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MS TITLE: Scaling of oscillatory kinematics and Froude efficiency in baleen whales

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ARTICLE TYPE: Research Article

Dear Dr. Gough,

We have now reached a decision on the above manuscript.

The reviewer reports are shown at the bottom of this email or can be accessed, together with a copy of this decision letter, by going to:

<https://submit-jeb.biologists.org>

and clicking on the 'Manuscripts with Decisions' queue in the Author Area.

As you will see, the reviewers are somewhat divided in their assessments of your paper. Whereas R1 is generally quite positive and raises only minor points of concern, R2 raises two major concerns with respect to your estimates of body mass based on length alone and particularly in regard to whether the field swimming data were well curated for those swimming activities that can be reasonably be considered steady state. The issues raised by R2 seem legitimate and of significant concern, which may well require that you not only make major revisions to your paper but also re-analyze your data to address.

If you think that you can deal satisfactorily with the criticisms on revision, I would be pleased to see a revised manuscript. We would then return it to the reviewers.

We are aware that, due to COVID-19 restrictions, you may be experiencing disruption to the normal running of your lab that makes experimental revisions challenging. If it would be helpful, we encourage you to contact us to discuss your revision in greater detail. Please send us a point-by-point response indicating where you are able to address concerns raised (either experimentally or by changes to the text) and where you will not be able to do so within the normal timeframe of a revision. We will then provide further guidance. Please also note that we are happy to extend revision timeframes as necessary.

In revising your manuscript, please take into account the formatting instructions detailed below (we accept over 95% of revision submissions and therefore hope you won't mind any extra work involved in reformatting your manuscript at this point).

Please ensure that you clearly highlight all changes made in the revised manuscript. Please avoid using 'Track changes' in Word files as these are lost in PDF conversion.

I would be grateful if you would also list how you have dealt with the points raised by the reviewers in the 'Response to Reviewers' box. Please attend to all of the reviewers' comments. If you do not agree with any of their criticisms or suggestions please explain clearly why this is so.

In order to promote timely publication, we generally ask that the revision be completed within 90 days from the date of this letter. However, as noted above, we recognise that this may not be possible under the current circumstances and will be happy to grant an extension where this is needed: please just contact the Editorial Office.

To submit your revised manuscript, please go to:
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I look forward to receiving your revised manuscript.

Best wishes

Andrew Biewener
Monitoring Editor
Journal of Experimental Biology

Significant Manuscript Edits:

- We have swapped Hayden J. Smith and William T. Gough in the author list. We believe that both of these authors have made similar contributions to the paper and we would like for them to both be recognized as co-first authors, if possible.
- In our methods section, we have updated many of our symbols and added a new table (Table S1) with a list of symbols and descriptions.

- We have reordered the segment detailing routine and lunge-associated tailbeats and have added significant detail on the lunge-associated in the form of a new paragraph starting on L215.
- We have updated the “Thrust Power, Efficiency, and Drag Coefficient Modeling” segment of our methods section with additional detail and new equations. Our new method of calculating drag coefficient (Equation 8a) takes into account acceleration and differing values for thrust and drag over the course of a tailbeat. We have also simplified our analysis of lunge-associated tailbeats and removed lunge-associated tailbeat data from our calculations of drag coefficient and Froude efficiency.
- We have expanded the “Statistical Analyses” segment of our methods section with more detail on our statistical models.
- We have updated the values in our results section and added a new paragraph starting on L354 that details the change in speed over the course of a tailbeat (ΔU).
- We have altered the “Froude Efficiency vs. Swimming Velocity” portion of our discussion section to reflect the removal of lunge-associated tailbeat data. Our new text focuses more heavily on the average (and median) routine swimming speeds in our dataset and how they align with ranges of migratory swimming speeds as well as the optimal speeds calculated by Gough et al. (2019). We are also more explicit in saying that 99% of our swimming speed datapoints fall below 4.5 m s^{-1} .
- We have rewritten our conclusion section to focus more heavily on the direct results of our study.
- We were erroneously showing \log^e data instead of \log^{10} data in Figure 3. We have fixed this oversight.
- Figure 4 has been updated with new values for lunge-associated tailbeat data.
- Figure 5 no longer includes lunge-associated tailbeat data. The routine swimming data shown now uses our new method of calculating drag coefficient.
- Figure 6 no longer includes lunge-associated tailbeat data. We have also included three horizontal lines (described in the figure legend) that related to the optimal speed (calculated by Gough et al., 2019), median speed in our dataset, and 99th percentile.

Reviewer 1 Comments for the Author:

The authors examined the allometric relationships of several kinematic parameters during swimming in baleen whales, based on tag data and morphological estimates using drones. This paper is related to Gough et al. (2019), where the team examined the allometry of swim speed and tailbeat frequency using a similar dataset. In this paper, the team goes beyond Gough et al. by estimating several mechanically important parameters such as thrust power, drag coefficient, and Froude efficiency. The main strength of this paper is that the analyses were done for the animal group with the largest body sizes by using the team's unique dataset. Overall, this is an excellent paper highly

relevant to the readership of JEB. Presentation is clear and analyses are well done. My comments are fairly minor.

L45 Froude efficiency is a ratio, not the amount of work.

We appreciate the correction in our definition of Froude efficiency. We have taken this into account and have updated the definition on L45 to state: “Froude efficiency, defined as the ratio of useful power output to the rate of energy input (Sloop, 1978), generally increased...”

L752: Sloop L. J., (1978). Appendix B: Liquid Hydrogen as a Propulsion Fuel, 1945-1959. NASA SP-4404, 324 pages, NASA, Washington, D.C.

L59 functionally analogous 'among' swimming animals such as...

We appreciate the reviewer's correction and have implemented it into the manuscript.

L72 'Energetic assumptions... were limited to deceased animals' - sounds strange.

We thank the reviewer for this comment and agree that the statement sounds strange. We have updated the sentence starting on L72 to read: “Attempts to study mysticetes and derive energetic assumptions (Sumich, 1983; Parry, 1949; Blix & Folkow, 1995) were constrained to breathing events at the water's surface, and morphological measurements were only attainable from animals that had stranded on beaches or been captured by whaling operations (Lockyer, 1976; Kahane-Rapport & Goldbogen, 2018).”

L166 'Matlab'

We thank the reviewer for the correction and have updated the manuscript accordingly.

L228 Define CT, as it doesn't seem to have appeared before. A list of symbols may be useful for this paper.

We thank the reviewer for pointing out this oversight and for their suggestion. We have defined C_T as the coefficient of thrust on L253 and added a new table to the manuscript (Table S1) with a list of symbols and their corresponding definitions as they appear in the text.

L232 Should 'u' be 'U'?

We appreciate the reviewer for this correction and have updated some of our symbols, including 'U' to be 'Uavg'. We have changed all instances of 'u' and 'U' to be 'Uavg'. Please reference the new Table S1 for more information on symbols used throughout the text.

L233 It seems that fluke area is Fa, not St.

We appreciate the reviewer for this correction and have removed the definition of fluke area from the sentence after equation 5 on L235. Fluke area (Fa) is now solely defined on L197 and in Table S1.

Were swim speed and tailbeat frequency extracted from the bottom phase of dives? Is the effect of buoyancy negligible? Consistency in the phase of dives examined seems important for interspecific comparisons.

We thank the reviewer for their questions and agree that consistency and transparency in our analytical methods is extremely important. For our analysis of tailbeats, each beat was determined to occur fully below 2m (similar threshold used for tailbeat analyses in Gough et al., 2019) from the surface to remove kinematic interference from the air-water interface. For a previous study (Gough et al., 2019), we performed a comparative analysis on the three submerged dive phases (dive descent, bottom stage, dive ascent). This segment ended up being cut from that manuscript for length and manuscript focus. We have included the cut paragraph below. The methods used to analyze and determine tailbeats were the same methods used in the current study. As a short summary, we found differences in oscillatory frequency between the dive descent and dive ascent when combining all of our tailbeats together into a single sample set, but these differences did not hold on the individual level, with differences only being found between surface and bottom stage tailbeats. For the current study, we felt it was reasonable on the level of the individual whale to remove all surface tailbeats and combine dive descent, bottom stage, and dive ascent tailbeats together.

Oscillatory Frequency vs. Dive Stages

We found a significant difference in oscillatory frequency between the dive descent and ascent stages for all species combined ($df = 137782$; $t = 29.02$; $p < 0.001$). We also found significant differences for the same analysis performed on a species-specific basis for the minke ($df = 12762$; $t = 14.81$; $p < 0.001$; Fig. 7A), humpback ($df = 101106$; $t = 26.31$; $p < 0.001$; Fig. 7B), and blue whales ($df = 18182$; $t = -4.45$; $p < 0.001$; Fig. 7C). Our models comparing the coefficient of variation of the oscillatory frequency for an individual whale between all four swimming stages showed a significant difference between surface swimming and the bottom stage ($df = 564$; $t = 2.33$; $p = 0.02$), but not between surface swimming and dive descent ($df = 564$; $t = -1.35$; $p = 0.18$), surface swimming and dive ascent ($df = 564$; $t = -0.61$; $p = 0.54$), or the dive descent and dive ascent ($df = 280$; $t = 0.72$; $p = 0.48$).

We did not perform a similar analysis for swimming speeds, but we feel that these oscillatory frequency trends give us a solid basis to combine our speed measurements at the level of the individual and disregard the effects of the dive phase or the influence of buoyancy at the present time. We also feel that our dataset is robust to minor behavioral variations for a few reasons. First, we have only included individuals in our dataset that have a large number of usable tailbeats (>200; taken from the methodology of Gough et al., 2019). Second, we have used similar thresholds for each individual whale and each species that define a usable tailbeat and remove outliers (again, taken from the methodology of Gough et al., 2019).

L246 Swim speed increases before lunges. Doesn't it mean that thrust exceeds drag, leading to an inaccurate estimate of drag coefficient?

We thank the reviewer for their question and agree that swimming speeds are constantly variable within both the routine and lunge-associated swimming periods. In order to understand and quantify this variability, we have performed some additional analyses to find the average speed variations (from the start of a tailbeat to the end of a tailbeat as both absolute and a percentage of swimming speed) for both swimming periods. Our findings in this analysis show that routine swimming speed variability is smaller (~12% of swimming speed) than lunge-associated swimming speed variability (~24%). We have added these findings into the manuscript as columns in Table 1 and have described the trends more fully in a paragraph starting on L354. We feel that this analysis gives the reader a clearer idea of the variability in our dataset.

Given the variability in our speed measurements across the timescale of a single tailbeat, we felt it necessary to recalculate our drag coefficients in a way that takes into account acceleration and potential differences between thrust and drag. Our updated values are found in Table 3 as well as Figure 5. We have also made changes to the manuscript starting on L272 to define this new method of calculating the drag coefficient. Equation 8a now includes a term $[k_{added} * M_{body} * (U_f - U_i / T_{beat}) * U_{avg}]$ that provides an offset value between the thrust and drag. This is based upon swimming speed at the start and end of a given tailbeat, the mass of the body, and a shape drag factor between 0.03-0.05 that has been calculated from CFD shape models of each species.

We have also rethought out approach to the lunge-associated tailbeat analyses. We determined that the change in speed for lunge-associated tailbeats was too great to assume steady-state or model Froude efficiency or drag coefficient. As a result, we have removed lunge-associated data from these measurements. For Figures 5 (A-C) and 6 (A-B), this means we are now only displaying data for routine swimming. In Figure 4, you will notice that we are still including lunge-associated data. In this case, we have calculated lunge-associated thrust power output in a new way using the average routine swimming drag coefficient for each whale (Equation 8b).

Given these changes to our data and methodology, we have updated our results and discussions sections to reflect our refocused approach. This is especially pronounced in the “Froude Efficiency vs. Swimming Velocity” portion of the discussion, where we have removed a paragraph discussing the Froude efficiency during foraging lunges and added new text to describing our routine swimming speeds more fully.

In addition to these changes, we have also expanded and clarified our description of the lunge-associated time period starting on L215 in response to these comments as well as comments from Reviewer 2. We thank the reviewer for suggesting these changes and hope that we have fully addressed their concerns.

L299-300 Repeated sentences on decreasing oscillatory frequency with increasing body size.

We thank the reviewer for finding this error and we have deleted the repeated sentence.

L312-313 Repeated sentences on constant swim speed across animal body size.

We thank the reviewer for finding this error and we have deleted the repeated sentence.

L480-498 I have difficulty in following this paragraph. Looking at Fig. 6A, Froude efficiency is maximized at max. possible speed (for routine swimming) or about 5 m/s for lunge-associated swimming, unlike 2-2.5 m/s as explained in the text. I cannot see how the curve fits in Fig. 6A were created. Why is the range of swim speed wider than other figures? Also, the relationship between COT and Froude efficiency may not be so straightforward. In the former, the effect of basal metabolic rates is strong, and I guess the minimum COT speed is not always the maximum Froude efficiency speed for a given species.

We appreciate the reviewer’s comments. The range of swim speed is wider in Fig. 6A than other figures because it does not show mean values of swim speed, but instead shows the swimming speeds for each individual tailbeat for every animal. Therefore, the figure encompasses hundreds of thousands of different swim speeds and has a larger range than the mean ~2-4 m/s. To make this more clear, we have updated the figure legend to state that “Curved fit line shown in A) is based upon each individual tailbeat measurement for all species combined and shows the plateau in Froude efficiency that occurs at 2-2.5 m s⁻¹.” We have also made it clear that 99% of our data falls below 4.5 m/s by stating that “The vertical grey dotted line at 4.5 m s⁻¹ in A) denotes the 99th percentile, with only 1% of the data falling to the right of the line.” We included all of our speed data for completeness, but the high swim speed trajectory (increasing) is likely a statistical anomaly due to low sample size.

In order to make this clear in the manuscript and to describe why we have only included routine swimming in this analysis, we have updated the text starting on L603 to state that “Only 1% of our speed measures fell above 4.5 m s^{-1} , meaning our ability to predict Froude efficiency at these high speeds is limited. The significantly unsteady nature of lunge-associated swimming also meant that we could not include that swimming style in our analysis of Froude efficiency.”

To make Figure 6A more clear, we have also included two vertical lines denoting the median speed calculated from our data and the optimal swimming speed (U_{opt}) calculated from Gough et al. 2019. We have included descriptions of both vertical lines in the figure legend for Figure 6: “Vertical black dashed line in A) denotes the median routine swimming speed across all species (2.06 m s^{-1}). Vertical grey dot-dashed line in A) denotes the optimal swimming speed (U_{opt} ; 1.97 m s^{-1}) calculated by Gough et al. (2019).”

L539 Again, this sentence is confusing given that Froude efficiency increases with speed (Fig. 6A), although I can understand that Froude efficiency during routine swimming is higher than that during lunge-associated swimming.

We thank the reviewer for their comments. We have rewritten our “Conclusion” section to focus more directly on the findings of our study. As a result, we believe that the sentence in question has been removed.

Reviewer 2 Comments for the Author:

Combining biologging and morphology measurements in baleen whales (six species ranging in body length from 5-25 m), some interesting values and relationships were indicated. I agree with the importance of these data to understand the morphology and the kinematics of swimming behavior of large whales, however, there are two main concerns in this paper.

First concern is morphology of cetaceans. As indicated in line 69, morphological measurements of large cetaceans have been difficult to obtain. Authors used drones to obtain morphological measurement of cetaceans under natural condition. However, only body lengths was used for estimating body mass. I wonder why authors did not use maximum body diameter to check geometrical similarity. As they quote in this paper, Hill (1950) first dealt with scaling of cetaceans. Hill predicted that running and swimming speed should be independent of body size for geometrically similar animals. Important point is geometrical similarity of animals. In land animals, to whom gravity becomes a predominant factor at extreme size, geometrical similarity is impossible over so wide a range. However, such geometrical similarity can be expected in aquatic animals like cetaceans because body weight is supported by buoyancy. I recommend authors to use both body length and width to evaluate geometrical similarity of cetaceans. Only

body length is used to estimate body mass and wetted surface area of the body using known regressions (line 195-197). Are these regressions obtained for each species? This point should be clarified. Authors should first examine geometrical similarity of cetaceans. If authors do not include detailed information on morphology, it is difficult for them to discuss about scaling.

We would like to thank the reviewer for their comments. We feel that we did not adequately explain our methodology in the initial manuscript. In order to remedy this, we have expanded on the methods section titled *UAS Operations and Morphometric Measurements* with additional detail about our body length scaling methods. In particular, we have extended the sentence starting on L195 to read “Body mass (M_{body} ; kg) was estimated from total body length using regressions derived for each of our six study species using a broad range of data compiled from both whaling operations and studies of stranded animals (Kahane-Rapport & Goldbogen, 2018).”

For our regressions equations of body length to determine body mass, we used the values provided in Kahane-Rapport and Goldbogen (2018). These values constitute one of the most comprehensive compilations of rorqual whale morphology to date and rely partially on whaling records (the *Discovery Report* investigations; Matthews, 1937; Matthews, 1938) to obtain high sample sizes for many of the measured morphological parameters.

For our scaling relationships between body size and wetted surface area, we used a series of measurements taken from the literature or from computations performed on morphologically accurate models (Kennedy, 2021). From these measurements, we obtained a unique surface area coefficient (surface area / body length) and/or equation for each species. These measurements and equations could then be used to calculate the wetted surface area for each species in our analysis. We have detailed these measurements and equations in a new Table S2.

Kennedy, J. H. (2021). Hydrodynamics of Rorquals. Ph.D. Dissertation, Saint Louis University.

Matthews, L. H. (1937). The humpback whale, *Megaptera nodosa*. *Discovery Reports*, 17 (pp. 9–89). Cambridge University Press.

Matthews, L. H. (1938). The sei whale, *Balaenoptera borealis*. *Discovery Reports*, 17 (pp. 185–290). Cambridge University Press.

Kahane-Rapport, S. R., Savoca, M. S., Cade, D. E., Segre, P. S., Bierlich, K. C., Calambokidis, J., Dale, J., Fahlbusch, J. A., Friedlaender, A. S., Johnston, D. W., Werth, A. J. and Goldbogen, J. A. (2020). Lunge filter feeding biomechanics constrain rorqual foraging ecology across scale. *J. Exp. Biol.* 279, jeb.224196.

Second concern of this paper is application of theoretical model to field observation data. Drags of swimming whales were estimated assuming steady state in which thrust is equal to drag (line 84-85 and equation 7). However, authors seem not to pay attention to the state when they extract data during routine and lunge-associated swimmings. For example, the period from 10-0 seconds prior to the lunge deceleration was defined as the lunge-associated period and all other tailbeats were classified as routine swimming (line 246-249). This classification does not confirm constant swim speed during the routine swimming. It can be problem when they applied the theoretical model to calculate drag. If authors follow their assumption, they should not use data during lunge-associated swimming.

We thank the reviewer for their comments and would like to clarify a few changes that we have made in response to their concerns. To start, we have performed additional analyses to quantify the average change in swimming speed over the course of a tailbeat for both routine (~12% change in swimming speed) and lunge-associated swimming (~24% change in swimming speed). We have added these findings into the manuscript as columns in Table 1 and have described the trends more fully in a paragraph starting on L340. We feel that this analysis gives the reader a clearer idea of the variability in our dataset.

Owing to this variability in swimming speed during a tailbeat, we agree with the reviewer that thrust does not equal drag. To account for this in our calculations of drag coefficient, we have included a term $[k_{added} * M_{body} * (U_f - U_i / T_{beat}) * U_{avg}]$ in Equation 8a that provides an offset value between the thrust and drag. This is based upon swimming speed at the start and end of a given tailbeat, the mass of the body, and a shape drag factor between 0.03-0.05 that has been calculated from CFD shape models of each species.

We have also refocused our analyses in regards to lunge-associated swimming and removed lunge-associated data from our calculations of Froude efficiency and drag coefficient. We agree with the reviewer that the variability in our lunge-associated tailbeats is too high to accurately estimate these values. For thrust power output, we have included lunge-associated tailbeat data, but recalculated it (Equation 8b) using the average drag coefficient for routine swimming from the same animal.

As a result of these changes, we have updated our methods section starting primarily on L258 to include greater detail for each equation used in our analyses. We have also updated our measured hydrodynamic values in Table 3 and updated Figures 5 (A-C) and 6 (A-B) to only include routine swimming data. Finally, we have updated our results and discussion sections, most significantly the “Froude Efficiency vs. Swimming Velocity” portion of our discussion (starting on L548), to reflect our shift in focus away from lunge-associated data for these measurements.

Whales accelerated swim speed and then decelerated suddenly during the lunge-associated swimming. And also whales opening their mouth (changes drag) and engulfing a large volume of water into the expansible throat pouch (changes mass and drag). These situation does not satisfy the condition of the steady state.

We thank the reviewer for their comments and we have expanded and clarified our description of the lunge-associated time period starting on L215 in the manuscript.

And authors measured swim speed using the amplitude of tag vibrations (Cade et al. 2018). I wonder whether this method can be applied for unsteady-state. There are several methods to measure swim speed of cetaceans. As same as a previous paper (Watanabe et al. 2010 J. Anim. Ecol.), comparative analysis is recommended to confirm accuracy of swim speed measurement.

We thank the reviewer for their comment and we have updated the sentence starting on L166 to include the clause: "...a method which has been shown to be robust and accurate above $\sim 1 \text{ m s}^{-1}$ in a variety of behavioral contexts." This method uses *in situ* regressions between the amplitude of tag vibrations and the orientation-corrected depth rate (OCDR) during periods of high pitch to increase the accuracy of the speed measurements throughout the tag deployment, regardless of tag orientation or position on the animal. This makes the method extremely accurate during routine swimming as well as higher-speed maneuvers and foraging lunges. Since our data set is limited to swimming (either routinely or in the lead-up to a lunge), we feel that this method is well-suited for our purposes.

This paper reports some interesting relationships. It seems that authors try to explain some parameters in view of scaling. For example, oscillatory frequency, swim speed, mass-specific thrust power and drag coefficient were compared with body size. It is reasonable that total body length is used as an index of body size because body mass is not measured. And it is worth comparing oscillatory frequency and swim speed with body length. However, relationships with body length were not clear because swim speed and oscillatory frequency of routine swimming and lunge-associated swimming include unsteady-state (accelerate and decelerate). The results were compared with a previous study (Sato et al. 2007(this paper is not in the list of references)). But the previous study dealt with cruising speed (steady state). This points should be discussed (line 445-449). And one important previous study (Watanabe et al. 2010 J. Anim. Ecol.) is not quoted.

We thank the reviewer for catching our oversight and have added Sato et al., 2007 into our reference list. We have also included Watanabe et al., 2010 with an in-text citation on L550.

On the topic of our scaling relationships, we do not fully agree with the reviewer's assertion that we would be unable to accurately measure the mean swimming speed or oscillatory frequency

using our methodology. We agree with the reviewer that there is variation in speed across tailbeats and we have addressed those concerns in the manuscript, but we reiterate that both swimming conditions occur with the mouth closed, suggesting that the main differences between the two are the swimming speed and the associated changes in the kinematic profile of the tailbeat.

By focusing on the time-scale of a single tailbeat, we can minimize the variation in speed in any given tailbeat and obtain a single measurement of oscillatory frequency (the period of that particular tailbeat). This also allows us to treat each tailbeat as a model for an animal of a given size swimming with the given kinematic parameters from that tailbeat (similar to the methods laid out in Gough et al., 2019). Over a large enough sample size (>200 tailbeats per deployment), we felt this gave an accurate portrait of the overall swimming performance of any single whale.

In looking back at the mentioned study (Sato et al., 2007), we believe that their methods defined and dealt with cruising (routine swimming) in a similar way to our present study. They used the OCSR method to determine swimming speed, a method which we indirectly make use of, and they used a Fast-Fourier Transformation (FFT) to determine the dominant stroking frequency instead of the average of individual measured tailbeat periods. We believe that our single-tailbeat method allows us to split our dataset in unique ways, such as we have done between routine and lunge-associated swimming, and model swimming under different conditions using the kinematic parameters of individual tailbeats.

This paper should be discussed in views of scaling and the cost of transport (line 479-498). It is doubtful to use mass-specific thrust power because of the same reason (body mass was not measured for each individual). Drag coefficients during lunge-associated swimming are doubtful because steady state is not satisfied. When you compare drag coefficients with values in previous studies, reference area (wetted surface area or cross sectional area) should be indicated.

We thank the reviewer for their comments. As we have detailed in earlier responses, we have included new analyses pertaining to speed change and we have updated our calculation of drag coefficient to account for acceleration and the lack of equality between thrust and drag in many cases. We have also removed data from lunge-associated tailbeats from Froude efficiency and drag coefficient calculations.

In regards to the cost of transport, we have included more text in the “Froude Efficiency vs. Swimming Velocity” segment that describes our swimming speeds in more detail and how they align with the optimal swimming speed calculated by Gough et al. (2019). We have also added a horizontal line to Figure 6A that denote the median speed of our dataset as well as this optimal speed, showing that they closely align with one another. We have updated the figure legend for Figure 6 to included details on these horizontal lines.

In regards to referenced surface area, each one was confirmed to be the wetted surface area of the body. These surface areas are referenced in the new Table S2.

Figures 6 and 7) Efficiency is compared with length and swim speed. “Propulsive efficiency” is appeared in the captions, but “Froude efficiency” is used in the figure. What is a definition of the propulsive efficiency? It is written that “Our calculations of thrust power, coefficient of drag, and Froude efficiency were based on a model of lunate tail propulsion using unsteady wing lifting surface theory (Chopra & Kambe 1977, Yates 1983, Fish 1998)”. It is better to indicate simple definition of the Froude efficiency.

We thank the reviewer for catching this error and we have adjusted the figure legends for Figures 6 and 7 to read “Froude efficiency” instead of propulsive efficiency.

Another concern is statistics used in this paper. It is stated that “we fit linear models to assess relationships” (line 276-277). However, I cannot confirm whether authors consider the error in the both x- and y-axes. One possible solution might be the reduced major axes analyses to estimate the scaling relationship.

We appreciate the reviewer’s thorough reading of the methods of this paper. We have revisited our “Statistical Analyses” section starting on L289 and filled it out with more detail about the linear mixed-effects models that we employed for our analyses. Following the reviewer’s suggestion, we considered a reduced major axes analysis, but feel that using it for these data would be inappropriate because we do not have variation in the x and y axes for a given point. We believe that using a linear mixed model is appropriate here because each point presented in Figures 3, 4, 5, and 6b is a point representing the measured length (a single measurement) and the average for each individual deployment’s measured values (O’s freq, swim speed, etc. as described in the Methods; L294-299). In other words, for each point there is no error in the x or y, they are point estimates. We used a linear mixed model, as opposed to a more straightforward linear model (i.e., standard linear regression) because we wanted to be able to control for the variation between species using species as a random effect.

We have also caught an error in L313 in which the “...using package lm in R” should now read “...using package lme4 in R”.

Data obtained under natural condition is very important to understand scaling-based understanding of oscillatory swimming in cetacean, however, above concerns prevent me to examine how reasonable the authors’ discussions are. Generally relationships between swimming parameters and body size are not so clear. Many plots varied from regression lines (Figs. 3-6). It seems to be difficult to compare scaling exponents with previous studies. I

recommend re-analyze and re-construct the story of paper. I ask to clarify above concerns in revised version of the manuscript.

We thank the reviewer for their comments and hope that we have adequately addressed their concerns in regards to our morphological measurement procedures, the description and validation of our lunge-associated swimming condition, the variability in swimming speeds within tailbeats, and our updated methods for calculating hydrodynamic parameters.

(Specific comments)

Line 217, equation 3) A parameter “c” is included. What is “c”? In line 193-194, chord length of the flukes was defined as “C” (a capital).

We appreciate the reviewer finding this discrepancy. We are referring to the chord length of the flukes in both locations and we have changed all instances of the parameter for chord length from “c” to “C” in order to maintain consistency. We have also included a new table (Table S1) in the manuscript with descriptions for each symbol used throughout the text. We hope that this clears up any further confusion related to symbols.

Line 232, equation 5) What is C_t ? It should be defined after the equation. “u” is not defined. “U” is defined as swimming velocity (line 208). And “Fa” is defined as the combined planar surface area of the flukes (line 192-193), but St is defined in line 233.

We thank the reviewer for their comments. We have defined C_T as the coefficient of thrust in L253, all instances of “u” and “U” have been changed to U_{avg} and defined as the average swimming velocity for a tailbeat, and “St” has been changed to “Fa” to define the combined planar surface area of the flukes. Please reference the new Table S1 for more details on symbols used in equations 1-11.

Line 239, equation 7) What is “Sa”? It should be explained after equation 7.

We thank the reviewer for pointing this out and apologize for the confusion. Sa is defined as the wetted surface area of the body. This definition is given on L203 and we have added it into the new list of symbols in Table S1.

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