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The most efficient metazoan swimmer creates a 'virtual wall' to enhance performance

Brad J. Gemmell, Kevin T. Du Clos, Sean P. Colin, Kelly R. Sutherland and John H. Costello

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Proc. R. Soc. B **288**: 20202494.
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Review timeline
Original submission: 6 October 2020
Revised submission: 30 November 2020
Final acceptance: 30 November 2020

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

Review History

RSPB-2020-2494.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?
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

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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?
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
General comments:
This manuscript describes how a jellyfish, swimming in the open ocean, can create a "virtual wall" using a vortex shed in one swimming cycle, to enhance swimming performance and efficiency in the next pulsatile cycle. In my view this a very good contribution to a collection of papers on the topic of propulsion in the Proceedings B journal, and this paper adds considerably to the current literature. Specifically, there has been a great deal of recent work on the effects of swimming near walls. Solid surfaces can boost swimming performance through a number of different mechanisms, and this process has been studied quite thoroughly using aquatic robotic systems and in swimming fishes. But to my knowledge no previous study has documented that shed vortex rings in an open water environment can act as a hydrodynamic wall that also boosts swimming performance in the absence of any solid boundary.

I have only a few minor comments (below) on the manuscript, but I do want to address one more significant issue with the research as presented here. I'm not sure what the authors can do to tackle this point except further analyses and experiments, but perhaps some caveats could be added to the manuscript to discuss the limitations of the approach so far. My main concern is that the statements regarding force production and efficiency are entirely inferential. That is, no measurements or even estimates of actual forces and the directions that they are exerted by the jellyfish on the fluid have been made. And there are no measurements of energetic cost that can be compared to sequences starting from rest that do not involve a virtual wall. As a result, the paper is completely observational and presents pressures estimated from PIV data on the jellyfish surface and flows in the wake, but no calculations were done on these data to estimate forces in x and y planes. Since these same authors have done these calculations in previous papers, the absence of force magnitudes and directions through a locomotor cycle was a bit surprising to me. And comparing forces and how they vary through time between the swimming and starting from rest sequences would be very useful. The paper would also benefit from an explicit comparison between a jellyfish swimming using a virtual wall, and one that does not using a computational approach, although I realize that this is outside the scope of the paper. What I'm getting at here is the need to show just what the quantitative benefit of the virtual wall is in terms of force and efficiency: what is the magnitude of the benefit? Is the benefit on the same order of what has been shown in previous studies of animals swimming near a solid wall?

Minor comments:

1. Table 1 title should read "…presence or absence".
2. Figures 3 and 4 need a length scale (similar to that shown in Fig. 2a).

3. Figure 5 caption. Please explain what the "H" stands for.

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?
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.
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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
Please find below my review of the paper "The most efficient metazoan swimmer creates a 'virtual wall' to enhance performance" for consideration for publication in the Proceedings of the Royal Society B. In this paper, the authors use particle image velocimetry to analyze the vortex-vortex interactions in the wake of the moon jellyfish Aurelia aurita. The authors find that the stopping vortex formed during bell expansion is positioned in such a way as to generate a wall effect (similar to a virtual vortex). The result is performance enhancement similar to what has been observed in other animals swimming near walls. This paper should be of broad interest to the readers of Proceedings B given the considerable interest in the fluid dynamics of animal locomotion, both as a way to provide insight into comparative biomechanics and as a way to inspire the design of autonomous underwater vehicles. The paper is generally well written, and

the schematic diagrams really help the reader interpret the underlying fluid dynamics. I have a few comments that should be addressed prior to the acceptance of the manuscript.

Figures 2, 3 – Consider using different color maps for vorticity and velocity since these two color maps are really similar.

Line 46 – "numerical models have suggested true vortex-vortex can, under the right circumstances, produce an equivalent effect" – Please clarify what is meant by true vortex-vortex (perhaps a word is missing here).

Line 91 – "The result is a significant increase in overall swimming performance and may also have important implications for understanding feeding in medusae, locomotion in other taxonomic groups as well as informing design principles for the engineering of bio-inspired vehicles." – Please elaborate a bit on these ideas in the main text since they set the stage for the significance of this work.

Line 122 – also define p as the pressure.

Figures – There are inconsistencies in referring to figures as Fig. or Figure.

Line 60 – "the vortex-vortex interactions and resulting impact" -> "the vortex-vortex interactions and the resulting impact"

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Line 108 "ensures accuracy" -> "ensures the accuracy"

Line 129 Reword "Data were input a time series of DPIV"

Line 136 "An important result which allows" -> "An important result that allows"

Line 211 "Engineers frequency consider" -> "Engineers frequently consider"

Line 223 "The link …. are" -> "The link…..is"

Line 234 "This causing a strong jet" -> "This causes a strong jet"

Line 244 "propulsion though a fluid" -> "propulsion through a fluid"

Decision letter (RSPB-2020-2494.R0)

11-Nov-2020

Dear Dr Gemmell

I am pleased to inform you that your manuscript RSPB-2020-2494 entitled "The most efficient metazoan swimmer creates a 'virtual wall' to enhance performance" has been accepted for publication in Proceedings B.

The referee(s) have recommended publication, but also suggest some minor revisions to your manuscript. Therefore, I invite you to respond to the referee(s)' comments and revise your manuscript. 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 us know.

To revise your manuscript, log into https://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, 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 referee(s) and upload a file "Response to Referees". You can use this to document any changes you make to the original 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.

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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".

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3) Electronic supplementary material: this should be contained in a separate file and where possible, all ESM should be combined into a single file. 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.

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].

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5) Data accessibility section and data citation
It is a condition of publication that data supporting your paper are made available either in the electronic supplementary material or through an appropriate repository. Please see our Data Sharing Policies https://royalsociety.org/journals/authors/author-guidelines/#data.

In order to ensure effective and robust dissemination and appropriate credit to authors the dataset(s) used should be fully cited. To ensure archived data are available to readers, authors should include a 'data accessibility' section immediately after the acknowledgements section. This should list the database and accession number for all data from the article that has been made publicly available, for instance:
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• Phylogenetic data: TreeBASE accession number S9123
• Final DNA sequence assembly uploaded as online supplemental material
• Climate data and MaxEnt input files: Dryad doi:10.5521/dryad.12311
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6) 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 revision. If you have any questions at all, please do not hesitate to get in touch.

Sincerely,
Dr Locke Rowe
mailto: proceedingsb@royalsociety.org

Associate Editor
Board Member: 1
Comments to Author:
Dear Authors,
Both reviewers rate your paper quite strong and of high quality. They also note that it fits well with our special feature issue. However, R1 does raise a major point, which I think is quite valid and one that you will need to address or, at least, add caveats to the interpretations you draw from their data. This also relates to R2's comment re: l. 91. R1 notes that you provide no quantitative results for forces and energetic efficiency in relation to swimming against a wall, akin to a virtual vortex; but instead present inferences of this drawn from your pressure measurements based on PIV. R1 notes that you and your colleagues have done this in the past, Consequently, they were surprised not to see similar quantitative analyses and results presented here to make a stronger case for the interpretations drawn from your data. Perhaps you can add such an analysis or provide a more circumspect evaluation of your results.

The other comments are minor and quite straightforward.

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Referee: 1
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General comments:
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Referee: 2
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Author's Response to Decision Letter for (RSPB-2020-2494.R0)

See Appendix A.

Decision letter (RSPB-2020-2494.R1)

30-Nov-2020

Dear Dr Gemmell

I am pleased to inform you that your manuscript entitled "The most efficient metazoan swimmer creates a 'virtual wall' to enhance performance" 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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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.

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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

Response to reviewer comments

<u>Authors:</u> We thank the editor and reviewers for their time and for the helpful comments on this manuscript. We were glad to see both reviewers held a positive assessment of the manuscript. We have addressed all concerns/comments and feel as though the manuscript has been significantly improved as a result of these revisions. Please find below our detailed responses to each comment.

Comments to Author:
Dear Authors,
Both reviewers rate your paper quite strong and of high quality. They also note that it fits well with our special feature issue. However, R1 does raise a major point, which I think is quite valid and one that you will need to address or, at least, add caveats to the interpretations you draw from their data. This also relates to R2's comment re: l. 91. R1 notes that you provide no quantitative results for forces and energetic efficiency in relation to swimming against a wall, akin to a virtual vortex; but instead present inferences of this drawn from your pressure measurements based on PIV. R1 notes that you and your colleagues have done this in the past, Consequently, they were surprised not to see similar quantitative analyses and results presented here to make a stronger case for the interpretations drawn from your data. Perhaps you can add such an analysis or provide a more circumspect evaluation of your results.

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Referee: 1

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My main concern is that the statements regarding force production and efficiency are entirely inferential. That is, no measurements or even estimates of actual forces and the directions that they are exerted by the jellyfish on the fluid have been made. And there are no measurements of energetic cost that can be compared to sequences starting from rest that do not involve a virtual wall. As a result, the paper is completely observational and presents pressures estimated from PIV data on the jellyfish surface and flows in the wake, but no calculations were done on these data to estimate forces in x and y planes. Since these same authors have done these calculations in previous papers, the absence of force magnitudes and directions through a locomotor cycle was a bit surprising to me. And comparing forces and how they vary through time between the swimming and starting from rest sequences would be very useful.

Authors: **We thank the reviewer for this valid concern and we certainly understand the desire for quantitative force estimates. We have added an estimate of force generated by positive pressures at the subumbrellar surface of the bell margin (lines 194-196). Total body force or thrust estimates are not feasible in this case however, due the fact that in order to resolve the fluid structures with the resolution needed to tease out the details of vortex-vortex interactions and obtain reliable pressures, we had to focus the entire camera's field of view on a very small subsection of the animal where the vortex interactions where occurring (Figs 3 and 4 are actually full frames and not cropped).**

Energetic costs of swimming for live animals typically require oxygen consumption data acquired over a period of at least several minutes. While the authors agree that direct energetic comparisons would be valuable here, the behavior of the jellyfish preclude obtaining comparative energetic data. While we know the cost of transport for a steady swimming Aurelia from previous studies (stopping vortex present case), the stopping vortex absent case only occurs when starting from rest and thus cannot be preformed on a continual basis to extract reliable oxygen consumption estimates. What we do know is that Aurelia makes the same kinematic movements in both cases. Assuming that the energetic expenditure is roughly the same in both cases, we know speed differs greatly and thus we can reliably speculate that cost of transport would rise without the presence of a stopping vortex. We now address these aforementioned points in lines (237-244).

The paper would also benefit from an explicit comparison between a jellyfish swimming using a virtual wall, and one that does not using a computational approach, although I realize that this is outside the scope of the paper. What I'm getting at here is the need to show just what the quantitative benefit of the virtual wall is in terms of force and efficiency: what is the magnitude of the benefit? Is the benefit on the same order of what has been shown in previous studies of animals swimming near a solid wall?

Authors: **We agree 100% with the reviewer that a computation approach would be a great next step in this line of research. It will be a priority of ours going forward to collaborate**

with experts in CFD to better understand this novel phenomenon.

Minor comments:

1. Table 1 title should read "…presence or absence".

Authors: Fixed

2. Figures 3 and 4 need a length scale (similar to that shown in Fig. 2a).

Authors: Thank you. Figure 4 does indeed have a scale bar (black bar in panel A), but there is indeed a scale bar missing from Figure 3. This has been corrected.

3. Figure 5 caption. Please explain what the "H" stands for.

Authors: We now define the letter 'H'.

Referee: 2

Comments to the Author(s)
Please find below my review of the paper "The most efficient metazoan swimmer creates a 'virtual wall' to enhance performance" for consideration for publication in the Proceedings of the Royal Society B. In this paper, the authors use particle image velocimetry to analyze the vortex-vortex interactions in the wake of the moon jellyfish Aurelia aurita. The authors find that the stopping vortex formed during bell expansion is positioned in such a way as to generate a wall effect (similar to a virtual vortex). The result is performance enhancement similar to what has been observed in other animals swimming near walls. This paper should be of broad interest to the readers of Proceedings B given the considerable interest in the fluid dynamics of animal locomotion, both as a way to provide insight into comparative biomechanics and as a way to inspire the design of autonomous underwater vehicles. The paper is generally well written, and the schematic diagrams really help the reader interpret the underlying fluid dynamics. I have a few comments that should be addressed prior to the acceptance of the manuscript.

Figures 2, 3 – Consider using different color maps for vorticity and velocity since these two color maps are really similar.

Authors: As suggested, we experimented with several different iterations of velocity vector color mapping. A contrasting uniform color such as black arrows made it too difficult to visually pick up on velocity differences as only the vector length provided any information. A different color scheme resulted in non-intuitive colors representing high or low flow speeds. Thus, while we appreciate the reviewer's point, the cold colors for low flow speeds and vorticity and warm colors for high flow speeds and vorticity seem to provide the best

visual information.

Line 46 – "numerical models have suggested true vortex-vortex can, under the right circumstances, produce an equivalent effect" – Please clarify what is meant by true vortex-vortex (perhaps a word is missing here).

Authors: There was indeed a word missing. This sentence has been clarified.

Line 91 – "The result is a significant increase in overall swimming performance and may also have important implications for understanding feeding in medusae, locomotion in other taxonomic groups as well as informing design principles for the engineering of bio-inspired vehicles." – Please elaborate a bit on these ideas in the main text since they set the stage for the significance of this work.

Authors: We have elaborated on these ideas lines 256-259 (feeding), lines 266-270 (locomotion in other taxa) and lines 274-277 (engineering).

Line 122 – also define p as the pressure.

Authors: Fixed.

Figures – There are inconsistencies in referring to figures as Fig. or Figure.

Authors: Thank you for catching this inconsistency. All references to a figure in the manuscript now follow the Proc B format.

Line 60 – "the vortex-vortex interactions and resulting impact" -> "the vortex-vortex interactions and the resulting impact"

Authors: Fixed.

Line 62 -> "of the stopping vortex (16) allowing" -> "of the stopping vortex (16), allowing"
Authors: Fixed.

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