

Migrating baleen whales transport high-latitude nutrients to tropical and subtropical ecosystems

Corresponding Author: Dr Joe Roman

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This file contains all reviewer reports in order by version, followed by all author rebuttals in order by version.

Attachments originally included by the reviewers as part of their assessment can be found at the end of this file.

Version 0:

Reviewer comments:

Reviewer #1

(Remarks to the Author)

General comments:

This study attempts to quantify the amount of energy that baleen whales transfer from high latitude feeding grounds to low latitude breeding grounds. While the conceptual idea of a global estimate of this is appealing, and of great importance for the management and conservation of large whales, there are some major shortcomings that prevents me from endorsing this study. This has to do mainly with the modelling approach and the parameter values used, as well as how the authors dealt with the many assumptions that needed to be made to carry out this kind of study on a global scale.

In regards to methodology, while the general approach is good, the actual modelling, calculations and assumptions are weak at best. First, there is no uncertainty given for any of the parameters, and consequently all the results are given as single values without any confidence intervals. That is very misleading for any reader, as it gives the false pretence that there is confidence behind these estimates, where in fact they are resting on a large number of assumptions and parameters with considerable uncertainty (which was not accounted for). This is a major weakness of the study, and needs to be addressed before the paper is accepted by any journal. The modelling approach includes many uncertain variables and parameters, going from population sizes, to body sizes, to residency times, to protein content etc. All of these variables/parameters comes with considerable uncertainty, and I suspect that when you add them all together you are going to end up with a huge confidence interval around your final predictions. That is fine; it is the nature of the game when you are trying to calculate something as complex as this, but it needs to be clearly shown throughout the process, and not hidden behind means or references to other papers. There are some places where it is not entirely clear what the input data was or where it comes from (empirical or theoretical). For example, what was the assumed body mass of the different whale species, and was a single value used for each species? Did you account for differences in age classes (and consequent mass)? A reference is provided, but when looking through that article, I could not find the data either (see specific comment below). Try to make it easy for the reader to see exactly what you did and provide a table where all your model parameter values are listed. Then add the confidence interval to each of these values, and run a sensitivity analysis to see what happens when you vary these parameter values within their known confidence intervals.

I also have some issues with the literature that is being cited, especially when choosing input parameter values and dealing with assumptions in your model. Many of the cited articles are very old, and while they are good articles, considerable work has been done in these fields and more recent (and accurate) estimates could be used instead. For example, it seems like the authors have missed the large number of bioenergetic studies of large whales coming out over the last five years, including empirical measurements as well as pure modelling exercises. I think this paper would greatly benefit from looking through those studies and updating many of their model assumptions with more appropriate (and ideally empirically based) estimates.

Finally, while the overall story of the paper is good and there is a nice flow, there are some major implications made in the text (e.g. about migration) and the referencing is poor (often with outdated references or sometimes no references).

I have provided some more specific comments below.

Based on the above, I do not think this study is of sufficient standard to be published in a prestigious journal like Nature Communications.

Specific comments:

Lines 57-59: What about the thermal benefits for young calves to be born in warmer temperature or tropical waters? I do not think the theories given for baleen whale migration here is exhaustive, and given a single reference for each theory is not enough. This is a huge question that is still not empirically answered, and that needs to be better reflected in these sentences.

Lines 64-66: Please provide some references here for the costs of gestation and lactation.

Lines 182-184: Is there any support for this speculation? Any references?

Line 216: What is the three month residency time of humpback mother-calf pairs based on? Residency time for individual whales on their breeding grounds (or feeding grounds for that matter) is poorly understood and this uncertainty needs to be incorporated in your estimates.

Line 226: 40 tonnes is a very high weight for a humpback whale. Where is the empirical justification for this value? What length was that based on? There is differences in the size of humpback whales between the northern and southern hemisphere. Many recent studies have measured the size (length) of whales with photogrammetry. Why not update your estimates with those findings.

Lines 238-240: The theory about cetaceans migrating to molt has been shown only in killer whales, and only from Antarctica. Hence, assuming that this could be a major reason for migration in other cetaceans is very speculative.

Lines 280-282: Southern right whales does not really conform to the traditional migration pattern between high and low latitudes. Over the last years, satellite-tagging studies have actually revealed that right whales make considerable longitudinal migrations during the feeding season, and some individuals does not travel very far south at all.

Lines 322-323: It is not clear from the text or tables what the assumed body masses were for the different species. There is a reference to Pershing et al., but that article too does not provide values of the body mass of the different species. It would be helpful if the authors could provide the input data for their calculations clearly in a table, with appropriate confidence intervals.

Lines 323-324: This equation is based on a study from 1997. There has been many advances in our knowledge of the body size (length and mass) of newborn baleen whales, which could provide more accurate estimates than Webb.

Lines 329-331: Is there no data on baleen whale placentas from historical whaling? Or commercial whaling? Surely, it would be better to base your estimate on a baleen whale rather than an odontocetes. Further, was there no confidence interval around the 10% value?

Line 331: Again, a single value is used for the protein content of the placenta. Surely, there must be some uncertainty around this value no? Is there no data from marine mammals?

Line 333: Is 16% an accurate value, or is there uncertainty around this value as well? If so, please provide it, or otherwise give a justification to why there is no variation.

Lines 338-339: These are major assumptions, without any justification. How does these values compare to those estimated from whaling records (see many of the papers from Lockyer, Vikingsson etc.). There must be considerable variations in these values, and differences between species, age-classes and reproductive states. That variation needs to be incorporated into these analyses, to see how it will affect the final estimates.

Lines 363-364: But calves grow very rapidly during the first months of their lives, which requires a lot of energy from their mothers. In addition, the mass-specific field metabolic rates is higher for smaller calves, which further increases the cost when they are younger/smaller. So although the calves are small, they are not energetically cheap for the mother.

Lines 365-366: The days spent on the calving grounds is no doubt a very important parameter in these calculations, yet the input data (summarized in Table S4) is not very accurate, and does not provide any confidence intervals. Why are the months rounded to the nearest value? Surely, that compromises accuracy no? Further, are these values based on the presence of whales (as populations) on their feeding/breeding grounds, or individual whales? In several places, the values does not match those provided from studies of the same species on their breeding and feeding grounds. For example, humpback whales migrate along both the western and eastern coastline of Australia between May and November, yet the start and ends months are given as 7 and 10. The same goes for southern right whales, which are present on their breeding grounds as early as May and leaves in October.

Lines 398-399: What is this based on? Even though it is an assumption, you need to provide some justification to it.

Reviewer #2

(Remarks to the Author)

This manuscript provides an interesting analysis of the potential role of great whales in transporting nutrients and material from high-latitude feeding grounds to low-latitude breeding grounds. The rationale of the analysis is that whales accumulate great amounts of energy during intensive summer feeding periods at high latitudes, and that these resources are used at breeding grounds, where excess material is excreted in feces and urine. In addition, the authors include estimates of the number of carcasses and placentas produced, and add these to the overall carbon and nutrient transport estimates. The authors conclude that the seasonal migrations of whales contribute very substantially to the overall global carbon and nutrient transport, and that this role would have been several times greater before commercial hunting decimated several of the world's great whale stocks.

The manuscript thus represents a contribution to the growing literature discussing the potential role of whales as ecosystem engineers, and thus the material in the manuscript is of great relevance and highly topical. However, I have several serious concerns about the approach taken and, in particular, with some of the very strong assumptions made by the authors in their calculations. I provide detailed comments and questions to the authors in the attached commented PDFs of the manuscript and supplementary materials documents. In short, my main concerns are with:

1. The estimate of reproductive females that migrate and give birth to calves. The authors assume that all females in the population do this. In fact, for many of the relevant species, about half of the females will be sexually immature. In addition to not giving birth (giving rise also to placentas and calf carcasses), they may not even migrate to low-latitude calving grounds.
2. The authors use estimates of calf and adult annual mortality to estimate the number of carcasses that may be added to the breeding grounds. This seems to assume that all of this annual mortality occurs at these calving grounds. This is highly unrealistic, and the number of carcasses is therefore likely highly overestimated.
3. I have trouble understanding how the ratios of feeding to breeding/calving grounds are calculated. Do they represent some ratio of number of observations, in which case this is problematic when using highly disparate, and partially opportunistic sightings, or do they represent geographic areas? This is not clearly described in the methods or SI
4. Finally, while the authors cite an online repository for the data and code used to calculate their estimates, this link does not exist. Presumably, this is planned to become live once the paper is published. However, similar to many other manuscripts submitted for review, I would have expected that data and code would be made available to the reviewers, so that they can evaluate the analyses and results. As it now stands, I tried to recreate the calculations as best I could, but arrive at very different numbers. My treatment of the results section is therefore cursory, as I suspect many of the estimates are biased from the strong assumptions made (and other issues detailed in my comments in the documents).

My recommendation is to not accept this manuscript for publication in its current form. There are simply too many assumptions and other potentially serious issues with the methodology that I feel must be addressed before reconsidering for publication. My recommendation is therefore that the authors are invited to resubmit a substantially reworked version of the manuscript. I would also encourage the authors to submit their data and code as part of the submission, so that reviewers are better able to evaluate the work.

Version 1:

Reviewer comments:

Reviewer #1

(Remarks to the Author)

The authors have done a great job with revising the article and incorporating uncertainty in their many parameters and estimates. They have also improved the justification of values used for the different model parameters, which I believe adds confidence to the estimates. Where the authors have disagreed with my previous comments and suggestions, they have done so with good justification and arguments. I am therefore happy to endorse this paper for publication. I list a few minor edits (mainly adding 95%CIs to the estimates presented in the text) below which I picked up reading through the last version of the manuscript:

The authors argue that "To our knowledge, direct observations of newborn whale calves are rare. Webb's allometric model gives us a consistent way of estimating calf size as a function of adult size". There are however, recent studies on humpback whales, gray whales and southern right whales that provide direct measurements of calf sizes (including birth sizes). Anyways, since it probably does not change the results much, the current approach is fine.

Lines 32-33 (Abstract): add Latin names of species.

Line 62: Add Latin name for killer whale.

Line 103: Please add 95%Cis also for biomass and C.

Line 106: Again, please add 95%CI to the C production estimate.

Lines 114-116: Please add 95%CIs to all estimates presented here.

Lines 142-143: Add 95%CIs to all estimates.

Lines 151-155: Add 95%CIs to all estimates.

Line 164: Add 95%CIs to all estimates.

Lines 166-168: Add 95%CIs to all estimates.

Lines 230-231: Add 95%CIs to all estimates.

Line 235: Add 95%CIs to estimate.

Double check that Latin names are added for all species mentioned in the paper

Please add 95%CIs to all estimates produced from this study.

I congratulate the authors on a very important and impressive study.

Fredrik Christiansen

Reviewer #2

(Remarks to the Author)

I have now gone through the responses from authors, and the changes made to the manuscript in response to issues raised by myself and the other reviewer. I note that the other reviewer broadly agreed with my original assessment, that 'while the general approach is good, the actual modelling, calculations and assumptions are weak at best'. While the authors have now included a sensitivity analysis to partially address this issue, I find the description of their approach to this sensitivity analysis lacking in detail. There is virtually no information on how the sensitivity analysis was actually carried out, which makes it very difficult to evaluate if their conclusions from this are valid. While the authors present a figure (Fig S6) supposedly showing the relative importance of the five main parameters in terms of how it contributes to the uncertainty, this appears almost entirely driven by the coefficients of variation the authors chose as input into the sensitivity analysis. Without any information about the sensitivity analysis approach itself, I was left wondering what this figure actually shows, other than what the input uncertainties were that the authors entered into the analysis. As pointed out by the other reviewer: 'All of these variables/parameters comes with considerable uncertainty, and I suspect that when you add them all together you are going to end up with a huge confidence interval around your final predictions. That is fine; it is the nature of the game when you are trying to calculate something as complex as this, but it needs to be clearly shown throughout the process, and not hidden behind means or references to other papers'. It is unclear if, and if so how, this was actually done in the sensitivity analysis. All that is now presented (aside from the somewhat uninformative Fig S6) is the uncertainty on total N in Table 1. I think the uncertainties should be traced all the way through the calculations, to make it clear where and how they affect the estimates.

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Thanks to both reviewers for their careful read of the manuscript. We believe the manuscript reads *much* better as a result—and it gives more acknowledgment of the uncertainty and assumptions.

Below, we address the substantive changes suggested by the reviewers. We have also accepted most of the grammatical and stylistic changes. And though we have not listed a response to all of the comments below (there were ~100 individual comments), in the rare case when we disagreed, we expressed it below.

We have now posted all data and calculations on figshare:
https://figshare.com/articles/dataset/Great_Whale_Conveyor_Belt/25021040. We have also updated the editorial policy checklist and the reporting summary.

Uncertainty values have been added for the total nitrogen transported by great whales, as requested by the reviewers. Sobel sensitivity indices (see Figure S6) have been included to explore the impact of model inputs. We focused on five parameters that generate most of the uncertainty in our estimation of whale nutrient transport. They overwhelm the impact of other parameters, such as placenta size and N concentration. We present these uncertainties in our updated text and explore how we can refine estimates in our discussion. We note, however, that even our lower estimates are comparable to known important fluxes of abiotic (e.g., upwelling) and biotic (e.g., seabird) inputs. Please see below and in the text for more details.

Our responses to the suggestions of the reviewers are below. In the vast majority of cases, we have taken their suggestions. When we didn't, we explained our reasoning below.

Response to Reviewer One

Uncertainty and sensitivity

1. This study attempts to quantify the amount of energy that baleen whales transfer from high latitude feeding grounds to low latitude breeding grounds. While the conceptual idea of a global estimate of this is appealing, and of great importance for the management and conservation of large whales, there are some major shortcomings that prevents me from endorsing this study. This has to do mainly with the modelling approach and the parameter values used, as well as how the authors dealt with the many assumptions that needed to be made to carry out this kind of study on a global scale.

In regards to methodology, while the general approach is good, the actual modelling, calculations and assumptions are weak at best. First, there is no uncertainty given for any of the parameters, and consequently all the results are given as single values without any confidence intervals. That is very misleading for any reader, as it gives the false pretence that there is confidence behind these estimates, where in fact they are resting on a large number of assumptions and parameters with considerable uncertainty (which was not accounted for). This is a major weakness of the study, and needs to be addressed before the paper is accepted by any journal. The modelling approach includes many uncertain

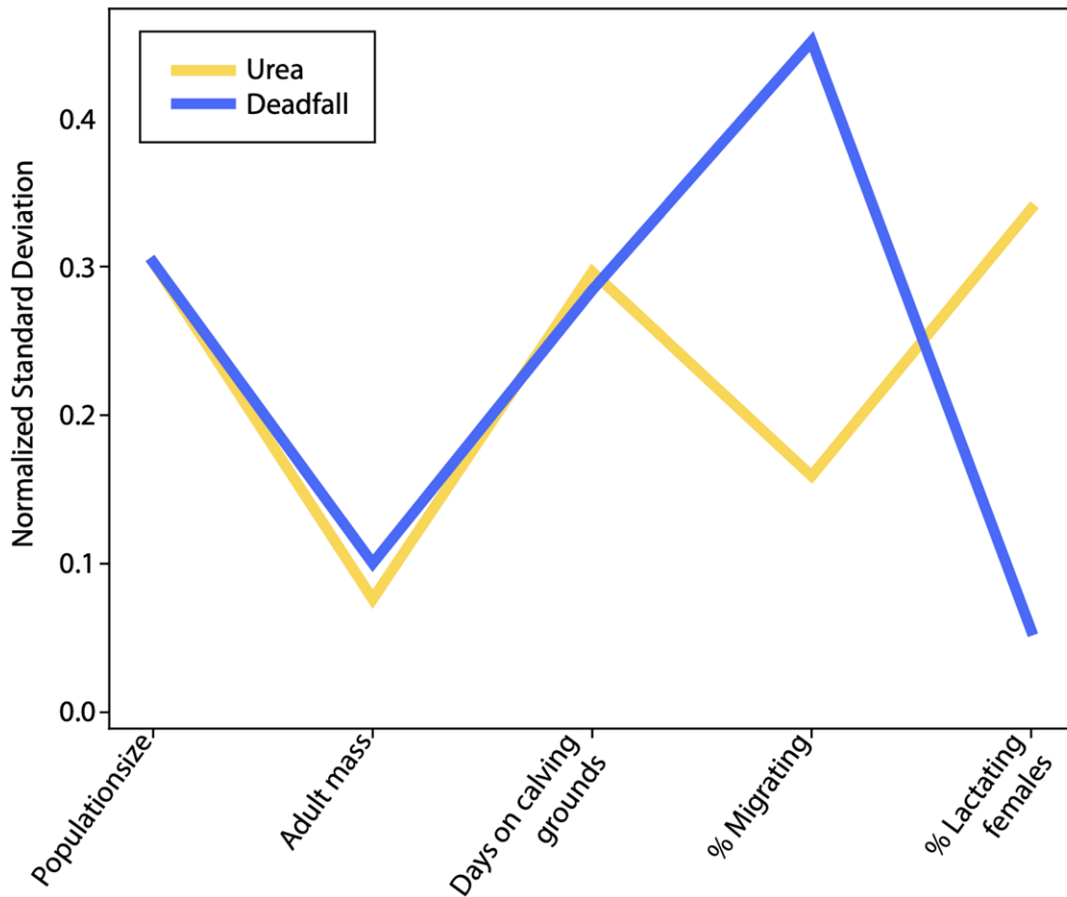
variables and parameters, going from population sizes, to body sizes, to residency times, to protein content etc.

All of these variables/parameters comes with considerable uncertainty, and I suspect that when you add them all together you are going to end up with a huge confidence interval around your final predictions. That is fine; it is the nature of the game when you are trying to calculate something as complex as this, but it needs to be clearly shown throughout the process, and not hidden behind means or references to other papers. There are some places where it is not entirely clear what the input data was or where it comes from (empirical or theoretical). For example, what was the assumed body mass of the different whale species, and was a single value used for each species? Did you account for differences in age classes (and consequent mass)? A reference is provided, but when looking through that article, I could not find the data either (see specific comment below). Try to make it easy for the reader to see exactly what you did and provide a table where all your model parameter values are listed. Then add the confidence interval to each of these values, and run a sensitivity analysis to see what happens when you vary these parameter values within their known confidence intervals.

We thank Reviewer 1 for raising this important concern. Originally, we included uncertainty within our calculations by considering both a conservative estimate (nutrient transport by only mothers and calves) and a best guess (all whales). However, we recognize that this overlooks relevant uncertainty inherent within each parameter of our model. We have now included uncertainty parameters for Total N and made the model and data openly available at https://figshare.com/articles/dataset/Great_Whale_Conveyor_Belt/25021040. The estimates provided are taken from the literature, and we have added cases where a range of variables is available (population sizes in particular).

We focus our sensitivity analysis on five major parameters in our model: population size, adult mass, time on wintering (breeding grounds), percent migrating, and percent lactating. While there are further parameter inputs for our model, we focused on these five as they have been identified as the primary drivers of uncertainty in whale nutrient subsidies (see Gilbert et al. 2023 *Nature Communications*, figure 7), and our preliminary tests established that uncertainty in these parameters overwhelmed the effects of other parameters (e.g., placenta size and N concentration).

In general, the uncertainty in our estimates was generated more by the population parameters (number of whales, % migrating) than by the biological parameters (adult mass and thus calf mass and any of the allometric terms). Examining the parameters most important for urea vs deadfall inputs, indicated that urea N is most sensitive to population size, days on the calving ground, and percentage of lactating females. In contrast, deadfall N is most sensitive to the percent of the population migrating (Fig. S6).



New Fig S6.

We recognize that our original presentation of results appeared to state our calculations definitively. We present uncertainty errors for Total N in Table 1 and throughout the manuscript to address this. Our analysis concludes that the population estimates and the number of days spent by different demographic groups on the calving grounds are critical to understanding the exact magnitude of whale nutrient subsidies. We refer to the need for such parameters to be better refined to advance our whale-nutrient-transport quantification. However, we note that even our conservative lower estimates are of significant importance when compared to known important abiotic (e.g., physical processes) and biotic (e.g., seabirds), indicating that whales likely have a meaningful impact on the biogeochemical cycles of subtropical ecosystems.

Regarding adult mass, we used an average adult mass for males and females. We did not include age classes, as they are unavailable for most species and even in cases where we might have some idea of age distribution, weight is not known for different age classes. We have noted this uncertainty and included it in our analysis. The sensitivity analysis indicates that population-level parameters, such abundance and percent of population migrating, have a greater impact on the final estimates.

2. I also have some issues with the literature that is being cited, especially when choosing input parameter values and dealing with assumptions in your model. Many of the cited articles are very

old, and while they are good articles, considerable work has been done in these fields and more recent (and accurate) estimates could be used instead. For example, it seems like the authors have missed the large number of bioenergetic studies of large whales coming out over the last five years, including empirical measurements as well as pure modelling exercises. I think this paper would greatly benefit from looking through those studies and updating many of their model assumptions with more appropriate (and ideally empirically based) estimates.

One of our co-authors, Dan Costa, has spent considerable time and effort on this interesting question and has been a co-author on several of the recent bioenergetic papers. Several recent whale bioenergetics models rely on either a best guess or an application of the only baleen whale empirical measurement of metabolic rate produced by Jim Sumich. However, this is irrelevant because we don't make an estimate of whale metabolic rate. Rather, we were interested in estimating the whale's fasting protein catabolism. There are no measures of protein catabolism for any cetacean, so we chose to use the closest proxy, which is a capital breeding elephant seal. The text was clarified to make this point, and a very recent reference to a review of cetacean metabolic rates was also added. For a more thorough response see below (note 61, reviewer 2).

3. Finally, while the overall story of the paper is good and there is a nice flow, there are some major implications made in the text (e.g. about migration) and the referencing is poor (often with outdated references or sometimes no references).

We have now updated our references. We have also streamlined our text to focus on only the details necessary for our study. For instance, we have reduced text on the possible causes of migration. While this point is interesting, it is clearly distracted from our main message, which is that a considerable number of baleen whales undertake vast migrations and, in doing so, transport nitrogen and other elements with them.

Specific Points

Lines 57-59: What about the thermal benefits for young calves to be born in warmer temperature or tropical waters? I do not think the theories given for baleen whale migration here is exhaustive, and given a single reference for each theory is not enough. This is a huge question that is still not empirically answered, and that needs to be better reflected in these sentences.

We have revised this paragraph. At least two publications question the role of thermoregulation (or reduction of thermal stress) in calves: Corkeron and Connor (1999) and Stern and Friedlaender (Encyclopedia of Marine Mammals 2018). In the interest of word count, we did not include this debate here and follow these and other publications.

Lines 64-66: Please provide some references here for the costs of gestation and lactation.

This section has been rewritten. We have included Costa and Maresh (2018) as a review (we'd have to delete another essential reference to add another at this point).

Lines 182-184: Is there any support for this speculation? Any references?

It is speculation, and we suspect that it is reasonable, but in the absence of empirical evidence, we have cut this sentence.

Line 216: What is the three-month residency time of humpback mother-calf pairs based on? Residency time for individual whales on their breeding grounds (or feeding grounds for that matter) is poorly understood and this uncertainty needs to be incorporated in your estimates.

Time spent on breeding grounds varies annually by individual, population and whale species. However, the exact timing is poorly understood. For our best estimate calculations, we used a conservative estimate of 90 days (see Table S4 for approximate start and end dates). However, we vary this number by $\pm 30\%$ in sensitivity tests to encapsulate uncertainty in total N.

Line 226: 40 tonnes is a very high weight for a humpback whale. Where is the empirical justification for this value? What length was that based on? There is differences in the size of humpback whales between the northern and southern hemisphere. Many recent studies have measured the size (length) of whales with photogrammetry. Why not update your estimates with those findings.

We use 26.6 tons as our central estimate of adult humpback mass. The 40-ton whale was a hypothetical example. We have modified the example to be consistent with our mass estimate. It reduces the numbers in the example but does not change the conclusion of stimulating more than a whale's worth of carbon.

Lines 238-240: The theory about cetaceans migrating to molt has been shown only in killer whales, and only from Antarctica. Hence, assuming that this could be a major reason for migration in other cetaceans is very speculative.

Yes, it is speculative, though it makes a lot of sense. There is some fundamental physiology associated with being a bare-skinned mammal in cold water, and this is consistent with what we know. See also reference 39, where underwater images show humpbacks exfoliating on breeding grounds, surrounded by fish, and new Fig. 4. We added a slight hedge. Thanks.

Lines 280-282: Southern right whales does not really conform to the traditional migration pattern between high and low latitudes. Over the last years, satellite-tagging studies have actually revealed that right whales make considerable longitudinal migrations during the feeding season, and some individuals does not travel very far south at all.

Thanks for this. We have added a reference to this information from Zerbini et al. 2021 on line 338. In this case, it's not a latitudinal gradient so much as a movement to inshore waters.

Lines 322-323: It is not clear from the text or tables what the assumed body masses were for the different species. There is a reference to Pershing et al., but that article too does not provide values of the body mass of the different species. It would be helpful if the authors could provide the input data for their calculations clearly in a table, with appropriate confidence intervals.

The masses are in Table 4 in Pershing et al. 2010. We have added $\pm 10\%$ for variation in adult biomass to our sensitivity analysis in the SI.

Lines 323-324: This equation is based on a study from 1997. There has been many advances in our knowledge of the body size (length and mass) of newborn baleen whales, which could provide more accurate estimates than Webb.

To our knowledge, direct observations of newborn whale calves are rare. Webb's allometric model gives us a consistent way of estimating calf size as a function of adult size.

Lines 329-331: Is there no data on baleen whale placentas from historical whaling? Or commercial whaling? Surely, it would be better to base your estimate on a baleen whale rather than an odontocetes. Further, was there no confidence interval around the 10% value?

We did a literature search but could find no data measuring placentas in the whaling literature. The best we could find is from killer whales, but with sample sizes too small for CI's. This is likely because baleen whales are not held in captivity and whalers didn't record their weight to our knowledge. Please note that placentas play a very small role in this transport and is likely to have a very small impact on overall estimates.

Line 331: Again, a single value is used for the protein content of the placenta. Surely, there must be some uncertainty around this value no? Is there no data from marine mammals?

Lean tissue has a very consistent protein content. There are no data on placenta content for any marine mammal. More importantly, the uncertainty on the protein content is not that important compared to the uncertainty in the mass of the placenta, and that is all tiny compared to the other variables. See for example our new Fig. 3. The N from placentas is so small it doesn't even register compared to urea and deadfall N.

Line 333: Is 16% an accurate value, or is there uncertainty around this value as well? If so, please provide it, or otherwise give a justification to why there is no variation.

The 16% value is what is used in the nutritional literature, typically without any measure of variation. It is based on the stoichiometry of an average of typical protein and is widely used throughout biology. There is no reason to assume that whales are substantially different. A change of 1-2% would have a very limited impact on our calculations, especially compared with numbers that are more uncertain like total population size.

Lines 338-339: These are major assumptions, without any justification. How does these values compare to those estimated from whaling records (see many of the papers from Lockyer, Vikingson etc.). There must be considerable variations in these values, and differences between species, age-classes and reproductive states. That variation needs to be incorporated into these analyses, to see how it will affect the final estimates.

Pershing et al. 2010 used Lockyer extensively in their 2010 paper to get the von Bertalanffy growth curves that allowed them to estimate adult mass. We have added uncertainty to these

values. In a literature review, we did not see estimates for dry weight and protein from Lockyer or Vikingsson.

Lines 363-364: But calves grow very rapidly during the first months of their lives, which requires a lot of energy from their mothers. In addition, the mass-specific field metabolic rates is higher for smaller calves, which further increases the cost when they are younger/smaller. So although the calves are small, they are not energetically cheap for the mother.

We don't estimate the energy intake of the female in the tropical waters when they are not feeding. They are fasting, so while the energy consumption is certainly high, we are only interested in the protein catabolism that results in urea excretion in the urine.

Lines 365-366: The days spent on the calving grounds is no doubt a very important parameter in these calculations, yet the input data (summarized in Table S4) is not very accurate and does not provide any confidence intervals. Why are the months rounded to the nearest value? Surely, that compromises accuracy no? Further, are these values based on the presence of whales (as populations) on their feeding/breeding grounds, or individual whales? In several places, the values does not match those provided from studies of the same species on their breeding and feeding grounds. For example, humpback whales migrate along both the western and eastern coastline of Australia between May and November, yet the start and ends months are given as 7 and 10. The same goes for southern right whales, which are present on their breeding grounds as early as May and leaves in October.

Our sensitivity analysis demonstrates that the number of days on the calving grounds is an important parameter (Fig. S6). In the absence of species-specific information, we have taken a conservative approach assuming an average of 90 days on the breeding ground. But, the reviewer is right, some individual whales arrive earlier and stay longer. We have added a note to that effect on line 603.

Most importantly, we have now included a range of values $\pm 30\%$ to address this uncertainty. and we hope that our study motivates further research on whale migration to reduce this uncertainty for particular populations and species.

Response to Reviewer Two

1. The estimate of reproductive females that migrate and give birth to calves. The authors assume that all females in the population do this. In fact, for many of the relevant species, about half of the females will be sexually immature. In addition to not giving birth (giving rise also to placentas and calf carcasses), they may not even migrate to low-latitude calving grounds.

Our calculations assume a steady-state population. Under this assumption, most females in the population will be sexually mature. We effectively assume that all females older than the calving interval are mature. In a growing population, the proportion of juveniles will be higher. If detailed age structure were available, they could be incorporated into the calculations. Our sensitivity analysis suggests that the nitrogen flux estimates are sensitive to the proportion of lactating females, and our uncertainty estimates include this factor. We have added a line to suggest that a growing population with a high proportion of juveniles will be at the low end of the estimates (line 554).

2. The authors use estimates of calf and adult annual mortality to estimate the number of carcasses that may be added to the breeding grounds. This seems to assume that all of this annual mortality occurs at these calving grounds. This is highly unrealistic, and the number of carcasses is therefore likely highly overestimated.

Our model assumes that mortality occurs equally across annual migration cycle, which is a conservative approach as nutritional/energy effort required for migration/lactation, along with male competition on the breeding grounds likely means more individuals will die in calving grounds (Smith et al. 2016, Roman et al. 2014).

3. I have trouble understanding how the ratios of feeding to breeding/calving grounds are calculated. Do they represent some ratio of number of observations, in which case this is problematic when using highly disparate, and partially opportunistic sightings, or do they represent geographic areas? This is not clearly described in the methods or SI.

As whales generally have vast feeding grounds, but relatively smaller breeding areas, we calculated the ratio of feeding area:breeding area to examine for a possible nutrient funneling effect of whale nutrient transport (i.e. whales accumulate nutrients from a wide area, but generally deposit in small coastal lagoons; see Fig 1). For this, we adopted a commonly used method to examine the area of utilization during different seasons (i.e., by using observation data during the feeding season and breeding season for each whale sub-population outlined in table S4). The exact methods we used to generate feeding/breeding areas are described in Supplementary Information text L0-90. However, as the reviewer correctly identifies, bias in observations used to generate feeding/breeding areas (e.g., near shorelines/shipping lanes, etc.) may skew our generated polygons. Consequently, we used a 95% kernel density (i.e. there was a 95% probability of finding an observed individual within the boundary) to incorporate as much of the data as possible, while still excluding uncommon or extralimital observations (e.g., laggard or non-migratory individuals). To ensure that our feeding:breeding area ratios are robust, we also undertook this procedure using a 90% and 99% kernel density (see figures S1-S5). Finally, we also undertook a systematic literature search and used expert opinion to generate

outlines of known/described calving grounds. Areas that overlapped from our observation dataset and the published literature, have a high degree of confidence for being where females/calves reside seasonally.

4. Finally, while the authors cite an online repository for the data and code used to calculate their estimates, this link does not exist. Presumably, this is planned to become live once the paper is published. However, similar to many other manuscripts submitted for review, I would have expected that data and code would be made available to the reviewers, so that they can evaluate the analyses and results. As it now stands, I tried to recreate the calculations as best I could, but arrive at very different numbers. My treatment of the results section is therefore cursory, as I suspect many of the estimates are biased from the strong assumptions made (and other issues detailed in my comments in the documents).

We have now made all data available at:

[https://figshare.com/articles/dataset/Great Whale Conveyor Belt/25021040](https://figshare.com/articles/dataset/Great_Whale_Conveyor_Belt/25021040)

Note 1. Done.

Note 2. 'Closest' relative to what? Do you mean they adhere closer to this pattern than they do to other patterns, or that they adhere closer to this pattern compared to other species?

The sentence has been recast.

Note 3. This makes it sound like simply by appearing further offshore, they show more behavioural plasticity. Surely the behavioural plasticity is more related to variations in the seasonal distribution patterns. Also, at least humpbacks appear offshore at least during migrations, so the offshore aspect isn't really the main difference I would say.

Fair enough, changed this to “a wider range of migratory behaviors” per Geijer et al. 2016.

Note 4. 1. Not sure about the journal's editorial rules, but I would suggest changing this to a complete sentence: 'Why do whales migrate?'. 2. In terms of migrating to avoid predation, since you specifically mention mothers, I assume you mean that they do this to avoid predation of the calves? However, pregnant females (i.e. not yet mothers in the true sense) usually migrate to lower latitudes, probably also to give birth in warmer waters to protect the calves from hypothermia. I would think this is at least an equally valid explanation as the ones you have given.

The paragraph has been revised and the sentence has been altered as suggested. As mentioned above, in response to Reviewer 1, at least two publications question the role of thermoregulation (or reduction of thermal stress) in calves: Corkeron and Connor (1999) and Stern and Friedlaender (*Encyclopedia of Marine Mammals* 2018). We did not include this debate here and follow these and other publications in the interest of word count.

Note 5. Insert “spatially and temporally.” Done.

Note 6. Insert “seasonal.” Done.

Note 7. More than males at what stage of the annual cycle? Given that also adult males undertake seasonal migrations to mate, they too must accumulate substantial lipid energy reserves prior to migration.

Males also store substantial lipid energy prior to migration, but females store more (according to these and other references), presumably because of the energetic costs of pregnancy and lactation. Please see references (Irvine et al. and Lockyer) for further information.

Note 8. These are of course larger in absolute terms, but are they also larger in relative terms, both in relation to total body size, and relative to energy demands?

In this case, we mean absolute terms.

Note 9. Related to my previous question, is this actually the case? That is, that they are capable of longer migrations compared to pinnipeds? I would argue that several pinnipeds would also be capable of undertaking such long migrations, but they don't have to. They can instead remain in relative vicinity of feeding grounds, since they have land- or ice-based breeding which makes pups less exposed to cold waters during the (much shorter) lactation period.

We are following several papers in the literature, including Rasmussen et al. 2007 and Mate et al. 2015, both *Biology Letters*, and many others. Pinnipeds travel long distances but not to our knowledge the 8,300 to 11,000 km distances recorded for whales. In that case, we consider whales and their movement of nitrogen worthy of study.

For an extensive contemplation on the relationship of pinnipeds and whales and a justification of our decision, please see the response to note 61 below.

Note 10. 'Unique' in what sense?

We have removed this word.

Note 11. Perhaps you should introduce the topic of nutrient cycling and the role of whales before you focus on the role of migrations in that context?

We have rewritten the introduction, though we have retained the order of migration, with nutrient cycling at the end, which we believe makes a better transition to the results.

Note 12. It's a bit unclear to me what the role of lactation is in terms of the latitudinal transport. Sure, calves also metabolize energy they receive through lactation, and excrete urine and feces while at low latitudes. But most of the nutrients received are actually bound in their body tissues, and should not be accounted for in terms of the (immediate) latitudinal transport.

Most mammals assimilate 90-95% of the material consumed as milk. There are very few if any data on this for any marine mammal. Therefore, there will be some fecal material produced and definitely some urea excreted in the urine. We did not estimate fecal N from calves, which produced an overall conservative estimate.

Note 13. 'Significant' in what sense? As there's no specific reference to this, it's difficult to evaluate how large these contributions are, in relation to the contribution of all other ecological processes that contribute to nutrient input into these areas.

Fine. We have changed this to “large,” in a way that reflects studies of strandings (Quagiotto et al. 2022) and whale falls (Smith et al. 2019). We are currently at the limit of words and references in this manuscript, or we would have happily added more references and text.

Note 14. And will likely remain so for the foreseeable future. A more realistic aim might be to provide some **reliable estimates**.

Sure.

Note 15. This sentence is a bit misplaced here. I would suggest that this topic be introduced further up, where I suggested you insert a paragraph introducing the whole idea of whales as ecosystem engineers. Or in the subsequent paragraph where you introduce the idea of how whale migrations might contribute to the latitudinal transport.

We have revised this paragraph.

Note 16. I think this issue deserves some more detailed treatment here, and could even be mentioned when you (as I suggest) introduce the 'whales as ecosystem engineers' topic. Especially since several earlier articles discuss exactly this topic, i.e. contrast preexploitation and current contributions. Also, I think it's worth mentioning the fact that several baleen whale stocks are now increasing, with some potentially reaching pre-exploitation levels.

Yes, we agree that this is important, but we are limited by reference and word count, so will have to leave that for another time, sadly. We do mention recovery, which is very important, at the end of the discussion.

Note 17. I have several issues and questions regarding the methods used, and my treatment of the results will therefore be done somewhat 'half blind'. I have also tried to re-create the calculations to figure out how things were done, but I cannot manage to get to the same results as those presented here. I understand that the code cannot be uploaded on an openly available repository until the paper is published. But given my concerns about some aspects of the calculations, it would have been much easier to evaluate the methods and results if links to the code had been provided to the reviewers as part of the submission.

We have now made all data and models available at:
https://figshare.com/articles/dataset/Great_Whale_Conveyor_Belt/25021040

Note 18. Again, it's a bit unclear to me when you focus on these species, and when you focus on the other two (blue and fin whales). Perhaps it can be better clarified in which contexts you focus on one or the other group, and why?

Please see the section: **Potential importance of other balaenopterid whales** on p. 8.

Note 19. But see my comments on the methods section about sexually mature females only representing perhaps half of all females in a population. This may then actually produce an upward bias that more than compensates for the supposed underestimate the authors discuss here.

As we mentioned above: "Our calculations assume a steady-state population. Under this assumption, most females in the population will be sexually mature. We effectively assume that all females older than the calving interval are mature. In a growing population, the proportion of juveniles will be higher. If detailed age structure were available, they could be incorporated into the calculations. Our sensitivity analysis suggests that the nitrogen flux estimates are sensitive to the proportion of lactating females, and our uncertainty estimates include this factor. We have added a line to suggest that a growing population with a high proportion of juveniles will be at the low end of the estimates."

Note 20. The proportion of these categories of animals that actually migrate is highly uncertain. Together with the likely overestimate in pregnant females, including these additional categories may not in fact provide a reliable population-level picture. Indeed, I would argue that this is a substantial overestimate.

Our estimate for pregnant females is reliable, accounting for immature animals and years when they don't breed. Much of the population travels for many species, including gray whales, humpbacks, and southern rights. And whereas every individual won't necessarily migrate every year, most of these populations, to the best of our knowledge, journey to lower latitudes. We believe this is made clear in lines 108-112.

Note 21. Indeed, and likely more than just 'some'.

Note 22. Or don't go there at all, but remain at high- or mid-latitude feeding grounds.

Note 23. I couldn't agree more! And until such data are available, I think any speculations must be treated with extreme caution.

To notes 21-23. We believe the new uncertainty ranges, updated references, and data make clear that our range of values, from reproductive females (most conservative) to entire population (possible upper bound), provides a good background for this long-distance movement of nitrogen and other nutrients. We have added another sentence to this paragraph to make clear that not all individuals migrate.

Note 24. Ratios of what? Abundance? Days present? See also my comments/questions to table 1 in the supplementary information document.

This refers to ratios of size. Seen Table 2 in manuscript.

Note 25. This now suggests that the ratios represent area ratios? Again, perhaps I've missed something, but this is not at all clear in the methods or SI sections.

We edited the paragraph for clarity.

Note 26. I would move this sentence to after the sentence that ends on line 115.

Done.

Note 27. But how much in relation to nutrients released by other marine organisms? This is something frequently missing in discussions about the relative importance of whales as ecosystem engineers.

See Fig. 3 for comparison to seabirds as an example.

Note 28. What does this mean? I assume you mean that they may not have regular and well-defined seasonal migration patterns, similar to those observed in e.g. grey and humpback whales?

Yes. Thanks.

Note 29. There are several recent papers suggesting this is no longer the case, but that fin whales are well on their way back towards preexploitation levels. See papers by e.g. Helena Herr et al, Sascha Viquerat et al., https://www.researchgate.net/publication/361825408_Return_of_large_fin_whale_feeding_aggregations_to_historical_whaling_grounds_in_the_Southern_Ocean

Fair enough. We have included this reference and a caveat.

Note 30. I still this is an oversimplification. Especially given the very strong and untested assumptions made in this analysis, as well as the lack of any comparison to similar studies on other organisms. At the very least, I would encourage the authors to note this, i.e. the possibility that several other marine organisms may contribute greatly to these types of transports.

Fair enough. We have added a hedge that there are possibilities that other species may play similarly large roles as more studies become available.

Note 31. While this may be true, several species actually feed mostly within the euphotic zone, and thus this vertical transport does not represent re-introduction of nutrients from other water masses, but simply a regeneration within the euphotic zone.

Yes, vertical movement can be recycled or add new nutrients. We have added “and within” for clarity.

Note 32. But how large is such horizontal transport compared to the natural advection by ocean currents? True, this process will be slower in terms of transport between high- and low-latitudes, but will likely be several orders of magnitude greater. And even if such advection has a delay of several years in reaching low latitudes, it is constant and may overall be much greater than the whale contribution.

The role of advection will differ considerably from place to place and across spatial scales. Our conceptual model is that oceanography sets the background conditions such as explaining why the Hawaiian calving grounds are oligotrophic. Horizontal transfer by migrating whales adds on top of this process. If the background state is oligotrophic—a common feature of most calving grounds, then the whale conveyor belt can be an important contribution. We show that this can be locally significant, but at a global scale, oceanography will dominate.

Note 33. This has been stated several times in the MS, and is indeed the foundation of the entire analysis. Seems weird to have this sentence so far into the discussion of the MS.

This sentence has been recast.

Note 34. Done.

Note 35. Surely, this depends on which seabirds we're talking about? Several species are known to migrate across distances that far exceed those of whales. Indeed, some seabirds seasonally migrate from pole to pole, thereby potentially moving nutrients between Arctic and Antarctic polar regions...

One of the main differences is that seabirds feed their chicks from prey they capture within flying distance of the breeding grounds. We now clarified that in the text.

Note 36. Again, while this may be correct for some species, it's certainly not the case any longer for several of them.

We recast the sentence.

Note 37. It's surprising that the IWC catch database has not been used, as it is one of the most comprehensive databases of historical whale catches. It can be obtained from the IWC upon request.

We used the databases that were publicly available to us online, but did not encounter the IWC data (except for some from Brazil). Thanks for the heads up that these data are available on request. We will consider this for future studies.

Note 38. This species is probably less tied to shallow waters than the other two?

Perhaps, but many are coastal-dwelling, so we have left as is.

Note 39. Conservative in what sense? I assume in this case you mean specifically in the number of breeding grounds, but you almost make it sound like it's conservative in terms of the estimates of nutrient transport, which is of course another matter altogether. If you use the same overall abundance estimates, but split them up into fewer breeding grounds than may actually be present, then the estimated contribution at each of these breeding grounds may actually be overestimated. So, you need to be more specific in terms of what you mean by 'conservative' here.

We originally intended this to mean that we were conservative in the number of breeding ground areas. We have updated our text to include the reviewer's point, as we agree it is a good one.

Note 40. I'm not sure why the issue of faster-swimming is important here? The point is that, for some species we have good knowledge regarding their breeding grounds, while for others we do not. This may be a result of (as you mention) them having more offshore breeding grounds and therefore not observed/identified.

Okay, we've cut that comment.

Note 41. This is in fact also the case for fin whales, so perhaps these too should have been excluded?

Although our understanding of fin and blue whales is more limited than it is for the more coastal species, we thought an examination of the two more pelagic species would be valuable to researchers, especially give their large size (even though they are placed in the SI). Minke whale estimates will need to await future studies, but could be important due to their high abundance.

Note 42. The estimate of North Atlantic humpback whale abundance used here (112,000, originally from Ruegg et al., 2013 based on genetics) should be treated with some caution. It is many times higher than some other estimates (e.g. an upper limit of 40,000–47,000 reported by Smith and Pike, 2009 based on catch data), and has been the target of substantial and as yet unresolved debate over the past few decades.

Fair enough. Our new range, based on Suárez et al. (2023, *Science*) is 20,488 (9,964-57,030).

Note 43. This equation ignores the fact that a substantial number of females in the population have not yet attained reproductive age (which occurs usually around 5-11 years age in baleen whales). Below is a rough back-of-the-envelope calculation for a humpback, using the values from Taylor et al (2007), which you've used for other life history parameters:

If we assume a life expectancy of 50 years, an age of first reproduction of 6 years, followed by a constant birth rate of $1/2.36=0.424$ until the age of 50, and further assuming a survival rate of 0.76 the first year and 0.96 every year thereafter, suggests that only about 45% are above the age of first reproduction. While this is of course a gross oversimplification, it illustrates the importance of considering also age at first reproduction. Since you use other values from Taylor et al (2007) I suggest you also include this.

As mentioned above, our calculations assume a steady-state population. This allows us to compare pre-whaling and modern populations. Under this assumption, most females in the population will be sexually mature. We effectively assume that all females older than the calving interval are mature. In a growing population, the proportion of juveniles will be higher. If detailed age structure were available, then that could be incorporated in the calculations. Our sensitivity analysis suggests that the nitrogen flux estimates are sensitive to the proportion of lactating females, and our uncertainty estimates include this factor. We have added a line to suggest that a growing population with a high proportion of juveniles will be at the low end of the estimates.

Note 44. This entire section is not very clear. It is frequently very challenging to understand exactly what is done in the different steps. The notation is confusing, as it you seem to sometimes use the same letters for different things, and switch between uppercase and lowercase letters. It is also not entirely clear when you try to create your allometric equations based on values from other studies, so I suggest you explain this explicitly to the reader. I also have several issues with the calculations themselves, but hopefully my issues are based on my poor understanding partly caused by the unclear description. But I would strongly urge you to double check all calculations to make absolutely sure they are correct.

We have double checked our calculations, and the results are now available online, and we have answered direct concerns about equations and steps.

Note 45. I cannot find actual mean body mass (I assume by 'size' you mean mass, and not length?) estimates in Pershing et al (2010). I assume you've obtained these by dividing biomass with abundance estimates in Table 1 from that paper?

Yes, by size we mean mass (clarified in text). The population-average masses were not published in Pershing (2010), but they were an intermediate step in their calculations. We obtained their original tables and use them in this study.

Note 46. I couldn't access the original article, so this bit left me somewhat confused. First of all, which of these two versions did you actually use? They give ever so slightly (unimportantly) different results, so I don't see the point of including both versions. More importantly, they don't seem to give reasonable results, whichever unit (g or tons) are used. Using g gives vastly underestimated calf masses (240 kg for a humpback whale calf, 720 kg for a blue whale calf). Using tons on the other hand, gives overestimated calf masses (4.4 tons for a humpback calf, 13.2 tons for a blue whale calf). More reasonable (though at the upper limit of reported) values are obtained assuming units are kilograms (1.03 tons for a humpback calf, 3.1 tons for a blue whale calf). This really needs clarification, as units here make a big difference.

It was hard for us to decipher from the PDF exactly what the reviewer is referring to here. We presume it is the equation for calf mass. The equation assumes that the calf mass is specified in kg (the reference to g in the text is a typo). The output is also in kg.

Notes 47 and 48. Would be good to add an 'A' as a subscript to denote adult. This should preferably be a subscript.

We have left these as is, since we think it is clear as written.

Note 49. This is almost certainly an overestimate, since calf survival estimates refer to survival throughout the entire first year. It is not unreasonable to assume that a substantial proportion of calves do not in fact die at the calving grounds, but during migration or at the feeding grounds. While the exact proportions are of course not known, I suggest you make some assumption about this proportion (say 50:50), or at the very least include a comment discussing the potential problem with your assumption.

Another detail, it would be better to denote calf survival as s with a 'c' as subscript, then you can replace the x for adult survival by s with an 'a' as subscript.

We compute the total annual number of calving deaths and then scale that by the percentage of the year spent on the calving grounds. This is actually a very conservative calculation as calf mortality is almost certainly highest during the first few days after birth.

We have left the notation as it.

Note 50. This seems high to me. I wasn't able to access the reference, but neither of the authors appear to be authorities on the subject?

To our knowledge, no one has done field measurements on the stoichiometry of whales (we've looked). We have no reason to doubt Jelmert and Oppen-Bentsen's estimates here.

Note 51. Difficult to judge how representative this might be for a baleen whale. Are there no estimates from more similar organisms?

Crocker et al. measured a urea production rate of 84 g day^{-1} during mid-lactation for a female elephant seal weighing an average of 432 kg.⁴⁶ We assume an allometric relationship:

$$U(m) = \text{urea (g day}^{-1}) = A m^{0.75}$$

We are not aware of any work on protein catabolism for baleen whales. Please see our response to 61 below.

Note 52. How do you include an estimate of adult survival here? Is it age specific? And is it an annual rate or proportion? How might that be affected by the fact that adults probably die throughout the year, not just at the calving grounds.

We assume that the number of deaths is evenly spaced throughout the year. For our calculations, we scale the total deaths by the proportion of the year on the calving ground. This is likely

conservative, since deaths on the breeding grounds could be higher than those on feeding grounds due to conflict and limited food resources.

Note 53. What is N here? Since you use N for nitrogen, it is confusing that you use N here too, and since you've already defined F as the number of pregnant females at the calving ground, it's unclear what this N refers to.

Good point. Thanks. N is the population size. We replace this with P.

Note 54. This is a slightly confusing way to denote. Does it mean U as a function of mass?

Yes, we are using standard function notation here. U is a function of mass.

Note 55. Done.

Note 56. Done.

Notes 57-58. See previous point about subscripts.

We are using standard function notation here.

Note 59. In this case, mass is in kg. Perhaps this is worth pointing out? And it's then also crucial that you stick to kg also for whales. You do so initially, but eventually you convert to tons. I'm not sure this is done correctly, but more on that later.

We use kilograms and tons for readability. We have confirmed the calculations. Thanks for the heads up.

Note 60. You may want to explain that this constant is calculated by re-arranging eq 1.

Done.

Note 61. Elephant seals are extreme capital breeders, with a very short lactation period compared to baleen whales (~3 weeks vs. over 2 years). I seriously doubt that these values are indicative of a late lactation baleen whale. In fact, most of the lactation period in a baleen whale does not occur at the breeding grounds, as females most likely leave soon after birth and continues their lactation enroute to feeding grounds, and subsequently during the first 2 or so years. Using elephant seal data, especially from some late lactation/ fasting stage, therefore doesn't seem very representative here.

The bioenergetics of capital breeding are discussed in Costa (1993) and Costa and Maresh (2017). Figure 6 in Costa and Maresh (below) shows that when you control body size the time to weaning is comparable between phocids and mysticete cetaceans. More importantly phocids and mysticetes are both extreme capital breeders. The only reason baleen whales can lactate while fasting for many months is because of their large size and the associated benefits that come with it.

[figure redacted]

To put this in perspective, metabolic rate generally scales with $\text{mass}^{0.75}$. It follows that other metabolic processes such as time to weaning should similarly scale as $\text{mass}^{0.75}$ (Calder 2001). Therefore, following the same scaling relationship, we can estimate the time to wean for an elephant seal if it were the size of a blue whale.

Metabolic rate (in energy units e.g. Joules per day, Watts, or Kcal per day) = $A \times \text{mass}^{0.75}$, Where A is the scaling constant

Thus, we solve for the constant A that scales time to weaning or lactation duration for a given body mass:

Elephant seal time to weaning 26 days; $26 \text{ days} = A (500 \text{ kg})^{0.75}$
 $A = 0.246$

A comparable time to wean for an elephant seal the size of a blue whale would be:
 $105,000 \text{ kg mass } 0.246 * (105,000 \text{ kg})^{0.75} = 1434 \text{ days or 4 years}$

Based on simple scaling relationships, whales are even more extreme capital breeders than elephant seals and our elephant seal extrapolation should be conservative.

An independent method of calculating the nitrogen excretion rate is to assume a metabolic rate based on simple scaling relationships. Villegas-Amtmann et al. (2015) estimated that migrating gray whales would have a field metabolic rate that is 1.3 times that predicted by Kleiber (1975). Assuming the same relationship for a 105,000 kg blue whale would be:

$\text{BMR} = 1,708,500 \text{ kJ/day} = 293 \text{ kJ/kg-day} * (105,000 \text{ kg})^{0.75}$ $\text{FMR} = 1.3 \times \text{BMR} = 2,221,050 \text{ kJ/day}$

7.9% of the energy provided in a fasting seal comes from protein in early lactation, which is low compared to other mammals. This increases to 11.2 % in late lactation.

Thus, protein oxidation is $7.9\% \times \text{FMR} = 175,463 \text{ kJ/day of protein}$

Protein has 18 kJ/gr and 16% of protein is Nitrogen: $175,463 \text{ kJ-day} / 18 \text{ kJ-gr} = 9.75 \text{ kg protein per day}$

$9.75 \text{ kg protein per day of which } 16\% \text{ is Nitrogen} = 1.56 \text{ kg Nitrogen per day being excreted early and } 2.21 \text{ kg/day late.}$

Calder, W. A. 2001. Ecological Consequences of Body Size. Encyclopedia of Life Sciences. John Wiley & Sons, Ltd.

Costa, D. P. 1993. The relationship between reproductive and foraging energetics and the evolution of the Pinnipedia. Pages 293-314 in I. L. Boyd, editor. Marine Mammals:

- Advances in Behavioural and Population Biology. Oxford University Press, Symposium Zoological Society of London.
- Costa, D. P., and J. L. Maresh. 2017. Energetics. Pages 329-335 in B. Würsig, J. G. M. Thewissen, and K. Kovacs, editors. Encyclopedia of Marine Mammals. Academic Press.
- Kleiber, M. 1975. The Fire of Life: An introduction to animal energetics. R.E. Krieger Publishing Co., Huntington.
- Villegas-Amtmann, S., L. K. Schwarz, J. L. Sumich, and D. P. Costa. 2015. A bioenergetics model to evaluate demographic consequences of disturbance in marine mammals applied to gray whales. *Ecosphere* **6**.

For notes 62-68. We refer the reviewer to the revised methods and figshare. Reviewer I did not have the same concerns. We have rechecked our numbers, and they are consistent throughout. Thanks for prompting a review. We have rewritten for clarity..

Note 62. This doesn't seem right to me. If the goal here is to convert to tons, you should surely divide eq 2 by 1000, not multiply, as you do in the last part of eq 3 to calculate B. And I don't see why you include the 0.75 power twice in the resulting equation. Perhaps I'm missing something here, but the description is not very clear of what you do and why in the different steps.

Comparing eq2 and the first part of eq3, it seems to me that $B=vA$. So where do you get the second part of eq3 from?

In the end, if you use $B=73.49$ in the first part of eq 3, and include the mass of a blue whale (now in tons rather than kg), you get: $n(m)=Bm^{0.75}=73.49*105^{0.75}=2410.57$, i.e. exactly the same as you get from eq2, and thus still in g. As far as I can tell, to convert this to tons of nitrogen, you'd have to divide by 1,000,000, which doesn't seem right.

We have rechecked our calculations.

Note 63. As far as I can tell, this refers back to the elephant seal numbers, but this is far from clear. It would perhaps be better to restructure this entire section, to make it easier to follow the logic.

We inserted “whale” for clarity.

Note 64. But this now throws me off a bit, as it suggests the more conservative numbers are simply chosen on the assumption that calves consume less milk, and has nothing to do with the numbers you took from elephant seals. All very confusing....

This refers to whales calves, since they likely consume less milk when younger.

Note 65. New subscript that hasn't been previously defined. I assume it means 'united' or something?

Yes, thanks, we have clarified.

Note 66. What does this survival estimate refer to? Calves I assume? But what about the mothers of calves that do not survive? Are they assumed to simply leave the calving grounds as soon as the calf dies?

We don't know how the death of a whale calf, and its timing, affects the time on breeding ground for a mother.

Note 67. Unclear what this refers to.

Not sure what you meant here on pdf.

Note 68. Surely this depends greatly on when a calf dies, and how large it is at that stage?

Sure. We are using a conservative average estimate for calf size.

Note 69. This makes it sound like the calf contribution isn't included in Nu, but surely it is? It would be better to say that 'Adults contribute 90% towards Nu, while calves contribute only 10%.'

Done.

Note 70. Almost certainly only the proportion of the population that actually migrates to breeding grounds. This may only be adult females that are pregnant or ready to mate, and males that are sexually active. The assumption that this makes up the majority of a population is probably wrong. Humpbacks, for example, can also be seen in wintertime at high latitudes, and old whaling records confirm humpbacks were taken at high northern latitudes also in winter.

Agreed. We set pregnant females as a lower bound. The entire population could be considered an upper bound, though males will often stay longer on the breeding grounds until the last of the females leaves. This seems like a reasonable range.

Note 71. Newer studies have also shown that humpbacks are in poor condition when they arrive at feeding grounds, and fatten up gradually throughout the summer. So, weight at feeding grounds probably also depend on the time when they were measured.

Fair enough. We have not added this given our effort to stay within the boundaries of word count and references.

Note 72. This is of course obvious, and is in fact the definition of fasting. If they didn't keep metabolizing reserves they would die.....

Fair enough. We cut since already mentioned.

Note 73. Done.

Note 74. The first paragraph is a more introductory one, and would actually be better placed at the start of the methods section. It helps to form the framework for details contained in the rest of the methods description. In fact, the entire section is very general, and doesn't even quite seem like it belongs in methods? I would argue that the first paragraph could go in the main introduction, and the last one is important for the discussion. I understand the need for shortening the main text for Nature Communications, but some of these points are critical for placing the results in some context, and especially for being upfront with the fact that some of the assumptions in your calculations may in fact lead to upward biases in your estimates of transport.

Fair enough. This section has been removed, with sections worked into the Introduction and Discussion. Thanks.

Note 75. Unclear what you mean by 'timings'. perhaps 'residence times' would be better?

Sure. Thanks.

Note 76. What do you mean by 'oceanic basin' here? I assume you mean feeding vs calving grounds for the specific populations/stocks?

We cut to avoid confusion.

Note 77. and, more importantly, great uncertainty

Added, with a range of values.

Note 78. But what proportion of the adult population did you assume does this? See earlier comments. Since many of these species are assumed to spend about 120 days on the feeding grounds, this leaves about 150 days on migration. This will also play a role in the nutrient transport.

We have revised this section, and now account for uncertainty in the proportion of adult population migrating and time on the feeding grounds in the Sobel Indices for N transport.

Note 79. Insert "rates used in our calculations are based on....."

Done.

Note 80. This may in fact be higher, or as high, at feeding grounds.

We cut that claim.

Note 81. Sounds likely. But starving animals presumably excrete much less feces and urine...?

Sure. In this case we are discussing carcasses, so not sure that feces and urine are relevant.

Note 82. This statement appears to suggest that you actually carry out some simulations, where you include a survival probability to estimate the numbers of adults (and calves) that die throughout the breeding period, and where everything else is also simulated. This is in fact not what you've done (at least as far as I can make out from the methods section), and so I suspect the use of s in your equations is actually an annual survival rate (proportion). In that case, you actually assume that all whales that die do so at the calving grounds.

As an aside, if you use (instantaneous) survival rates (more accurately, probabilities) to continuously estimate changes in population size, these actually have to be modelled as $s = \exp(-m)$

From the Pershing et al. 2010 steady state model, we have annual survival percentages. We use these to calculate the number of adults and calves dying. We then scale this number by the number of days on the calving grounds divided by 365. The scaling step is now documented in the methods.

Note 83. What proportion of calves born does this represent?

As far as we could tell, the total proportion was not reported in the paper, though it could be inferred from Fig. 3. See Rowntree et al. 2013.

Note 84. Yes, but it can also be high elsewhere. Right whales may be an extreme example, in the sense that they are easily visible in their calving lagoons, and mortalities there more easily quantified than in other places (and for other species in general).

Sure, but we are assuming that first-year calves are 25% likely to die on the breeding grounds. This is almost certainly an underestimate, but it seems like a reasonable conservative assumption. We have added some text to clarify.

Note 85. But you don't make an attempt to provide any estimates (or justification for assumptions) of these mortalities. So the purpose or relevance of this section is unclear to me.

We added a new sentence to help explain why, showing that our approach is likely conservative in light of calf mortality on breeding areas.

Note 86. Insert “largely.” Done.

Note 87. This does not seem right to me, except perhaps for some species (i.e. grey whales). In the case of many of these large baleen whales, most of them have very long lactation periods, spanning often several years. Most of this lactation period is in fact NOT spent on the calving grounds, but either in migration or at feeding grounds.

Fair enough. We have changed this to “early lactation often”

Note 88. Done

Note 89. Done

Note 90. I assume this N stands for 'Nitrogen'? It probably should not appear in the unit like this? It also looks strange to me to talk about mmol of N per m², as it is a volumetric unit. I guess what you mean is, that under every area of 1m², there is a vertical movement of X m³ of water, with a N concentration of 0.048 mmol. You should probably report X here, as this is critical for how you arrive at 0.06 g/m² (which is again a bit confusing, but again makes sense assuming it means 'under every area of 1m²').

The number cited is a flux—an amount moving through an area, hence per m². We are reporting the number and units as reported in the Letscher et al. paper, which are consistent with the oceanographic literature. Multiplying by area and time gives us the total mass of N that is brought into the system by the physics. This number is directly comparable with the mass units from our calculations.

Note 91. This sort of statement does not belong in the methods section.

It has been cut.

Note 92. The repository is not yet available, presumably since the article isn't published yet. But as a reviewer, I would have liked to take a closer look at this, as there are several points in calculations that are not well described in the methods section.

The repository is now available at
[https://figshare.com/articles/dataset/Great Whale Conveyor Belt/25021040](https://figshare.com/articles/dataset/Great_Whale_Conveyor_Belt/25021040).

Thanks to both reviewers for their careful read of the manuscript. Below we address the suggestions of both reviewers.

Reviewer #1

We are thrilled to see that Reviewer #1 is pleased with our changes. We address each of his concerns below.

The authors have done a great job with revising the article and incorporating uncertainty in their many parameters and estimates. They have also improved the justification of values used for the different model parameters, which I believe adds confidence to the estimates. Where the authors have disagreed with my previous comments and suggestions, they have done so with good justification and arguments. I am therefore happy to endorse this paper for publication. I list a few minor edits (mainly adding 95% CIs to the estimates presented in the text) below which I picked up reading through the last version of the manuscript:

Great thanks!

The authors argue that “To our knowledge, direct observations of newborn whale calves are rare. Webb’s allometric model gives us a consistent way of estimating calf size as a function of adult size”. There are however, recent studies on humpback whales, gray whales and southern right whales that provide direct measurements of calf sizes (including birth sizes). Anyways, since it probably does not change the results much, the current approach is fine.

Thanks for this attention to detail. We agree that future studies can help refine our estimates, but as noted—and as we’ve found with the sensitivity analysis—they are likely to have a very small impact on these global estimates.

Lines 32-33 (Abstract): add Latin names of species.

Latin names for all species have now been added to the text. In reading over other *Nature Communications* abstracts (e.g., <https://www.nature.com/articles/s41467-024-47635-4>), it appears that Latin names are not always included in the abstract. In this case we did not add them as we feel it could reduce readability. We defer to the editor here and are happy to add them.

Lines 32-33 (Abstract): add Latin names of species.

Latin names for all species have now been added to the text. In reading over other *Nature Communications* abstracts (e.g., <https://www.nature.com/articles/s41467-024-47635-4>), it appears that Latin names are not always included in the abstract. In this case we did not add them as we feel it could reduce readability. We defer to the editor here and are happy to include them.

Line 62: Add Latin name for killer whale.

Done.

Line 103: Please add 95% CIs also for biomass and C.

Line 106: Again, please add 95% CI to the C production estimate.

Lines 114-116: Please add 95% CIs to all estimates presented here.

Lines 142-143: Add 95% CIs to all estimates.

Lines 151-155: Add 95% CIs to all estimates.

Line 164: Add 95% CIs to all estimates.

Lines 166-168: Add 95% CIs to all estimates.

Lines 230-231: Add 95% CIs to all estimates.

Line 235: Add 95% CIs to estimate.

Latin names and CI estimates have now been added to all numbers.

I congratulate the authors on a very important and impressive study.

Thank you!

Reviewer #2

We broadly address the concerns of Reviewer #2 below. As suggested by the editor, “To address some of the concerns of reviewer #2, please consider whether more nuance and/or caveats could be added to the main text along with further discussion of the robustness and generality of your estimates. Please also make sure that uncertainty is always reported when estimates are stated or take out numerical results that can't be expressed together with the uncertainty, such as in the Abstract.”

I have now gone through the responses from authors, and the changes made to the manuscript in response to issues raised by myself and the other reviewer. I note that the other reviewer broadly agreed with my original assessment, that 'while the general approach is good, the actual modelling, calculations and assumptions are weak at best'. While the authors have now included a sensitivity analysis to partially address this issue, I find the description of their approach to this sensitivity analysis lacking in detail. There is virtually no information on how the sensitivity analysis was actually carried out, which makes it very difficult to evaluate if their conclusions from this are valid. While the authors present a figure (Fig S6) supposedly showing the relative importance of the five main parameters in terms of how it contributes to the uncertainty, this appears almost entirely driven by the coefficients of variation the authors chose as input into the sensitivity

analysis. Without any information about the sensitivity analysis approach itself, I was left wondering what this figure actually shows, other than what the input uncertainties were that the authors entered into the analysis. As pointed out by the other reviewer: 'All of these variables/parameters comes with considerable uncertainty, and I suspect that when you add them all together you are going to end up with a huge confidence interval around your final predictions.'

That is fine; it is the nature of the game when you are trying to calculate something as complex as this, but it needs to be clearly shown throughout the process, and not hidden behind means or references to other papers'. It is unclear if, and if so how, this was actually done in the sensitivity analysis. All that is now presented (aside from the somewhat uninformative Fig S6) is the uncertainty on total N in Table 1. I think the uncertainties should be traced all the way through the calculations, to make it clear where and how they affect the estimates.

We have now added confidence intervals throughout the paper, with a clearer presentation of the approach. To our knowledge, nothing is hidden, though, of course, we rely on findings and assumptions in the published literature. We believe these references make the source of our parameters clear and reproducible. We think the sensitivity analysis is valuable in revealing the parameters' influence on the final output value, showing that population numbers generate the most uncertainty and future studies targeting these parameters will better inform our estimates. Future studies of particular populations, trends, and habitats will enhance our understanding of the resource subsidies provided by great whales.

Response to reviewer comments in text:

1. Uncertainty in

Done

2. Most abundance estimates are presented along with their coefficient of variation (CV). These can indeed be expressed as percentages (representing the SD as a percentage of the mean value). So, that's how I would express this ('30% from the best estimate' isn't a very rigorous way to describe it).

Also, bear in mind, that if you carry out a sensitivity analysis by simulating a set of realisations, in the case of population size you need to sample from a log-normal distribution, after properly transforming your mean and sd. That way, you also avoid sampling negative values.

Sampling from a uniform distribution with positive bounds cannot produce negative values. We feel that using uniform distributions is more appropriate for the inputs into our model.

3. **This is very little. For instance, Smith et al (2015) assume 20%: Smith, L. A., Link, J. S., Cadrin, S. X., & Palka, D. L. (2015). Consumption by marine mammals on the Northeast U.S. continental shelf. Ecological Applications, 25(2), 373–389. <https://doi.org/10.1890/13-1656.1>**

We have expanded to 20%.

4. **Why and when was this necessary?**

This has been cut. We used $\pm 50\%$ from the best estimate.

5. **Of course, because you allowed more variation in these parameters...**

True enough, but even if we allowed the biological parameters, such as N concentration of carcass, to vary more, they would have a smaller impact than the number of whales and time on breeding grounds.

6. **The point of a sensitivity analysis isn't necessarily to find which parameters cause most of the uncertainty, but to incorporate the cumulative uncertainty of all variables in your calculations, to examine the overall resulting uncertainty. Since you've provided no information on how you carried out your sensitivity analysis, it is impossible to know if this has in fact been done, and therefore what the uncertainty reported in Total N in Table 1 represents.**

We have now added CI's to all calculations and tables and revised the Sensitivity Analysis section for clarity.

Page 3

What does 'Normalised standard deviation' mean? I assume it's the same as coefficient of variation (CV) which is simply $sd/mean$. This is pretty much the same as what you describe in your section on sensitivity analysis in the supplementary file (but there expressed as percentages).

Main point here, does this plot show you anything more than the uncertainty you decided to use for these various variables? For population size, your Normalized sd seems to be around 0.3, i.e. similar to the 30% you mentioned in the supplementary section. Same for body mass (10%). So, what have you actually shown with this figure, other than what's stated there?

The correspondence identified by the reviewer between the normalized SD of the inputs and the sensitivity of the final calculation indicates that the model is close to linear. We feel that the figure has important additional information such as the fact that uncertainty in the percentage of the population that migrates leads to higher uncertainty in the deadfall estimates relative to the urea estimates.

What is an “uncertainty error”? ;)



See my extended comments to the supplementary file. There's really not enough information on how the sensitivity analysis was carried out for me to judge the validity of this.

We have now redone our confidence intervals and rewritten the section on sensitivity analysis for clarity.

Is this really a lower conservative estimate? Depends on how the sensitivity analysis was carried out. E.g. did you accumulate all uncertainty from the five variables?

Our new confidence intervals now incorporate the uncertainty from the five variables.

Again, with the caveat that I've no idea how you actually carried out your sensitivity analysis, the conclusion made here is almost certainly due to the fact that you've assumed a much more restrictive uncertainty on body mass (10%) compared to what was used for abundance and percentage migrating. This is of course not wrong per-se, but without a full description of how uncertainty is transferred through the calculations, it's impossible to make an informed judgement.

As stated elsewhere, I think this is too restricted. Other authors e.g. Smith et al (2015); Skern-Mauritzen et al (2022), use 20% uncertainty.

We have now revised body mass to include 20% uncertainty.

Where is the logic in this? This will surely depend on several life history parameters, such as age at first reproduction, juvenile and adult mortality, inter-birth intervals etc. (see next comment)

How can this be a valid assumption for cetaceans? According to Taylor et al. (2007, see below), age at first reproduction for baleen whales average about 10 years, while the calving interval averages around 2.5 years. In Table 1 in that paper, they also report estimated proportions of adults in the population, assuming both an intrinsic max population growth rate and a stable population. Even in the case of stable populations, their estimated proportion of adults is only about 71%. This drops to about 50% if you assume the estimated intrinsic maximum growth rate for the different species (mean: 4.8% across baleen whale species). there is no reason why this intrinsic maximum growth rate should not be valid, given that many baleen whales appear to be recovering.

In any case, given that estimates do exist for several of these critical life history parameters, there is no reason not to use them in important studies such as this one. Taylor, B. L.,

Chivers, S. J., Larese, J., & Perrin, W. F. (2007). Generation length and percent mature estimates for IUCN assessments of cetaceans. Administrative Report LJ-07-01 National Marine Fisheries, January, 24 pp.

Yes, but it does not account for the consistent downward bias in number of lactating females due to the juvenile component of the population. Why not use the estimated adult proportions from Taylor et al. (2007) in your calculations?

Fair enough. We have now updated percent mature per Taylor et al.

How much is actually known about this across species? I'm not convinced this has strong support.

The kernel density approach is intended to deal with this lack of knowledge. Not all whales migrate in all species, so this approach excludes whales that remained on their feeding grounds or were otherwise not seen on breeding grounds. These areas are pretty well established in the literature, and much of the data comes from winter surveys on or near breeding grounds.

It is also unfortunate that the two species of focus (right and humpback whales) are known for their coastal breeding habits, while many other baleen whale species have more offshore (and often poorly known) breeding areas. So, it is perhaps questionable to assume similar nutrient funneling for these other species. While the authors do not explicitly state that their conclusions in this context should be extended to other species than the two focus species, the overall conclusions and message of the paper will perhaps become biased. I would encourage the authors to state this clearly.

We focused on the five species that are known to have coastal breeding habits: Southern, North Atlantic, and North Pacific right whales, humpbacks, and grays. (North Pacific right whales are sadly, ecologically extinct at this point, and we don't know where they breed.) We say quite clearly in the text (e.g., line 171-184) that movement by the fins and blues are not as well-known and are thus included in a separate table in the SI.

As already stated, I don't agree with this assumption. I would argue that the most realistic estimate of proportion of adults in a population is around 50-60%, which would substantially reduce your estimates.

Change made.

No, it is not reliable, because it doesn't fully account for the proportion of immature animals. Again, see Taylor et al. Table 1.

We have now updated the percent mature per Taylor et al. and cite it on lines 371-373.

Sensitivity analysis not explained.

We have updated and revised the sensitivity analysis and methods.

Number of reproductive females remain overestimated relative to what's been estimated elsewhere (e.g. Taylor et al., 2007).

Fixed.

There is also a recently published paper on fin whale abundance in the Scotia Sea that might be worth including: https://link.springer.com/article/10.1038/s41598-024-57378-3?utm_source=rct_congratemail&utm_medium=email&utm_campaign=oa_20240329&utm_content=10.1038/s41598-024-57378-3

This is very cool! We will certainly include it in any future research of fin whales in the South Atlantic and Southern Hemisphere.

Yes, I agree. At least for species that breed in small, well defined coastal breeding areas, but perhaps not for oceanic breeding areas.

Fair enough. It's why we focus on coastal species.

Again, I don't agree with this, and I suggest the authors account for the non-adult proportion. Most simply by using the estimates in Table 1 in Taylor et al. (2007).

We have now added new terms for growing and stable populations from Taylor et al. 2007.

OK, thanks. Just be clear then, that your estimates are at the upper limit of those reported.

We think it's a reasonable estimate. The N from calf carcasses is a small sliver of total. We added a caveat on line 469 to be safe.

While I agree in terms of dividing feeding and calving geographically and temporally, there is an important difference in terms of lactation and time to weaning. I would argue that extreme capital breeders are those where females fast completely from birth to weaning. I don't think that holds for cetaceans, which lactate for several years while feeding, and where weaning is most likely gradual (i.e. calves start feeding before they stop suckling). Anyways, since you end up using the lower numbers, i.e. from mid-lactation, I guess it's OK. The late lactation numbers for elephant seals are probably irrelevant, as they still fast at that stage (as opposed to cetaceans).

Okay, thanks. We will keep these numbers as best available estimates.

I don't see how you can refer to time to weaning as a purely metabolic process. Again, surely this time should depend greatly on whether weaning is abrupt (as in e.g. elephant seals) or gradual (as is likely in most cetaceans). But, this is becoming an academic argument without real implications for the MS, so I'll just leave it.

Thanks.

**Sure, but again, why is this relevant, given the very different lactation strategies?
Fine, but again I don't think this late lactation point is relevant, given the different lactation strategies.**

As mentioned above, these are the best available estimates for capital breeders and seem reasonable assumptions for baleen whales.

And? Was my original point based on a misunderstanding on my part? Should I simply trust that the authors have done it correctly, without any explanation being given? I'm simply trying to make sure all calculations are correct, as this topic is of great importance. I'm not trying to prevent publication, I'm simply trying to be helpful.

The equation is correct as written, and we apologize for not providing more details. The factor of $1000^{0.75}$ converts from mass in tons to mass in kg. It may be easier to see this starting from the desired equation expressing nitrogen as a function of mass in tons:

$$N(\text{mass in tons}) = B (\text{mass in tons})^{0.75}$$

We don't know what B is, but we do know that the coefficient is vA if mass is in kg. So, we multiply by 1000 underneath the exponent:

$$N(\text{mass in tons}) = v A (\text{mass in tons} \times 1000)^{0.75}$$

We can then pull the constant terms together:

$$N(\text{mass in tons}) = v A (1000)^{0.75} (\text{mass in tons})^{0.75}$$

Implying that $B = v A (1000)^{0.75}$ as written in the text.

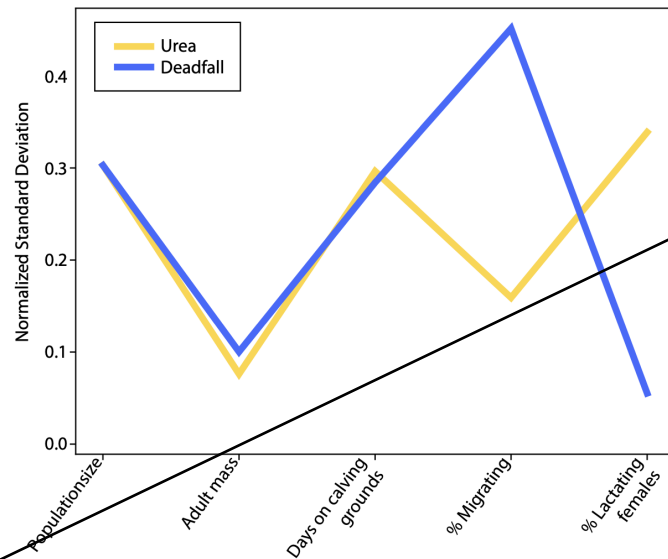
Yes, I now understand. Apologies for the confusion, and for being overly pedantic.

Thanks!

I understand that this is not known, but what do you assume in your modelling? In your calculations, does a mother leave as soon as her calf dies? I'm not questioning what you've done, I just want to understand and make sure things are clear.

We do not assume an early departure, but it would be worth exploring in future work.

Summary of comments on 433186_1_rebuttal_8634327_s8cl2g_com mented



New Fig S6.

We recognize that our original presentation of results appeared to state our calculations definitively. We present **uncertainty errors** for Total N in Table 1 and throughout the manuscript to address this. Our analysis concludes that the population estimates and the number of days spent by different demographic groups on the calving grounds are critical to understanding the exact magnitude of whale nutrient subsidies. We refer to the need for such parameters to be better refined to advance our whale-nutrient-transport quantification. However, we note that even our **conservative lower estimates** are of significant importance when compared to known important abiotic (e.g., physical processes) and biotic (e.g., seabirds), indicating that whales likely have a meaningful impact on the biogeochemical cycles of subtropical ecosystems.

Regarding adult mass, we used an average adult mass for males and females. We did not include age classes, as they are unavailable for most species and even in cases where we might have some idea of age distribution, weight is not known for different age classes. We have noted this uncertainty and included it in our analysis. The sensitivity analysis indicates that population-level parameters, such as abundance and percent of population migrating, have a greater impact on the final estimates.

2. I also have some issues with the literature that is being cited, especially when choosing input parameter values and dealing with assumptions in your model. Many of the cited articles are very

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What does 'Normalised standard deviation' mean? I assume it's the same as coefficient of variation (CV) which is simply $sd/mean$. This is pretty nmuch the same as what you describe in your section on sensitivity analysis in the supplementary file (but there expressed as percentages).

Main point here, does this plot show you anything more than the uncertainty you decided to use for these various variables? For population size, your Normalized sd seems to be around 0.3, i.e. similar to the 30% you mentioned in the supplementary section. Same for body mass (10%). So, what have you actually shown with this figure, other than what's stated there?

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Type: Highlight Subject: Highlight Date: 01/04/2024, 12:12:34

What's an 'uncertainty error'? ;)

Page: 3

Type: Highlight Subject: Highlight Date: 30/03/2024, 16:59:58

See my extended comments to the supplementary file. There's really not enough information on how the sensitivity analysis was carried out for me to judge the validity of this.

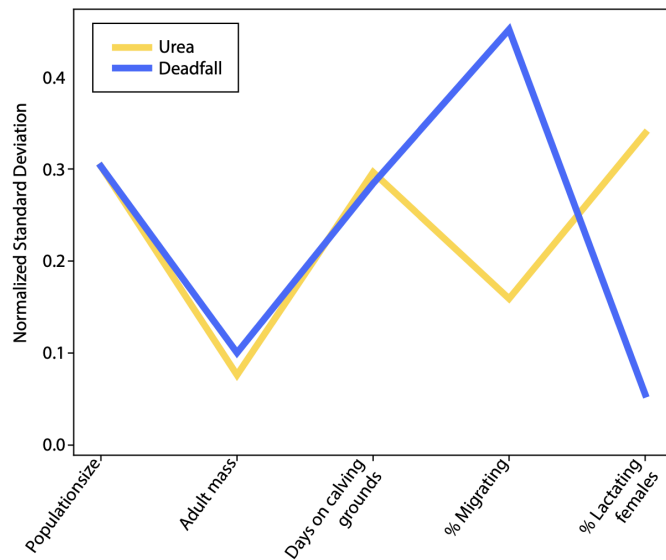
Page: 3

Type: Highlight Subject: Highlight Date: 30/03/2024, 11:53:41

Is this really a lower conservative estimate? Depends on how the sensitivity analysis was carried out. E.g. did you accumulate all uncertainty from the five variables?

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Type: Highlight Subject: Highlight Date: 01/04/2024, 12:44:34



New Fig S6.

We recognize that our original presentation of results appeared to state our calculations definitively. We present **uncertainty errors** for Total N in Table 1 and throughout the manuscript to address this. Our analysis concludes that the population estimates and the number of days spent by different demographic groups on the calving grounds are critical to understanding the exact magnitude of whale nutrient subsidies. We refer to the need for such parameters to be better refined to advance our whale-nutrient-transport quantification. However, we note that even our **conservative lower estimates** are of significant importance when compared to known important abiotic (e.g., physical processes) and biotic (e.g., seabirds), indicating that whales likely have a meaningful impact on the biogeochemical cycles of subtropical ecosystems.

Regarding adult mass, we used an average adult mass for males and females. We did not include age classes, as they are unavailable for most species and even in cases where we might have some idea of age distribution, weight is not known for different age classes. We have noted this uncertainty and included it in our analysis. The sensitivity analysis indicates that **population-level parameters, such as abundance and percent of population migrating, have a greater impact on the final estimates.**

2. I also have some issues with the literature that is being cited, especially when choosing input parameter values and dealing with assumptions in your model. Many of the cited articles are very

Again, with the caveat that I've no idea how you actually carried out your sensitivity analysis, the conclusion made here is almost certainly due to the fact that you've assumed a much more restrictive uncertainty on body mass (10%) compared to what was used for abundance and percentage migrating. This is of course not wrong per-se, but without a full description of how uncertainty is transferred through the calculations, it's impossible to make an informed judgement.

As stated elsewhere, I think this is too restricted. Other authors e.g. Smith et al (2015); Skern-Mauritzen et al (2022), use 20% uncertainty.

The masses are in Table 4 in Pershing et al. 2010. We have added $\pm 10\%$ for variation in adult biomass to our sensitivity analysis in the SI.

Lines 323-324: This equation is based on a study from 1997. There has been many advances in our knowledge of the body size (length and mass) of newborn baleen whales, which could provide more accurate estimates than Webb.

To our knowledge, direct observations of newborn whale calves are rare. Webb's allometric model gives us a consistent way of estimating calf size as a function of adult size.

Lines 329-331: Is there no data on baleen whale placentas from historical whaling? Or commercial whaling? Surely, it would be better to base your estimate on a baleen whale rather than an odontocetes. Further, was there no confidence interval around the 10% value?

We did a literature search but could find no data measuring placentas in the whaling literature. The best we could find is from killer whales, but with sample sizes too small for CI's. This is likely because baleen whales are not held in captivity and whalers didn't record their weight to our knowledge. Please note that placentas play a very small role in this transport and is likely to have a very small impact on overall estimates.

Line 331: Again, a single value is used for the protein content of the placenta. Surely, there must be some uncertainty around this value no? Is there no data from marine mammals?

Lean tissue has a very consistent protein content. There are no data on placenta content for any marine mammal. More importantly, the uncertainty on the protein content is not that important compared to the uncertainty in the mass of the placenta, and that is all tiny compared to the other variables. See for example our new Fig. 3. The N from placentas is so small it doesn't even register compared to urea and deadfall N.

Line 333: Is 16% an accurate value, or is there uncertainty around this value as well? If so, please provide it, or otherwise give a justification to why there is no variation.

The 16% value is what is used in the nutritional literature, typically without any measure of variation. It is based on the stoichiometry of an average of typical protein and is widely used throughout biology. There is no reason to assume that whales are substantially different. A change of 1-2% would have a very limited impact on our calculations, especially compared with numbers that are more uncertain like total population size.

Lines 338-339: These are major assumptions, without any justification. How does these values compare to those estimated from whaling records (see many of the papers from Lockyer, Vikingsson etc.). There must be considerable variations in these values, and differences between species, age-classes and reproductive states. That variation needs to be incorporated into these analyses, to see how it will affect the final estimates.

Pershing et al. 2010 used Lockyer extensively in their 2010 paper to get the von Bertalanffy growth curves that allowed them to estimate adult mass. We have added uncertainty to these

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Where is the logic in this? This will surely depend on several life history parameters, such as age at first reproduction, juvenile and adult mortality, inter-birth intervals etc. (see next comment)

A Type: Highlight Subject: Highlight Date: 30/03/2024, 13:58:17

How can this be a valid assumption for cetaceans? According to Taylor et al. (2007, see below), age at first reproduction for baleen whales average about 10 years, while the calving interval averages around 2.5 years. In Table 1 in that paper, they also report estimated proportions of adults in the population, assuming both an intrinsic max population growth rate and a stable population. Even in the case of stable populations, their estimated proportion of adults is only about 71%. This drops to about 50% if you assume the estimated intrinsic maximum growth rate for the different species (mean: 4.8% across baleen whale species). there is no reason why this intrinsic maximum growth rate should not be valid, given that many baleen whales appear to be recovering.

In any case, given that estimates do exist for several of these critical life history parameters, there is no reason not to use them in important studies such as this one.

Taylor, B. L., Chivers, S. J., Larese, J., & Perrin, W. F. (2007). Generation length and percent mature estimates for IUCN assessments of cetaceans. Administrative Report LJ-07-01 National Marine Fisheries, January, 24 pp.

A Type: Highlight Subject: Highlight Date: 30/03/2024, 13:56:29

Yes, but it does not account for the consistent downward bias in number of lactating females due to the juvenile component of the population. Why not use the estimated adult proportions from Taylor et al. (2007) in your calculations?

Response to Reviewer Two

1. The estimate of reproductive females that migrate and give birth to calves. The authors assume that all females in the population do this. In fact, for many of the relevant species, about half of the females will be sexually immature. In addition to not giving birth (giving rise also to placentas and calf carcasses), they may not even migrate to low-latitude calving grounds.

Our calculations assume a steady-state population. Under this assumption, most females in the population will be sexually mature. We effectively assume that all females older than the calving interval are mature. In a growing population, the proportion of juveniles will be higher. If detailed age structure were available, they could be incorporated into the calculations. Our sensitivity analysis suggests that the nitrogen flux estimates are sensitive to the proportion of lactating females, and our uncertainty estimates include this factor. We have added a line to suggest that a growing population with a high proportion of juveniles will be at the low end of the estimates (line 554).

2. The authors use estimates of calf and adult annual mortality to estimate the number of carcasses that may be added to the breeding grounds. This seems to assume that all of this annual mortality occurs at these calving grounds. This is highly unrealistic, and the number of carcasses is therefore likely highly overestimated.

Our model assumes that mortality occurs equally across annual migration cycle, which is a conservative approach as nutritional/energy effort required for migration/lactation, along with male competition on the breeding grounds likely means more individuals will die in calving grounds (Smith et al. 20169, Roman et al. 2014).

3. I have trouble understanding how the ratios of feeding to breeding/calving grounds are calculated. Do they represent some ratio of number of observations, in which case this is problematic when using highly disparate, and partially opportunistic sightings, or do they represent geographic areas? This is not clearly described in the methods or SI.

As whales generally have vast feeding grounds, but relatively smaller breeding areas, we calculated the ratio of feeding area:breeding area to examine for a possible nutrient funneling effect of whale nutrient transport (i.e. whales accumulate nutrients from a wide area, but generally deposit in small coastal lagoons; see Fig 1). For this, we adopted a commonly used method to examine the area of utilization during different seasons (i.e., by using observation data during the feeding season and breeding season for each whale sub-population outlined in table S4). The exact methods we used to generate feeding/breeding areas are described in Supplementary Information text L0-90. However, as the reviewer correctly identifies, bias in observations used to generate feeding/breeding areas (e.g., near shorelines/shipping lanes, etc.) may skew our generated polygons. Consequently, we used a 95% kernel density (i.e. there was a 95% probability of finding an observed individual within the boundary) to incorporate as much of the data as possible, while still excluding uncommon or extralimital observations (e.g., laggard or non-migratory individuals). To ensure that our feeding:breeding area ratios are robust, we also undertook this procedure using a 90% and 99% kernel density (see figures S1-S5). Finally, we also undertook a systematic literature search and used expert opinion to generate

Response to Reviewer Two

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How much is actually known about this across species? I'm not convinced this has strong support.

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It is also unfortunate that the two species of focus (right and humpback whales) are known for their coastal breeding habits, while many other baleen whale species have more offshore (and often poorly known) breeding areas. So, it is perhaps questionable to assume similar nutrient funneling for these other species. While the authors do not explicitly state that their conclusions in this context should be extended to other species than the two focus species, the overall conclusions and message of the paper will perhaps become biased. I would encourage the authors to state this clearly.

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As already stated, I don't agree with this assumption. I would argue that the most realistic estimate of proportion of adults in a population is around 50-60%, which would substantially reduce your estimates.

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No, it is not reliable, because it doesn't fully account for the proportion of immature animals. Again, see Taylor et al. Table 1.

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Sensitivity analysis not explained

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Number of reproductive females remain overestimated relative to what's been estimated elsewhere (e.g. Taylor et al., 2007).

Note 18. Again, it's a bit unclear to me when you focus on these species, and when you focus on the other two (blue and fin whales). Perhaps it can be better clarified in which contexts you focus on one or the other group, and why?

Please see the section: **Potential importance of other balaenopterid whales** on p. 8.

Note 19. But see my comments on the methods section about sexually mature females only representing perhaps half of all females in a population. This may then actually produce an upward bias that more than compensates for the supposed underestimate the authors discuss here.

As we mentioned above: "Our calculations assume a steady-state population. Under this assumption, most females in the population will be sexually mature. We effectively assume that all females older than the calving interval are mature. In a growing population, the proportion of juveniles will be higher. If detailed age structure were available, they could be incorporated into the calculations. Our sensitivity analysis suggests that the nitrogen flux estimates are sensitive to the proportion of lactating females, and our uncertainty estimates include this factor. We have added a line to suggest that a growing population with a high proportion of juveniles will be at the low end of the estimates."

Note 20. The proportion of these categories of animals that actually migrate is highly uncertain. Together with the likely overestimate in pregnant females, including these additional categories may not in fact provide a reliable population-level picture. Indeed, I would argue that this is a substantial overestimate.

Our estimate for pregnant females is reliable, accounting for immature animals and years when they don't breed. Much of the population travels for many species, including gray whales, humpbacks, and southern rights. And whereas every individual won't necessarily migrate every year, most of these populations, to the best of our knowledge, journey to lower latitudes. We believe this is made clear in lines 108-112.

Note 21. Indeed, and likely more than just 'some'.

Note 22. Or don't go there at all, but remain at high or mid-latitude feeding grounds.

Note 23. I couldn't agree more! And until such data are available, I think any speculations must be treated with extreme caution.

To notes 21-23. We believe the new uncertainty ranges, updated references, and data make clear that our range of values, from reproductive females (most conservative) to entire population (possible upper bound), provides a good background for this long-distance movement of nitrogen and other nutrients. We have added another sentence to this paragraph to make clear that not all individuals migrate.

Note 24. Ratios of what? Abundance? Days present? See also my comments/questions to table 1 in the supplementary information document.

There is also a recently published paper on fin whale abundance in the Scotia Sea that might be worth including:

https://link.springer.com/article/10.1038/s41598-024-57378-3?utm_source=rct_congratemail&utm_medium=email&utm_campaign=oa_20240329&utm_content=10.1038/s41598-024-57378-3

This refers to ratios of size. Seen Table 2 in manuscript.

Note 25. This now suggests that the ratios represent area ratios? Again, perhaps I've missed something, but this is not at all clear in the methods or SI sections.

We edited the paragraph for clarity.

Note 26. I would move this sentence to after the sentence that ends on line 115.

Done.

Note 27. But how much in relation to nutrients released by other marine organisms? This is something frequently missing in discussions about the relative importance of whales as ecosystem engineers.

See Fig. 3 for comparison to seabirds as an example.

Note 28. What does this mean? I assume you mean that they may not have regular and well-defined seasonal migration patterns, similar to those observed in e.g. grey and humpback whales?

Yes. Thanks.

Note 29. There are several recent papers suggesting this is no longer the case, but that fin whales are well on their way back towards preexploitation levels. See papers by e.g. Helena Herr et al., Sascha Viquerat et al., https://www.researchgate.net/publication/361825408_Return_of_large_fin_whale_feeding_aggregations_to_historical_whaling_grounds_in_the_Southern_Ocean

Fair enough. We have **included this reference** and a caveat.

Note 30. I still think this is an oversimplification. Especially given the very strong and untested assumptions made in this analysis, as well as the lack of any comparison to similar studies on other organisms. At the very least, I would encourage the authors to note this, i.e. the possibility that several other marine organisms may contribute greatly to these types of transports.

Fair enough. We have added a hedge that there are possibilities that other species may play similarly large roles as more studies become available.

Note 31. While this may be true, several species actually feed mostly within the euphotic zone, and thus this vertical transport does not represent re-introduction of nutrients from other water masses, but simply a regeneration within the euphotic zone.

Yes, I agree. At least for species that breed in small, well defined coastal breeding areas, but perhaps not for oceanic breeding areas.

Yes, vertical movement can be recycled or add new nutrients. We have added “and within” for clarity.

Note 32. But how large is such horizontal transport compared to the natural advection by ocean currents? True, this process will be slower in terms of transport between high- and low-latitudes, but will likely be several orders of magnitude greater. And even if such advection has a delay of several years in reaching low latitudes, it is constant and may overall be much greater than the whale contribution.

The role of advection will differ considerably from place to place and across spatial scales. Our conceptual model is that oceanography sets the background conditions such as explaining why the Hawaiian calving grounds are oligotrophic. Horizontal transfer by migrating whales adds on top of this process. If the background state is oligotrophic—a common feature of most calving grounds, then the whale conveyor belt can be an important contribution. We show that this can be **locally significant**, but at a global scale, oceanography will dominate.

Note 33. This has been stated several times in the MS, and is indeed the foundation of the entire analysis. Seems weird to have this sentence so far into the discussion of the MS.

This sentence has been recast.

Note 34. Done.

Note 35. Surely, this depends on which seabirds we're talking about? Several species are known to migrate across distances that far exceed those of whales. Indeed, some seabirds seasonally migrate from pole to pole, thereby potentially moving nutrients between Arctic and Antarctic polar regions...

One of the main differences is that seabirds feed their chicks from prey they capture within flying distance of the breeding grounds. We now clarified that in the text.

Note 36. Again, while this may be correct for some species, it's certainly not the case any longer for several of them.

We recast the sentence.

Note 37. It's surprising that the IWC catch database has not been used, as it is one of the most comprehensive databases of historical whale catches. It can be obtained from the IWC upon request.

We used the databases that were publicly available to us online, but did not encounter the IWC data (except for some from Brazil). Thanks for the heads up that these data are available on request. We will consider this for future studies.

Note 38. This species is probably less tied to shallow waters than the other two?

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Again, I don't agree with this, and I suggest the authors account for the non-adult proportion. Most simply by using the estimates in Table 1 in Taylor et al. (2007).

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OK, thanks. Just be clear then, that your estimates are at the upper limit of those reported.

As mentioned above, our calculations assume a steady-state population. This allows us to compare pre-whaling and modern populations. Under this assumption, most females in the population will be sexually mature. We effectively assume that all females older than the calving interval are mature. In a growing population, the proportion of juveniles will be higher. If detailed age structure were available, then that could be incorporated in the calculations. Our sensitivity analysis suggests that the nitrogen flux estimates are sensitive to the proportion of lactating females, and our uncertainty estimates include this factor. We have added a line to suggest that a growing population with a high proportion of juveniles will be at the low end of the estimates.

Note 44. This entire section is not very clear. It is frequently very challenging to understand exactly what is done in the different steps. The notation is confusing, as it you seem to sometimes use the same letters for different things, and switch between uppercase and lowercase letters. It is also not entirely clear when you try to create your allometric equations based on values from other studies, so I suggest you explain this explicitly to the reader. I also have several issues with the calculations themselves, but hopefully my issues are based on my poor understanding partly caused by the unclear description. But I would strongly urge you to double check all calculations to make absolutely sure they are correct.

We have double checked our calculations, and the results are now available online, and we have answered direct concerns about equations and steps.

Note 45. I cannot find actual mean body mass (I assume by 'size' you mean mass, and not length?) estimates in Pershing et al (2010). I assume you've obtained these by dividing biomass with abundance estimates in Table 1 from that paper?

Yes, by size we mean mass (clarified in text). The population-average masses were not published in Pershing (2010), but they were an intermediate step in their calculations. We obtained their original tables and use them in this study.

Note 46. I couldn't access the original article, so this bit left me somewhat confused. First of all, which of these two versions did you actually use? They give ever so slightly (unimportantly) different results, so I don't see the point of including both versions. More importantly, they don't seem to give reasonable results, whichever unit (g or tons) are used. Using g gives vastly underestimated calf masses (240 kg for a humpback whale calf, 720 kg for a blue whale calf). Using tons on the other hand, gives overestimated calf masses (4.4 tons for a humpback calf, 13.2 tons for a blue whale calf). More reasonable (though at the upper limit of reported) values are obtained assuming units are kilograms (1.03 tons for a humpback calf, 3.1 tons for a blue whale calf). This really needs clarification, as units here make a big difference.

It was hard for us to decipher from the PDF exactly what the reviewer is referring to here. We presume it is the equation for calf mass. The equation assumes that the calf mass is specified in kg (the reference to g in the text is a typo). The output is also in kg.

conservative, since deaths on the breeding grounds could be higher than those on feeding grounds due to conflict and limited food resources.

Note 53. What is N here? Since you use N for nitrogen, it is confusing that you use N here too, and since you've already defined F as the number of pregnant females at the calving ground, it's unclear what this N refers to.

Good point. Thanks. N is the population size. We replace this with P.

Note 54. This is a slightly confusing way to denote. Does it mean U as a function of mass?

Yes, we are using standard function notation here. U is a function of mass.

Note 55. Done.

Note 56. Done.

Notes 57-58. See previous point about subscripts.

We are using standard function notation here.

Note 59. In this case, mass is in kg. Perhaps this is worth pointing out? And it's then also crucial that you stick to kg also for whales. You do so initially, but eventually you convert to tons. I'm not sure this is done correctly, but more on that later.

We use kilograms and tons for readability. We have confirmed the calculations. Thanks for the heads up.

Note 60. You may want to explain that this constant is calculated by re-arranging eq 1.

Done.

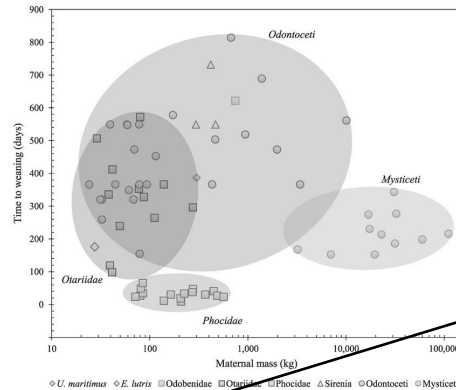
Note 61. Elephant seals are extreme capital breeders, with a very short lactation period compared to baleen whales (~3 weeks vs. over 2 years). I seriously doubt that these values are indicative of a late lactation baleen whale. In fact, most of the lactation period in a baleen whale does not occur at the breeding grounds, as females most likely leave soon after birth and continues their lactation enroute to feeding grounds, and subsequently during the first 2 or so years. Using elephant seal data, especially from some late lactation/ fasting stage, therefore doesn't seem very representative here.

The bioenergetics of capital breeding are discussed in Costa (1993) and Costa and Maresh (2017). Figure 6 in Costa and Maresh (below) shows that when you control body size the time to weaning is comparable between phocids and mysticete cetaceans. **More importantly phocids and mysticetes are both extreme capital breeders.** The only reason baleen whales can lactate while fasting for many months is because of their large size and the associated benefits that come with it.

While I agree in terms of dividing feeding and calving geographically and temporally, there is an important difference in terms of lactation and time to weaning. I would argue that extreme capital breeders are those where females fast completely from birth to weaning. I don't think that holds for cetaceans, which lactate for several years while feeding, and where weaning is most likely gradual (i.e. calves start feeding before they stop suckling). Anyways, since you end up using the lower numbers, i.e. from mid-lactation, I guess it's OK. The late lactation numbers for elephant seals are probably irrelevant, as they still fast at that stage (as opposed to cetaceans).

I don't see how you can refer to time to weaning as a purely metabolic process. Again, surely this time should depend greatly on whether weaning is abrupt (as in e.g. elephant seals) or gradual (as is likely in most cetaceans). But, this is becoming an academic argument without real implications for the MS, so I'll just leave it.

Sure, but again, why is this relevant, given the very different lactation strategies?



To put in perspective, metabolic rate generally scales with mass^{0.75}. It follows that other metabolic processes such as time to weaning should similarly scale as mass^{0.75} (Calder 2001). Therefore, following the same scaling relationship, we can estimate the time to wean for an elephant seal if it were the size of a blue whale.

Metabolic rate (in energy units e.g. Joules per day, Watts, or Kcal per day) = $A \times \text{mass}^{0.75}$, Where A is the scaling constant

Thus, we solve for the constant A that scales time to weaning or lactation duration for a given body mass:

Elephant seal time to weaning 26 days; $26 \text{ days} = A (500 \text{ kg})^{0.75}$
 $A = 0.246$

A comparable time to wean for an elephant seal the size of a blue whale would be:
 $105,000 \text{ kg mass } 0.246 * (105,000 \text{ kg})^{0.75} = 1434 \text{ days or 4 years}$

Based on simple scaling relationships, whales are even more extreme capital breeders than elephant seals and our elephant seal extrapolation should be conservative.

An independent method of calculating the nitrogen excretion rate is to assume a metabolic rate based on simple scaling relationships. Villegas-Amtmann et al. (2015) estimated that migrating gray whales would have a field metabolic rate that is 1.3 times that predicted by Kleiber (1975). Assuming the same relationship for a 105,000 kg blue whale would be:

$\text{BMR} = 1,708,500 \text{ kJ/day} = 293 \text{ kJ/kg-day} * (105,000 \text{ kg})^{0.75}$
 $\text{FMR} = 1.3 \times \text{BMR} = 2,221,050 \text{ kJ/day}$

Fine, but again I don't think this late lactation point is relevant, given the different lactation strategies.

And? Was my original point based on a misunderstanding on my part? Should I simply trust that the authors have done it correctly, without any explanation being given? I'm simply trying to make sure all calculations are correct, as this topic is of great importance. I'm not trying to prevent publication, I'm simply trying to be helpful.

7.9% of the energy provided in a fasting seal comes from protein in early lactation, which is low compared to other mammals. This increases to 11.2 % in late lactation.

Thus, protein oxidation is $7.9\% \times \text{FMR} = 175,463 \text{ kJ/day}$ of protein

Protein has 18 kJ/gr and 16% of protein is Nitrogen: $155,473 \text{ kJ-day} / 18 \text{ kJ-gr} = 9.75 \text{ kg protein per day}$

9.75 kg protein per day of which 16 % is Nitrogen = 1.56 kg Nitrogen per day being excreted early and 2.21 kg/day late.

Calder, W. A. 2001. Ecological Consequences of Body Size. Encyclopedia of Life Sciences. John Wiley & Sons, Ltd.

Costa, D. P. 1993. The relationship between reproductive and foraging energetics and the evolution of the Pinnipedia. Pages 293-314 in I. L. Boyd, editor. Marine Mammals: Advances in Behavioural and Population Biology. Oxford University Press, Symposium Zoological Society of London.

Costa, D. P., and J. L. Maresh. 2017. Energetics. Pages 329-335 in B. Würsig, J. G. M. Thewissen, and K. Kovacs, editors. Encyclopedia of Marine Mammals. Academic Press.

Kleiber, M. 1975. The Fire of Life: An introduction to animal energetics. R.E. Krieger Publishing Co., Huntington.

Villegas-Amtmann, S., L. K. Schwarz, J. L. Sumich, and D. P. Costa. 2015. A bioenergetics model to evaluate demographic consequences of disturbance in marine mammals applied to gray whales. Ecosphere 6.

For notes 62-68. We refer the reviewer to the revised methods and figshare. Reviewer I did not have the same concerns. We have rechecked our numbers, and they are consistent throughout. Thanks for prompting a review. We have rewritten for clarity..

Note 62. This doesn't seem right to me. If the goal here is to convert to tons, you should surely divide eq 2 by 1000, not multiply, as you do in the last part of eq 3 to calculate B. And I don't see why you include the 0.75 power twice in the resulting equation. Perhaps I'm missing something here, but the description is not very clear of what you do and why in the different steps.

Comparing eq2 and the first part of eq3, it seems to me that $B=vA$. So where do you get the second part of eq3 from?

In the end, if you use $B=73.49$ in the first part of eq 3, and include the mass of a blue whale (now in tons rather than kg), you get: $n(m)=Bm^{0.75}=73.49*105^{0.75}=2410.57$, i.e. exactly the same as you get from eq2, and thus still in g. As far as I can tell, to convert this to tons of nitrogen, you'd have to divide by 1,000,000, which doesn't seem right.

We have rechecked our calculations.

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Yes, I now understand. Apologies for the confusion, and for being overly pedantic.

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I understand that this is not known, but what do you assume in your modelling? In your calculations, does a mother leave as soon as her calf dies? I'm not questioning what you've done, I just want to understand and make sure things are clear.

Note 63. As far as I can tell, this refers back to the elephant seal numbers, but this is far from clear. It would perhaps be better to restructure this entire section, to make it easier to follow the logic.

We inserted "whale" for clarity.

Note 64. But this now throws me off a bit, as it suggests the more conservative numbers are simply chosen on the assumption that calves consume less milk, and has nothing to do with the numbers you took from elephant seals. All very confusing....

This refers to whales calves, since they likely consume less milk when younger.

Note 65. New subscript that hasn't been previously defined. I assume it means 'united' or something?

Yes, thanks, we have clarified.

Note 66. What does this survival estimate refer to? Calves I assume? But what about the mothers of calves that do not survive? Are they assumed to simply leave the calving grounds as soon as the calf dies?

We don't know the death of a whale calf, and its timing, affects the time on breeding ground for a mother.

Note 67. Unclear what this refers to.

Not sure what you meant here on pdf.

Note 68. Surely this depends greatly on when a calf dies, and how large it is at that stage?

Sure. We are using a conservative average estimate for calf size.

Note 69. This makes it sound like the calf contribution isn't included in Nu, but surely it is? It would be better to say that 'Adults contribute 90% towards Nu, while calves contribute only 10%.'

Done.

Note 70. Almost certainly only the proportion of the population that actually migrates to breeding grounds. This may only be adult females that are pregnant or ready to mate, and males that are sexually active. the assumption that this makes up the majority of a population is probably wrong. Humpbacks, for example, can also be seen in wintertime at high latitudes, and old whaling records confirm humpbacks were taken at high northern latitudes also in winter.