**
No

**Do you have any concerns about statistical analyses in this paper? If so, please specify them explicitly in your report.**
No

**It is a condition of publication that authors make their supporting data, code and materials available - either as supplementary material or hosted in an external repository. Please rate, if applicable, the supporting data on the following criteria.**

**Is it accessible?**
Yes

**Is it clear?**
Yes

**Is it adequate?**
Yes

**Do you have any ethical concerns with this paper?**
No

**Comments to the Author**
In a convincing analysis of several cores from the northern Adriatic Sea, the authors demonstrate that the recent stratigraphic record preserves decadal scales in the body size of the bivalve Corbula gibba. Moreover, they demonstrate that the increase in body size corresponds with a change in community composition, a decrease in bioturbation, an increase in the frequency of hypoxia events, and that the current state of the system lies well outside of any previous states. Not only is this study a strong demonstration that a conservation-paleobiology approach can reveal ecological changes in the stratigraphic record at a higher resolution than generally thought, it also demonstrates that changes in bioturbation control the nature and temporal resolution of the stratigraphic record during these environmental changes. This study is an informed and nuanced reading of the stratigraphic record, backed by rigorous numerical analysis, and it is a model for ecologists and paleontologists on how to approach these problems.

In my previous review, I had three main concerns: (1) that the manuscript sacrificed its strongest point in attempting to address ancient mass extinctions, (2) that the manuscript contradicted itself over the scope of modern relative to ancient mass extinctions, and (3) that the manuscript was difficult to follow, largely owing to excessive convoluted sentences. The authors have addressed all of my concerns well, most notably by focusing the study on recent environmental and ecological change rather than those in deep time. The writing is much improved, and the text is now clear. The authors have addressed my previous comments keyed to line numbers, and their careful modifications of the figures have made them easier to understand.

As such, I am completely satisfied with this manuscript and recommend its acceptance. There are a few minor errors (e.g., HolocenIts on line 268), but these will be easily found and corrected in the copy-editing phase.

The authors should feel free to contact me with regard to any aspect of this review.

Steven Holland
stratum@uga.edu

## Review form: Reviewer 3 (Evan Edinger)

**Recommendation**
Accept with minor revision (please list in comments)

**Scientific importance: Is the manuscript an original and important contribution to its field?**
Excellent

**General interest: Is the paper of sufficient general interest?**
Excellent

**Quality of the paper: Is the overall quality of the paper suitable?**
Excellent

**Is the length of the paper justified?**
Yes

**Should the paper be seen by a specialist statistical reviewer?**
No

**Do you have any concerns about statistical analyses in this paper? If so, please specify them explicitly in your report.**
No

**It is a condition of publication that authors make their supporting data, code and materials available - either as supplementary material or hosted in an external repository. Please rate, if applicable, the supporting data on the following criteria.**

> **Is it accessible?**
> Yes
>
> **Is it clear?**
> Yes
>
> **Is it adequate?**
> Yes

**Do you have any ethical concerns with this paper?**
No

**Comments to the Author**
Summary:
This paper provides carefully documented evidence of a shift in the size of a dominant shallow water bivalve species, and a shift in the species composition of shallow water bivalves, in response to increasingly prevalent anoxia in shallow waters of the northern Adriatic Sea. The paper is a sort of capstone paper, following on a series of previous publications that amassed raw data on shell sizes and species composition. This paper provides the overview. The fundamental biological concepts in the paper are ecological release from competition, and possibly from

predation, by an already common bivalve that is much more tolerant of dysoxia or even temporary anoxia, than most of the other bivalves that occur in the life assemblage and death assemblage of bivalves in the shallow water sediments. The paper is supported by carefully documented chronologies of the bivalves in sediment cores, as well as living and death assemblages of bivalves from surface grab samples.

Evaluation.
This paper provides a clear example of the application of Conservation Paleobiology to nearshore molluscan assemblages. Taphonomical studies of bivalves, especially those comparing living and death assemblages, have a long history, but this one adds to it a carefully documented temporal component. The paper examines both the average size and the size frequency distribution, and uses the size of the 95th percentile log-length of shells, and the variance in mean log-length of shells as an important measure, in addition to the average size of shells, and shell morphometry.

The authors propose that the shift in size composition is made visible by a decrease in sediment mixing caused by bioturbation. They demonstrate the change in degree of bioturbation by comparing chronological records and stratigraphic records of the same cores, based on extensively dated shell records within the cores. The authors are able to pin-point the onset of the Anthropocene regime of frequent dysoxia to the 1950's.

Finally, the authors present modelling results to demonstrate the shift in the scale of time-averaging with the onset of Anthropocene conditions. The modelling results were somewhat opaque to me; in my opinion, the species composition presented in the supplementary material was more compelling that the modelling results. As is, the authors present a multivariate demonstration of a changed species composition without reference to the nature of the species being over or under-represented, and relegate the data on species composition to the supplementary material. Although the authors discuss the change in degree of bioturbation, they present no visual data on the sediment evidence for change in bioturbation, nor geochemical measures of bioturbation (e.g. radiogenic isotopes). Although these were presented in a previous publication, Tomasovych et al. 2018 Paleobiology, some visual representation of this change in bioturbation might be worth including, either in the main paper or the supplementary materials.

I have also read the authors' response to two previous reviewers. Although I have not seen the original version, the authors' responses appear to address the reviewers' concerns.

Overall, the paper is fairly well-written, and requires relatively little in terms of proofreading-type corrections. The figures are well-composed, although in figure 1 it is difficult to see the location of the 16 points included in figure 2B. There are a few minor writing corrections indicated in marginal comments.

Additional marginal comments are included in the marked-up copy of the MS.

Overall, the paper is an important contribution in Conservation Paleobiology, and is of general interest to ecologists, paleoecologists, and geologists addressing the Anthropocene. It definitely merits publication. The main change I would recommend is that I think the authors should find a way to present within the main manuscript the shift in species composition by reference to guilds or other shifts demonstrating release from predation and competition, in addition to the multivariate analyses demonstrating a quantitative shift in composition.

# Decision letter (RSPB-2020-0695.R0)

07-May-2020

Dear Dr Tomasovych:

Your manuscript has now been peer reviewed and the reviews have been assessed by an Associate Editor. The reviewers' comments (not including confidential comments to the Editor) and the comments from the Associate Editor are included at the end of this email for your reference. As you will see, the reviewers and the Editors have raised some concerns with your manuscript and we would like to invite you to revise your manuscript to address them.

We do not allow multiple rounds of revision so we urge you to make every effort to fully address all of the comments at this stage. If deemed necessary by the Associate Editor, your manuscript will be sent back to one or more of the original reviewers for assessment. If the original reviewers are not available we may invite new reviewers. Please note that we cannot guarantee eventual acceptance of your manuscript at this stage.

To submit your revision please log into http://mc.manuscriptcentral.com/prsb and enter your Author Centre, where you will find your manuscript title listed under "Manuscripts with Decisions." Under "Actions", click on "Create a Revision". Your manuscript number has been appended to denote a revision.

When submitting your revision please upload a file under "Response to Referees" in the "File Upload" section. This should document, point by point, how you have responded to the reviewers' and Editors' comments, and the adjustments you have made to the manuscript. We require a copy of the manuscript with revisions made since the previous version marked as 'tracked changes' to be included in the 'response to referees' document.

Your main manuscript should be submitted as a text file (doc, txt, rtf or tex), not a PDF. Your figures should be submitted as separate files and not included within the main manuscript file.

When revising your manuscript you should also ensure that it adheres to our editorial policies (https://royalsociety.org/journals/ethics-policies/). You should pay particular attention to the following:

Research ethics:
If your study contains research on humans please ensure that you detail in the methods section whether you obtained ethical approval from your local research ethics committee and gained informed consent to participate from each of the participants.

Use of animals and field studies:
If your study uses animals please include details in the methods section of any approval and licences given to carry out the study and include full details of how animal welfare standards were ensured. Field studies should be conducted in accordance with local legislation; please include details of the appropriate permission and licences that you obtained to carry out the field work.

Data accessibility and data citation:
It is a condition of publication that you make available the data and research materials supporting the results in the article. Datasets should be deposited in an appropriate publicly available repository and details of the associated accession number, link or DOI to the datasets must be included in the Data Accessibility section of the article (https://royalsociety.org/journals/ethics-policies/data-sharing-mining/). Reference(s) to datasets should also be included in the reference list of the article with DOIs (where available).

In order to ensure effective and robust dissemination and appropriate credit to authors the dataset(s) used should also be fully cited and listed in the references.

If you wish to submit your data to Dryad (http://datadryad.org/) and have not already done so you can submit your data via this link http://datadryad.org/submit?journalID=RSPB&manu=(Document not available), which will take you to your unique entry in the Dryad repository.

If you have already submitted your data to dryad you can make any necessary revisions to your dataset by following the above link.

For more information please see our open data policy http://royalsocietypublishing.org/data-sharing.

Electronic supplementary material:
All supplementary materials accompanying an accepted article will be treated as in their final form. They will be published alongside the paper on the journal website and posted on the online figshare repository. Files on figshare will be made available approximately one week before the accompanying article so that the supplementary material can be attributed a unique DOI. Please try to submit all supplementary material as a single file.

Online supplementary material will also carry the title and description provided during submission, so please ensure these are accurate and informative. Note that the Royal Society will not edit or typeset supplementary material and it will be hosted as provided. Please ensure that the supplementary material includes the paper details (authors, title, journal name, article DOI). Your article DOI will be 10.1098/rspb.[paper ID in form xxxx.xxxx e.g. 10.1098/rspb.2016.0049].

Please submit a copy of your revised paper within three weeks. If we do not hear from you within this time your manuscript will be rejected. If you are unable to meet this deadline please let us know as soon as possible, as we may be able to grant a short extension.

Thank you for submitting your manuscript to Proceedings B; we look forward to receiving your revision. If you have any questions at all, please do not hesitate to get in touch.

Best wishes,
Dr Daniel Costa
mailto: proceedingsb@royalsociety.org

Associate Editor
Comments to Author:
Rev 1, who was most critical about the original submission is completely happy with the revision and suggests no changes except for minor typographical errors. Rev 3 is new and is also positive, with the opinion that the original reviewers' comments have been adequately taken on board. However, Rev 3 did have some additional concerns that the authors may want to consider. Perhaps the most important is making the shift in species composition more a feature of the main text than the supplemental material. The reviewer thought that reference to the actual species being over or under-represented in the main text would make the multivariate modelling a bit less opaque. He also suggests making the location of the 16 points in Fig. 2B more visible, and including information on the sedimentary evidence for changes in bioturbation (either main text or supplemental material). He has provided a marked-up ms with additional comments/edits.

Reviewer(s)' Comments to Author:

Referee: 1

Comments to the Author(s).
In a convincing analysis of several cores from the northern Adriatic Sea, the authors demonstrate that the recent stratigraphic record preserves decadal scales in the body size of the bivalve Corbula gibba. Moreover, they demonstrate that the increase in body size corresponds with a change in community composition, a decrease in bioturbation, an increase in the frequency of hypoxia events, and that the current state of the system lies well outside of any previous states. Not only is this study a strong demonstration that a conservation-paleobiology approach can reveal ecological changes in the stratigraphic record at a higher resolution than generally thought, it also demonstrates that changes in bioturbation control the nature and temporal resolution of the stratigraphic record during these environmental changes. This study is an informed and nuanced reading of the stratigraphic record, backed by rigorous numerical analysis, and it is a model for ecologists and paleontologists on how to approach these problems.

In my previous review, I had three main concerns: (1) that the manuscript sacrificed its strongest point in attempting to address ancient mass extinctions, (2) that the manuscript contradicted itself over the scope of modern relative to ancient mass extinctions, and (3) that the manuscript was difficult to follow, largely owing to excessive convoluted sentences. The authors have addressed all of my concerns well, most notably by focusing the study on recent environmental and ecological change rather than those in deep time. The writing is much improved, and the text is now clear. The authors have addressed my previous comments keyed to line numbers, and their careful modifications of the figures have made them easier to understand.

As such, I am completely satisfied with this manuscript and recommend its acceptance. There are a few minor errors (e.g., HolocenIts on line 268), but these will be easily found and corrected in the copy-editing phase.

The authors should feel free to contact me with regard to any aspect of this review.

Steven Holland
stratum@uga.edu

Referee: 3

Comments to the Author(s).
Summary:
This paper provides carefully documented evidence of a shift in the size of a dominant shallow water bivalve species, and a shift in the species composition of shallow water bivalves, in response to increasingly prevalent anoxia in shallow waters of the northern Adriatic Sea. The paper is a sort of capstone paper, following on a series of previous publications that amassed raw data on shell sizes and species composition. This paper provides the overview. The fundamental biological concepts in the paper are ecological release from competition, and possibly from predation, by an already common bivalve that is much more tolerant of dysoxia or even temporary anoxia, than most of the other bivalves that occur in the life assemblage and death assemblage of bivalves in the shallow water sediments. The paper is supported by carefully documented chronologies of the bivalves in sediment cores, as well as living and death assemblages of bivalves from surface grab samples.

Evaluation.
This paper provides a clear example of the application of Conservation Paleobiology to nearshore molluscan assemblages. Taphonomical studies of bivalves, especially those comparing living and death assemblages, have a long history, but this one adds to it a carefully documented temporal

component. The paper examines both the average size and the size frequency distribution, and uses the size of the 95th percentile log-length of shells, and the variance in mean log-length of shells as an important measure, in addition to the average size of shells, and shell morphometry.

The authors propose that the shift in size composition is made visible by a decrease in sediment mixing caused by bioturbation. They demonstrate the change in degree of bioturbation by comparing chronological records and stratigraphic records of the same cores, based on extensively dated shell records within the cores. The authors are able to pin-point the onset of the Anthropocene regime of frequent dysoxia to the 1950's.

Finally, the authors present modelling results to demonstrate the shift in the scale of time-averaging with the onset of Anthropocene conditions. The modelling results were somewhat opaque to me; in my opinion, the species composition presented in the supplementary material was more compelling that the modelling results. As is, the authors present a multivariate demonstration of a changed species composition without reference to the nature of the species being over or under-represented, and relegate the data on species composition to the supplementary material. Although the authors discuss the change in degree of bioturbation, they present no visual data on the sediment evidence for change in bioturbation, nor geochemical measures of bioturbation (e.g. radiogenic isotopes). Although these were presented in a previous publication, Tomasovych et al. 2018 Paleobiology, some visual representation of this change in bioturbation might be worth including, either in the main paper or the supplementary materials.

I have also read the authors' response to two previous reviewers. Although I have not seen the original version, the authors' responses appear to address the reviewers' concerns.

Overall, the paper is fairly well-written, and requires relatively little in terms of proofreading-type corrections. The figures are well-composed, although in figure 1 it is difficult to see the location of the 16 points included in figure 2B. There are a few minor writing corrections indicated in marginal comments.

Additional marginal comments are included in the marked-up copy of the MS.

Overall, the paper is an important contribution in Conservation Paleobiology, and is of general interest to ecologists, paleoecologists, and geologists addressing the Anthropocene. It definitely merits publication. The main change I would recommend is that I think the authors should find a way to present within the main manuscript the shift in species composition by reference to guilds or other shifts demonstrating release from predation and competition, in addition to the multivariate analyses demonstrating a quantitative shift in composition.

## Author's Response to Decision Letter for (RSPB-2020-0695.R0)

See Appendix C.

# Decision letter (RSPB-2020-0695.R1)

24-May-2020

Dear Dr Tomasovych

I am pleased to inform you that your manuscript entitled "Ecological regime shift preserved in the Anthropocene stratigraphic record" has been accepted for publication in Proceedings B.

You can expect to receive a proof of your article from our Production office in due course, please check your spam filter if you do not receive it. PLEASE NOTE: you will be given the exact page length of your paper which may be different from the estimation from Editorial and you may be asked to reduce your paper if it goes over the 10 page limit.

If you are likely to be away from e-mail contact please let us know. Due to rapid publication and an extremely tight schedule, if comments are not received, we may publish the paper as it stands.

If you have any queries regarding the production of your final article or the publication date please contact procb_proofs@royalsociety.org

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Electronic supplementary material:
All supplementary materials accompanying an accepted article will be treated as in their final form. They will be published alongside the paper on the journal website and posted on the online figshare repository. Files on figshare will be made available approximately one week before the accompanying article so that the supplementary material can be attributed a unique DOI.

Thank you for your fine contribution. On behalf of the Editors of the Proceedings B, we look forward to your continued contributions to the Journal.

Sincerely,
Dr Daniel Costa
Editor, Proceedings B
mailto: proceedingsb@royalsociety.org

Associate Editor:
Board Member
Comments to Author:
I am happy that the authors have adequately addressed all of the remaining (minor) issues pointed out in the final stage of reviews. The paper looks great and should be a great addition to

the literature.  Many thanks to the authors for their careful attention to the reviewer's final comments.

# Appendix A

Summary: Perhaps I have just never liked the term "regime shift" with its overt political connotation (at least in the US), but whether a change in size of one species is really a regime shift seems to stretch the definition. According to the authors' reference "*We define ECOLOGICAL REGIME SHIFTS as dramatic, abrupt changes in the community structure that are persistent in time, encompass multiple variables, and include key structural species" (*Rocha et al 2015). I see no data that the proposed shift (*Corbula* getting larger) involves changes in community composition (though it is claimed that this is true, ie certain species supposedly disappear due to anoxia and this allows the survivor (*Corbula*) to be released from competition (Line 38)). It is also claimed that the shift correlates with intensity of bioturbation, which I suppose could be considered an indicator of community structure, but data presentation is cryptic and I am not sure if this is actually demonstrated (mostly bioturbation is just categorized as either "highly" or "weakly" averaged. The "regime" terminology is further clouded by its use for the physical environment (the new "disturbance regime", line 305). So the claim is that the regime shift in bivalve size was caused by the regime shift in disturbance.

Overall, I find the paper hard to evaluate because the basic data and methods are barely alluded to. While there are supplementary on-line files, even here I can't find some of the most basic methods (ex what is the diameter of the cores?, how many shells were dated?) and data (what was the precision/time averaging in the cores?, what were the average sizes of shells before and after the anoxic events? When were the anoxic events)? I assume the issue is that this is a capstone study built on a number of other papers that I would have to go carefully pick through to find the answers. I do note however, that the crux of the paper (the recent increase in size) come from only two cores: "chronological trends in body size are based on two cores" (Sup Line 53-54); Po3 and Po4) due to low sample sizes elsewhere. These two sites are adjacent to each other calling the regional significance of the pattern into question.

If it is all true, I suppose it is interesting, but I remain too unclear on the data and the results to be sure that it is. For example, while anoxic events may be responsible for large size via loss of "burrowing shrimp, echinoderms and holothurians, predatory asteroids (sic, holothurians and asteroids are echinoderms) and muricids" I am not sure there is really any evidence to support this conjecture. For example, is large size correlated with decrease in muricid predatory bore holes? Were there really no anoxic events prior to the Anthropocene?

Perhaps a reviewer better versed in the underlying data can evaluate the results and the relevance of the various models that are based on the data, and whether there is evidence that supports the proposed ecological cascade. Without much more effort I don't feel comfortable doing this.

# Appendix B

Dear PRSB Associate Editor,

here we would like to resubmit a revised version of the manuscript "Ecological regime shift preserved in the Anthropocene stratigraphic record".

We have revised the manuscript according to all AE recommendations and according to the comments of the two reviewers that were very helpful, with two main clarifications regarding the comments of Reviewer 2 (where the two concerns were that the crux of the message is in two cores only and that information on data and methods is not sufficient).

First, as we explain in detail below, the chronological nature of the shift (punctuation) is preserved in more than two cores - it is also preserved at Po prodelta (two stations) and in the Gulf of Trieste (Isonzo prodelta). The decadal-scale punctuation cannot be of course preserved at sites with slow sedimentation but the pre-Anthropocene segment in size structure that is preserved everywhere shows invariable small sizes of C. gibba in the whole Northern Adriatic. Therefore, the comparison visualized in Figure 1 shows that the major size (and also compositional shift in Figure 2) occurred in the whole northern Adriatic.

Second, the primary data in this manuscript are represented by the shell-length data. We have waited with the submission of our manuscript so that all former geochronological, time averaging or bioturbation data are published so that we do not need to explain myriads of background details that come with these data and which can be tracked in these peer-reviewed studies. However, we have expanded the ESM so that these are explained better. We have added source codes in R that show all methods associated with size analyses (ESM 3) and with time averaging simulations (ESM 4).

In addition to the raw shell-length data, we are also adding a source code in R (as another supplementary file) that shows all methodological steps and figures.

Our detailed responses to the AE comments and the reviewers are appended below.

with best regards

Adam Tomasovych (on the behalf of all co-authors)

##################################################################################

Associate Editor
Reviewer 1 was satisfied with the approach, analysis and goals of the ms and was overall positive about publication.  However, s/he believes the paper needs substantial re-writing, particularly how the manuscript is pitched, the comparison of modern to ancient extinctions, and the writing overall. Rev 1 makes several valid points: 1) that it is misleading to imply that we can read the fine-scale record of deep-time events as an accurate chronology of that event in a single environment. The rev recommends dropping that pitch and focusing on the fact that the most recent fossil record is a high-quality archive of ecological change;

**Response: We follow the advice from reviewer 1 and avoid extrapolations about fine-scale resolution observed in Anthropocene records into deep-time record. We have thus limited our inference that in prodelta environments, the fine-scale stratigraphic record in Anthropocene cores does qualitatively capture the size shift in the same way as the chronologic record.**

2) drop the issue of how the modern compares to the ancient and focus on the record of relatively recent ecological changes in the youngest fossil record;

**Response: We have removed the comparison of modern with the deep-time fossil record.**

3) clarify text and figure captions.

**Response: We have revised the convoluted statements in the main text and have clarified figure captions.**

Rev 2 was more critical, particularly with respect to the concept of regime shift.

**Response: In Methods, we have added our conceptual definition (that then translates to several statistical ways how this can be detected in Methods):** *"We use three approaches to detect the regime shifts (i.e., a large, abrupt, and persistent shift in ecosystem structure), here approximated by shift in the size structure of one of the most abundant molluscan species)."*

S/he was also less favourable about linking the change in body size to the change in community composition or bioturbation.

**Response: We have added a new compositional analysis (based on a large-scale compilation of community data from our and other sources, so this analysis is at genus level). We have added three new subplots into Figure 2 that visualize this analysis and thus should clarify the point of reviewer 2 asking for additional support of the regime shift beyond the size effect. The shift in bioturbation is documented in our former paper - the timing of the decline in bioturbation was documented to occur in mid 20th century by Tomasovych et al. 2018 Paleobiology – so we use this observation in the Discussion as one potential covariate that coincides with the shifts in size and composition.**

S/he also found the paper difficult to evaluate due to lack of sufficient information on basic data and methods;

**Response: The primary data in this manuscript are represented by the shell-length data only. However, we have expanded the ESM so that these data and sources are explained better.**

if the paper is largely based on just two cores, then the reviewer questions the regional significance of the study.

**Response: We have clarified in the revised version that the main result is not based just on two cores. Although the strict chronological-stratigraphic comparison is limited to two cores, the stratigraphic record with an abrupt (punctuation) shift is also preserved in the Gulf of Trieste in two cores (Panzano M28 and M29). We suggest that the shift can be inferred in the whole northern Adriatic because the pre-Anthropocene assemblages are invariably formed by small-sized specimens whereas Anthropocene assemblages, also at sites with slow sedimentation, show significantly higher proportions of larger individuals. In the revised version, the size shift is now visualized in Figure 1A and the compositional shift in figure 2B-C.**

**To clarify this in the main text, we have updated these statements in the Results:** *"Stratigraphic records at sites with relatively high sedimentation"*.

*"However, although the signature of the size increase in the 20th century is lost at these sites, TST and HST assemblages are consistently dominated by small-size individuals".*

**In the Discussion, we have added this clarification:** *"The abrupt increase in size of C. gibba detected in the stratigraphic records from the Po and Isonzo prodeltas and the observation that large individuals are invariably rare in the pre-Anthropocene assemblages at sites with slow sedimentation demonstrate that the shift in maximum shell size from 5 to 10-15 mm occurred in the whole northern Adriatic Sea (figures 1A, 2A)."*

#######################################################################

Referee: 1

In this manuscript, the authors demonstrate that the most recent fossil record of the Adriatic Sea preserves decadal-scale changes in body size of the bivalve Corbula gibba. They also make a convincing case that these changes are linked to increasing frequency of hypoxia events. This is a remarkable demonstration from one of the best data sets available for the latest Pleistocene to modern shelf settings. As such, it has important implications for understanding modern biotic changes in the oceans, especially in areas where historical records are lacking. The patterns are well-documented, and the interpretations are well-supported. I have no substantive criticisms of what the authors argue from the data. The manuscript is methodologically sound, and I have no suggested changes to the analyses. Threshold regression is appropriate, and using the adjusted R^2 and F-tests is a standard way of avoiding overfitting. Even so, the breaks implied by this approach are quite subtle. For example, looking at the time series in Figure 2A, I'm certain I would not have guessed that the breaks would exist where threshold regression placed them. Finally, the authors include all of the shell size data in the supplemental material, an admirable level of openness that I wish was standard.

**Response: We note that the magnitude of size shift depends on whether the mean or the 95th percentile size (as an approximation of maximum size) is assessed. The shift is well-visible with the 95th percentile size, corresponding to a 2-fold increase from ~5 mm to above 10 mm (changes in the mean size are also affected by changes in abundance of juveniles – those are also informative, but in general are less affected by changes in the size of adults). The effect is most pronounced when comparing longer series that include most of the highstand phase (Fig. 2B at Po based on the Po Plain and Po prodelta cores) because the shorter cores collected at Po (Fig. 2A) do not penetrate much beyond the 20th century.**

**In the Discussion, we have added***: "...The abrupt increase in size of C. gibba detected in the stratigraphic records from the Po and Isonzo prodeltas and the observation that large individuals are invariably rare in the pre-Anthropocene assemblages at sites with slow sedimentation demonstrate that the shift in maximum shell size from 5 to 10-15 mm occurred in the whole northern Adriatic Sea (figures 1A, 2A)."*

My main concerns are not on the data and their interpretation, but on how the manuscript is pitched, the comparison of modern to ancient extinctions, and the writing overall. I highly recommend publication once these issues are addressed, which will require some rewriting of the beginning and ending of the manuscript. I regard these as minor revisions in that no re-analysis or re-interpretation of the data is required.

1) The manuscript is pitched towards comparing modern and deep-time biodiversity crises (lines 30–31, 41–44, 64-81, etc.). The problem in the deep-time record is only partly a matter of time resolution within beds. The second and potentially much bigger problem is the stratigraphic context of most major biotic crises (the K-Pg is perhaps the best exception). Deep-time events are consistently associated with surfaces that reflect prolonged erosion, non-deposition, or stratigraphic condensation. Just as importantly and often glossed over, these surfaces record significant changes in depositional environment and their associated communities. As a result, stratigraphic columns are rarely if ever simple time series (see 48–50), as they reflect sampling from completely different environments with nearly non-overlapping communities. Even if every bed has decadal-scale time resolution, it would not address the challenges posed by stratigraphic architecture.

**Response: We have removed the comparisons with the deep-time mass extinctions from the whole manuscript (keeping one sentence about mass extinctions in the Introduction – to highlight the fact that deep-time stratigraphic records have different resolution and completeness).**

What the fossil record preserves at ancient mass extinctions would be like having a record of modern ecological change up through the 1950's from a mesic forest, followed by a record beginning in the 2000's from grasslands. Time is missing from that data series, but the more severe issue is that the record is from fundamentally different communities. Even with perfect time resolution in this data set, the time points before and after the extinction cannot be compared.

**Response: We agree, we have removed the mass extinction vs Holocene-Anthropocene stratigraphic record comparison from the ms.**

As such, it is highly misleading to imply that we could now read the fine-scale record of deep-time events as an accurate chronology of that event in a single environment. I recommend dropping that pitch and focusing on what this manuscript significantly offers, *that the most recent fossil record is a high-quality archive of ecological change (as the manuscript argues well beginning on line 82).* That alone makes this a valuable contribution to Proceedings of the Royal Society B.

**Response: We agree, we have removed those parts and focus solely on the Holocene-Anthropocene event.**

2) The manuscript makes conflicting statements about the scope of the modern biodiversity crisis relative to ancient mass extinctions. The text begins by stating that the emerging biodiversity crisis is comparable to ancient mass extinctions (47, 60–62). Shortly after this, it suggests that equivalence is an unanswered question (64–66). Near the end, the manuscript states that the modern crisis is not of the same intensity as ancient mass extinctions (355–356). I'm not aware of any fair comparison that indicates that modern rates of change are comparable to ancient ones (fair in the sense that they compare the same settings, in settings where we have a good fossil record). The data I've seen suggests we are thankfully nowhere close to the shocking calamities of the past (but give us time...). Regardless, the entire issue of how the modern compares to the ancient goes away if the authors focus on the record of relatively recent ecological changes in the youngest fossil record.

**Response: We agree, we have removed the deep-time vs 6th mass extinction comparisons from the text.**

3) My main criticism with the manuscript is that the text and the figures are frequently hard to understand.

For example, many sentences are too long and convoluted (e.g., 109–112, 116–123, 130–134, 135–143, 152–157, 345–350, 564–569, and many others). I found myself reading these multiple times to understand them. Splitting them would make these much easier to parse.

**Response: We have shortened and split sentences that were overly long and have attempted to simplify them.**

The figures are complex, which is not a problem in itself, but the captions could do more to help the reader understand what is shown in the figures. Many of the captions describe what is to be learned from the figure, but they don't describe what is being shown. Many of the figures have numerous lines, but these are described in the captions rather than labeled directly on the figures.

**Response: We have fixed the figure captions, adding an introductory statement what is shown in figures, and have attempted to simplify figures. We have also simplified all four figures so that their density if smaller. The captions are still relatively long but we think this should be still helpful. Their headings are as follows:**

**Figure 1.** *Size distributions of C. gibba in Holocene (TST and HST) and Anthropocene (20th century) death assemblages in the northern Adriatic Sea (with the exception of three Anthropocene sites from < 10 m depth, all sites are > 10 m deep).*

**Figure 2.** *The size and compositional regime shift between Holocene and Anthropocene assemblages and the effect of oxygen concentrations on shell size of C. gibba.*

**Figure 3.** *Chronological and stratigraphic records in the mean (black points) and 95th percentile log-length (white points) of Corbula gibba and the corresponding likelihood models for temporal changes in the 95th percentile log-length.*

**Figure 4.** *The sensitivity of size shifts to empirical and simulated time averaging.*

Minor comments

38: enemies: predators?
**Response: yes, fixed**

54: should this be highly time-averaged?
**Response: yes, fixed**
109: shifts (typo).
**Response: fixed**

130–133: It would help to lay out the three main time increments in order, and with their corresponding age spans: TST, HST, and the Anthropocene (which should be described as the latest part of the HST). These are outlined on 167–172, but this should be defined the first time these terms are used.

**Response: We have fixed this as follows (not that TST deposits are not captured in the Bay of Panzano in our sediment cores):** *"Net sedimentation rate was ~0.3 cm/y during the transgressive phase (TST) and 1-2 cm/y during the highstand phase (HST) at Po prodelta, 0.2-0.4 cm/y during the HST phase at Isonzo prodelta, and ~0.01 cm/y during the TST and HST phases off Istria and in the Gulf of Venice*

*(36-40). The uppermost HST increments (corresponding to 20th century sediments) do not show any signs of increased or decreased sedimentation rate (36).”*

195: precursor (typo)
**Response: fixed**

195: sentence fragment: "Under the so-called strict stasis, omega=0."
**Response: fixed**

Figure 1A: The caption indicates that there are three types of distributions (black, gray, and white), but I see only two: dark (the lower of each pair) and light (the upper). In addition, it is unclear what the arrows under the light size distributions indicate.

**Response: We have simplified the figure 1A and replaced the gray shading in histograms with white histograms only, thus showing simply the comparison of pre-Anthropocene HST distribution with the 20th century Anthropocene distributions.**

Figure 1B: The caption is quite difficult for me to parse, and I'm still not sure I follow it correctly. I think the authors are trying to say this: "... separation between two groups: the first group consists of transgressive (TST), highstand (HST), and shallow-water (< 10 m) Anthropocene sites (white triangles), and the second group consists only of deeper-water (> 10 m), high-sedimentation Anthropocene sites (white circles). High-averaging Anthropocene sites bridge these two groups." Even this, though, raises the question of whether there are deep-water low-sedimentation sites.

**Response: We have added that with the exception of the three shallow-water sites, all other assemblages are deep (> 10 m). In other words, deep-water low-sedimentation sites are the highly-averaged Anthropocene sites (and deep-water low-sedimentation Holocene sites are in the TST-HST group).**
**The new heading for the figure caption:** *“Size distributions of C. gibba in Holocene (TST and HST) and Anthropocene (20th century) death assemblages in the northern Adriatic Sea (with the exception of three Anthropocene sites from < 10 m depth, all sites are > 10 m deep).”*

Part of the problem is that it seems like certain groups are described in different ways: for example, the caption refers to the white circles as "sites > 10 m water depth with high sedimentation rates" but the figure refers to these as "Anthropocene (ANT) (low averaging)"; a consistent set of terms should be used to connect the text, caption, and figures.

**Response: We have removed the subset of the legend to avoid the confusion. The three shallow assemblages are not used in** PERMANOVA or analogue matching, but they are used in the Discussion where the connection is made with the hypoxic events and the thermocline (shallow-water are not exposed to those events, and thus did not undergo the shift).

The final sentence would be clearer if it stated "sites with high time averaging are based on shells that have periostracum and those that do not" (based on what is described in lines 172–176).

**Response: In PCO, ANT-HST assemblages are based just on shells with periostracum (and thus do not use size distributions of shells without periostracum –those are captured by subsurface increments well). To clarify this in Methods, we have modified the periostracum approach as:** ***“****Periostracum is usually not preserved on shells older than 19th-20th century, and the size distributions based on shells with periostracum better approximate Anthropocene conditions (figure S4).”*

Figure 2: This figure is complex, and the caption should begin by stating what is being plotted, rather than doing this in the second sentence.

**Response: This figure is now figure 3. The new heading is as follows:** "*Chronological and stratigraphic records in the mean (black points) and 95th percentile log-length (white points) of Corbula gibba and the corresponding likelihood models for temporal changes in these two size metrics.*"

The caption also describes the relationship of these patterns to sedimentation rates, but the sedimentation rates are not indicated on the figures, so it is hard for readers to make the connection themselves.
**Response: We have added one bar on the top that discriminates between the sections with high and low sedimentation rate.**

Figure 3: The last sentence was unclear to me, and the phrasing suggests that some of the points are based on six cores and others on the three sites with paired cores, but which is which?

**Response: We have clarified this explanation as follows:** *"The negative relationship between time averaging and the variance in mean log-length (ω) observed in the HST increments. ω (with 95% confidence intervals) was estimated at seven sites (two cores at Po, Isonzo, Piran, and one core at Brijuni) and in three pooled cores (Po, Isonzo, Piran)."*

Figure 4: In the last sentence, is this all the localities, or were some excluded? If so, why?

**Response: Only stations where instrumental oxygen concentrations were directly measured or approximated could be included into this plot. This is explained in the ESM as follows:** "*We have found instrumental data that can be matched with 16 sites with surface or top-core Anthropocene (20th and 21st centuries) death assemblages. These locations include two stations in the Gulf of Venice, two stations at the Po prodelta (Po 3 and Po 4), seven stations in the Bay of Panzano, two stations off Piran, two stations off Rovinj, and one station at Brijuni."*

Figure S7: Was threshold regression constrained to stasis (this figure makes it appear so). For example, in the lower right, why doesn't the fitted red dash show a positive slope to match the data in the second window?

**Response: Yes, the threshold regression is constrained to stasis. It is compared relative to the gradual trends. It is used to assess the first-order question about the presence of an abrupt shift. The likelihood framework allows for more complicated patterns with all variations.**

359: Anthropocene (typo)
**Response: fixed**

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**Referee 2**
Summary: Perhaps I have just never liked the term "regime shift" with its overt political connotation (at least in the US), but whether a change in size of one species is really a regime shift seems to stretch the definition. According to the authors' reference "We define ECOLOGICAL REGIME SHIFTS as dramatic, abrupt changes in the community structure that are persistent in time, encompass multiple variables, and include key structural species" (Rocha et al 2015). I see no data that the proposed shift (Corbula getting larger) involves changes in community composition (though it is claimed that this is true, ie certain species supposedly disappear due to anoxia and this allows the survivor (Corbula) to be released from competition (Line 38)).

**Response: We note that initially we have referred to previous (our own) studies and qualitative observations where the major shift in the community composition in the Northern Adriatic Sea was observed (Kowalewski et al. 2015, Tomasovych et al. 2018). To respond and clarify this better, we have added new compositional analyses into the Results, adding the subplots into one of the figures (now Figure 2). We document the compositional shifts using principal coordinate analysis and analogue matching analysis, using a large newly compiled dataset with core, surface death, and living assemblages.**
**We have added this information into the Methods:** *"Second, we compare the taxonomic composition of molluscan assemblages with TST and HST assemblages on one hand (deposited prior to the 20th century or during the earliest 20th century, 95 assemblages from the same cores used in analyses of shell size) with 54 Anthropocene death assemblages (late 20th century) and 223 Anthropocene living assemblages collected since 1980s on the other hand (Van Veen grab samples compiled from published sources). The Anthropocene data are based on multiple studies by various authors of soft-bottom habitats in the Po prodelta and in the Gulf of Trieste between 10-30 m water depth (with sample size exceeding 30, details in the electronic supplementary material) and are thus standardized to genus level. The compositions of Anthropocene living assemblages are not affected by mixing and thus help to constrain the compositional state of the latest 20th century communities. Compositional differences are analyzed with principal coordinate analysis, PERMANOVA (Bray-Curtis distances based on square-root transformed proportional abundances of genera), and with the analogue matching by evaluating whether Anthropocene assemblages extend beyond the variation defined by the Holocene assemblages (using Bray-Curtis distances between the Holocene centroid and individual Anthropocene assemblages, 41-45)."*

**In the Results, we have expanded our description of compositional shifts as follows:** *"The size shift coincides with a shift in the molluscan composition. The Bray-Curtis distances show that 82% of Anthropocene living assemblages are further from the Holocene centroid than 97.5% of individual Holocene assemblages (figure 2B). The Holocene-Anthropocene transition is characterized by a major increase in abundance of C. gibba from ~20-30% (95% confidence intervals on the median value) in TST and HST increments to 50-60% in time-averaged death assemblages and to 63-75% in Anthropocene non-averaged living assemblages (figure 2C). The increase in abundance of C. gibba is compensated by the decline in abundance of commensals, predators and scavengers (figure S8). Principal coordinate analyses and PERMANOVA show that the overlap between Anthropocene living and death assemblages on one hand and TST and HST assemblages on the other hand is negligible (figure 2E, table S5)."*

It is also claimed that the shift correlates with intensity of bioturbation, which I suppose could be considered an indicator of community structure, but data presentation is cryptic and I am not sure if this is actually demonstrated (mostly bioturbation is just categorized as either "highly" or "weakly" averaged.)

**Response: In the Discussion, we have clarified our point about bioturbation (based again on former studies) as follows:** *"This release hypothesis is congruent with the decline in abundance of predatory gastropods observed here and with the 20th century decline in the depth of the surface mixed layer declined from several decimeters documented at Po and Isonzo prodeltas on the basis of higher preservation of flood layers, reduced mottling, and reduced time averaging (36)."*

The "regime" terminology is further clouded by its use for the physical environment (the new "disturbance regime", line 305). So the claim is that the regime shift in bivalve size was caused by the regime shift in disturbance.

**Response: To avoid confusion, we have replaced "disturbance regime" by "higher frequency of seasonal hypoxia".**

Overall, I find the paper hard to evaluate because the basic data and methods are barely alluded to. While there are supplementary on-line files, even here I can't find some of the most basic methods (ex what is the diameter of the cores?, how many shells were dated?) and data (what was the precision/time averaging in the cores?,

**Response: As we mention above, all details about geochronological and time averaging analyses were published in referenced papers (including information about the core diameter and about the numbers of dated shell). These data are used as covariates (time averaging) so we define them in the Methods, but all details are explained in those primary references.**

**We have added R source code in the Supplement. We have revised our text so that it should be clear that the primary data in our manuscript are represented by *Corbula gibba* length data. All other data - geochronological, time averaging, environmental and compositional data were published in our former studies or in the studies of other authors. Those studies include information about the errors associated with time averaging, the methods used to compute time averaging**
**We specify them in the Electronic Supplementary Material (where information about the core diameter and about the numbers of dated shells is also given) and cite the main source also in the main text.**

what were the average sizes of shells before and after the anoxic events?

**Response: This information is not available (only that C. gibba grows to > 10 mm immediately after the events). We do not make inferences about size changes before and after *individual* seasonal events. We claim that size structure changed from low-frequency of seasonal events (~per decade or longer) to high frequency seasonal events.**

When were the anoxic events?

**Response: We do not infer the timing of individual past hypoxic events prior to the 20th century (those events cannot be of course preserved even under the decadal averaging), just that the decadal frequency of hypoxic events was smaller prior to the 20th century.**
**The timing of hypoxic events directly observed in the late 20th century was revised in the ESM as follows:** *"One year with summer anoxia during ~30 years of observations (~decadal hypoxia) was detected at sites off Rovinj and Brijuni (in 1989, Hrs-Brenko et al. 1994), 3 out of 31 years at Piran 1 (in 1983, 1987, and 1988, Giani et al. 2015) and 2 out of 31 years at Piran 2 (in 1983, 1987, Stachowitsch 1991, Giani et al. 2015). Inter-annual hypoxia was detected at a station in the Bay of Panzano where two cores were collected (M28 and M29), plus three stations (Panzano 4, 6, and 8 in Fig. S1) also collected with Van Veen grabs in the Bay of Panzano at depths below 10 m. These stations can be comparable to the station AA1 (Cibic et al. 2019) where 6 years with hypoxic events were observed during 16 years (Giani et al. 2015). Almost annual hypoxia was detected at Po Prodelta: 18 years with hypoxia out of 40 years at SJ101 that is close to Po 3 site, 21 out of 40 years at SJ108 that is close to Po 4 site, and 12 out of 40 years at SJ103 that is close to D2 site (Djakovac et al. 2015)."*

I assume the issue is that this is a capstone study built on a number of other papers that I would have to go carefully pick through to find the answers.

**Response: The revised ESM explains and references now all data sources and methods.**

I do note however, that the crux of the paper (the recent increase in size) come from only two cores: "chronological trends in body size are based on two cores" (Sup Line 53-54); Po3 and Po4) due to low sample sizes elsewhere. These two sites are adjacent to each other calling the regional significance of the pattern into question. If it is all true, I suppose it is interesting, but I remain too unclear on the data and the results to be sure that it is.

**See our response to the AE above. We have clarified that this is incorrect - although the two cores allow the strict chronologic-stratigraphic comparison, but both cores at Po prodelta and Isonzo prodelta (four stations in total) capture the punctuated size shifts. We have revised our point in the Discussion:** *"The abrupt increase in size of C. gibba detected in the stratigraphic records from the Po and Isonzo prodeltas and the observation that large individuals are invariably rare in the pre-Anthropocene assemblages at sites with slow sedimentation demonstrate that the shift in maximum shell size from 5 to 10-15 mm occurred in the whole northern Adriatic Sea."*

For example, while anoxic events may be responsible for large size via loss of "burrowing shrimp, echinoderms and holothurians, predatory asteroids (sic, holothurians and asteroids are echinoderms) and muricids" I am not sure there is really any evidence to support this conjecture.

**Response: we hypothesize that hypoxic events can drive the shift via the release hypothesis – of course this is open to the future testing, and we do not want to get in the loop where we test something that follows from our analyses with the same non-independent data. We have improved our reasoning behind the hypotheses as follows:**

**In the Discussion, we have revised our statement about the preferential loss of predators and active burrowers:** *"Direct biological observations showed that seasonal mass mortalities in the Adriatic Sea negatively affected predators and substrate-destabilizing burrowers, including burrowing shrimps, echinoids, holothurians, predatory asteroids and muricid gastropods (53), in contrast to hypoxia-tolerant C. gibba (54-55). The recovery of these taxa in the wake of hypoxic events is delayed and occurs over several years (56), allowing Corbula dominance also in years without seasonal hypoxic events."*

**About the release hypothesis:** *"The size and dominance increase following the shift to higher frequency might be hypothesized to be driven by the predatory and competitive release and by high tolerance of C. gibba to seasonal hypoxia (57).*

**Our new statement about bioturbation in The Discussion follows also from a formerly-published study – the timing of the shift in size and compositions coincides with the timing of the decline in bioturbation – see our statement above.**

For example, is large size correlated with decrease in muricid predatory bore holes?

**Response: Analyses of drilling predation are ongoing. We suggest our interpretation as a potential explanation that can be assessed with other data (see also below). However, the key point is the documentation of the regime shift, regardless of underlying causes.**

Were there really no anoxic events prior to the Anthropocene?

**Response: We do not claim that there were no anoxic events. Tomasovych et al. 2017 Geology suggested some hypoxic events probably occurred also during the highstand phase. We infer that their frequency was not so high as in the late 20th century.**

Perhaps a reviewer better versed in the underlying data can evaluate the results and the relevance of the various models that are based on the data, and whether there is evidence that supports the proposed ecological cascade. Without much more effort I don't feel comfortable doing this.

**Response: The revised Discussion summarizes our points about the potential *causes* of the regime shift – these are qualitative indicators where (1) several lines of evidence indicate that seasonal hypoxia increased in frequency in the 20th century, (2) direct biological observations (again, not our study) show that (inevitably) hypoxia-sensitive predators and active burrowers suffer from mass mortality during these seasonal events, and (3) sedimentological evidence indicates that bioturbation also declined.**

# Appendix C

Dear PRSB Associate Editor,

here we would like to resubmit a revised version of the manuscript "Ecological regime shift preserved in the Anthropocene stratigraphic record" (ID RSPB-2020-0695).

We have revised the manuscript according to all AE recommendations and according to the additional comments of the Reviewer 3. Our detailed responses to the AE comments and to the reviewers are appended below (and attached in the separate response letter).

The manuscript has now 7,300 words and four figures and should fit within ten printed pages.

We have also prepared all (six) ESM files for Data Dryad upload (and have added the link dx.doi.org/10.5061/dryad.t4b8gthzr to the manuscript – although this link is under review by Dryad).

Thank you very much for your consideration

with best regards

Adam Tomasovych (on the behalf of all co-authors)

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Associate Editor
Comments to Author:
However, Rev 3 did have some additional concerns that the authors may want to consider.  Perhaps the most important is making the shift in species composition more a feature of the main text than the supplemental material. The reviewer thought that reference to the actual species being over or under-represented in the main text would make the multivariate modelling a bit less opaque. He also suggests making the location of the 16 points in Fig. 2B more visible, and including information on the sedimentary evidence for changes in bioturbation (either main text or supplemental material). He has provided a marked-up ms with additional comments/edits.
**Response: As we explain below in more detailed, we have followed all suggestions:**
**1. We have added more information about the compositional shift into the main text, listing also the most important taxa (genera, as the communit-level analyses had to be taxonomically standardized).**
**2. We have added explanation to the figure 1 caption concerning the locality labels. The localities are listed now in the ESM.**
**3. The discussion about the evidence for the declining bioturbation was expanded.**

**Referee: 1**
As such, I am completely satisfied with this manuscript and recommend its acceptance. There are a few minor errors (e.g., HolocenIts on line 268), but these will be easily found and corrected in the copy-editing phase.
**Response: We are glad that the reviewer is satisfied with the revision. We have now corrected also all typos.**

**Referee: 3**

Finally, the authors present modelling results to demonstrate the shift in the scale of time-averaging with the onset of Anthropocene conditions. The modelling results were somewhat opaque to me; in my opinion, the species composition presented in the supplementary material was more compelling that the modelling results. As is, the authors present a multivariate demonstration of a changed species composition without reference to the nature of the species being over or under-represented, and relegate the data on species composition to the supplementary material.
**Reponse: We have attempted to make the explanation of modelling more compact – it is supporting our argument that natural bioturbation would generate time averaging that would obliterate the signal of abrupt shift. We have added more information about the under- and over-represented genera and functional groups and also have added information about the decline of echinoids (see below our detailed responses).**

Although the authors discuss the change in degree of bioturbation, they present no visual data on the sediment evidence for change in bioturbation, nor geochemical measures of bioturbation (e.g. radiogenic isotopes). Although these were presented in a previous publication, Tomasovych et al. 2018 Paleobiology, some visual representation of this change in bioturbation might be worth including, either in the main paper or the supplementary materials.

**Response: We have expanded our explanation of changes in bioturbation (as also mentioned below). The photographic documentation based on x-ray was published in the paper we refer to (Paleobiology 2018). The key part of our inference also follows from the observation that sedimentation rates did not change during the 20th century, and the empirical change towards lower time averaging in the late 20th century cannot be explained by an increase in sedimentation rate. We have added this clarification into Discussion:**
*"Time averaging of the present-day 10-20 cm-thick mixed layer (35, 57) can be expected to be ~10-20 years under sedimentation rates of 1 cm/y at Po prodelta, which is consistent with the observed values of time averaging in the late 20th century sediments. However, time averaging attaining ~50 years at Po prodelta, the lack of preservation of flood layers and stronger mottling in Holocene relative to Anthropocene increments indicate that the thickness of the mixed layer exceeded ~25 cm prior to 1950 AD (35). This decline in time averaging was not associated with an increase in sedimentation rates. Therefore, under naturally-deeper sediment mixing prior to anthropogenic increase in hypoxia, multi-decadal time averaging would obliterate the stratigraphic signal of abrupt ecological shifts even under high sedimentation rates (figure 4D-E). "*

Overall, the paper is fairly well-written, and requires relatively little in terms of proofreading-type corrections. The figures are well-composed, although in figure 1 it is difficult to see the location of the 16 points included in figure 2B. There are a few minor writing corrections indicated in marginal comments.
**Response: Not all sites could be used in this correlation (Po Plain core not collected in the sea, and periostracum was not scored in all samples). The list of sites is now given at the end of the caption to figure S10 in the ESM. In the caption to Figure 1, we have specified that the number 6 on the map in 1A corresponds to a transect with multiple sites:** *"The labels summarize sites analyzed in this study: 1 – Po Plain core S10, 2 – Po 4, 3 – Po 3, 4 – Venice, 5 – Site D2, 6 – Bay of Panzano (transect with seven Van Veen grab sites and two sites with sediment cores), 7 – Piran 1, 8 – Piran 2, 9-10 – Rovinj 120 and 38, 11 – Brijuni."*

**In the Supplement, we have added:** "The relative frequency of hypoxic years during 1980-2010, defined as the number of years when minimum monthly concentrations of dissolved oxygen were at least once per year less than 2 ml/L relative to the total number of years) is estimated for 16 out of 19 sites according to data in Stachowitsch (1991), Justic (1991), Hrs-Brenko et al. (1994), Hrs-Brenko (2003), Giani et al. (2015), and Djakovac et al. (2015)."

Overall, the paper is an important contribution in Conservation Paleobiology, and is of general interest to ecologists, paleoecologists, and geologists addressing the Anthropocene. It definitely merits publication. The main change I would recommend is that I think the authors should find a way to present within the main manuscript the shift in species composition by reference to guilds or other shifts demonstrating release from predation and competition, in addition to the multivariate analyses demonstrating a quantitative shift in composition.

**Response: In Results, we have added this information into the main text:** *"This increase in abundance of C. gibba in soft-bottom habitats is associated with an increase in abundance of deposit-feeders (from 7 to 22%, mainly by the infaunal bivalve Nucula). It is compensated by the decline in abundance of the suspension-feeding gastropod Turritella communis (from 20% to 1.5%, excluding Corbula) and in abundance of commensals (bivalves Kurtiella from 20% to 8% and Musculus from 3% to <1%,), drilling gastropods (Euspira) and scavengers (Nassarius) (figure S7)."*

**In Discussion, we have added:** *"Although C. gibba was a persistent subset of molluscan communities during the Holocene (44-45), it became dominant relative to molluscan suspension-feeders and other functional groups in the 20th century (figure S7)."*
*"This release hypothesis is congruent with the decline in abundance of predatory gastropods observed here and with a major decline in abundance of bulldozing infaunal echinoids (that can negatively affect slow-burrowing bivalves such as C. gibba), which was observed in the northern Adriatic Sea during the late 20th century (55-56)."*

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Responses to the comments
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**1. We have added "hypersaline".**

2. "cores allows us to directly compare chronological (i.e., ages of fossils in time series do not depend on their stratigraphic position, here partitioned into 5-year age cohorts) and stratigraphic records (i.e., ages of fossils refer to the mean age of a sedimentary layer in which they are embedded). " This sentence is difficult to read - rephrase.

**Response: We have revised this as follows:**
*"Absolute dating of multiple shells embedded in sediment cores allows reconstructing the chronological record regardless of time averaging (i.e., fossils can be aligned into a time series independently of their stratigraphic position) and contrasting it against the stratigraphic record (i.e., fossils are assigned to the mean age of a sedimentary layer in which they are embedded)."*

3. Provide more details on coring methods: were these gravity cores, piston cores, vibrocores? Diver cores? What was core diameter? Different coring methods cause diffferent amounts of disturbance to upper sediment layers.
**Response: In the main text, we have added that the 1.5 m cores collected from the sea-floor were taken with piston cores (and wireline coring at Po Plain – but this was already on land). Owing to the word limit in the main text, we have added additional information about core diameters into the Supplement:** *"The core diameter was 16 cm at Po 2, Po 4, Panzano, and Piran, and 9 cm at Venice and Brijuni (Gallmetzer et al. 2019), and 10 cm at S10 core."*

4. This section – "Detection of regime shifts and sensitivity to time averaging" is rather opaque.
**Response: We have shortened this section, and started with** *"We assessed whether abrupt shifts in (i) the mean and (ii) the 95% percentile log-length detected in the chronological records are preserved also in the stratigraphic records."*

5. Line 216 "to constrain"
**Response: This sentence was removed.**

6. Line 259-261 "The mean and the 95th percentile log-length of C. gibba in death assemblages correlate positively with the 1980-2010 measurements of yearly frequency of seasonal hypoxia at 16 sites (Spearman r = 0.91, p = 0.005) and the 95th percentile log-length (Spearman r = 0.82, p < 0.0001)."
This is confusing. Is this a spatial correlation among sites or a temporal correlation among years?
**Response: this refers to geographic correlation. We have modified this as follows:** ***"****The mean and the 95th percentile log-length of C. gibba in 16 DAs correlate positively with the proportion of years with at least one hypoxic event at each of these sites (Spearman r [mean] = 0.91, p = 0.005, r [95th percentile] = 0.82, p < 0.0001)."*

The relationship between these 16 sites and the 11 sites shown in figure 1A is not clear.
**Response: "For the figure 1A, we have added that the number 6 (Panzano) is a transect with several sites. Out of 19 sites, 16 sites can be matched with some instrumental observations of dissolved oxygen. 16 sites are listed in the ESM.**

7. "The increase in abundance of C. gibba is compensated by the decline in abundance of commensals, predators and scavengers (figure S7)"
Species composition, and especially guild composition, is really important. Why bury it in the Supplementary material?
**Response: we have expanded the description of the shift by referring to several genera and functional groups in the main text – see our response to general comments above.**

8. Line 300-301 Is this figure reference correct? Do you mean figure 4C?
**Response:** The reference was changed to figure 3D

9. Line 316 No discussion of figure 4F?
**Response:** Figure 4F was mis-typed as "FF", it is now corrected in the section "***Chronological and stratigraphic record of size shifts"***

10. Line 327 "Although C. gibba was a persistent subset of molluscan communities during the Holocene (49-50), it became dominant relative to other molluscan species in the 20th century." Here the data in figure S7 are really important.
**Response: We have added more information but are limited by space constraints:** *"Although C. gibba was a persistent subset of molluscan communities during the Holocene (47-48), it became dominant relative to molluscan suspension-feeders and other functional groups in the 20th century (figure S7)."*
**In Discussion, we have also added independent information that adds more to an overall community compositional shift:** *"This release hypothesis is congruent with the decline in abundance of predatory gastropods observed here and with a major decline in abundance of bulldozing infaunal echinoids (that can negatively affect slow-burrowing bivalves such as C. gibba) that was observed in the northern Adriatic Sea during the late 20th century (59-60)."*

11. Line 328 This bimodality is not clearly evident in figure 2C.
**Response: the reference should be to Figure 2D. We refer to two modes in Holocene and Anthropocene living assemblages (death assemblages are intermediate as they are mixed). We have modified this sentence as follows:** *"The bimodality of abundances of C. gibba prior to (mode = ~20%) and after the transition in the 20th century (mode > 90% in living assemblages, figure 2D) is a diagnostic attribute of abrupt ecological transitions (49)."*

12. Discussion
What is the sedimentary signature of this reduced bioturbation in the cores? Is there any visible reduction in bioturbation index (cf. ichnofabric, Bottjer & Droser 1994)? What geochemical evidence from the numerous previous papers published in this area by the co-authors can be cited to further substantiate this interpretation? I think the interpretation is likely correct, but it could be better supported here.
**Response: Although geochemical data were published in several papers focused on the uppermost core increments at Po prodelta, they do not trace down to pre-20th century sediments or estimates of the historical mixed-layer thickness (and abrupt geochemical signals that would be indicative of weak bioturbation were not reported). We have added reference to Tesi et al. 2012 (that parallel earlier works on the thickness of active mixed layer from Po prodelta) that indicates present-day mixing to about 10 cm (our estimates in 2018 Paleobiology indicate maximum of 20 cm) and expanded the discussion as cited in our response to the general comments above.**

13. Figure 1 caption
"Three Anthropocene assemblages at < 10 m water depth are represented by white triangles." These are completely different from the other ANTH assemblages. depth-related differences? How comparable in terms of sedimentological mixing?
**Response: These sites are too shallow to be affected by stratification. We have expanded this explanation in the Discussion:** *"C. gibba populations that did not experience an increase in size during the 20th century were limited to the shallowest or high-energy habitats at the Isonzo prodelta and off Venice. They were thus not subjected to seasonal hypoxia, in contrast to deeper habitats located below the thermocline and experiencing annual to inter-annual frequencies of hypoxic events at the Po prodelta (48) and less regular hypoxic events in the Gulf of Trieste (49)."*

14. Figure 2. Where are the additional 5 sites?  Not clear in Figure 1A.
**Response: In the caption to 1A, we have added** *“6 – Bay of Panzano transect with seven Van Veen grab sites and two sites with sediment cores”.* **The total number of unique sites is 19. 16 sites refer to those for which oxygen measurements were available. This is now explained in the ESM (*Relationship between hypoxia frequency and size)***