THE ROYAL SOCIETY
PUBLISHING

ROYAL SOCIETY
OPEN SCIENCE

A ctenophore (comb jelly) employs vortex rebound dynamics and outperforms other gelatinous swimmers

Brad J. Gemmell, Sean P. Colin, John H. Costello and Kelly R. Sutherland

Article citation details
R. Soc. open sci. **6**: 181615.
http://dx.doi.org/10.1098/rsos.181615

Review timeline
Original submission: 16 October 2018
Revised submission: 30 January 2019
Final acceptance: 31 January 2019

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

Note: This manuscript was transferred from another Royal Society journal without peer review.

Review History

RSOS-181615.R0 (Original submission)

Review form: Reviewer 1

Is the manuscript scientifically sound in its present form?
Yes

Are the interpretations and conclusions justified by the results?
Yes

Is the language acceptable?
Yes

Is it clear how to access all supporting data?
Yes

Do you have any ethical concerns with this paper?
No

Have you any concerns about statistical analyses in this paper?
No

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

Comments to the Author(s)
Please find attached my review of the paper "A ctenophore (comb jelly) employs vortex rebound dynamics and outperforms other gelatinous swimmers" for consideration for publication in Royal Society Open Science. In this paper, the authors use particle image velocimetry to quantify the propulsive flows generated by the ctenophore Ocyropsis. In particular, the authors consider swimming mode in which the lobes of the comb jelly are "rowed" (in addition to any flows generated by the ciliary plates). They find that during the escape mode, this come jellyfish can reach dimensionless speeds nearly double that of other gelatinous animals. The fluid dynamic mechanism behind the swimming behavior appears to be representative of a vortex rebound mechanism. Comparisons are made to the jellyfish A. aurita which also uses a rowing or paddling mode of propulsion that seems similar to the comb jellyfish escape swimming mode. Interesting differences in contraction kinematics and the resulting wake can be seen, however, which explain the difference in swimming speeds. The experimental work in the paper is of solid quality, the results are clearly presented, and the work should be of broad interest to the biomechanics and biofluids communities.

Minor comments
1) It is stated in the abstract and the discussion that the results might inform the bio-inspired design of propulsive systems. Some elaboration on this point seems worthwhile.
2) Figure 3 and Supplemental Figure 1 use a very similar color map for the vorticity and for the velocity vectors. It would be preferable to use some other color scheme. It is very difficult to see the velocity vectors in Figure 3.
3) Additional discussion of the flows generated by the ciliary plates would help contrast the escape mode from other propulsive modes in this species and other comb jellyfish. It is likely worth explaining further that these are ciliary fused plates rather than individually spinning cilia.

Review form: Reviewer 2

Is the manuscript scientifically sound in its present form?
Yes

Are the interpretations and conclusions justified by the results?
Yes

Is the language acceptable?
Yes

Is it clear how to access all supporting data?
Yes

Do you have any ethical concerns with this paper?
No

Have you any concerns about statistical analyses in this paper?
No

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

Comments to the Author(s)
Major;

None

Minor;

-In the introduction the authors consistently talk about the highly efficient of swimming in certain medusa, I would like to see some values included to give this claim of efficiency some context.

-Pg. 7, Line 15 appears to be missing 'of the'.

-Pg. 7, Line 38; 'newly forming starting vortex as while the stopping vortex remained', sounds odd, consider revising.

-Pg.7, Line 56; 'in' should be 'it'.

- How did the authors measure body length for the individual species? What size were the animals that the proficiency measurements were being compared to?

-The comparison to other gelatinous swimmers is valid and interesting, however, I think that more context needs to be given to the different types of propulsion system being looked at. i.e, Ocyropsis may well have a maximum normalised body speed of twice that of Stomolophus meleagris, but ecologically speaking they are completely different locomotor modes, with one being an escape response and one being a continuous cruising style of swimming. I understand the authors are looking at proficiency, but I feel as the manuscript is written now it is hard to know which species are cruisers and which are an escape swim. Something as simple as an extra line in the figure legend would help clarify this.

- In the discussion the authors talk about the increased range of motion in O. maculate being bought about by increased muscle fibre layers. Have the authors considered how changes in the material properties of the mesoglea might affect the range of motion achievable in these species?

-How does the musculature compare between Ocyropsis and other ctenophores that do not perform these escape swims?

-In the videos of the swims the animals often appear very close the wall of the aquarium, are the authors confident this did not affect the measurements?

-As a reader I would also be keen to see a video showing multiple swimming strokes at normal speed.

Decision letter (RSOS-181615.R0)

04-Jan-2019

Dear Dr Gemmell

On behalf of the Editors, I am pleased to inform you that your Manuscript RSOS-181615 entitled "A ctenophore (comb jelly) employs vortex rebound dynamics and outperforms other gelatinous swimmers" has been accepted for publication in Royal Society Open Science subject to minor revision in accordance with the referee suggestions. Please find the referees' comments at the end of this email.

The reviewers and handling editors have recommended publication, but also suggest some minor revisions to your manuscript. Therefore, I invite you to respond to the comments and revise your manuscript.

• Ethics statement
If your study uses humans or animals please include details of the ethical approval received, including the name of the committee that granted approval. For human studies please also detail whether informed consent was obtained. For field studies on animals please include details of all permissions, licences and/or approvals granted to carry out the fieldwork.

• Data accessibility
It is a condition of publication that all supporting data are made available either as supplementary information or preferably in a suitable permanent repository. The data accessibility section should state where the article's supporting data can be accessed. This section should also include details, where possible of where to access other relevant research materials such as statistical tools, protocols, software etc can be accessed. If the data has been deposited in an external repository this section should list the database, accession number and link to the DOI for all data from the article that has been made publicly available. Data sets that have been deposited in an external repository and have a DOI should also be appropriately cited in the manuscript and included in the reference list.

If you wish to submit your supporting data or code to Dryad (http://datadryad.org/), or modify your current submission to dryad, please use the following link:
http://datadryad.org/submit?journalID=RSOS&manu=RSOS-181615

• Competing interests
Please declare any financial or non-financial competing interests, or state that you have no competing interests.

• Authors’ contributions
All submissions, other than those with a single author, must include an Authors’ Contributions section which individually lists the specific contribution of each author. The list of Authors should meet all of the following criteria; 1) substantial contributions to conception and design, or acquisition of data, or analysis and interpretation of data; 2) drafting the article or revising it critically for important intellectual content; and 3) final approval of the version to be published.

All contributors who do not meet all of these criteria should be included in the acknowledgements.

We suggest the following format:

AB carried out the molecular lab work, participated in data analysis, carried out sequence alignments, participated in the design of the study and drafted the manuscript; CD carried out the statistical analyses; EF collected field data; GH conceived of the study, designed the study, coordinated the study and helped draft the manuscript. All authors gave final approval for publication.

• Acknowledgements
Please acknowledge anyone who contributed to the study but did not meet the authorship criteria.

• Funding statement
Please list the source of funding for each author.

Please note that we cannot publish your manuscript without these end statements included. We have included a screenshot example of the end statements for reference. If you feel that a given heading is not relevant to your paper, please nevertheless include the heading and explicitly state that it is not relevant to your work.

Because the schedule for publication is very tight, it is a condition of publication that you submit the revised version of your manuscript before 13-Jan-2019. Please note that the revision deadline will expire at 00.00am on this date. If you do not think you will be able to meet this date please let me know immediately.

To revise your manuscript, log into https://mc.manuscriptcentral.com/rsos and enter your Author Centre, where you will find your manuscript title listed under "Manuscripts with Decisions". Under "Actions," click on "Create a Revision." You will be unable to make your revisions on the originally submitted version of the manuscript. Instead, revise your manuscript and upload a new version through your Author Centre.

When submitting your revised manuscript, you will be able to respond to the comments made by the referees and upload a file "Response to Referees" in "Section 6 - File Upload". You can use this to document any changes you make to the original manuscript. In order to expedite the processing of the revised manuscript, please be as specific as possible in your response to the referees. We strongly recommend uploading two versions of your revised manuscript:

1) Identifying all the changes that have been made (for instance, in coloured highlight, in bold text, or tracked changes);
2) A 'clean' version of the new manuscript that incorporates the changes made, but does not highlight them.

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

1) A text file of the manuscript (tex, txt, rtf, docx or doc), references, tables (including captions) and figure captions. Do not upload a PDF as your "Main Document";
2) A separate electronic file of each figure (EPS or print-quality PDF preferred (either format should be produced directly from original creation package), or original software format);
3) Included a 100 word media summary of your paper when requested at submission. Please ensure you have entered correct contact details (email, institution and telephone) in your user account;
4) Included the raw data to support the claims made in your paper. You can either include your data as electronic supplementary material or upload to a repository and include the relevant doi within your manuscript. Make sure it is clear in your data accessibility statement how the data can be accessed;

5) All supplementary materials accompanying an accepted article will be treated as in their final form. Note that the Royal Society will neither edit nor typeset supplementary material and it will be hosted as provided. Please ensure that the supplementary material includes the paper details where possible (authors, article title, journal name).

Supplementary files will be published alongside the paper on the journal website and posted on the online figshare repository (https://rs.figshare.com/). The heading and legend provided for each supplementary file during the submission process will be used to create the figshare page, so please ensure these are accurate and informative so that your files can be found in searches. 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 note that Royal Society Open Science charge article processing charges for all new submissions that are accepted for publication. Charges will also apply to papers transferred to Royal Society Open Science from other Royal Society Publishing journals, as well as papers submitted as part of our collaboration with the Royal Society of Chemistry (http://rsos.royalsocietypublishing.org/chemistry).

If your manuscript is newly submitted and subsequently accepted for publication, you will be asked to pay the article processing charge, unless you request a waiver and this is approved by Royal Society Publishing. You can find out more about the charges at http://rsos.royalsocietypublishing.org/page/charges. Should you have any queries, please contact openscience@royalsociety.org.

Once again, thank you for submitting your manuscript to Royal Society Open Science and I look forward to receiving your revision. If you have any questions at all, please do not hesitate to get in touch.

Kind regards,
Andrew Dunn
Royal Society Open Science Editorial Office
Royal Society Open Science
openscience@royalsociety.org

on behalf of Professor Brooke Flammang (Associate Editor) and Kevin Padian (Subject Editor)
openscience@royalsociety.org

Associate Editor Comments to Author (Professor Brooke Flammang):

Both reviewers find this manuscript to be a significant contribution and suggest minor edits for clarification. Please incorporate their suggestions into your revision.

Reviewer comments to Author:
Reviewer: 1

Comments to the Author(s)
Please find attached my review of the paper "A ctenophore (comb jelly) employs vortex rebound dynamics and outperforms other gelatinous swimmers" for consideration for publication in Royal Society Open Science. In this paper, the authors use particle image velocimetry to quantify the propulsive flows generated by the ctenophore Ocyropsis. In particular, the authors consider swimming mode in which the lobes of the comb jelly are "rowed" (in addition to any flows

generated by the ciliary plates). They find that during the escape mode, this come jellyfish can reach dimensionless speeds nearly double that of other gelatinous animals. The fluid dynamic mechanism behind the swimming behavior appears to be representative of a vortex rebound mechanism. Comparisons are made to the jellyfish A. aurita which also uses a rowing or paddling mode of propulsion that seems similar to the comb jellyfish escape swimming mode. Interesting differences in contraction kinematics and the resulting wake can be seen, however, which explain the difference in swimming speeds. The experimental work in the paper is of solid quality, the results are clearly presented, and the work should be of broad interest to the biomechanics and biofluids communities.

Minor comments
1) It is stated in the abstract and the discussion that the results might inform the bio-inspired design of propulsive systems. Some elaboration on this point seems worthwhile.
2) Figure 3 and Supplemental Figure 1 use a very similar color map for the vorticity and for the velocity vectors. It would be preferable to use some other color scheme. It is very difficult to see the velocity vectors in Figure 3.
3) Additional discussion of the flows generated by the ciliary plates would help contrast the escape mode from other propulsive modes in this species and other comb jellyfish. It is likely worth explaining further that these are ciliary fused plates rather than individually spinning cilia.

Reviewer: 2

Comments to the Author(s)
Major;

None

Minor;

-In the introduction the authors consistently talk about the highly efficient of swimming in certain medusa, I would like to see some values included to give this claim of efficiency some context.

-Pg. 7, Line 15 appears to be missing 'of the'.

-Pg. 7, Line 38; 'newly forming starting vortex as while the stopping vortex remained', sounds odd, consider revising.

-Pg.7, Line 56; 'in' should be 'it'.

- How did the authors measure body length for the individual species? What size were the animals that the proficiency measurements were being compared to?

-The comparison to other gelatinous swimmers is valid and interesting, however, I think that more context needs to be given to the different types of propulsion system being looked at. i.e, Ocyropsis may well have a maximum normalised body speed of twice that of Stomolophus meleagris, but ecologically speaking they are completely different locomotor modes, with one being an escape response and one being a continuous cruising style of swimming. I understand the authors are looking at proficiency, but I feel as the manuscript is written now it is hard to know which species are cruisers and which are an escape swim. Something as simple as an extra line in the figure legend would help clarify this.

- In the discussion the authors talk about the increased range of motion in O. maculate being bought about by increased muscle fibre layers. Have the authors considered how changes in the material properties of the mesoglea might affect the range of motion achievable in these species?

-How does the musculature compare between Ocyropsis and other ctenophores that do not perform these escape swims?

-In the videos of the swims the animals often appear very close the wall of the aquarium, are the authors confident this did not affect the measurements?

-As a reader I would also be keen to see a video showing multiple swimming strokes at normal speed.

Author's Response to Decision Letter for (RSOS-181615.R0)

See Appendix A.

Decision letter (RSOS-181615.R1)

31-Jan-2019

Dear Dr Gemmell,

I am pleased to inform you that your manuscript entitled "A ctenophore (comb jelly) employs vortex rebound dynamics and outperforms other gelatinous swimmers" is now accepted for publication in Royal Society Open Science.

You can expect to receive a proof of your article in the near future. Please contact the editorial office (openscience_proofs@royalsociety.org and openscience@royalsociety.org) to let us know if you are likely to be away from e-mail contact. Due to rapid publication and an extremely tight schedule, if comments are not received, your paper may experience a delay in publication.

Royal Society Open Science operates under a continuous publication model (http://bit.ly/cpFAQ). Your article will be published straight into the next open issue and this will be the final version of the paper. As such, it can be cited immediately by other researchers. As the issue version of your paper will be the only version to be published I would advise you to check your proofs thoroughly as changes cannot be made once the paper is published.

On behalf of the Editors of Royal Society Open Science, we look forward to your continued contributions to the Journal.

Kind regards,
Royal Society Open Science Editorial Office
Royal Society Open Science
openscience@royalsociety.org

on behalf of Professor Brooke Flammang (Associate Editor) and Professor Kevin Padian (Subject Editor)
openscience@royalsociety.org

Appendix A

Response to reviewer comments:

Authors' overview: *We thank the reviewers for their time and helpful comments. We have made the suggested changes to improve the clarity to readers and feel that the manuscript has been significantly improved as a result. The specific changes made are outlined below.*

Reviewer: 1
Comments to the Author(s)
Minor comments
1) It is stated in the abstract and the discussion that the results might inform the bio-inspired design of propulsive systems. Some elaboration on this point seems worthwhile.

Authors: *We have added some text to the conclusion that addresses how bio-inspired underwater vehicles may benefit from employing the fluid/vortex arrangement that has been identified in this study.*

2) Figure 3 and Supplemental Figure 1 use a very similar color map for the vorticity and for the velocity vectors. It would be preferable to use some other color scheme. It is very difficult to see the velocity vectors in Figure 3.

Authors: *We have gone back to the figure data and played around with several other color schemes in Lavision's DaVis software program and they all give similar looking results. We also tried to make the vectors thicker and more pronounced as well as making all the vectors a unicolor black shade. This resulted in the obscuring of the vorticity color palette (which is the main focus of the figure). Ultimately, we feel the problem of clearly seeing the vector field was mostly likely the result of the low resolution of the figure in the initial submission. We have replaced all figures in the revision with high resolution copies and feel that this resolves the issue with not being able to clearly resolve the velocity vectors.*

3) Additional discussion of the flows generated by the ciliary plates would help contrast the escape mode from other propulsive modes in this species and other comb jellyfish. It is likely worth explaining further that these are ciliary fused plates rather than individually spinning cilia.

Authors: *we have added text in the first paragraph of the discussion that reflects the reviewer's comment about clarity of the cilia-based mode locomotion found in all ctenophores, including Ocyropsis.*

Reviewer: 2

Comments to the Author(s)
Minor;

-In the introduction the authors consistently talk about the highly efficient of swimming in certain medusa, I would like to see some values included to give this claim of efficiency some context.

Authors: *We have added that jellyfish can achieve energetic swimming efficiencies as low as 0.3 J* kg^{-1} m^{-1} *to the second paragraph of the introduction.*

-Pg. 7, Line 15 appears to be missing 'of the'.

Authors: *Fixed.*

-Pg. 7, Line 38; 'newly forming starting vortex as while the stopping vortex remained', sounds odd, consider revising.

Authors: *This sentence has been reworded.*

-Pg.7, Line 56; 'in' should be 'it'.

Authors: *Fixed.*

- How did the authors measure body length for the individual species? What size were the animals that the proficiency measurements were being compared to?

Authors: *We have added details to the methods to clarify the point that body size was measured at the longest axis and length data on all species is available in the online data depository.*

-The comparison to other gelatinous swimmers is valid and interesting, however, I think that more context needs to be given to the different types of propulsion system being looked at. i.e, Ocyropsis may well have a maximum normalised body speed of twice that of Stomolophus meleagris, but ecologically speaking they are completely different locomotor modes, with one being an escape response and one being a continuous cruising style of swimming. I understand the authors are looking at proficiency, but I feel as the manuscript is written now it is hard to know which species are cruisers and which are an escape swim. Something as simple as an extra line in the figure legend would help clarify this.

Authors: *We appreciate this point and as suggested have added a line to the figure legend for clarity.*

- In the discussion the authors talk about the increased range of motion in O. maculate being bought about by increased muscle fibre layers. Have the authors considered how changes in the material properties of the mesoglea might affect the range of motion achievable in these species?

Authors: *The reviewer brings up an interesting point. While we are unable to address the question in detail, we added text that speculates there could be material properties other than muscle that allow for the greater range of motion.*

-How does the musculature compare between Ocyropsis and other ctenophores that do not perform these escape swims?

Authors: *We are unaware of any detailed physiological descriptions of oceanic ctenophores, so we are unable to provide any insight into this interesting question.*

-In the videos of the swims the animals often appear very close the wall of the aquarium, are the authors confident this did not affect the measurements?

Authors: *While some swimming sequences occurred with a small part of the ctenophore body somewhat close to a wall, we are very confident that this did not affect any of our measurements for the following reasons: 1) We did not use data from any animals touching a wall. 2) The swimming performance for the few individuals that were close to the wall was not significantly different that those in the middle of the filming tank. 3) Fluid structures (vortices) that formed somewhat close to a wall, did not appear altered or to dissipate any faster than those in the middle of the tank.*

-As a reader I would also be keen to see a video showing multiple swimming strokes at normal speed.

Authors: *Unfortunately in all of our underwater field videos (the only ones with a field of view large enough to capture multiple swimming strokes) the animals quickly swam out of plane/focus and so we do not have any high quality videos of this.*