Foetal growth, birth size and energetic cost of gestation in southern right whales

Fredrik Christiansen, Marcela M Uhart, Lars Bejder, Phil Clapham, Yulia Ivashchenko, Dmitry Tormosov, Nicolás Lewin, and Mariano Sironi

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The following individual(s) involved in review of this submission have agreed to reveal their identity: Ken D O'Halloran (Referee #4)

Review Timeline:

| Event                      | Date      |
|----------------------------|-----------|
| Submission Date            | 07-Sep-2021|
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Reviewing Editor: Janna Morrison

Transaction Report:

(Note: With the exception of the correction of typographical or spelling errors that could be a source of ambiguity, letters and reports are not edited. Depending on transfer agreements, referee reports obtained elsewhere may or may not be included in this compilation. Referee reports are anonymous unless the Referee chooses to sign their reports.)
Dear Dr Christiansen,

Re: JP-RP-2021-282351 “Foetal growth, birth size and energetic cost of gestation in southern right whales” by Fredrik Christiansen, Marcela M Uhart, Lars Bejder, Phil Clapham, Yulia Ivashchenko, Dmitry Tormosov, and Mariano Sironi

Thank you for submitting your manuscript to The Journal of Physiology. It has been assessed by a Reviewing Editor and by 4 expert Referees and I am pleased to tell you that it is considered to be acceptable for publication following satisfactory revision.

Please advise your co-authors of this decision as soon as possible.

The reports are copied at the end of this email. Please address all of the points and incorporate all requested revisions, or explain in your Response to Referees why a change has not been made.

NEW POLICY: In order to improve the transparency of its peer review process The Journal of Physiology publishes online as supporting information the peer review history of all articles accepted for publication. Readers will have access to decision letters, including all Editors' comments and referee reports, for each version of the manuscript and any author responses to peer review comments. Referees can decide whether or not they wish to be named on the peer review history document.

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If you have any queries please reply to this email and staff will be happy to assist.
EDITOR COMMENTS

Reviewing Editor:

Ethics Concerns:
The Ethics Editor has reviewed the paper. Commercial whaling has a negative tone to it in the current time and data from the past is included in the paper. I just wanted to make sure that it was appropriately described.

Comments to the Author:
This is an interesting paper determining fetal growth trajectories in SRW.

The paper would benefit from some editing to assist the broad readership of Journal of Physiology. For example, it is not clear that the SRW is one of many baleen species and that other baleen species have been studied. It would also be important to identify what is and isn't known in these different species and what new knowledge this study presents. Some of the figures are complex and it would be useful to a figure that simplifies the data presentation.

It should also be noted that Journal of Physiology does not have supplementary files. All data should be included in the paper. As such, would all tables/figures be required in the paper. It is permissible to include data on a public repository such as figshare and to reference that site in the paper.

In many places, ‘fetus’ is used but this should be ‘fetal’. Eg fetal length, fetal growth.

Line 53 - placental energy content

Line 82 - However, high offspring growth rates incur large... would be more appropriate. If 'However' is used in the middle of a sentence, it should be preceded by a semicolon. There are several instances where this is the case.

Whaling is a controversial area, and the authors must include information about ethics approvals for collecting and using the data in this paper. The acknowledgements section has information about approvals for the recent data collection using drones. This information should be moved to the methods section. Please refer to Grundy for information about what details are required [1] and the JP guidelines to authors for formatting. The fetal length data was from Russian ships commercial whaling records that have been published. The methods should have detail that clearly explains what data came from where. Was there ethics approval to collect/access this data? Please ensure that it is very clear that published data was used. The results say that the fetuses were extracted from the mothers; however, there was no information about how the mothers or fetus were killed or the ethics to do this.

Line 222 - Pease include the appropriate citations for ref 7 and 8.

Line 465 - the equations suggest that the fetus is 0.30m at conception. This doesn't see possible. However, how big is the
REFEREE COMMENTS

Referee #1:

This manuscript describes studies of fetal growth birth size and the energetic costs of gestation in southern right whales.

On page 4 of the introduction (lines 100-102) the authors note that some studies suggest a slowing of growth in late gestation. This certainly occurs in the human and sheep. It would be interesting to see if this also occurs in aquatic mammals. I do not see how this could done in baleen whales, but it could be possible in captive dolphins using serial ultrasound observations of fetal size.

I have no concerns with the manuscript, although I am not familiar with the equations used in the study and their viability. I believe that the study provides new data on reproduction in southern right whales and should be published.

[1] Grundy D. Principles and standards for reporting animal experiments in The Journal of Physiology and Experimental Physiology. Exp Physiol. 2015;100:755-8.

[2] Morrison JL. Sheep models of intrauterine growth restriction: fetal adaptations and consequences. Clin Exp Pharmacol Physiol. 2008;35:730-43.

[3] McMillen IC, Adams MB, Ross JT, Coulter CL, Simonetta G, Owens JA, et al. Fetal growth restriction: adaptations and consequences. Reprod. 2001;122:195-204.

[4] McMillen IC, Robinson JS. Developmental origins of the metabolic syndrome: prediction, plasticity, and programming. Physiological reviews. 2005;85:571-633.

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Referee #2:

This study demonstrated fetus development and birth sizes of southern right whales by the regression models with some potential covariates. The relationship between maternal body length and calf birth length and calf birth sizes are new findings and useful for monitoring this endanger species. I think the modelling exercises are appropriately done and the outputs are definitely useful, and overall the manuscript it well written and organized. However the authors need to be careful to assume biological input data since fetuses and animals after birth have different circumstances and demands of nutritive composition for their growths.

Better to use "common" minke whales (Balaenoptera acutorostrata)

L320-326 The authors made a choice to uses the mean lipid and protein concentrations from adult animals not from those from fetus records. I do not see the justification for choosing a data from adult animals even if the sample size is small. Fetus does not need much lipid reserves during their growth, and fast fattening just after birth are well known in many marine mammals. It is also reasonable that fetuses have less lipid contents than adult animals. I would encourage the authors to add a calculation using the assumption of these data from Lockyer et al. (1985).

L422 The authors used the foetus data range in length from 0.017 to 4.75m. I think a more thorough explanation of the current thoughts on the foetus proportion is required. For example, the proportion of early stage of gestation differ from those at giving birth (ex. Lanzetti et al. 2020).

L560-564 The difference of fetus growing speed among maternal size is a biologically important finding. The authors are required to mention the timing of conception between larger and smaller females to justify the larger females growing their foetus faster.

L625-628 The authors concluded the foetus was already 2%ML at the time of fertilization. Again, a better explanation needs to be given with the morphological difference between early and late stage of gestation. I agree the point that the cost of foetus growth is negligible in the early stage of gestation.

Referee #3:

I was asked to take an initial look at this paper due to the presence of some complicated equations. I have substantial experience in allometry, and in my opinion the modelling conducted in this paper is robust. Multi-model selection was approached appropriately using information theoretic approaches, and there was rigorous checking of underpinning model assumptions, which is refreshing to see.
Referee #4:

Thank you for submitting your manuscript to The Journal of Physiology.

The Methods section ordinarily starts with the subheading "Ethical approval". There is no mention of ethical approval for your study. I recognise that the data collected were from aerial photographs (or historical data sets). The de novo data from the aerial photographs was collected at a time when ethical approval for all studies involving animals is the (required) norm. Was the study considered by an ethics committee at both institutions? Were other forms of institutional approval in place?

Whereas I recognise that the data gathered was from observations of the animals during normal behaviours, it is nevertheless necessary for a consideration of whether the act of gathering the data in any way affected the behaviours. This issue is best considered a priori by an ethics committee, even in circumstances where one might reasonably consider that the impact is small or even negligible. It is best practice for an independent evaluation of these issues so that the judgement does not sit exclusively with the investigators.

END OF COMMENTS
Response to reviewers comments from the submission to the Journal of Physiology (JP-RP-2021-282351)

**Manuscript ID number:** JP-RP-2021-282351  
**Manuscript title:** Foetal growth, birth size and energetic cost of gestation in southern right whales  
**Author(s):** F. Christiansen, M.M Uhart, L. Bejder, P. Clapham, Y. Ivashchenko, D. Tormosov, N. Lewin, and M. Sironi

**General comments:**
We are very thankful to the editor and the four reviewers for their fair and constructive criticism, which helped to improve the manuscript substantially. Following the journal requirements, four of the tables in supplementary materials have been moved to the main manuscript. The remaining supplementary material (i.e. 4 tables) has been moved to a public repository (figshare) as suggested by the editor, which is now referenced in the manuscript. In response to the editor and one of the reviewers, a correction factor has been added to the growth curve for relative foetal length so that the time of conception now corresponds to a foetal (embryo) length of 0. This step is described in Eqn. 21-22. We also clarified some of the methodology by adding equations for relative calf length at birth (Eqn. 17-18). Finally, following the advice of one of the reviewers, we added a fourth modelling approach to estimate the energetic cost of gestation (Approach 4), which uses the lipid and protein concentrations of a fin whale foetus presented in Lockyer et al. (1985).

Answers to the specific questions and recommendations from the reviewers follow in this document. The line numbers refer to the numbering in the revised manuscript with track changes (“Manuscript showing edits.doc”), except for the reviewers comments which are referring to the original version of the manuscript.

Thank you very much for your time and effort in reviewing this manuscript. We hope that you find this new version to be improved and a valuable contribution to the Journal of Physiology.

Best regards,

Fredrik Christiansen

**Answers to comments from editor:**

**Ethics Concerns:**
The Ethics Editor has reviewed the paper. Commercial whaling has a negative tone to it in the current time and data from the past is included in the paper. I just wanted to make sure that it was appropriately described.

**AUTHOR REPLY:** It is unclear what the journal expects us to do in terms of ethics approval for data that are more than half a century old, and which were collected in conjunction with commercial whaling operations that have long since ceased to exist. In the recent past, ethical concerns certainly have been raised with regard to data collected from current, ongoing whaling operations (such as those of Japan and Norway), since research has sometimes been used as a partial, and arguably spurious, justification for such lethal "sampling". Indeed, some journals reject publications based upon contemporary whaling
data, and one of us (Phil Clapham) was involved in establishing such a policy for two Royal Society journals for which he was an Associate Editor. However, the Soviet whaling fleet that was the source of the data used in this paper ceased operations in 1975, and archived historical whaling data from numerous sources are routinely used to address various scientific questions. It is unclear how one could reasonably require ethics approval for the use of data collected decades ago.

We added the following explanation in the methods (lines 246-251):
“...we used archived data of foetal length from 207 pregnant SRW females of known length that were caught (killed) in commercial catch operations by the Soviet whaling fleet Yuri Dolgorukiy, operating in the Southern Hemisphere between 1961 and 1967 (Fig. 1). Some of these data (155 of 207 measurements) were published in Best (1994) as refs 7 (Best, Mikhalev & Brownell, in prep.) and 8 (Tormosov, pers. comm.) in Table 2 in that paper; the full data set is archived at the International Whaling Commission (Cambridge, UK).”

Regarding ethics approval for the UAV work, the following paragraph was added at the beginning of the methods section (lines 129-151):
“Ethical approval
The UAV research in Argentina was carried out under permits from the Sub Secretaría de Conservación y Áreas Protegidas (#43-SsCyAP/18) and Dirección de Fauna y Flora Silvestres (#106/2018.SsG-M.P.), Chubut, Argentina. The UAV research in Australia was carried out under research permits from the Department for Environment and Water (DEW), South Australia (M26501-2, M26501-4, M26501-5 and M26501-6), and Marine Parks permits (MR00082-3-V, MO00082-4-R, MO00082-5-R and MO00082-6-R). The UAV was operated under UAV operator’s certificates with the necessary remotely piloted aircraft system licenses in accordance with regulations by the Australian Civil Aviation Safety Authority. The UAV research in both Australia and Argentina was carried out under animal ethics permits from Murdoch University (O2819/16), Western Australia, and DEW (4/2016), South Australia. Research has shown that the noise of the UAV used in this study (see model specifications in the next section) cannot be heard by the whales while close to the surface (Christiansen et al., 2016b). Further, a behavioural impact assessment found no differences in the behaviour of SRW mother-calf pairs in the presence and absence of the UAV, even when flying at a very low altitude (5m) (Christiansen et al., 2020b).”

Comments to the Author:
This is an interesting paper determining fetal growth trajectories in SRW. The paper would benefit from some editing to assist the broad readership of Journal of Physiology. For example, it is not clear that the SRW is one of many baleen species and that other baleen species have been studied. It would also be important to identify what is and isn't known in these different species and what new knowledge this study presents.

AUTHOR REPLY: We thank the editor for this suggestion and have edited the introduction to make it clearer that the SRW is one of 16 species of baleen whales (line 75): “Baleen whales, which comprise 16 species, are the largest animals on the planet (Lockyer, 1976)...”
The third paragraph in the introduction provides an overview of what is known in regards to foetal growth in baleen whales. This paragraph has now been edited to make it clearer which species are being referred to (lines 95-106):

“Based on data from humpback (Megaptera novaeangliae), blue (Balaenoptera musculus), fin (B. physalus), sei (B. borealis), common minke (B. acutorostrata) and gray whales (Eschrichtius robustus), Frazer & Huggett (1973) argued that baleen whale foetal length can be described by a single straight line through most of gestation. However, Laws (1959) demonstrated, using data from the same species (except gray whales), that foetal growth pattern in baleen whales follows a concave curve-like parabola, with initial linear slow growth followed by rapid exponential growth. This curvilinear pattern is supported by several other studies on the same species (Nishiwaki, 1959; Rice & Wolman, 1971; Masaki, 1976; Ivashin & Mikhailov, 1978; Christiansen et al., 2014b), with some studies (on gray whales) suggesting a deceleration in foetal growth towards the end of pregnancy (Zimushko & Ivashin, 1980; Rice, 1983).”

The novelty of this study was highlighted in the last paragraph of the discussion in the original version of the manuscript. This part has now been moved to the beginning of the discussion to better emphasize what new knowledge this study presents (lines 632-636):

“This study presents the first estimates of the cost of gestation in SRWs based on empirical data on foetal growth and calf birth sizes. We show that the daily cost of gestation can be high for baleen whales, and that maternal body size has a large influence on foetal growth rates and birth size. Further, we show that the vast majority of gestation costs were incurred during the third trimester.”

Some of the figures are complex and it would be useful to a figure that simplifies the data presentation.

AUTHOR REPLY: We are not sure which of the figures the editor is specifically referring to, or what is confusing about them, and hence it is difficult to address this question. We have tried to make the figures as simple as possible, but since the aim of this paper is to provide a comprehensive and detailed estimate of the cost of gestation in southern right whales, we didn’t want to compromise the information provided in the figures by simplifying them too much. Following the editor’s suggestion, we have made some simplifications to Fig. 7, by reducing the amount of information provided in sub-figures C and D.

It should also be noted that Journal of Physiology does not have supplementary files. All data should be included in the paper. As such, would all tables/figures be required in the paper. It is permissible to include data on a public repository such as figshare and to reference that site in the paper.

AUTHOR REPLY: We have moved Tables S1-S4 into the main manuscript and named them Table 1-4, respectively. The original Tables 1 and 2 are now renamed to Tables 5 and 6. The remaining four tables in the supplementary materials have been uploaded on figshare and a DOI number is now referred to in the manuscript (DOI: 10.6084/m9.figshare.17121446). The link is currently not active, but will be activated once the paper is at the proof stage.
In many places, 'fetus' is used but this should be 'fetal'. Eg fetal length, fetal growth.

**AUTHOR REPLY:** “Foetus” has been changed to “foetal” throughout the manuscript.

Line 53 - placental energy content

**AUTHOR REPLY:** Corrected.

Line 82 - However, high offspring growth rates incur large... would be more appropriate. If 'However' is used in the middle of a sentence, it should be preceded by a semicolon. There are several instances where this is the case.

**AUTHOR REPLY:** This has been corrected throughout the manuscript.

Whaling is a controversial area, and the authors must include information about ethics approvals for collecting and using the data in this paper. The acknowledgements section has information about approvals for the recent data collection using drones. This information should be moved to the methods section. Please refer to Grundy for information about what details are required [1] and the JP guidelines to authors for formatting. The fetal length data was from Russian ships commercial whaling records that have been published. The methods should have detail that clearly explains what data came from where. Was there ethics approval to collect/access this data? Please ensure that it is very clear that published data was used. The results say that the fetuses were extracted from the mothers; however, there was no information about how the mothers or fetus were killed or the ethics to do this.

**AUTHOR REPLY:** It is unclear what the journal expects us to do in terms of ethics approval for data that are more than half a century old, and which were collected in conjunction with commercial whaling operations that have long since ceased to exist. In the recent past, ethical concerns certainly have been raised with regard to data collected from current, ongoing whaling operations (such as those of Japan and Norway), since research has sometimes been used as a partial, and arguably spurious, justification for such lethal "sampling". Indeed, some journals reject publications based upon contemporary whaling data, and one of us (Phil Clapham) was involved in establishing such a policy for two Royal Society journals for which he was an Associate Editor. However, the Soviet whaling fleet that was the source of the data used in this paper ceased operations in 1975, and archived historical whaling data from numerous sources are routinely used to address various scientific questions. It is unclear how one could reasonably require ethics approval for the use of data collected decades ago.

To clarify where the catch data came from, we have revised the “Foetal length and volume” section in the methods (lines 246-251):

“We used archived data of foetal length from 207 pregnant SRW females of known length that were caught (killed) in commercial catch operations by the Soviet whaling fleet Yuri Dolgorukiy, operating in the Southern Hemisphere between 1961 and 1967 (Fig. 1). Some of these data (155 of 207 measurements) were published in Best (1994) as refs 7 (Best, Mikhalev & Brownell, in prep.) and 8 (Tormosov, pers. comm.) in Table 2 in that paper; the full data set is archived at the International Whaling Commission (Cambridge, UK).”

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Line 222 - Please include the appropriate citations for ref 7 and 8.
AUTHOR REPLY: Best 1994 only referenced 7 as “Best, Mikhailov & Brownell, in prep.” (this article was never published) and 8 as “Tormosov, pers. comm.”. We have edited the methods section to include this information (lines 249-251):

“Some of these data (155 of 207 measurements) were published in Best (1994) as refs 7 (Best, Mikhailov & Brownell, in prep.) and 8 (Tormosov, pers. comm.) in Table 2 in that paper; the full data set is archived at the International Whaling Commission (Cambridge, UK).”

Line 465 - The equations suggest that the fetus is 0.30m at conception. This doesn’t seem possible. However, how big is the oocyte?
AUTHOR REPLY: The 0.3m foetal length at conception (or actually 2% ML) was an consequence of the GLM being used. The model uses a log link to prevent negative values, but which also means that the regression line will never reach absolute zero. One solution to overcome this model limitation is to force the regression line of the relative foetal length model to 0 at -365 days (the day of conception based on a gestation length of 1 year) by adding a correction factor of -0.02116519 to the back-transformed model. This however would result in a birth length of the calves of 0.34980628-0.02116519 = 0.3286411, which would not correspond with the predicted relative birth length of calves (34.97% ML) from Model 2 in Table 2. Hence, instead of applying a fixed correction factor, we applied a gradual correction factor, which reduced the relative foetal length from 0 (at birth) to -0.021 at conception. We explained this additional step in the result section (lines 480-500):

“From the refitted GLMs, the estimated days to birth (Julian day-134) had a significant positive effect on relative foetal length ($F_{1,205}=360.4$, p-value<0.001, Fig. 6A). The model explained 63.7% (pseudo-$R^2$) of the deviance in the data. Days to birth (DTB) had a positive log-linear effect (mean=0.769% ML, SE=0.037, on the log-scale) on relative foetal length ($FL_{Rel}$) (Fig. 6A). $FL_{Rel}$, in prop. ML, could hence be predicted from:
\[ FL_{\text{Rel}} = \exp(-1.050376 + 0.007685 \times \text{DTB}) \]  \hfill (20)

Assuming a gestation period of one year (365 days), the size of the foetus (i.e. embryo) at the time of conception (DTB=-365) was:

\[ FL_{\text{Rel(conception)}} = \exp(-1.050376 + 0.007685 \times -365) = 0.021165 \]  \hfill (21)

A relative foetal (embryo) length of 2.1%ML at conception is unrealistic, and hence the following correction factor was added to Eqn. 20 to bind the size at conception (DTB=-365) to zero, while keeping the relative birth length at 34.97%ML (DTB=0):

\[ FL_{\text{Rel}} = \exp(-1.050376 + 0.007685 \times \text{DTB}) + (0.021165/365) \times \text{DTB} \]  \hfill (22)

“Equations 23-28 were also updated with this new correction factor. The correction factor did not significantly change any of the results, but made the foetal growth model more biologically realistic.

Line 501 - Should 'though' be 'through'
AUTHOR REPLY: Yes, this has been corrected.

Line 544 - Should the Pv=, Hob= have more detail?
AUTHOR REPLY: We apologize for having forgotten to enter these details. The sentence has been corrected to (lines 626-629):

“The cost of gestation differed only slightly between locations (PV=164.6 GJ, HoB=156.5 GJ, based on a 14m long female) as a consequence of the higher BBC of calves in PV compared to HoB, and both estimates were similar to that of calves born at an average body condition (BBC=0) (Fig. 7D).”

Line 553 - The details about data collection in different locations should be clearly outlined in the methods.
AUTHOR REPLY: The sample sizes were mentioned again in the discussion to highlight the scale of this study and the strength of the data set. The details about the data collection is provided at the beginning of the methods section for each relevant sub-section. The sample sizes of each data set is provided in the result section at the beginning of the relevant sub-sections.

Line 555-557 -Does the Christiansen 2020a paper use the same dataset as this paper? How do the two papers differ?
AUTHOR REPLY: Christiansen 2020a used data from four populations of right whales (North Atlantic, New Zealand, Argentina and Australia), including some of the Argentinian (part of the 2018 data) and Australian (part of the 2016 data) data sets used in the current paper. One of the models in the paper analyses calf length relative to maternal length. However the analyses does not include repeated measurements from the same mother and calf pair, and does not include birth size of calves based on re-sightings of late pregnant and early lactating females. The positive relationship found between calf body length and maternal body length in Christiansen et al. 2020a does not account for
differences in growth rates of calves as a function of maternal body size, and hence does not show that the difference in calf body length is caused by differences in birth size of calves as a function of maternal body length. The current paper therefore provides a significant advancement in our understanding of how maternal body size affect offspring body size in southern right whales.

Line 573 - Fetal growth restriction is common across species and occurs in the third trimester. Thus, it is not surprising that this may also occur in whales. There is evidence from other species that FGR is associated with poor outcomes in the neonatal period as well as late in life [2-4].

AUTHOR REPLY: We thank the editor for bringing these papers to our attention. We added some information about this in the discussion (lines 662-666): “Foetal (intrauterine) growth restriction is also common across mammalian species and can be caused by factors relating to the mother, the placenta or the foetus itself (for reviews, see McMillen et al., 2001 and Morrison, 2008). Foetal growth restriction has been associated with poor perinatal health outcomes as well as increased risk of disease in adult life (McMillen & Robinson, 2005).”

Line 655 - Miscarriage is likely a better term that abortion.

AUTHOR REPLY: This has been changed.

Line 698 - Please provide a copy of the paper that is under review. Is there overlap between the two papers?

AUTHOR REPLY: A copy of the manuscript “Christiansen et al. in review” has been uploaded with this submission. The aim of that paper was to estimate the energetic cost of postnatal somatic growth in southern right whales, from birth to adulthood. Both papers refer to each other, but does not overlap in terms of content, analyses or findings.

Three of the authors 'provided data'. Did they collect the data? Did they participate in data interpretation or conceive of the project?

AUTHOR REPLY: This sentence has been revised to (lines 836-837):
“SRW foetal data was processed, collated and provided by P.C., Y.I. and D.T.”

Line 740 - should the xxx and xxx be numbers?

AUTHOR REPLY: Yes, these will be added at the proof stage of the article by the University of Hawaii.

Line 744- 747 and 751-757 should be in the methods.

AUTHOR REPLY: Corrected.

Answers to comments from reviewer 1:
This manuscript describes studies of fetal growth birth size and the energetic costs of gestation in southern right whales.

On page 4 of the introduction (lines 100-102) the authors note that some studies suggest a slowing of growth in late gestation. This certainly occurs in the human and sheep. It would be interesting to see if this also occurs in aquatic mammals. I do not see how this could done in baleen whales, but it could be possible in captive dolphins using serial ultrasound observations of
fetal size.

**AUTHOR REPLY:** We agree with reviewer 1 that it would be very interesting to investigate a slowing in foetal growth in late gestation in marine mammals. As reviewer 1 points out though, there is no captive studies of baleen whales that would make such a study possible. However, there are several facilities that keep and breed dolphins, and in such a setting it would be possible to investigate foetal growth restriction from ultrasound measurements through gestation. Obtaining a sufficiently large sample size to say something conclusively would take time, but it could be worthwhile to pursue.

In regards to foetal growth restriction, we added the following text to the discussion (lines 662-666):

“Foetal (intrauterine) growth restriction is also common across mammalian species and can be caused by factors relating to the mother, the placenta or the foetus itself (for reviews, see McMillen et al., 2001 and Morrison, 2008). Foetal growth restriction has been associated with poor perinatal health outcomes as well as increased risk of disease in adult life (McMillen & Robinson, 2005).”

I have no concerns with the manuscript, although I am not familiar with the equations used in the study and their viability. I believe that the study provides new data on reproduction in southern right whales and should be published.

**AUTHOR REPLY:** We thank the reviewer for endorsing our manuscript. In regards to the equations, we refer to reviewer 3s evaluation of the paper (see below).

**Answers to comments from reviewer 2:**
This study demonstrated fetus development and birth sizes of southern right whales by the regression models with some potential covariates. The relationship between maternal body length and calf birth length and calf birth sizes are new findings and useful for monitoring this endanger species. I think the modelling exercises are appropriately done and the outputs are definitely useful, and overall the manuscript it well written and organized. However the authors need to be careful to assume biological input data since fetuses and animals after birth have different circumstances and demands of nutritive composition for their growths.

**AUTHOR REPLY:** We thank the reviewer for his/her comments. We agree with the reviewer that both the tissue composition and tissue energy content is likely to differ between foetuses and animals after birth. We have therefore followed the later suggestion of the reviewer (see comment for L320-326 below) to add a calculation of foetal growth costs based on the foetal data presented in Lockyer et al. (1985). See answer to comment L320-326 below.

184 Better to use "common" minke whales (Balaenoptera acutorostrata)

**AUTHOR REPLY:** This has been corrected throughout the manuscript.

L320-326 The authors made a choice to use the mean lipid and protein concentrations from adult animals not from those from fetus records. I do not see the justification for choosing a data from adult animals even if the sample size is small. Fetus does not need much lipid reserves during their growth, and fast fattening just after birth are well known in many marine mammals. It is also reasonable that fetuses have less lipid contents than adult animals. I would encourage the authors to add a calculation using the assumption of these data from Lockyer et al. (1985).
AUTHOR REPLY: We agree with the reviewer that there are large uncertainties in regards to what the actual lipid and protein concentration of various tissues are in SRW foetuses. We have therefore followed the reviewer’s advice and added a calculation of the cost of gestation based on the foetal lipid and protein concentrations reported for a fin whale foetus in Lockyer et al. (1985). This is referred to as Approach 4 in the paper in the methods section (lines 370-373):

“In the fourth (Approach 4), the tissue energy density was based on the fin whale foetus measured in Lockyer et al., (1985). Since no values for lipid or protein concentrations were provided for the bones of the fin whale foetus, we used the same values as for foetal muscle.”

And in the result section (lines 623-626):

“Both the total cost and the maximum daily cost of gestation was lower for modelling Approach 3 (assuming a fixed energy content for all tissues) and modelling Approach 4 (assuming the same tissue energy content as a fin whale foetus), with the latter being slightly lower.”

The uncertainty regarding the tissue energy content of SRW foetuses has been highlighted in the discussion (lines 785-800):

“In addition, the costs of foetal growth are based on assumed tissue energy densities derived from juvenile and adult whales from other species, and might hence not be representative for SRW foetuses. Lipid and protein concentration in blubber, muscle and visceral tissues has been shown to vary significantly seasonally across the body of whales, and also between species and reproductive classes (Lockyer et al., 1984, 1985; Lockyer, 1987a; Aguilar & Borrell, 1990; Vikingsson, 1990; Vikingsson et al., 2013). Christiansen et al. (in review) demonstrated through model simulations that varying these tissue energy densities within their reported ranges can result in nearly a doubling in energy expenditure from the lowest to the highest values. This was also evident in our study when comparing the results from modelling approaches 1 and 2 with that of modelling approach 3 and 4 which assumed an overall lower tissue energy content. Which of these modelling approaches is closest to the true cost of gestation in SRWs is unknown, and this uncertainty needs to be acknowledged (or incorporated) in bioenergetic models relating to foetal growth in baleen whales. With empirical data on foetal energy content lacking, we encourage researchers to measure this from either stranded pregnant females or animals accidentally caught in fishing gear.”

L422 The authors used the foetus data range in length from 0.017 to 4.75m. I think a more thorough explanation of the current thoughts on the foetus proportion is required. For example, the proportion of early stage of gestation differ from those at giving birth (ex. Lanzetti et al. 2020).

AUTHOR REPLY: We assume that the reviewer is referring to the relationship between foetal volume and foetal length, and/or the relationship between different body parts (e.g. head size versus foetal length), throughout gestation. We agree with the reviewer that body morphometrics are likely to change during gestation, however we had no data to inform this pattern. We knew from photogrammetric studies of newborn SRW calves what the body volume to length relationship would look like for a calf at birth, as well as the relationship between body length, body width and body height (dorso-lateral distance). Since we knew that the foetus would end up having these proportions at the time of birth,
and that the overall costs of foetus growth would be more or less the same irrespective of how this relationship would vary through gestation, we assumed that the body volume to length relationship would remain constant through gestation. To make this clear in the paper, we added the following text to the discussion (lines 800-809):

“Finally, our estimates of growth in foetal volume and mass are based on the body volume to length relationship of newborn SRW calves, which might not be representative for a foetus throughout gestation. Lanzetti et al., (2020) used 3D landmarks to demonstrate changes in the cranial morphology of humpback whale foetuses relative to a juvenile specimen, and found significant differences. While a similar approach would have been desirable in our study, such data was not available for SRWs. Since we knew that the growing foetus would ultimately obtain a similar body shape as that of a newborn SRW calf (for which we had data), and we assumed that the absolute energetic cost of reaching those body proportions would be the same irrespective of how the body shape varied throughout gestation, we extrapolated the body volume to length relationship of newborn SRWs to the entire gestation period.”

L560-564 The difference of fetus growing speed among maternal size is a biologically important finding. The authors are required to mention the timing of conception between larger and smaller females to justify the larger females growing their foetus faster.

AUTHOR REPLY: We do not know the exact timing of conception for individual whales, however we could calculate the day of birth of calves based on the growth rate in calf volume and the assumed birth volume of the calves. Assuming a one year gestation period, the timing of conception should be the same as the day of birth minus one year. We found no effect of maternal length of the day of birth (and hence time of conception) in SRWs. We added this to the result section (lines 479-480):

“Day of birth (and hence the time of conception) was not affected by maternal body length.”

L625-628 The authors concluded the foetus was already 2%ML at the time of fertilization. Again, a better explanation needs to be given with the morphological difference between early and late stage of gestation. I agree the point that the cost of foetus growth is negligible in the early stage of gestation.

AUTHOR REPLY: Based on this comment and that of the editor, we added a gradual correction factor to the foetal length growth model to bind it to 0%ML at conception. We explained this additional step in the result section (lines 480-500):

“From the refitted GLMs, the estimated days to birth (Julian day-134) had a significant positive effect on relative foetal length (F_{L_{rel}}=360.4, p-value<0.001, Fig. 6A). The model explained 63.7% (pseudo-R^2) of the deviance in the data. Days to birth (DTB) had a positive log-linear effect (mean=0.769%ML, SE=0.037, on the log-scale) on relative foetal length (F_{L_{rel}}) (Fig. 6A). F_{L_{rel}}, in prop. ML, could hence be predicted from:

\[ F_{L_{rel}} = \exp(-1.050376 + 0.007685 \times DTB) \]  

(20)

Assuming a gestation period of one year (365 days), the size of the foetus (i.e. embryo) at the time of conception (DTB=-365) was:
\[ FL_{\text{Rel}(\text{conception})} = \exp(-1.050376 + 0.007685 \times -365) = 0.021165 \] (21)

A relative foetal (embryo) length of 2.1\%ML at conception is unrealistic, and hence the following correction factor was added to Eqn. 20 to bind the size at conception (DTB=-365) to zero, while keeping the relative birth length at 34.97\%ML (DTB=0):

\[ FL_{\text{Rel}} = \exp(-1.050376 + 0.007685 \times DTB) + (0.021165/365) \times DTB \] (22)

Equations 23-28 were also updated with this new correction factor. The correction factor did not significantly change any of the results, but made the foetal growth model more biologically realistic.

Answers to comments from reviewer 3:
I was asked to take an initial look at this paper due to the presence of some complicated equations. I have substantial experience in allometry, and in my opinion the modelling conducted in this paper is robust. Multi-model selection was approached appropriately using information theoretic approaches, and there was rigorous checking of underpinning model assumptions, which is refreshing to see.

AUTHOR REPLY: We thank the reviewer for endorsing the modelling conducted in this paper. We are also grateful to the editor for sending this paper to a specialist in allometry, to double check the validity of our approach.

Answers to comments from reviewer 4:
Thank you for submitting your manuscript to The Journal of Physiology.
The Methods section ordinarily starts with the subheading "Ethical approval". There is no mention of ethical approval for your study. I recognise that the data collected were from aerial photographs (or historical data sets). The de novo data from the aerial photographs was collected at a time when ethical approval for all studies involving animals is the (required) norm. Was the study considered by an ethics committee at both institutions? Were other forms of institutional approval in place?

AUTHOR REPLY: Yes all UAV data was collected under appropriate animal ethics approvals. This has been clarified in the methods section (lines 129-147):

“Ethical approval
The UAV research in Argentina was carried out under permits from the Sub Secretaría de Conservación y Áreas Protegidas (#43-SsCyAP/18) and Dirección de Fauna y Flora Silvestres (#106/2018.SsG-M.P.), Chubut, Argentina. The UAV research in Australia was carried out under research permits from the Department for Environment and Water (DEW), South Australia (M26501-2, M26501-4, M26501-5 and M26501-6), and Marine Parks permits (MR00082-3-V, MO00082-4-R, MO00082-5-R and MO00082-6-R). The UAV was operated under UAV operator’s certificates with the necessary remotely piloted aircraft system licenses in accordance with regulations by the Australian Civil Aviation Safety Authority. The UAV research in both Australia and Argentina was carried out under animal ethics permits from Murdoch University (O2819/16), Western Australia, and DEW (4/2016), South Australia.”
Whereas I recognise that the data gathered was from observations of the animals during normal behaviours, it is nevertheless necessary for a consideration of whether the act of gathering the data in any way affected the behaviours. This issue is best considered a priori by an ethics committee, even in circumstances where one might reasonably consider that the impact is small or even negligible. It is best practice for an independent evaluation of these issues so that the judgement does not sit exclusively with the investigators.

AUTHOR REPLY: We agree with the reviewer that it is important to collect data with minimum impact on the study species. In an earlier study we investigated the underwater noise level of UAVs (the same model as the one used in this study) when flying at different altitudes, and found that the noise was negligible (below that of ambient noise) at 1m depth. In another study, we measured the potential behavioural response of southern right whale mother-calf pairs to low flying (5m altitude) UAVs. Potential changes to horizontal behavior (swim speed and turning angle) and surfacing pattern (inter-breath intervals) were investigated by comparing mother-calf behaviour before and during UAV approaches. Changes in respiration rate were used to quantify energetic effects. We also explored acoustic cue perceptibility of the UAV at 5, 10, and 30m altitude, by measuring the received UAV underwater noise level on whales equipped with acoustic tags (DTAGs). No behavioural response to the UAV was observed, providing support for UAVs as a non-invasive tool to study baleen whale behaviour and ecophysiology. To clarify this in the manuscript, we added the following text to the methods section (lines 147-151):

“Research has shown that the noise of the UAV used in this study (see model specifications in the next section) cannot be heard by the whales while close to the surface (Christiansen et al., 2016b). Further, a behavioural impact assessment found no differences in the behaviour of SRW mother-calf pairs in the presence and absence of the UAV, even when flying at a very low altitude (5m) (Christiansen et al., 2020b).”
Dear Dr Christiansen,

Re: JP-RP-2021-282351R1 "Foetal growth, birth size and energetic cost of gestation in southern right whales" by Fredrik Christiansen, Marcela M Uhart, Lars Bejder, Phil Clapham, Yulia Ivashchenko, Dmitry Tormosov, Nicolás Lewin, and Mariano Sironi

I am pleased to tell you that your paper has been accepted for publication in The Journal of Physiology.

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Yours sincerely,

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EDITOR COMMENTS

Reviewing Editor:

Thank you for revising the manuscript.

REFEREE COMMENTS

I thank the authors that my concern was agreed and an additional calculation was made for the foetal growth before parturition. I admit the revised manuscript satisfied my question in the previous review.

Right whale is one of the most endangered whale species in large baleen whales. Authors used data both from advanced technology and old records from commercial whaling.

1st Confidential Review 08-Dec-2021