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High heart rates in hunting harbour porpoises

Birgitte I. McDonald, Siri L. Elmegaard, Mark Johnson, Danuta M. Wisniewska, Laia Rojano-Doñate, Anders Galatius, Ursula Siebert, Jonas Teilmann and Peter T. Madsen

Article citation details
Proc. R. Soc. B **288**: 20211596.
http://dx.doi.org/10.1098/rspb.2021.1596

Review timeline

Original submission:	7 July 2020
1st revised submission:	14 July 2021
2nd revised submission:	23 September 2021
3rd revised submission:	19 October 2021
Final acceptance:	19 October 2021

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

Review History

RSPB-2020-1628.R0 (Original submission)

Review form: Reviewer 1

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

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

General interest: Is the paper of sufficient general interest?
Good

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.
Yes

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?
N/A

Is it clear?
N/A

Is it adequate?
N/A

Do you have any ethical concerns with this paper?
No

Comments to the Author
See attached file for comments to the author. (See Appendix A)

Review form: Reviewer 2

Recommendation
Accept with minor revision (please list in comments)

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

General interest: Is the paper of sufficient general interest?
Good

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

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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
This study looks at heart rate, movement, and breathing in the wild harbor porpoise in Denmark. Because these animals are active hunters, the authors hypothesized that the porpoises will have a strong exercise response in heart rate than porpoises in human care. The methods allow the researchers to obtain heart rate, activity, and breathing rates in free ranging animals.
- Can you include the genus and species name for your porpoise? I don't think I saw it in the manuscript, just the key words.
- It was not immediately clear to me how you determined ventilation of the animals. I think that this was done through the stereo sound? I would combine 120 and 121: " …(MATLAB code…) to identify ventilation and feeding buzzes[15,21].

Line 185: how was the ADL calculated? I don't think you should be citing a paper that is in prep and unavailable, provide details.
- Figures: For the box plots, provide description of boxes and the data points on the figures. Are the points outliers?
- Line 197: While the smaller animals may have lower oxygen stores, won't they also have lower oxygen needs?

Review form: Reviewer 3

Recommendation
Reject – article is scientifically unsound

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?
Yes

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Yes

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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
Please see my comments in the attached file. (See Appendix B)

Review form: Reviewer 4

Recommendation
Accept as is

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

General interest: Is the paper of sufficient general interest?
Acceptable

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?
Yes

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

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Is it accessible?
N/A

Is it clear?
N/A

Is it adequate?
N/A

Do you have any ethical concerns with this paper?
No

Comments to the Author
This is a detailed investigation into the physical effects of tags on terrestrial mammal locomotion. As such, it is useful to gauge the potential effects that might alter behavior and other performance metrics. However, those of us that use tags to study animals accept that the tag will have some sort of influence and that it should always be as small as possible. Generally, tags do not remain attached to wild animals long enough to pose a threat to survival, or at least they should not. However, the3-5% body mass rule still seems a reasonable for maximum tag size given the uncertainties of performance-related effects. The ethical treatment of animals must always be considered, but I do not want to see a ban on animal-borne instruments.

Decision letter (RSPB-2020-1628.R0)

16-Nov-2020

Dear Dr McDonald:

I am writing to inform you that your manuscript RSPB-2020-1628 entitled "High heart rates in hunting harbour porpoises" 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. Your manuscript was reviewed by four referees. Two of them were quite critical and two were positive, but the two positive reviews were rather superficial. A major concern that was brought up by the two more critical referees was that your study was rather narrow in focus. However, we are willing to give you an opportunity to revise your manuscript and respond to the two more negative reviews. I would also ask that you try to put your work in a large context, one that would make it of interest to the wide readership of Proc B. A specifc example is in the Abstract you make reference to a DTAG, most ProcB readers will have no idea what a DTAG is. However, on line 87 you refer to using "suction-cup-attached biologging tags that can uniquely measure heart rate, breathing, exercise and foraging" 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.
4) Data - please see our policies on data sharing to ensure that you are complying (https://royalsociety.org/journals/authors/author-guidelines/#data).

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:
Thank you for submitting your manuscript "High heart rates in hunting harbour porpoises" to Proceedings B. I've now received four reviews of your manuscript and reviewed the paper myself. The reviewers opinion of the paper were mixed, but two reviewers raised significant concerns about the interpretation of the data, how the data were handled (e.g., lumping of age classes), and data analysis. There's also some indication that the results are quite species and even population specific and therefore the results are somewhat incremental in nature.

Reviewer(s)' Comments to Author:
Referee: 1
Comments to the Author(s)
See attached file for comments to the author

Referee: 2
Comments to the Author(s)
This study looks at heart rate, movement, and breathing in the wild harbor porpoise in Denmark. Because these animals are active hunters, the authors hypothesized that the porpoises will have a strong exercise response in heart rate than porpoises in human care. The methods allow the researchers to obtain heart rate, activity, and breathing rates in free ranging animals.
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Referee: 3
Comments to the Author(s)
Please see my comments in the attached file.

Referee: 4
Comments to the Author(s)
This is a detailed investigation into the physical effects of tags on terrestrial mammal locomotion. As such, it is useful to gauge the potential effects that might alter behavior and other performance metrics. However, those of us that use tags to study animals accept that the tag will have some

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Author's Response to Decision Letter for (RSPB-2020-1628.R0)

See Appendix C.

RSPB-2021-1596.R0

Review form: Reviewer 3

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?
Acceptable

Quality of the paper: Is the overall quality of the paper suitable?
Marginal

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

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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
Please see attached comments (See Appendix D)

Review form: Reviewer 5

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:
The authors have investigated heart rate responses in foraging harbor porpoises. With use of one of the most sophisticated bio-logging recorders available, they have assessed heart rate responses in relation to depth, activity (minimum specific acceleration – MSA) during dives, foraging behavior (echolocation buzzes) during dives as well as respirations during surface intervals of one of the world's smallest cetaceans. This is a remarkable technical accomplishment.

In these shallow-diving porpoises, dive heart rate was relatively moderate (40-50 beats per minute) and considered independent of dive duration, activity, and type of dive (foraging versus non-foraging). However, heart rate during surface intervals was higher after longer and more active dives. Dives (up to about 3.5 min in duration) were considered within aerobic limits for the species; routine maximum depths were predominantly less than 10 m. The authors conclude that although an extreme dive response (severe bradycardia) may occur in deeper or exceptional dives of harbor porpoises, this was not observed in the routine shallow dives of harbor porpoises in the study location.

The methodology and analysis were well detailed. The statistical analysis was rigorous. The data were well organized and presented. I think concerns expressed by other reviewers on heart rate during different phases of the dive and on possible effects of ontogeny on heart rate responses of juveniles versus adults in the study were adequately addressed in the revision. This included requested analyses and graphics of heart rate responses of the individual animals, and of heart rate responses during different phases of the dive.

I agree with the authors that a full-scale analysis of the ontogeny of the dive response in harbor porpoises is beyond the scope of the paper; it was not the goal of the research and there is not an adequate age range or sample size of animals for such a study. In the revision, analyses of individual animals did not reveal differences in responses between the juvenile and adult animals.

Analyses of heart rate responses during different phases of the dives and in longer dives are now included in the revision. The results reinforce the authors' original interpretations and conclusions.

Previous reviews also raised the issue of the author's interpretation of statistical significance versus biological relevance. In their data presentation, the authors have reviewed and re-emphasized this important concept, i.e., that although a result may be statistically significant, it may not be biologically relevant. These interpretations are now made quite clear in their presentation and should be of value to readers.
Lastly, there are no animal welfare concerns.

General Comments:

Line 41: suggest changing "that hunt thousands of small prey daily" to "that hunt thousands of small prey daily during continuous shallow diving". Or something to that effect. Or perhaps the suggested changes in lines 47-48 are adequate.

Line 47-48: suggest changing "dive response, for these shallow-diving cetaceans, it is more efficient to maintain circulation while diving: extreme heart-rate gymnastics are for emergencies, not everyday use" to "dive response, for these continuously shallow diving, frequently foraging cetaceans, it is more efficient to maintain some circulation while diving: extreme heart-rate gymnastics are for deeper/longer dives or emergencies, not everyday use."

I realize this increases the word count in the abstract, but I think these changes address concerns of other reviewers that these dives are not characteristic of all harbor porpoise populations, and that the physiological responses found may be different in other populations in different locations. Although not relevant to this paper, similar arguments could be made for other species - there may be physiological differences (in addition to documented hematological differences) in coastal vs off-shore bottlenose dolphins.

Line 230: Explanations for elevated heart rates in the smallest animal (26 kg) are logical. For example, if this animal was studied later in the season and was smaller than other juveniles, occult disease (infection, poor nutrition) may well be a factor in the high respiratory rates and heart rates. I agree with presentation of the analyses both with and without this animal. The overall conclusions are the same.

Line 245: "by minimizing blood flow to exercising muscle": suggest changing to: exercising muscle and other organs. This reinforces arguments that the moderate (relatively elevated heart rates) during dives contribute to increased metabolism and digestion in these continuously feeding porpoises (as described in the next paragraph of the manuscript). Indeed, even at these moderate heart rates, most blood flow may be for digestion/thermoregulation and not to exercising muscle, which may still predominantly rely on its myoglobin-oxygen store.

In addition, although not necessary to add to text, moderate heart rates during shallow dives (with no alveolar collapse) will help maintain pulmonary gas exchange and access to the lung oxygen store (the lungs comprise about 20% the estimated total body oxygen store in most studies; the lung store may be an even greater percentage of the total oxygen store, dependent on what the blood volume actually is (blood volume is not documented in the harbor porpoise).

Line 267-290: Prediction of extreme bradycardia in the harbor porpoise diving to 410 meters off Greenland. Agree with the prediction. The deep-diving harbor porpoise probably undergoes alveolar collapse at some point unlike the shallow-diving harbor porpoise. Effects on lung stretch receptor reflexes, etc. as well as minimization of pulmonary gas exchange during deep dives will affect heart rate and oxygen store management differently than in the shallow dives.

Line 328-329: "extreme heart-rate gymnastics are for emergencies": Suggest changing to "deeper or exceptional dives and emergencies." Many of the deeper dives of Greenland harbor porpoises cited in Nielsen et al are probably foraging dives, not emergencies.

Specific comments:

Line 221: "than" check grammar and word usage

Line 222: suggesting changing more extreme bradycardia to more intense bradycardia because the main point of the paper is that these porpoises do not have an extreme bradycardia

Line 333: suggest changing "physiological capacities" to "physiological responses"

Reference 16: I am not sure of the citation format, but shouldn't the last author in this reference at least get an "et al.", rather than not be listed. Note that the eleventh author in Ref 6 got an "et al."

Reference 38: citation is incomplete - ? journal or book source

Fig S2 x axis legend: should this not be "Time into dive" rather than "dive duration".

Decision letter (RSPB-2021-1596.R0)

03-Sep-2021

Dear Dr McDonald:

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 (https://royalsociety.org/journals/authors/author-guidelines/#data). 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

Reviewer(s)' Comments to Author:
Referee: 3
Comments to the Author(s).
Please see attached comments

Referee: 5
Comments to the Author(s).
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Reference 38: citation is incomplete - ? journal or book source

Fig S2 x axis legend: should this not be “Time into dive” rather than “dive duration”.

Author's Response to Decision Letter for (RSPB-2021-1596.R0)

See Appendix E.

RSPB-2021-1596.R1

Review form: Reviewer 3

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?
Good

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?**
> No
>
> **Is it clear?**
> N/A
>
> **Is it adequate?**
> N/A

Do you have any ethical concerns with this paper?
No

Comments to the Author
Please see attached comments. (See Appendix F)

Decision letter (RSPB-2021-1596.R1)

14-Oct-2021

Dear Dr McDonald

I am pleased to inform you that your Review manuscript RSPB-2021-1596.R1 entitled "High heart rates in hunting harbour porpoises" has been accepted for publication in Proceedings B.

However, the referee have recommended some minor revisions. The referee went to considerable effort to document items that require attention. Therefore, please proof-read your manuscript carefully and upload your final files for publication. Because the schedule for publication is very tight, it is a condition of publication that you submit the revised version of your manuscript within 7 days. If you do not think you will be able to meet this date please let me know immediately.

To upload your 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 Revision." Your manuscript number has been appended to denote a revision.

You will be unable to make your revisions on the originally submitted version of the manuscript. Instead, upload a new version through your Author Centre.

Before uploading your revised files please make sure that you have:

1) A text file of the manuscript (doc, txt, rtf or tex), including the references, tables (including captions) and figure captions. Please remove any tracked changes from the text before submission. PDF files are not an accepted format for the "Main Document".

2) A separate electronic file of each figure (tiff, EPS or print-quality PDF preferred). The format should be produced directly from original creation package, or original software format. Please note that PowerPoint files are not accepted.

3) Electronic supplementary material: this should be contained in a separate file from the main text and the file name should contain the author's name and journal name, e.g authorname_procb_ESM_figures.pdf
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 see: https://royalsociety.org/journals/authors/author-guidelines/

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Once again, thank you for submitting your manuscript to Proceedings B and I look forward to receiving your final version. If you have any questions at all, please do not hesitate to get in touch.

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

Reviewer(s)' Comments to Author:
Referee: 3
Comments to the Author(s)
Please see attached comments

Decision letter (RSPB-2021-1596.R2)

19-Oct-2021

Dear Dr McDonald

I am pleased to inform you that your manuscript entitled "High heart rates in hunting harbour porpoises" 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.

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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,
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Appendix A

GENERAL COMMENTS AND SUGGESTIONS FOR RE-ANALYZING THE DATA

I have read the manuscript, "High heart rates in hunting harbour porpoises" by McDonald et al. I applaud the authors for collecting heart rate data from free-ranging cetaceans, that certainly is a difficult task. However, this manuscript cannot be accepted as is; the way in which the data were analyzed has undoubtedly obscured the significance of their findings. If the authors have the patients to reexamine the data per the comments below, they will have the opportunity to potentially have a landmark study, showing both the influence of ontogeny and activity on diving heart rate (HR) in a free-ranging cetacean. Currently we have a very limited understanding of the influence of ontogeny and activity on HR in cetaceans

Specifically, the authors must examine the data from the 2 adults and 3 juveniles separately; clumping data from physiologically mature and immature porpoises together undoubtedly added noise to your dataset which lowered your significance when you explored the effect of dive duration and activity on diving HR. The authors admit to excluding a juvenile JM3 because it was immature, and it was the smallest animal (26 kg), and appeared to have a variable HR respose. Yet Table 1 reveals that of the 5 porpoises analyzed, 3 of the animals were juveniles and all 3 juveniles were close in size (26-30kg). Just excluding one juvenile raises a "red flag", as if the authors were cherry picking the data. There is a paper published on cetaceans that shows that diving bradycardia is refined with age throughout the juvenile stage (Noren et al. 2004) and it is highly likely that this is the case for porpoise, given that they show postnatal development of other aspects of diving physiology (Noren et al. 2014).

Noren, S. R., Cuccurullo, V. and Williams, T. M. (2004). The development of diving bradycardia in bottlenose dolphins (Tursiops truncatus). *J. Comp. Phys. B*. 174, 139-147.

Noren SR, Noren DP, Gaydos JK. 2014. Living in the fast lane: rapid development of the locomotor muscle in immature harbor porpoise (Phocoeana phocoena). Journal of Comparative Physiology B 184(8):1065-1076.

Another issue with analyzing all of the dives at once is that the HR response to short, medium and long duration dives is very different. Within each age class (juv and adult) they need to sub-categorize the dives into "short duration dive", middle duration dives", "long duration dives, approaching cADL". By examining the longest dives independent of the other dives they will clearly see the effect of activity releasing a portion of the bradycardia that accompanies the dive response. As an aside, it is extremely perplexing that even with all the noise of combining age classes and all of the very different dive types, the authors DID show significance YET they consistently dismissed it by stating "but this is not biologically relevant (or significant)". No one has measured how blood flow and oxygen utilization is linked to heart rate so no one can comment on the level of change in HR that is biologically relevant. Why do the authors want to ignore the influence of activity on HR, when clearly their data show the opposite? Why did the authors chose to not site the recent study on dolphins that clearly shows the influence of activity on HR (Noren et al. 2012).

Noren SR, Williams TM, Kendall T, Cuccurullo V. 2012. The dive response redefined: underwater behavior influences cardiac variability in freely diving dolphins *Journal of Experimental Biology* 215:2735-2741.

The authors also act surprised that the porpoises do not show dramatic changes in HR; but if they just examined each porpoises 5 longest dives they would see a dramatic change in HR. This is because marine mammals do not lower HR to extreme levels unless they have to and they only do this when approaching their diving limits; the median dive durations of the animals in this study do not even come close to approximating the diving capacity of these animals, as indicated by the published calculated aerobic dive limits for harbor porpoises (Noren et al. 2014). The mediocre heart rate response of these porpoises is therefore not surprising, but as presented by the authors suggests that this result potentially separates the porpoises from other cetaceans. As an aside, the authors chose to ignore yet another published paper; Noren et al. 2014 that provides cADLs for porpoises, but these authors chose to site a paper in prep for their cADLs instead.

One of the reasons the authors surmise that the harbor porpoise limits bradycardia is because of the thermoregulatory demands of harbor porpoise (small body in cold water). However, the vasoconstriction at the periphery that accompanies bradycardia during the dive response can actually lower thermoregulatory costs by safeguarding the internal temperature of the brain and heart because blood flow is directed away from the periphery where heat is lost to the environment. Vasoconstriction during the dive response in relation to thermoregulation is really only a concern for marine mammals exercising in warm water because they can't dump heat which could lead to hyperthermia. There is a lot of literature on adaptations for thermoregulating in cold environment, which includes vasoconstriction in marine mammals that dates back to Scholander in the 1940's and recent work on how heart rate and thermoregulation are linked and concerns about hyperthermia in exercising dolphins in warm water.

Noren D.P., Williams T.M., Berry P., Butler E. (1999) Thermoregulation during swimming and diving in bottlenose dolphins, *Tursiops truncatus*. The Journal of Comparative Physiology (B) 169: 93-99.

Williams T.M., Noren D., Berry P., Estes J.A., Allison C., Kirtalnd J. (1999) The diving physiology of bottlenose dolphins (*Tursiops truncatus*) III. Thermoregulation at depth. The Journal of Experimental Biology 202:2763-2769.

I would also like to see in Table 1 the median and range values for porpoise for "median middle dive heart rate". This metric is probably the best metric to pick up differences in the ability for bradycardia. Although, you need to reassess how you determined what HR would be included in this metric. In your analyses you state that you cut off 10 sec at the beginning and end of the dive, and the remaining HR was the "median middle dive heart rate". But cutting off 10 sec at the beginning and end of the dive is arbitrary, especially since you have such variation in dive durations. To account for the different dive durations, you should consider excluding HR at the beginning and end of the dive based on a percentage of the dive time. For example, the "median middle dive heart" represents the heart response during the dive, which excludes the 1st 25% and last 25% of the dive duration; in this way you are only looking at HR during 50% of the dive time and excluding HR artifacts associated with the surface respiratory event and excluding HR artifacts associated with anticipatory tachycardia. This will give you the lowest HR response during the dive, which is what you are trying to quantify. You may have to play with this percentage to make sure that your “median middle dive heart rate” ONLY includes HR that occurs when the HR is consistently flat in its response, no decline or incline associated with the previous breath or anticipation of the next breath, respectively. I.e maybe you cut off the first and last 30% of the dive HR and only examine the middle 40% of the HR.

The data collected by the authors is difficult to obtain, therefore there is value in including all of the dives to show that during a typical day in the life of a harbor porpoise they are not required to have a dramatic change in HR because they rarely approach their diving limits. This is the case for many cetaceans; and is not novel to porpoises. BUT by ONLY doing this, the authors have introduced too much noise into the dataset to pick up signals for the variables they are trying to explore. (effect of dive duration and activity on diving HR). Which is why I suggested categorizing your dives into short, medium, and long duration dives and doing separate analyses for each category. To look for ontogenetic effects, you should look at ONLY the 5 longest dives for each porpoise, as done by Noren et al. (2004).Examining maximum performance to determine the maximum physiological response is what is done in physiology; and this is what needs to be done before you can make an argument about the differences between the adult and immature porpoises. It is likely that when examining the 5 longest dives that the adults were below their cADLs and the immatures were approaching or exceeding their cADLs. As a result you likely got the most pronounced bradycardia response from the immatures that they were capable of, but is unlikely you captured the most pronounced bradycardia response that the adults were capable of. Doing this analysis gives you the opportunity to reveal the influence of ontogeny on diving heart rate in a cetacean in the field – which has never been done before. OR if you show that immature porpoises have a mature ability for bradycardia early in life – this is also of value since to date the only study to investigate the development of bradycardia in a cetacean was on captive bottlenose dolphins. However, to make the later statement, both the adult and immature groups must have their field dives be a similar proportion of the cADLs (see Noren et al. 2014 for porpoise cADLs)

SPECIFIC COMMENTS

ABSTRACT

Line 36-38. This statement is incorrect. There has been a study that examined how increased swim speeds (as would be required during hunting) can alter the dive response (Noren et al. 2012) AND also two studies have discussed the implications of the dive response and thermoregulation (Noren et al. 1999; Williams et al. 1999).

Rewrite the sentence to “Previous studies on marine mammals have focused on the role of the dive response in maximizing dive duration, but few have addressed how these adjustments may negatively impact the capability to hunt, digest and thermoregulate.”

Lines 38-39 is an overstatement of what your study is accomplishing. You state, "Here we use heart-rate DTAGs to investigate how O2 management is balanced between the need to dive,.." BUT you are not measuring O2 management. You are measuring heart rate, and to date no one has done a study to link O2 management with heart rate. Therefore you need to reword this sentence to reflect what your study is actually investigating.

Rewrite sentence to "Here we use heart-rate DTAGs to investigate how alterations in heart rate are balanced between the need to dive,.."

Line 41: Insert the range of dive durations that were measured in your study into this sentence. if you have a narrow range of dive durations, and dive durations that do not approach the cADL for the harbor porpoise, then it is not surprising that HR was moderate. Marine mammals will only lower HR to dramatic levels when necessary, because to your point it is beneficial to keep HR elevated to support muscular activity and digestion. BUT please note that in cold environments, especially for small bodied mammals, it is beneficial to shut down blood flow to the extremities (as occurs during the dive response) to assist with thermoregulation to protect core body temperature from heat loss (see Noren et al. 2008). The vasoconstriction that occurs during the dive response actually is more problematic for thermoregulation for an exercising marine mammal in warm water because they cannot dump heat and can possibly become hyperthermic (Noren et al. 1999, Williams et al. 1999).

Noren SR, Pearson LE, Davis JW, Trumble SJ, Kanatous SB. 2008. Different thermoregulatory strategies in nearly weaned pup, yearling, and adult Weddell seals (Leptonychotes weddelli). Physiological and Biochemical Zoology 81(6):868-879.

LINE 45-47 This statement is not novel. "despite having the capacity to prolong dives by lowering cardiac output, for these shallow-diving cetaceans, it is more efficient to maintain circulation: extreme heart-rate gymnastics are for emergencies, not everyday use."

As mentioned above all marine mammals studied to date do not show large reductions in HR unless they are prolonging dive durations. Also "gymnastics" would be better used in layman article, not a scientific article.

Rewrite to the sentence to "Like other marine mammals, harbor porpoise do not have dramatic reductions in heart rate during normal free-ranging activities, although is it likely that porpoise can reduce heart rate further for emergencies.

BACKGROUND

Line 60 Noren et al. (2012) discusses the effect of exercise and volition. Should include in the references for this sentence

Line 59-60 Among the factors influencing the ability for diving bradycardia is postnatal development. This has been shown in seals and dolphins. You should include this because your sample includes immature porpoise, and it has been shown in bottlenose dolphins that this development is not complete until 3.5 years postpartum. See Noren et al. 2004 and Greaves et al. 2005

Greaves D.K., Schreer, J. F., Hammill, M. O. and Burns, J. M. (2005). Diving heart rate development in seals. *Phys. Biochem. Zool.* 78, 9–17.

Line 68 These studies did not look at “O2 management” they looked at heart rate adjustments. Change O2 management to heart rate adjustments. Do this for all places in the text where you have written O2 management for studies that investigated HR adjustments. Your line prior to this one discusses the probable link between HR and O2 management so that link has been provided for the reader, but when commenting on your study and past studies you must report what was actually measured, and that was HR (not O2 management).

Line 71 missing the word “are”

Line 76. After talking about O2 management should put in another sentence to remind the reader about O2 and HR link so that the reader understands why the next sentence and the rest of the paragraph you talk about HR.

Line 79 “influenced by….volition. Include Noren et al. 2012, who was among the first to suggest the idea of the influence of volition on HR in diving marine mammals.

METHODS

Lines 176-177 What was the estimated age of JM3? You measured body length, so you can estimate the age from published age vs. length curves, which are available for porpoise. See Noren et al.2014 for these references. Little is known about the HR response of immature marine mammals, particularly young cetaceans so the higher HR variability in the juvenile porpoise is an important finding in this study.

RESULTS AND DISCUSSION

Line 184, please also include the range of maximum dive durations across the 5 porpoises you studied, making sure to note which value is associated with the juvenile porpoise.

Line 187-189. This result is NOT surprising given that the median duration of the dives where HR was measured was 43-76 seconds. When looking for “extreme bradycardia” you need to analyze ONLY the “extreme dive durations”, as in Noren et al. 2004 where ONLY the 5 longest dives for each dolphin were analyzed; and this needs to be done with adults and juveniles separate. The approach of examining extreme performance (i.e. longest dive durations) to understand the ability for a physiological response is not a novel ideal; this is done throughout the physiological literature when investigating the physiological capacities of animals.

Line 191 move the range of mass (28-67 kg) earlier in the sentence to just after the word the words estimated mass. And include the entire range of mass, the lowest mass was 26 kg.

Having looked at TABLE 1 now, I see that you have 3 juveniles, close in mass 26, 28, 30kg. this makes it completely arbitrary that you ONLY excluded JM3 (26 kg) from the analyses, given that JM2 and JM1 are only 2-4 kg heavier than JM3. While the adults are much larger, at 44 kg and 67 kg. Your data are compounded by a sample of 2 adults and 3 juveniles. These age classes should NOT be combined for your analyses based on the findings of Noren et al. 2004. Indeed the muscle biochemistry of harbor porpoises is underdeveloped in porpoises less than 134 cm long, which affects diving capacity. See Noren et al. 2014

Line 194-197 It is NOT surprising that the bradycardia of the juveniles is lower than the adults, because the juveniles are probably pushing their dive limits more than that adults. In order to compare across ages classes you must look at their extreme physiological response, which is why you need to also include in you analyses an examination of ONLY the 5 longest dives for each animal. To determine if the adult and juveniles are pushing their physiology equally, for each porpoise you need to divide their average dive time over their 5 longest dives by their cADL to determine how close they were approximating their physiological capacity. For example, if adults are only holding their breath for half their cADL then they should not need to lower HR as much compared to juveniles if they are holding their breath for their full cADL.

Moreover, you excluded one of the juveniles because it didn't fit your conclusion; that is cherry picking data. JM3 is the youngest, thus you expect higher respiratory rates, ,higher HR, and more variable HR response while diving as shown in Noren et al. 2004. Please see additional thoughts in the general response paragraph I provided at the beginning of this review.

Table 1: I don't agree with your cADL calculations; you cite a paper that is in prep when calculations for harbor porpoise have already been well described in Noren et al. (2014)

Line 207-208. This is not surprising. If you examine just the extreme dives, say the 25 longest dives for each animal I suspect that your relationship for HR and dive duration will improve. Short duration dives often have high variability in HR, this is because sometimes an animal may lower HR in anticipation of a long dive but then something interrupts the animals to that it ends up terminating the dive after only a short duration. You cannot control for this in the wild. My insight about how sensitive HR is to external factors is from simultaneously analyzing over 24 hours of underwater behaviors of a dolphin in combination with instantaneous heart rate data. Indeed, you do point out that there is a relationship for HR and dive duration in captive porpoises; this is because the measurements are taken in a more controlled environment (less variables for the porpoise to have to worry about while on a dive). As an aside, how do you know that 3 bpm for one min increase in dive duration is not "biologically relevant".?

Line 215 This is what is happening. You should state this up front.

Line 239 Why is Noren et al. 2012 not mentioned here. They were among the first to point out the relationship between HR and exercise in a cetacean.

Line 243. It has been shown in the past (I believe by Rosen) that it is hard to link MSA to HR. There is too much noise. It is very possible that had you measured fluke stroke frequency that you would have found a relationship between HR and exercise as in Noren et al. (2012). You have to mention the limits of your study (using MSA instead of Stroke frequency) and how this could have influenced this result.

Line 247-250. Again you dismiss a significant result, stating “there is no biological relevant difference”…. How do you know that? Have you measured how blood flow and oxygen utilization patterns change with small changes in HR?. You need to delete the use of “there is no biological relevant difference” and “there is no biological significance” throughout your manuscript.

Line 251-252 “while the association between MSA and LQ was significant, a unit of increase in one MSA… Why are you again dismissing a significant result? It is as if you want your study to show no influence of activity on HR, but your data says the opposite. And I bet that once you separate the juveniles and adults out from each other and analyze each age class separately your results will become more significant. And I suspect that if you create sub categories within each age class (i.e. short duration, medium duration, and extended duration dives) and analyze each sub category separately that your results will become even more significant. Short duration dive HR has a lot of noise and variation so it is hard to see the patterns; and HR is already relatively high so effect of exercise is not as dramatic. When the animal is pushing itself during extended duration dives that is when you see the effects of exercise, as it must release some of the dive response to deal with oxygen debt at the muscle. See Noren et al. 2012.

Line 277 get rid of “lack of biologically significant difference”

Line 289-290. If you look at your data categorically within each age class, “short duration dive”, “medium duration dive”, and “long duration dive” I suspect that you cannot make this statement. Undoubtedly during their longer dives porpoises do employ a comparatively deep bradycardia. Moreover, even as you analyzed the data (with the noise of combining age classes and also combining disparately different dive types) your results were significant for dive duration and activity, but you chose to dismiss them.

Line 294 “delete “are a step too far”

Line 295 delete “gymnastics”

Line 295 Change to “shallow-feeding shot duration diving porpoises”.

Line 297-300 The point here is that your porpoises were generally not pushing themselves physiologically when they forage, as shown in Table 1 by the dive durations exhibited. They rarely approached their dive limits. Bottlenose dolphins do the same thing, shallow short dive durations are not accompanied by dramatic bradycardia. This is not unique to porpoise, but your closing line makes it seem like it is unique to porpoises.

Figure 1 legend. Line 362-364 change “had higher metabolic rate” to “suggests a higher metabolic rate”. You did not measure metabolic rate so you can’t state the animal had a higher metabolic rate.

Figure 2 legend. Line 372 delete “not biologically significant”.

Foraging dive HR is higher – why do you want to state the opposite. AND if you get ride of noise by looking at age classes separately and within age classes look at sub-categories based on dive duration, your noise will decrease and this result will be even more significant, and is undoubtedly biologically significant.

Figure 3 delete “no biologically significant” throughout this legend!

foraging dives have higher HR!

Appendix B

Firstly, I want to congratulate the authors for conducting a study that is important in assessing a critical part of the dive response in harbor porpoises. This component of the dive responses is particularly difficult to study due to the technological requirements and the complexities of the data analysis. It is not surprising that there are relatively few scientists that have tackled this area of investigation in marine mammals, particularly cetaceans, which are even more difficult to study than pinnipeds, because they do not haul out on land.

Having said that, it is possible that the findings of this study would be different if the data were analyzed in a different manner. Because heart rate at depth is highly variable, including over one dive cycle, it is important to critically analyze heart rates on a dive by dive basis, rather than take a cookie cutter approach across all dives. Other researchers have meticulously analyzed diving heart rates on a dive by dive basis in free-swimming cetaceans and have also assessed how heart rates at depth are influenced by activity (e.g., Noren et al. 2004, 2012; Williams et al. 2015, 2017). Furthermore, the development of diving bradycardia with age has also been investigated in dolphins (Noren et al. 2004). It was surprising to see that the authors did not attempt to analyze their data in a similar manner, nor cite some of these highly relevant earlier studies, particularly Noren et al. 2012. Furthermore, the authors did not analyze the heart rate data from the three juvenile and the two adult harbor porpoises separately, despite the findings of earlier studies on the development of bradycardia at depth. Not only does the heart rate response to diving vary by age in marine mammals, including toothed cetaceans (Noren et al. 2004 and references cited within), the total oxygen storage capacity and calculated aerobic dive limits of marine mammals, including harbor porpoises (Noren et al. 2014), differ from that of adults. Both factors influence dive capacity. Besides these highly relevant studies, there is now a relatively large volume of publications that demonstrate how several physiological aspects of diving, including bradycardia, are influenced by age and development in many marine mammal species. Yet, the development of diving, including the HR response, was not acknowledged, nor investigated, despite its potential to greatly impact the results of the study.

Given the authors' relatively coarse analytical approach with a fairly small sample size, it is likely that they were unable to detect important factors that contribute to the HR response in harbor porpoise. As such, significant reanalysis will be required in order to adequately address these important issues and assess whether the HR response in harbor porpoises is influenced by activity and if the response in juveniles differs from that of adults.

Below, I provide specific comments:

Abstract

Page 2 (line 39) and throughout the manuscript, the authors state that they investigate "how O_2 management" is balanced, etc. This study only investigated heart rate. There are a suite of physiological adjustments that relate to O_2 management on a dive, including for example, peripheral vasoconstriction, which were not investigated in the present study. It would be more accurate for the authors to specify that they investigated one component of O_2 management in the abstract and simply use "changes in heart rate" in other parts of the manuscript, as appropriate.

Page 2 (line 43): “A moderate dive response, allowing for some perfusion of peripheral tissues”. Similar to the statement above, although changes in heart rate may be related to perfusion of peripheral tissues, this study did not investigate changes in peripheral perfusion. Changes in peripheral perfusion is achieved by vasoconstriction and vasodilation of blood vessels, which may occur independently of changes in heart rate. Changes in heart rate, which this study investigated, are more indicative of changes in metabolic rates, or the rate that oxygen stores are being utilized. The authors should consider rewording these statements to accurately reflect what their study investigates.

Background

Page 2, lines 57-60 describes some components of the “so-called dive response”. This section of the manuscript focuses on regulating the magnitude and distribution of peripheral blood flow to conserve blood for critical tissues, which is correct. But, there is also another vital component, which is the reduction in the rate at which O_2 stores are utilized. Reduction in heart rate (bradycardia) is one component of this part of the dive response. Bradycardia and potentially reduced metabolic rates should be mentioned here as well. The study primarily focuses on bradycardia, rather than perfusion.

Page 2, line 59-60 One of the important factors that influences the dive response is age or development, but it was not included here. Particularly relevant to this manuscript is the publication on the development of bradycardia by Noren et al. 2004, and it should be cited here.

Methods

Page 5, lines 139-148: The relatively coarse methods to determine heart rates during various parts of the dive cycle and also the arbitrary exclusion of the initial and final 10 sec of the dive undoubtedly make it difficult to detect the differences in heart rates that are likely present. Given results from studies on other cetaceans, arbitrarily excluding 10 sec periods at the beginning and at the end of dives may not sufficiently exclude the heart rate changes that occur during descent and ascent in all dives. By not adequately excluding the ascent and descent periods of the dives, the heart rate variables that were calculated for the “middle phase” of the dives are likely to be erroneous and more variable. The appropriate duration of time to exclude can vary by dive duration/depth as well as by subject age. The appropriate method would be to exclude ascent and descent phases on a dive by dive basis. Indeed, for bottlenose dolphins with similar dive durations reported for harbor porpoises in the present study, steady state heart rates were often not reached until well after 10 sec following submergence (Noren et al. 2004). Similarly, heart rates prior to surfacing also began to increase more than 10 sec before the end of submergence for several dives (Noren et al. 2004). Furthermore, older dolphins demonstrate greater overall reductions in heart rate during diving, compared to immature dolphins, and the ability to reduce heart rate improves as calves mature (Noren et al. 2004). Finally, there is substantial variation across dives, including dives by the same individual (Noren et al. 2004 (dolphins), Williams et al. 2017 (narwhals)). The best approach to address these complex issues with the harbor porpoise dive data is to analyze each dive to determine when the heart rate reaches a relative steady state at depth. The minimum steady state heart rate at depth could then be compared across dives and also compared to steady state heart rates at the surface. Similarly, the minimum steady state heart rate at depth should be compared across adults and juveniles. The current method of analysis undoubtedly adds quite a lot of variability which may also obscure statistical and biologically significant differences in heart rates across dive types. Furthermore, because juvenile porpoises have limited dive capacities (Noren et al. 2014) and potentially limited bradycardia responses (Noren et al. 2004), it is not appropriate to combine adult and juvenile harbor porpoises in the analysis. Development of bradycardia has also been reported for pinniped species (see references within Noren et al. 2004), which suggests that this necessary developmental period is ubiquitous across marine mammal species.

Page 6-7, lines 176-178: Excluding the juvenile male (JM3) from the analysis is not appropriate. This animal is the smallest in the study and is potentially the animal that has not fully developed the bradycardia response yet. As such, it is not surprising that its heart rate data were much more variable than the other four animals. Furthermore, this animal had the longest tag deployment. With a longer duration of data collection, it is expected that this individual would demonstrate greater variability in dive behavior and consequently more variable heart rates. Indeed, during this tag deployment, JM3 demonstrated a relatively extreme range in dive depths (Table 1 and Fig 3 from Rojano-Doñate et al. 2018). In light of results from previous studies on dive behavior and heart rate (e.g., Noren et al. 2004, 2012 and Williams et al. 2017), this high degree of individual heart rate variability is not surprising. Rather than exclude JM3 from the analyses, more careful attention to how the heart rate data are analyzed is warranted.

Results and Discussion

General Comment: I suspect once the data are analyzed in a meticulous manner, as described above, many of the findings will change.

Page 7, lines 194-203 The discussion regarding the lack of difference between juvenile and adult diving heart rates is interesting. However, differences in heart rates between juveniles and adults probably exist, but are likely being obscured, given the coarse methods of heart rate data analysis in the present study. As stated above, given the larger sample size from JM3, the smallest individual, it isn’t surprising that the analysis showed that this individual had highly variable and higher heart rates than the other individuals. This finding aligns with those from previous studies (Noren et al. 2004 and references within), which were not cited by the authors.

Page 8, lines 208-214. The discussion regarding the association between dive duration and heart rate is a little confusing to me. First, the authors state that despite a statistically significant association between dive duration and heart rate (when JM3 is excluded), the slope coefficient is not biologically relevant. Yet, this follows the expected physiological response. Despite this relationship, the authors then state that this finding is unusual for diving marine mammals since heart rate typically decreases with increasing dive duration. But wasn’t that the finding stated a few sentences prior?

Page 8, line 215-220: The authors state that the porpoises performed short dives that rarely approach their cADL (cADLs reported in Table 1). I was surprised to see that the cADL values in Table 1 are single point estimates from a paper that is in prep, rather than published cADL values for harbor porpoises. There are quite a few considerations when calculating ADL values, and these are thoroughly discussed for harbor porpoise in Noren et al. 2014. Indeed, cADL values for harbor porpoises of all ages are published in that paper. The authors should cite the appropriate range of cADL values for adult and juvenile harbor porpoises from Noren et al. 2014. For some of the harbor porpoise subjects the cADL values in Noren et al. 2014 are a bit different from the values in Table 1.

Furthermore, the authors suggest that since harbor porpoise regularly do not approach their cADL, there is no requirement to modify heart rate to maximize dive duration. If harbor porpoise dive durations do not approach their cADL (but see comment above about published cADLs), then this argument seems logical. However, the authors then suggest that harbor porpoises minimize their dive durations in order to continue to digest their food, almost out of necessity. With a sample size of 5 harbor porpoise, I caution the authors against suggesting that their data are representative of all harbor porpoises and that short dive times are an adaptation for digestion. The authors do not evaluate how their harbor porpoise dive data compare to the somewhat substantial number of harbor porpoise dive duration and/or depth values in the published literature. For example, other publications on free-ranging harbor porpoises (e.g., Berga et al. 2015, Otani 2000, Otani et al. 1998, Linnernschmidt et al. 2012, Solsona et al. 2015, Westgate et al.1995) have shown that these cetaceans repeatedly dive to depths that are substantially greater than median, 2.5 quartile and 97.5 quartile max dives reported in Table 1. Consequently, due to the small sample size, the present study many not have been able to capture the full dive capacity and the subsequent range of HR responses in harbor porpoise. The authors should compare their data to dive depths and times reported by other studies (the list above is likely not complete) to add context. Furthermore, they need to be transparent and acknowledge that their study did not capture the full diving capacity of this species. As Berga et al. 2015 acknowledged in their study with a small sample size (n=12, which is larger than the sample size reported in the present study), large variation among animals may obscure subtle effects on the diving behavior of porpoises. This could also be said about the HR response in the present study. Later in lines 228-233, the authors do acknowledge that harbor porpoise in Danish waters primarily dive to relatively shallow depths, compared to porpoises in Greenland waters, and that these differences in diving behavior could elicit different heart rate responses. Given the findings from other studies, it is likely that many harbor porpoises dive to greater depths than the animals in the present study. As such, the findings in this study may not reflect the physiological response to diving for most harbor porpoises. This is critical to acknowledge.

Page 9, lines 246-250: The authors predicted that the increase in activity would lead to higher diving heart rates, but “there was no biologically relevant difference in LQ, MM, or minimum dive heart rate between foraging and non-foraging dives” This statement seems to contradict their findings. There is a statistical difference, which supports the hypothesis and is a result that has also been reported by others (e.g., Noren et al. 2012; Williams et al. 2015, 2017). Also, as mentioned above, the coarse methods of parsing out heart rates in the different dive components is expected to lead to a great deal of variability. Consequently, it isn't surprising that a low percentage of variation in the data is explained.

Table 1: It is curious that the authors did not report the absolute max dive depth and duration values. When investigating the range of responses, it is of interest to also evaluate the responses at the most extreme diving capacities. In this case, dive duration is likely to have a significant effect on the HR response, and it is also likely that there were significant differences in max dive duration across juvenile and adult harbor porpoise subjects. Indeed dive duration data in Table 1 for the two smallest juveniles suggest that these animals in particular are not diving to the capacity that the two adult harbor porpoise are. As mentioned elsewhere, differences in dive duration and HR response between juveniles and adults should be explored. See, for example, Noren et al. 2004.

Conclusions

Page 10, lines 287-290: "…demonstrate how these consummate divers juggle the conflicting demands of a deep bradycardia to prolong dives in search of prey while still delivering the O_2 needed for active hunting and digestion. We find that porpoises in shallow water forgo deep bradycardia and instead maintain a stable diving heart rate that is not influenced by size, dive duration, or activity."

Compared to other harbor porpoise worldwide, these subjects are diving to shallow depths and are also diving for shorter periods. Consequently, deep bradycardia may not be necessary. Some of these results are not surprising. However, this study has a relatively small sample size and the authors' coarse analytical methods may have precluded them from finding significant influences of size, dive duration, or activity, which may exist.

References

Berga A.S., Wright A.J., Galatius A., Sveegaard S., Teilmann J. (2015) Do larger tag packages alter diving behavior in harbor porpoises? Mar Mam Sci 31:756-763.

Linnenschmidt M., Teilmann J., Akamatsu T., Dietz R., Miller L.A. (2013) Biosonar, dive, and foraging activity of satellite tracked harbor porpoises (*Phocoena phocoena*). Mar Mam Sci 29: E77–E97

Noren S.R., Cuccurullo V., Williams T.M. (2004) The development of diving bradycardia in bottlenose dolphins (*Tursiops truncatus*). J Comp Physiol B 174: 139-147

Noren S.R., Kendall T., Cuccurullo V., Williams T.M. (2012) The dive response redefined: underwater behavior influences cardiac variability in freely diving dolphins. J Exp Biol 215: 2735-2741

Noren S.R., Noren D.P., Gaydos J.K. (2014) Living in the Fast Lane: rapid development of the locomotor muscle in immature harbor porpoises (*Phocoena phocoena*). J Comp Physiol B 184:1065-1076

Otani S. (2000) Diving behavior and swimming speed of a free-ranging harbor porpoise, *Phocoena phocoena*. Mar Mam Sci 16:811-814

Otani S., Naito Y., Kawamura A., Kawasaki M., Nishiwaki S., Kato A. (1998) Diving behavior and performance of harbor porpoises, Phocoena phocoena, in Funka Bay, Hokkaido, Japan. Mar Mamm Sci 14:209-220

Solsona Berga A., Wright A.J., Galatius A., Sveegaard S., Teilmann J. (2015) Do larger tag packages alter diving behavior in harbor porpoises? Mar Mam Sci 31:756-763

Westgate A.J., Read A.J., Berggren P., Koopman H.N., Gaskin D.E. (1995) Diving behaviour of harbour porpoise, *Phocoena phocoena*. Can J Fish Aquat Sci 52:1064-1073.

Williams T.M., Fuiman L.A., Kendall T., Berry P., Richter B., Noren S.R., Thometz N., Shattock M.J., Farrell E., Stamper A.M., Davis R.W. (2015) Exercise at depth alters bradycardia and incidence of cardiac anomalies in deep-diving marine mammals. Nat. Commun. 6:6055 doi: 10.1038/ncomms7055 (2015).

Williams T.M., Blackwell S.B., Richter B., Sinding M.-H. S., Heide-Jørgensen M.P. (2017) Paradoxical escape responses by narwhals (*Monodon monoceros*). Science 358 (6368), 1328-1331.

Appendix C

Response to Reviewers

We thank the reviewers for their comments. We have performed additional analyses as suggested by some of the reviewers and modified some of the text. These analyses support our previous conclusions and we believe have strengthened the manuscript. Please see below for specific responses to the reviewer's comments.

Reviewer 1

Firstly, I want to congratulate the authors for conducting a study that is important in assessing a critical part of the dive response in harbor porpoises. This component of the dive responses is particularly difficult to study due to the technological requirements and the complexities of the data analysis. It is not surprising that there are relatively few scientists that have tackled this area of investigation in marine mammals, particularly cetaceans, which are even more difficult to study than pinnipeds, because they do not haul out on land.

Thank you for your kind words.

Having said that, it is possible that the findings of this study would be different if the data were analyzed in a different manner. Because heart rate at depth is highly variable, including over one dive cycle, it is important to critically analyze heart rates on a dive by dive basis, rather than take a cookie cutter approach across all dives. Other researchers have meticulously analyzed diving heart rates on a dive by dive basis in free-swimming cetaceans and have also assessed how heart rates at depth are influenced by activity (e.g., Noren et al. 2004, 2012; Williams et al. 2015, 2017). Furthermore, the development of diving bradycardia with age has also been investigated in dolphins (Noren et al. 2004). It was surprising to see that the authors did not attempt to analyze their data in a similar manner, nor cite some of these highly relevant earlier studies, particularly Noren et al. 2012. Furthermore, the authors did not analyze the heart rate data from the three juvenile and the two adult harbor porpoises separately, despite the findings of earlier studies on the development of bradycardia at depth. Not only does the heart rate response to diving vary by age in marine mammals, including toothed cetaceans (Noren et al. 2004 and references cited within), the total oxygen storage capacity and calculated aerobic dive limits of marine mammals, including harbor porpoises (Noren et al. 2014), differ from that of adults. Both factors influence dive capacity. Besides these highly relevant studies, there is now a relatively large volume of publications that demonstrate how several physiological aspects of diving, including bradycardia, are influenced by age and development in many marine mammal species. Yet, the development of diving, including the HR response, was not acknowledged, nor investigated, despite its potential to greatly impact the results of the study.

Given the authors' relatively coarse analytical approach with a fairly small sample size, it is likely that they were unable to detect important factors that contribute to the HR response in harbor porpoise. As such, significant reanalysis will be required in order to adequately address these important issues and assess whether the HR response in harbor porpoises is influenced by activity and if the response in juveniles differs from that of adults.

Thank you for your thoughtful comments. We address the comments below and in the manuscript.

With respect to our analytical approach, we opted for a relatively coarse-grained approach to summarize the data because of both broad variability in activity level and the unknown state of health (e.g., parasite load) of five individuals. We therefore selected variables that provided relatively simple

but effective descriptions of the observed heart rate profiles. Given the concern expressed by reviewers 1 and 3 about missing details with this approach, we have conducted additional analyses. First we divided the dive into three phases: 1) dive decent, 2) bottom time (start time is when the porpoise reached within 1 body length of maximum depth and ends the last time the porpoise is at that depth), and 3) dive ascent. While this resulted is some changes in the summary data of one individual (JM3), it did not change any of the conclusions (Supplemental Figure S3 and Supplemental Table S4).

In addition to redefining bottom time, we analyzed the relationship between activity and heart rate within the dive. The bottom of the dive was divided into 5 second intervals. Mixed models with a correlation structure were used to evaluate the relationship between dive duration, interval MSA (an activity measure), and interval heart rate. The results further support our initial findings using dive-level metrics. I.e. MSA has some influence in the full dataset – but explains less than 7% of the variation in the data. When JM3 is excluded (which improves the model assumptions by removing the outlier), interval MSA did not influence interval heart rate. Heart rate tended to be lower in longer dives when JM3 was excluded, but the effect size was small and the fixed effects only explained 3% of the variation in the data indicating that the model offered little predictive value. This suggests, that that while significant, the fixed effect is not biologically relevant (Nakagawa and Cuthill 2007, Edwards et al 2008, Wasserstein and Lazar 2016). We have added these citations to the tables and have added the extended analyses to the methods and the result/discussion sections.

Regarding the comments about investigating the ontogenetic development of diving bradycardia, while we think this is an interesting question, this was beyond the scope of this paper. As we are opportunistically instrumenting porpoises captured in fishing nets, we cannot select for age. Our dataset comprises 3 juveniles and 2 adults as assessed by body length, and with this sample size we do not have the statistical power to try to compare animals of different ages, especially given the unknown life histories of these individuals. However, recognizing that age, amongst many other factors, can influence heart rate, we show the data separately for each individual and use mixed effects models to account for individual differences. This approach is appropriate given the literature on diving ontogeny in porpoises: Juvenile porpoises of similar size to individuals in our study have been reported to have fully developed O_2 stores (even myoglobin) and similar cADLs to adults (Noren et al 2014). In comparison, bottlenose dolphins mature more slowly, taking 3 years to exhibit a decrease in diving heart rate similar to adults, but they also take much longer to develop adult level O_2 stores. The 3-year-old dolphins were likely at a similar developmental state as the juvenile porpoises in this study given the rapid maturation of porpoise. Due to the rapid maturation of porpoises, we would need data from neonates and calves to address the theme raised by the reviewer. Nonetheless, we followed the suggestion of reviewer 3 and plotted the 5 longest dives for each porpoise (Fig 2). There was no difference in the dive heart rate response in these dives compared to average duration dives. Additionally, both the figure with the 5 longest dives (Fig 2) and the interval summary figure (Supplemental Figure S2) do not support any consistent differences between juveniles and adults.

We thank the reviewer for the suggested references and have added Noren et al 2004, Noren et al 2012, and Noren et al 2014 citations throughout the paper.

Below, I provide specific comments:

Abstract Page 2 (line 39) and throughout the manuscript, the authors state that they investigate "how O2 management" is balanced, etc. This study only investigated heart rate. There are a suite of physiological adjustments that relate to O2 management on a dive, including for example, peripheral vasoconstriction, which were not investigated in the present study. It would be more accurate for the authors to specify that they investigated one component of O2 management in the abstract and simply use "changes in heart rate" in other parts of the manuscript, as appropriate.

While we appreciate this suggestion, our statement accurately reflects the literature on O_2 management in diving animals. Heart rate is, as the main driver of cardiac output, a direct indicator of peripheral vasoconstriction (Grinnell et al 1942, Zapol et al 1979, Davis and Kanatous 1999, Jobsis et al 2001, Butler et al 2020). When submersion triggers peripheral vasoconstriction, the heart rate must drop to keep blood pressure stable. Endotherms are finely tuned to maintain a relatively stable blood pressure (Butler et al 2020). Accordingly, at this time, heart rate is the best indicator of O_2 management in freely diving cetaceans. There is not room in the abstract to expand on this, but we explain this link briefly in the introduction (lines 61-67)

Grinnell, S. W., Irving, L., & Scholander, P. F. (1942). Experiments on the relation between blood flow and heart rate in the diving seal. Journal of Cellular and Comparative Physiology, 19(3), 341-350.

Zapol, W. M., Liggins, G. C., Schneider, R. C., Qvist, J., Snider, M. T., Creasy, R. K., & Hochachka, P. W. (1979). Regional blood flow during simulated diving in the conscious Weddell seal. Journal of Applied Physiology, 47(5), 968-973.

Davis, R. W., & Kanatous, S. B. (1999). Convective oxygen transport and tissue oxygen consumption in Weddell seals during aerobic dives. Journal of Experimental Biology, 202(9), 1091-1113.

Jobsis, P. D., Ponganis, P. J., & Kooyman, G. L. (2001). Effects of training on forced submersion responses in harbor seals. Journal of Experimental Biology, 204(22), 3877-3885.

Butler, P. J., Brown, J. A., Stephenson, D. G., & Speakman, J. R. (2021). Animal Physiology: An Environmental Perspective. Oxford University Press.

Page 2 (line 43): "A moderate dive response, allowing for some perfusion of peripheral tissues". Similar to the statement above, although changes in heart rate may be related to perfusion of peripheral tissues, this study did not investigate changes in peripheral perfusion. Changes in peripheral perfusion is achieved by vasoconstriction and vasodilation of blood vessels, which may occur independently of changes in heart rate. Changes in heart rate, which this study investigated, are more indicative of changes in metabolic rates, or the rate that oxygen stores are being utilized. The authors should consider rewording these statements to accurately reflect what their study investigates.

As discussed in the previous comment, heart rate and vasoconstriction and vasodilation are tightly correlated. While we cannot determine which tissues are perfused by studying heart rate, we do know that an increase in perfusion to some tissues will result in an increase in heart rate that we can measure. We posit accordingly that our wording is accurate as written.

Background
Page 2, lines 57-60 describes some components of the "so-called dive response". This section of the manuscript focuses on regulating the magnitude and distribution of peripheral blood flow to conserve blood for critical tissues, which is correct. But, there is also another vital component, which is the reduction in the rate at which O2 stores are utilized. Reduction in heart rate (bradycardia) is one component of this part of the dive response. Bradycardia and potentially reduced metabolic rates should be mentioned here as well. The study primarily focuses on bradycardia, rather than perfusion.

Thank you for pointing this out. We had mentioned that the dive response consists of vasoconstriction and bradycardia in the abstract, but realize we should also mention it here. We have modified the sentence before this statement to make it clear that the peripheral vasoconstriction and bradycardia during diving minimizes O_2 consumption (lines 57-58). We think it is important to keep this statement about how the dive response regulates the magnitude and distribution of peripheral blood flow. This statement is accurate even if we are not measuring blood flow. And as mentioned earlier, at this time, heart rate is the best tool we have to examine the dive response in freely diving cetaceans. We have added a few sentences to explain the link between heart rate and perfusion (lines 63-67).

Page 2, line 59-60 One of the important factors that influences the dive response is age or development, but it was not included here. Particularly relevant to this manuscript is the publication on the development of bradycardia by Noren et al. 2004, and it should be cited here.

Good point. We have added information on age and this reference (lines 61).

Methods

Page 5, lines 139-148: The relatively coarse methods to determine heart rates during various parts of the dive cycle and also the arbitrary exclusion of the initial and final 10 sec of the dive undoubtedly make it difficult to detect the differences in heart rates that are likely present. Given results from studies on other cetaceans, arbitrarily excluding 10 sec periods at the beginning and at the end of dives may not sufficiently exclude the heart rate changes that occur during descent and ascent in all dives. By not adequately excluding the ascent and descent periods of the dives, the heart rate variables that were calculated for the "middle phase" of the dives are likely to be erroneous and more variable. The appropriate duration of time to exclude can vary by dive duration/depth as well as by subject age. The appropriate method would be to exclude ascent and descent phases on a dive by dive basis. Indeed, for bottlenose dolphins with similar dive durations reported for harbor porpoises in the present study, steady state heart rates were often not reached until well after 10 sec following submergence (Noren et al. 2004). Similarly, heart rates prior to surfacing also began to increase more than 10 sec before the end of submergence for several dives (Noren et al. 2004). Furthermore, older dolphins demonstrate greater overall reductions in heart rate during diving, compared to immature dolphins, and the ability to reduce heart rate improves as calves mature (Noren et al. 2004). Finally, there is substantial variation across dives, including dives by the same individual (Noren et al. 2004 (dolphins), Williams et al. 2017 (narwhals)). The best approach to address these complex issues with the harbor porpoise dive data is to analyze each dive to determine when the heart rate reaches a relative steady state at depth. The minimum steady state heart rate at depth could then be compared across dives and also compared to steady state heart rates at the surface. Similarly, the minimum steady state heart rate at depth should be compared across adults and juveniles. The current method of analysis undoubtedly adds quite a lot of variability which may also obscure statistical and biologically significant differences in heart rates across dive types. Furthermore, because juvenile porpoises have limited dive capacities (Noren et al. 2014) and potentially limited bradycardia responses (Noren et al. 2004), it is not appropriate to combine adult and juvenile harbor porpoises in the analysis. Development of bradycardia has also been reported for pinniped species (see references within Noren et al. 2004), which suggests that this necessary developmental period is ubiquitous across marine mammal species.

Thank you for this thoughtful feedback. Based on the suggestions above, we have expanded our analyses to include descent, bottom, and ascent dive phases defined based on the dive profile (bottom time is defined as the time the porpoise first reaches a depth within one body length of maximum

depth and the time when the porpoise was last at that depth)(Rojano-Doñate, Ph.D. dissertation, 2020). We have redone the analysis using these new definitions with corresponding changes to the methods and results sections. While this resulted is some changes in the summary data of one individual (JM3), it did not change any of the conclusions (Supplemental Figure S3 and Supplemental Table S4).

We also conducted fine-scale analysis within the dive, which we described earlier in response to the general comments. The results further support our initial findings using dive-level metrics. I.e. MSA has some influence in the full dataset – but explains less than 7% of the variation in the data. When JM3 is excluded (which improves the model assumptions by removing the outlier), interval MSA did not influence interval heart rate. Heart rate tended to be lower in longer dives when JM3 was excluded, but the effect size was small and the fixed effects only explained 3% of the variation in the data indicating that the model offered little predictive value.

Although interesting, some of the other analysis suggestions raised by the reviewer are not appropriate for wild cetaceans. For animals that perform short active transit and foraging dives, we did not expect to see a steady state dive or surface heart rate. Unlike the captive studies the reviewer cites, researchers cannot control the behavior of the animal (e.g., have the animal swim at a steady state or rest at surface). After careful examination of the raw data, we concluded that the use of bottom-of-dive heart rate in addition to the fine-scale interval analysis is an appropriate way to examine the dive heart rate in relation to behavior.

In reference to the development of diving bradycardia, based on the two papers the reviewer cites, and the other limited studies, we would not expect juvenile porpoises to differ from the adults in their heart rate response. In Noren et al 2014, juvenile porpoises of similar size to those in this study had fully developed oxygen stores and similar cADLs. Also, in Noren et al 2004, bradycardia in juvenile bottlenose dolphins at a similar developmental state as the juveniles in our study (even if different ages) did not differ from adults. Consistent with this, our data provides no evidence that juveniles differ from adults in heart rate response within the range of dives that is typical in Danish waters. We have added some new figures to the manuscript and supplemental material that demonstrate this (Figures 2 and S2). While we briefly mention there was no difference, we do not want to make this a focus of the paper as we do not have the appropriate dataset to robustly investigate the development of diving bradycardia.

Page 6-7, lines 176-178: Excluding the juvenile male (JM3) from the analysis is not appropriate. This animal is the smallest in the study and is potentially the animal that has not fully developed the bradycardia response yet. As such, it is not surprising that its heart rate data were much more variable than the other four animals. Furthermore, this animal had the longest tag deployment. With a longer duration of data collection, it is expected that this individual would demonstrate greater variability in dive behavior and consequently more variable heart rates. Indeed, during this tag deployment, JM3 demonstrated a relatively extreme range in dive depths (Table 1 and Fig 3 from Rojano-Doñate et al. 2018). In light of results from previous studies on dive behavior and heart rate (e.g., Noren et al. 2004, 2012 and Williams et al. 2017), this high degree of individual heart rate variability is not surprising. Rather than exclude JM3 from the analyses, more careful attention to how the heart rate data are analyzed is warranted.

We are puzzled by this critique: In the methods we state that all the models were run with and without JM3 (Lines 189-191), we reiterate this in the results/discussion (lines 232-233) and we report

all of these results in the tables (S1, S2, S3, and S4). We also include data from JM3 in most figures (Figs 2-5 and supplemental figures) so it is clear that this animal is an outlier. Running the models with and without an influential outlier is a common way to deal with data with outliers, and is the most appropriate way to analyze these data. It would certainly be inappropriate to only report the results from the full data set. At times we focus on the data analysis without JM3 in the text, because this is likely a better estimate of what most porpoises do. However, we also devote several lines of results and discussion to this individual (lines 226-232, 299-300)

In regards to the high variability in heart rate observed in JM3, this is likely not due to the longer deployment. Despite the longer deployment, this porpoise has the lowest variability in the range of dive durations (longest dive was 100s). Moreover, the heart rate was highly variable within dives (This is clear in the new Figure 2). This variability could be because it is young, but as we suggest, it could also relate to unknown health issues or time of year (this tag was deployed later in the year than the others). JM3 is not the smallest porpoise we have studied (Rojano-Doñate, Ph.D. thesis 2020, Rojano-Doñate et al 2018), but even compared to these other small animals that are of similar age/size, its ventilation rate and heart rate are unusual. Unfortunately, with this data set we cannot determine why this porpoise is an outlier with a high and variable heart rate. Therefore, we report the data, but we think the models without JM3 are likely a better representation of the relationship between behavior and heart rates in porpoises.

Results and Discussion

General Comment: I suspect once the data are analyzed in a meticulous manner, as described above, many of the findings will change.
It is great to make a prediction, thank you: We have performed the suggested analyses that are appropriate for our data. However, these additional analyses did not change our results and further strengthen our conclusions.

Page 7, lines 194-203 The discussion regarding the lack of difference between juvenile and adult diving heart rates is interesting. However, differences in heart rates between juveniles and adults probably exist, but are likely being obscured, given the coarse methods of heart rate data analysis in the present study. As stated above, given the larger sample size from JM3, the smallest individual, it isn’t surprising that the analysis showed that this individual had highly variable and higher heart rates than the other individuals. This finding aligns with those from previous studies (Noren et al. 2004 and references within), which were not cited by the authors.

Our results do not change with the fine-scale analysis. As can be seen from the new figures (Figure 2 and S2), there was no difference in the dive response between adults and JM1 and JM2. JM3 is unusual, but because JM3 is not much smaller than the other juveniles, we cannot determine if this variability is due to age or other factors. As discussed above, the papers cited by the reviewer do not predict age-related variability in a porpoise at this developmental stage - quite the opposite.

Page 8, lines 208-214. The discussion regarding the association between dive duration and heart rate is a little confusing to me. First, the authors state that despite a statistically significant association between dive duration and heart rate (when JM3 is excluded), the slope coefficient is not biologically relevant. Yet, this follows the expected physiological response. Despite this relationship, the authors then state that this finding is unusual for diving marine mammals since heart rate typically decreases with increasing dive duration. But wasn’t that the finding stated a few sentences prior?

We kindly believe that the reviewer perhaps is confusing statistical significance with explanatory power here. The main point we are making in this section was that in contrast to our predictions, when we use the data set that excludes the outlier (the most appropriate dataset for porpoises in general), there is no biologically relevant relationship between dive duration and LQ, bottom-of-dive, or minimum-in-dive heart rate. Although the model assigns a p-value < 0.05 to dive duration as an explanatory factor, it is essential to consider effect size and predictive power when assessing biological relevance, i.e., the amount of variation in the data that the model accounts for (Nakagawa & Cuthill, 2007; Wasserstein and Lazar, 2016; Whitlock & Schluter, 2020).

This quote from Wasserstein and Lazer (2016) sums up the issue nicely: "A p-value, or statistical significance, does not measure the size of an effect or the importance of a result. Statistical significance is not equivalent to scientific, human, or economic significance. Smaller p-values do not necessarily imply the presence of larger or more important effects, and larger p-values do not imply a lack of importance or even lack of effect. Any effect, no matter how tiny, can produce a small p-value if the sample size or measurement precision is high enough, and large effects may produce unimpressive p-values if the sample size is small or measurements are imprecise."

We accordingly included a sentence in the manuscript to exemplify the small effect size "i.e. 1 min increase in dive duration (which is a doubling of the median dive duration) only resulted in a 3 bpm decrease in LQ and MM dive heart rate)" and refer the reader to a table that summarized how little of the variation the fixed effects account for in the model (Lines 240-242). We have added some explanatory references in the paper (Line 242) and supplemental material, but do not believe that the difference between significance and relevance need to be explained explicitly in the paper since this is a fundamental (if often misunderstood) concept in statistics.

Wasserstein, R.L. and Lazar, N.A., 2016. The ASA statement on p-values: context, process, and purpose. A p-value, or statistical significance, does not measure the size of an effect or the importance of a result.

Nakagawa, S., & Cuthill, I. C. (2007). Effect size, confidence interval and statistical significance: a practical guide for biologists. Biological reviews, 82(4), 591-605.

Whitlock, M. C., & Schluter, D. (2020). Why statistical significance is not the same as biological importance. In The Analysis of Biological Data 3rd edition, pg 176-177

Edwards, L. J., Muller, K. E., Wolfinger, R. D., Qaqish, B. F., & Schabenberger, O. (2008). An R2 statistic for fixed effects in the linear mixed model. Statistics in medicine, 27(29), 6137-6157.

Nakagawa, S., & Schielzeth, H. (2013). A general and simple method for obtaining R2 from generalized linear mixed-effects models. Methods in Ecology and Evolution, 4(2), 133-142.

Page 8, line 215-220: The authors state that the porpoises performed short dives that rarely approach their cADL (cADLs reported in Table 1). I was surprised to see that the cADL values in Table 1 are single point estimates from a paper that is in prep, rather than published cADL values for harbor porpoises. There are quite a few considerations when calculating ADL values, and these are thoroughly discussed for harbor porpoise in Noren et al. 2014. Indeed, cADL values for harbor porpoises of all ages are published in that paper. The authors should cite the appropriate range of cADL values for adult and juvenile harbor porpoises from Noren et al. 2014. For some of the harbor porpoise subjects the cADL values in Noren et al. 2014 are a bit different from the values in Table 1.

Thank you. We added the values from the Noren et al 2014 to Table 1 and Fig 2 as a reference (we had to estimate these from points on a figure since the values were not provided in the paper). We have also retained the single point estimates because they were calculated based on the mass and metabolic rate of each porpoise in the study. We have added the reference to the published thesis and we provide a brief explanation of the method in the supplemental material. Even when we use the Noren et al estimates, the porpoises are still diving below the cADL.

Furthermore, the authors suggest that since harbor porpoise regularly do not approach their cADL, there is no requirement to modify heart rate to maximize dive duration. If harbor porpoise dive durations do not approach their cADL (but see comment above about published cADLs), then this argument seems logical. However, the authors then suggest that harbor porpoises minimize their dive durations in order to continue to digest their food, almost out of necessity. With a sample size of 5 harbor porpoise, I caution the authors against suggesting that their data are representative of all harbor porpoises and that short dive times are an adaptation for digestion. The authors do not evaluate how their harbor porpoise dive data compare to the somewhat substantial number of harbor porpoise dive duration and/or depth values in the published literature. For example, other publications on free-ranging harbor porpoises (e.g., Berga et al. 2015, Otani 2000, Otani et al. 1998, Linnernschmidt et al. 2012, Solsona et al. 2015, Westgate et al.1995) have shown that these cetaceans repeatedly dive to depths that are substantially greater than median, 2.5 quartile and 97.5 quartile max dives reported in Table 1. Consequently, due to the small sample size, the present study many not have been able to capture the full dive capacity and the subsequent range of HR responses in harbor porpoise.
The authors should compare their data to dive depths and times reported by other studies (the list above is likely not complete) to add context. Furthermore, they need to be transparent and acknowledge that their study did not capture the full diving capacity of this species. As Berga et al. 2015 acknowledged in their study with a small sample size (n=12, which is larger than the sample size reported in the present study), large variation among animals may obscure subtle effects on the diving behavior of porpoises. This could also be said about the HR response in the present study. Later in lines 228-233, the authors do acknowledge that harbor porpoise in Danish waters primarily dive to relatively shallow depths, compared to porpoises in Greenland waters, and that these differences in diving behavior could elicit different heart rate responses. Given the findings from other studies, it is likely that many harbor porpoises dive to greater depths than the animals in the present study. As such, the findings in this study may not reflect the physiological response to diving for most harbor porpoises. This is critical to acknowledge.

This is an important point and one that we have been careful to address in the manuscript. We are therefore sorry that the reviewer has misunderstood our conclusions and their applicability to other populations. The dive behavior we documented is typical of porpoises in Danish waters and we have added more references (lines: 211, 266-267) to reinforce this point. We acknowledge in the manuscript that porpoises elsewhere often perform longer/deeper dives and likely manage O_2 differently on those longer dives (lines 268-271). While it is likely that we have not captured all possible behaviors, our data are very typical for porpoises tagged in Danish waters (there have been many studies documenting this now) and are also similar to observations of porpoises in Japanese waters (Otani 2000, Otani et al. 1998). In the interest of brevity, we only cite the most relevant papers, both of populations with similar dive behavior as our animals, and populations where diving is more extreme. Our results likely are typical of other populations of harbor porpoises when they perform

aerobic dives and this study provides insight into how other active, shallow diving species manage O_2. As physiologists we often focus on extreme dives, but it is also essential to understand how these animals function when performing routine behaviors.

Page 9, lines 246-250: The authors predicted that the increase in activity would lead to higher diving heart rates, but "there was no biologically relevant difference in LQ, MM, or minimum dive heart rate between foraging and non-foraging dives" This statement seems to contradict their findings. There is a statistical difference, which supports the hypothesis and is a result that has also been reported by others (e.g., Noren et al. 2012; Williams et al. 2015, 2017). Also, as mentioned above, the coarse methods of parsing out heart rates in the different dive components is expected to lead to a great deal of variability. Consequently, it isn't surprising that a low percentage of variation in the data is explained.

As we explain before, it would be inappropriate to report significance without evaluating the biological relevance. It would also be inappropriate to only examine the model with all porpoises since JM3 is an outlier. We evaluate the biological relevance by examining the effect size and the amount of variation in the data the fixed effects explain. We explain our interpretation by providing an example of the increase in heart rate in relation to change in MSA (Line 291-292, i.e. an increase in mean MSA of 1 m s^{-2} only results in an increase of heart rate of 1.8 bmp (range of MSA – 0.2 – 2.8 m s^{-2})). As suggested earlier by the reviewer, we have added a finer-scale analysis. Within dives there is no relationship between activity and heart rate when JM3 is excluded. Results for all models are presented in the supplemental material (Tables S1 and S2) and the data from all porpoises are included in the figures.

Table 1: It is curious that the authors did not report the absolute max dive depth and duration values. When investigating the range of responses, it is of interest to also evaluate the responses at the most extreme diving capacities. In this case, dive duration is likely to have a significant effect on the HR response, and it is also likely that there were significant differences in max dive duration across juvenile and adult harbor porpoise subjects. Indeed dive duration data in Table 1 for the two smallest juveniles suggest that these animals in particular are not diving to the capacity that the two adult harbor porpoise are. As mentioned elsewhere, differences in dive duration and HR response between juveniles and adults should be explored. See, for example, Noren et al. 2004.

Because these porpoises are bathymetrically constrained and did not perform any extreme dives (e.g., compared to dives reported from other populations in deeper waters), this paper focuses on the typical dive response. While studying the extremes can inform on the physiological limits, it is also important to understand how animals manage oxygen during typical transit and foraging dives. Many studies support the notion that most individuals dive within the cADL most of the time (Kooyman et al 1980, McDonald and Ponganis 2013, Ponganis 2015) and characterizing their routine behavior is therefore valuable. Nonetheless, we have added the range of depths and durations observed to Table 1.
As mentioned earlier, we do not have a large enough sample size to compare juveniles and adults statistically. Moreover, there is little basis in the literature to expect much difference in animals of the sizes used in this study. Nonetheless, Figures 2 – 5, and supplemental figures S1 and S2, show the data from the 5 porpoises so the reader can visually evaluate inter-individual differences.

G.L. Kooyman, E.A. Wahrenbrock, M.A. Castellini, R.W. Davis, E.E. Sinnett. Aerobic and anaerobic metabolism during diving in Weddell seals: evidence of preferred pathways from blood chemistry and behavior J. Comp. Physiol., 138:335-346. 1980.

McDonald, B.I. and P.J. Ponganis. Insights from venous oxygen profiles: oxygen utilization and management in diving California sea lions. JEB 217:3332-3341. 2013.

Ponganis, P.J. Diving Physiology of Marine Mammals and Seabirds. Cambridge University Press, Cambridge, 2015.

Conclusions

Page 10, lines 287-290: "…demonstrate how these consummate divers juggle the conflicting demands of a deep bradycardia to prolong dives in search of prey while still delivering the O2 needed for active hunting and digestion. We find that porpoises in shallow water forgo deep bradycardia and instead maintain a stable diving heart rate that is not influenced by size, dive duration, or activity." Compared to other harbor porpoise worldwide, these subjects are diving to shallow depths and are also diving for shorter periods. Consequently, deep bradycardia may not be necessary. Some of these results are not surprising. However, this study has a relatively small sample size and the authors' coarse analytical methods may have precluded them from finding significant influences of size, dive duration, or activity, which may exist.

Although we continually strive to increase our dataset, our manuscript reports more wild cetacean heart rate data than any other publication. This is only the 3rd study on wild cetaceans. The preceding two papers report data from a few dives performed by 5 stressed narwhals (published in Science), and 8 hrs of data from one blue whale (published in PNAS). Our manuscript therefore comprises the most comprehensive study to date on heart rates in wild cetaceans. At the reviewers' suggestion, we have made finer-scale analyses and found that our conclusions are robust to analysis scale. Harbour porpoises are most definitely capable of greater diving feats than those documented in our manuscript. However, our results characterize a much more conservative routine behavior that likely represents the most common behavior in many cetaceans; we believe those are important observations to report.

References ***(with annotation if the paper presents data on shallow diving harbour porpoises)***

Berga A.S., Wright A.J., Galatius A., Sveegaard S., Teilmann J. (2015) Do larger tag packages alter diving behavior in harbor porpoises? Mar Mam Sci 31:756-763. – ***short shallow dives in Danish waters***

Linnenschmidt M., Teilmann J., Akamatsu T., Dietz R., Miller L.A. (2013) Biosonar, dive, and foraging activity of satellite tracked harbor porpoises (Phocoena phocoena). Mar Mam Sci 29: E77–E97 – ***short shallow dive in Danish waters***

Noren S.R., Cuccurullo V., Williams T.M. (2004) The development of diving bradycardia in bottlenose dolphins (Tursiops truncatus). J Comp Physiol B 174: 139-147

Noren S.R., Kendall T., Cuccurullo V., Williams T.M. (2012) The dive response redefined: underwater behavior influences cardiac variability in freely diving dolphins. J Exp Biol 215: 2735-2741

Noren S.R., Noren D.P., Gaydos J.K. (2014) Living in the Fast Lane: rapid development of the locomotor muscle in immature harbor porpoises (Phocoena phocoena). J Comp Physiol B 184:1065-1076

Otani S. (2000) Diving behavior and swimming speed of a free-ranging harbor porpoise, Phocoena. Mar Mam Sci 16:811-814 - ***mostly shallow dives***

Otani S., Naito Y., Kawamura A., Kawasaki M., Nishiwaki S., Kato A. (1998) Diving behavior and performance of harbor porpoises, Phocoena phocoena, in Funka Bay, Hokkaido, Japan. Mar Mamm Sci 14:209-220 ***– mostly short shallow dives >70% less than 20 m mean dive dur ~1.5 min***

Westgate A.J., Read A.J., Berggren P., Koopman H.N., Gaskin D.E. (1995) Diving behaviour of harbour porpoise, Phocoena phocoena. Can J Fish Aquat Sci 52:1064-1073. ***– Some deeper dives - most < 100 m***

Williams T.M., Fuiman L.A., Kendall T., Berry P., Richter B., Noren S.R., Thometz N., Shattock M.J., Farrell E., Stamper A.M., Davis R.W. (2015) Exercise at depth alters bradycardia and incidence of cardiac anomalies in deep-diving marine mammals. Nat. Commun. 6:6055 doi: 10.1038/ncomms7055 (2015).

Williams T.M., Blackwell S.B., Richter B., Sinding M.-H. S., Heide-Jørgensen M.P. (2017) Paradoxical escape responses by narwhals (Monodon monoceros). Science 358 (6368), 1328- 1331.

Reviewer 2

Comments to the Author(s)
This study looks at heart rate, movement, and breathing in the wild harbor porpoise in Denmark. Because these animals are active hunters, the authors hypothesized that the porpoises will have a strong exercise response in heart rate than porpoises in human care. The methods allow the researchers to obtain heart rate, activity, and breathing rates in free ranging animals.

- Can you include the genus and species name for your porpoise? I don't think I saw it in the manuscript, just the key words.
This is included on line 77, the first time we mention the species. We have now added it to the abstract (line 41)

- It was not immediately clear to me how you determined ventilation of the animals. I think that this was done through the stereo sound? I would combine 120 and 121: " …(MATLAB code…) to identify ventilation and feeding buzzes[15,21].
Thanks for catching this oversight. We made the suggested change to clarify how we determined ventilations (lines 126-129)

Line 185: how was the ADL calculated? I don't think you should be citing a paper that is in prep and unavailable, provide details.
We added the cADL ranges from the Noren et al 2014 to Table 1 and Fig 2 as a reference, in addition to the single point cADL estimates for each porpoise. We retained the single point estimates because they were calculated based on the mass and metabolic rate of each porpoise in this study. We have

added the reference to the published thesis where this was first calculated and we provide a brief explanation of the method in the supplemental material.

- Figures: For the box plots, provide description of boxes and the data points on the figures. Are the points outliers?
Good point. We added the following to the box plot figure text:

The bottom and top of the box correspond the 25th and 75th percentiles. The lower and upper whisker extend to the smallest and largest value that is no further than 1.5 * the inter-quartile range. Data beyond the end of the whiskers are outliers and are plotted individually.

- Line 197: While the smaller animals may have lower oxygen stores, won't they also have lower oxygen needs?
In theory the ADL of smaller animals should be a little shorter than larger individuals due to differences in the scaling exponent of O_2 stores and Metabolic rate. Oxygen stores tend to scale linearly with mass, while metabolic rate tends to scales to the power of 0.7 (Schmidt-Nielsen 1984, Goldbogen and Madsen 2018, Williams and Maresh 2016). We have now added the individual cADL calculated for each porpoise in this study, and the range based on age class from Noren et al 2014 to Table 1 and Figure 2 so it is easier to see how they differ. The difference in cADL is small between juveniles and adult porpoises.

Schmidt-Nielsen K. (1984). Scaling: Why is animal size so important. Cambridge University Press.

Goldbogen, J. A., & Madsen, P. T. (2018). The evolution of foraging capacity and gigantism in cetaceans. *Journal of Experimental Biology*, *221*(11), jeb166033.

Williams T.M. and J.L. Maresh. Exercise energetics. In: Marine Mammal Physiology. Editors: M.A. Castellini and J-A. Mellish. CRC Press.

Reviewer 3

GENERAL COMMENTS AND SUGGESTIONS FOR RE-ANALYZING THE DATA

I have read the manuscript, "High heart rates in hunting harbour porpoises" by McDonald et al. I applaud the authors for collecting heart rate data from free-ranging cetaceans, that certainly is a difficult task. However, this manuscript cannot be accepted as is; the way in which the data were analyzed has undoubtedly obscured the significance of their findings. If the authors have the patients to reexamine the data per the comments below, they will have the opportunity to potentially have a landmark study, showing both the influence of ontogeny and activity on diving heart rate (HR) in a free-ranging cetacean. Currently we have a very limited understanding of the influence of ontogeny and activity on HR in cetaceans

Specifically, the authors must examine the data from the 2 adults and 3 juveniles separately; clumping data from physiologically mature and immature porpoises together undoubtedly added noise to your dataset which lowered your significance when you explored the effect of dive duration and activity on diving HR. The authors admit to excluding a juvenile JM3 because it was immature, and it was the smallest animal (26 kg), and appeared to have a variable HR respose. Yet Table 1 reveals that of the 5 porpoises analyzed, 3 of the animals were juveniles and all 3 juveniles were close in size (26-30kg). Just

excluding one juvenile raises a “red flag”, as if the authors were cherry picking the data. There is a paper published on cetaceans that shows that diving bradycardia is refined with age throughout the juvenile stage (Noren et al. 2004) and it is highly likely that this is the case for porpoise, given that they show postnatal development of other aspects of diving physiology (Noren et al. 2014).
Noren, S. R., Cuccurullo, V. and Williams, T. M. (2004). The development of diving bradycardia in bottlenose dolphins (Tursiops truncatus). J. Comp. Phys. B. 174, 139-147.
Noren SR, Noren DP, Gaydos JK. 2014. Living in the fast lane: rapid development of the locomotor muscle in immature harbor porpoise (Phocoeana phocoena). Journal of Comparative Physiology B 184(8):1065-1076.

Thanks for this feedback. Unfortunately, with a sample size of 3 juveniles and 2 adults, we do not have the statistical power to try to compare animals of different ages. However, we were aware of ontogeny as a potential factor and so most definitely did not 'clump' the data across individuals. We both show the data separately for each individual (Fig 2-5), and use mixed effects models to allow for individual differences. If the reviewer re-examines both the fine- and course-scale results it will be apparent that there is no substantial difference in heart rate response between two of the juveniles and adults. The third juvenile, JM3, is a clear outlier and we do not have sufficient data to conclude whether this animal differs due to being in an earlier growth stage or due to an unknown health status.

The lack of difference between juveniles and adults is consistent with the findings of Noren et al (2014) showing that juvenile porpoises of similar size to individuals in our study had fully developed O_2 stores (even myoglobin) and similar cADLs. In comparison, it took the slower maturing bottlenose dolphins 3 years to exhibit a decrease in diving heart rate similar to adults, but they were likely at a similar developmental state to the juveniles in our study. We did follow the reviewer's suggestion to compare the 5 longest dives for each porpoise (New figure 2). There was no difference between juvenile and adults in the dive heart rate response in these dives that were all shorter than the cADL (irrespective of whether cADL is taken from Noren et al. 2014 or from Rojano-Doñate, L. 2020 (Ph.D. thesis, Aarhus University). The interval summary figure in the supplemental material (Fig S2) also indicates no consistent differences between adults and juveniles.

We definitely agree with the reviewer that arbitrarily removing an animal from an analysis would be unacceptable cherry-picking. Because juvenile JM3 was an obvious outlier with strong influence both because of the long data recording on this animal and the low number of individuals, we ran all models with and without JM3 and we report results from both classes of model in the tables (Tables S1, S2, S3, and S4) and often briefly discuss the differences in the manuscript (f.ex. lines 287-300). We also include data from JM3 in all figures so it is clear that this animal in an outlier. Running models with and without outliers is a common way to deal with data with influential outliers and seems to be the most appropriate approach in this case. Although we discuss JM3 throughout the results and discussions, some of our conclusions are drawn from the models excluding JM3 because, as we explain in the text, this is likely a better estimate of what most porpoises do.

Another issue with analyzing all of the dives at once is that the HR response to short, medium and long duration dives is very different. Within each age class (juv and adult) they need to sub-categorize the dives into “short duration dive”, middle duration dives”, “long duration dives, approaching cADL”. By examining the longest dives independent of the other dives they will clearly see the effect of activity releasing a portion of the bradycardia that accompanies the dive response. As an aside, it is extremely perplexing that even with all the noise of combining age classes and all of the very different dive types, the authors DID show significance YET they consistently dismissed it by stating “but this is not biologically relevant (or significant)”. No one has measured how blood flow and oxygen utilization is linked to heart rate so no one can comment on the level of change in HR that is biologically relevant. Why do the authors want to ignore the influence of activity on HR, when clearly their data show the opposite? Why did the authors chose to not site the recent study on dolphins that clearly shows the influence of activity on HR (Noren et al. 2012).

Noren SR, Williams TM, Kendall T, Cuccurullo V. 2012. The dive response redefined: underwater behavior influences cardiac variability in freely diving dolphins Journal of Experimental Biology 215:2735-2741.

Thanks for these interesting perspectives. Like the reviewer, we predicted that activity would influence heart rate; however, our results do not support this. Based on a suggestion from reviewer one, we divided the bottom of each dive into 5 second intervals and examined the relationship between interval MSA and heart rate with mixed effects models. These fine-scale models support the course-scale analysis, i.e., that there is no substantial effect of activity on heart rate. We are puzzled by why the reviewer insists that long dives would show the greatest sensitivity to activity. The opposite was found in wild sea lions where the influence of activity was strongest in short dives and much weaker in the long dives (McDonald et al 2020). However, in our porpoise models, dive duration received no support as an explanatory covariate. Nonetheless, Figure 5 and supplemental figure S2 now separate the data into dive duration bins of 0.5-1, 1-2, and >2 min to make it easier for the reader to see the lack of relationships.

McDonald, B. I., Tift, M. S., Hückstädt, L. A., Jeffko, M., & Ponganis, P. J. (2020). Stroke effort and relative lung volume influence heart rate in diving sea lions. Journal of Experimental Biology, 223(5).

Regarding the comment about evaluating the biological relevance of the data: Activity does have a p-value < 0.05 as an explanatory variable in our models but it is essential to consider effect size in tandem with statistical significance (Nakagawa & Cuthill, 2007; Wasserstein and Lazar, 2016; Whitlock & Schluter, 2020). See the response to reviewer one for a more detailed explanation of the difference between statistical significance and biological relevance.

In our models, the fixed effects explain very little of the variation in the data and therefore offer little predictive power, the acid test of biological relevance. We summarize this result both in a table and with a sentence exemplifying the small effect size “1 min increase in dive duration (which is a doubling of the median dive duration) only resulted in a 3 bpm decrease in LQ and bottom-of-dive f_H and dive duration explained less than 3% of the variation in f_H” (lines 240-242). We have added some references to the bottom of the tables and the text (Line 242) that explain the important distinction between significance and relevance. See references provided in response to reviewer 1.

The authors also act surprised that the porpoises do not show dramatic changes in HR; but if they just examined each porpoises 5 longest dives they would see a dramatic change in HR. This is because marine mammals do not lower HR to extreme levels unless they have to and they only do this when approaching their diving limits; the median dive durations of the animals in this study do not even come close to approximating the diving capacity of these animals, as indicated by the published calculated aerobic dive limits for harbor porpoises (Noren et al. 2014). The mediocre heart rate response of these porpoises is therefore not surprising, but as presented by the authors suggests that this result potentially separates the porpoises from other cetaceans. As an aside, the authors chose to ignore yet another published paper; Noren et al. 2014 that provides cADLs for porpoises, but these authors chose to site a paper in prep for their cADLs instead.

We do not "act" surprised. Can we please kindly ask this reviewer to carefully consider the tone in future reviews? The argumentative manner adopted here is not consistent with the professional and courteous tone that we as a community should expect and strive to offer in reviews. To answer the specific critique, we had hypothesized that wild porpoises would exhibit a greater range of dive responses than captive porpoises due to a greater range of activity (transiting, foraging, etc.). The results did not match this prediction: We saw a greater exercise response and a more severe bradycardia in the captive porpoises. While we would not expect a severe bradycardia in the range of dives exhibited, it was surprising that we did not detect an exercise response or lower heart rates in longer dives as has been observed in captive porpoises, wild sea lions and harbor seals, even in dives that are shorter than the cADL (Thompson and Fedak 1993, McDonald et al 2018, McDonald and Ponganis 2014). As the reviewer suggested, we did examine the five longest dives from each porpoise. Even in the longest dives, we did not observe a dramatic change. In contrast, heart rate was moderate and similar to shorter duration dives.

We initially only presented the individual cADLs because these values were determined specifically for each porpoise in this study based on size and metabolic rate estimated from respiration rate (Rojano-Donate et al, JEB, 2018). We have now added a short paragraph explaining this method in the supplemental material and cite a published thesis (Rojano-Donate, Aarhus University, 2020). We have also added the cADL range for juveniles and adults from Noren et al 2014 to Table 1 and Figure 2.

McDonald, B.I., Johnson, M. & Madsen, P.T. 2018 Dive heart rate in harbour porpoises is influenced by exercise and expectations. J Exp Biol 221, jeb168740.

McDonald, B.I. & Ponganis, P.J. 2014 Deep-diving sea lions exhibit extreme bradycardia in long duration dives. J Exp Biol 217, 1525-1534.

Thompson, D. & Fedak, M.A. 1993 Cardiac responses of grey seals during diving at sea. J Exp Biol 174, 139-154.

One of the reasons the authors surmise that the harbor porpoise limits bradycardia is because of the thermoregulatory demands of harbor porpoise (small body in cold water). However, the vasoconstriction at the periphery that accompanies bradycardia during the dive response can actually lower thermoregulatory costs by safeguarding the internal temperature of the brain and heart because blood flow is directed away from the periphery where heat is lost to the environment. Vasoconstriction during the dive response in relation to thermoregulation is really only a concern for marine mammals exercising in warm water because they can't dump heat which could lead to hyperthermia. There is a lot of literature on adaptations for thermoregulating in cold environment, which includes vasoconstriction in marine mammals that dates back to Scholander in the 1940's and recent work on how heart rate and thermoregulation are linked and concerns about hyperthermia in exercising dolphins in warm water.
Noren D.P., Williams T.M., Berry P., Butler E. (1999) Thermoregulation during swimming and diving in bottlenose dolphins, Tursiops truncatus. The Journal of Comparative Physiology (B) 169: 93-99.
Williams T.M., Noren D., Berry P., Estes J.A., Allison C., Kirtalnd J. (1999) The diving physiology of bottlenose dolphins (Tursiops truncatus) III. Thermoregulation at depth. The Journal of Experimental Biology 202:2763-2769.

Thanks for raising this interesting point, but we are a bit unsure what the reviewer is asking and are hence unsure how to respond. The working swimming muscles still produce heat no matter if they receive blood or not via a weak or strong vasoconstriction/diving response. Moreover, all of our animals were tagged in the warm water season in Denmark during which porpoises reduce their blubber layer so dumping heat is likely not an issue. Our main point, is that as a small mammal that lives in cold water, they have a high metabolic rate (Rojano-Donate et al, JEB, 2018), and this can impact dive duration. As we did not collect data that allows us to directly investigate thermoregulation, in the interests of brevity, we prefer to not delve into what would be a lengthy peripheral discussion in this manuscript.

I would also like to see in Table 1 the median and range values for porpoise for "median middle dive heart rate". This metric is probably the best metric to pick up differences in the ability for bradycardia. Although, you need to reassess how you determined what HR would be included in this metric. In your analyses you state that you cut off 10 sec at the beginning and end of the dive, and the remaining HR was the "median middle dive heart rate". But cutting off 10 sec at the beginning and end of the dive is arbitrary, especially since you have such variation in dive durations. To account for the different dive durations, you should consider excluding HR at the beginning and end of the dive based on a percentage of the dive time. For example, the "median middle dive heart" represents the heart response during the dive, which excludes the 1st 25% and last 25% of the dive duration; in this way you are only looking at HR during 50% of the dive time and excluding HR artifacts associated with the surface respiratory event and excluding HR artifacts associated with anticipatory tachycardia. This will give you the lowest HR response during the dive, which is what you are trying to quantify. You may have to play with this percentage to make sure that your "median middle dive heart rate" ONLY includes HR that occurs when the HR is consistently flat in its response, no decline or incline associated with the previous breath or anticipation of the next breath, respectively. I.e maybe you cut off the first and last 30% of the dive HR and only examine the middle 40% of the HR.

Thank you, these are good points. Based also on a suggestion from the first reviewer, we have re-analyzed the data with dives divided into dive descent, bottom-of-dive, and dive ascent based on the depth profile (method explained Lines:155-157). Bottom-of-dive heart rate has been added to the table and bottom-of-dive heart rate has replaced median middle-of-dive in the models (Supplemental tables and figures).

In the revised manuscript we also divided the bottom phase of the dive into 5 sec intervals to better examine the relationship between activity and heart rate at a finer scale within dives.

The data collected by the authors is difficult to obtain, therefore there is value in including all of the dives to show that during a typical day in the life of a harbor porpoise they are not required to have a dramatic change in HR because they rarely approach their diving limits. This is the case for many cetaceans; and is not novel to porpoises. BUT by ONLY doing this, the authors have introduced too much noise into the dataset to pick up signals for the variables they are trying to explore. (effect of dive duration and activity on diving HR). Which is why I suggested categorizing your dives into short, medium, and long duration dives and doing separate analyses for each category. To look for ontogenetic effects, you should look at ONLY the 5 longest dives for each porpoise, as done by Noren et al. (2004). Examining maximum performance to determine the maximum physiological response is what is done in physiology; and this is what needs to be done before you can make an argument about the differences between the adult and immature porpoises. It is likely that when examining the 5 longest dives that the adults were below their cADLs and the immatures were approaching or exceeding their cADLs. As a result you likely got the most pronounced bradycardia response from the immatures that they were capable of, but is unlikely you captured the most pronounced bradycardia response that the adults were capable of. Doing this analysis gives you the opportunity to reveal the influence of ontogeny on diving heart rate in a cetacean in the field – which has never been done before. OR if you show that immature porpoises have a mature ability for bradycardia early in life – this is also of value since to date the only study to investigate the development of bradycardia in a cetacean was on captive bottlenose dolphins. However, to make the later statement, both the adult and immature groups must have their field dives be a similar proportion of the cADLs (see Noren et al. 2014 for porpoise cADLs)

Our focus in the manuscript is on the typical cardiac response of porpoises during foraging rather than on their capabilities under extreme conditions. Indeed, the bathymetric constraints in Danish waters results in porpoises in our study performing exclusively shallow dives. Nonetheless, as the reviewer requested we have examined the 5 longest dives from each porpoise in relation to the individual cADL and the age class cADL range (New Figure 2). None of the porpoises exceed their cADL. The heart rate profiles of the longest dives are similar between individuals (except for JM3 that has higher and more variable bottom-of-dive heart rate) even when some of the dives approach the cADL. They are also similar to short dives (for example in Figure 1 and supplemental figure S2). There is no evidence in the longest dives, nor in the dataset as a whole, that the dive heart rate response is different in juveniles. As mentioned earlier, this is consistent with previous studies that suggest juvenile porpoises have fully developed O_2 stores (Noren et al 2014) and bottlenose dolphins at a similar developmental stage had a similar dive response to adults (Noren et al 2004)

SPECIFIC COMMENTS
ABSTRACT
Line 36-38. This statement is incorrect. There has been a study that examined how increased swim speeds (as would be required during hunting) can alter the dive response (Noren et al. 2012) AND also two studies have discussed the implications of the dive response and thermoregulation (Noren et al. 1999; Williams et al. 1999).
Rewrite the sentence to "Previous studies on marine mammals have focused on the role of the dive response in maximizing dive duration, but few have addressed how these adjustments may negatively impact the capability to hunt, digest and thermoregulate."

Thanks, we have made the suggested change (lines 36-38).

Lines 38-39 is an overstatement of what your study is accomplishing. You state, "Here we use heart-rate DTAGs to investigate how O2 management is balanced between the need to dive,.." BUT you are not measuring O2 management. You are measuring heart rate, and to date no one has done a study to link O2 management with heart rate. Therefore you need to reword this sentence to reflect what your study is actually investigating. Rewrite sentence to "Here we use heart-rate DTAGs to investigate how alterations in heart rate are balanced between the need to dive,.."

We appreciate this suggestion; however, our statement accurately reflects the literature on O_2 management in diving animals. While O_2 management also includes other adjustments such as peripheral vasoconstriction, heart rate is a good indicator of peripheral vasoconstriction and O_2 use (Grinnell et al 1942, Zapol et al 1979, Davis and Kanatous 1999, Jobsis et al 2001, and summarized nicely in Ponganis 2015 and Butler et al 2020). When a marine mammal submerges, peripheral

vasoconstriction is associated with a drop in heart rate which maintains blood pressure. Endotherms are fine tuned to maintain a relatively stable blood pressure (Butler et al 2020). At this time, heart rate is the best indicator of O_2 management in freely diving cetaceans.

Grinnell, S. W., Irving, L., & Scholander, P. F. (1942). Experiments on the relation between blood flow and heart rate in the diving seal. Journal of Cellular and Comparative Physiology, 19(3), 341-350.

Zapol, W. M., Liggins, G. C., Schneider, R. C., Qvist, J., Snider, M. T., Creasy, R. K., & Hochachka, P. W. (1979). Regional blood flow during simulated diving in the conscious Weddell seal. Journal of Applied Physiology, 47(5), 968-973.

Davis, R. W., & Kanatous, S. B. (1999). Convective oxygen transport and tissue oxygen consumption in Weddell seals during aerobic dives. Journal of Experimental Biology, 202(9), 1091-1113.

Jobsis, P. D., Ponganis, P. J., & Kooyman, G. L. (2001). Effects of training on forced submersion responses in harbor seals. Journal of Experimental Biology, 204(22), 3877-3885.

Butler, P. J., Brown, J. A., Stephenson, D. G., & Speakman, J. R. (2021). Animal Physiology: An Environmental Perspective. Oxford University Press.

Ponganis, P.J. Diving Physiology of Marine Mammals and Seabirds. Cambridge University Press, Cambridge, 2015.

Line 41: Insert the range of dive durations that were measured in your study into this sentence. If you have a narrow range of dive durations, and dive durations that do not approach the cADL for the harbor porpoise, then it is not surprising that HR was moderate. Marine mammals will only lower HR to dramatic levels when necessary, because to your point it is beneficial to keep HR elevated to support muscular activity and digestion. BUT please note that in cold environments, especially for small bodied mammals, it is beneficial to shut down blood flow to the extremities (as occurs during the dive response) to assist with thermoregulation to protect core body temperature from heat loss (see Noren et al. 2008). The vasoconstriction that occurs during the dive response actually is more problematic for thermoregulation for an exercising marine mammal in warm water because they cannot dump heat and can possibly become hyperthermic (Noren et al. 1999, Williams et al. 1999).

Noren SR, Pearson LE, Davis JW, Trumble SJ, Kanatous SB. 2008. Different thermoregulatory strategies in nearly weaned pup, yearling, and adult Weddell seals (Leptonychotes weddelli). Physiological and Biochemical Zoology 81(6):868-879.

We have added the range of durations to the abstract (line 43).

LINE 45-47 This statement is not novel. “despite having the capacity to prolong dives by lowering cardiac output, for these shallow-diving cetaceans, it is more efficient to maintain circulation: extreme heart-rate gymnastics are for emergencies, not everyday use.”

As mentioned above all marine mammals studied to date do not show large reductions in HR unless they are prolonging dive durations. Also “gymnastics” would be better used in layman article, not a scientific article.

Rewrite to the sentence to “Like other marine mammals, harbor porpoise do not have dramatic reductions in heart rate during normal free-ranging activities, although is it likely that porpoise can reduce heart rate further for emergencies.

Thank you for the suggestion. We think that the reviewer is objecting to the style here rather than the message as the suggested alternative appears to say the same thing. For the abstract, we adopted a deliberately eye-catching wording in the hope to attract broader interest.

BACKGROUND

Line 60 Noren et al. (2012) discusses the effect of exercise and volition. Should include in the references for this sentence

Added (line 61)

Line 59-60 Among the factors influencing the ability for diving bradycardia is postnatal development. This has been shown in seals and dolphins. You should include this because your sample includes immature porpoise, and it has been shown in bottlenose dolphins that this development is not complete until 3.5 years postpartum. See Noren et al. 2004 and Greaves et al. 2005

Greaves D.K., Schreer, J. F., Hammill, M. O. and Burns, J. M. (2005). Diving heart rate development in seals. Phys. Biochem. Zool. 78, 9–17.

We added age as one of the factors that can influence heart rate, but we are not going to make this a focus of the paper. We believe it is beyond the scope of this paper as explained above (added line 61).

Line 68 These studies did not look at "O2 management" they looked at heart rate adjustments. Change O2 management to heart rate adjustments. Do this for all places in the text where you have written O2 management for studies that investigated HR adjustments. Your line prior to this one discusses the probable link between HR and O2 management so that link has been provided for the reader, but when commenting on your study and past studies you must report what was actually measured, and that was HR (not O2 management).

Heart rate adjustments are key to O_2 management in diving animals and it is appropriate to use this term as explained above.

Line 71 missing the word "are"

Thanks, we modified the text in this area.

Line 76. After talking about O2 management should put in another sentence to remind the reader about O2 and HR link so that the reader understands why the next sentence and the rest of the paragraph you talk about HR.

In the previous paragraph we state: "Due to the challenge of studying blood flow and cardiac output in wild marine mammals, heart rate (f_H) is often measured as a proxy for evaluating dive response and O_2 management."

We added two sentences following the statement to make more clear why heart rate is a good proxy (lines 63-67)

Because we just explain the link between heart rate and O2 a few sentence previously it seems repetitive to repeat here so we did not add anything in order to keep the intro concise

Line 79 "influenced by....volition. Include Noren et al. 2012, who was among the first to suggest the idea of the influence of volition on HR in diving marine mammals.

We cite this paper previously. In this paragraph we are talking specifically about porpoises so it is not appropriate to cite here.

METHODS

Lines 176-177 What was the estimated age of JM3? You measured body length, so you can estimate the age from published age vs. length curves, which are available for porpoise. See Noren et al.2014 for these references. Little is known about the HR response of immature marine mammals, particularly young cetaceans so the higher HR variability in the juvenile porpoise is an important finding in this study.

While we cannot determine the specific age of porpoises in this study, we determined the three smallest porpoises (113-120 cm) were juveniles (1- <3 years) based on standard length (Lockyer & Kinze, 2003). Using the references from Noren et al 2014 we come to the same conclusion. These animals are in the same size range as the porpoises classified as juveniles in Noren et al 2014 which found juveniles had fully developed O_2 stores. We cannot be more specific than calling them juveniles.

RESULTS AND DISCUSSION

Line 184, please also include the range of maximum dive durations across the 5 porpoises you studied, making sure to note which value is associated with the juvenile porpoise.

This information is provided in the table 1 now. We initially included the 2.5% and 97.5% quantiles in the table, but have changed this to range.

Line 187-189. This result is NOT surprising given that the median duration of the dives where HR was measured was 43-76 seconds. When looking for "extreme bradycardia" you need to analyze ONLY the "extreme dive durations", as in Noren et al. 2004 where ONLY the 5 longest dives for each dolphin were analyzed; and this needs to be done with adults and juveniles separate. The approach of examining extreme performance (i.e. longest dive durations) to understand the ability for a physiological response is not a novel ideal; this is done throughout the physiological literature when investigating the physiological capacities of animals.

The goal of this paper was not to examine the extreme behavior, but to examine the heart rate response during routine dives in wild porpoises. In the wild we hypothesized to see some longer dives, or potentially some dives where they were disturbed, which is why we stated occasionally extreme bradycardias. It was surprising how moderate and consistent the heart rate was over the range dive durations and activity levels we observed. As suggested by the reviewer, we did examine the five longest dives for each porpoise (New figure 2). This figure further supports the moderate and consistent heart rate, even in the longer dives. These porpoises don't do anything extreme, and that is exactly the take-home-message of our paper.

Line 191 move the range of mass (28-67 kg) earlier in the sentence to just after the word the words estimated mass. And include the entire range of mass, the lowest mass was 26 kg.

Thanks, Changed (line 218)

Having looked at TABLE 1 now, I see that you have 3 juveniles, close in mass 26, 28, 30kg. this makes it completely arbitrary that you ONLY excluded JM3 (26 kg) from the analyses, given that JM2 and JM1 are only 2-4 kg heavier than JM3. While the adults are much larger, at 44 kg and 67 kg. Your data are compounded by a sample of 2 adults and 3 juveniles. These age classes should NOT be combined for your analyses based on the findings of Noren et al. 2004. Indeed the muscle biochemistry of harbor porpoises is underdeveloped in porpoises less than 134 cm long, which affects diving capacity. See Noren et al. 2014

As explained above, all analyses were performed with and without JM3. JM3 was not excluded because of his small size, but because he is an outlier and one of the most appropriate ways to deal with an outlier is to perform the analysis with and without the outlier. We tried to make this clearer in the methods by stating he is an outlier (Lines: 189-191) and again when presenting results (Lines 232-233). It is also mentioned in the notes for all the supplemental tables.

While we would have loved to look at the ontogeny of bradycardia, it is not possible with this data set. We do not have the ability to separate the data into two small groups due to lost statistical power. Additionally, we would need more age classes to do this well. After careful examination of the data, we decided to analyze all porpoises together since there were no consistent differences in heart rate between juveniles and adults (Fig 2-5). Later, we determined it would be best to run the models with and without JM3, not because JM3 was the smallest porpoise (just by 3 cm), but because he is an outlier. We do not pool the data in the figures and we used mixed effects models (with individual as a random effect). This allows the reader to examine the data and see that there is no consistent difference in heart rate between the adults and JM1 and JM2.

Line 194-197 It is NOT surprising that the bradycardia of the juveniles is lower than the adults, because the juveniles are probably pushing their dive limits more than that adults. In order to compare across ages classes you must look at their extreme physiological response, which is why you need to also include in you analyses an examination of ONLY the 5 longest dives for each animal. To determine if the adult and juveniles are pushing their physiology equally, for each porpoise you need to divide their average dive time over their 5 longest dives by their cADL to determine how close they were approximating their physiological capacity. For example, if adults are only holding their breath for half their cADL then they should not need to lower HR as much compared to juveniles if they are holding their breath for their full cADL. Moreover, you excluded one of the juveniles because it didn't fit your conclusion; that is cherry picking data. JM3 is the youngest, thus you expect higher respiratory rates, ,higher HR, and more variable HR response while diving as shown in Noren et al. 2004. Please see additional thoughts in the general response paragraph I provided at the beginning of this review.

We are a little surprised by the reviewer's comments. The papers referred to earlier in the review suggests that younger animals don't have the ability to decrease heart rate as low as the adults. Additionally, younger smaller animals typically have higher heart rates. So it was a little surprising that in our study the heart rate was similar to the adults. However, our results are consistent with Noren et al 2014 that estimated cADL of juvenile porpoises to be similar to adults, and Noren et al 2004 that found dolphins at a similar developmental stage to have a similar dive heart rate response as adults. We plotted the 5 longest dives for each porpoise in relation to cADL as suggested (New figure 2) and did not see any evidence to support the reviewer's claims. The adults and juveniles are pushing their physiology equally. The adult male performs dives that are closer to its cADL, yet still has a moderate dive response. JM2 tends to have the lowest dive heart rate (still moderate), but is not coming as close to his cADL as the adult male. Heart rate is moderate and consistent across a range of aerobic dive durations. This analysis further supports our conclusions.

Again we would like to emphasize, that we are not cherry picking our data. JM3's data is in all figures and all models are performed with and without JM3 as is appropriate when you have outliers. It is clear in all the figures (including the new figure with the 5 longest dives) that JM3 is an outlier. This

animal is not much smaller than the other juveniles in this study and, lacking information about state of health and life history, we cannot conclude that age is the cause of the difference.

Table 1: I don't agree with your cADL calculations; you cite a paper that is in prep when calculations for harbor porpoise have already been well described in Noren et al. (2014)

We have added the values from the Noren paper to Table 1 and Figure 2 (we had to estimate these from points on a figure since the values were not provided in the paper). We believe the single point estimates we provide are a better reference for this study because they were calculated based on the mass and metabolic rate of each porpoise in the study. We added a short paragraph in the supplemental material to explain the calculation and we added the reference to the published thesis.

Line 207-208. This is not surprising. If you examine just the extreme dives, say the 25 longest dives for each animal I suspect that your relationship for HR and dive duration will improve. Short duration dives often have high variability in HR, this is because sometimes an animal may lower HR in anticipation of a long dive but then something interrupts the animals to that it ends up terminating the dive after only a short duration. You cannot control for this in the wild. My insight about how sensitive HR is to external factors is from simultaneously analyzing over 24 hours of underwater behaviors of a dolphin in combination with instantaneous heart rate data. Indeed, you do point out that there is a relationship for HR and dive duration in captive porpoises; this is because the measurements are taken in a more controlled environment (less variables for the porpoise to have to worry about while on a dive). As an aside, how do you know that 3 bpm for one min increase in dive duration is not "biologically relevant".?

This result was a bit surprising and different from other studies. While we agree that if these porpoises did perform more extreme dives, we would likely see more extreme bradycardia; however, one would still expect to see a graded response based on captive studies and studies on wild pinnipeds over the range of dive durations we observed (i.e. McDonald et al, JEB, 2018, McDonald et al, JEB 2014). You can see from the interval profiles (Supplemental figure S2) that the diving bradycardia is consistent in the range of dive durations we observed. We also are a bit confused about the reviewer's point about not being able to control for things in the wild. The purpose of this study was to see what they do in the wild.
Please see above comments about biological relevance. The small effects size (3 bpm) combined with the very low r^2 of 0.03 (which means only 3% of the variation in the data are accounted for by the fixed effects) indicated duration is not biologically relevant.

Line 215 This is what is happening. You should state this up front.
We are not sure what the reviewer is requesting. We first describe our results and put in context with other studies. As soon as we do that, we clearly state this as a topic sentence in the following paragraph to explain why our results are different. This is, we believe, the most appropriate location to make this statement.

Line 239 Why is Noren et al. 2012 not mentioned here. They were among the first to point out the relationship between HR and exercise in a cetacean.

We have added the reference (line 277)

Line 243. It has been shown in the past (I believe by Rosen) that it is hard to link MSA to HR. There is too much noise. It is very possible that had you measured fluke stroke frequency that you would have found a relationship between HR and exercise as in Noren et al. (2012). You have to mention the limits of your study (using MSA instead of Stroke frequency) and how this could have influenced this result.

All activity measures have strengths and weaknesses. For example, with stroke rate one loses information about the magnitude of the stroke. In comparison, MSA tracks stroke magnitude and rate, and has a clear connection with mechanical energy expenditure. We would argue that, as a proxy for energy, there is no more 'noise' in this metric than in fluke rate or ODBA. A recent study on California sea lions found that MSA and stroke rate were highly correlated, but MSA was a better predictor of heart rate (McDonald et al 2020). There is also some indication that MSA may be a better estimate of effort than stroke rate (Mason Cole, manuscript in progress). Therefore, there is no indication currently that the use of MSA limits the study. We have however added a sentence to justify the benefit of using MSA (Line 145-147).

Line 247-250. Again you dismiss a significant result, stating “there is no biological relevant difference”.... How do you know that? Have you measured how blood flow and oxygen utilization patterns change with small changes in HR?. You need to delete the use of “there is no biological relevant difference” and “there is no biological significance” throughout your manuscript.

We respectfully disagree with this statement. What the reviewer is requesting would be inappropriate. It is essential to evaluate the effect size and r^2. Both of these support our conclusion that this relationship is not biological relevant. Please see references above.

Line 251-252 “while the association between MSA and LQ was significant, a unit of increase in one MSA... Why are you again dismissing a significant result? It is as if you want your study to show no influence of activity on HR, but your data says the opposite. And I bet that once you separate the juveniles and adults out from each other and analyze each age class separately your results will become more significant. And I suspect that if you create sub categories within each age class (i.e. short duration, medium duration, and extended duration dives) and analyze each sub category separately that your results will become even more significant. Short duration dive HR has a lot of noise and variation so it is hard to see the patterns; and HR is already relatively high so effect of exercise is not as dramatic. When the animal is pushing itself during extended duration dives that is when you see the effects of exercise, as it must release some of the dive response to deal with oxygen debt at the muscle. See Noren et al. 2012. Line 277 get rid of “lack of biologically significant difference”

We are interpreting the data correctly. We also predicted there would be a relationship, but the data does not support this. By including duration in our models we are already accounting for that noise so we do not need to break the data into arbitrary categories. Our results do not support the reviewers' statements. This is also clear in some of the figures (Fig 3, 4, 5, and supplemental figures S1).

Please refer to the above references about properly evaluating p values by examining effect size and r^2. And as stated before, we do not have a large enough sample size to evaluate juveniles and adults separately, but if you look at the data you can see there is no difference in adults and JM1 and JM2 (Fig 2-5, supplemental figures). As mentioned before, JM3 is an outlier from all the porpoises and we cannot determine why.

Line 289-290. If you look at your data categorically within each age class, “short duration dive”, “medium duration dive”, and “long duration dive” I suspect that you cannot make this statement.

Undoubtedly during their longer dives porpoises do employ a comparatively deep bradycardia. Moreover, even as you analyzed the data (with the noise of combining age classes and also combining disparately different dive types) your results were significant for dive duration and activity, but you chose to dismiss them.

We believe this statement is correct as written. All of our analyses (intervals within a dive, dive variables) support this statement.
Added word relatively. I.e. "… instead maintain a relatively stable diving heart rate that is not influenced…."

Line 294 "delete "are a step too far"

Modified to "are not needed"

Line 295 delete "gymnastics"

Thanks for the suggestion, but it seems the reviewer is objecting to the style rather than the message. The editor should advise if our wording does not meet the style requirements of the journal.

Line 295 Change to "shallow-feeding short duration diving porpoises".
Changed

Line 297-300 The point here is that your porpoises were generally not pushing themselves physiologically when they forage, as shown in Table 1 by the dive durations exhibited. They rarely approached their dive limits. Bottlenose dolphins do the same thing, shallow short dive durations are not accompanied by dramatic bradycardia. This is not unique to porpoise, but your closing line makes it seem like it is unique to porpoises.
We prefer to keep as written. While this may not be unique to porpoises (and we do not state that it is), this is the first time it has been documented in wild cetaceans. This study provides insight into how shallow diving species manage O_2 during routine diving behavior.

Figure 1 legend. Line 362-364 change "had higher metabolic rate" to "suggests a higher metabolic rate". You did not measure metabolic rate so you can't state the animal had a higher metabolic rate.

We kindly prefer how it is currently written. We state "indicating" earlier in the sentence, which has a similar meaning to suggesting. It is repetitive to state it again.

Figure 2 legend. Line 372 delete "not biologically significant". –
Foraging dive HR is higher – why do you want to state the opposite. AND if you get ride of noise by looking at age classes separately and within age classes look at sub-categories based on dive duration, your noise will decrease and this result will be even more significant, and is undoubtedly biologically significant.
We have moved this figure to supplemental material. As stated before, we cannot delete "not biologically significant", but will modify to "not biologically relevant". This is an important qualification of the result which would be misleading to omit. Please see the comments above about importance of evaluating effect size and r^2 to access biological relevance. The conclusions are further supported by the interval analysis.

Again we reiterate that we performed the most appropriate analyses. It is clear in the figures there is no difference in the heart rate response between adults and juveniles. There is no need to divide the dives into three arbitrary dive duration categories for analysis because dive duration is included in all the models.

Figure 3 delete “no biologically significant” throughout this legend! foraging dives have higher HR!

As discussed above, it would be misleading to delete this characterization of the effect size. We have modified it to “unlikely to be biologically relevant”.

Appendix D

I appreciate the authors' efforts to address the reviewer comments, particularly with regards to the analysis of the dive data. I believe that the manuscript has greatly improved and that this study provides some valuable new data. However, there are a few, outstanding issues that should be addressed. Most are relatively minor, and all only require changes in wording or presentation. Some of the suggested changes do, however, require some substantial reevaluation of the significance and interpretation of the results. I appreciate that the authors' study system constrained their ability to measure the full diving capacity of harbor porpoises, but I reiterate that these constraints must be acknowledged upfront. Furthermore, because of the constraints, the authors should be careful about speculating on the adaptive response of moderate bradycardia at depth. It is clear from the dive depths and durations that these subjects were diving within their cADL, as the authors do acknowledge. However, without comparable HR data on dives beyond their cADL or other physiological measurements that provide data on digestion, for example, it is not appropriate to speculate that the porpoises' diving behavior is driven by other physiological processes. There was no mention of bathymetry, depth, or prey abundance and behavior (e.g., depth, density, etc.) in the study area, so harbor porpoise diving behavior could simply be an artifact of the environment in which they forage. Although the other physiological responses/systems may benefit from shorter dives with moderate bradycardia, it is likely that the reduced dive duration, rather than the other physiological processes, drive the harbor porpoise's moderate bradycardia response at depth. These are interesting observations and could be discussed, but the authors need to carefully convey that these benefits are likely an artifact of these shorter dives, rather than the other physiological processes driving the harbor porpoise diving behavior and subsequent heart rate response. Furthermore, as harbor porpoises throughout the world tend to be found in higher latitudes, some of the physiological issues (e.g., thermoregulation in cold water) are not unique to this specific study population. However, in contrast to the dives reported in the present study, harbor porpoises elsewhere dive for longer durations and to greater depths. It might be helpful to provide comparative background information on diving rates/capabilities of other porpoise populations in the introduction to support the authors' statements that this harbor porpoise population is very different from others. Regardless, I think most diving literature suggests that most marine mammals do not typically dive beyond their cADL, so some reframing is necessary and some of the concluding statements should be reevaluated. Finally, the authors should carefully consider how they cite specific studies because the findings do not necessarily support their statements. Please also see specific comments below.

Title: "High heart rates in hunting harbour porpoises" is somewhat misleading. This title implies that heart rates of hunting harbor porpoises may be elevated. However, the authors have shown that during dives (both foraging and non-foraging) heart rates are lower at depth, following a somewhat typical, moderate dive response. Consequently, harbour porpoises do not have unusually high heart rates at depth. Indeed, the diving heart rates of 40-50 bpm are lower than heart rates for the harbor porpoises measured at the surface. Furthermore, these diving heart rates are on par with the heart rates of several other marine mammals (e.g., sea lions, Weddell seals, and dolphins) that are also diving within their cADL, similar to the harbor porpoises in this study. The heart rate data for the other marine mammals diving within their cADL can be found in the references the authors cite. The results from this study suggest that foraging activity has minimal impact on the heart rate in these harbor porpoises at depth, which in this study was relatively shallow. There were reductions in heart rate at depth during both foraging and non-foraging dives, but there doesn't seem to be a difference in heart rates during these two activities. I would suggest modifying the title to one that more accurately states the findings. For example, “Shallow water hunting activity has minimal impact on harbour porpoise heart rates at depth”, or something more eloquent.

Abstract:

Lines 36-42: “Many studies have focused on the extreme role of the dive response in maximizing dive duration in marine mammals, but few have addressed how these adjustments may compromise the capability to hunt, digest and thermoregulate. Here we use DTAGs which record heart rate together with foraging and movement behaviour to investigate how O_2 management is balanced between the need to dive, forage, and digest in five wild harbour porpoises (Phocoena phocoena) that hunt thousands of small prey daily.”

The study focused on changes in heart rate in relatively short, shallow dives. The method of the study was to use DTAGs that recorded heart rate and acoustic signals. Since no other measurements were made to evaluate hunting efficiency, digestion or thermoregulation, the present study also doesn’t address how these diving adjustments compromise those activities or how O_2 management is balanced between the need to dive, forage, and digest. Although these are interesting discussion points, I think the focus of the study needs to be more accurately represented in the abstract.

Lines 42-43: “Surprisingly, dive heart rate (f_H) was moderate (40-50 bpm) and relatively stable across dive types, dive duration (0.5-3.3 min), and activity.”

I am having a difficult time reconciling the diving heart range of 40-50 bpm with Table 1 and the figures SI A and B, S2, and S3 in the supplemental information. In my interpretation, minimum dive heart rates are being reported for the depth phase (not descent or ascent), but it appears that most minimum dive heart rates are greater than 40-50 (even with removing J3). The range of minimum dive heart rates in Table 1 (excluding J3) range from 40-73. The max minimum heart rate for J3 is 86. If it is the minimum dive heart rate that is being reported, then the range is 40-86, but if it is the entire range (not just minimum), the range is much larger. If this is the correct interpretation, please correct the range and indicate that the dive heart rate that is being reported is the minimum dive heart rate or whichever heart rate descriptor applies.

Lines 45-50: “A moderate dive response, allowing for some perfusion of peripheral tissues, may be essential for fuelling the high field metabolic rates required to maintain body temperature and support digestion during diving in these small, continuously-feeding cetaceans. Thus, despite having the capacity to prolong dives via a strong dive response, for these shallow-diving cetaceans, it is more efficient to maintain circulation while diving: extreme heart-rate gymnastics are for emergencies, not everyday use.”

Please see comment above regarding extrapolation. Is there some way to measure/determine that these porpoises are consciously ending dives relatively early? Is there something in their habitat such as bathymetry or prey behaviour that also factors into determining their dive behaviour? Although there may be some physiological benefits to these shorter dives, the methods of this study cannot be used to determine what diving strategy is most efficient or if the porpoises are consciously performing shorter dives to reap these postulated benefits. Also, please see comments below regarding harbour porpoise metabolic rates compared to those of other marine mammals.

Lines 70-73: “a single foraging blue whale (8.5 hours, *Balaenoptera musculus*, the largest baleen whale, ~70,000 kg) [16], and five narwhals (~5 dives each, *Monodon monoceros*) released from prolonged net entanglement and stranding (mid-size odontocete, ~1000-1600 kg) [17].”

For consistency with the blue whale information, suggest including the size of the narwhals in the parentheses with the species and dive information: “a single foraging blue whale (8.5 hours, *Balaenoptera musculus*, the largest baleen whale, ~70,000 kg) [16], and five narwhals (~5 dives each, *Monodon Monoceros*, mid-size odontocete, ~1000-1600 kg) released from prolonged net entanglement and stranding [17].”

Lines 154-155: “duration between the respiration ending a dive, and the respiration starting the following dive” should be “duration between the respiration ending a dive and the respiration starting the following dive” without a comma.

Lines 229-230: “Figures 2, 3B and 4A ,” remove extra space between 4A and ,

Lines 250-258: “Although the associations between dive duration and bottom-of-dive and LQ ƒH were statistically significant when JM3 was excluded, the slope coefficient was not biologically relevant; i.e. a1 min increase in dive duration (which is a doubling of the median dive duration) only resulted in a 3 bpm decrease in LQ and bottom-of-dive ƒH and dive duration explained less than 3% of the variation in ƒH (Table S1)[37, 38]. This is unusual for diving mammals as ƒH typically decreases with increasing dive duration even during aerobic dives (dives shorter than ADL) [4, 8, 39, 40], and a decrease in ƒH with increased dive duration was documented in captive porpoises performing short dives [8, 23].”

To be clear, I understand and appreciate the difference between statistical significance and explanatory power, or biological relevance. However, despite the results from the present study not being biologically relevant, per statistical criteria, this does not mean that the results of this study are “unusual for diving mammals.” The previous studies that the authors cite reported a significant decrease in heart rate with increasing dive duration, but mainly for dives that extended beyond the species’ cADL. As written, the authors are using the lack of biological significance (not statistical significance) to present the findings as unusual and different from previous studies. Only if the authors of the previous studies ran similar analytical tests and found that their results were both statistically and biologically relevant, can the authors of the present study make such statements. I consulted the cited references and none of the authors evaluated the biological relevance of their findings. Similar to many of the previous studies, the results of the present study report a statistically significant relationship between dive duration and heart rates at depth. Unlike the present study, however, many of the previous studies collected data over a larger range of dive durations, including dives that exceeded the cADL. Importantly, the heart rate response is most pronounced during dives that were at the upper limit of or exceed the cADL, which many of the previous studies also emphasized. As the authors of the present study report, the harbor porpoises in the present study were diving within their cADL. The data and results from the previous studies are indeed similar to the findings reported here for harbor porpoises. Across the studies, individuals that were diving within their cADL demonstrated relatively minimal changes in heart rate at depth. For example, Hill et al. (1987) reported variable results for individual free-diving Weddell seals. Only for dives greater than 20 min in duration, which are at and beyond the cADL for Weddell seals, was there a correlation between heart rate and dive duration. In contrast, there was no correlation between dive duration and heart rate for dives under 20 min in duration. Similar results were reported for sea lions that were diving within their cADL (McDonald et al 2018). Sea lions only displayed typical true bradycardia in mid- to long-duration dives; these dives were near the upper limit of their cADL or beyond their cADL. Across all studies, the extreme reductions in heart rates typically occurred during the longer dives that exceeded cADL. It was also interesting to observe that many of the heart rates measured at depth for seals and sea lions diving within their cADL were similar to the values reported in the present study for harbor porpoises. So, to summarize, because other studies have not evaluated the predictive power, or biological significance of their results, only statistical results and patterns can be compared across studies. In particular, the appropriate pattern to compare is how diving heart rate varies with dive duration for dives that fall within the cADL. The results from previous studies on freely diving marine mammals demonstrate that the pattern is similar to that reported in the present study for harbor porpoises diving within their cADL. Harbor porpoise dive duration and/or depth in other environments (e.g., Berga et al. 2015, Otani 2000, Otani et al. 1998, Linnernschmidt et al. 2012, Solsona et al. 2015, Westgate et al.1995) are substantially greater than those reported in the present study and we might expect to see some effect of dive duration on heart rate in these populations.

Lines 261-262: “The generally high ʃH is likely required to support the high field metabolic rates documented in porpoises to keep small bodies warm in high latitude waters[19]”.

As mentioned above, the heart rates reported at depth for harbor porpoises are lower than their corresponding heart rates measured at the surface and similar to heart rates recorded for other marine mammals, including bottlenose dolphins, diving within their cADL. As such, it isn’t appropriate to classify fH as generally high in harbour porpoises, and it is also beyond the scope of this study to correlate these heart rates with metabolic rates to support thermoregulation. Other harbor porpoise populations, all of which inhabit cold waters in high latitudes, perform longer and deeper dives, so thermoregulation is not likely to be a major driver for this specific population’s diving behavior. Furthermore, harbor porpoise FMRs are not unusually high compared to other marine mammals. Indeed, Rojano-Doñate et al. (2018) reported that “harbour porpoises have FMRs that are elevated in comparison to terrestrial mammals of the same size, even when comparing with terrestrial carnivores, but lower than similar-sized marine pinnipeds and mustelids.” Thus, Rojano-Doñate et al. (2018) did not conclude that harbor porpoises have unusually high FMRs. In fact, across other marine mammal species, the estimated FMR of harbor porpoises (3–4 times higher than the BMR predicted from Kleiber’s equation, Rojano-Doñate et al. 2018) is not unusually high. Several studies on pinnipeds and dolphins have measured and estimated FMRs that are up to 5-8 times higher than BMR predicted from Kleiber’s equation. See references in Noren 2011 and Bejarano et al. 2017. Also, it is interesting to note that metabolic rates are not necessarily correlated with food consumption in marine mammals. For example see the study by Williams et al. 2007 on sea lions. The authors found that BMR did not increase with increasing food consumption requirements, though admittedly, the lack of correlation between BMR and food consumption occurred during relatively energetically demanding periods of time (e.g., molting, lactation).

Lines 308-310: “The lack of relationship between activity and dive ʃH in most of the porpoises could be a by-product of a consistent moderate dive response that allows for digestion during diving.”

As mentioned above, these are interesting discussion points, but since the study didn’t measure digestive processes, I would suggest rephrasing slightly to something like: “The lack of relationship between activity and dive ƒH in most of the porpoises could be a by-product of a consistent moderate dive response that may also allow for digestion during diving.”

Lines 344-347: “These first longer-term, continuous heart rate data from multiple, unstressed wild cetaceans demonstrate how these consummate divers juggle the conflicting demands of a deep bradycardia to prolong dives in search of prey while still delivering the O_2 needed for active hunting and digestion.”

Please see comments above about extrapolating beyond what was measured in the study. My impression is that it is not typical for marine mammals to extend their dive durations beyond their cADL while foraging unless there are extreme circumstances. For example, see the data for Weddell seals in Hill et al. 1987. The number of dives that were within the cADL (n=152) were far greater than the number of dives that were at or above the cADL (n=37). Indeed, one seal never performed dives that were greater than the cADL. Do the authors think that we should not expect the same for harbor porpoises? If so, what are the other potential reasons/factors to suggest that the harbor porpoises are intentionally not pushing their limits during foraging dives? Was there a difference in depth/duration of foraging versus non-foraging dives? Is this a relatively shallow or deep environment? Are the prey typically found in shallow or deep water or difficult to capture? The sample size from this study is impressive, so it is intriguing that the dives fell within the cADL, but it is difficult to presume that the animals are intentionally forgoing long dives without compelling information to suggest that they would be expected to perform deeper, longer dives in their environment. If there is evidence that these dives would be expected, then there might be some justification for a tradeoff.

Lines 347-349: “We find that porpoises in shallow waters forgo deep bradycardia and instead maintain a relatively stable diving heart rate that is not influenced by size, dive duration, or activity.”

This needs some rephrasing. Per typical marine mammal diving response for short, shallow dives, the harbor porpoises are diving within their cADL so there is no need for deep bradycardia. They aren’t “forgoing” it. Also, the authors state that “heart rate is not influenced by size, dive duration, or activity”. I suggest removing “size” since evaluating the relationship between size and diving heart rate was not one of the goals of this study. If that was the goal, then a larger diversity of animals should have been studied, including much smaller animals. As written, a reader could inappropriately misinterpret that statement as a lack of influence of body size on diving capabilities for harbor porpoises, in general, rather than the lack of an effect of size for the relatively narrow range of porpoise body sizes in this study.

Lines 349-353: “This moderate bradycardia may be essential for providing cardiac output to support the high metabolic rate and upholding digestion during near-continuous feeding. Thus, for porpoises in this environment, extreme dive responses enabling extended dive durations, that may be critical for efficient foraging in marine mammals elsewhere, are not needed; extreme heart-rate gymnastics are for emergencies, not everyday use.”

Per comments above, the question remains whether this moderate bradycardia is simply a consequence of their short/shallow dives that are related to the environment in which they live or whether their dive behavior is the result of a conscientious decision to maintain these shorter dives in order to provide essential cardiac output to support other physiological processes. The authors have not presented any compelling data to suggest the latter.

Please remove “high metabolic rate” per comments from above regarding marine mammal FMRs that are all relatively high

Lines 353-355: “Instead, shallow-feeding short duration diving porpoises adopt a strategy of moderate dive heart rate combined with high surface heart rate to balance the demands of prey capture, digestion, and thermoregulation.”

It is more likely that the harbor porpoise adopt a shallow-feeding short duration diving strategy and the heart rate response follows, rather than “adopt a heart rate strategy”. Also, please consider rephrasing to qualify that the other benefits are postulated.

Suggestion: “Instead, shallow-feeding short duration diving porpoises have moderate dive heart rates combined with high surface heart rates that may help balance the demands of prey capture, digestion, and thermoregulation.”

Lines 356-359: As mentioned before, most marine mammals do not regularly dive beyond their limits, so it is unclear how the results of this study support the concluding sentence. I suggest deleting the final concluding sentence.

Table 1 - The additional information is quite helpful. Thanks for adding it.

Table Header: “Median and range provided form dive duration and maximum dive depth, Median and 2.5 - 97.5 quantiles provided for dive duration, maximum dive depth, minimum dive, median bottom-of-dive, and maximum surface, and dive cycle ƒH.”

“provided form dive duration” should be “provided for dive duration”

“and maximum dive depth, Median and 2.5-97.5” should be “and maximum dive depth. Median and 2.5-2.75”

Column Header: “Median bottom-of-dive ƒH (bmp)” should be “Median bottom-of-dive ƒH (bpm)”

Fig 2. Thanks for adding this figure. It is a great visualization of the dive data and individual dive responses.

Figs S2 and S3 are really quite compelling, and it is a shame that they are not part of the main paper. If the journal requirements will not allow for more figures to be added to the main paper, I suggest adding Fig S2 as a panel to Figure 2.

Fig S3: For consistency with Figs 3 A and B, I suggest replacing the text at the top “Foraging? No buzzes or buzzes” with the key that is presented in Fig. 3. Simply code blue bars as “non-foraging dives” and red bars as “foraging dives”.

References:

Bejarano A.C., Wells R.S., Costa D.P. (2017) Development of a bioenergetic model for estimating energy requirements and prey biomass consumption of the bottlenose dolphin *Tursiops truncatus*. Ecological Modelling 356: 162-172.

Berga A.S., Wright A.J., Galatius A., Sveegaard S., Teilmann J. (2015) Do larger tag packages alter diving behavior in harbor porpoises? Mar Mam Sci 31:756-763.

Linnenschmidt M., Teilmann J., Akamatsu T., Dietz R., Miller L.A. (2013) Biosonar, dive, and foraging activity of satellite tracked harbor porpoises (Phocoena phocoena). Mar Mam Sci 29: E77–E97

Noren D.P. (2011) Estimated field metabolic rates and prey requirements of resident killer whales. Marine Mammal Science 27:60–77.

Otani S. (2000) Diving behavior and swimming speed of a free-ranging harbor porpoise, Phocoena phocoena. Mar Mam Sci 16:811-814

Otani S., Naito Y., Kawamura A., Kawasaki M., Nishiwaki S., Kato A. (1998) Diving behavior and performance of harbor porpoises, Phocoena phocoena, in Funka Bay, Hokkaido, Japan. Mar Mamm Sci 14:209-220

Solsona Berga A., Wright A.J., Galatius A., Sveegaard S., Teilmann J. (2015) Do larger tag packages alter diving behavior in harbor porpoises? Mar Mam Sci 31:756-763

Westgate A.J., Read A.J., Berggren P., Koopman H.N., Gaskin D.E. (1995) Diving behaviour of harbour porpoise, Phocoena phocoena. Can J Fish Aquat Sci 52:1064-1073.

Williams T.M., Rutishauser M., Long B., Fink T., Gafney J., Mostman-Liwanag H., Casper D. 2007. Seasonal variability in otariid energetics: implications for the effects of predators on localized prey resources. Physiological and Biochemical Zoology 80:433-443.

Appendix E

Response to reviewers

Reviewer 5

Comments to the Author(s).

Summary:

The authors have investigated heart rate responses in foraging harbor porpoises. With use of one of the most sophisticated bio-logging recorders available, they have assessed heart rate responses in relation to depth, activity (minimum specific acceleration – MSA) during dives, foraging behavior (echolocation buzzes) during dives as well as respirations during surface intervals of one of the world's smallest cetaceans. This is a remarkable technical accomplishment.

In these shallow-diving porpoises, dive heart rate was relatively moderate (40-50 beats per minute) and considered independent of dive duration, activity, and type of dive (foraging versus non-foraging). However, heart rate during surface intervals was higher after longer and more active dives. Dives (up to about 3.5 min in duration) were considered within aerobic limits for the species; routine maximum depths were predominantly less than 10 m. The authors conclude that although an extreme dive response (severe bradycardia) may occur in deeper or exceptional dives of harbor porpoises, this was not observed in the routine shallow dives of harbor porpoises in the study location.

The methodology and analysis were well detailed. The statistical analysis was rigorous. The data were well organized and presented. I think concerns expressed by other reviewers on heart rate during different phases of the dive and on possible effects of ontogeny on heart rate responses of juveniles versus adults in the study were adequately addressed in the revision. This included requested analyses and graphics of heart rate responses of the individual animals, and of heart rate responses during different phases of the dive.

I agree with the authors that a full-scale analysis of the ontogeny of the dive response in harbor porpoises is beyond the scope of the paper; it was not the goal of the research and there is not an adequate age range or sample size of animals for such a study. In the revision, analyses of individual animals did not reveal differences in responses between the juvenile and adult animals.

Analyses of heart rate responses during different phases of the dives and in longer dives are now included in the revision. The results reinforce the authors' original interpretations and conclusions.

Previous reviews also raised the issue of the author's interpretation of statistical significance versus biological relevance. In their data presentation, the authors have reviewed and re-emphasized this important concept, i.e., that although a result may be statistically significant, it may not be biologically relevant. These interpretations are now made quite clear in their presentation and should be of value to readers.

Lastly, there are no animal welfare concerns.

We thank the reviewer for thoughtful comments and appreciation of the dataset. We are pleased the reviewer concludes that we address the concerns of the reviewers in our revision and that our analysis and interpretation are robust.

General Comments:

Line 41: suggest changing "that hunt thousands of small prey daily" to "that hunt thousands of small prey daily during continuous shallow diving". Or something to that effect. Or perhaps the suggested changes in lines 47-48 are adequate.

Thank you for the suggestion. We have changed to

'… that hunt thousands of small prey daily during continuous shallow diving.' (line 41-42)

Line 47-48: suggest changing "dive response, for these shallow-diving cetaceans, it is more efficient to maintain circulation while diving: extreme heart-rate gymnastics are for emergencies, not everyday use" to "dive response, for these continuously shallow diving, frequently foraging cetaceans, it is more efficient to maintain some circulation while diving: extreme heart-rate gymnastics are for deeper/longer dives or emergencies, not everyday use."

I realize this increases the word count in the abstract, but I think these changes address concerns of other reviewers that these dives are not characteristic of all harbor porpoise populations, and that the physiological responses found may be different in other populations in different locations. Although not relevant to this paper, similar arguments could be made for other species - there may be physiological differences (in addition to documented hematological differences) in coastal vs off-shore bottlenose dolphins.

We have made the excellent suggested change to add deep/long dives. While we liked the suggestion to add "frequently foraging cetaceans", we did not include in an effort to keep the number of words in the abstract down. It is mentioned in the previous sentence. We hope this will also satisfy concerns of reviewer 3.

"Thus, despite having the capacity to prolong dives via a strong dive response, for these shallow-diving cetaceans, it is more efficient to maintain circulation while diving: extreme heart-rate gymnastics are for deep/long dives and emergencies, not everyday use. (lines 46-49)

Line 230: Explanations for elevated heart rates in the smallest animal (26 kg) are logical. For example, if this animal was studied later in the season and was smaller than other juveniles, occult disease (infection, poor nutrition) may well be a factor in the high respiratory rates and heart rates. I agree with presentation of the analyses both with and without this animal. The overall conclusions are the same.

Thank you for this comment. We are happy to learn that you think we handled this outlier appropriately.

Line 245: "by minimizing blood flow to exercising muscle": suggest changing to: exercising muscle and other organs. This reinforces arguments that the moderate (relatively elevated heart rates) during dives contribute to increased metabolism and digestion in these continuously feeding porpoises (as described in the next paragraph of the manuscript). Indeed, even at these moderate heart rates, most blood flow may be for digestion/thermoregulation and not to exercising muscle, which may still predominantly rely on its myoglobin-oxygen store.

Great suggestion. We have made the suggested change (lines 248-249).

In addition, although not necessary to add to text, moderate heart rates during shallow dives (with no alveolar collapse) will help maintain pulmonary gas exchange and access to the lung oxygen store (the lungs comprise about 20% the estimated total body oxygen store in most studies; the lung store may be an even greater percentage of the total oxygen store, dependent on what the blood volume actually is (blood volume is not documented in the harbor porpoise).

Thank you for this thought.

Line 267-290: Prediction of extreme bradycardia in the harbor porpoise diving to 410 meters off Greenland. Agree with the prediction. The deep-diving harbor porpoise probably undergoes alveolar collapse at some point unlike the shallow-diving harbor porpoise. Effects on lung stretch receptor reflexes, etc. as well as minimization of pulmonary gas exchange during deep dives will affect heart rate and oxygen store management differently than in the shallow dives.

Thank you.

Line 328-329: "extreme heart-rate gymnastics are for emergencies": Suggest changing to "deeper or exceptional dives and emergencies." Many of the deeper dives of Greenland harbor porpoises cited in Nielsen et al are probably foraging dives, not emergencies.

This is a great point and we have made the suggested change to:

"; extreme heart-rate gymnastics are for deep/long dives and emergencies." (line 332)

Specific comments:

Line 221: "than" check grammar and word usage

Thank you for this suggestion. We have consulted the Merriam-Webster dictionary and it appears that our usage is appropriate: than is used when you are talking about comparisons; then is used when you are talking about something relating to time. In this case we are comparing between adults and juveniles so "than" appears the correct choice?

Line 222: suggesting changing more extreme bradycardia to more intense bradycardia because the main point of the paper is that these porpoises do not have an extreme bradycardia

Great suggestions. We have made the change. (line 225)

Line 333: suggest changing "physiological capacities" to "physiological responses"

Great suggestion. We have made the change (Line 336)

Reference 16: I am not sure of the citation format, but shouldn't the last author in this reference at least get an "et al.", rather than not be listed. Note that the eleventh author in Ref 6 got an "et al."

Thank you for catching that. There was an error in the imported citation that is now corrected. It now states et. al. since more than 10 authors.

Reference 38: citation is incomplete - ? journal or book source

Thank you for catching this. There was an error in the imported citation that is now corrected.

Fig S2 x axis legend: should this not be "Time into dive" rather than "dive duration".
Thank you for catching this. This has been changed.

Reviewer 3

I appreciate the authors' efforts to address the reviewer comments, particularly with regards to the analysis of the dive data. I believe that the manuscript has greatly improved and that this study provides some valuable new data. However, there are a few, outstanding issues that should be addressed. Most are relatively minor, and all only require changes in wording or presentation. Some of the suggested changes do, however, require some substantial reevaluation of the significance and interpretation of the results. I appreciate that the authors' study system constrained their ability to measure the full diving capacity of harbor porpoises, but I reiterate that these constraints must be acknowledged upfront.

We are pleased that the reviewer thinks the manuscript is greatly improved and provides valuable data. We have responded to the detailed comments below. We wish to reiterate that the purpose of this study was not to measure the full diving capacity of harbor porpoises; we acknowledge in the abstract, intro (line 77), and discussion (line 213) that the porpoises perform shallow dives, and we have added a few more phrases to highlight this (Line 77 & 80). Therefore we would rarely expect to see extreme physiology and behaviour. The goal of this study was to investigate how these porpoises regulate heart rate during routine behaviors. We are upfront with this in the introduction and in the discussion, and we specifically discuss how porpoises in other locations may manage O_2 differently. We therefore argue that there is no need to present the shallow depth of the environment as a constraint on the study: extreme diving behaviour was not the focus of the study. However, we have emphasized our focus by adding "during routine dives" in the abstract on lines 38-39.

Furthermore, because of the constraints, the authors should be careful about speculating on the adaptive response of moderate bradycardia at depth. It is clear from the dive depths and durations that these subjects were diving within their cADL, as the authors do acknowledge. However, without comparable HR data on dives beyond their cADL or other physiological measurements that provide data on digestion, for example, it is not appropriate to speculate that the porpoises' diving behavior is driven by other physiological processes. There was no mention of bathymetry, depth, or prey abundance and behavior (e.g., depth, density, etc.) in the study area, so harbor porpoise diving behavior could simply be an artifact of the environment in which they forage. Although the other physiological responses/systems may benefit from shorter dives with moderate bradycardia, it is likely that the reduced dive duration, rather than the other physiological processes, drive the harbor porpoise's moderate bradycardia response at depth. These are interesting observations and could be discussed, but the authors need to carefully convey that these benefits are likely an artifact of these shorter dives, rather than the other physiological processes driving the harbor porpoise diving behavior and subsequent heart rate response. Furthermore, as harbor porpoises throughout the world tend to be found in higher latitudes, some of the physiological issues (e.g., thermoregulation in cold water) are not unique to this specific study population. However, in contrast to the dives reported in the present study, harbor porpoises elsewhere dive for longer durations and to greater depths. It might be helpful to provide comparative background information on diving rates/capabilities of other porpoise populations in the introduction to support the authors' statements that this harbor porpoise population is very different from others. Regardless, I think most diving literature suggests that most marine mammals do not typically dive beyond their cADL, so some reframing is necessary and some of the concluding statements should be reevaluated. Finally, the authors should carefully consider how they cite specific studies because the findings do not necessarily support their statements. Please also see specific comments below.

We are a little unclear what the reviewer is requesting here. We believe we are reporting our results accurately and discuss them in relation to previous findings. We are not arguing that are results are unique to this population. As stated in the response to the first revision, most porpoise populations studied perform short shallow dives (Berga et al 2015, and Linnenschmidt et al 2013 – short shallow dives in Danish waters; Otani 2000, Otani et al 1998 - mostly shallow dives less than 20 m and 1.5 min; Westgate et al 1995, some deeper dives, but most < 100m). While it would be interesting to discuss why porpoises in other locations behave differently, we do not believe it is within the scope of this paper. The focus of this manuscript is the dive response during routine dives, not behavior. We also do not disagree that most dives will be below the cADL and we do not suggest otherwise in the paper. In contrast we suggest that the heart rate response we observe will be typical in many shallow diving species. We do hypothesize what we think the heart rate response would be in porpoises performing more extreme dives. We believe it is the job of the authors to make some speculations on what the results mean that can then be tested in future studies. We make it clear when we are speculating by using the words "may", "could" or "suggest". Our speculations are based on current state of knowledge and we therefore believe they are appropriate. We address the reviewer's specific comments below.

Title: "High heart rates in hunting harbour porpoises" is somewhat misleading. This title implies that heart rates of hunting harbor porpoises may be elevated. However, the authors have shown that during dives (both foraging and non-foraging) heart rates are lower at depth, following a somewhat typical, moderate dive response. Consequently, harbour porpoises do not have unusually high heart rates at depth. Indeed, the diving heart rates of 40-50 bpm are lower than heart rates for the harbor porpoises measured at the surface. Furthermore, these diving heart rates are on par with the heart rates of several other marine mammals (e.g., sea lions, Weddell seals, and dolphins) that are also diving within their cADL, similar to the harbor porpoises in this study. The heart rate data for the other marine mammals diving within their cADL can be found in the references the authors cite. The results from this study suggest that foraging activity has minimal impact on the heart rate in these harbor porpoises at depth, which in this study was relatively shallow. There were reductions in heart rate at depth during both foraging and non-foraging dives, but there doesn't seem to be a difference in heart rates during these two activities. I would suggest modifying the title to one that more accurately states the findings. For example, "Shallow water hunting activity has minimal impact on harbour porpoise heart rates at depth", or something more eloquent.

We thank the reviewer for the suggestion, but we prefer our original title. In this study we report the highest surface and some of the highest diving heart rates observed in wild marine mammals.

Additionally, heart rates were regularly higher than what has been observed in captive porpoises. We believe that our title more accurately represents our study than the suggested title.

Abstract:

Lines 36-42: "Many studies have focused on the extreme role of the dive response in maximizing dive duration in marine mammals, but few have addressed how these adjustments may compromise the capability to hunt, digest and thermoregulate. Here we use DTAGs which record heart rate together with foraging and movement behaviour to investigate how O_2 management is balanced between the need to dive, forage, and digest in five wild harbour porpoises (Phocoena phocoena) that hunt thousands of small prey daily."

The study focused on changes in heart rate in relatively short, shallow dives. The method of the study was to use DTAGs that recorded heart rate and acoustic signals. Since no other measurements were made to evaluate hunting efficiency, digestion or thermoregulation, the present study also doesn't address how these diving adjustments compromise those activities or how O_2 management is balanced between the need to dive, forage, and digest. Although these are interesting discussion points, I think the focus of the study needs to be more accurately represented in the abstract.

We have revise the second sentence to only include the need to balance diving and foraging. We are documenting for the first time heart rate in a foraging cetacean and we are directly comparing heart rate in foraging and non-foraging dives. Therefore, we think this statement is appropriate, but we have removed digest from the second sentence. We still discuss this in the paper because foraging porpoises must digest.

Modified sentence:

"Here we use DTAGs which record heart rate together with foraging and movement behaviour to investigate how O2 management is balanced between the need to dive and forage in five wild harbour porpoises that hunt thousands of small prey daily during continuous shallow diving." (Lines 39- 42)

Lines 42-43: "Surprisingly, dive heart rate (f_H) was moderate (40-50 bpm) and relatively stable acrossdive types, dive duration (0.5-3.3 min), and activity."

I am having a difficult time reconciling the diving heart range of 40-50 bpm with Table 1 and the figuresSI A and B, S2, and S3 in the supplemental information. In my interpretation, minimum dive heart ratesare being reported for the depth phase (not descent or ascent), but it appears that most minimum diveheart rates are greater than 40-50 (even with removing J3). The range of minimum dive heart rates in Table 1 (excluding J3) range from 40-73. The max minimum heart rate for J3 is 86. If it is the minimum dive heart rate that is being reported, then the range is 40-86, but if it is the entire range (not just minimum), the range is much larger. If this is the correct interpretation, please correct the range and indicate that the dive heart rate that is being reported is the minimum dive heart rate or whichever heart rate descriptor applies.

Thank you for catching this. We forgot to update the values when we switched the variable we were reporting. We have modified to:

"The dive heart rate was moderate (median minimum 47-69 bpm) and relatively stable across dive

types, dive duration (0.5-3.3 min), and activity." (lines 42-43)

Lines 45-50: "A moderate dive response, allowing for some perfusion of peripheral tissues, may be essential for fuelling the high field metabolic rates required to maintain body temperature and support digestion during diving in these small, continuously-feeding cetaceans. Thus, despite having the capacity to prolong dives via a strong dive response, for these shallow-diving cetaceans, it is more efficient to maintain circulation while diving: extreme heart-rate gymnastics are for emergencies, not everyday use."

Please see comment above regarding extrapolation. Is there some way to measure/determine that these porpoises are consciously ending dives relatively early? Is there something in their habitat such as bathymetry or prey behaviour that also factors into determining their dive behaviour? Although there may be some physiological benefits to these shorter dives, the methods of this study cannot be used to determine what diving strategy is most efficient or if the porpoises are consciously performing shorter dives to reap these postulated benefits. Also, please see comments below regarding harbour porpoise metabolic rates compared to those of other marine mammals.

Thank you for this perspective. It is common in studies of free-ranging animals to interpret their consistent natural behaviour, observed over multiple individuals, as reflecting a degree of optimality (in the full sense of balancing conflicting demands and constraints across physiology, environment, sensory capabilities, prey availability, perception of predation risk etc.). We are invoking this idea here by presuming that if there was a more efficient way to manage heart rate during foraging in this study location, porpoises would adopt it. As we point out in the introduction, even though the environment restricts the dive depth, a shallow dive can still be long and so require deeper heart rate modulation. The sentences highlighted by the reviewer speculate that, whatever drives the relatively short dive durations, the efficient behaviour appears to be to maintain blood flow. In that spirit, we have now modified the second sentence to emphasise that we are speculating based on best available data: "… for these shallow-diving cetaceans, it appears to be more efficient……" (line 47)

Lines 70-73: "a single foraging blue whale (8.5 hours, *Balaenoptera musculus*, the largest baleen whale, ~70,000 kg) [16], and five narwhals (~5 dives each, *Monodon monoceros*) released from prolonged net entanglement and stranding (mid-size odontocete, ~1000-1600 kg) [17]."

For consistency with the blue whale information, suggest including the size of the narwhals in the parentheses with the species and dive information: "a single foraging blue whale (8.5 hours, *Balaenoptera musculus*, the largest baleen whale, ~70,000 kg) [16], and five narwhals (~5 dives each, *Monodon Monoceros*, mid-size odontocete, ~1000-1600 kg) released from prolonged net entanglement and stranding [17]."

Great suggestion. We have made the change (line 70)

Lines 154-155: "duration between the respiration ending a dive, and the respiration starting the following dive" should be "duration between the respiration ending a dive and the respiration starting the following dive" without a comma.

Thank you – we have corrected. (line 150)

Lines 229-230: "Figures 2, 3B and 4A ," remove extra space between 4A and ,

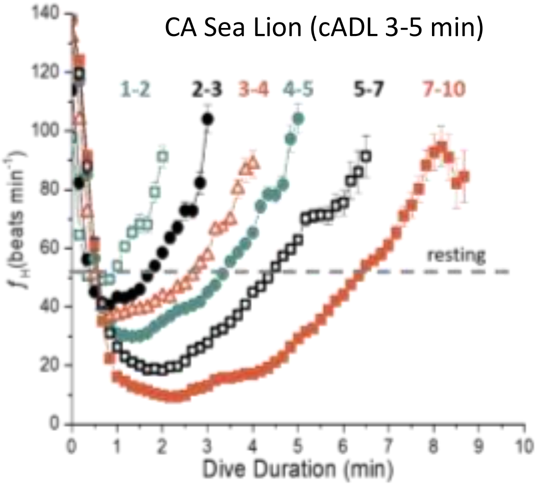
Thank you – we could not find that error on our version, but it did lead us to fix another spacing issue nearby.

Lines 250-258: "Although the associations between dive duration and bottom-of-dive and LQ ƒH were statistically significant when JM3 was excluded, the slope coefficient was not biologically relevant; i.e. a1 min increase in dive duration (which is a doubling of the median dive duration) only resulted in a 3 bpm decrease in LQ and bottom-of-dive ƒH and dive duration explained less than 3% of the variation in ƒH (Table S1)[37, 38]. This is unusual for diving mammals as ƒH typically decreases with increasing dive duration even during aerobic dives (dives shorter than ADL) [4, 8, 39, 40], and a decrease in ƒH with increased dive duration was documented in captive porpoises performing short dives [8, 23]."

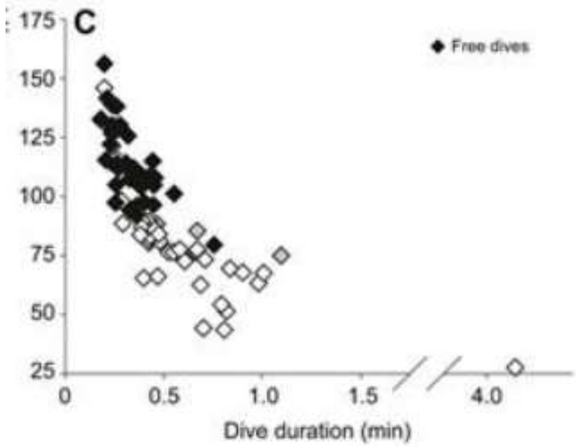
To be clear, I understand and appreciate the difference between statistical significance and explanatory power, or biological relevance. However, despite the results from the present study not being biologically relevant, per statistical criteria, this does not mean that the results of this study are "unusual for diving mammals." The previous studies that the authors cite reported a significant decrease in heart rate with increasing dive duration, but mainly for dives that extended beyond the species' cADL. As written, the authors are using the lack of biological significance (not statistical significance) to present the findings as unusual and different from previous studies. Only if the authors of the previous studies ran similar analytical tests and found that their results were both statistically and biologically relevant, can the authors of the present study make such statements. I consulted the cited references and none of the authors evaluated the biological relevance of their findings. Similar to many of the previous studies, the results of the present study report a statistically significant relationship between dive duration and heart rates at depth. Unlike the present study, however, many of the previous studies collected data over a larger range of dive durations, including dives that exceeded the cADL. Importantly, the heart rate response is most pronounced during dives that were at the upper limit of or exceed the cADL, which many of the previous studies also emphasized. As the authors of the present study report, the harbor porpoises in the present study were diving within their cADL. The data and results from the previous studies are indeed similar to the findings reported here for harbor porpoises. Across the studies, individuals that were diving within their cADL demonstrated relatively minimal changes in heart rate at depth. For example, Hill et al. (1987) reported variable results for individual free-diving Weddell seals. Only for dives greater than 20 min in duration, which are at and beyond the cADL for Weddell seals, was there a correlation between heart rate and dive duration. In contrast, there was no correlation between dive duration and heart rate for dives under 20 min in duration. Similar results were reported for sea lions that were diving within their cADL (McDonald et al 2018). Sea lions only displayed typical true bradycardia in mid- to long-duration dives; these dives were near the upper limit of their cADL or beyond their cADL. Across all studies, the extreme reductions in heart rates typically occurred during the longer dives that exceeded cADL. It was also interesting to observe that many of the heart rates measured at depth for seals and sea lions diving within their cADL were similar to the values reported in the present study for harbor porpoises. So, to summarize, because other studies have not evaluated the predictive power, or biological significance of their results, only statistical results and patterns can be compared across studies. In particular, the appropriate pattern to compare is how diving heart rate varies with dive duration for dives that fall within the cADL. The results from previous studies on freely diving marine mammals demonstrate that the pattern is similar to that reported in the present study for harbor porpoises diving within their cADL. Harbor porpoise dive duration and/or depth in other environments (e.g., Berga et al. 2015, Otani 2000, Otani et al. 1998, Linnernschmidt et al. 2012, Solsona et al. 2015, Westgate et al.1995) are substantially greater than those reported in the present study and we might expect to see some effect of dive duration on heart rate in these populations.

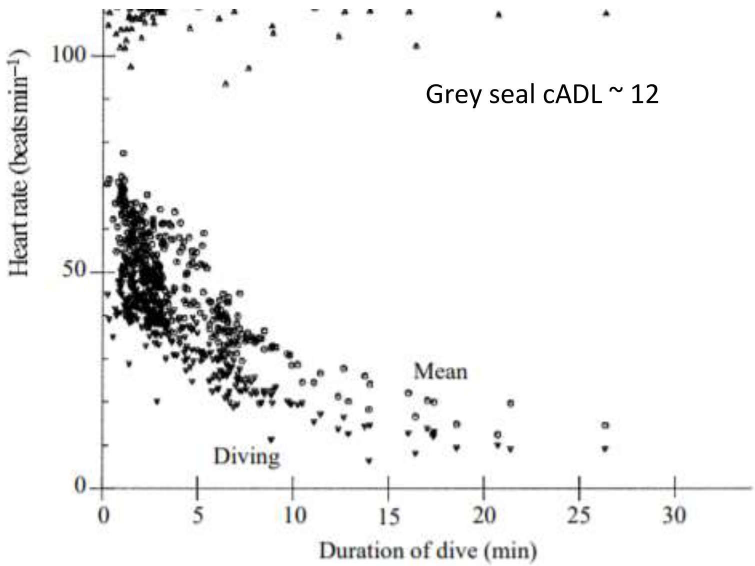
We respectfully disagree with the statement that we cannot compare our results to previous studies because they did not specifically evaluate biological relevance. From many of these papers it is straightforward to determine the effect size and biological relevance from the reported data and statistics. While it is good practice to discuss both, common practice is to only report statistical significance when the biological relevance is clear.

We also respectfully disagree that there is not a relationship between dive heart rate and dive duration even in aerobic dives. As can be seen in the below figures from 3 of the citations (California sea lions, Porpoises, and grey seals), even in dives below the cADL there is a strong relationship between dive duration and dive heart rate. We have removed the Weddell seal citation because there is not enough data provided for dives below the ADL to compare.



Harbor porpoise





Lines 261-262: “The generally high ʃH is likely required to support the high field metabolic rates documented in porpoises to keep small bodies warm in high latitude waters[19]”.

As mentioned above, the heart rates reported at depth for harbor porpoises are lower than their corresponding heart rates measured at the surface and similar to heart rates recorded for other marine mammals, including bottlenose dolphins, diving within their cADL. As such, it isn't appropriate to classify fH as generally high in harbour porpoises, and it is also beyond the scope of this study to correlate these heart rates with metabolic rates to support thermoregulation. Other harbor porpoise populations, all of which inhabit cold waters in high latitudes, perform longer and deeper dives, so thermoregulation is not likely to be a major driver for this specific population's diving behavior. Furthermore, harbor porpoise FMRs are not unusually high compared to other marine mammals. Indeed, Rojano-Doñate et al. (2018) reported that “harbour porpoises have FMRs that are elevated in comparison to terrestrial mammals of the same size, even when comparing with terrestrial carnivores, but lower than similar-sized marine pinnipeds and mustelids.” Thus, Rojano-Doñate et al. (2018) did not conclude that harbor porpoises have unusually high FMRs. In fact, across other marine mammal species, the estimated FMR of harbor porpoises (3–4 times higher than the BMR predicted from Kleiber's equation, Rojano-Doñate et al. 2018) is not unusually high. Several studies on pinnipeds and dolphins have measured and estimated FMRs that are up to 5-8 times higher than BMR predicted from Kleiber's equation. See references in Noren 2011 and Bejarano et al. 2017. Also, it is interesting to note that metabolic rates are not necessarily correlated with food consumption in marine mammals. For example see the study by Williams et al. 2007 on sea lions. The authors found that BMR did not increase with increasing food consumption requirements, though admittedly, the lack of correlation between BMR and food consumption occurred during relatively energetically demanding periods of time (e.g., molting, lactation).

We respectfully disagree with this critique. The surface (median maximum = 188-219 bpm) and dive heart rates (median minimum = 47-69) of porpoises in our study are both higher than what is observed in the few other species studied (f.ex. captive bottlenose dolphins heart rates in dives < cADL: surface maximum ~150-160 bpm, dive minimum ~30-40 bpm (Noren et al 2012), adult California sea lions heart rate in 1-3 min dives surface = ~100-130 bpm , bottom of 1-3 min dives = 30-40 bpm (McDonald and Ponganis, 2014), captive juvenile California sea lions heart rates in 2 min dives of similar mass to porpoises in this study: surface = 150-200 bpm, dive minimum 20-25 bpm (Ponganis et al 1997), wild grey seal heart rates in dives of ~ 5 min (~50% of cADL): surface: 100-120 bpm, dive heart rate 40-55 bpm (so minimum heart rate even lower)(Thompson and Fedak 1993)). Additionally, porpoises do indeed have high metabolic rates compare to terrestrial carnivores and as small marine mammals they have high FMR (not has high as an otter, but still high). We modified the sentence so it does not refer to cold water, but we believe the statement is relevant to explain that the high heart rates would be needed to meet metabolic demands of an animal with a high mass specific FMR (Smaller animals, and marine mammals in particular have high mass specific metabolic rates).
Modified to:
The generally high fH is likely required to support the high field metabolic rates documented in porpoises [19]. (Lines 250-251)

Lines 308-310: “The lack of relationship between activity and dive ʃH in most of the porpoises could be a by-product of a consistent moderate dive response that allows for digestion during diving.”

As mentioned above, these are interesting discussion points, but since the study didn't measure digestive processes, I would suggest rephrasing slightly to something like: "The lack of relationship between activity and dive ƒH in most of the porpoises could be a by-product of a consistent moderate dive response that may also allow for digestion during diving."

We do not believe it is necessary to add an additional "may" - it is already made clear that this is a discussion point and speculation by our use of the word "could" earlier in the sentence.

Lines 344-347: "These first longer-term, continuous heart rate data from multiple, unstressed wild cetaceans demonstrate how these consummate divers juggle the conflicting demands of a deep bradycardia to prolong dives in search of prey while still delivering the O_2 needed for active hunting and digestion."

Please see comments above about extrapolating beyond what was measured in the study. My impression is that it is not typical for marine mammals to extend their dive durations beyond their cADL while foraging unless there are extreme circumstances. For example, see the data for Weddell seals in Hill et al. 1987. The number of dives that were within the cADL (n=152) were far greater than the number of dives that were at or above the cADL (n=37). Indeed, one seal never performed dives that were greater than the cADL. Do the authors think that we should not expect the same for harbor porpoises? If so, what are the other potential reasons/factors to suggest that the harbor porpoises are intentionally not pushing their limits during foraging dives? Was there a difference in depth/duration of foraging versus non-foraging dives? Is this a relatively shallow or deep environment? Are the prey typically found in shallow or deep water or difficult to capture? The sample size from this study is impressive, so it is intriguing that the dives fell within the cADL, but it is difficult to presume that the animals are intentionally forgoing long dives without compelling information to suggest that they would be expected to perform deeper, longer dives in their environment. If there is evidence that these dives would be expected, then there might be some justification for a tradeoff.

We agree that it would be both fascinating and informative to examine the driving forces on dive duration in porpoises at this and other locations, but that is well beyond the scope of this study. We are simply recognizing in the highlighted sentence that longer dive durations inevitably come at a cost: there is an ineluctable trade-off between deep bradycardia and maintenance of functions such as digestion. Species that often approach and exceed the cADL (f.ex. beaked whales, elephant seals, Australia sea lions, New Zealand sea lions, California sea lions, harbor porpoises in Greenland, etc) must solve this trade-off by serializing physiological processes that can be postponed during long dives. We are just making the point that shallow diving species may adopt a different strategy allowing them to balance conserving O2 with other important functions. To contextualize this point, we give examples in the text of species that appear to separate these functions

Lines 347-349: "We find that porpoises in shallow waters forgo deep bradycardia and instead maintain a relatively stable diving heart rate that is not influenced by size, dive duration, or activity."

This needs some rephrasing. Per typical marine mammal diving response for short, shallow dives, the harbor porpoises are diving within their cADL so there is no need for deep bradycardia. They aren't "forgoing" it. Also, the authors state that "heart rate is not influenced by size, dive duration, or activity".I suggest removing "size" since evaluating the relationship between size and diving heart rate was not one of the goals of this study. If that was the goal, then a larger diversity of animals should have been studied, including much smaller animals. As written, a reader could inappropriately misinterpret that statement as a lack of influence of body size on diving capabilities for harbor porpoises, in general, rather than the lack of an effect of size for the relatively narrow range of porpoise body sizes in this study.

As discussed in response to an earlier point, bradycardia does not just switch on when animals dive beyond cADL. It is typically a graded response influenced by dive duration even in dives shorter than cADL (f.ex. McDonald and Ponganis 2014, McDonald et al 2018, Thompson and Fedak 1993, Reed et al 2000, Meir et al 2008). Thus our finding that heart rate is independent of dive duration points to a distinct strategy which we have encapsulated in the highlighted line. Although we have less strong evidence for the conclusion regarding size, as this was not the focus of the study, our data do cover a doubling of mass with no appreciable difference in heart rate. Nonetheless, we have rearranged the sentence to acknowledge the weaker evidence for size (line 329-330).

Modified sentence:

We find that porpoises in shallow waters forgo deep bradycardia and instead maintain a relatively stable diving heart rate that is not influenced by dive duration or activity, and possibly size.

Lines 349-353: "This moderate bradycardia may be essential for providing cardiac output to support the high metabolic rate and upholding digestion during near-continuous feeding. Thus, for porpoises in this environment, extreme dive responses enabling extended dive durations, that may be critical for efficient foraging in marine mammals elsewhere, are not needed; extreme heart-rate gymnastics are for emergencies, not everyday use."

Per comments above, the question remains whether this moderate bradycardia is simply a consequence of their short/shallow dives that are related to the environment in which they live or whether their dive behavior is the result of a conscientious decision to maintain these shorter dives in order to provide essential cardiac output to support other physiological processes. The authors have not presented any compelling data to suggest the latter.

Our study does not seek to identify the causal factors underlying the diving behaviour (which would be extremely difficult to do in wild animals). But, given the continuous high foraging rates and fast digestive turnover of harbour porpoises in this location, digestion must largely occur in parallel with foraging. The highlighted text is simply pointing out that this constrains bradycardia. Thus, whatever the driving factor(s) behind the dive duration, the diving behaviour, bradycardia, prey availability and environment are all interlinked into an integrated foraging strategy.
In response to reviewer 5's comments we have modified the final phrase of the highlighted text to: "extreme heart-rate gymnastics are for long/deep dives and emergencies, not everyday use." which emphasizes dive duration as an elective factor influencing the depth of bradycardia.(Line 332)

Please remove "high metabolic rate" per comments from above regarding marine mammal FMRs that are all relatively high

Compared to terrestrial carnivores, porpoises have high metabolic rates. Rojano-Doñate et al. (2018) also acknowledge that their FMR estimates are conservative and true FMR is likely higher. Additionally, Rojano-Donate et al discuss how food intake increases seasonally even when metabolic rate remains relatively stable so one way they avoid an even higher metabolic rate is by increasing food intake so can increase insulation (blubber).

Lines 353-355: “Instead, shallow-feeding short duration diving porpoises adopt a strategy of moderate dive heart rate combined with high surface heart rate to balance the demands of prey capture, digestion, and thermoregulation.”

It is more likely that the harbor porpoise adopt a shallow-feeding short duration diving strategy and the heart rate response follows, rather than “adopt a heart rate strategy”. Also, please consider rephrasing to qualify that the other benefits are postulated.

Suggestion: “Instead, shallow-feeding short duration diving porpoises have moderate dive heart rates combined with high surface heart rates that may help balance the demands of prey capture, digestion, and thermoregulation.”

Thank you: We have made the suggested change. (Lines 333-335)

Lines 356-359: As mentioned before, most marine mammals do not regularly dive beyond their limits, so it is unclear how the results of this study support the concluding sentence. I suggest deleting the final concluding sentence.

In response to reviewer 5 we have modified the last statement to:

This new understanding on how one of the smallest marine mammals manages O2 during active foraging dives provides insight into how physiological responses are not necessarily taken to their extremes in the wild. (lines 335-337)

We believe this re-wording also addresses the concern raised here.

Table 1 - The additional information is quite helpful. Thanks for adding it.

Table Header: “Median and range provided form dive duration and maximum dive depth, Median and 2.5 - 97.5 quantiles provided for dive duration, maximum dive depth, minimum dive, median bottom-of-dive, and maximum surface, and dive cycle ƒH.”

“provided form dive duration” should be “provided for dive duration”

Thank you for catching this error – corrected.

“and maximum dive depth, Median and 2.5-97.5” should be “and maximum dive depth. Median and 2.5-2.75”

Thank you for catching this error – corrected.

Column Header: “Median bottom-of-dive ƒH (bmp)” should be “Median bottom-of-dive ƒH (bpm)”

Thank you for catching this error – corrected.

Fig 2. Thanks for adding this figure. It is a great visualization of the dive data and individual dive responses.

We are pleased you like the figure.

Figs S2 and S3 are really quite compelling, and it is a shame that they are not part of the main paper. If the journal requirements will not allow for more figures to be added to the main paper, I suggest adding Fig S2 as a panel to Figure 2.

We are pleased you like the supplemental figures. Unfortunately, with the additions during the first round of revisions we are at the maximum page length so we cannot add a figure or make the included figures larger.

Fig S3: For consistency with Figs 3 A and B, I suggest replacing the text at the top "Foraging? No buzzes or buzzes" with the key that is presented in Fig. 3. Simply code blue bars as "non-foraging dives" and red bars as "foraging dives".

Thanks for the suggestion.

References:

Bejarano A.C., Wells R.S., Costa D.P. (2017) Development of a bioenergetic model for estimating energy requirements and prey biomass consumption of the bottlenose dolphin *Tursiops truncatus*. Ecological Modelling 356: 162-172.

Berga A.S., Wright A.J., Galatius A., Sveegaard S., Teilmann J. (2015) Do larger tag packages alter diving behavior in harbor porpoises? Mar Mam Sci 31:756-763.

Linnenschmidt M., Teilmann J., Akamatsu T., Dietz R., Miller L.A. (2013) Biosonar, dive, and foraging activity of satellite tracked harbor porpoises (Phocoena phocoena). Mar Mam Sci 29: E77–E97

Noren D.P. (2011) Estimated field metabolic rates and prey requirements of resident killer whales. Marine Mammal Science 27:60–77.

Otani S. (2000) Diving behavior and swimming speed of a free-ranging harbor porpoise, Phocoena phocoena. Mar Mam Sci 16:811-814

Otani S., Naito Y., Kawamura A., Kawasaki M., Nishiwaki S., Kato A. (1998) Diving behavior and performance of harbor porpoises, Phocoena phocoena, in Funka Bay, Hokkaido, Japan. Mar Mamm Sci 14:209-220

Solsona Berga A., Wright A.J., Galatius A., Sveegaard S., Teilmann J. (2015) Do larger tag packages alter diving behavior in harbor porpoises? Mar Mam Sci 31:756-763

Westgate A.J., Read A.J., Berggren P., Koopman H.N., Gaskin D.E. (1995) Diving behaviour of harbour porpoise, Phocoena phocoena. Can J Fish Aquat Sci 52:1064-1073.

Williams T.M., Rutishauser M., Long B., Fink T., Gafney J., Mostman-Liwanag H., Casper D. 2007. Seasonal variability in otariid energetics: implications for the effects of predators on localized prey resources. Physiological and Biochemical Zoology 80:433-443.

Appendix F

This study is exceptional in that it is one of a very few number of studies to measure heart rates in free ranging cetaceans. As such the data are very important. I truly appreciate the efforts by the authors to revise this manuscript. I believe that the additional analyses, reframing of some statements, and supplemental figures have improved the manuscript greatly. Because these are the only heart rate data obtained from free ranging small odontocetes, it is critical that the findings are represented as accurately as possible with respect to other data on marine mammal heart rates and metabolic rates. Given that, I have one editorial and three relatively minor comments/requested revisions that stem from previous comments and author responses. None of these suggested changes will alter the main points that the authors are trying to convey, but rather should strengthen the paper.

1) Following up on Reviewer 5's comment "Line 221: "than" check grammar and word usage", I noted that it was not resolved. "than" now appears on line 224, within the statement, "That two juveniles (JM1 and JM2) exhibited similar dive ƒH **than** the two adults (Figures 2, 3B, 4, 5 and supplemental figures S1 and S2) suggests that the juveniles are employing a relatively more intense bradycardia, allowing 226 them to dive similarly to adults despite smaller absolute oxygen stores due to their smaller size."

From the dictionary: Than is used in comparisons as a conjunction (as in "she is younger than I am") and as a preposition ("he is taller than me"). It would be appropriate to use "than" here if juvenile dive fH was "greater", "higher" or "lower" than adult fH, for example. However, this sentence discusses "similar" values. So, it is necessary to rephrase the earlier part of the sentence to something like: "That the two juveniles (JM1 and JM2) and two adults exhibited similar dive ƒH (Figures 2,…."

2) Lines 219-228 "Despite a large range in estimated mass (26-67 kg), when the smallest porpoise was excluded, porpoises exhibited remarkably similar dive ƒH (Figures 2, 3B and 4A, i.e. 95% of all Lower Quartile (LQ) ƒHs fell between 55 and 84 bpm). This is unexpected because among mammals, small young animals generally have higher ƒH than larger adults (Table 1)[35]. That two juveniles (JM1 and JM2) exhibited similar dive ƒH than the two adults (Figures 2, 3B, 4, 5 and supplemental figures S1 and S2) suggests that the juveniles are employing a relatively more intense bradycardia, allowing them to dive similarly to adults despite smaller absolute oxygen stores due to their smaller size. These results are consistent with a previous study that determined juvenile and adult porpoises have similar cADL's [34]."

This is indeed an interesting phenomenon to ponder. The authors have obtained data that could be used to determine whether or not juvenile harbor porpoises employ relatively more intense bradycardia, so I wonder why they present a hypothesis, rather than data to support it?

While I agree that juveniles should theoretically have higher heart rates, it isn't obvious to me that the data from this study support that the juvenile harbor porpoises in the present study (JM1 and JM2) have elevated surface fH. After reviewing Table 1, it is evident that surface fH for JM1 is only marginally greater than the two adult porpoises, while the surface and dive fHs for JM2 are actually lower than both adults. Figure 3D demonstrates that dive cycle fH for JM1 is similar to adults, while JM2 is consistently lower. Similarly, figures S1C and S2 show considerable overlap in data across all subjects (with the exception of JM3, the outlier). In particular S1C and S2 show that data from JM1 and AF are nearly identical, including post dive fH at the surface. With so much overlap in heart rate data from juveniles and adults plus the somewhat inconsistent results for JM1 and JM2, it is inappropriate to speculate that bradycardia in juveniles is more intense than the adults. Given the small sample size (n=4 animals with quality data (2 juveniles and 2 adults)), the disparate results for surface and diving fH for the two juveniles, and the fact that the data do not appear to demonstrate that the juvenile harbor porpoises have elevated surface fH, compared to the adults, nor that they are employing more intense bradycardia at depth, I suggest removing these sentences, or at the very least deleting the statement “suggests that the juveniles are employing a relatively more intense bradycardia, allowing them to dive similarly to adults despite smaller absolute oxygen stores”.

If the authors’ disagree with my interpretation of their data, then they should report results on differences in surface heart rates, dive heart rates, and bradycardia intensity between harbor porpoise juveniles and adults to support their statements. There is no need to speculate. Indeed the results of such an analysis would be very interesting.

Also, the paper on harbor porpoise cADLs (reference 34) only incorporated age-specific total body oxygen stores and estimated diving metabolic rates (based on body mass alone), with no correction in metabolic responses by age. The main reasons that juvenile and adult harbor porpoises were found to have similar cADLs is that harbor porpoise body oxygen stores are fully developed at a relatively young age and there is only a marginal difference in body size between juvenile and adult harbor porpoises. The early oxygen storage development and marginal difference in body size between juvenile and adult porpoises may also explain why heart rates are similar. This also supports the conclusion that age does not seem to be a large factor in the fH response to diving in juvenile and adult porpoises from the present study.

3) Lines 244-247: “This is unusual for diving mammals as ƒH typically decreases with increasing dive duration even during aerobic dives (dives shorter than ADL) [4, 8, 39, 40], and a decrease in ƒH with increased dive duration was documented in captive porpoises performing short dives [8, 23].”

The author rebuttal states, “We have removed the Weddell seal citation because there is not enough data provided for dives below the ADL to compare”, yet the reference is still cited (reference 39 in lines 244-247 from the manuscript).

However, I disagree that the authors should ignore this citation. The study reported that there is no change in heart rate with increasing dive duration for “short dives” (<20 min, which is the approximate ADL). In contrast, there was a significant increase in heart rate with dive duration for dives that were ≥20 min. The authors concluded that HR does not change with dive duration for dives within the Weddell seal ADL. These findings are not that surprising, given that the Weddell seals have cADLs that are substantially greater than the other marine mammals that are presented for comparison in the present paper. Furthermore, the plots of data that include dives of all durations (0 to >20 min in duration) from two individual seals that regularly performed longer dives (see Fig 2 A and B from Hill et al. 1987, pasted below) do not show the same pattern as the figures presented in the authors’ rebuttal. These are the same/similar relationships that are presented in the authors’ rebuttal so they are comparable. The sample size for the Weddell seal study is also substantial and surpasses the sample size of data presented in the captive harbor porpoise study. Weddell seal physiology is geared towards long duration diving, so differing results could be expected. Another illustration of this is that dissimilar to the results from the present study, Weddell seal post-dive heart rate also did not vary by dive duration (Fig 2 C and D from Hill et al. 1987, pasted below).

Therefore, there is no basis to remove the Weddell seal citation. Given how relatively few studies there are on heart rates in freely diving marine mammals and the numerous biological and ecological factors that influence heart rate at depth, it is important to acknowledge the findings that differ.

I suggest a compromise to simply temper this statement that I hope the authors find suitable:

"This is unusual for many marine mammals. While Weddell seals do not appear to modify fH with dive duration during aerobic dives (dives shorter than estimated ADL) [39], ƒH decreases with increasing dive duration during aerobic dives in other free-ranging pinnipeds [4, 40] as well as captive porpoises performing short dives [8, 23]."

Estimated cADL for Weddell seals is 20 min. Dive HR for dives up to 20 min do not appear to decline with dive duration for the two seals in the study that regularly performed very long dives (panels A and B).

R348 HEART RATE AND TEMPERATURE OF WEDDELL SEALS

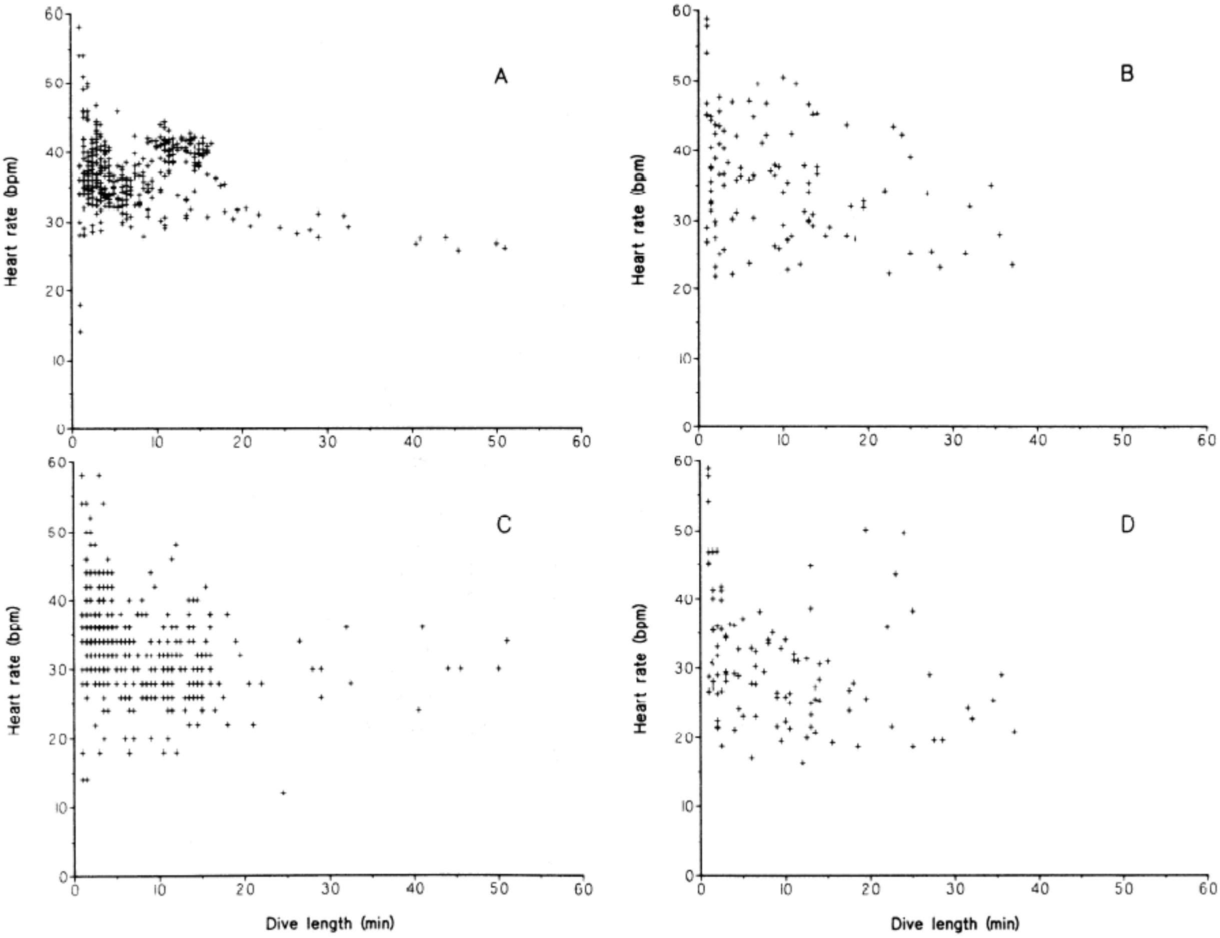


FIG. 2. Mean heart rate variations with dive duration. *A*: whole-dive heart rate averages for *seal 82/2*, predive heart rate = 60.2 ± 2.2 beats/min. *B*: whole-dive heart rate averages for *seal 83/4*, predive heart rate = 64.9 ± 1.9 beats/min. *C*: average heart rate for *seal 82/2* between 30 and 60 s after diving. *D*: average heart rate for *seal 83/4* between 30 and 60 s after diving.

4) Lines 249-251: "Even in the longest dives performed by each porpoise of up to 3.3 min, ƒH was moderate and no different from shorter dives (Figures 2 and S2). The generally high ƒH is likely required to support the high field metabolic rates documented in porpoises [19]."

I note and appreciate that the authors have removed the statements regarding thermoregulation. However, the entire statement regarding the moderate fH supporting high metabolic rates should not be included. If this moderate fH is specifically “required” to support high metabolic rates, then we would expect to see this phenomenon in all marine mammals that have elevated metabolic rates, compared to terrestrial animals. Per my previous review, harbor porpoises do not have exceptionally high metabolic rates compared to other marine mammals. I’ve included a figure from a relatively new reference that illustrates the main point I was trying to convey in the previous review. As mentioned previously, the study that is being cited does not report that harbor porpoises have high metabolic rates when compared to other marine mammals. Indeed, despite the title of the paper, Rojano-Doñate et al. (2018) reported that “harbour porpoises have FMRs that are elevated in comparison to terrestrial mammals of the same size, even when comparing with terrestrial carnivores, **but lower than similar-sized marine pinnipeds and mustelids**.” With respect, the comparison to terrestrial mammals in the rebuttal letter is irrelevant because terrestrial mammals do not dive. The relevant comparison is across marine mammals. As mentioned previously, the estimated FMR of harbor porpoises (3–4 times higher than the BMR predicted from Kleiber’s equation, Rojano-Doñate et al. 2018) is not high compared to other marine mammals. In addition to the references I mentioned previously, Jeanniard-du-Dot et al. 2017 provides a good review on pinniped FMRs. More importantly, recent results from Rimbach et al. (2021) are more compelling. They present new data on bottlenose dolphin FMRs and an exceptional comparison with other marine mammals, including harbor porpoises (Fig 5, see below). Rimbach et al. 2021, found that harbour porpoises (P. phocoena) spend 14.3% <u>**less energy**</u> than expected for their size, compared to other <u>**marine mammals**</u>. Similar to Rojano-Doñate et al. (2018), Rimbach et al. (2021) also reported that harbor porpoise FMRs are not elevated compared to other marine mammals.

RESEARCH ARTICLE   Journal of Experimental Biology (2021) 224, jeb242218. doi:10.1242/jeb.242218

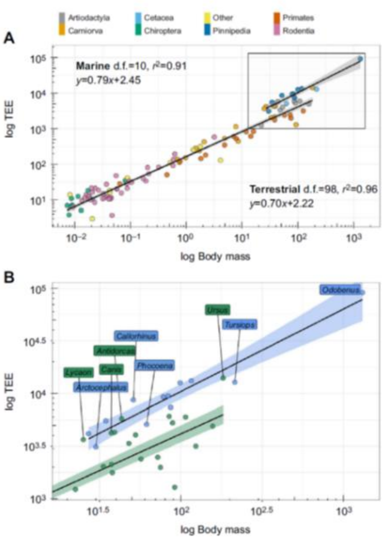


Fig. 5. Body mass and TEE in eutherian mammals. (A) TEE (kcal day^{-1}) versus body mass (kg) for eutherian mammals (*n*=112 species). Separate linear regression lines are presented for terrestrial (*n*=100 species) and marine (*n*=12 species) mammals. Shading represents the 95% CI for the linear regressions. The s.e. is smaller than the symbols for the species. (B) Inset from A in more detail, showing marine mammals in blue and terrestrial mammals in green. Specific taxa of marine and mammals are highlighted to allow inter-specific comparisons.

The point here is, if the low/no reduction in fH for dives within the cADL is “required” to support the “high field metabolic rates” of porpoises, then logic suggests that the harbor porpoise fH response to diving should be prevalent across all marine mammals, including those which are reported to have relatively higher FMRs (for their body size) than porpoises (see Fig 5b, Rimbach et al. 2021). However, as the authors have pointed out, the fH response in harbor porpoises is unlike other marine mammals.

Thus, the proposed link between the heart rate response supporting high metabolic rates is tenuous. If porpoises are not lowering their fH to manage their high metabolic rate, then why are other marine mammals, including pinnipeds and bottlenose dolphins, with similarly high metabolic rates, reducing their fH while diving for longer durations within their cADLs? As mentioned elsewhere by the authors, the short duration dives that can be accomplished on a repetitive basis may serve the role of allowing the harbor porpoises to continuously capture and digest more food. As indicated in my previous review (see Williams et al. 2007), food consumption rates are not necessarily correlated with metabolic rates. In their rebuttal, the authors also mention that "Rojano-Donate et al discuss how food intake increases seasonally even when metabolic rate remains relatively stable so one way they avoid an even higher metabolic rate is by increasing food intake so can increase insulation (blubber)". I agree with this, so again the driver is prey consumption, possibly to build blubber reserves, not necessarily supporting a high metabolic rate, which all marine mammals tend to have. Furthermore, all marine mammals that have insufficient blubber for their environment will also increase their metabolic rates – this is a ubiquitous response. The paper will not suffer from deleting, "The generally high ƒH is likely required to support the high field metabolic rates documented in porpoises [19]." Indeed, by deleting this statement, the paper will not perpetuate an inaccurate interpretation of harbor porpoise FMRs relative to other marine mammals.

References

Jeanniard-du-Dot, T, Trites, AW, Arnould, JPY, Speakman, JR, Guinet, C. Activity-specific metabolic rates for diving, transiting, and resting at sea can be estimated from time–activity budgets in free-ranging marine mammals. *Ecol Evol*. 2017; 7: 2969– 2976. https://doi.org/10.1002/ece3.2546

Bejarano A.C., Wells R.S., Costa D.P. (2017) Development of a bioenergetic model for estimating energy requirements and prey biomass consumption of the bottlenose dolphin Tursiops truncatus. Ecological Modelling 356: 162-172.

Noren D.P. (2011) Estimated field metabolic rates and prey requirements of resident killer whales. Marine Mammal Science 27:60–77.

Rimbach, R, Amireh, A, Allen, A, Hare, B, Guarino, E, Kaufman, C, Salomons, H, Pontzer, H. Total energy expenditure of bottlenose dolphins (Tursiops truncatus) of different ages. J Exp Biol 1 August 2021; 224 (15): jeb242218. doi: https://doi.org/10.1242/jeb.242218

Williams T.M., Rutishauser M., Long B., Fink T., Gafney J., Mostman-Liwanag H., Casper D. 2007. Seasonal variability in otariid energetics: implications for the effects of predators on localized prey resources. Physiological and Biochemical Zoology 80:433-443.