Peer Review File

Manuscript Title: Baleen whale prey consumption based on high resolution foraging measurements

Editorial Notes:

Reviewer Comments & Author Rebuttals

Reviewer Reports on the Initial Version:

Referee #1 (Remarks to the Author):

This manuscript is based on an impressive data set comprising field observations of feeding behaviour of various species of tagged baleen whales in relation to available prey density from which consumption rates were deduced. These measurements come as close to direct observations as one can get in the pelagic realm and they have been carried out on both types of baleen-whale feeding mode (lunge and ram feeding) by different research groups working in different sites of the world ocean. The overall conclusion from these comprehensive results was that all the whale species studied consumed much more prey than current estimates. This finding on its own, scaled up to the pre-whaling population sizes, would warrant publication in Nature and the authors make a convincing case for why current estimates of past and current whale consumption derived from various assumptions and considerations are likely to be too low. The authors assume that the much higher productivity of the whale feeding grounds required to support the much larger prey populations to feed the actual demands of the whales is provided by the recycling of essential nutrients in the surface layer by the whales, in particular iron in the Southern Ocean.
I need to point out at here that, as the originator of the "whale manuring hypothesis" invoked in 2005 and laid out in 2007, I am favourably inclined to the results presented here (references at the end). In the 2010s the hypothesis captured the public imagination as the "power of whale poo" (Monbiot in the Guardian) and was promoted by various green movements but was disregarded by most mainstream krill scientists. Further, models parameterised with current values not surprisingly cast doubt on its functioning since the hypothesis was based on the pre-whaling krill stocks. The matter remains controversial until the experiments to test the hypothesis I outlined (2007) are carried out, for which there is unfortunately great reluctance in the community. So, the measurements presented here, which indicate that the biomass of prey organisms is underestimated and is likely to have been at least more than double in the presence of intact whale stocks, are grist to my mill and I acknowledge my bias.
I accept that consumption rates during the observations were higher than expected but the reasoning behind the extrapolations of observed and deduced feeding rates to daily, seasonal and from there to annual and global scales is not well explained in the text and can be easily contested. The authors chose to highlight the higher values (like fivefold, or 30% of body weight eaten on one day) that are hard to believe and undermine the real message – that the pre-whaling stocks of baleen whales will indeed have acted as ecosystem engineers. Exaggeration will unnecessarily raise scepticism about the overall veracity of the results. The authors have chosen this path because they are trying to elevate the implications of their findings to the carbon-cycle stage where "more is better" without regard to the physical-chemical constraints on the ecosystems they invoke to support their estimated prey stocks. The carbon framework is not only detrimental to the message of this paper but the reasoning behind the estimates of the whale-mediated carbon sink is flawed. In Table 1 the estimates of carbon export from whale and krill-fertilized phytoplankton are based on observations made on diatom blooms under low grazing pressure – the norm in today's

megafauna-bereft oceans. During a time station we were carrying out in the Weddell-Scotia Confluence in 1988, I had the good fortune to observe, without seeing it at the surface, a krill swarm suddenly appear in the water below the ship, and graze down the diatom bloom we were studying by severalfold in a matter of hours. They darkened the light profiles we were taking, individuals were attached to the CTD and masses were collected by all the nets we deployed, even hand nets. They left behind a cloud of faecal strings, the bulk of which did not sink out, evident from vertical profiles of depth distribution. The situation was very different in an iron-fertilized diatom bloom without krill where we observed massive sinking out of diatom aggregates to the deep sea in its aftermath.

It is now well established that the iron supply determines productivity of the Southern Ocean and that iron has a short life time in the surface layer reflected in satellite images of the location and duration of phytoplankton blooms: restricted areas along the coasts and islands that receive terrestrial or sedimentary sources of iron, as well as the short life times (weeks to a month or two) of blooms in regions fertilized by dust or melting ice bergs in today's oceans. In the relative absence of krill swarms, the diatoms responsible for this iron-enhanced productivity sink out of the surface layer taking the iron with them. Microbial recycling communities with tenfold lower biomass replace the diatoms in the iron-impoverished surface layer: the classic HNLC condition. The current krill populations are apparently unable to adequately utilize diatom blooms in the above-mentioned regions where iron is supplied from external sources. However, in the pre-whaling Southern Ocean, whale stocks were one to two orders of magnitude higher than today implying that krill stocks must have also been much larger to provide the food necessary to sustain them. Since the supply of new iron entering the system is not likely to have changed much between then and now, if at all it has increased as a result of retreating glaciers in the Peninsula, various islands and Patagonia, the only way to explain the much larger krill stocks is to invoke maintenance of the iron in animal tissue that is then recycled in the surface layer. In other words, iron lost by sinking diatoms but also krill faeces and cadavers must have been substantially reduced in the pre-whaling phytoplankton blooms. An efficiently functioning recycling system by definition binds but does not sink carbon. You can't have your cake and eat it. So the assumption of whale- and krill-fertilized diatom blooms sinking carbon to the deep sea is invalid and all conclusions drawn from it should be removed from the manuscript. The concept of "carbon sink" dealt with here as an amount removed from the atmosphere and not delivered back elsewhere is faulty. Reference to the Amazon rain forest is a case of cabbages and kings. For example, prior to the industrial age atmospheric CO2 levels had remained fairly constant around 280 ppm (~600 Gt) over the Holocene. A sustained annual sink of the magnitude proposed by the authors (0.4 Gt) and not compensated elsewhere would have drained the atmospheric pool to glacial levels of 180 ppm within 500 years as opposed to the tens of millennia that transitions recorded in ice cores over past climate cycles actually took.

In this light, can whales contribute to carbon sequestration? As shown by Lavery et al (2010) sperm whales can do so by feeding on deep-sea squids and releasing the iron contained in them by defecation at the surface, the condition being that the C/Fe ratios in squids is substantially lower than in the phytoplankton biomass fertilized by surface-defecating whales that eventually sinks out. This condition does not apply to baleen whales feeding on krill and copepods, because even if the latter retreat to depth for some hours, they are essentially creatures of the surface layer that contain iron (and carbon) in their tissues collected there. Indeed, the carbon in krill and zooplankton biomass enhanced by whale recycling will be the major sink term in the carbon cycle. A krill biomass of around 600 Mt maintained by the whales in the pre-whaling era is equivalent to around 60 Mt of carbon which is not much compared to around 2 Gt taken up by the ocean's solubility pump annually. But it contains enough iron to fertilize diatom blooms over millions of km2 as this calculation shows. Taking a generous area of 2 million km2 for the former whaling grounds in the SW Atlantic sector of the SO, 600 Mt of krill biomass (the stock necessary to feed the pre-whaling whales), is equivalent to 300 g or about 600 krill m-2. This is a lot of animal biomass and, converting biomass to carbon, about 30 gCm-2. Compare this figure with the biomass of a prominent diatom bloom in satellite imagery: 10 – 20 gCm-2. Carbon in animal biomass would have contributed the bulk of the POC pool. As ocean iron fertilization experiments have shown, a diatom bloom takes about 3 weeks to reach this peak, with aggregation and sinking out of portions of the bloom occurring in subsequent weeks. Given the constraints on phytoplankton growth rates in the Southern Ocean, the size of the animal biomass accommodated in this recycling ecosystem will be influenced by grazer density and behaviour, but there will be an upper carrying capacity regardless of the mode of harvesting (timing and intensity) by grazers. In satellite images, had they been available, the pre-whaling feeding grounds are likely to have resembled a patchwork quilt in the tens of km range. Observations made in the early last century described feeding whales from horizon to horizon with the surrounding water coloured red with krill swarms. I have spent over two years in the Southern Ocean and never seen a krill swarm at the surface nor a blue whale.

What the whales of the past were maintaining were giant recycling systems based not on the microbes of the current recycling systems, bereft of their large fauna, but on a diatom-krill-whale based ecosystem. In this scenario the iron pool on which the system functioned was located in the overwintering krill and zooplankton pools that was released back to the phytoplankton by whale faeces. The net long-term carbon sink to the deep sea emanating from this system depends on the C/Fe ratio of sinking particles. I have explained the scenario in Smetacek (2007).

Since there is an upper limit to the amount of blubber a whale can put on, the total number of days spent feeding will depend on the energetic costs of lunge-feeding in relation to prey density as also the efficiency of digestion, assimilation and proportion of krill biomass incorporated into blubber. At the greater prey densities reported by visual observations of surface krill swarms during the whaling era, the costs of converting prey into blubber will have been lower. Further, since the intact whale populations herded krill to the surface, iron leaching out of krill faeces would be more effectively utilised by phytoplankton than deep feeding, now more prevalent with fewer whales. Another factor promoting recycling would be the biomixing caused by the whales (described in this manuscript) as this would break-up and disperse friable krill faecal strings and copepod pellets thereby retaining their contents in the surface layer. In short, the more whales, the more efficient the recycling. Hence, I caution the authors not to overplay their hand by invoking fivefold higher feeding rates over current estimates as these are hard to imagine. For instance, comparing herbivores with known inefficient digestion (elephants) feeding on terrestrial plants consisting largely of cellulose and lignin with krill-feeding whales does not make sense (Line 662). Both are ecosystem engineers but in very different ways. Elephants defecate huge amounts, mostly undigested remains, but can the same be said of whales? The indigestible krill chitin exoskeleton is a relatively small fraction of biomass. Besides, krill secrete powerful proteases that promote autolysis of crushed krill to such an extent that fishing vessels pump krill out of the cod ends of fishing nets while fishing, to prevent them becoming mush. What counts here is not the mass of the faeces but their iron content and its immediate availability to photoautotrophs. Having said all this, I need to point out that krill, when offered high food densities in aquaria, feed and defecate continuously. Copepods are also wasteful feeders in the wild, evidenced by the many intact cells commonly seen in their faeces. I have argued the recycling benefit of this “superfluous feeding”, so would not be surprised if the whales were doing the same in dense krill swarms. This would imply that whales consuming 30% of body weight per day would be defecating a greater proportion of undigested food than an individual feeding at its metabolic capacity. In human terms all these animals enjoy eating because gluttony has a positive feedback on the system sustaining them.

It might be worthwhile pointing out that the annual food demands of intact whales populations - >200 Mt – is more than twice the world fish catch. The former was sustainable because the whales were putting back the crucial element iron whereas fishing vessels only remove biomass but do not return anything.

I had some problems with the figures that need to be redone. I did not understand Fig. 2. Why is there no scaling on the Y axes? For Figs 3 and 4 I recommend linear instead of logarithmic scales. The latter is useful when lower numbers need to be deciphered, but here it is the higher numbers that need highlighting particularly the differences between species. These figures need to be better discussed and presented in the main text. Space will be gained for this if text on the purported impacts on the carbon cycle is removed. Also, I think it would be more appropriate in the cartoon to have the arrows from phytoplankton to krill and whales pointing in the other direction as this would be more indicative of recycling. In any case this cartoon is not particularly informative at this level of resolution and could be dropped or more relevant details included.

I recommend resubmission of a manuscript with major revisions in which the emphasis is on ecosystem engineering instead of the global carbon cycle.

Ref.

Smetacek, V. & Nicol, S. (2005) Polar ocean ecosystems in a changing world. Insight review. Nature 437: 362-368.

Smetacek, V. (2008) Are declining Antarctic krill stocks a result of global warming or of the decimation of the whales? In Duarte, C. M. (ed.) “Impacts of global warming on polar ecosystems.” Fundación BBVA, www.fbbva.es, ISBN: 978-84-96515-74-1, 45-83 (available on the web).

Referee #2 (Remarks to the Author):

This is an outstanding manuscript, using a massive set of data on the foraging behavior of baleen whales. Every tag deployment – especially those collected in polar waters – would have been difficult to obtain. The manuscript also combines three modern technologies for collecting data on baleen whale foraging in a novel manner. These are: suction cup tagging to elucidate foraging behavior, using scientific echosounders from small vessels, and UAS (drone) photogrammetry. With over 300 tag deployments and more than 70,000 feeding events recorded over a decade, just the suction-cup tagging data set is the most comprehensive published (to my knowledge) to date.

Then, adding photogrammetry to estimate engulfment capacity of rorquals with sounder-derived estimates of prey density to this data set reframes our knowledge of rorqual foraging ecology. The foraging estimates for balaenids in the manuscript are less well informed than those of the rorquals, and do not have data on prey fields from scientific echosounders, unfortunately. However, the information provided is still an improvement on our current understanding of their foraging ecology.

The authors then take this information and give it context. The finding that baleen whales’ prey consumption has been underestimated substantially is a major new finding, and in itself warrants publication in a high-profile journal. The authors then explore the implications of this finding for marine biogeochemical cycling quite comprehensively. Their findings are exciting, and somewhat alarming. They indicate that the important role that baleen whales play in marine nutrient cycling has been seriously underestimated.

Yet their models are quite conservative – they leave out some baleen whale species that are also likely significant (sei whales, for example), and they assume that baleen whales feed for a maximum of 6 months, when we know that some are present in polar waters for longer than that (e.g. Van Opzeeland et al. 2013). And while the authors consider most of the known biogeochemical contributions by baleen whales, they miss at least one. The nutrient contribution to relatively nutrient-poor tropical systems by baleen whales’ annual calving migrations is likely significant, when baleen whale populations recover. The afterbirths, stillborns and neonatal mortality of hundreds to thousands of female baleen whales probably provide a significant annual nutrient pulse to tropical calving grounds. I mention it not to require the authors to mention this particular example, but to note that there are other aspects of baleen whales’ role in marine biogeochemical cycles that could have been considered.

Finally, the authors then explore what this means for carbon sequestration, and possible role of baleen whales in natural climate solutions. This is a very exciting aspect of the work, as it is well quantified. There have been previous discussions of this general idea. But this manuscript, because it shows that we've underestimated the amount that baleen whales forage, takes the idea further than it has been previously. This work should help change the conversation on the importance of recovering baleen whale populations internationally, by demonstrating its climate benefit. It also shows the climate cost of prior whaling, and should re-frame the discussion of the utility, and ecosystem consequences of current commercial whaling.

While the role of baleen whales in natural climate solutions is important and justifiably the focus of the manuscript, there are a couple of other management implications of this work that area not mentioned in the manuscript., It may be that space considerations prevent these from being raise, but I'll mention them anyway, in case the authors find them worthwhile. The point that more whales mean more productivity should be considered in national strategies to enact ecosystem-based fisheries management (EBFM). Encouraging baleen whales' recovery is valuable not only for conservation and for climate, but for sustainable fisheries - as more whales should lift carrying capacity of marine ecosystems. I'm not aware of any national EBFM strategy that includes this idea, so it might be worth mentioning. Similar reasoning applies to national management when legislation specifically links management of whale populations to ecosystem carrying capacity (e.g. the US Marine Mammal Protection Act, see https://www.fisheries.noaa.gov/national/marine-mammal-protection/marine-mammal-protection-act).

I see no flaws in this manuscript that should prohibit its publication. I believe that this manuscript will be of great significance in several disciplines: marine ecology, conservation biology, the science of carbon management, marine management. I suspect it could be a paper that help drive a major change in how we think about managing whales, internationally and so could be hugely significant. Given the level of public interest in whales generally, and in the current climate crisis, I believe this manuscript, when published will also be of substantial general interest to a wide audience.

The data and analyses seem fine. I checked the first author's GitHub repo listed in the manuscript and all seems appropriate. My only concern with the figures is that I can't see where the boxplots are defined, which needs addressing (unless I missed that somewhere, but I can't find it). All other statistical presentation seems appropriate. I see no problems with the authors' interpretation of their data. To me the conclusions seem robust, valid and reliable. The manuscript is well, and copiously, referenced. The Abstract is clear and a valid representation of the paper. All sections of the manuscript seem appropriate.

Apart from my comment on the boxplots' detail, I have a very few minor clarifications that could help.

Line 35-36 – is this the Antarctic whale-krill-carbon pump, or world-wide? Clarification would help.
Line 189 - nearly all anthropogenic CO_2 emissions, presumably at the time, but it's not quite clear.
Line 367 – "Using diet composition (Z) from 77" ends abruptly. Is something missing?

The reference I cited above is:
Van Opzeeland I, Van Parijs S, Kindermann L, Burkhardt E, Boebel O (2013) Calling in the Cold: Pervasive Acoustic Presence of Humpback Whales (Megaptera novaeangliae) in Antarctic Coastal Waters. PLoS ONE 8(9): e73007. https://doi.org/10.1371/journal.pone.0073007

Referee #3 (Remarks to the Author):

B. Originality and significance: if not novel, please include reference

This manuscript tries to do a big job by synthesizing numerous diverse and unique datasets from several different research groups. Its very challenging thing to do and success relies on very clearly explaining all the various methods in a cohesive and comprehensive manner. This is not easy and the authors should be commended for their effort. A lot of work has been put into the modeling component of this manuscript and the approaches appear quite sophisticated. Unfortunately this draft did not quite succeed in communicating the information with clarity and so for that reason I cannot evaluate its significance to the field. I think that with a revision of the manuscript text with careful attention to clarity it is possible to achieve the goal.

A. Summary of the key results

I reviewed up to about half way through the methodology and I was so confused that I stopped my review because I could no longer follow the thread of the paper. There are issues with the clarity of the manuscript that need to be addressed before I can continue my review.

C. Data & methodology: validity of approach, quality of data, quality of presentation

The most concerning issue is that I cannot evaluate the methods section because the supplementary figures are peppered throughout it but I cannot find most of them cited in the text of the methods section, and so I do not know what information is being presented and why.

I am not an expert on animal metabolism and so I cannot comment on the appropriateness of the metabolic models or parameterization of those models used in this study. However, as a non-expert reader, I find a number of apparent inconsistencies between statements made in the text and the model equations. My general comment the model parameters and units need to be better explained so that the statements written in the text are straightforward to interpret for non-expert readers based on the information given about the model equations.
I have expertise using bioacoustics to measure zooplankton and I could not interpret the methodology used to measure krill biomass from echosounder data because not enough information was provided. For example, the frequencies of the echosounders used were not given. The section would benefit considerably from including example krill biomass data and associated calculations from a specific whale to better illustrate how the acoustic data were processed on lines 475-490.

C. Appropriate use of statistics and treatment of uncertainties

Very often the sample sizes are not given, and the choice of error bars used in the figures is not described (i.e., do they represent confidence limits, standard error, or standard deviation).

D. Conclusions: robustness, validity, reliability

I cannot evaluate the conclusions of the manuscript.

E. Clarity and context: lucidity of abstract/summary, appropriateness of abstract, introduction and conclusions

The authors do not state their study objective in the main text. After reading through the manuscript, I suggest that the objective stated on Line 28 of the abstract (i.e., calculate prey consumption) is an incomplete description of the study objective. My interpretation is that the objective is to model the contribution of baleen whale foraging biology to ocean carbon cycling using a box model approach (illustrated in Fig. 1c), where particular attention is given to parameterizing the model with novel field data on whale foraging.

A number of terms are used in the main text and there is no language that clearly defines or links these terms, which makes it a challenge for the reader to interpret the authors rationale. Terms include: prey consumption, ingestion rates, prey requirements, feeding rates, digestion time, prey patch quality, filtration, consumption. Units are not provided for any of the terms.

I find quite a few inconsistencies and contradictions in the abstract and main text that I highlight in the line-by-line editorial comments.

Editorial comments
Title:

Line 1: The authors should explain why they chose the term climate engineers. Climate engineering is the intentional large-scale intervention in the Earth's climate system to counter climate change. Whales are not influencing earth's climate intentionally.

Main Text:
Line 25: whales are referred to as climate engineers in the title and ecosystem engineers in the abstract. Why are two different terms used, and what is the difference between the two?

Line 30: Remove the 's'

Line 33: Sentence reads as though each whale required an order of magnitude more prey prior to whaling. I think the authors mean that the whale populations were larger and so the total prey consumed was greater in the pre-whaling era.

Line 35: If this study shows that past studies have underestimated prey consumption, then the authors should justify why it is appropriate to then reference the size of the global carbon sink generated by whales to past studies (citations 6, 7). This approach makes it difficult for the reader to understand which results described in the abstract are novel and which are not.

Line 38: Suggest rewording to "mysticete populations should be considered as a natural climate solution" so the authors do not have to list other natural climate solutions.

Line 43: Add "s" to depend. Understanding one thing depends on another thing.

Line 43: What kind of direct measurements?

Line 49: add 'ocean' before surface

Line 49: Are prey consumption and ingestion rate to be interpreted interchangeably in this sentence? Ingestion rate has a specific definition and unit, whereas to me, prey consumption is a more general term.

Lines 51-54: These two sentences as written appear to contradict one another. The first sentence says that methods to directly measure prey consumption have been unavailable. The second cites literature on methods used to directly measure prey consumption, which means methods have been available prior to the current study under review.

Line 58: change relationship to ratio.

Line 60: If theory says the ratio between basal and field metabolic rate is 1:3, then this means field metabolic rate is 3X larger than basal, not 2-5X larger.

Line 68: Suggest rewording so it is more clear to the reader that 'limiting' refers not to nutrients that are limiting to whale nutrition, but instead limiting to primary productivity in the ocean.

Line 72: reference to Fig. 1 comes before the methods and so a lot of the terms in the captions are not easy to understand. For example, in Fig 1b, the caption states "time by depth plot over the full day" but the reader hasn't yet read the methodology and doesn't know how many days the study was. This might be remedied by moving panel 1c, which illustrates the 'whale pump' to panel 1a, and changing the figure reference in the main text to Fig. 1a.

Line 80: The objective of the study is not stated in the main text.

Methods:

General comment: I cannot make heads or tails of the methods section because many of the supplementary figures are not cited in the text. Are the supplementary figures supposed to be cited in the methods section? If not, move them to a separate section at the end.

Line 333: The methods section would benefit a lot from a section at the front end briefly explaining the general methodological steps. Without that roadmap, its impossible for the reviewer to link together the various disparate methods sections and ensure that one follows logically from another in a meaningful sequence. Its also impossible to understand why various equipment was used. For example, why was a drone needed? What information was derived from tagging data? I assume these instruments are used to estimate some key parameters of the carbon export model, but which ones?

Lines 334-402: This section is a very nice historical overview of methodologies for calculating prey consumption, but it is lengthy, and the rationale for including it is unclear to me. I suggest removing it.

Line 348: Provide units for mean daily consumption. Is mean daily consumption (MDC) different than a daily mean prey consumption rate? Or can you reduce the number of different terms you use in the manuscript by using prey consumption rate in units of g day-1?

Line 367: sentence fragment.

Eq 2: I think that this is a body-size dependent metabolic rate equation but its unclear because the parameters R, M, alpha and beta are not defined or given units.

Line 377: It is not clear to me from looking at equation 2 that there is an inherent assumption in the model about daily ingestion rate being equal throughout the year. There is no time-dependency in the equation I think (although not units are given).

Line 409 and 413: The correct terminology for the audio device is a hydrophone

Line 423: Please provide more statistics on tag duration (sample size and variance)

Lines 434-435: Using the presence of a single lunge to classify a day as a feeding day does not seem to be a conservative approach. One lunge is the minimum number of lunges that could indicate a feeding day. Please justify why this approach is characterized as conservative.

Line 436: Please explain the term whale-frame.

Line 443-445: This is really interesting! Please either cite the source of this method or describe in detail how the authors infer prey type from tagging data. Please also tell us which species or populations generally feed on multiple prey types (beyond providing one example).

Line 445-447: Provide information on how many and which tag deployments contained direct observations of prey using each of video or acoustic approaches. Perhaps this data is best presented in a table. This is important to identify potential biases in the analysis that could be introduced because of regional differences in prey sampling method.

Line 452: Please be specific about sample sizes throughout the manuscript. How many whales were measured for their body length, by species?

Line 456: In my experience using drones without LIDAR, the height measurements drift over time during a deployment. Was that source of error measured?

Line 462: How was the 'best' estimate of length determined?

Line 467: Is it correct Nature style to end a sentence with a subscripted citation number as opposed to (author, year)? Perhaps delete this sentence and move the citation to line 463.

Line 491: define the acronym ENP.

Line 492 - 494: I cannot interpret this apparent method of drawing inference using 'gulp-sized cells'.

Line 475: Why only krill data when the whale species feed on krill, copepods and/or fish? Multifrequency acoustical instruments can differentiate between prey size class. What frequencies were used in the study?

General remark: If only modeling rorqual whale feeding, then why are North Atlantic right whales displayed in Fig. S3?

Line 477: Was cell size constant? If so, what was the size of the cell, in meters squared?

Line 482-487: I cannot interpret these three sentences. For example, the prey data were only "included" - included in what? Please revise.

Figures:

General comment: The figures contain a lot of information and so the completeness and clarity of the figure captions is really important. I find quite a few gaps in the information and so all captions should be revisited to ensure the reader can easily follow them.

Fig. 1 A caption. The authors need to revisit the figure caption with the following suggestions in mind. ENP is not defined in the main text before the first reference of Fig 1 and so should be defined here. Circles are not 'hollow', they are unfilled. Euphotic zone is not highlighted, it is labeled. Raw echosounder data is not translated, it is bin-averaged. Describe the color scale and define Sv biomass.

Fig 1 B: What does overall mean in "overall proportion"

Fig 1B caption:

Extended Data Fig 1, Line 260: Reword caption: The images are of four different whale species defecating, which leads to nutrient recycling. Is figure B a fin whale defecating underwater? This could be important to note in the caption. Define the ENP acronym.

Extended Data Fig 1: Authors should check if permit numbers need to be listed in the figure caption.

I stopped my review at line 487 because I could no longer follow the narrative thread of the manuscript due to a lack of clarity in the main text and methodology section. It would not be helpful to the authors for me to review any further until the major comments I listed above are addressed.

Referee #4 (Remarks to the Author):

Authors pool together an impressive global data base of empirical measurements of baleen whale foraging to create a much more field-driven perspective on whale consumption rates. They conclude most previous studies of baleen whale consumption were inaccurately low. Based on these higher measures of consumption, they then update calculations of the influence of the "whale pump" mechanism on carbon sinks – with a special emphasis on the Southern Ocean. The biogeochemical significance of the whale pump in carbon cycling (especially in the S Ocean) has been considered previously. However, the novelty of this contribution is reporting underestimation in these calculations.

Please find below major and minor comments on the MS:

Line 27 – Noting that a number of the ecosystem services of whales described elsewhere are non-trophic (e.g. benthic habitat modification). Authors are referring to the sub-set of ES associated with feeding). Consider generally how well the dynamics here fit a classic definition of "ecosystem engineer" sensu Johns, Lawton, Schchak 1994 Oikos

Line 32 Not yet clear in abstract mechanism by which whales support ocean productivity; i.e. for readers approaching the whale pump subject for the first time

Lines 73-75 as written suggests that Boyce et al attribute whales loss as a mechanism for putative ocean productivity declines. These authors do not – but instead suggest climate/warming as primary mechanism. In general, the possible role of ocean warming (and other potential abiotic drivers) affecting primary producer bases should be better considered.

Just as some of the terrestrial literature that quantifies and highlights sometimes under-appreciated carbon sequestration potential of forests (e.g. Bastin et al 2019) but also considers some of the future instabilities and lost opportunities in this potential that may be caused by CC – here also author's could (in a sentence or 2) speculate how effects of CC may affect the under-appreciated carbon sequestration potential of whales in a future climate-altered ocean.

Some brief additional discussion on geographic variability of prey consumption/filtration rates captured in their empirical data set may be in order. Also, further discussion is merited regarding any anticipated geographic variation in respect to the contribution of whale fecal inputs to stimulating ocean productivity and the biological pump. There is the tacit assumption (sensu line 178) in this report that nutrient contributions in fecal inputs are limiting in all contexts. More discussion on this point would be valuable. Authors focus on iron. Could some brief discussion be had on relative role of other nutrients, especially outside S Ocean (e.g. nitrogen sensu Roman/McCarthy)

It would be interesting to better understand how whale recoveries (for populations that have increased after whaling) have potentially affected whale pump/carbon sequestration potential

It would be insightful to have authors comment on what elements of the metabolic models that previously predicted much lower levels of consumption by whales were incorrect. It is potentially worth noting that these new consumption rates reported here were most similar to estimate generated in references 61,62 (as represented in Fig 3). Please explain what seemed “more accurate” in these estimates. In Line 93 – be clearer in main text which values are used to quantify how much higher their estimates are from previous estimates (e.g. their mean value versus highest previously reported value?).

Not a resolvable issue, but noting that there is a disconnect in that the vast majority of the tagging and consumption estimates were conducted in the ENP (i.e. Fig. S3) – whereas some of the most heavily emphasized conclusions, as they relate to carbon capture, come from the Southern Ocean. This may not be an issue unless feeding behavior/consumption rates (e.g. for blue whales) differ significantly between ENP and S Ocean. Some discussion by authors on this point and the exportability of ENP heavy estimates to other regions is in order.

I would suggest it would be prudent to include in the conclusion that any putative positive benefits for global carbon sequestration that can come from enhanced whale conservation and increase in whale populations – should be coupled with suggestion of the need for aggressive reduction in anthropogenic emissions. Regardless of the outlet where this report is published, I would advise authors review the messaging and response from the scientific community associated with such terrestrial reports as Bastin et al 2019. Central arguments of these authors were diminished by (deserved or undeserved) criticism that authors were over-emphasizing the confidence we can place on one pathway for combating CC using nature-based carbon capture.

There is a need (briefly) to connect with more detail these observation to examples of mechanism and species case studies in literature from other contexts on how megafaunal nutrient vectoring and trophic effects shape ecosystem productivity and carbon dynamics; sensu https://www.pnas.org/content/116/51/25707?ijkey=180e111b8828560fa9f6d262d7301c3a6de6cd9b&keytype2=tf_ipsecsha and papers contained within PNAS 2016 special edition (some already cited)

Please include some perspective on what dynamics may have been introduced in regarding nutrient transport and C sequestration as associated with putative increases in non-whale krill predators following whaling? Relatedly, please provide some very brief sense of interpretation of how the importance of whales may have ranked in an ocean before whaling and before over-hunting and overfishing of other large marine predators? E.g. in an ocean that had more whales, but also had many more large fishes, how important were whales? How should we think of their importance in an ecosystem context?

Please provide some discussion of how changes in winter sea ice/ice algae play into forecasting future importance of whales as the dominant force regulating krill abundance in the S Ocean

In the conclusion, it might be prudent to acknowledge and remind readers that there is a decent amount of inherent uncertainly in the chain of calculations that takes the authors from whale tagging data to whale influence on ocean-level estimates of C sink.

Referee #5 (Remarks to the Author):

The authors present a synthesis of in situ feeding determinations of baleen whales providing, in limited view, the first global estimates of the impacts of present and historic whale populations impacts on the global ocean ecology and biogeochemistry. I am nowhere near an expert in whale ecology / physiology and I can only take the authors' work in quantifying these processes and scaling them to the global ocean. The few papers I have read about "whale falls" and their impacts have been highly speculative with wild guesses from scant observations. This work surely helps in putting some bounds on these processes through their synthesis using modern methods over a range of environments.

The problem with this manuscript is that many aspects of their analysis of the impacts of baleen whales on the ocean's ecology and carbon cycle are, at best, overstated, and, too often, incorrect. For example from lines 115-131, the authors estimate the amount of filtration that whales do today and did 100 years age for the Southern Ocean. They estimate that whaling reduced the total amount of "biomixing" by whales globally tenfold, from 2000 to 200 km3 yr-1. Seems like a lot. But does it scale to global scales? According to Wikipedia, the area of the Southern Ocean is ~7.85 million square miles (or 20e6 km^2). Assuming (conservatively) a layer of influence of whale "biomixing" of 100 m, it would take roughly 1000 years for the upper layers of the Southern Ocean to filtered through the historic whale population (2e6 km3 / 2000 km3/y). Clearly whale "biomixing' is NOT impactful on global scales – although it surely will be local space and time scales (km's and days). Thus statements of enhanced nutrient supply and iron recycling due to whale ingestion made throughout the text are simply incorrect. Something is wrong here – either the global estimates of whale filtration are factors of >1000 too small or whales do not contribute this ecosystem service on global scales.

Further, the authors' analysis of the carbon cycle impacts of baleen whale is simply incorrect and frankly misleading. The authors state repeatably throughout the paper that whaling reduced the ocean carbon sink by nearly 400 Mt/y (0.4 PgC/y in proper units) through the lost processing of organic carbon by baleen whales. They then state that is 20% of the global carbon sink. Based upon the reference cited, I am assuming that the authors are stating that this "whale carbon sink" is 20% of the global air-sea exchange of CO2 carbon (which is ~2 Pg/y). This is the wrong component of the ocean C cycle to make a meaningful comparison with baleen whale processing of organic C. Whales are transforming organic carbon in the form of krill and small fishes into both detrital organic carbon, which will be recycled by microbes back to CO2 and nutrients, and into CO2, via whale population respiration. Most of this recycled organic matter and respired CO2 will be taken up by phytoplankton via photosynthesis to make more organic matter. Only a fraction will be exported from the surface ocean to depth. The correct comparison with the global C cycle would be with the export of organic carbon from the surface ocean to depth via sinking particles and vertically migrating metazoans where that exported carbon might be sequestered at depth on decadal and longer time scales. The global magnitude of the contributions of the sinking and migrant pathways to the biological pump is roughly 8 PgC/y. As mentioned above, some fraction of the whale carbon demand is exported from the upper ocean to depth; generously let's let that fraction be 50% (globally its 10%). Therefore, whaling has reduced the biological pump historically by no more than 0.2 PgC/y, which is ~2.5% of the magnitude of export for the present global biological carbon pump. This in no way supports any of the ascertains made throughout the paper that baleen whale populations if reestablished to historic levels would be "global climate engineers" (particularly, lines 160 -194).

In summary, this paper is not publishable in Nature and, in its present form, in any other journal - to do so would be irresponsible. The global estimates of baleen whale feeding, filtering and respiration rates are valuable and should be published. Again, I cannot speak to the voracity of these estimates; just that if these estimates are correct, they do not support the speculations / conclusions drawn. There's more beyond the two examples listed here that are either incorrect or over stated – but this is more than enough in my book to reject the paper.

Author Rebuttals to Initial Comments:

Referees' comments:

Referee #1 (Remarks to the Author):

This manuscript is based on an impressive data set comprising field observations of feeding behaviour of various species of tagged baleen whales in relation to available prey density from which consumption rates were deduced. These measurements come as close to direct observations as one can get in the pelagic realm and they have been carried out on both types of baleen-whale feeding mode (lunge and ram feeding) by different research groups working in different sites of the world ocean. The overall conclusion from these comprehensive results was that all the whale species studied consumed much more prey than current estimates. This finding on its own, scaled up to the pre-whaling population sizes, would warrant publication in Nature and the authors make a convincing case for why current estimates of past and current whale consumption derived from various assumptions and considerations are likely to be too low. The authors assume that the much higher productivity of the whale feeding grounds required to support the much larger prey populations to feed the actual demands of the whales is provided by the recycling of essential nutrients in the surface layer by the whales, in particular iron in the Southern Ocean.

I need to point out at here that, as the originator of the "whale manuring hypothesis" invoked in 2005 and laid out in 2007, I am favourably inclined to the results presented here (references at the end). In the 2010s the hypothesis captured the public imagination as the "power of whale poo" (Monbiot in the Guardian) and was promoted by various green movements but was disregarded by most mainstream krill scientists. Further, models parameterised with current values not surprisingly cast doubt on its functioning since the hypothesis was based on the pre-whaling krill stocks. The matter remains controversial until the experiments to test the hypothesis I outlined (2007) are carried out, for which there is unfortunately great reluctance in the community. So, the measurements presented here, which indicate that the biomass of prey organisms is underestimated and is likely to have been at least more than double in the presence of intact whale stocks, are grist to my mill and acknowledge my bias.

I accept that consumption rates during the observations were higher than expected but the reasoning behind the extrapolations of observed and deduced feeding rates to daily, seasonal and from there to annual and global scales is not well explained in the text and can be easily contested. The authors chose to highlight the higher values (like fivefold, or 30% of body weight eaten on one day) that are hard to believe and undermine the real message – that the pre-whaling stocks of baleen whales will indeed have acted as ecosystem engineers. Exaggeration will unnecessarily raise scepticism about the overall veracity of the results. The authors have chosen this path because they are trying to elevate the implications of their findings to the carbon-cycle stage where "more is better" without regard to the physical-chemical constraints on the ecosystems they invoke to support their estimated prey stocks. The carbon framework is not only detrimental to the message of this paper but the reasoning behind the estimates of the whale-mediated carbon sink is flawed. In Table 1 the estimates of carbon export from whale and krill-fertilized phytoplankton are based on observations made on diatom blooms under low grazing pressure – the norm in today's megafauna-bereft oceans. During a time station we were carrying out in the Weddell-Scotia Confluence in 1988, I had the good fortune to observe, without seeing it at the surface, a krill swarm suddenly appear in the water below the ship, and graze down the diatom bloom we were studying by severalfold in a matter of hours. They darkened the light profiles we were taking, individuals were attached to the CTD and masses were collected by all the nets we deployed, even hand nets. They left behind a cloud of faecal strings, the bulk of which did not sink out, evident from vertical profiles of depth distribution. The situation was very different in an iron-fertilized diatom bloom without krill where we observed massive sinking out of diatom aggregates to the deep sea in its aftermath.

It is now well established that the iron supply determines productivity of the Southern Ocean and that iron has a short life time in the surface layer reflected in satellite images of the location and duration of phytoplankton blooms: restricted areas along the coasts and islands that receive terrestrial or sedimentary sources of iron, as well as the short life times (weeks to a month or two) of blooms in regions fertilized by dust or melting ice bergs in today's oceans. In the relative absence of krill swarms, the diatoms responsible for this iron-enhanced productivity sink out of the surface layer taking the iron with them. Microbial recycling communities with tenfold lower biomass replace the diatoms in the iron-impoverished surface layer: the classic HNLC condition. The current krill populations are apparently unable to adequately utilize diatom blooms in the above-mentioned regions where iron is supplied from external sources. However, in the pre-whaling Southern Ocean, whale stocks were one to two orders of magnitude higher than today implying that krill stocks must have also been much larger to provide the food necessary to sustain them. Since the supply of new iron entering the system is not likely to have changed much between then and now, if at all it has increased as a result of retreating glaciers in the Peninsula, various islands and Patagonia, the only way to explain the much larger krill stocks is to invoke maintenance of the iron in animal tissue that is then recycled in the surface layer. In other words, iron lost by sinking diatoms but also krill faeces and cadavers must have been substantially reduced in the pre-whaling phytoplankton blooms. An efficiently functioning recycling system by definition binds but does not sink carbon. You can't have your cake and eat it. So the assumption of whale- and krill-fertilized diatom blooms sinking carbon to the deep sea is invalid and all conclusions drawn from it should be removed from the manuscript. The concept of "carbon sink" dealt with here as an amount removed from the atmosphere and not delivered back elsewhere is faulty. Reference to the Amazon rain forest is a case of cabbages and kings. For example, prior to the industrial age atmospheric CO2 levels had remained fairly constant around 280 ppm (~600 Gt) over the Holocene. A sustained annual sink of the magnitude proposed by the authors (0.4 Gt) and not compensated elsewhere would have drained the atmospheric pool to glacial levels of 180 ppm within 500 years as opposed to the tens of millennia that transitions recorded in ice cores over past climate cycles actually took.

In this light, can whales contribute to carbon sequestration? As shown by Lavery et al (2010) sperm whales can do so by feeding on deep-sea squids and releasing the iron contained in them by defecation at the surface, the condition being that the C/Fe ratios in squids is substantially lower than in the phytoplankton biomass fertilized by surface-defecating whales that eventually sinks out. This condition does not apply to baleen whales feeding on krill and copepods, because even if the latter retreat to depth for some hours, they are essentially creatures of the surface layer that contain iron (and carbon) in their tissues collected there. Indeed, the carbon in krill and zooplankton biomass enhanced by whale recycling will be the major sink term in the carbon cycle. A krill biomass of around 600 Mt maintained by the whales in the pre-whaling era is equivalent to around 60 Mt of carbon which is not much compared to around 2 Gt taken up by the ocean's solubility pump annually. But it contains enough iron to fertilize diatom blooms over millions of km2 as this calculation shows. Taking a generous area of 2 million km2 for the former whaling grounds in the SW Atlantic sector of the SO, 600 Mt of krill biomass (the stock necessary to feed the pre-whaling whales), is equivalent to 300 g or about 600 krill m-2. This is a lot of animal biomass and, converting biomass to carbon, about 30 gCm-2. Compare this figure with the biomass of a prominent diatom bloom in satellite imagery: 10 – 20 gCm-2. Carbon in animal biomass would have contributed the bulk of the POC pool. As ocean iron fertilization experiments have shown, a diatom bloom takes about 3 weeks to reach this peak, with aggregation and sinking out of portions of the bloom occurring in subsequent weeks. Given the constraints on phytoplankton growth rates in the Southern Ocean, the size of the animal biomass accommodated in this recycling ecosystem will be influenced by grazer density and behaviour, but there will be an upper carrying capacity regardless of the mode of harvesting (timing and intensity) by grazers. In satellite images, had they been available, the pre-whaling feeding grounds are likely to have resembled a patchwork quilt in the tens of km range. Observations made in the early last century described feeding whales from horizon to horizon with the surrounding water coloured red with krill swarms. I have spent over two years in the Southern Ocean and never seen a krill swarm at the surface nor a blue whale.

What the whales of the past were maintaining were giant recycling systems based not on the microbes of the current recycling systems, bereft of their large fauna, but on a diatom-krill-whale based ecosystem. In this scenario the iron pool on which the system functioned was located in the overwintering krill and zooplankton pools that was released back to the phytoplankton by whale faeces. The net long-term carbon sink to the deep sea emanating from this system depends on the C/Fe ratio of sinking particles. I have explained the scenario in Smetacek (2007).
Since there is an upper limit to the amount of blubber a whale can put on, the total number of days spent feeding will depend on the energetic costs of lunge-feeding in relation to prey density as also the efficiency of digestion, assimilation and proportion of krill biomass incorporated into blubber. At the greater prey densities reported by visual observations of surface krill swarms during the whaling era, the costs of converting prey into blubber will have been lower. Further, since the intact whale populations herded krill to the surface, iron leaching out of krill faeces would be more effectively utilised by phytoplankton than deep feeding, now more prevalent with fewer whales. Another factor promoting recycling would be the biomixing caused by the whales (described in this manuscript) as this would break-up and disperse friable krill faecal strings and copepod pellets thereby retaining their contents in the surface layer. In short, the more whales, the more efficient the recycling. Hence, I caution the authors not to overplay their hand by invoking fivefold higher feeding rates over current estimates as these are hard to imagine. For instance, comparing herbivores with known inefficient digestion (elephants) feeding on terrestrial plants consisting largely of cellulose and lignin with krill-feeding whales does not make sense (Line 662). Both are ecosystem engineers but in very different ways. Elephants defecate huge amounts, mostly undigested remains, but can the same be said of whales? The indigestible krill chitin exoskeleton is a relatively small fraction of biomass. Besides, krill secrete powerful proteases that promote autolysis of crushed krill to such an extent that fishing vessels pump krill out of the cod ends of fishing nets while fishing, to prevent them becoming mush. What counts here is not the mass of the faeces but their iron content and its immediate availability to photoautotrophs. Having said all this, I need to point out that krill, when offered high food densities in aquaria, feed and defecate continuously. Copepods are also wasteful feeders in the wild, evidenced by the many intact cells commonly seen in their faeces. I have argued the recycling benefit of this "superfluous feeding", so would not be surprised if the whales were doing the same in dense krill swarms. This would imply that whales consuming 30% of body weight per day would be defecating a greater proportion of undigested food than an individual feeding at its metabolic capacity. In human terms all these animals enjoy eating because gluttony has a positive feedback on the system sustaining them.

This is a thorough and captivating review that has further honed the message of the paper. On behalf of all co-authors, we thank you this reviewer for their deeply informed and well-reasoned response to, and evaluation of, our manuscript. We are in agreement with all of Smetacek's major points and have removed the carbon and climate connections from this updated manuscript. We agree that those links were the most extrapolated in the initial version of the paper. His detailed explanation has convinced us that our paper is indeed stronger (in addition to being better connected to the field data we collected), by replacing discussion of carbon export or climate engineering with discussion of baleen whales as ecosystem engineers.

In our new section on whales as ecosystem engineers (lines 172-203), we reference and discuss the Antarctic Polar Plume that he references in his 2008 book chapter as perhaps the best example of where the removal of baleen whales likely catalyzed a reduction in overall productivity and initiated a regime shift from a krill- to a salp-based system (Atkinson et al. 2004). We have also toned down our wording of how much higher our prey consumption estimates are then previous estimates. Finally, we made we made a simple, but important change to the title, substituting the word “climate” for “ecosystem” as suggested.

It might be worthwhile pointing out that the annual food demands of intact whales populations - >200 Mt – is more than twice the world fish catch. The former was sustainable because the whales were putting back the crucial element iron whereas fishing vessels only remove biomass but do not return anything.

This is an excellent point. We now mention this specifically in the updated Abstract (lines 37-38).

I had some problems with the figures that need to be redone. I did not understand Fig. 2. Why is there no scaling on the Y axes? For Figs 3 and 4 I recommend linear instead of logarithmic scales. The latter is useful when lower numbers need to be deciphered, but here it is the higher numbers that need highlighting particularly the differences between species. These figures need to be better discussed and presented in the main text. Space will be gained for this if text on the purported impacts on the carbon cycle is removed. Also, I think it would be more appropriate in the cartoon to have the arrows from phytoplankton to krill and whales pointing in the other direction as this would be more indicative of recycling. In any case this cartoon is not particularly informative at this level of resolution and could be dropped or more relevant details included.

We appreciate knowing where the first versions of our figures were unclear. We have taken these suggestions and flipped Figure 2 90° such that the scaling values are on the y-axis. We also changed the scales in Figures 3 and 4 from logarithmic to linear to better show the large differences not only pre- and post-whaling, but also among species. These changes highlight how the removal of the two largest species – fin and blue whales – have had effects throughout the ecosystem over decades. In Extended Figure 4, we have removed the cartoon as suggested.

I recommend resubmission of a manuscript with major revisions in which the emphasis is on ecosystem engineering instead of the global carbon cycle.

Done. See the two fully revised sections of the main text: Mysticetes as global ecosystem engineers and Conclusions (lines 172-235).

Ref.

Smetacek, V. & Nicol, S. (2005) Polar ocean ecosystems in a changing world. Insight review. Nature 437: 362-368.

Smetacek, V. (2008) Are declining Antarctic krill stocks a result of global warming or of the decimation of the whales? In Duarte, C. M. (ed.) “Impacts of global warming on polar ecosystems.” Fundación BBVA, www.fbbva.es, ISBN: 978-84-96515-74-1, 45-83 (available on the web).

Thank you for these references, in particular your 2008 book chapter, which we now cite in the revised manuscript.

Referee #2 (Remarks to the Author):

This is an outstanding manuscript, using a massive set of data on the foraging behavior of baleen whales. Every tag deployment – especially those collected in polar waters – would have been difficult to obtain. The manuscript also combines three modern technologies for collecting data on baleen whale foraging in a novel manner. These are: suction cup tagging to elucidate foraging behavior, using scientific echosounders from small vessels, and UAS (drone) photogrammetry. With over 300 tag deployments and more than 70,000 feeding events recorded over a decade, just the suction-cup tagging data set is the most comprehensive published (to my knowledge) to date.

Then, adding photogrammetry to estimate engulfment capacity of rorquals with sounder-derived estimates of prey density to this data set reframes our knowledge of rorqual foraging ecology. The foraging estimates for balaenids in the manuscript are less well informed than those of the rorquals, and do not have data on prey fields from scientific echosounders, unfortunately. However, the information provided is still an improvement on our current understanding of their foraging ecology.

The authors then take this information and give it context. The finding that baleen whales' prey consumption has been underestimated substantially is a major new finding, and in itself warrants publication in a high-profile journal. The authors then explore the implications of this finding for marine biogeochemical cycling quite comprehensively. Their findings are exciting, and somewhat alarming. They indicate that the important role that baleen whales play in marine nutrient cycling has been seriously underestimated.

Yet their models are quite conservative – they leave out some baleen whale species that are also likely significant (sei whales, for example), and they assume that baleen whales feed for a maximum of 6 months, when we know that some are present in polar waters for longer than that (e.g. Van Opzeeland et al. 2013). And while the authors consider most of the known biogeochemical contributions by baleen whales, they miss at least one. The nutrient contribution to relatively nutrient-poor tropical systems by baleen whales' annual calving migrations is likely significant, when baleen whale populations recover. The afterbirths, stillborns and neonatal mortality of hundreds to thousands of female baleen whales probably provide a significant annual nutrient pulse to tropical calving grounds. I mention it not to require the authors to mention this particular example, but to note that there are other aspects of baleen whales' role in marine biogeochemical cycles that could have been considered.

Finally, the authors then explore what this means for carbon sequestration, and possible role of baleen whales in natural climate solutions. This is a very exciting aspect of the work, as it is well quantified. There have been previous discussions of this general idea. But this manuscript, because it shows that we've underestimated the amount that baleen whales forage, takes the idea further than it has been previously. This work should help change the conversation on the importance of recovering baleen whale populations internationally, by demonstrating its climate benefit. It also shows the climate cost of prior whaling, and should re-frame the discussion of the utility, and ecosystem consequences of current commercial whaling.

While the role of baleen whales in natural climate solutions is important and justifiably the focus of the manuscript, there are a couple of other management implications of this work that area not mentioned in the manuscript., It may be that space considerations prevent these from being raise, but I'll mention them anyway, in case the authors find them worthwhile. The point that more whales mean more productivity should be considered in national strategies to enact ecosystem-based fisheries management (EBFM). Encouraging baleen whales' recovery is valuable not only for conservation and for climate, but for sustainable fisheries - as more whales should lift carrying capacity of marine ecosystems. I'm not aware of any national EBFM strategy that includes this idea, so it might be worth mentioning. Similar reasoning applies to national management when legislation specifically links management of whale populations to ecosystem carrying capacity (e.g. the US Marine Mammal Protection Act, see https://www.fisheries.noaa.gov/national/marine-mammal-protection/marine-mammal-protection-act).

I see no flaws in this manuscript that should prohibit its publication. I believe that this manuscript will be of great significance in several disciplines: marine ecology, conservation biology, the science of carbon management, marine management. I suspect it could be a paper that help drive a major change in how we think about managing whales, internationally and so could be hugely significant. Given the level of public interest in whales generally, and in the current climate crisis, I believe this manuscript, when published will also be of substantial general interest to a wide audience.

The data and analyses seem fine. I checked the first author's GitHub repo listed in the manuscript and all seems appropriate. My only concern with the figures is that I can't see where the boxplots are defined, which needs addressing (unless I missed that somewhere, but I can't find it). All other statistical presentation seems appropriate. I see no problems with the authors' interpretation of their data. To me the conclusions seem robust, valid and reliable. The manuscript is well, and copiously, referenced. The Abstract is clear and a valid representation of the paper. All sections of the manuscript seem appropriate.

Apart from my comment on the boxplots' detail, I have a very few minor clarifications that could help.

We thank this reviewer for pointing out our oversight by not initially explaining what the boxplots represent. We have now done so in all the relevant figure captions.

Overall, we thank this reviewer for the kind words and thorough review of our paper. The applied perspective on the potential benefits of whales to fisheries yield and EBFM were not lost on us, and we wove those points in more explicitly than we had previously (see lines 79-82, 167-170). The key point, as the reviewer mentions, is that when humans extract resources, we do not recycle them, thereby supporting the ecosystem that sustains us. In contrast, this is precisely what whales (and all non-human consumers) do, and what makes their substantial prey consumption not a hindrance to ecosystem productivity, but a boon to it.

Further, the note about our estimates on baleen whales as ecosystem engineers are indeed conservative not only because we did not include every baleen whale species or population in our estimates, but also because we only dealt with their effects on the foraging grounds. Whales had (and have) so many impacts on ocean ecosystems we did not have the space to address them all in this manuscript. However, the point regarding whales on the breeding grounds is well taken. We have colleagues who are working on a paper detailing this "great whale conveyor belt" to assess how whales affect the ecosystems not just in their high-latitude feeding grounds, but also in their lower-latitude breeding grounds. In any event, we agree that further discussion isn't warranted in this manuscript.

Line 35-36 – is this the Antarctic whale-krill-carbon pump, or world-wide? Clarification would help.
Our focus was solely on the Antarctic whale-krill-carbon pump, but based on suggestions from other reviewers and the editor, we have removed and quantifications of carbon sequestration and export from the revised version of the manuscript and instead focus the paper more on the data we collected (tag, drone, and echosounder data), and on the subsequent ramifications of those findings on ecosystem ecology.

Line 189 - nearly all anthropogenic CO 2 emissions, presumably at the time, but it's not quite clear.
Yes, our text was supposed to mean "nearly all anthropogenic CO_2 emissions at the time," but as mentioned in reply to another reviewer, this section was removed from the revised manuscript.

Line 367 – "Using diet composition (Z) from 77" ends abruptly. Is something missing?
Yes, we appreciate having this omission pointed out. We have now updated this sentence to say: Diet composition (Z) values were obtained from (Pauly et al. 1998).

The reference I cited above is:
Van Opzeeland I, Van Parijs S, Kindermann L, Burkhardt E, Boebel O (2013) Calling in the Cold: Pervasive Acoustic Presence of Humpback Whales (Megaptera novaeangliae) in Antarctic Coastal Waters. PLoS ONE 8(9): e73007. https://doi.org/10.1371/journal.pone.0073007

Referee #3 (Remarks to the Author):

B. Originality and significance: if not novel, please include reference

This manuscript tries to do a big job by synthesizing numerous diverse and unique datasets from several different research groups. Its very challenging thing to do and success relies on very clearly explaining all the various methods in a cohesive and comprehensive manner. This is not easy and the authors should be commended for their effort. A lot of work has been put into the modeling component of this manuscript and the approaches appear quite sophisticated. Unfortunately this draft did not quite succeed in communicating the information with clarity and so for that reason I cannot evaluate its significance to the field. I think that with a revision of the manuscript text with careful attention to clarity it is possible to achieve the goal.
We thank this reviewer for evaluating our manuscript and providing feedback that it needed to be clearer. Upon re-reading our methods, we agree. We have made several major changes in our presentation of the methods and results that we describe in more detail below to improve clarity. We hope these changes will elucidate our analytical procedure to permit a full evaluation of the scope and potential impact of our work.

A. Summary of the key results

I reviewed up to about half way through the methodology and I was so confused that I stopped my review because I could no longer follow the thread of the paper. There are issues with the clarity of the manuscript that need to be addressed before I can continue myreview.
We apologize for the lack of clarity in the initial presentation of our methodology and have addressed this issue in several important ways in the revised manuscript. First, we now include a flow chart illustrating how we went from data collection, analysis, synthesis and inference (see page 26). This graphic includes labeling each methods section such that it is clearer how the data were generated from one portion of the analysis fed into the next portion. Second, we include a summary data table immediately following this flow chart that gives a broad overview of our findings – taking the qualitative information displayed in the flowchart and presenting it quantitatively (page 27). Third, the krill prey methods section has been streamlined and simplified (lines 509-562); to reduce confusion we now present our one “best estimate” on daily krill consumption, and compare that to results using older methodology (see Figs 3 and Extended Fig. 2E and F). Finally, because we have removed the carbon and climate information the last section in the methods, “Iron recycling calculations,” has been considerably reduced (lines 741-767).

C. Data & methodology: validity of approach, quality of data, quality of presentation

The most concerning issue is that I cannot evaluate the methods section because the supplementary figures are peppered throughout it but I cannot find most of them cited in the text of the methods section, and so I do not know what information is being presented and why.
This is a critically important point, and we appreciate it bring brought to our attention. We have now carefully gone through the revised manuscript and made sure that each figure is cited in the text of the paper itself. In addition, we provide further context for many of these figures in both the main text and the methods sections. Furthermore, these figures are also referred to (when relevant) in the new Analysis Flowchart and Summary Data Table (Table S2) in the revised manuscript.

I am not an expert on animal metabolism and so I cannot comment on the appropriateness of the metabolic models or parameterization of those models used in this study. However, as a non-expert reader, I find a number of apparent inconsistencies between statements made in the text and the model equations. My general comment the model parameters and units need to be better explained so that the statements written in the text are straightforward to interpret for non-expert readers based on the information given about the model equations.
We thank the reviewer for this feedback. We have addressed these concerns with a more streamlined and better referenced Prior estimation of consumption section (lines 347-409), and an improved description of only the essential ideas in the main text (lines 60-66). Also see a more thorough explanation of our preliminary metabolic findings in the response to reviewer #4.

I have expertise using bioacoustics to measure zooplankton and I could not interpret the methodology used to measure krill biomass from echosounder data because not enough information was provided. For example, the frequencies of the echosounders used were not given. The section would benefit considerably from including example krill biomass data and associated calculations from a specific whale to better illustrate how the acoustic data were processed on lines 475-490.
The methodology we used to transfer our raw acoustic data to biomass units for our prey consumption calculations was initially based on a currently unpublished method. It was our hope that the manuscript that fully described this method would be published and citable by now, but that is not the case as it is in revision elsewhere. As a result, we have used a previously published methodology (Goldbogen et al. 2019) that we think is easier to follow and justify (see lines 509-562). This method calculates a gulp-sized patch of prey for each whale species which is then geometrically averaged to define a patch density. We also provide an Analytical Flowchart and Table S2 (pages 26-28) that describes the methods we used to convert measured krill patches into estimates of prey consumed by foraging whales.

C. Appropriate use of statistics and treatment of uncertainties

Very often the sample sizes are not given, and the choice of error bars used in the figures is not described (i.e., do they represent confidence limits, standard error, or standard deviation).
We think that we have brought clarity on these essential details in the revision.
First, the sample sizes of our whale tag deployments, prey mapping, and drone measurements are now provided in our summary data tables (Tables S2 and S3) along with mean and standard deviations of each derived parameter (Table S2). We used bootstrapping with replacement (1000 samples for each feeding day, see Daily prey consumption methods for rorquals section on page 42 for details) to create probability distributions for the daily and annual prey consumption and nutrient recycling results (e.g., Figs 2, 3, 4, and S6). As we are using a custom sampling function to generate thousands of iteration of possibilities for each whale-prey-ecosystem combination (e.g., a humpback whale, feeding on krill, in the Eastern North Pacific), the way we chose to display and discuss those results is as a median and interquartile range (25^{th} – 75^{th} percentile) in parentheses in the text. In the figures we represented the full spread of our sampled distributions using vertical density plots (e.g., Fig 2) and boxplots. For annual figures (Figs. 3 and 4), we showed the median as the thick line and interquartile range (the shaded area). We explain all of this this more clearly now in both the text and the figure captions.

D. Conclusions: robustness, validity, reliability

I cannot evaluate the conclusions of the manuscript.
With the extensive changes we have made to improve the clarity of the methods, we hope this problem has been remedied.

E. Clarity and context: lucidity of abstract/summary, appropriateness of abstract, introduction and conclusions

The authors do not state their study objective in the main text. After reading through the manuscript, I suggest that the objective stated on Line 28 of the abstract (i.e., calculate prey consumption) is an incomplete description of the study objective. My interpretation is that the objective is to model the contribution of baleen whale foraging biology to ocean carbon cycling using a box model approach (illustrated in Fig. 1c), where particular attention is given to parameterizing the model with novel field data on whale foraging.
We have taken this comment to heart and now provide more detail in both the Abstract (lines 30-33) and the main text at the end of the introductory section (lines 82-91) that more explicitly describe our study's primary objectives and how we set out to achieve them.

A number of terms are used in the main text and there is no language that clearly defines or links these terms, which makes it a challenge for the reader to interpret the authors rationale. Terms include: prey consumption, ingestion rates, prey requirements, feeding rates, digestion time, prey patch quality, filtration, consumption. Units are not provided for any of the terms.
We think that our revision provides better definitions for all of these terms in the introductory section of the main text (lines 85-88, 99-100) including providing units of measurement. We also provide units in the Summary Data Table (Table S2) in the methods section.

I find quite a few inconsistencies and contradictions in the abstract and main text that I highlight in the line-by-line editorial comments.

Editorial comments
Title:

Line 1: The authors should explain why they chose the term climate engineers. Climate engineering is the intentional large-scale intervention in the Earth's climate system to counter climate change. Whales are not influencing earth's climate intentionally.
Changed from "climate" to "ecosystem engineers" in title. However, when talking about ecosystem engineering, intentionality – to the degree it can be assessed – is not included in our definition. Many examples of ecosystem engineers, from bison to beaver engineer their ecosystems as a byproduct (i.e., positive externality) of their actions. We have removed the carbon and climate analysis from the revised manuscript.

Main Text:
Line 25: whales are referred to as climate engineers in the title and ecosystem engineers in the abstract. Why are two different terms used, and what is the difference between the two?
We have now removed any mention of climate engineering from the revised manuscript and focus instead on ecosystem engineers.

Line 30: Remove the 's'
Done.

Line 33: Sentence reads as though each whale required an order of magnitude more prey prior to whaling. I think the authors mean that the whale populations were larger and so the total prey consumed was greater in the pre-whaling era.
Correct. We have now added the phrase "the global population of" to make it clear that we are speaking about the prey requirements of a population of whales, not an individual whale.

Line 35: If this study shows that past studies have underestimated prey consumption, then the authors should justify why it is appropriate to then reference the size of the global carbon sink generated by whales to past studies (citations 6, 7). This approach makes it difficult for the reader to understand which results described in the abstract are novel and which are not.
We have now removed any mention of the specifics of a potential carbon sink from the revised manuscript. This should make it clear that what previous studies have underestimated is baleen whale prey consumption.

Line 38: Suggest rewording to "mysticete populations should be considered as a natural climate solution" so the authors do not have to list other natural climate solutions.
Thank you for this suggestion - we have removed any mention of mysticetes being an untapped natural climate solution from the revised manuscript.

Line 43: Add "s" to depend. Understanding one thing depends on another thing.
Done.

Line 43: What kind of direct measurements?
When we say “direct measurements” we are referring to field measurements from living animals and include things such as measuring rorqual feeding rate via tags and engulfment capacity (derived here using length measurements) via drone photogrammetry, as well as and prey biomass density. These direct measurements are what has been lacking from prior studies.

Line 49: add 'ocean' before surface
Done.

Line 49: Are prey consumption and ingestion rate to be interpreted interchangeably in this sentence? Ingestion rate has a specific definition and unit, whereas to me, prey consumption is a more general term.
Correct: we mean prey consumption more broadly here and ingestion rate (as in prey consumed per mouthful, per day, per year, etc) is more specific. However, that sentence is left intentionally broad on purpose to indicate that there is little to no information derived from direct field measurements on baleen whale prey consumption at any temporal scale.

Lines 51-54: These two sentences as written appear to contradict one another. The first sentence says that methods to directly measure prey consumption have been unavailable. The second cites literature on methods used to directly measure prey consumption, which means methods have been available prior to the current study under review.
Yes, it is accurate to say that methods to directly measure prey consumption have been unavailable. Over the past decade, our multi-institutional research group has developed methods that allow us to finally address that question at ecosystem and global scales. We directly measure feeding rates and prey biomass in the environment where whales feed. From these direct measures, we calculate prey consumption. Some of the data presented here have been published before and are cited throughout the paper. Several examples include (Hazen et al. 2015, Cade et al. 2016, 2020, Calambokidis et al. 2019, Friedlaender et al. 2019, Goldbogen et al. 2019). We leveraged those previously published data on feeding effort and prey density and add more, unpublished original data in the present manuscript. It is important to note that previously published studies by our research group had different goals that summarized and reported the data differently to meet their goals. Largely those studies focused on biomechanics, physiology, behavior, and ecology at finer scales.

Line 58: change relationship to ratio.
Done.

Line 60: If theory says the ratio between basal and field metabolic rate is 1:3, then this means field

metabolic rate is 3X larger than basal, not 2-5X larger.
We have simplified these two sentences for clarity and brevity.

Line 68: Suggest rewording so it is more clear to the reader that 'limiting' refers not to nutrients that are limiting to whale nutrition, but instead limiting to primary productivity in the ocean.
Added “to primary producers” to enhance clarity.

Line 72: reference to Fig. 1 comes before the methods and so a lot of the terms in the captions are not easy to understand. For example, in Fig 1b, the caption states "time by depth plot over the full day" but the reader hasn't yet read the methodology and doesn't know how many days the study was. This might be remedied by moving panel 1c, which illustrates the 'whale pump' to panel 1a, and changing the figure reference in the main text to Fig. 1a.
We have now updated Figure 1, which includes the removal of the whale pump section. Further we have made considerable edits to the Figure 1 caption with this comment in mind. We now feel as though Figure 1 can stand alone and be interpreted even before reading the Methods.

Line 80: The objective of the study is not stated in the main text.
We now clearly state the main aims of our study at the end of the introductory section (see lines 79-85).

Methods:

General comment: I cannot make heads or tails of the methods section because many of the supplementary figures are not cited in the text. Are the supplementary figures supposed to be cited in the methods section? If not, move them to a separate section at the end.
All supplementary figures are now cited in either the main text, the methods text, or both. After a brief description of how previous studies have generated baleen whale prey consumption estimates, we have added an Analysis Flowchart and Summary Data Table that describes the sample sizes and methods that we used to generate our results presented in this paper. To further enhance clarity, we labeled each section of the methods (sections A.1 through A.11) we used so they could be referred to more easily.

Line 333: The methods section would benefit a lot from a section at the front end briefly explaining the general methodological steps. Without that roadmap, its impossible for the reviewer to link together the various disparate methods sections and ensure that one follows logically from another in a meaningful sequence. Its also impossible to understand why various equipment was used. For example, why was a drone needed? What information was derived from tagging data? I assume these instruments are used to estimate some key parameters of the carbon export model, but which ones?
This helpful comment led us to realize that the best way to describe our methods and logic was first to present it as an overview in a flow chart so that a reader can follow the steps that lead from the data we collected in the field, the data we amassed from other studies (e.g., iron concentration in mysticete feces), to how they were processed and synthesized to reach our results and draw our conclusions. We hope that this flow chart and Table S2 now makes the answers to these questions (e.g., why was a drone needed?) clearly.

Lines 334-402: This section is a very nice historical overview of methodologies for calculating prey consumption, but it is lengthy, and the rationale for including it is unclear to me. I suggest removing it.
We appreciate this comment, but we feel this overview of how previous studies estimated mysticete prey consumption (and indeed, many have) is critical to put our results in context. We have condensed that section to only the material that we deem is essential for describing what other studies have done.

Line 348: Provide units for mean daily consumption. Is mean daily consumption (MDC) different than a daily mean prey consumption rate? Or can you reduce the number of different terms you use in the manuscript by using prey consumption rate in units of g day-1?
Thank you for bringing this to our attention. We have now provided units for daily consumption (kg d^{-1}) and have simplified the terminology and streamlined the units wherever possible.

Line 367: sentence fragment.
Thanks again for catching this. We have made this change now.

Eq 2: I think that this is a body-size dependent metabolic rate equation but its unclear because the parameters R, M, alpha and beta are not defined or given units.
The daily ration ("R") and the body mass ("M") are both in kg. The text is now updated to reflect that (lines 368-371). Alpha and beta are the metabolic scaling constant and exponent terms and do not have units. An extended review and discussion of these metabolic scaling equations is available in (White and Kearney 2014), which is also now cited in the text (line 380).

Line 377: It is not clear to me from looking at equation 2 that there is an inherent assumption in the model about daily ingestion rate being equal throughout the year. There is no time-dependency in the equation I think (although not units are given).
The daily ration ("R") as shown in equations 1 and 2 does assume that whales eat a consistent amount each day of the year, which is known from field observations to be unrealistic. To convert from the daily ration ("R") to an amount of prey ingested per feeding day by previous studies, you need to convert from R to a mean daily consumption (MDC; equation 3), using the known natural history of mysticete feeding ecology.

Line 409 and 413: The correct terminology for the audio device is a hydrophone.
Another good catch; we have made this change.

Line 423: Please provide more statistics on tag duration (sample size and variance)
Thank you for pointing out this oversight. We have now provided a table (Table S3) in the Tagging methods section that provides this information.

Lines 434-435: Using the presence of a single lunge to classify a day as a feeding day does not seem to be a conservative approach. One lunge is the minimum number of lunges that could indicate a feeding day. Please justify why this approach is characterized as conservative.
This is a conservative approach because our goal was to quantify an "average" feeding day. The presence of a few (or only one) lunges is not an average feeding day. In most cases, an average feeding day consistent of hundreds, and occasionally thousands (e.g., Antarctic minke whales), of lunges. By using a criteria of inclusion where we are using any day of data with one lunge in, it we are likely skewing our estimates low, which is why we consider this aspect of our approach "conservative".

Line 436: Please explain the term whale-frame.
The term "whale-frame" is best described by the term "whale-reference frame", which is the orientation of the whale relative to the orientation of the tag. Because the tags cannot be placed perfectly aligned with the whale's longitudinal, lateral, and dorso-ventral axes, a correction must be made to convert from the data retrieved from the tag (i.e., the "tag-frame") to the position of the whale itself. This is now explained in the text as well (lines 490-492).

Line 443-445: This is really interesting! Please either cite the source of this method or describe in

detail how the authors infer prey type from tagging data. Please also tell us which species or populations generally feed on multiple prey types (beyond providing one example).
We are able to discriminate between prey type individual whales were foraging on using three different methods (or a combination thereof): kinematic differences in foraging behavior (Cade et al. 2016), videos collected by the tag itself, or acoustically determining the prey type in the patch being fed on by the focal whale(s). In the revised manuscript, we provide an example of the results we are referring to (in Fig. 2) and also cite several relevant papers where the differences in behavior and kinematics between individuals feeding on different prey types has been described and discussed (see lines 498-506).

Line 445-447: Provide information on how many and which tag deployments contained direct observations of prey using each of video or acoustic approaches. Perhaps this data is best presented in a table. This is important to identify potential biases in the analysis that could be introduced because of regional differences in prey sampling method.
We now include this information in Table S3.

Line 452: Please be specific about sample sizes throughout the manuscript. How many whales were measured for their body length, by species?
We appreciate this important point. Sample sizes are provided now in the new Tables S2 and S3.

Line 456: In my experience using drones without LIDAR, the height measurements drift over time during a deployment. Was that source of error measured?
To accommodate for error due to barometric drift, we flew the quadcopter at altitudes known to reduce error (20-60m) and calibrated altitude readings by measuring the known length of the boat. This has now been clarified in the manuscript.

Line 462: How was the 'best' estimate of length determined?
Thank you for bringing this to our attention. “Best” is misleading and has been omitted from the manuscript.

Line 467: Is it correct Nature style to end a sentence with a subscripted citation number as opposed to (author, year)? Perhaps delete this sentence and move the citation to line 463.
We have deleted this sentence and moved the citation as you have suggested.

Line 491: define the acronym ENP.
Done.

Line 492 - 494: I cannot interpret this apparent method of drawing inference using 'gulp-sized cells'.
We hope this is now more clear in the revised text (specifically see lines 509-533). Briefly each measured krill patch was divided into species specific gulp sized volumes (i.e., S_{v_gulp}). The log mean (i.e., geomean) and standard deviation (GSD) of these distributions (see ‘Prey biomass density’ column in Table S2) is what was used to generate of S_{v_gulp} is what was used to generate prey consumption estimates in the present manuscript. Specifically, see lines 527-538 in the revised manuscript. See Goldbogen et al. (2019) for more details on this method.

Line 475: Why only krill data when the whale species feed on krill, copepods and/or fish? Multifrequency acoustical instruments can differentiate between prey size class. What frequencies were used in the study?
We now have three different subsections of our Prey Methods section describing how we arrived at the measurements we used (which are displayed in Table S2). Briefly, we derived krill biomass estimates from active acoustics of krill patches that rorquals were foraging on or near. We used estimates from the published literature on the density of copepods and forage fish schools that baleen whales have been shown to feed on. In future studies, better estimating the prey density of copepods and fish schools that whales are actually feeding would improve our estimates presented

herein.

General remark: If only modeling rorqual whale feeding, then why are North Atlantic right whales displayed in Fig. S3?
We are estimating daily prey consumption of all seven species of mysticete shown in Figure S3 (and Table S2). However, the most (and highest quality) data of both predator and prey is focused on krill-feeding rorqual whales; as a result, we only estimate annual consumption (Fig. 3) and ecosystem effects (Fig. 4) on this subset of mysticetes.

Line 477: Was cell size constant? If so, what was the size of the cell, in meters squared?
The gulp-sized cells are constant for each species (i.e., they are species-specific). Cell dimensions were as follows: Minke whales, had cells of 1.44 m (vertical) x 3.54 m (horizontal), humpbacks were 2.82 x 7.45, fins were 3.95 x 11.29, blues were 5.02 x 14.71. See Goldbogen et al. (2019) for more details.

Line 482-487: I cannot interpret these three sentences. For example, the prey data were only "included" - included in what? Please revise.
We agree this is confusing, and this wording has now been removed. Please see revised Krill prey methods section (509-562).

Figures:

General comment: The figures contain a lot of information and so the completeness and clarity of the figure captions is really important. I find quite a few gaps in the information and so all captions should be revisited to ensure the reader can easily follow them.
Point well taken. We have simplified the figures (e.g., Figs 1 and 4) and improved the captions.

Fig. 1 A caption. The authors need to revisit the figure caption with the following suggestions in mind. ENP is not defined in the main text before the first reference of Fig 1 and so should be defined here. Circles are not 'hollow', they are unfilled. Euphotic zone is not highlighted, it is labeled. Raw echosounder data is not translated, it is bin-averaged. Describe the color scale and define Sv biomass.
We have made all the requested changes to the Figure 1 caption.

Fig 1 B: What does overall mean in "overall proportion"
It is meant to indicate the overall proportion of lunge feeding in orange, and total time in green. This is now shown explicitly in the figure's x-axis itself.

Fig 1B caption:

Extended Data Fig 1, Line 260: Reword caption: The images are of four different whale species defecating, which leads to nutrient recycling. Is figure B a fin whale defecating underwater? This could be important to note in the caption. Define the ENP acronym.
This is now part C of our main Figure 1 and we have made the edits you suggest.

Extended Data Fig 1: Authors should check if permit numbers need to be listed in the figure caption.
Permit numbers are now listed in the caption of Figure 1.

I stopped my review at line 487 because I could no longer follow the narrative thread of the manuscript due to a lack of clarity in the main text and methodology section. It would not be helpful to the authors for me to review any further until the major comments I listed above are addressed.
We have addressed all of the comments up to this point, and we think it has greatly improved the manuscript; we appreciate such a detailed review.

Referee #4 (Remarks to the Author):

Authors pool together an impressive global data base of empirical measurements of baleen whale foraging to create a much more field-driven perspective on whale consumption rates. They conclude most previous studies of baleen whale consumption were inaccurately low. Based on these higher measures of consumption, they then update calculations of the influence of the "whale pump" mechanism on carbon sinks – with a special emphasis on the Southern Ocean. The biogeochemical significance of the whale pump in carbon cycling (especially in the S Ocean) has been considered previously. However, the novelty of this contribution is reporting underestimation in these calculations.

Please find below major and minor comments on the MS:

Line 27 – Noting that a number of the ecosystem services of whales described elsewhere are non-trophic (e.g. benthic habitat modification). Authors are referring to the sub-set of ES associated with feeding). Consider generally how well the dynamics here fit a classic definition of "ecosystem engineer" sensu Johns, Lawton, Schchak 1994 Oikos
This is an excellent point and reference. The first two sentences of that paper: "Ecosystem engineers are organisms that directly or indirectly modulate the availability of resources to other species, by causing physical state changes in biotic or abiotic materials. In so doing they modify, maintain and create habitats" (Jones et al. 1994), suggests that the foraging based ecosystem services provided by baleen whales, detailed extensively in our paper, would qualify baleen whales as ecosystem engineers. This is a good point: the capacity of whales to serve as ecosystem engineers does not end with foraging, but also includes other aspects of their life and death (e.g., whalefalls). A deep dive into all the ways in which whales serve as ecosystem engineers is beyond the scope of this paper, but is provided by (Roman et al. 2014), which is cited throughout the main text.

Line 32 Not yet clear in abstract mechanism by which whales support ocean productivity; i.e. for readers approaching the whale pump subject for the first time
Thank you for bringing this to our attention, we hope that our updated abstract (specifically lines 40-42) has now cleared this up.

Lines 73-75 as written suggests that Boyce et al attribute whales loss as a mechanism for putative ocean productivity declines. These authors do not – but instead suggest climate/warming as primary mechanism. In general, the possible role of ocean warming (and other potential abiotic drivers) affecting primary producer bases should be better considered.
This is another good point. We have now changed the wording from "has been implicated in the" to "has coincided with," to make that lack of causal connection by the referenced studies clear.

Just as some of the terrestrial literature that quantifies and highlights sometimes under-appreciated carbon sequestration potential of forests (e.g. Bastin et al 2019) but also considers some of the future instabilities and lost opportunities in this potential that may be caused by CC – here also author's could (in a sentence or 2) speculate how effects of CC may affect the under-appreciated carbon sequestration potential of whales in a future climate-altered ocean.
We have now removed the section on whales as climate engineers, as well as any explicit discussion of whales as a "natural climate solution," including any quantifications of the ability of whales and their food web to sequester atmospheric carbon. We allude to this potential in the updated Conclusion section (lines 205-235), including how climate change itself may hamper these ecosystem services, but leave a more thorough evaluation of this topic for another paper.

Some brief additional discussion on geographic variability of prey consumption/filtration rates captured in their empirical data set may be in order. Also, further discussion is merited regarding any anticipated geographic variation in respect to the contribution of whale fecal inputs to stimulating ocean productivity and the biological pump. There is the tacit assumption (sensu line 178) in this report that nutrient contributions in fecal inputs are limiting in all contexts. More discussion on this point would be valuable. Authors focus on iron. Could some brief discussion be had on relative role of other nutrients, especially outside S Ocean (e.g. nitrogen sensu Roman/McCarthy)
This is a good point. We focus on the Southern Ocean in this paper because this is the ecosystem that had the greatest, and most rapid, removal of large whales and also because the Southern Ocean is known to influence global ecology and biogeochemistry. While we allude to these effects (e.g., lines 40-42) not being confined to the Southern Ocean (e.g., the Gulf of Maine is another location that has been studied for this effect as the reviewer points out), we think the narrative flows best focusing on the Southern Ocean ecosystem when considering the global effects of whale removal.

It would be interesting to better understand how whale recoveries (for populations that have increased after whaling) have potentially affected whale pump/carbon sequestration potential.
We totally agree; however, based on the suggestion from the editor and other reviewers, we have removed the carbon and climate discussion and projections from the present manuscript. The point of the impact of whale recoveries on carbon cycling and sequestration is something that we would like to consider in a future paper.

It would be insightful to have authors comment on what elements of the metabolic models that previously predicted much lower levels of consumption by whales were incorrect. It is potentially worth noting that these new consumption rates reported here were most similar to estimate generated in references 61,62 (as represented in Fig 3). Please explain what seemed "more accurate" in these estimates.

This question, which boils down to: "why are your results are more similar to predictions by (Klumov 1963) and Method 3 in (Tamura and Ohsumi 2000) than other, more recent estimates?" is an important one because these studies used a field metabolic scaling exponent (β) of 1, whereas β for most endothermic taxa fall between 0.67 and 0.85 (Nagy et al. 1999, Glazier 2010, Speakman and Król 2010). We think the apparent similarity between our results and the β=1 models is driven by a combination of isometric scaling of daily energy intake and uncertain (but likely negative) allometry of feeding season duration.

For example, if we assume all rorqual species feed half the year, then the predicted FMR allometric equation is $FMR=184.25M^{1.04}$ (FMR in kJ day-1, M is body mass in kg, see figure below). Similarly, in Fig. 3, the β=1 predictions are close to the predicted value when "Days feeding" approaches half the year (182.5 days).

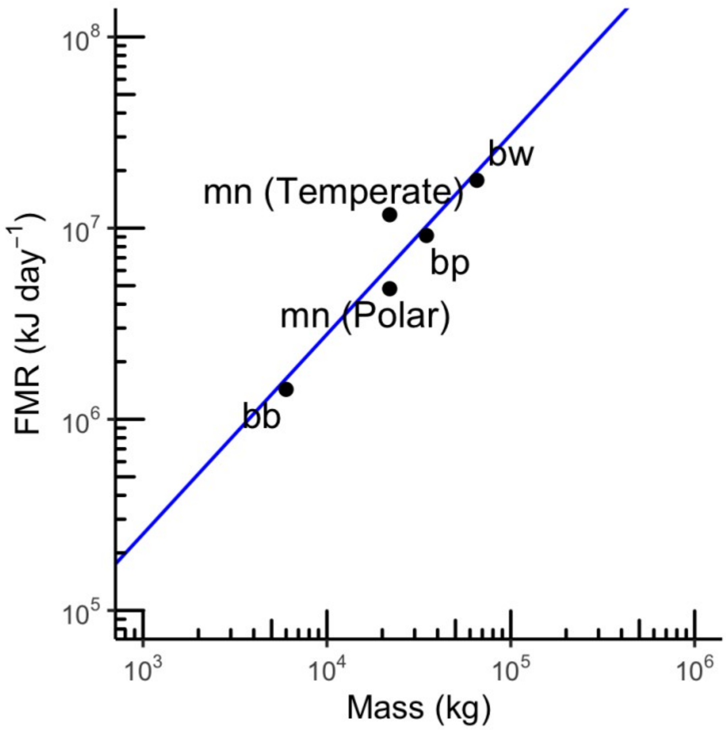

Figure showing daily FMR by body mass assuming 182.5 feeding days per year. Bb = Balaenoptera bonaerensis; mn = Megaptera novaeangliae; bp = Balaenoptera physalus; bw = Balaenoptera musculus

However, evidence from whaling records suggests smaller-bodied rorquals have longer feeding seasons (Lockyer 1981a, 1981b) Although the allometry of feeding season duration is unknown, 6 months for a minke whale, 4.5 months for a humpback whale, and 3 months for fin and blue whales is not unreasonable. Comparing estimates of annually-averaged FMR using these feeding season durations, the predicted β decreases to a more typical value of 0.73. The figure below compares our estimates (green line) based on these feeding season durations to three other published estimates. The orange line represents the 2.5xBMR model used in other recent estimates of cetacean prey consumption (Croll et al. 2006, Barlow et al. 2008). Using these feeding season duration assumptions, our estimates are approximately three-fold greater. The blue line is the FMR allometric equation for eutherian mammals from (Nagy et al. 1999), which is greater than the 2.5x BMR model due to the higher scaling exponents of FMR relative to BMR. Our estimates (again with the assumptions regarding feeding season duration) are approximately two-fold greater. However, (Kolokotrones et al. 2010) challenged the fundamental assumption of metabolic scaling, namely linearity in log-log space. Their analysis indicated a significant quadratic term, necessary for accurately predicting the elevated metabolic rates of very small and very large mammals. The purple line represents 2.5x BMR as predicted by the quadratic metabolic scaling model, which is on the same order as our estimates (given these feeding season duration assumptions). Therefore, we feel confident our results are within the range of biological plausibility and the 2.5xBMR model used in previous estimates is under-predicting prey consumption by baleen whales.

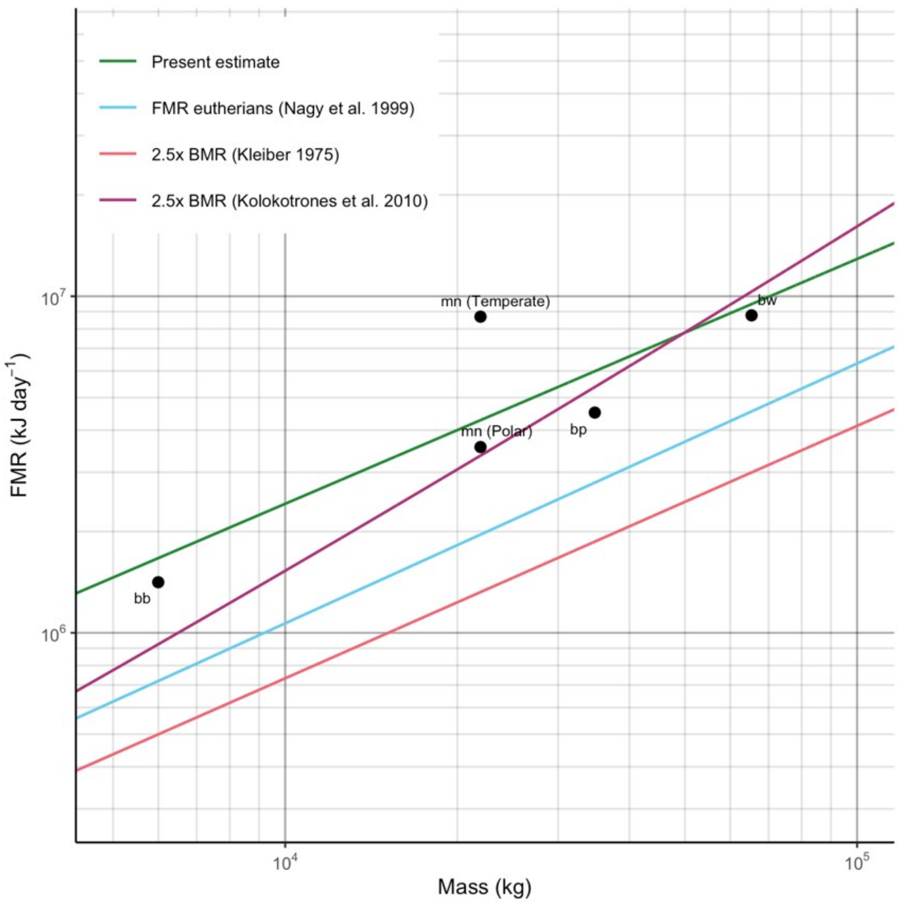

Figure showing daily FMR by body mass assuming 182.5 feeding days per year, comparing our estimate (green line) to prior estimates using different scaling power laws. Bb = Balaenoptera bonaerensis; mn = Megaptera novaeangliae; bp = Balaenoptera physalus; bw = Balaenoptera musculus

In Line 93 – be clearer in main text which values are used to quantify how much higher their estimates are from previous estimates (e.g. their mean value versus highest previously reported value?).

In this section of the main text we are comparing the median to the measure of central tendency in previous studies, usually the mean or median. However, we have removed quantitative comparisons like this to past studies because as you indicate the measures they report as compared to the measures we report (not to mention the methods themselves) may be different.

Not a resolvable issue, but noting that there is a disconnect in that the vast majority of the tagging and consumption estimates were conducted in the ENP (i.e. Fig. S3) – whereas some of the most heavily emphasized conclusions, as they relate to carbon capture, come from the Southern Ocean. This may not be an issue unless feeding behavior/consumption rates (e.g. for blue whales) differ significantly between ENP and S Ocean. Some discussion by authors on this point and the exportability of ENP heavy estimates to other regions is in order.

This is an important point; however, there is key issue in our inability to directly address this point. So many large whales (e.g., fin and blue) were killed in the 20th century that they remain rare, and exceedingly wary of boats, even to this day (Calderan et al. 2020). However, as the reviewer points out, there is no reason to think that the feeding rates or energetic demands would differ substantially between blue and fin whales in the North Pacific vs. the Southern Ocean. Hopefully over the course of the 21st century, the measurements we have described here – largely for Northern Hemisphere whales – can be done on baleen whales in the Southern Ocean. That would be an exciting future study.

I would suggest it would be prudent to include in the conclusion that any putative positive benefits for global carbon sequestration that can come from enhanced whale conservation and increase in whale populations – should be coupled with suggestion of the need for aggressive reduction in anthropogenic emissions. Regardless of the outlet where this report is published, I would advise authors review the messaging and response from the scientific community associated with such terrestrial reports as Bastin et al 2019. Central arguments of these authors were diminished by (deserved or undeserved) criticism that authors were over-emphasizing the confidence we can place on one pathway for combating CC using nature-based carbon capture.
This is a very prudent note of caution, and we appreciate it. Taking this, and the feedback of other reviewers to heart, we have now removed all quantification of carbon sequestration benefits provided by whales and removed any explicit discussion of baleen whales as a natural climate solution. We hope these substantial revisions let's our data and measurements shine through and will hopefully thus avoid the quagmire you describe in this comment.

There is a need (briefly) to connect with more detail these observation to examples of mechanism and species case studies in literature from other contexts on how megafaunal nutrient vectoring and trophic effects shape ecosystem productivity and carbon dynamics; sensu https://www.pnas.org/content/116/51/25707?ijkey=180e111b8828560fa9f6d262d7301c3a6de6cd9b&keytype2=tf_ipsecsha and papers contained within PNAS 2016 special edition (some already cited)
This is an excellent point and key reference. We have added two sentences in the Conclusion section discussing this point (see lines 217-220).

Please include some perspective on what dynamics may have been introduced in regarding nutrient transport and C sequestration as associated with putative increases in non-whale krill predators following whaling? Relatedly, please provide some very brief sense of interpretation of how the importance of whales may have ranked in an ocean before whaling and before over-hunting and overfishing of other large marine predators? E.g. in an ocean that had more whales, but also had many more large fishes, how important were whales? How should we think of their importance in an ecosystem context?
Thank you for this comment. Putting whales into their proper context is important as you mention; however, it is difficult to tease apart the effects of industrial whaling and overfishing on ecosystem services and productivity. No doubt they definitely both effected ecosystem productivity and carbon sequestration in similar ways (Mariani et al. 2020), and we mention that idea generally in the revised manuscript (lines 183-191). However to speak quantitatively on this point we feel is beyond the scope of this paper, but future studies such as these you outline are critically important, and likely very exciting, future work.

Please provide some discussion of how changes in winter sea ice/ice algae play into forecasting future importance of whales as the dominant force regulating krill abundance in the S Ocean.
While do explicitly recognize that climate change may hinder the recovery (and hence the recovery of the ecosystem services) of baleen whales (lines 226-232), delving too much into the specific highly speculative future possible feedbacks between sea ice/ice algae, krill, and whales is outside the scope of the present manuscript.

In the conclusion, it might be prudent to acknowledge and remind readers that there is a decent amount of inherent uncertainly in the chain of calculations that takes the authors from whale tagging data to whale influence on ocean-level estimates of C sink.

We agree. Based on this and the comments of other reviewers we have removed any quantitative estimates of the whale carbon sink.

Referee #5 (Remarks to the Author):

The authors present a synthesis of in situ feeding determinations of baleen whales providing, in limited view, the first global estimates of the impacts of present and historic whale populations impacts on the global ocean ecology and biogeochemistry. I am nowhere near an expert in whale ecology / physiology and I can only take the authors' work in quantifying these processes and scaling them to the global ocean. The few papers I have read about "whale falls" and their impacts have been highly speculative with wild guesses from scant observations. This work surely helps in putting some bounds on these processes through their synthesis using modern methods over a range of environments.

The problem with this manuscript is that many aspects of their analysis of the impacts of baleen whales on the ocean's ecology and carbon cycle are, at best, overstated, and, too often, incorrect. For example from lines 115-131, the authors estimate the amount of filtration that whales do today and did 100 years age for the Southern Ocean. They estimate that whaling reduced the total amount of "biomixing" by whales globally tenfold, from 2000 to 200 km3 yr-1. Seems like a lot. But does it scale to global scales? According to Wikipedia, the area of the Southern Ocean is ~7.85 million square miles (or 20e6 km^2). Assuming (conservatively) a layer of influence of whale "biomixing" of 100 m, it would take roughly 1000 years for the upper layers of the Southern Ocean to filtered through the historic whale population (2e6 km3 / 2000 km3/y). Clearly whale "biomixing' is NOT impactful on global scales – although it surely will be local space and time scales (km's and days). Thus, statements of enhanced nutrient supply and iron recycling due to whale ingestion made throughout the text are simply incorrect. Something is wrong here – either the global estimates of whale filtration are factors of >1000 too small or whales do not contribute this ecosystem service on global scales.
While it is true that if you average out across the entire ocean, biomixing by foraging whales will pale in comparison to abiotic forces such as the wind and tides. However, historic populations of whales filtering thousands of cubic kilometers each year in regions that are already primed by geologic or oceanographic forces to be productive may have positive impacts on ecosystem productivity that are unexpectedly large. Also, our estimates of the water mixed by whales is massively underestimated because we only considered the water that is filtered (i.e., moved and mixed) in the mouth and through the baleen. In future work, we hope to add in a key factor that we have omitted in the present paper: the quantity of water mixed by the rest of the whale's body, and specifically by the propulsive surfaces (e.g., the fluke). For example, in the acceleration phase leading up to a lunge, rorqual species have several powerful, high-amplitude fluke strokes. We have examined this quantitatively for a subset of our tag deployments and present it here:

Species	N	Mean strokes leading up to lunge	St Dev
Blue	22	3.68	0.71
Fin	2	3.38	1.17
Humpback	9	2.04	0.77
Minke	10	2.93	0.74

This means that on an average day feeding, a single minke whale has ~3500 lunge-associated fluke strokes (lunges per day * fluke strokes leading up to the lunge) and a blue whale has ~750 lunge-associated fluke strokes. The amount of water each fluke stroke displaces is unknown but adding this to the biomixing totals (which we don't in the paper itself and just share here for your reference) in future studies will add to amount of biomixing baleen whales contribute to the ecosystem, especially prior to whaling.

Further, the authors' analysis of the carbon cycle impacts of baleen whale is simply incorrect and frankly misleading. The authors state repeatably throughout the paper that whaling reduced the ocean carbon sink by nearly 400 Mt/y (0.4 PgC/y in proper units) through the lost processing of organic carbon by baleen whales. They then state that is 20% of the global carbon sink. Based upon the reference cited, I am assuming that the authors are stating that this "whale carbon sink" is 20% of the global air-sea exchange of CO_2 carbon (which is ~2 Pg/y). This is the wrong component of the ocean C cycle to make a meaningful comparison with baleen whale processing of organic C. Whales are transforming organic carbon in the form of krill and small fishes into both detrital organic carbon, which will be recycled by microbes back to CO_2 and nutrients, and into CO_2, via whale population respiration. Most of this recycled organic matter and respired CO_2 will be taken up by phytoplankton via photosynthesis to make more organic matter. Only a fraction will be exported from the surface ocean to depth. The correct comparison with the global C cycle would be with the export of organic carbon from the surface ocean to depth via sinking particles and vertically migrating metazoans where that exported carbon might be sequestered at depth on decadal and longer time scales. The global magnitude of the contributions of the sinking and migrant pathways to the biological pump is roughly 8 PgC/y. As mentioned above, some fraction of the whale carbon demand is exported from the upper ocean to depth; generously let's let that fraction be 50% (globally its 10%). Therefore, whaling has reduced the biological pump historically by no more than 0.2 PgC/y, which is ~2.5% of the magnitude of export for the present global biological carbon pump. This in no way supports any of the ascertains made throughout the paper that baleen whale populations if reestablished to historic levels would be "global climate engineers" (particularly, lines 160 -194).
We thank this reviewer for the time and effort to review our carbon-climate engineering hypothesis and providing this critical feedback. Due to this, and suggestions from another reviewer and the editor, we have removed any quantifications of carbon sequestration and export from the revised version of the manuscript and instead focus the paper on the data we collected (tag, drone, and echosounder data), and on the subsequent ramifications of those findings on ecosystem ecology and productivity.

In summary, this paper is not publishable in Nature and, in its present form, in any other journal - to do so would be irresponsible. The global estimates of baleen whale feeding, filtering and respiration rates are valuable and should be published. Again, I cannot speak to the voracity of these estimates; just that if these estimates are correct, they do not support the speculations / conclusions drawn. There's more beyond the two examples listed here that are either incorrect or over stated – but this is more than enough in my book to reject the paper.
As previously mentioned, we have now removed any quantification of the carbon sequestration and export benefits provided by larger populations of baleen whale, instead re-focusing the discussion of our paper on mysticetes potential as ecosystem engineers (see lines 172-203). We no longer mention the term "natural climate solution," and instead focus on prey consumption and nutrient recycling by whales. A topic that is closer to our expertise and for which better data exists to make more definitive statements and predictions. We hope you agree and that our changes allow you to see the value in the data presented in the revised manuscript.

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Reviewer Reports on the First Revision:

Referee #1 (Remarks to the Author):

Reading the other reviews was heartening since there seems to be general agreement that the data presented here, the first comprehensive, quantitative field measurements of whale feeding rates, are worthy of publication in Nature. All the more so because the results are quite startling: more than double the rates of the prevailing view. The new figures now render the data acquisition process transparent and instil confidence in the veracity of the feeding rates. The revised version is a great improvement over the rather impetuous first version and I recommend publication, albeit after attention to a few points listed below.

General comments
The results presented here imply that the much higher demand for food by whales and its apparent provision by the ecosystem fertilized with recycled iron by the whales was not only sustainable but also stable, reflected in the large body sizes of the organisms involved: diatoms, krill, whales. At the time of the whales, productivity for the Southern Ocean has been estimated to have been an order of magnitude higher and achieved with just 10,000 tons of recycled iron. The calculations do make ball-park sense but the efficiency of recycling, i.e. how big the losses to sinking might be, has not been considered and would need to be determined experimentally. Models are only as good as the values and processes built into them, and these will need to be obtained from in situ experiments: nevertheless,

how do your new values compare with the model of recycling iron run by Ratnarajah et al. you quoted as Ref 138; I think one of the outcomes was that the recycling loop only functioned at very high animal and iron concentrations. Perhaps one could revisit their model results and see whether their “high” values now conform with your new findings.

Since high latitudes are widely associated with low productivity, because of a terrestrial bias in thinking, it is worth pointing out that, in the presence of adequate nutrients, including iron, the upper limit on primary production is set by light availability (photon flux) which, during the peak summer months of high latitudes, is the same as at low latitudes because lower sun angle is compensated by the longer day length. Regular, storm-induced mixing of the deep mixed layer ensures efficient illumination of the entire water column, so that primary production levels can be as high as anywhere in the world. Indeed, the highest in situ rates of primary production were recorded in the shallow, hence iron-replete, Beaufort Sea along the northern coast of Alaska, the feeding grounds of bowhead and grey whales. A half sentence that pelagic production at high latitudes ranks amongst the highest in the world ocean would remind readers that the high productivity being invoked here is entirely possible.

In the section on iron recycling (starting at Line 743) the term “excretion” is often used in its more colloquial sense as the opposite of ingestion in places where defecation is meant. I would recommend replacing with the more neutral “egestion” as in line 73. Take lines 761/2 as an example: if the word iron were substituted with nitrogen, the term excretion would be correctly used. Excretion is defined as removal of substances from within the body, (the contents of the gastro-intestinal tract are outside the body) and is carried out primarily by the kidneys removing waste products from body fluids involving largely nitrogen (as ammonia or urea) but also phosphate and other ions. Iron, however, is never excreted, say the textbooks. Nevertheless, from a biological and ecological perspective, lumping liquid urine and particulate faeces under “excreta” does not make sense the way it does for municipalities. Because humans, and by extension all mammals, cannot excrete iron due to its insolubility, once the animal’s iron depots are filled, uptake from ingested food through the gut walls is stopped and all the iron is defecated.

Clearly, the much higher molar C:Fe ratios of terrestrial plants vs. animals is due to the large amounts of bulk C in cellulose and lignin, that also happen to be fairly indigestible and are defecated by elephants because their feeding strategy is centred around increasing throughput vs. uptake efficiency. In a nutshell: because elephants enjoy long lifespans, they don’t chew their cud like cows, (they have to go easy on their teeth) so they defecate what they don’t manage to grind. Elephant molars are replaced multiple times and individual life spans are determined by the condition of the last molars. Whales on the other hand are eating proteins and lipids encased in flimsy chitin carapaces that are easily crushed, so I am sure they are digesting and taking up the bulk of the organic carbon of the krill they ingest. This does not apply to iron in the case of adult whales, meaning that most iron ingested with the krill is defecated out again. Against this background, comparing elephants with whales in terms of the volume and the C:Fe ratio of ingested and egested food is not relevant. But see my comments on superfluous feeding in the first review.

It is worthwhile mentioning that an important function of whale filtering and stirring is breaking up and mixing friable krill faecal strings and copepod pellets in the water column. The effect would be akin to ploughing in a terrestrial field: crumbling the earth. Whale feeding and fertilizing prolonged the bloom and stirring broke up and mixed krill and copepod faeces but also diatom aggregates in the surface layer preventing their sinking out.

That the krill stock functioned as a biological iron reservoir could be stressed a bit more in the text to counter the one-way food chain concept that has been holding sway for so long.

Specific comments
Title: “global” in the title is no longer valid, it should be substituted with “ocean ecosystem engineers”

Abstract:
Line 29: I would substitute “services” with “functioning” here.
Line 37: I would substitute “current” with “estimated” just to underscore the fact that current krill stock estimates are highly uncertain.
Line 39: an order of magnitude is a bit daring. I try to imagine what today’s satellites would have seen over the former whale feeding grounds: presumably, extensive seaward extension of the high chlorophyll concentrations currently restricted to the coastline. On the other hand, at the turn of the last century, krill swarms were reported to colour the water red for miles and miles and feeding blue whales were seen from horizon to horizon. To support all that animal biomass, the water must have indeed been coloured green with chlorophyll. This would imply that the whale feeding grounds in the current Southern Ocean are largely degraded, microbial-dominated pelagic ecosystems.
Line 44: here the term “services” is appropriate because it refers to a specific function: iron fertilization.
Lines 114 to 116: “buffer generalists against variability”. I would argue that the specialist blue whales are the top engineers (movers and shakers) compared to other whales (before the invention of the explosive harpoon) in recycling ecosystems although highly specialised to feed only on euphausiids. Such recycling-based systems are buffered against ocean variability caused by multiyear cycles such as the El Nino Southern Oscillation because they are based on biological pools of iron. Ecosystem stability will enable top engineers to attain very large individual sizes in accordance with the other rule: The larger the area of the habitat, the larger the individual sizes of top predators and herbivores.
Line 173 What are “global results”? I suggest dropping “global”. Our results based on field-collected…. (drop global and switch based and on)
Line 189: replace “excreting” with “transferring”.
Line 193 “Antarctic Peninsula Plume” not Polar
Line 213/214: add “long-term” and “short-term” alongside “indirect” and “direct” respectively.
Line 227 food chain of the giants, (diatoms-krill-whales) instead of phytoplankton. Diatoms are the largest phytoplankton and some Antarctic diatom species are the largest in the world and beyond the reach of copepods: a conspicuous case of size escape. But krill can handle them because of their size and their diatom-shell-crushing gizzards. This is the food chain of the giants in each of the size classes: the largest diatoms (phytoplankton), the largest euphausiids and the largest whales.

End of manuscript review

The following is general information for whom it may concern or interest. I don’t expect the authors to mention this subject matter in the final version of the manuscript.

So where do we go from here? The authors begin their last sentence of the Conclusions with “Allowing cetacean populations to recover…..” will have multiple benefits. But blue whales have been allowed to recover since the moratorium was passed in 1964 yet the signs so far are discouraging. The recent sighting of some 15 or so individuals around S. Georgia made the international news and is consoling in that there are at least a few left. But for years before that, hardly any whales were sighted despite excellent coverage, not only from cruise ships. What is also no longer seen are krill swarms at the surface. The last extensive, krill “super” swarms, that extended for many kms on the surface, were reported in the early 1980s. In this light “allowing” whales to recover sounds too much like sit-and-wait to see what happens. Unfortunately, encouraging them to recover by providing the lost iron artificially is a red-hot iron no one seems willing to touch, even at the price of losing the whales altogether.
Clearly, current productivity in the Scotia Sea is not high enough, for lack of iron, to allow build-up of krill stocks. Iron entering the sea from land and sediments is not recycled but has a short life-time as indicated by the restricted areal extent and short duration of phytoplankton blooms along the coast and islands in satellite images. The blooms growing around two islands have been studied as examples of natural iron fertilization. Nowhere have there been reports of toxic algae jeopardising the rich animal life supported by iron leached from sediments and land runoff in island plumes. Nor has anoxia and production of methane and nitrous oxide been found in association with natural blooms. The final argument against OIF, that it will cause permanent damage to the pelagic ecosystem is belied by the

coast-to-ocean wide transition from iron-rich to iron-impoverished water that occurs annually around the continent, in island wakes and along frontal regions receiving enhanced dust supply. Pelagic ecosystems are subject to fundamental changes in the course of seasonal succession, with productive systems evolving into impoverished ones as essential nutrients are lost via sinking particles.
According to Discovery-era scientists and based on observations of slaughtered whales, blue whales needed less than 5 years from egg to egg. Alister Hardy marvelled at the extraordinary growth rate of embryos and calves and ranked the underlying cell division rates amongst the highest in the animal kingdom. And this in the largest animal, despite the belief that metabolism slows with increasing size. Clearly, the krill/blue whale relationship is something very special. That their total numbers after many decades are still just a few thousand should ring alarm bells. The return of the humpbacks is due to their feeding on overwintering krill stocks in fjords along the Western Antarctic Peninsula that used to be ice-covered. This is not encouraging as the fertilization effect under these conditions is minimal. In short there is no reason to expect krill stocks to increase in the near future. My anxiety for the whales is based on knowledge of how Southern Ocean ecosystems respond to iron addition based on numerous field observations (transect cruises) and 3 iron fertilization experiments. Unless grazer populations are built up, diatom blooms will continue to simply sink out en masse taking the iron with them.
The obvious solution is to test the whale-fertilizing hypothesis by mimicking their ecosystem engineering by releasing iron solution from a ship, studying the build-up of diatom blooms and following the effects of krill grazing on the bloom but also on the reproductive response of the krill. The females are opportunistic spawners that build up their ovaries in response to the food supply. The eggs then sink to depth along the continental shelf where they hatch, the larvae returning to the surface in a hungry state. Again, the feeding grounds of the larvae in the following year could be prepared with artificially induced blooms to ensure an abundant food supply and promote recruitment. From where else will come the iron necessary to restart the recycling ecosystem? None of the 5 experiments carried out in the Southern Ocean so far were located in krill territory, so this aspect of the effect of iron on the ecosystem is waiting to be addressed. It would be ecosystem recuperation and the opposite of what the detractors of ocean iron fertilization (OIF) claim. I would compare this type of action with the establishment of permanent water holes with water pumped from artesian wells in drought-prone African savannahs to save elephants and other megafauna from dying of thirst or migrating to regions where they are not wanted. Scientific OIF experiments mimicking feeding whales can be applied for and carried out anytime soon, with the permission of the London Convention that has passed an internationally binding moratorium on large-scale iron fertilization but explicitly allows scientific experiments. Someone has to take the initiative….

Referee #2 (Remarks to the Author):

As this is a review of a revised manuscript, I'm not going to repeat my general comments from the initial iteration of this work. The authors have addressed my comments satisfactorily. The manuscript's new focus – away from carbon cycling, in response to other reviewers' comments – makes it a much stronger paper, in my opinion.

This re-sets our understanding of the role of baleen whales in the marine ecosystems at a global scale, and in historical context. It is an extremely significant paper, and will be likely to drive scientific impetus to changing the manner in which society views the role of baleen whales in marine ecosystems.

I have a only a couple of comments on the current iteration of the manuscript, regarding two papers that the authors seem to have missed.

First, with the manuscript's revised focus on prey consumption and ecosystem engineering, with a emphasis particularly on the Antarctic system, it's appropriate that the authors cite Willis' 2014 paper in

Marine Ecology Progress Series entitled “Whales maintained a high abundance of krill; both are ecosystem engineers in the Southern Ocean” - https://www.int-res.com/abstracts/meps/v513/p51-69/.

Second, do the data from Miller et al’s recent paper in Scientific Reports on krill swarms and blue whales (https://www.nature.com/articles/s41598-019-52792-4) inform your analyses, if at all?

And a couple of minor issues in Figures.
Figure 2 isn’t identified correctly. Bb/Mn are A,C&E.

Extended data figure 2 D – I can't see the lighter shaded parts of these plots.

Referee #3 (Remarks to the Author):

I thank that authors of this paper for providing a revised manuscript that has significantly improved in its clarity. The authors addressed most of the concerns laid out in my first review of the paper. I find the newest version very readable. I think the addition of a roadmap through the methods was very helpful. I think that the estimation of whale prey consumption rates is sophisticated and there is strong evidence supporting the conclusion that previous models have underestimated prey consumption. One of the most fascinating findings is that animals that prey-switch seem to keep their energy intake constant across prey types. This analysis is the most novel piece of the paper and will be of great interest to a broad readership.

My major issue with the manuscript is with the direct relationships drawn between whale-regenerated nutrients, iron limitation and the impact of whales on primary production across the global oceans. This is the least supported topic of the paper. While top-down control on primary production by whales is an interesting hypothesis, the authors have not made a convincing argument in support of this hypothesis based on their synthesis. The paper greatly oversimplifies the processes that impact primary production, and in doing this the impact of whale nutrient cycling on ecosystem functioning is biased high. The authors also provide too few supporting numbers from the literature, relying at times on one number or one paper to make very significant statements about their results in relation to ocean-wide or decadal-scale primary and secondary production (see my comments on Lines 157 and 197).

My impression is that the conceptual model in the paper assumes an epipelagic zone that is constantly nutrient limited while whales are present, and where the nutrients generated by whale poop are immediately and entirely used up by phytoplankton. That is not the case throughout much of the high primary productivity zones of the global oceans.

First, nutrient limitation is one of many controls on primary production; others being light and temperature. Second, iron is one of a few nutrients that can limit primary production. Iron is important in some places, like the southern ocean, and not important in other places, like the continental shelf and coastal regions of the Atlantic ocean, which are also productive Mysticete habitats. This second issue could be remedied by including other important nutrients in the analysis.

Thirdly, the estimates do not consider important information about the annual cycles of regional whale occurrence and controls on primary production. For example, much of the primary production in the temperate continental shelf regions occurs during the spring bloom, months after the whales feeding in the region departed the previous autumn. If we assume a 6 month feeding season in a temperate zone, a spring bloom in May would need to somehow be influenced by nutrients generated in the surface zone by whales the previous October. During winter, primary production is light limited, and so the whale poop-generated nutrients from the previous fall may not be used up until the following spring. It is unlikely, given that ocean currents can transport and disperse water thousands of kilometers over a six month period, that nutrients generated by whales in areas that produce phytoplankton and zooplankton would remain entirely in those areas for 6 months. Further, vertical mixing by wind in winter mixes nutrients from the deep ocean throughout the water column such that primary production in the spring bloom is not nutrient limited, it is light-limited. This is just one example of a significant amount of primary production in global whale habitats that is not likely to be directly influenced much, if at all, by whale poop generated in the photic zone in those habitats.

However, there are certain locations and times of year (e.g., summer in the temperate zones) when vertical stratification of the water column is known to limit vertical nutrient exchange. This could be a time when regenerated nutrients from poop could make some direct contribution to the primary production in the surface layer.

The authors argue that whales, as a source of fecal nutrient recycling in the photic zone of the ocean, are keystone organisms facilitating ecosystem productivity. They argue this based on the idea that a decline in whale biomass due to whaling may have reduced iron cycling by an estimated 1.1 x 10^4 tonnes of iron per year in the southern ocean. But no context is provided for interpreting the importance of this number. Is this is high number relative to other sources of iron cycling such as wind-driven upwelling and terrestrial sources? Further, there is no evidence in the primary literature the authors provided that primary production has declined in the southern ocean concurrently as whales declined from over-harvest.

Not considering how oceanographic factors would impact whale-regenerated nutrient loss terms (i.e., nutrients that go unused in primary production) would lead to an overestimate of the amount of primary production that could be generated by regenerated nutrients released by whale poop. I think these nuances need to be discussed, or this analysis removed from what is an otherwise very nice synthesis study.

As the manuscript stands, the statement on line 39-41 of the abstract about historical primary production being an order of magnitude higher than present due to a higher whale population is biased high. I also disagree with the statement that this likely reflects a global pattern, based on the reasons I stated above. The statements about broad applicability of the paper's results across the global oceans is overstated. In my opinion, these issues must be addressed before the manuscript is publishable. I believe that these issues could be fairly easily remedied with more contextual information about how primary productivity is limited in whale feeding zones, perhaps consideration of additional loss terms in their models, and some revision of key statements.

Overall, the study went into significant detail to improve estimates of whale prey consumption, and provided a highly convincing and publishable argument based on those estimates. I think those portions of the paper are very strong. In comparison, the oceanographic portion of the study was given very limited attention, and the resulting 'bigger picture" argument about the role of whales in ecosystem functioning was not convincing.

Line-by-Line comments:

Line 39: Not more productive 'oceans' since the calculations in the paper are for only one ocean, the southern ocean.
Line 61: from whales carcasses, not from whaling
Line 66: Not only smaller but also physiologically and evolutionarily distinct and occupying different foraging niches. To my knowledge there are no smaller filter-feeding marine mammals. I don’t expect metabolism to be the same a priori beyond just changes in body size.
Line 69: quantity not quality (quality would be nutritional content per unit biomass)
74: facilitating, not maximizing
Line 82: This is speculation, and either needs to be removed from the introduction, or the authors need

to provide a lot more evidence to support drawing this relationship. The Boyce et al reference analyzes chlorophyll data from across the entire globe (not only whale feeding habitats) and so the decline in primary productivity they measure cannot be attributed to whale feeding. If the pattern they measure is real (and there is considerable debate about this in the literature), relating it to a top-down control mechanism would be a tall order. In that paper they draw statistical conclusions about physical forcing of the variation in primary production (light and temperature).
Line 83: Mysticetes are not universally recovering (e.g., Northwest Atlantic blue whale). I wonder where this statement came from. It would be helpful to explain how Mysticete populations are changing globally.
Lines 134-135: I think that, for me, this is the main take-home message from the paper. This is incredible. Going the next step to linking this result to altering ecosystem function needs more attention.
Line 152: I don't quite understand this result. Predicted by whom? Are you discussing your prediction, or how your prediction compares to predictions made in past studies?
Line 152-157: Please include the uncertainties around each of these estimates.
Line 157: Reference number 4 states in the abstract that 379 Mt yr is the average over the period of 1926 - 2004, so I conclude that it does not represent the contemporary state of the krill biomass in the southern ocean relative to the 20th century. Please address this apparent discrepancy. This is critical since this one number is central to the entire argument that whale removal reduced ecosystem productivity.
Line 197: Since the time series in Reference 18 only goes back to 1976 (post whaling) its not possible to conclude that whaling caused of the declining trend. There have been many changes to the southern ocean ecosystem during this period that could have caused the decline.
Line 197: Reference 18 does not include any time series analysis of primary production, so I cannot see how the authors drew the conclusion that it was modest over this period.
Line 375: Is diet composition on a 0-1 scale for a single species? E.g. 0.5 = 50% krill and 50% forage fish?
Line 393: Figs S1 and S2 are uncited in the text of the main paper text or supplement. The (I assume) error bars are not defined in the figures. How were these statistics generated? Please ensure that all figures and tables are cited somewhere in the paper or supplement and a full description of the information in each figure is written in the caption.
Line 405: what calculations? Do you mean the data presented in Figs S1 and S2?
Line 405-406: what is your justification that the metabolic rates are extremely low? Is it because they are basal estimates based on body size alone (assume no activity)? One or two explanatory sentences here would be helpful.
Line 385: minor point; mid- to high latitudes. Include the temperate regions in your description of feeding range.
Line 742: missing reference
Line 746: There is no information provided in this section about the stoichiometry of fertilizing nutrients to primary production.

Referee #4 (Remarks to the Author):

I don't disagree with other reviewers calls to remove estimates of carbon sequestration by whales from the previous draft - my colleagues make a compelling case for the many challenges and uncertainties in generating these carbon estimates. I look forward, however, to the authors advancing that dialogue about the historic vs contemporary role of whales as agents of carbon in an alternate forum, for I do think beginning to identify and consequently fill gaps in these whale carbon sequestration estimates is a scientifically important and deserving exercise. With these estimates removed, the principal contribution of the paper becomes creating first empirical estimates of consumption rates for whales – using a combination of extensive tagging data, drone measurements of tagged whales, and mapping of prey biomass. These field measurements are very useful and interesting. They help here – and will similarly help in future research attempting to assess the trophic dynamics of whales and their influence on ecosystems. I'm not certain, however, that this contribution by itself merits publication Nature.

The authors efforts to use these new directly measured prey consumption rates to create estimates of the influence of whales on biogeochemistry in the Southern Ocean are interesting and certainly the next logical extension for application of these empirical consumption rates. But the base suggestion that numerically larger pre-whaling whale populations had an elevated impact on ocean ecosystem ecology and biogeochemistry is not in of itself new – and stems back at least as far a literature from the early 2000s (all adequately cited by these authors; e.g. Whales, Whaling, and Ocean Ecosystems 2007 UC Press). I am also left with some minor misgivings about missed opportunities to discuss any possible role of applying field data collected in one ocean to nutrient recycling rates in another ocean and opportunities to, even very briefly, consider possible alternate hypothesis associated with what has been written about relationships between climate change and the krill paradox.

Referee #5 (Remarks to the Author):

Review of "High-resolution foraging measurements reveal baleen whales as global ecosystem engineers"

Authors have revised their original submission to this journal focusing on their estimates of feeding rates and implications on ecosystem dynamics. As suggested by the editor and some of the reviewers (incl. mind), they removed all of the wildly speculative ascertains connecting the reestablishment of whale populations and atmospheric CO_2 levels. This makes this a more palatable paper and one that is possibly publishable in Nature. I am generally favorable with this resubmission. From my admittedly limited point of view, the ingestion rates synthesis appear to be an excellent contribution to the literature.

However, the authors have fallen short of convincing me that baleen whales really are "global ecosystem engineers" as stated in the title. In the abstract, the authors state "By extension, larger whale populations prior to 20th-century the whaling supported more productive oceans, with prey and primary production an order of magnitude higher than present.". Their conclusion hinges on what seems to me to be a few rather weak pieces of evidence. The strongest piece of evidence (Lines 142-160) is this paper's primary ecological result that krill abundances must have been much larger than they are today to support the historic whale populations. That appears to me to be the interesting and important finding of this work.

The problem is with the "why" there are more krill in the Southern Ocean pre-whaling. The suggestion that the NPP is higher is not entirely convincing to me based upon the flawed Boyce et al. result (see below) and the rather crude Primary Production Required (PPR) estimate (see below). Further, the biomixing leading to more nutrient recycling argument also doesn't make sense to me. It is at best a local mechanism and cannot scale to ocean basin scales as is suggested here (see my earlier review). The new production hypothesis taught in every 1st year grad Bio Oce class suggests that more recycling would lead to lower NPP and smaller phytoplankton and a longer trophic distance between phytoplankton and whales.

To be acceptable, the authors need to focus harder on their results and the implications of these results and limit the wilder speculation. I suppose to be acceptable by Nature there needs to be important global implications so its relatable to material scientists and protein folders. But pushing the story too far is not acceptable as the adverse damage it creates is reqal. There is a lot of interest now in both national science agencies and NGOs in global benefits of the restoring ecosystems to the conditions that preceded the anthrocene. This work has an important part to play in that dialogue but needs to stick to its story.

My detailed comments follow…

Lines 38-29 – Statement should be downplayed.

Lines 40-41 – Iron recycling – It is not clear to me why that is relevant on its own. I suppose the authors could assume a phytoplankton C/Fe ratio for Fe depleted conditions and figure out what that mean in enhanced NPP in the Southern Ocean. Further following my previous review's statement that biomixing is a local mechanism and cannot scale to ocean basin scales not sure how this has “broad implications”. Actually virtually nothing is stated in the main text about whale recycling of iron besides this statement in the abstract. Probably should be removed.

Lines 81-82 – Boyce paper. There are many concerns in the biological oceanography community about the veracity of the Boyce paper's results. Many of their results have merit, but their ascertain of a 1% per year decrease in median ocean phytoplankton biomass over the last century is simply unrealistic and it should not have been allowed to be published. It implies that the global median phytoplankton pigment biomass levels were ~2.7 times greater than they are today. It is inconceivable that the blue oceans of today (the median) were moderately eutrophic 100 years ago. Clearly, there must be issues in their extrapolation of the historical, sparse, poor quality Secchi disk observations to the present satellite record using statistical models in the Boyce paper. BUT it does point out how difficult it is to correct obviously incorrect results once they are published.

Lines 139-140 – Again I must restate that the biomixing argument is irrelevant. It is obviously unimportant on a global scale as stated in my last review. The statement here is accurate – but is misleading as it implies that there is a significant role for mysticetes in ocean ecosystems, which may actually be true on global scales.

Line 165-166 – Not sure how they are concluding that “current ecosystem models may underestimate the quantity of prey and primary productivity required to support current and historic populations of baleen whales”

.

Line 170 – see comment above

Lines 174-178 – Two things. First, I am not sure why whale falls are mentioned here. They do supply organic matter to the seafloor and support benthic communities but do export organic matter from the surface ocean exasperating the NPP issue. I likely does not matter much anyways as I suspect it is a tiny number compared with other export pathways. Second, not sure that recycling makes sense for increasing NPP as commented previously.

Lines 189 – 190 – The terrestrial sink of organic matter via birds and seals is probably not a real big term on global scales – but could easily be important on local scales.

Lines 197-199 – I am not buying this. Sorry. I do not see how your finding support these statements.

Lines 227-230 – Again this is way too speculative and should be cut. Arguments are made throughout that whales lived in a time where NPP may have been higher which could leasd to higher carbon export and sequestration. BUT arguments are also made that whales recycle nutrients in the euphotic zone which would reduce the fraction of NPP that is exported. You cannot make both arguments.

Lines 561-562 – I have issue with the logic with the statement “Finally, in our calculations we assumed maximal engulfment and 100% capture of krill as previously published recognizing this may be overestimate.” The authors should be developing their best conservative estimates of the ecosystem impacts of baleen whales, not an overestimate. In the previous section (Lines 555-557), they chose the more conservative of two methods. So, first consistency is needed throughout. But by choosing the overestimate, it raises doubts in the readers' mind whether the authors find that whales are impactful because they really are or because the authors used overestimates in their analyses.

Lines 732-342 – The PPR estimates are central to statements that mysticetes have significant roles in ocean ecosystems. I wish there were a better description why the mathematical formulation given in equation 9 actually quantifies PPR. I am not following how this works. Also units are missing for P_c and C_p. Most importantly, I wish this section detailed how the PPR quoted in Lines 163 and 164 were actually calculated. This should be shored up if used.

Author Rebuttals to First Revision:

Referees' comments:

Referee #1 (Remarks to the Author):

Reading the other reviews was heartening since there seems to be general agreement that the data presented here, the first comprehensive, quantitative field measurements of whale feeding rates, are worthy of publication in Nature. All the more so because the results are quite startling: more than double the rates of the prevailing view. The new figures now render the data acquisition process transparent and instil confidence in the veracity of the feeding rates. The revised version is a great improvement over the rather impetuous first version and I recommend publication, albeit after attention to a few points listed below.

General comments

The results presented here imply that the much higher demand for food by whales and its apparent provision by the ecosystem fertilized with recycled iron by the whales was not only sustainable but also stable, reflected in the large body sizes of the organisms involved: diatoms, krill, whales. At the time of the whales, productivity for the Southern Ocean has been estimated to have been an order of magnitude higher and achieved with just 10,000 tons of recycled iron. The calculations do make ball-park sense but the efficiency of recycling, i.e. how big the losses to sinking might be, has not been considered and would need to be determined experimentally. Models are only as good as the values and processes built into them, and these will need to be obtained from in situ experiments: nevertheless, how do your new values compare with the model of recycling iron run by Ratnarajah et al. you quoted as Ref 138; I think one of the outcomes was that the recycling loop only functioned at very high animal and iron concentrations. Perhaps one could revisit their model results and see whether their "high" values now conform with your new findings.

Since high latitudes are widely associated with low productivity, because of a terrestrial bias in thinking, it is worth pointing out that, in the presence of adequate nutrients, including iron, the upper limit on primary production is set by light availability (photon flux) which, during the peak summer months of high latitudes, is the same as at low latitudes because lower sun angle is compensated by the longer day length. Regular, storm-induced mixing of the deep mixed layer ensures efficient illumination of the entire water column, so that primary production levels can be as high as anywhere in the world. Indeed, the highest in situ rates of primary production were recorded in the shallow, hence iron-replete, Beaufort Sea along the northern coast of Alaska, the feeding grounds of bowhead and grey whales. A half sentence that pelagic production at high latitudes ranks amongst the highest in the world ocean would remind readers that the high productivity being invoked here is entirely possible.

In the section on iron recycling (starting at Line 743) the term “excretion” is often used in its more colloquial sense as the opposite of ingestion in places where defecation is meant. I would recommend replacing with the more neutral “egestion” as in line 73.
Take lines 761/2 as an example: if the word iron were substituted with nitrogen, the term excretion would be correctly used. Excretion is defined as removal of substances from within the body, (the contents of the gastro-intestinal tract are outside the body) and is carried out primarily by the kidneys removing waste products from body fluids involving largely nitrogen (as ammonia or urea) but also phosphate and other ions. Iron, however, is never excreted, say the textbooks. Nevertheless, from a biological and ecological perspective, lumping liquid urine and particulate faeces under “excreta” does not make sense the way it does for municipalities. Because humans, and by extension all mammals, cannot excrete iron due to its insolubility, once the animal’s iron depots are filled, uptake from ingested food through the gut walls is stopped and all the iron is defecated.

Clearly, the much higher molar C:Fe ratios of terrestrial plants vs. animals is due to the large amounts of bulk C in cellulose and lignin, that also happen to be fairly indigestible and are defecated by elephants because their feeding strategy is centred around increasing throughput vs. uptake efficiency. In a nutshell: because elephants enjoy long lifespans, they don’t chew their cud like cows, (they have to go easy on their teeth) so they defecate what they don’t manage to grind. Elephant molars are replaced multiple times and individual life spans are determined by the condition of the last molars.
Whales on the other hand are eating proteins and lipids encased in flimsy chitin carapaces that are easily crushed, so I am sure they are digesting and taking up the bulk of the organic carbon of the krill they ingest. This does not apply to iron in the case of adult whales, meaning that most iron ingested with the krill is defecated out again.
Against this background, comparing elephants with whales in terms of the volume and the C:Fe ratio of ingested and egested food is not relevant. But see my comments on superfluous feeding in the first review.

It is worthwhile mentioning that an important function of whale filtering and stirring is breaking up and mixing friable krill faecal strings and copepod pellets in the water column. The effect would be akin to ploughing in a terrestrial field: crumbling the earth. Whale feeding and fertilizing prolonged the bloom and stirring broke up and mixed krill and copepod faeces but also diatom aggregates in the surface layer preventing their sinking out.

That the krill stock functioned as a biological iron reservoir could be stressed a bit more in the text to counter the one-way food chain concept that has been holding sway for so long.

Thank you once again for providing an incredibly thorough and thought-provoking review. Your comment about the models, like those of (Ratnarajah et al. 2016), is well taken; the authors of that study remark: “However, only when all parameter estimates are at their upper limits does there appear to be this significant role for whales in enhancing primary productivity, and thus we need to assess the likelihood of these values arising.” And in particular “future research will need to refine our understanding of five influential model parameters: iron content in krill; krill consumption rates by whales; persistence of whale faecal iron in the photic zone; bioavailability of this retained iron; and the carbon-to-iron ratio of phytoplankton.” Our study has better resolved two of these parameters. First that the krill consumption rate by whales is at least as much (and likely greater) than the maximum consumption rates used by Ratnarajah et al. (2016). For example, Ratnarajah et al. (2016) reported a *maximum* estimate of 4130 kg d^{-1}, while our *median* estimate was 4193 kg d^{-1}. Second, our tags confirm that whales we have tagged typically forage at depth (>>20m) but spend the majority of their total time budget at, or near, the surface (<20m), which is where the majority of their defecation is likely to occur (see Fig. 1). Consequently, the persistence of whale feces in the photic zone is maximized. On a related note, the vast surface krill swarms noted by researchers in the early 20th century (Marr 1964, Ozawa and Sato 1967, Mackintosh 1973) may have been driven and/or kept at the surface, in large part, by heavy predation pressure from whales (Willis 2014). If true, then whales would have had another indirect positive effect on this process in that both the krill and whale fecal retention in the photic zone would have been maximized.

We have addressed the remaining issues you raised in several ways in our revisions. First, we explicitly mention how our values compare to model inputs from other researchers (Ratnarajah et al. 2016) (see lines 160-166). Second, we substitute excretion for egestion, as you recommend. Third, we retain our biomixing results and interpretation because, we similarly think that the fluid dynamics of whale swimming and feeding by dense concentrations of whales could have a significant effect in areas already primed for high productivity. And finally we have also added the sentence “More broadly, pelagic production at high latitudes ranks amongst the highest in the world ocean (Falkowski et al. 1998), and this was likely even more pronounced prior to industrial whaling.” (lines 153-155) at your recommendation.

Specific comments

Title: “global” in the title is no longer valid, it should be substituted with “ocean ecosystem engineers”

We agree. Synthesizing all the feedback from the editor and all reviewers our new proposed title is: Baleen whale prey consumption enables their ecosystem engineering potential

Abstract:
Line 29: I would substitute “services” with “functioning” here. Done.

Line 37: I would substitute “current” with “estimated” just to underscore the fact that current krill stock estimates are highly uncertain.
We added the word “estimated” after “current” to note that present estimates of krill biomass could not have supported past populations of whales.

Line 39: an order of magnitude is a bit daring. I try to imagine what today’s satellites would have seen over the former whale feeding grounds: presumably, extensive seaward extension of the high chlorophyll concentrations currently restricted to the coastline. On the other hand, at the turn of the last century, krill swarms were reported to colour the water red for miles and miles and feeding blue whales were seen from horizon to horizon. To support all that animal biomass, the water must have indeed been coloured green with chlorophyll. This would imply that the whale feeding grounds in the current Southern Ocean are largely degraded, microbial-dominated pelagic ecosystems.
We have toned this sentence down:
“By extension, larger whale populations prior to 20th-century whaling supported more productive oceans, with greater prey and primary production than at present.”

Line 44: here the term “services” is appropriate because it refers to a specific function: iron fertilization.
Thank you for the clarification.

Lines 114 to 116: “buffer generalists against variability”. I would argue that the specialist blue whales are the top engineers (movers and shakers) compared to other whales (before the invention of the explosive harpoon) in recycling ecosystems although highly specialised to feed only on euphausiids. Such recycling-based systems are buffered against ocean variability caused by multiyear cycles such as the El Nino Southern Oscillation because they are based on biological pools of iron. Ecosystem stability will enable top engineers to attain very large individual sizes in accordance with the other rule: The larger the area of the habitat, the larger the individual sizes of top predators and herbivores.
We agree on the point you make, however in this sentence we were merely discussing population viability in the face of climate variability and change. Blue whales do not efficiently feed on fish (Cade et al. 2020; see Fig S7b) and can only feed on swarming krill species; whereas many populations of humpbacks, like those found off the west

coast of North America regularly eat fish and krill. The ability to switch from one prey type to another will likely allow generalist humpbacks to be less effected by ocean variability than specialist blue whales (Fleming et al. 2015, Hazen et al. 2019).

Line 173 What are "global results"? I suggest dropping "global". Our results based on field-collected…. (drop global and switch based and on)

Done.

Line 189: replace "excreting" with "transferring". Done.

Line 193 "Antarctic Peninsula Plume" not Polar

Thank you for noticing this, we have made this change.

Line 213/214: add "long-term" and "short-term" alongside "indirect" and "direct" respectively.

Done.

Line 227 food chain of the giants, (diatoms-krill-whales) instead of phytoplankton. Diatoms are the largest phytoplankton and some Antarctic diatom species are the largest in the world and beyond the reach of copepods: a conspicuous case of size escape. But krill can handle them because of their size and their diatom-shell-crushing gizzards. This is the food chain of the giants in each of the size classes: the largest diatoms (phytoplankton), the largest euphausiids and the largest whales.

I knew this to be true for the krill and whales, but not for the phytoplankton. The food chain of the giants indeed! We have included this interesting bit of natural history in the parenthetical in line 237.

End of manuscript review

The following is general information for whom it may concern or interest. I don't expect the authors to mention this subject matter in the final version of the manuscript.

So where do we go from here? The authors begin their last sentence of the Conclusions with "Allowing cetacean populations to recover….." will have multiple benefits. But blue whales have been allowed to recover since the moratorium was passed in 1964 yet the signs so far are discouraging. The recent sighting of some 15 or so individuals around

S. Georgia made the international news and is consoling in that there are at least a few left. But for years before that, hardly any whales were sighted despite excellent coverage, not only from cruise ships. What is also no longer seen are krill swarms at the surface. The last extensive, krill "super" swarms, that extended for many kms on the surface, were reported in the early 1980s. In this light "allowing" whales to recover sounds too much like sit-and-wait to see what happens. Unfortunately, encouraging them to recover by providing the lost iron artificially is a red-hot iron no one seems willing to touch, even at the price of losing the whales altogether.

Clearly, current productivity in the Scotia Sea is not high enough, for lack of iron, to allow build-up of krill stocks. Iron entering the sea from land and sediments is not recycled but has a short life-time as indicated by the restricted areal extent and short duration of phytoplankton blooms along the coast and islands in satellite images. The blooms growing around two islands have been studied as examples of natural iron fertilization. Nowhere have there been reports of toxic algae jeopardising the rich animal life supported by iron leached from sediments and land runoff in island plumes. Nor has anoxia and production of methane and nitrous oxide been found in association with natural blooms. The final argument against OIF, that it will cause permanent damage to the pelagic ecosystem is belied by the coast-to-ocean wide transition from iron-rich to iron-impoverished water that occurs annually around the continent, in island wakes and along frontal regions receiving enhanced dust supply. Pelagic ecosystems are subject to fundamental changes in the course of seasonal succession, with productive systems evolving into impoverished ones as essential nutrients are lost via sinking particles.

According to Discovery-era scientists and based on observations of slaughtered whales, blue whales needed less than 5 years from egg to egg. Alister Hardy marvelled at the extraordinary growth rate of embryos and calves and ranked the underlying cell division rates amongst the highest in the animal kingdom. And this in the largest animal, despite the belief that metabolism slows with increasing size. Clearly, the krill/blue whale relationship is something very special. That their total numbers after many decades are still just a few thousand should ring alarm bells. The return of the humpbacks is due to their feeding on overwintering krill stocks in fjords along the Western Antarctic Peninsula that used to be ice-covered. This is not encouraging as the fertilization effect under these conditions is minimal. In short there is no reason to expect krill stocks to increase in the near future. My anxiety for the whales is based on knowledge of how Southern Ocean ecosystems respond to iron addition based on numerous field observations (transect cruises) and 3 iron fertilization experiments. Unless grazer populations are built up, diatom blooms will continue to simply sink out en masse taking the iron with them.

The obvious solution is to test the whale-fertilizing hypothesis by mimicking their ecosystem engineering by releasing iron solution from a ship, studying the build-up of diatom blooms and following the effects of krill grazing on the bloom but also on the reproductive response of the krill. The females are opportunistic spawners that build up their ovaries in response to the food supply. The eggs then sink to depth along the continental shelf where they hatch, the larvae returning to the surface in a hungry state. Again, the feeding grounds of the larvae in the following year could be prepared with artificially induced blooms to ensure an abundant food supply and promote recruitment. From where else will come the iron necessary to restart the recycling ecosystem? None of the 5 experiments carried out in the Southern Ocean so far were located in krill territory, so this aspect of the effect of iron on the ecosystem is waiting to be addressed. It would be ecosystem recuperation and the opposite of what the detractors of ocean iron fertilization (OIF) claim. I would compare this type of action with the establishment of permanent water holes with water pumped from artesian wells in drought-prone African savannahs to save elephants and other megafauna from dying of thirst or migrating to regions where they are not wanted. Scientific OIF experiments mimicking feeding whales can be applied for and carried out anytime soon, with the permission of the London Convention that has passed an internationally binding moratorium on large- scale iron fertilization but explicitly allows scientific experiments. Someone has to take the initiative….

These ideas are intriguing. We have explicitly considered how rapidly blue whales (and all rorquals more generally) can reproduce, despite their immense size. Their mass- specific reproductive rate is off the charts. Therefore, it is indeed interesting, and distressing, that the Antarctic blue whale population has not recovered after ~50 years without whaling, whereas the humpback populations have roared back in the region (Pallin et al. 2018). This may be is a function of niche segregation and climate change. As krill biomass shifts poleward and contracts toward Antarctica itself (Atkinson et al. 2019), humpback and Antarctic minke whales, which thrive in the small, sheltered bays of the West Antarctic Peninsula and the Gerlache Strait are doing quite well. By comparison, larger sei, fin, and blue whales – which whaling records show were most often caught in open waters (e.g., Bransfield Strait, Scotia Sea, off South Georgia) – have not recovered at nearly the same rate. It seems as though the removal of ~1 million blue and fin whales from this region instigated an ecosystem regime shift from which there may be no going back, particularly in the face of near-future climate change…

Also, despite extensive reading on the topic of OIF, including the experiments you were a part of, I did not realize that none of them were located in "krill territory". It does seem like a targeted experiment to gauge the food web response to an experimental input of iron is pressing. After the conclusion of this review process, it would be a great pleasure to discuss these ideas and possibilities with you, if interested.

Referee #2 (Remarks to the Author):

As this is a review of a revised manuscript, I'm not going to repeat my general comments from the initial iteration of this work. The authors have addressed my comments satisfactorily. The manuscript's new focus – away from carbon cycling, in response to other reviewers' comments – makes it a much stronger paper, in my opinion.

This re-sets our understanding of the role of baleen whales in the marine ecosystems at a global scale, and in historical context. It is an extremely significant paper, and will be likely to drive scientific impetus to changing the manner in which society views the role of baleen whales in marine ecosystems.

I have a only a couple of comments on the current iteration of the manuscript, regarding two papers that the authors seem to have missed.

Thank you for your kind words and recognition of our work. Furthermore, the two papers you suggest we consider in our revision (below) are ones that provide key pieces of evidence to buttress our story. We also hope that our paper changes the way society views the role of baleen whales in marine ecosystems. Thank you again for your useful input.

First, with the manuscript's revised focus on prey consumption and ecosystem engineering, with a emphasis particularly on the Antarctic system, it's appropriate that the authors cite Willis' 2014 paper in Marine Ecology Progress Series entitled "Whales maintained a high abundance of krill; both are ecosystem engineers in the Southern Ocean" - https://www.int-res.com/abstracts/meps/v513/p51-69/.
This reference is very helpful. We have included it at several points in the revised manuscript (see lines 163-165, 212). The key addition is the notion that baleen whales may have important non-consumptive effects on krill (Peckarsky et al. 2008): whale presence maintains krill surface swarming behavior, which was commonly noted in the early whaling period (Mackintosh 1934, 1973, Marr 1964), but has rarely been observed post-whaling. If indeed the "landscape of fear" (Madin et al. 2011) caused by whales kept vast krill swarms at the surface, this would have the rippling effect of amplifying nutrient recycling of both krill and whales.

Second, do the data from Miller et al's recent paper in Scientific Reports on krill swarms and blue whales (https://www.nature.com/articles/s41598-019-52792-4) inform your analyses, if at all?
This paper lends credence to our suggestion that, if anything, we have underestimated prey consumption by the largest mysticete species (blue and fin whales) in the Southern Ocean. The fact that these authors (Miller et al. 2019) were able to find blue whales in this region is extraordinary because this population is rare, inconspicuous, and extremely hard to access. One of their key results is that Antarctic blue whales were more likely to be found around large krill swarms with high biomass densities of ≳300 g m^{-3}, which is twice the density we measured around Antarctic minke and humpback whales (see Table S2) and used to extrapolate to Antarctic fin and blue whales.
Furthermore, Miller et al. (2019) found that Antarctic blue whales were more likely to be found as krill swarm density increased (sometimes above 1000 g m^{-3}). In the eastern North Pacific, we have also reported a positive correlation between blue whale feeding rate and krill biomass density (Goldbogen et al. 2015, Hazen et al. 2015). As Miller et al. (2019) suggests, the same pattern is likely to hold true for Antarctic blue whales, and if so, we likely underestimated prey consumption in the present manuscript, perhaps driving ecosystem implications of our work even higher.

And a couple of minor issues in Figures.
Figure 2 isn't identified correctly. Bb/Mn are A,C&E.

Thank you for pointing out this oversight, we have corrected the figure caption accordingly.

Extended data figure 2 D – I can't see the lighter shaded parts of these plots.
We have fixed this part of the figure to make the lighter shaded parts of Extended data figure 2D more visible.

Referee #3 (Remarks to the Author):

I thank that authors of this paper for providing a revised manuscript that has significantly improved in its clarity. The authors addressed most of the concerns laid out in my first review of the paper. I find the newest version very readable. I think the addition of a roadmap through the methods was very helpful. I think that the estimation of whale prey consumption rates is sophisticated and there is strong evidence supporting the conclusion that previous models have underestimated prey consumption. One of the most fascinating findings is that animals that prey-switch seem to keep their energy intake constant across prey types. This analysis is the most novel piece of the paper and will be of great interest to a broad readership.

My major issue with the manuscript is with the direct relationships drawn between whale-regenerated nutrients, iron limitation and the impact of whales on primary production across the global oceans. This is the least supported topic of the paper. While top-down control on primary production by whales is an interesting hypothesis, the authors have not made a convincing argument in support of this hypothesis based on their synthesis. The paper greatly oversimplifies the processes that impact primary production, and in doing this the impact of whale nutrient cycling on ecosystem functioning is biased high. The authors also provide too few supporting numbers from the literature, relying at times on one number or one paper to make very significant statements about their results in relation to ocean-wide or decadal-scale primary and secondary production (see my comments on Lines 157 and 197).

My impression is that the conceptual model in the paper assumes an epipelagic zone that is constantly nutrient limited while whales are present, and where the nutrients generated by whale poop are immediately and entirely used up by phytoplankton. That is not the case throughout much of the high primary productivity zones of the global oceans.

First, nutrient limitation is one of many controls on primary production; others being light and temperature. Second, iron is one of a few nutrients that can limit primary production. Iron is important in some places, like the southern ocean, and not important in other places, like the continental shelf and coastal regions of the Atlantic ocean, which are also productive Mysticete habitats. This second issue could be remedied by including other important nutrients in the analysis.

Thirdly, the estimates do not consider important information about the annual cycles of regional whale occurrence and controls on primary production. For example, much of the primary production in the temperate continental shelf regions occurs during the spring bloom, months after the whales feeding in the region departed the previous autumn. If we assume a 6 month feeding season in a temperate zone, a spring bloom in May would need to somehow be influenced by nutrients generated in the surface zone by whales the previous October. During winter, primary production is light limited, and so the whale poop-generated nutrients from the previous fall may not be used up until the following spring. It is unlikely, given that ocean currents can transport and disperse water thousands of kilometers over a six month period, that nutrients generated by whales in areas that produce phytoplankton and zooplankton would remain entirely in those areas for 6 months. Further, vertical mixing by wind in winter mixes nutrients from the deep ocean throughout the water column such that primary production in the spring bloom is not nutrient limited, it is light-limited. This is just one example of a significant amount of primary production in global whale habitats that is not likely to be directly influenced much, if at all, by whale poop generated in the photic zone in those habitats.

However, there are certain locations and times of year (e.g., summer in the temperate zones) when vertical stratification of the water column is known to limit vertical nutrient exchange. This could be a time when regenerated nutrients from poop could make some direct contribution to the primary production in the surface layer.

The authors argue that whales, as a source of fecal nutrient recycling in the photic zone of the ocean, are keystone organisms facilitating ecosystem productivity. They argue this based on the idea that a decline in whale biomass due to whaling may have reduced iron cycling by an estimated 1.1 x 10^4 tonnes of iron per year in the southern ocean. But no context is provided for interpreting the importance of this number. Is this is high number relative to other sources of iron cycling such as wind-driven upwelling and terrestrial sources? Further, there is no evidence in the primary literature the authors provided that primary production has declined in the southern ocean concurrently as whales declined from over-harvest.

Not considering how oceanographic factors would impact whale-regenerated nutrient loss terms (i.e., nutrients that go unused in primary production) would lead to an overestimate of the amount of primary production that could be generated by regenerated nutrients released by whale poop. I think these nuances need to be discussed, or this analysis removed from what is an otherwise very nice synthesis study.

As the manuscript stands, the statement on line 39-41 of the abstract about historical primary production being an order of magnitude higher than present due to a higher whale population is biased high. I also disagree with the statement that this likely reflects a global pattern, based on the reasons I stated above. The statements about broad applicability of the paper's results across the global oceans is overstated. In my opinion, these issues must be addressed before the manuscript is publishable. I believe that these issues could be fairly easily remedied with more contextual information about how primary productivity is limited in whale feeding zones, perhaps consideration of additional loss terms in their models, and some revision of key statements.

Overall, the study went into significant detail to improve estimates of whale prey consumption, and provided a highly convincing and publishable argument based on those estimates. I think those portions of the paper are very strong. In comparison, the oceanographic portion of the study was given very limited attention, and the resulting 'bigger picture" argument about the role of whales in ecosystem functioning was not convincing.

First, thank you for sharing that the clarity of our work has improved and that the refined text and graphics has enabled you to better consider our results and discern the patterns and implications we extracted from the data. We also agree that baleen whales appearing to gain a similar amount mass-specific energy across species, regions, and prey types is remarkable. However, mass-specific energy intake appears to decrease with body size for whales feeding on krill in the North Pacific, and this may reflect the negative allometry of metabolic rate. However, the scaling of metabolic rate in mysticetes is not known. The reason this is not discussed more in the present manuscript is because this study focuses on the ecological ramifications of baleen whale prey consumption, but we do hope that the energetic implications of this finding spur future work in this arena.

As to your remaining concerns, we included more cautionary language that the loss of whale recycled nutrients was *the* driver of the ecosystem shift in the Antarctic, and instead we hypothesize that it played a role. Your comments on light and temperature controlling epipelagic primary production are well taken. There is considerable anecdotal evidence from the early whaling period (pre-1940) that krill were not only more abundant, but were more commonly found in dense surface swarms (Mackintosh 1934, 1973, Marr 1964, Ozawa and Sato 1967). More recent work has suggested that whale presence is responsible for maintaining high krill density near the surface (Willis 2014), thus increasing iron recycling benefits of both krill and whales (see additions on lines 163-165, 212). Taken together, the implications are that whale presence had ecosystem impacts well beyond their direct effects of prey consumption and defecation. Krill being more abundant at the surface (possibly as a result of whale presence) would have enhanced their iron recycling capabilities. In addition, this would have kept whales nearer to the surface, thereby maximizing their nutrient recycling potential as well.

Given the short-term nature of our tag deployments, we cannot say for sure how this increase in whale-recycled nutrients and biomixing affects productivity across seasons and years. However, given the timing of whale presence and foraging in temperate and polar regions, and the known phenology of phytoplankton blooms, it is most likely to extend blooms in space and time in the autumn, rather than impacting the initiation of the spring bloom the following year. However, it was our mistake to not discuss the role and function of the iron recycled by whales in the later parts of the paper. We have now rectified this (see lines 179-187). We now also a Southern Ocean-specific paper in our revision with measurements of a reduction in primary productivity following the cessation of whaling (Lee et al. 2010).

Finally, when we said this "reflects a broader global pattern," we didn't mean to imply that these processes were happening uniformly across the ocean, but rather were likely happening in many other similar systems (coastal and neritic systems in temperate latitudes and higher) around the world that were rapidly defaunated in the 19th and 20th centuries. We have made this point clearer in the revised manuscript, see specific comments below for examples of where an how we have done so.

Line-by-Line comments:

Line 39: Not more productive 'oceans' since the calculations in the paper are for only one ocean, the southern ocean.
This sentence now says: "Acting as ecosystem engineers (Roman and McCarthy 2010, Roman et al. 2014, 2016), these larger whale populations may have sustained higher productivity in large marine regions through enhanced recycling of limiting nutrients."

Line 61: from whales carcasses, not from whaling Good point, change made.

Line 66: Not only smaller but also physiologically and evolutionarily distinct and occupying different foraging niches. To my knowledge there are no smaller filter-feeding marine mammals. I don't expect metabolism to be the same a priori beyond just changes in body size.
You are correct that the filter-feeding mechanism and physiology is unique to mysticetes among marine mammals. You are also correct that baleen whales are physiologically and evolutionarily distinct from any organism whose metabolic rates have been empirically measured. The overall point being that our best guesses for mysticetes' metabolic parameters could be further refined with future research and technological development for a variety of reasons. To reflect our agreement on this point we have now added the clause ", with disparate physiology and evolutionary histories" at the end of the sentence you reference.

Line 69: quantity not quality (quality would be nutritional content per unit biomass) Changed "quality" to "density".

74: facilitating, not maximizing We have made this change.

Line 82: This is speculation, and either needs to be removed from the introduction, or the authors need to provide a lot more evidence to support drawing this relationship. The Boyce et al reference analyzes chlorophyll data from across the entire globe (not only whale feeding habitats) and so the decline in primary productivity they measure cannot be attributed to whale feeding. If the pattern they measure is real (and there is

considerable debate about this in the literature), relating it to a top-down control mechanism would be a tall order. In that paper they draw statistical conclusions about physical forcing of the variation in primary production (light and temperature).
This point is well taken. We have removed the following sentence from the manuscript entirely.

> "While mysticetes also compete with other krill predators, and possibly forage (krill or fish) fisheries (Gerber et al. 2009, Morissette et al. 2012, Ruzicka et al. 2013), the sequential timing of mysticete defaunation followed by reductions in primary and secondary productivity(Atkinson et al. 2004, Boyce et al. 2010) suggests that industrial whaling had unforeseen ecosystem-wide effects."

Furthermore, we remove any references to the Boyce et al. (2010) paper given that its findings remain controversial. We replace it with a paper that is focused on Southern Ocean productivity and CO_2 uptake specifically (Wang and Moore 2012).

Line 83: Mysticetes are not universally recovering (e.g., Northwest Atlantic blue whale). I wonder where this statement came from. It would be helpful to explain how Mysticete populations are changing globally.
This was an overgeneralization on our part. North Atlantic and North Pacific right whales are also not recovering. However, we don't want to sacrifice the flow of this part of the paper by going into the asymmetry of mysticete recoveries here. We do that at the end of the main text. To address your concern, we replaced the word "globally" with the phrase "changes over time".

Lines 134-135: I think that, for me, this is the main take-home message from the paper. This is incredible. Going the next step to linking this result to altering ecosystem function needs more attention.
We have, to the extent practicable, improved our discussion of ecosystem effects by placing our prey consumption and iron recycling results in better context (see lines 179- 187).

It is impossible with the data we have, however impressive, to say anything definitive about historic (pre-1900) oceans beyond that they must have functioned very differently with considerably more biomass concentrated in the 'food-chain-of-the-giants' (Smetacek 2008) than at present. This is supported by both modeling studies (Wiedenmann et al. 2011, Surma et al. 2014, Willis 2014, Tulloch et al. 2018) and anecdotal observations from the early whaling period (Hart 1934, Marr 1964, Mackintosh 1973). The advance we have provided is field data to support these reports based on our estimated prey/energetic requirements of rorqual whales extrapolated to pre-whaling populations.

Re-creating how the Southern Ocean appeared and functioned >100 years ago is akin to looking through foggy glasses: only simple outlines and basic patterns are visible, but every new piece of information we learn about the biology and ecology of the food- chain-of-the-giants makes the picture a bit clearer.

Line 152: I don't quite understand this result. Predicted by whom? Are you discussing your prediction, or how your prediction compares to predictions made in past studies? We are referring to the original prediction from (Laws 1977). We make that clear now (see line 145).

Line 152-157: Please include the uncertainties around each of these estimates. Thank you for picking this up. We now include a median and interquartile range (25th- 75th percentile) around these estimates.

Line 157: Reference number 4 states in the abstract that 379 Mt yr is the average over the period of 1926 - 2004, so I conclude that it does not represent the contemporary state of the krill biomass in the southern ocean relative to the 20th century. Please address this apparent discrepancy. This is critical since this one number is central to the entire argument that whale removal reduced ecosystem productivity.
Thank you for bringing this point to our attention. To ensure the best possible answer – and information for the paper itself – we contacted Dr. Angus Atkinson, the authority on this topic, to weigh in. He confirms that the often-cited 379 Mt yr^{-1} is the average over the period of 1926 – 2004 (Atkinson et al. 2009), and that the best guess number of total Antarctic krill biomass in 2000 is 215 Mt yr^{-1}. He described to us how to make this calculation and we added a new paragraph to the Methods (see section A.10) to describe how we came to this number, which we provide here for your review.

> "To estimate the total circumpolar biomass of *E. superba* in 2000 to compare to mysticete prey requirements, we used the same methods in (Atkinson et al.
> 2009), but with an updated estimate of 60.3Mt of *E. superba* in the CCAMLR synoptic survey area (Hill et al. 2016). This region contains ~28% of the total biomass of *E. superba*. Dividing the 60.3Mt from this region by 0.28 reveals an estimate of 215.36 Mt as the total circumpolar biomass of *E. superba* in 2000. The total biomass of *E. superba* in 1900 is believed to be greater than that, but how much greater is unknown. The largest decline of *E. superba* in the 20th century was observed in the Southwest Atlantic Sector (the region containing the APP) (Atkinson et al. 2004, 2008)."

While it is unknown if, and by how much, Antarctic krill populations have declined over the past 150 years, this reduction in our initial best guess for krill available for consumption by whales (revised down from 379 to 215 Mt yr^{-1}) further implies that krill populations needed to have been much larger in the past then at present, simply because of the prey demand of the great whales alone.

Line 197: Since the time series in Reference 18 only goes back to 1976 (post whaling) its not possible to conclude that whaling caused of the declining trend. There have been many changes to the southern ocean ecosystem during this period that could have caused the decline.
This is true. We cannot say for certain that the removal baleen whales was *the* mechanistic driver of the decline in krill that has been noted since the 1970s, but our

data do support the notion – as has been previously suggested other author researchers (Smetacek 2008, Roman and McCarthy 2010, Nicol et al. 2010, Roman et al. 2016) – that the loss of whale recycled nutrients, iron in this case, was *a* driver.

Line 197: Reference 18 does not include any time series analysis of primary production, so I cannot see how the authors drew the conclusion that it was modest over this period.
Reference 18 (Atkinson et al. 2004) was meant to refer to the decline in krill; we have moved this reference after that part in the sentence to be clearer. The argument regarding primary productivity in the APP in the latter half of the 20^{th} century is supported by (Falkowski et al. 1998), which we have now referenced at the end of the sentence.

Line 375: Is diet composition on a 0-1 scale for a single species? E.g. 0.5 = 50% krill and 50% forage fish?
Yes, that is correct. We now add the clause "a proportion ranging from 0 to 1" to the sentence to make that point clear.

Line 393: Figs S1 and S2 are uncited in the text of the main paper text or supplement. The (I assume) error bars are not defined in the figures. How were these statistics generated? Please ensure that all figures and tables are cited somewhere in the paper or supplement and a full description of the information in each figure is written in the caption.
Thank you for bringing this to our attention. We have now cited these figures both in the Main Text (lines 67 and 99) and the Supplement (lines 390 and 415). Further, we have scrutinized the full manuscript and can confirm that all figures are cited somewhere in the text.

Line 405: what calculations? Do you mean the data presented in Figs S1 and S2? Yes, exactly. We now reference those figures in this sentence.

Line 405-406: what is your justification that the metabolic rates are extremely low? Is it because they are basal estimates based on body size alone (assume no activity)? One or two explanatory sentences here would be helpful.
More specifically, what we meant by this was: due to their immense size, baleen whales are predicted to have low mass-specific metabolic rates as compared other eutherians. Our findings suggest that mysticetes, and rorquals in particular, mass-specific metabolic rates are closer to 1 than has been previously assumed (see β values in Table S1). We have not updated this section of the text to say:

> "These prey consumption estimates (Figs. S1 and S2) are based on predicted mass-specific metabolic rates for mysticetes, which are low compared to other eutherians. However, numerous aspects of mysticete life history and ecology correlate with elevated metabolic rates including their aquatic lifestyle (Schmitz and Lavigne 1984), rapid pace of reproduction (Nagy et al. 1999), muscular physiology (Rivero 2018), and energetically demanding feeding strategies (Goldbogen et al. 2017)."

Line 385: minor point; mid- to high latitudes. Include the temperate regions in your description of feeding range.
This is a good point; the sentence now reads "…mid- to high latitudes…"

Line 742: missing reference
We have removed this section, and any discussion of the PPR calculations, from the revised manuscript.

Line 746: There is no information provided in this section about the stoichiometry of fertilizing nutrients to primary production.
Thank you for noticing this. This was an erroneous holdover from the previous version of the paper that did so. We have removed the phrase "…and stoichiometry of fertilizing nutrients to primary production," from the updated manuscript.

Referee #4 (Remarks to the Author):

I don't disagree with other reviewers calls to remove estimates of carbon sequestration by whales from the previous draft - my colleagues make a compelling case for the many challenges and uncertainties in generating these carbon estimates. I look forward, however, to the authors advancing that dialogue about the historic vs contemporary role of whales as agents of carbon in an alternate forum, for I do think beginning to identify and consequently fill gaps in these whale carbon sequestration estimates is a scientifically important and deserving exercise. With these estimates removed, the principal contribution of the paper becomes creating first empirical estimates of consumption rates for whales – using a combination of extensive tagging data, drone measurements of tagged whales, and mapping of prey biomass. These field measurements are very useful and interesting. They help here – and will similarly help in future research attempting to assess the trophic dynamics of whales and their influence on ecosystems. I'm not certain, however, that this contribution by itself merits publication Nature.

The authors efforts to use these new directly measured prey consumption rates to create estimates of the influence of whales on biogeochemistry in the Southern Ocean are interesting and certainly the next logical extension for application of these empirical consumption rates. But the base suggestion that numerically larger pre-whaling whale populations had an elevated impact on ocean ecosystem ecology and biogeochemistry is not in of itself new – and stems back at least as far a literature from the early 2000s (all adequately cited by these authors; e.g. Whales, Whaling, and Ocean Ecosystems 2007 UC Press). I am also left with some minor misgivings about missed opportunities to discuss any possible role of applying field data collected in one ocean to nutrient recycling rates in another ocean and opportunities to, even very briefly, consider possible alternate hypothesis associated with what has been written about relationships between climate change and the krill paradox.

Taken in isolation, we agree with the argument that baleen whales eat more than we thought is not novel–hence why our revised title does not follow one of the suggested structures simply making that point. Instead, our findings are firmly placed in two contexts: a) ecosystem function, and b) marine defaunation, which is necessarily a historical context. Put bluntly, it's not just that whales eat more than we thought, but that they eat *far* more than we thought, which also means more mixing (through fluking and filtering) and more nutrient recycling (via defecation) than we thought. By extension, past oceans that supported many more whales must have had a different function than the defaunated one that we see, across the world, today. We have addressed your remaining concerns – considering other nutrients in other oceans (see lines 185-187), and the relationship between climate change and the krill paradox (see lines 198-201) – in the revised manuscript.

Like you, we feel as though this study will be important to start the conversation about redefining the role of baleen whales in past, present, and future ecosystems. Including, eventually, using these new measurements to more accurately evaluate their role in the global carbon cycle. However, as the reviewers and editor have suggested, this manuscript is not the place for that. Considering that this is the first comprehensive dataset of baleen whale prey consumption using high-resolution field data, the surprising results we found, and the implications of our findings on marine ecosystems warrant publication of this manuscript.

Referee #5 (Remarks to the Author):

Review of "High-resolution foraging measurements reveal baleen whales as global ecosystem engineers"

Authors have revised their original submission to this journal focusing on their estimates of feeding rates and implications on ecosystem dynamics. As suggested by the editor and some of the reviewers (incl. mind), they removed all of the wildly speculative ascertains connecting the reestablishment of whale populations and atmospheric CO2 levels. This makes this a more palatable paper and one that is possibly publishable in Nature. I am generally favorable with this resubmission. From my admittedly limited point of view, the ingestion rates synthesis appear to be an excellent contribution to the literature.

However, the authors have fallen short of convincing me that baleen whales really are "global ecosystem engineers" as stated in the title. In the abstract, the authors state "By extension, larger whale populations prior to 20th-century the whaling supported more productive oceans, with prey and primary production an order of magnitude higher than present.". Their conclusion hinges on what seems to me to be a few rather weak pieces of evidence. The strongest piece of evidence (Lines 142-160) is this paper's primary ecological result that krill abundances must have been much larger than they are today to support the historic whale populations. That appears to me to be the interesting and important finding of this work.

The problem is with the "why" there are more krill in the Southern Ocean pre-whaling. The suggestion that the NPP is higher is not entirely convincing to me based upon the flawed Boyce et al. result (see below) and the rather crude Primary Production Required (PPR) estimate (see below). Further, the biomixing leading to more nutrient recycling argument also doesn't make sense to me. It is at best a local mechanism and cannot scale to ocean basin scales as is suggested here (see my earlier review). The new production hypothesis taught in every 1st year grad Bio Oce class suggests that more recycling would lead to lower NPP and smaller phytoplankton and a longer trophic distance between phytoplankton and whales.

To be acceptable, the authors need to focus harder on their results and the implications of these results and limit the wilder speculation. I suppose to be acceptable by Nature there needs to be important global implications so its relatable to material scientists and protein folders. But pushing the story too far is not acceptable as the adverse damage it creates is real. There is a lot of interest now in both national science agencies and NGOs in global benefits of the restoring ecosystems to the conditions that preceded the anthrocene. This work has an important part to play in that dialogue but needs to stick to its story.

Thank you for your careful reading of our revised manuscript. Our revisions should address your remaining issues. First, we have removed the word "global" from the title. Second, we have removed the wording implying a mechanistic relationship between whale removal and a decline in primary production. Further, we have removed the troubling Boyce et al. (2010) reference from the paper altogether. Finally, we have removed the primary production required (PPR) calculations from this revision because it is not essential to the paper and the coarseness of the calculation may do more harm than good.

We did not mean to suggest that whale filtering (considered 'biomixing' in the manuscript) was an important process in a globally homogenous way, like winds and tides are. These effects from whales would be spatiotemporally limited to locations with aggregations of feeding whales, as was typical during the summer and fall months in neritic waters at temperate and high latitudes before whaling. Reviewer #1 summarizes why we think this mixing is worth considering:

> "…an important function of whale filtering and stirring is breaking up and mixing friable krill faecal strings and copepod pellets in the water column. The effect would be akin to ploughing in a terrestrial field: crumbling the earth. Whale feeding and fertilizing prolonged the bloom and stirring broke up and mixed krill and copepod faeces but also diatom aggregates in the surface layer preventing their sinking out."

As with other arguments brought up in the paper (e.g., equivalent energetic gain among whales across species, regions and prey types), our analysis and discussion of biomixing via filtration was intended to provide a lower bound estimate for what is possible. Others have considering biogenic mixing from cetacean fluking (Lavery et al. 2012), but filtration has yet to be considered in this process.

My detailed comments follow…

Lines 38-29 – Statement should be downplayed.
We have now edited this sentence to read: Acting as ecosystem engineers (Roman and McCarthy 2010, Roman et al. 2014, 2016), these larger whale populations may have sustained higher productivity in large marine regions through enhanced recycling of limiting nutrients.

Lines 40-41 – Iron recycling – It is not clear to me why that is relevant on its own. I suppose the authors could assume a phytoplankton C/Fe ratio for Fe depleted conditions and figure out what that mean in enhanced NPP in the Southern Ocean. Further following my previous review's statement that biomixing is a local mechanism and cannot scale to ocean basin scales not sure how this has "broad implications".
Actually virtually nothing is stated in the main text about whale recycling of iron besides this statement in the abstract. Probably should be removed.
We feel as though the iron recycling information is a major component of this paper. As such, we thank you for catching our omission of discussing our iron recycling results in more detail towards the end of the main text of this revision. This was an oversight on our part. While transitioning the text between our initial submission and our first revision, we accidentally omitted this portion. We have now incorporated this in the "Mysticetes as ecosystem engineers section," saying:

> "In the iron-limited Southern Ocean, pre-whaling populations of Antarctic minke, humpback, fin, and blue whales recycled 1.2×10^4 tonnes iron yr-1 (IQR: 0.65- 1.5×10^4 tonnes yr-1) (Fig. 4C). Considering the extremely low concentration of bioavailable iron in the Southern Ocean epipelagic (~0.03nmol L^{-1} in the top 200m(Bowie et al. 2009), approximately 6.3×10^4 tonnes total(Nicol et al. 2010)), pre-whaling populations of whales may have augmented the labile iron pool in these waters by 10-24%. Other regions that are limited by macronutrients, such as nitrogen or phosphorous (Roman and McCarthy 2010, Doughty et al. 2016, Roman et al. 2016), likely saw similar reductions in ecosystem services following the rapid removal of baleen whales (Roman and Palumbi 2003)."

Lines 81-82 – Boyce paper. There are many concerns in the biological oceanography community about the veracity of the Boyce paper's results. Many of their results have merit, but their ascertain of a 1% per year decrease in median ocean phytoplankton biomass over the last century is simply unrealistic and it should not have been allowed to be published. It implies that the global median phytoplankton pigment biomass levels were ~2.7 times greater than they are today. It is inconceivable that the blue oceans of today (the median) were moderately eutrophic 100 years ago. Clearly, there must be issues in their extrapolation of the historical, sparse, poor quality Secchi disk observations to the present satellite record using statistical models in the Boyce paper.

BUT it does point out how difficult it is to correct obviously incorrect results once they are published.
Multiple reviewers have brought up concerns with this paper. We thank you, and the other reviewers, for bringing these concerns to our attention. As a result, we have removed this manuscript altogether, and have replaced it with regional assessments (Lee et al. 2010, Wang and Moore 2012).

Lines 139-140 – Again I must restate that the biomixing argument is irrelevant. It is obviously unimportant on a global scale as stated in my last review. The statement here is accurate – but is misleading as it implies that there is a significant role for mysticetes in ocean ecosystems, which may actually be true on global scales.
See our comments above regarding biomixing. But to avoid any confusion or misinterpretation, we have removed this sentence from the revised manuscript.

Line 165-166 – Not sure how they are concluding that "current ecosystem models may underestimate the quantity of prey and primary productivity required to support current and historic populations of baleen whales"
We have concluded this because of the main finding of our paper – that baleen whales eat more (in some cases, much more) than we thought. Before this work, prey consumption were largely based on metabolic models and static measures of gut contents that, as we describe both in the introduction (lines 55-67) and in a detailed supplemental section (Prior estimation of prey consumption section), have chronically underestimated actual prey consumption. Once these prey consumption estimates are updated in ecosystem models the quantity of resources that whales requires will also increase. One study in particular that makes this very clear is Ratnarajah et al. (2016). In this modeling study, the authors use 4130 kg d^{-1} of krill consumed as a *maximum* consumption estimate for an Antarctic blue whale, while our *median* estimate was 4193 kg d^{-1}. In addition, our tags confirm that whales we have tagged typically forage at depth (>>20m) but spend the majority of their total time budget at, or near, the surface (<20m). Thus they are also likely to defecate most commonly at, or near, the surface, thereby increasing the persistence of whale feces in the photic zone, which is another key assumption of their model they have likely underestimated due to a lack of data.

Line 170 – see comment above See response to previous point.

Lines 174-178 – Two things. First, I am not sure why whale falls are mentioned here. They do supply organic matter to the seafloor and support benthic communities but do export organic matter from the surface ocean exasperating the NPP issue. I likely does not matter much anyways as I suspect it is a tiny number compared with other export pathways. Second, not sure that recycling makes sense for increasing NPP as commented previously.
The whale falls were not mentioned from a carbon export standpoint; this exact calculation has already been done (Pershing et al. 2010), they were mentioned as one of the ways in which whales serve as ecosystem engineers, which is the topic of this

section. This follows from the definition of an ecosystem engineer from (Jones et al. 1994), which states:

> "Ecosystem engineers are organisms that directly or indirectly modulate the availability of resources to other species, by causing physical state changes in biotic or abiotic materials."

A whale fall follows this definition precisely as it provides a temporary ecosystem unto itself.

Lines 189 – 190 – The terrestrial sink of organic matter via birds and seals is probably not a real big term on global scales – but could easily be important on local scales.
We agree that in terms of overall global primary production and nutrient cycling, the amount of nutrients that seabirds and pinnipeds transfer from sea to land is probably not important. However, this process is known to play an important role in the ecology and biogeochemistry regionally (Ellis et al. 2006, McCauley et al. 2012, Shatova et al. 2016).

Lines 197-199 – I am not buying this. Sorry. I do not see how your finding support these statements.
In addition to adding discussion on iron recycling, we have also toned down this sentence such that it now says:
"Our findings implicate the removal of large whales from the APP as a mechanism underlying the regime shift from a high-productivity krill-dominated system to a lower- productivity salp-based system (Atkinson et al. 2004, Smetacek 2008). "

Lines 227-230 – Again this is way too speculative and should be cut. Arguments are made throughout that whales lived in a time where NPP may have been higher which could lead to higher carbon export and sequestration. BUT arguments are also made that whales recycle nutrients in the euphotic zone which would reduce the fraction of NPP that is exported. You cannot make both arguments.
We have modified this statement such that it no longer references carbon sequestration or export. It now reads:
"For example, restoring the so-called 'food chain of the giants' (phytoplankton-krill- whales) (Smetacek 2008) would affect ecosystem structure and function in the Southern Ocean."

Lines 561-562 – I have issue with the logic with the statement "Finally, in our calculations we assumed maximal engulfment and 100% capture of krill as previously published recognizing this may be overestimate." The authors should be developing their best conservative estimates of the ecosystem impacts of baleen whales, not an overestimate. In the previous section (Lines 555-557), they chose the more conservative of two methods. So, first consistency is needed throughout. But by choosing the overestimate, it raises doubts in the readers' mind whether the authors find that whales are impactful because they really are or because the authors used overestimates in their analyses.
We appreciate that this sounds inconsistent. We mean to communicate that we have not observed krill escapement in the hundreds of hours of video and tens of thousands of lunges we have observed. Picking a value below this at random based on escape

behavior we have yet to observe would be arbitrary, and arguably a worse approach. In fact, it is possible that the pressure differential of a rapidly expanding mouth (a blue whale's mouth area expands to $8m^2$ in 2-5 seconds) could actually draw krill in from outside the 'engulfment zone', which would result in a capture of greater than 100%. To address this, we have updated this to say:

> "Finally, in our calculations we assumed maximal engulfment and 100% capture of krill, as has been previously published (Goldbogen et al. 2019, Cade et al. 2020). We recognize this may be an overestimate, but we have no evidence to suggest a lower capture rate. This is based on extensive tag-video observations – where we have not observed krill escape behavior – as well as at least a fivefold difference between a lunging whale (Goldbogen et al. 2011, Cade et al. 2016) and maximum krill escape speeds (Hamner 1984). Suction created by mouth opening in rorqual whales could also maximize capture rate (Potvin et al. 2009), and rorqual rolling behaviors could increase the quantity of prey engulfed within a given volume (Potvin et al. 2010, Goldbogen et al. 2013)."

Lines 732-342 – The PPR estimates are central to statements that mysticetes have significant roles in ocean ecosystems. I wish there were a better description why the mathematical formulation given in equation 9 actually quantifies PPR. I am not following how this works. Also units are missing for P_c and C_p. Most importantly, I wish this section detailed how the PPR quoted in Lines 163 and 164 were actually calculated.

This should be shored up if used.

We have decided to remove the PPR calculations from the revised manuscript. We have done so for two reasons. First, the PPR calculation is indeed crude, and using it may raise concerns about its calculation, which has been discussed elsewhere (Pauly and Christensen 1995, Young and Phillips 2002, Barlow et al. 2008) and is outside the scope of this manuscript. Second, to address other important concerns regarding other nutrients recycled by whales and to put our iron recycled values in better context needed several sentences to do so (see lines 179-187). As we are approaching the word limit for this paper, we felt as though the PPR calculation and implications will be better discussed in a separate follow-up paper.

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Reviewer Reports on the Second Revision:

Referee #1 (Remarks to the Author):

Review of third round

Baleen whale prey consumption enables vast ecosystem engineering potential
I am happy with this manuscript and recommend it for publication but request the authors to clarify an important point regarding the amount of iron potentially recycled by the whales. First, what is the area considered in mill km2? It couldn't be the entire SO? Since the whole issue of ecosystem engineering by animals is that the effect is regionally and seasonally concentrated, so the dimensions in space and time need to be defined. I would suggest taking the krill distribution map of Marr but see also Atkinson et al 2004 as the historical, close to pre-whaling area. If you average your projections for the pre-whaling krill stock onto that area per metre square and compare the krill contribution to the iron pool in comparison with an average diatom bloom of 10 – 20 g C m-2 you will get a better impression of the size of the krill iron reservoir. You could take C:Fe ratios for diatoms from the literature as in the case of krill. This way you could also show how the recycled iron was estimated on a regional basis.
The comparison from Nicol et al 2010 with dissolved iron in seawater (Line 181 -184) is faulty because iron at those low concentrations is inaccessible, so virtually non-existent locally. If you multiply a very low number with a huge volume you of course get a significant amount. Which is why you have to

specify the area and volume chosen. I would jettison the entire sentence, the comparison with a diatom bloom is much more convincing.
I still have some questions and comments below are not critical.
Title: I like the juxtaposition in the title but would suggest replacing “vast” with “effective” because it’s not the area but the intensity that is important here.
Line 121/122: I would shift “each” forward for emphasis: in this ecosystem each require >2 Mill t krill. But this is a matter of taste, so you could as well leave it. Normally, each at the end is a highlight, but the figure before casts a shadow over it. I had to read the sentence twice before I got it.
Line 172: check “based”
Line 180 tonnes Fe yr-1 or iron
Line 201 Half the Scotia Sea (part of the APP) is ice-covered annually.
Line 221 and 222 text missing
Line 241: Replace Allowing with Encouraging.
Line 243: replace oceanic with “regional” as not the entire ocean will be affected.

Referee #3 (Remarks to the Author):

With the additions of the roadmap through the methods and a more nuanced discussion about the impact of whale foraging on primary production, as well as their many additional edits, the authors have fully addressed the concerns I laid out in my previous two reviews and I have no further comments. The manuscript is acceptable. Good job!

Kind regards,

Dr. Kimberley Davies

Referee #5 (Remarks to the Author):

Savoca and colleagues provide a further refined version of their paper on baleen whale feeding and its impacts on ocean processes. This draft is far improved from the initial submissions. However, there are still passages that are too speculative in its conclusions. In particular, I find the discussion about iron recycling by whales in the Southern Ocean that would support more krill biomass does not have the evidence needed to support the conclusions. That section (lines 170 to 190) should be much more quantitative so that the links between whale recycling of krill Fe to increased phytoplankton NPP makes sense. The amount of krill iron recycled by whale feeding is calculated in section A.10 and hence you know the additional flux of recycled iron that would be there pre-hunting from today (not 100% will be recycled). Dividing that number by known iron to carbon ratios in phytoplankton would give you the missing of phytoplankton NPP and some fraction of that (10% or ??) would be krill production. Then one can test whether the amount of krill production would support the missing whale population or not. The arguments made are not quantified to see if they are reasonable. Now it is only speculative. I think the draft needs some improvement on these issues or this speculation needs to be removed. As such, this draft is not acceptable at this time. This should not be too hard, most of the hard work is done.

My specific comments follow. They mostly follow concerns described above.

The revised title is horrible - “…enables vast ecosystem engineering potential”? What does that mean? It either is or it isn’t.

35-40 – The speculation about ecosystem function lost and whale ecosystem services needs quantification as described above.

154 – likely is too strong of a word.

167-169 – Not buying this without some quantification. Otherwise, it's too speculative.

196-198 – I do not think sea to land nutrient transport is important for the oceans. For land it is for sure. Need a reference there.

199-200 – Not sure where this is going.

223-227 – Again this statement needs some back up from the data presented.

Author Rebuttals to Second Revision:

Referees' comments:

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The comparison from Nicol et al 2010 with dissolved iron in seawater (Line 181 -184) is faulty because iron at those low concentrations is inaccessible, so virtually non-existent locally. If you multiply a very low number with a huge volume you of course get a significant amount. Which is why you have to specify the area and volume chosen. I would jettison the entire sentence, the comparison with a diatom bloom is much more convincing.
Your points are well taken. Thank you for indicating where our contextualization of iron recycling was misguided. In this revision, we have chosen to present the amount of iron recycled by whales in the Southern Ocean, and specifically mention how the majority of this recycling occurred in the Southwest Atlantic sector. We have edited the text to ensure that we do not erroneously calculate or misrepresent our findings in the context of bioavailable iron in the system. Once this paper is published, we are very interested in discussing these ideas with you further to give them the attention and context they deserve in a follow-up paper.

I still have some questions and comments below are not critical.

Title: I like the juxtaposition in the title but would suggest replacing "vast" with "effective" because it's not the area but the intensity that is important here.
While we are generally in agreement with your assessment of the previous draft's title, we have changed the title based on feedback from Reviewer #5 and the editor. As such, we have landed on: "High prey intake reveals ecosystem role of whales before and after whaling" for a title.
However, we would be happy to consider modifications to this updated title.

Line 121/122: I would shift “each” forward for emphasis: in this ecosystem each require >2 Mill t krill. But this is a matter of taste, so you could as well leave it. Normally, each at the end is a highlight, but the figure before casts a shadow over it. I had to read the sentence twice before I got it.
Good point, we have made this change.

Line 172: check “based”
Thank you for pointing out this typo; however, we have now removed the “Mysticetes as ecosystem engineers” section

Line 180 tonnes Fe yr-1 or iron
Thank you for catching this. We have corrected this omission.

Line 201 Half the Scotia Sea (part of the APP) is ice-covered annually.
Thank you for this clarification, though we have removed this section from the revised text.

Line 221 and 222 text missing
Thank you for bringing this to our attention. This issue should be remedied in the revised draft.

Line 241: Replace Allowing with Encouraging. We have made this change.

Line 243: replace oceanic with “regional” as not the entire ocean will be affected. We have made this change.

Referee #3 (Remarks to the Author):

With the additions of the roadmap through the methods and a more nuanced discussion about the impact of whale foraging on primary production, as well as their many additional edits, the authors have fully addressed the concerns I laid out in my previous two reviews and I have no further comments. The manuscript is acceptable. Good job!

Kind regards,

Dr. Kimberley Davies

Thank you, on behalf of all the co-authors, for providing multiple rounds of thoughtful and helpful review. In particular, your suggestions prompted us to provide the roadmap of the methods and the summary tables of the outputs. The inclusion of these items, at your suggestion, have made the paper more easily interpretable and, we hope, useable for future researchers who want to build on our work. We are very appreciative of your efforts making this a better paper.

Referee #5 (Remarks to the Author):

Savoca and colleagues provide a further refined version of their paper on baleen whale feeding and its impacts on ocean processes. This draft is far improved from the initial submissions.
However, there are still passages that are too speculative in its conclusions. In particular, I find the discussion about iron recycling by whales in the Southern Ocean that would support more

krill biomass does not have the evidence needed to support the conclusions. That section (lines 170 to 190) should be much more quantitative so that the links between whale recycling of krill Fe to increased phytoplankton NPP makes sense. The amount of krill iron recycled by whale feeding is calculated in section A.10 and hence you know the additional flux of recycled iron that would be there pre-hunting from today (not 100% will be recycled). Dividing that number by known iron to carbon ratios in phytoplankton would give you the missing of phytoplankton NPP and some fraction of that (10% or ??) would be krill production. Then one can test whether the amount of krill production would support the missing whale population or not. The arguments made are not quantified to see if they are reasonable. Now it is only speculative. I think the draft needs some improvement on these issues or this speculation needs to be removed. As such, this draft is not acceptable at this time. This should not be too hard, most of the hard work is done.
Thank you for again giving a critical read of our manuscript. Given the word constraints and the primary data we have on whale prey consumption (and the data we don't have on the conversion of recycled iron into phytoplankton biomass), we have cut the "Mysticetes as ecosystem engineers" from this draft per your and the editor's suggestion. We agree that this information would be best suited for follow-up work, where we could expand on these ideas to give them the proper attention, context, and quantification they deserve.

My specific comments follow. They mostly follow concerns described above.

The revised title is horrible - "…enables vast ecosystem engineering potential"? What does that mean? It either is or it isn't.
The key aspect we are trying to convey is that the ecosystem role of baleen whales, which is already assumed to be considerable (Roman et al., 2014), has been underestimated due to widespread underestimates of their prey consumption. In response to your feedback and the editor's suggestion, we have now changed the title to: High prey intake reveals ecosystem role of whales before and after whaling.

We are still willing to consider a concise and informative title that is representative of our findings if you or the editor have further suggestions.

35-40 – The speculation about ecosystem function lost and whale ecosystem services needs quantification as described above.
The ecosystem service we quantify is the amount of limiting nutrients recycled by whales to primary producers. In this paper, we calculate the amount of iron whales recycled in the Southern Ocean, which has not been estimated accurately before since it was unknown how much whales were ingesting. We have further honed this section of the abstract to clarify that this is the primary ecosystem service we are referring to.

154 – likely is too strong of a word.
Changed from "was likely" to "may have been".

167-169 – Not buying this without some quantification. Otherwise, it's too speculative. We have removed this sentence from the revised manuscript.

196-198 – I do not think sea to land nutrient transport is important for the oceans. For land it is for sure. Need a reference there.
Fair point. We have now removed the “Mysticetes as ecosystem engineers” section entirely.

199-200 – Not sure where this is going.
This was to address the role of climate change in the changing productivity of the Southwest Atlantic sector of the Southern Ocean; however, we have now removed the “Mysticetes as ecosystem engineers” section entirely.

223-227 – Again this statement needs some back up from the data presented. We have removed this statement from the updated draft.

Reviewer Reports on the Third Revision:

Referee #1 (Remarks to the Author):

The current title: "High prey intake reveals ecosystem role of whales before and after whaling" is confusing for the first-time reader. I suggest:

High-resolution measurements reveal much higher baleen whale prey consumption than currently assumed

References need rechecking: Ref 1 does not appear before 2-4 in line 26. Refs 3 and 7 are the same. I didn’t check further, meaning more mistakes likely.

Referee #5 (Remarks to the Author):

Authors have provided another version of their paper. It is getting closer to being publishable in Nature. They still do not provide any context for their conclusion that recovered whale populations will drive higher primary productivity rates. They quote a missing pre-whaling iron recycling estimate of 1.2e4 ton iron /yr recycled in the Southern Ocean and then state that that proves their conclusion. This Fe recycling rate aggregated over the entire southern ocean is meaningless to most oceanographers and I am sure any general reader of the journal.

The authors MUST turn that missing pre-whaling iron recycling estimate into something meaningful. I think it is easy to estimate the missing recycled phytoplankton primary production rate. The recycled iron rate quoted Neds to be converted into an areal rate (drive by area) and then converted into a phytoplankton C recycled uptake rate by dividing by Fe/C ratios taken from the literature. This rate should then be compared with NPP rates (in molC/m2/y) from the present. If it is 10% or more this will be important finding and you have a Nature paper. If that value is less than 1% of present mean NPP values, this whole discussion about reestablished whales driving ocean productivity needs to be cut out. Then the decision of the novelty of the result is in question.

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References need rechecking: Ref 1 does not appear before 2-4 in line 26. Refs 3 and 7 are the same. I didn't check further, meaning more mistakes likely.

Thank you for this fine reading of our paper and References. We have double-checked and revised them for accuracy.

Referee #5 (Remarks to the Author):

Authors have provided another version of their paper. It is getting closer to being publishable in Nature. They still do not provide any context for their conclusion that recovered whale populations will drive higher primary productivity rates. They quote a missing pre-whaling iron recycling estimate of 1.2e4 ton iron /yr recycled in the Southern Ocean and then state that that proves their conclusion. This Fe recycling rate aggregated over the entire southern ocean is meaningless to most oceanographers and I am sure any general reader of the journal.

The authors MUST turn that missing pre-whaling iron recycling estimate into something meaningful. I think it is easy to estimate the missing recycled phytoplankton primary production rate. The recycled iron rate quoted Neds to be converted into an areal rate (drive by area) and then converted into a phytoplankton C recycled uptake rate by dividing by Fe/C ratios taken from the literature. This rate should then be compared with NPP rates (in molC/m2/y) from the present. If it is 10% or more this will be important finding and you have a Nature paper. If that value is less than 1% of present mean NPP values, this whole discussion about reestablished whales driving ocean productivity needs to be cut out. Then the decision of the novelty of the result is in question.

We understand the reviewer's point that the iron recycling rate (1.2×10^4 tonnes Fe yr^{-1}) is meaningless when considered over the entire Southern Ocean. To address this comment, we focus on the Scotia Sea as an area of interest. This ~900,000 km^2 pelagic region contains the Drake Passage, the Scotia Arc, as well as South Georgia Island and its shelf. The Scotia Sea is both extremely iron-limited, and also the region of the most intense whaling. Following whaling, this region also had the steepest decline of krill biomass in the second half of the 20th century (Atkinson et al. 2004). The removal of whale-recycled iron has been hypothesized as the driver of this ecosystem shift (Smetacek 2008).

We conservatively estimated that half of all Southern Ocean rorquals were taken from this region, and therefore that 6 x 10^3 tonnes of whale-recycled Fe yr^{-1} was lost from the Scotia Sea region. Converting that to an areal rate is ~120 µmol Fe m^{-2} yr^{-1}, all of which would have been recycled during a feeding season that is assumed to be 90-120 days long. Using a conservative assumption of 120-day feeding season, the average iron recycled by whales across the Scotia Sea is ~1 µmol Fe m^{-2} d^{-1}. Using Fe : C ratios of Southern Ocean phytoplankton from the literature (Quigg et al. 2003, Twining et al. 2004, Strzepek et al. 2011), we estimate that the presence of large mysticete populations pre-whaling may have increased NPP in this region by ~1.7 g C m^{-2} d^{-1} or ~0.15 mol C m^{-2} d^{-1} across the Scotia Sea during the whale feeding season. This is potentially a quadrupling (400%) of primary production (see lines 177-184; 749-778 for detailed explanation). Incidentally, this is very similar to what Smetacek and colleagues recorded (0.13 mol C m^{-2} d^{-1} incorporated) in their iron addition experiment that stimulated a powerful diatom bloom (Smetacek et al. 2012).

As a second test of the effect of whale-recycled iron on primary productivity, we used a trophic calculation to estimate how much primary production would have been needed to sustain the krill stock that supported historic whale populations. This is the same approach that you suggested we try in your third-round of review (as well as what Reviewer 1 suggested in their first review). Reassuringly, the outcome of this investigation yielded a nearly identical estimate (2 g C m^{-2} d^{-1} of primary production across the Scotia Sea pre-whaling) to the iron-fertilization approach described above. To assess the validity of the previous calculations, we have consulted with Oscar Schofield (Rutgers University), an expert on Southern Ocean phytoplankton biology and ecology.

We believe this finding is important not just because the magnitude, but also because it is the first time this estimate has been made based on field data, despite widespread research interest and media speculation (Smetacek 2008, Nicol et al. 2010, Krulwich 2014, Ratnarajah et al. 2014, 2018, Chami et al. 2019).

There are still many uncertainties that need to be clarified with future empirical work. First, we assume homogenously distributed whale-recycled iron, whereas in reality this effect would have been patchy and ephemeral. We also assume that 25% of whale-recycled iron is incorporated by phytoplankton, as has been previously assumed (Ratnarajah et al. 2016). While preliminary research suggests that this is indeed the case (Smith et al. 2013), more work is needed to enhance the precision and understanding of these mechanisms. Despite simplifying assumptions of these unknown parameters, our calculations redefine the role of large cetaceans in stimulating primary production.

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Referee reports on fourth version:

Referee #1 (Remarks to the Author):

This manuscript is indeed an improvement over the previous version. The primary production levels calculated to support the
whales' demands for prey biomass are high as expected but, in the context of rapid recycling, make sense.
The title is also fine with me.
The paper is ready for publication.

Referee #5 (Remarks to the Author):

The authors have revised their submission again attempting to improve the impacts part of their story. I appreciate their efforts on these revisions. Problem is I am not getting to the same conclusions they do using their total estimates of iron released via krill ingestions / egestion by baleen whales. Using their total Southern Ocean (SO) release of iron due to baleen whales (1.2e4 ton Fe / year), the assumption that ¼ of the released iron is utilized by phytoplankton and their literature mean iron to carbon ratio for diatoms (~3 micromole Fe / mole C), I get an enhancement of SO net primary production (NPP) of ~200 Tg C / year. This is a big number and although its uncertainty is very high (could be factor of 5) – but it is nowhere near the fourfold increase presented in the text. For example, Arrigo et al. (2008; JGR-Oceans) show that modern day spatially integrated NPP for the entire SO is nearly 2000 Tg C/year. So this enhancement could be 10% (accounting for uncertainties this could be as much as 50% or as little as 5%). Arrigo et al. state that for the Scotia / Weddell Sea region the total NPP is ~500 Tg C / year. If one-half of the whale induced NPP increase occurs in the Scotian Sea as posited in the text, it will still be a substantive fraction of the present-day total, roughly an increase of 20% for the average - but nowhere near the fourfold increase presented in the text. I have tried to recreate this calculation but am simply not understanding how they got to where they did.

It seems that the authors are trying too hard to make the case that baleen whale feeding will have an outsized role in ocean ecosystem function. The example presented in the text (as well as their previous attempts) is far too complicated and the nested set of assumptions makes it hard to see what is robust. The key result of the paper seems to be the aggregated whale feeding / filtering rates and, through a set of assumptions, the SO iron recycling rates. The iron rates keep making it to the abstract, so the authors must think it is important and hopefully robust. Getting it to biogeochemical impacts is more difficult and in particular the uncertainties in the phytoplankton C:Fe ratio are large, and likely taxa and environmental specific. So, I would focus on a simple example (i.e., the one given above), describe outcomes (whales are important to recycling iron and if restored to pre-hunted levels one would expect a substantial effect on SO regional NPP levels), and describe uncertainties in the calculation and providing caution from over interpreting the results as well as providing an agenda for future work (predicting C:Fe ratios, iron content in krill, missing whale taxa, etc.). This way the results are presented in a defendable manner and do not look like the "books were cooked".

My goal here is to help the authors keep their paper focused on what they do best and not extrapolating their results incorrectly in ways that will create lasting damage in policy arenas. The initial submission suggested with little support that restoring whale populations will magically fix our climate / excess CO_2 problem. It won't. But many, especially in the ocean conservation world, want to believe that is the case. It is very hard to put that toothpaste back in the tube once it is squeezed out and in doing so it distracts from the potentially viable solutions to the important issues society has in front of it.

Author Rebuttals to Fourth Revision:

Referees' comments:

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On behalf of all authors, thank you for your numerous dedicated reviews of this manuscript and suggestions for improvements. Your perspective and expertise have greatly improved the final paper.

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The difference between your estimates and ours is a matter of scale. The calculations you suggest are done with annual values of NPP at an oceanic scale, whereas our calculations in the previous submission (R4) were done with daily values of NPP on the spatial scale of m^2. We did so because that is the spatiotemporal scale that best matches our whale data, not to mention the whales are not present and feeding in the Southern Ocean for two-thirds of the year.

That said, there is power in simplicity, particularly due to the complex nature of the topic and the uncertainty of the estimates. Therefore, we have conducted the precise calculations you request and present them step-by-step in Extended Data Table 2. Reassuringly, we get the same answer as you (enhancement of Southern Ocean NPP of ~200 Tg C yr^{-1}) when doing the calculations over at an annual scale over the entire extent of the Southern Ocean (Arrigo et al. 2008). We include updates to the main text (lines 184-189) and Methods (lines 760-773) to reflect these changes.

We appreciate your guidance to omit explicit references and calculations of the carbon cycle or the fact that rebuilding whale populations globally will 'fix' our CO_2 problem. As such, there are now no remaining mentions of it in the final manuscript.

Literature cited

Arrigo, K. R., G. L. van Dijken, and S. Bushinsky. 2008. Primary production in the Southern Ocean, 1997-2006. Journal of Geophysical Research: Oceans 113:C08004.