

Linking hunting weaponry to attack strategies in sailfish and striped marlin

M. J. Hansen, S. Krause, M. Breuker, R. H. J. M. Kurvers, F. Dhellemmes, P. E. Viblanc, J. Müller, C. Mahlow, K. Boswell, S. Marras, P. Domenici, A. D. M. Wilson, J. E. Herbert-Read, J. F. Steffensen, G. Fritsch, T. B. Hildebrandt, P. Zaslansky, P. Bach, P. S. Sabarros and J. Krause

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Review timeline

Original submission: 24 September 2019

1st revised submission: 6 December 2019

2nd revised submission: 12 December 2019

Final acceptance: 12 December 2019

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

Review History

RSPB-2019-2228.R0 (Original submission)

Review form: Reviewer 1

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

This study provides novel observations of the feeding behaviour of striped marlin, and comparative analyses to better understand billfish feeding strategies. It was well-written and figures were well-laid-out. Minor edits or comments are provided below:

- In the supplement, provide explanation/support that rostra collected in the Indian Ocean for morphological examination would be similar to rostra used in behavioural observations (in the Gulf of Mexico and in the Pacific Ocean). Do these fish eat the same species in different regions?
- In the discussion, recommend using examples of comparative work with other fishes first, i.e., move lines 310-318 earlier in the section. This paragraph puts the morphological and behavioural results in context, and justifies the switch in parallel construction (other sections always start with behaviour then morphology). In the current lay-out, discussing birds first (line 299), particularly birds that primarily eat a very different prey type (bivalves), distracts from comparative component. The inclusion of oystercatchers as it relates to remodelling makes sense, I just didn't expect this inter-phyla comparison first. Citation in line 301 should only be #3, unless another sentence could be included to relate this trend to billfish (#5).
- Supplement figures were excellent for understanding the morphology and analyses, particularly S2. Only concern is that orange and pink are not colour-blind accessible, and can be difficult to distinguish.

Review form: Reviewer 2

Recommendation

Major revision is needed (please make suggestions in comments)

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

Acceptable

General interest: Is the paper of sufficient general interest?

Acceptable

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

Acceptable

Is the length of the paper justified?

Yes

Should the paper be seen by a specialist statistical reviewer?

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General comments

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Microteeth, this is the first-time billfishes teeth have been described with modern technology, but you don't explain why you think these are teeth, I agree they are but you should briefly state what makes them teeth (pulp cavity, enamel...). Following these lines, you performed a chemical analysis that could help support this idea but this is on the supplementary data and it is not even mentioned on the methods. I think this is relevant and needs to be addressed on the main part of the paper.

Try to specify striped marlin instead of marlin, you go back and forth and is not consistent in addition as you know there are multiple marlin species and it is confusing.

Abstract

L75- how this statement fits the scope of your study? These animals are closely related and the differences are not as clear as in other billfishes' species. How this species differs in their physical environment?

Introduction

L71-Misspelling- specializations, please check all the manuscript as is repeated multiple times. The intro needs work, background data in bill morphology make your case stronger, you based all your hypothesis on that yet there is not a single figure that shows the differences, you have micro CT data, I encourage you to show a good image sets the idea of the paper. See Atkins et al for an example.

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100- I think this statement is not strong and even perhaps contradicts the whole premise of your study, yes they are very similar as they are closely related....can you point strong differences? I'm a bit concerned about the question in this study I respectfully wonder if this question is trying to accommodate a comparison of two billfish species that are most available to study in the field instead of the other way around. You already had sailfish data and striped marlin are the perhaps the other easier species to collect in the field. I think you either need to shift the goal of the study or make a stronger case on why these two species are relevant to be compared.

Please add a phylogenetic tree showing their relationship as well as bill morphologies

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How do you know the chemical composition? You did a whole extra analysis that needs to be noted at least mention it on the methods otherwise the results come unexpected.

Discussion

Your analytical approach is complex but there are some important aspects that are not clear, how do you compensate with neighboring effect, sailfish were way more abundant? How do you compensate for the effect of having a larger number of prey items?

315- you mention how important is to show how morphology affects function and behavior and how is best to do this in the field, yet you are not comparing the most extreme morphologies that are extremely difficult to capture in the field (swordfish). Yes, the field is ideal but you are aware of the limitations, so I think saying this is the best approach to translate form functional complexes in species that almost look alike is not a strong statement. In addition, undermines previous works done in a different setting.

322- you are not making a fair comparison you are trying to compare a swordfish rostra with an istiophorid one, when in reality these two species are much more similar.

343- explain further, why intriguing what do you mean with that?

Please consider additional explanations for these results, what about the vertebral column on this species? Nakamura has described them for all species and as with the rostrum the major differences are between xiphias and istiophorids, however maybe worth it to explore, maybe there are some other explanations for the differences in movement.

Please consider including whole body differences between species, what do you think about the sail in sailfishes? What about spearing behavior? What other factors can support your observations?

Supplementary Fig S2. Orient the reader on the cross sectional area

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In my opinion as the idea of this work stands in a morphological difference among species is much more relevant to see the structures and then you can report the information on your graphs on a table or both.

Decision letter (RSPB-2019-2228.R0)

06-Nov-2019

Dear Dr Hansen:

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.

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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:

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

Use of animals and field studies:

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

Data accessibility and data citation:

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

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

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

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

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

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

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

Associate Editor
Board Member: 1

Comments to Author:

Both reviewers responded with general positivity towards the work and point out several areas for improvement. The second reviewer in particular, brings up interesting questions, including a central concern regarding the confounds and potential trade-offs of studying two such similar species. Addressing these issues directly and thoroughly will increase the impact of the work. The authors should also include more information about how the fish were treated when they were scanned and the efforts the authors made to follow ethical guidelines (ARRIVE/ARROW/Association for the Study of Animal Behaviour/Animal Behavior Society Guidelines for the Use of Animals in Research).

Reviewer(s)' Comments to Author:

Referee: 1

Comments to the Author(s)

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Referee: 2

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Author's Response to Decision Letter for (RSPB-2019-2228.R0)

See Appendix A.

Decision letter (RSPB-2019-2228.R1)

09-Dec-2019

Dear Dr Hansen

I am pleased to inform you that your Review manuscript RSPB-2019-2228.R1 entitled "Linking hunting weaponry to attack strategies in sailfish and striped marlin" has been accepted for publication in Proceedings B.

The referee(s) do not recommend any further changes. 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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It is a condition of publication that data supporting your paper are made available. Data should be made available either in the electronic supplementary material or through an appropriate repository. Details of how to access data should be included in your paper. Please see <https://royalsociety.org/journals/ethics-policies/data-sharing-mining/> for more details.

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

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5) For more information on our Licence to Publish, Open Access, Cover images and Media summaries, please visit <https://royalsociety.org/journals/authors/author-guidelines/>.

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:

As the authors mention, both reviewers found Fig S2 to be of use – would it be possible to include it in the main MS, or are the figure limitations a “hard” rule? Second, my strong preference is for the authors to mention in the main text that “no animals were experimentally manipulated or harmed in anyway” and that for the morphological analyses “scanning was carried out on dead fish that were bycatch of purse-seine fisheries.” In addition to being relevant to the ethical standards of our journal, there is also work showing an association (admittedly not causal) between ethical reporting and citations. In any event, it seems like scientific best practices should be front and center in our articles when possible.

Decision letter (RSPB-2019-2228.R2)

12-Dec-2019

Dear Dr Hansen

I am pleased to inform you that your manuscript entitled "Linking hunting weaponry to attack strategies in sailfish and striped marlin" has been accepted for publication in Proceedings B.

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

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

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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,

Editor, Proceedings B

mailto: proceedingsb@royalsociety.org

Appendix A

Dear Dr Hansen:

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.

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Data accessibility and data citation:

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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](mailto:proceedingsb@royalsociety.org)

Associate Editor

Board Member: 1

Comments to Author:

Both reviewers responded with general positivity towards the work and point out several areas for improvement. The second reviewer in particular, brings up interesting questions, including a central concern regarding the confounds and potential trade-offs of studying two such similar species. Addressing these issues directly and thoroughly will increase the impact of the work. The authors should also include more information about how the fish were treated when they were scanned and the efforts the authors made to follow ethical guidelines (ARRIVE/ARROW/Association for the Study of Animal Behaviour/Animal Behavior Society Guidelines for the Use of Animals in Research).

THANK YOU FOR YOUR CONSIDERATION AND THOUGHTFUL FEEDBACK. WE HAVE ADDRESSED ALL THE REVIEWER COMMENTS BELOW AND MADE ADJUSTMENTS TO OUR TEXT WHERE NECESSARY. WE HAVE INCLUDED MORE DETAILS ON OUR ETHICAL TREATMENT OF ANIMALS IN THE METHODS AS YOU REQUESTED. THE STUDY WAS PERFORMED TO THE ASAB/ABS ETHICAL GUIDELINES. OUR STUDY INVOLVED OBSERVATIONAL FIELDWORK IN A SETTING WHERE THE FISH VOLUNTARILY STAY IN OUR VICINITY IN THE OPEN OCEAN AND ARE FREE TO MOVE ELSEWHERE AT ANY TIME. NO ANIMALS WERE EXPERIMENTALLY MANIPULATED OR HARMED IN ANY WAY. THE SCANNING WAS CARRIED OUT ON DEAD FISH THAT WERE BYCATCH OF PURSE-SEINE FISHERIES (SABARROS PS, CAUQUIL P, DAMIANO A, MOEC E, BACH P. 2005-2015. BYCATCH OF ISTIOPHORIDAE SPECIES IN FRENCH PURSE-SEINE FISHERY IN THE INDIAN OCEAN). OUR DATA IS AVAILABLE AS SUPPLEMENTARY MATERIAL. IF THE JOURNAL REQUIRES IT TO BE UPLOADED TO A SEPARATE REPOSITORY, WE ARE OF COURSE HAPPY TO COMPLY.

Reviewer(s)' Comments to Author:

Referee: 1

Comments to the Author(s)

This study provides novel observations of the feeding behaviour of striped marlin, and comparative analyses to better understand billfish feeding strategies. It was well-written and figures were well-laid-out. Minor edits or comments are provided below:

- In the supplement, provide explanation/support that rostra collected in the Indian Ocean for morphological examination would be similar to rostra used in behavioural observations (in the Gulf of Mexico and in the Pacific Ocean). Do these fish eat the same species in different regions?

AUTHOR RESPONSE: TSAI ET AL. 2014 SHOWED THAT (IN ADDITION TO STRIPED MARLIN AND SAILFISH HAVING COMPARABLE DIETS) THAT SAILFISH IN TWO DIFFERENT REGIONS SHOWED NO DIFFERENCE IN TROPHIC SIGNATURES USING STABLE ISOTOPE ANALYSIS. WE HAVE THIS REFERENCE IN THE SUPPLEMENT ALREADY. DIFFERENCES IN STOMACH CONTENTS IN BILLFISHES HAVE BEEN REPORTED. HOWEVER, IT IS UNKNOWN WHETHER THESE DIFFERENCES REFLECT SEASONAL/ANNUAL AVAILABILITY OF PREY, SMALLER-SCALE SPATIAL HETEROGENEITY, CONSISTENT REGIONAL DIFFERENCES OR OTHER FACTORS. PAPERS THAT HAVE LOOKED AT ROSTRA STRUCTURE OF MARLIN OR SAILFISH FROM DIFFERENT REGIONS DO NOT GIVE ANY EVIDENCE FOR DIFFERENCES WITHIN SPECIES, HOWEVER, THEY DO NOT SPECIFICALLY TEST FOR THIS (NAKAMURA 1983; FIERSTINE & VOIGT 1996).

- In the discussion, recommend using examples of comparative work with other fishes first, i.e., move lines 310-318 earlier in the section. This paragraph puts the morphological and behavioural results in context, and justifies the switch in parallel construction (other sections always start with behaviour then morphology). In the current lay-out, discussing birds first (line 299), particularly birds that primarily eat a very different

prey type (bivalves), distracts from comparative component. The inclusion of oystercatchers as it relates to remodelling makes sense, I just didn't expect this inter-phyla comparison first. Citation in line 301 should only be #3, unless another sentence could be included to relate this trend to billfish (#5).

AUTHOR RESPONSE: THANK YOU FOR THIS RECOMMENDATION, WE HAVE MOVED THE COMPARATIVE WORK WITH FISHES EARLIER AND AGREE THIS IMPROVES THE DISCUSSION.

REMOVED #5, REPLACED WITH #4. THIS WAS A TYPO, WE APOLOGISE

- Supplement figures were excellent for understanding the morphology and analyses, particularly S2. Only concern is that orange and pink are not colour-blind accessible, and can be difficult to distinguish.

AUTHOR RESPONSE: WE HAVE RE-DONE THE WITH THE "TOL" COLOUR SCHEME TO MAKE IT COLOUR-BLIND ACCESSIBLE.

Referee: 2

Comments to the Author(s)
General comments

The work by Hansen et al, attempts to address the idea on how different bill morphologies in billfishes can translate into different feeding behaviors. The publication is generally well written and utilizes a good approach in terms of data analysis, however, I think it is necessary to bring a stronger case on why these two morphologies are needed to be addressed. How do they differ?

Since the entire paper is based on this difference in morphologies, the authors need to build a strong case by showing this clearly (figure and on the text). This needs to be the point of departure. An ideal case would show the differences between swordfishes and a marlin (as done in previous studies) but I'm aware of the limitations associated to test this in the two most extreme anatomical ends of the spectrum (swordfish vs marlin). Nevertheless, if the authors think these two morphologies are different enough to explore how they can translate into possible feeding behaviors the case has to be shown in a stronger context otherwise the rest of the research will not have a strong foundation.

AUTHOR RESPONSE: THANK YOU FOR YOUR CONSIDERED COMMENT. WE HAVE RE-WRITTEN PARTS OF THE INTRODUCTION TO MAKE OUR RATIONALE FOR COMPARING THE TWO SPECIES BEHAVIOURS AND ROSTRAL MORPHOLOGIES. IN PARTICULAR WE NOTE THAT WHILE ISTIOPHORIDAE ROSTRA ARE OF COURSE MORE SIMILAR TO EACH OTHER THAN THEY ARE TO XIPHIIDAE, SEVERAL PAPERS HAVE NOTED DIFFERENCES, INCLUDING NAKAMURA 1983 AND FIERSTINE & VOIGT 1996. THE LATTER NOTED THAT 26/32 OF THE CHARACTERISTICS ROSTRAL CHARACTERISTICS WERE SIGNIFICANTLY DIFFERENT BETWEEN SAILFISH AND STRIPED MARLIN. WE HAVE, HOWEVER, DOWNPLAYED THE BIOMECHANICAL PREDICTIONS WE PREVIOUSLY MADE BASED ON HADEGGER ET AL. 2015 AS WE AGREE WITH YOU THAT THE MORPHOLOGICAL DIFFERENCE BETWEEN THOSE SPECIES WERE EXTREME COMPARED TO THOSE IN OUR STUDY. NONETHELESS, WE BELIEVE THERE IS EVIDENCE FOR MORE SLENDER AND ROUNDER ROSTRA IN SAILFISH COMPARED TO STRIPED MARLIN, AND HAVE PROVIDED REFERENCES.

MOREOVER, DIFFERENCES IN MICROTOOTH MORPHOLOGY HAVE NOT BEEN EXPLORED IN GREAT DETAIL BETWEEN SPECIES OF BILLFISH. FIERSTINE & VOIGT 1996 DO NOTE THAT STRIPED MARLIN HAD A SMALLER AREA OF DENTICLES ON THE DORSAL SURFACE COMPARED TO SAILFISH. WE MENTION THIS IN OUR INTRODUCTION. AS XIPHIIDAE DO NOT HAVE MICRO-TEETH, AND MICROTEETH ARE ABSOLUTELY CENTRAL TO OUR MORPHOLOGICAL ANALYSIS, IT MAKES SENSE TO COMPARE TWO SIMILARLY SIZED ISTIOPHORIDAE.

THE OTHER REASON WE COMPARED THESE TWO SPECIES IS THAT DESPITE MANY SIMILARITIES BETWEEN THE SPECIES, INCLUDING THE FACT THEY BOTH GROUP HUNT SCHOOLS OF PREY FISH, SAILFISH ARE KNOWN TO USE THEIR ROSTRA EXTENSIVELY IN PREY CAPTURE WHILST THERE ARE ANECDOTAL REPORTS THAT STRIPED MARLIN DO NOT (WISNER 1958, HARVERY ET AL. 2000). WE THEREFORE THINK THEY ARE AN APPROPRIATE CHOICE OF SPECIES TO COMPARE BEHAVIOUR AND MORPHOLGY.

WE HAVE INCLUDED A REFERENCE TO FIG S2 HERE IN THE INTRODUCTION AS YOU SUGGEST.

Microteeth, this is the first-time billfishes teeth have been described with modern technology, but you don't explain why you think these are teeth, I agree they are but you should briefly state what makes them teeth (pulp cavity, enamel...). Following these lines, you performed a chemical analysis that could help support this idea but this is on the supplementary data and it is not even mentioned on the methods. I think this is relevant and needs to be addressed on the main part of the paper.

AUTHOR RESPONSE: INCLUDED NEW TEXT ON LINE 91 OF INTRODUCTION AND LINE OF 197-198 of METHODS

Try to specify striped marlin instead of marlin, you go back and forth and is not consistent in addition as you know there are multiple marlin species and it is confusing.

AUTHOR RESPONSE: CHANGED TO STRIPED MARLIN THROUGHOUT

Abstract

L75- how this statement fits the scope of your study? These animals are closely related and the differences are not as clear as in other billfishes' species. How this species differs in their physical environment?

AUTHOR RESPONSE: THE SENTENCE YOU REFER TO HERE WAS POORLY WORDED BY US AND THEREFORE HAS BEEN MISINTERPRETED. THIS IS OUR FAULT AND, REGARDLESS, WE HAVE REMOVED IT FROM THE NEW VERSION OF THE MANUSCRIPT. WE WERE NOT ACTUALLY REFERRING TO THE DIFFERENCES IN PHYSICAL ENVIRONMENT THAT EITHER SPECIES' INHABITS, BUT RATHER THAT THEY BOTH LIVE IN THE SAME OPEN WATER PELAGIC ENVIRONMENT, WHICH MAY EMBODY INTERESTING AND UNIQUE SELECTIVE PRESSURES

Introduction

L71-Misspelling- specializations, please check all the manuscript as is repeated multiple times

AUTHOR RESPONSE: CHANGED

The intro needs work, background data in bill morphology make your case stronger, you based all your hypothesis on that yet there is not a single figure that shows the differences, you have micro CT data, I encourage you to show a good image sets the idea of the paper. See Atkins et al for an example.

AUTHOR RESPONSE: PLEASE SEE ABOVE RESPONSE DETAILING CHANGES MADE TO INTRODUCTION AND REFERENCE TO MICRO-CT IMAGES IN FIG S2 F, G.

Your references need work, pioneer people like Nakamura are not listed. Fierstine has published in billfishes more than anybody else and I only see one paper cited.

AUTHOR RESPONSE: YES, THESE UNFORTUNATELY WERE REMOVED DURING THE INITIAL EDITING PROCESS BUT WE HAVE NOW RE-INCLUDED NAKAMURA 1983, 1985 and FIERSTINE et al. 1997

L81- misspelling defense

AUTHOR RESPONSE: PRSB REQUIRES BRITISH SPELLING FROM OXFORD DICTIONARY. WE BELIEVE DEFENCE WITH A 'C' IS CORRECT. BUT WILL LET THE EDITOR DECIDE.

L81- please cite other literature that supports this idea, your previous study is not the only one.

AUTHOR RESPONSE: WE HAVE RE-WORDED THE SENTENCE STARTING ON LINE 80 TO ALSO INCLUDE HADEGGER ET AL 2015.

100- I think this statement is not strong and even perhaps contradicts the whole premise of your study, yes they are very similar as they are closely related...can you point strong differences? I'm a bit concerned about the question in this study I respectfully wonder if this question is trying to accommodate a comparison of two billfish species that are most available to study in the field instead of the other way around. You already had sailfish data and striped marlin are the perhaps the other easier species to collect in the field. I think you either need to shift the goal of the study or make a stronger case on why these two species are relevant to be compared.

Please add a phylogenetic tree showing their relationship as well as bill morphologies

AUTHOR RESPONSE: WE HAVE REVISED THIS SECTION TO BETTER REFLECT THE RATIONALE OF OUR STUDY.

IN REGARD TO A PHYLOGENETIC TREE, WE HAVE COLLECTED NO DATA ON PHYLOGENETIC RELATIONSHIPS, AND WE HAVE NOTHING SUBSTANTIAL TO ADD TO THIS AREA OF RESEARCH AND MAKE NO NEW CLAIMS. WE THEREFORE CANNOT SEE THE VALIDITY OF INCLUDING A PHYLOGENETIC TREE. THERE ARE OTHER STUDIES THAT SPECIFICALLY EXPLORE THE PHYLOGENETIC RELATIONSHIP BETWEEN BILLFISHES AND WE CITED THEM IN OUR ORIGINAL SUBMISSION. E.G. COLETTE ET AL. 2006.

108- ok based on that, bring up the idea of swordfish why do you think that, there is already evidence for that

AUTHOR RESPONSE: WE HAVE PREVIOUSLY REFERENCED HABEGGER ET AL. 2015 AND SWORDFISH. WE APOLOGISE FOR NOT REFERENCING IT AGAIN HERE BUT THOUGHT IT WAS OBVIOUS. REGARDLESS, WE HAVE REMOVED THIS SENTENCE FROM THE NEW MS.

It is not clear how many NEW animals this study has and also if the sailfish data is new or an older dataset, please clarify. Also, please make sure to define you "n" number. Are these schools, animals?

AUTHOR RESPONSE: ALL OF THE STRIPED MARLIN DATA IS NEW. IN TERMS OF SAILFISH, WE UTILISED SOME OF THE SAME VIDEOS THAT WERE AVAILABLE FROM PREVIOUS STUDIES HOWEVER WE RE-ANALYSED THEM AS WE HAD TO DEFINE THE STATES OF THE MARKOV CHAIN DIFFERENTLY FOR A SPECIES COMPARISON. IN THE PROCESS WE ALSO ANALYSED SAILFISH ATTACKS THAT WERE NEVER PUBLISHED IN PREVIOUS WORK.

WE ARE UNSURE OF WHAT N NUMBER YOU ARE REFERRING TO HERE, HOWEVER, WE HAVE MADE AN EFFORT TO GO THROUGHOUT THE MANUSCRIPT AND MAKE IT OBVIOUS WHAT THE REPLICATE IS.

WE SAY N 'SCHOOLS' ON LINE 138 AND 167

LINE 188 AND 189 WE SAY 'ROSTRA'
Line 227 WE SAY 'SECTIONS'
LINE 155 AND 166 AND 175 WE HAVE ADDED 'ATTACK SEQUENCES'

How do you know the chemical composition? You did a whole extra analysis that needs to be noted at least mention it on the methods otherwise the results come unexpected.

AUTHOR RESPONSE: WE ARE UNCLEAR TO WHAT SECTION OF THE MANUSCRIPT YOU ARE REFERRING TO.

ON LINE 91 OF THE INTRODUCTION WE HAVE NOW MENTIONED THAT THE MICROTEETH ARE "TRUE TEETH COMPOSED OF AN ORGANIC PULP CAVITY AND ENAMEL CAP" AND REFER THE READER TO THE SUPPLEMENTARY MATERIALS AND FIG S2 FOR MORE DETAILS.

WE DIDN'T REFER TO THE ANALYSIS IN THE METHODS SECTION AS THE COMPOSITION OF THE MICROTEETH IS NOT CENTRAL TO THIS MANUSCRIPT. HOWEVER, WE HAVE ADDED A LINE (LINE 197) TO REFER TO THE READER AGAIN TO THE SUPPLEMENTARY MATERIAL IF THEY ARE INTERESTED IN THE CHEMICAL COMPOSITION.

ON LINE 277 WE ALSO REFER THE READER TO THE SUPPLEMENTARY MATERIALS

WE HOPE THAT YOU FIND THIS SUFFICIENT

Discussion

Your analytical approach is complex but there are some important aspects that are not clear, how do you compensate with neighboring effect, sailfish were way more abundant?

AUTHOR RESPONSE: WE DO NOT THINK SAILFISH WERE WAY MORE ABUNDANT. UNFORTUNATELY, WE COULD ONLY APPROXIMATE GROUP SIZES FOR EITHER BILLFISH SPECIES. IT WAS NOT POSSIBLE TO SAY HOW MANY NEIGHBOURS WERE PRESENT FOR EACH ATTACK OR HOW CLOSE THEY WERE TO THE FOCAL ATTACKER. HOWEVER, WE BELIEVE GROUP SIZES WERE COMPARABLE BETWEEN SPECIES (6-40 FOR SAILFISH AND 12-40 FOR STRIPED MARLIN)

How do you compensate for the effect of having a larger number of prey items?

AUTHOR RESPONSE: UNFORTUNATELY, WE DO NOT HAVE THE PREY NUMBERS FOR EACH ATTACK. WE HAVE APPROXIMATIONS OF THE BAITBALL SIZES THAT THE TWO BILLFISH SPECIES ATTACKED. 25-150 SARDINES FOR THE SAILFISH AND 50-200 SARDINES FOR STRIPED MARLIN. IN THE CONTEXT OF POSSIBLE BAITBALL SIZES IN NATURE, THESE ARE VERY SIMILAR, AND THEREFORE COMPARABLE.

315- you mention how important is to show how morphology affects function and behavior and how is best to do this in the field, yet you are not comparing the most extreme morphologies that are extremely difficult to capture in the field (swordfish). Yes, the field is ideal but you are aware of the limitations, so I think saying this is the best approach to translate form functional complexes in species that almost look alike is not a strong statement. In addition, undermines previous works done in a different setting.

AUTHOR RESPONSE: WE ARE NOT INTERESTED IN THE COMPARISON BETWEEN SAILFISH AND SWORDFISH FEEDING BEHAVIOUR. THEY HAVE VERY DIFFERENTLY SHAPED ROSTRA (SWORDFISH DO NOT EVEN HAVE MICROTEETH AND THAT IS AN ANALYSIS CENTRAL TO OUR STUDY). ALSO, TO THE BEST OF OUR KNOWLEDGE THEY HUNT DIFFERENT PREY. THE TWO SPECIES WE STUDIED BOTH GROUP HUNT SCHOOLING FISH AT THE OCEAN'S SURFACE, AND YET, AS WELL AS HAVING DIFFERENTLY SHAPED BILLS, THERE ARE

ALSO REPORTS THAT ONE SPECIES BUT NOT THE OTHER USES THEIR BILL TO CAPTURE PREY. WE THEREFORE WANTED TO ASSESS WHETHER THERE WAS A DIFFERENCE IN THE WAY THEY HUNTED THIS SIMILAR PREY AND WHETHER THE DISTRIBUTION OF MICROTEETH WAS IN ANY WAY INFORMATIVE OF THESE POTENTIAL DIFFERENCES.

WE DO BELIEVE THAT COMBINING HIGH RESOLUTION VIDEO OF REAL ATTACKS FROM THE FIELD WITH MORPHOLOGICAL WORK IS A PROMISING APPROACH. HOWEVER, IN LINE WITH YOUR SUGGESTION WE HAVE TONED DOWN THE LANGUAGE WE USED. OUR INTENTION WAS NEVER TO UNDERMINE PREVIOUS WORK DONE IN A DIFFERENT SETTING. WE THINK WE HAVE ADDED TO THIS WORK AND TOGETHER HELPED FORM A BETTER COLLECTIVE UNDERSTANDING OF FORM AND FUNCTION OF BILLFISH ROSTRA.

322- you are not making a fair comparison you are trying to compare a swordfish rostra with an istiophorid one, when in reality these two species are much more similar.

AUTHOR RESPONSE: WE HAVE REMOVED THIS FROM THE MANUSCRIPT. WE DO TALK ABOUT HADEGGER ET AL. 2015 IN THE DISCUSSION ON LINE 341, BUT MOSTLY AS RATIONALE THAT BIOMECHANICS ARE PROBABLY NOT A REASON WHY THE SPECIES USE THEIR BILL DIFFERENTLY, AS THE DIFFERENCES WITHIN ISTIOPORIDAE ARE NOT ANYWHERE AS EXTREME AS BETWEEN ISTIOPORIDAE AND XIPHIIDAE.

343- explain further, why intriguing what do you mean with that?

AUTHOR RESPONSE: WE THINK IT IS INTERESTING THAT THE SPECIES WITH THE LOWEST RELATIVE BITE FORCE ALSO USES ITS BILL THE MOST AS IT CAN BE SEEN AS A FORM OF FOOD HANDLING OR COMPENSATORY FEEDING STRUCTURE. THIS IS MENTIONED IN THE INTRODUCTION. IF SAILFISH USE THEIR BILL MORE FOR FOOD CAPTURE THEY WILL BE MOUTHING WEAKER AND ALREADY DAMAGED PREY. MARLIN USE THEIR BILL LESS, AND HAVE A STRONGER RELATIVE BITE FORCE, LIKELY BECAUSE THEY NEED TO HANDLE STRONGER, UNINJURED PREY.

WE HAVE MADE SOME ADDITIONS TO THE TEXT IN THE DISCUSSION TO MAKE THIS CLEARER TO THE READER.

Please consider additional explanations for these results, what about the vertebral column on this species? Nakamura has described them for all species and as with the rostrum the major differences are between xiphias and istiophorids, however maybe worth it to explore, maybe there are some other explanations for the differences in movement.

Please consider including whole body differences between species, what do you think about the sail in sailfishes? What about spearing behavior? What other factors can support your observations?

AUTHOR RESPONSE: WE THANK THE REFEREE FOR THESE COMMENTS. WE HAVE AMENDED THE TEXT IN THE DISCUSSION AND ADDED VARIOUS CONSIDERATIONS.

A NUMBER OF BODY DESIGN DIFFERENCES BETWEEN SAILFISH AND STRIPED MARLIN ARE IN ACCORDANCE WITH THE OBSERVED DIFFERENCES IN THEIR HUNTING BEHAVIOUR, I.E. HIGH OCCURRENCE OF IN-LINE DASHING IN STRIPED MARLIN VS. HIGH OCCURRENCE OF MANOEUVRING AND SLASHING WITH THE BILL IN SAILFISH.

(1) THE THIN, ROUNDED SHAPE OF THE SAILFISH ROSTRUM MAY BE RELATED TO VISUAL OR TACTILE CAMOUFLAGE, ALLOWING IT TO BE INSERTED INTO THE SARDINE SHOAL WITHOUT THE PREY DISPERSING (DOMENICI 2015), AND FOLLOWED BY A SLASH. THE STRIPED MARLIN BILL IS STOUTER AND MORE Laterally COMPRESSED (NAKAMURA 1983, FIERSTINE & VOIGT 1996).

(2) SAILFISH HAVE A MUCH LARGER DORSAL FIN THAN STRIPED MARLIN (NAKAMURA 1983), WHICH IS EXTENDED DURING FORAGING AND MANOEUVRING (DOMENICI ET AL

2014). IT IS KNOWN THAT LARGE VERTICAL SURFACES SUCH AS EXTENDED DORSAL FINs, CAN PROVIDE CONTROL SURFACES THAT MAXIMIZE MANOEUVRABILITY (LAUDER AND DRUCKER 2004 . IEEE J OCEAN ENG 29:556-71). FURTHERMORE, THE LARGE DORSAL FIN OF THE SAILFISH CAN PROVIDE A CONTROL SURFACE THAT MINIMIZES THE YAW OF THE BILL WHILE SWIMMING BEHIND A SCHOOL OF PREY, THUS MINIMIZING DISTURBANCE PRIOR TO SLASHING (DOMENICI ET AL 2014; MARRAS ET AL 2015) AND AID IN RESISTING LATERAL FORCES IN THE OPPOSITE DIRECTION OF THE SLASH, THUS INCREASING ITS EFFECTIVENESS (MARRAS ET AL 2015). ON THE OTHER HAND, A LARGE DORSAL FIN WOULD NOT BE ADVANTAGEOUS BECAUSE OF THE INCREASED DRAG DURING FAST IN-LINE DASHING SUCH AS THOSE USED BY STRIPED MARLIN.

(3) THE CROSS-SECTIONAL AREA OF SAILFISH IS MORE Laterally COMPRESSED THAN THAT OF STRIPED MARLIN (MAX. DEPTH/WIDTH AT ORIGIN OF FIRST ANAL FIN: 1.45 AND 2.16 FOR STRIPED MARLIN AND SAILFISH, RESPECTIVELY CALCULATED BASED ON NAKAMURA 1983). LATERAL COMPRESSION IS ASSOCIATED WITH HIGH LATERAL FLEXIBILITY (ALEEV, Y. G. 1969. FUNCTION AND GROSS MORPHOLOGY IN FISH. KETER PRESS, JERUSALEM), THUS A POTENTIALLY HIGHER MANOEUVRABILITY (E.G. IN TERMS OF TURNING RADIUS AND TURNING RATE, DOMENICI 2001 COMPARATIVE BIOCHEMISTRY AND PHYSIOLOGY PART A: MOLECULAR & INTEGRATIVE PHYSIOLOGY. 131: 169-82) IN SAILFISH AS OPPOSED TO A ROUNDER (THUS LESS FLEXIBLE) BODY SUCH AS THAT OF STRIPED MARLIN, IN ACCORDANCE WITH THEIR IN-LINE DASHING WHILE FEEDING.

IN REGARDS TO VERTEBRAE, WE WOULD NOT LIKE TO SPECULATE. INDEED STRIPED MARLIN HAVE WIDER VERTEBRAE (SINCE THEY ARE THICKER Laterally), AND DIFFERENT SHAPED NEURAL SPINES COMPARED TO SAILFISH BUT IT IS NOT EASY TO RELATE THESE DIFFERENCES TO SWIMMING STYLE OR PERFORMANCE.

THERE WERE VERY FEW SPEARING EVENTS, OUR PERSONAL OBSERVATIONS ARE THAT THESE ARE MORE COMMON ON LARGER PREY FISH, E.G. MACKEREL.

Supplementary Fig S2. Orient the reader on the cross-sectional area

AUTHOR RESPONSE: FIG 2 F AND G ARE THE TWO CROSS SECTIONS AND THEY HAVE THE CROSS-SECTIONAL POSITIONS NAMED IN THE FIGURE CAPTION

IT IS POSSIBLE THAT YOU WERE CONFUSED BY THE TWO IMAGES IN FIG 2C. THE COLOUR MESH ONE HAS NOW BEEN REMOVED SO THERE SHOULD BE NO FURTHER CONFUSION. 2C IS SIMPLY A RANDOM SECTION OF ROSTRA SURFACE. IT DOES NOT DIRECTLY RELATE TO 2A OR 2B

Not sure if this should be part of the supplementary data, I think you have a lot of valuable info here. I'm also not sure on what you are trying to show in A and B, please show the reader exactly where those points are in the cross section. It is not easy to understand

This graph collapsed a lot of info, can you just separate them?

AUTHOR RESPONSE: WE WILL BE HAPPY TO SEPARATE FIG2C IN ANY WAY THE EDITOR DEEMS REASONABLE. FOR EXAMPLE, WE COULD HAVE FIG 2A AND B TOGETHER AND FIG2 C-K TOGETHER IN TWO SEPARATE FIGURES?

WE ARE ALSO HAPPY TO PUT ALL OF FIG S2 OR PARTS OF IT IN THE MAIN DOCUMENT, HOWEVER, WE WERE CONCERNED ABOUT JOURNAL SPACE REQUIREMENTS.

FIG S2 A AND B ARE DESCRIBED IN THE FIGURE AND ITS CAPTION.

THE CAPTION READS... SUPPLEMENTARY FIG 2. "EXAMPLES OF MICRO-CT OVERVIEW IMAGES DISPLAYING THE POSITIONS OF ALL MICRO-TEETH MEASURED ON THE ROSTRUM, COLOURED BY MICRO-TEETH TYPE, FOR ONE A.) SAILFISH, AND B.) STRIPED MARLIN SPECIMEN. GREEN DOTS/ARROWS REPRESENT INTACT MICRO-TEETH, PINK DOTS/ARROWS REPRESENT BROKEN MICRO-TEETH AND YELLOW DOTS/ARROWS REPRESENT RE-GROWING MICRO-TEETH IN ALL IMAGES. THE X-AXIS (H MM) REPRESENTS THE DISTANCE FROM BILL TIP (0 ON THE FAR LEFT) TOWARDS THE HEAD (50 ON THE FAR RIGHT). THE Y-

AXIS AND PURPLE LINES SHOW THE ANGULAR POSITION OF THE MICRO-TEETH IN DEGREES FROM THE ROLL-AXIS OF THE ROSTRUM. 0° IS THE DEXTRAL SIDE, 90° IS THE DORSAL SIDE, 180° IS THE SINISTRAL SIDE AND 270° IS THE VENTRAL SIDE..."

WE THINK MAYBE YOU ARE CONFUSED BY OUR WORDING FOR C.) „MICRO-TEETH LABELLED IN TWO 3D COMPUTER VISUALISATIONS OF THE SAME SECTION, LEFT: VOLUME RENDERING AND RIGHT: AS COLOURED MESH."

THAT THE TWO SECTIONS ON DISPLAY IN 2C ARE THE SAME SECTION, BUT THE LEFT IS VOLUME RENDERED AND THE RIGHT IS COLOURED MESH.

UPON RE-READING WE UNDERSTAND THIS IS CONFUSING, THEREFORE WE WE HAVE CHANGED THIS TO READ... „C.) 3D COMPUTER VISUALISATION WITH VOLUME RENDERING OF A RANDOM SECTION OF ROSTRA SURFACE DISPLAYING MICRO-TEETH"

WE HAVE ONLY USED ONE IMAGE FOR FIG 2 C NOW BECAUSE I.) WE WISH TO AVOID FURTHER CONFUSION, AND II.) THE COLOUR MESH WILL BE TOO DIFFICULT FOR COLOUR-BLIND PEOPLE TO DISTINGUISH.

In my opinion as the idea of this work stands in a morphological difference among species is much more relevant to see the structures and then you can report the information on your graphs on a table or both.

AUTHOR RESPONSE: WE HAVE REFERENCED THE KNOWN MORPHOLOGICAL DIFFERENCES IN ROSTRA IN THE INTRODUCTION AND ALSO REFERRED THE READER TO THE SUPPLEMENTARY MATERIAL SO THEY CAN SEE FIG S2 AS WE UNDERSTAND THAT MAY HELP SOME READERS.

HOWEVER, A MAJOR PART OF THE MS IS TO ASSESS WHETHER THERE IS A MORPHOLOGICAL DIFFERENCE AMONG SPECIES IN TERMS OF THEIR MICROTEETH. WE DON'T THINK IT IS LOGICAL TO PUT OUR RESULTS IN THE INTRODUCTION AS THE REASON WE DID THE WORK.