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Decadal changes in blood $\delta^{13}C$ values, at-sea distribution, and weaning mass of southern elephant seals from Kerguelen Islands

Julie Mestre, Matthieu Authier, Yves Cherel, Rob Harcourt, Clive R. McMahon, Mark A. Hindell, Jean-Benoît Charrassin and Christophe Guinet

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Review timeline

Original submission:	13 March 2020
1st revised submission:	29 June 2020
2nd revised submission:	24 July 2020
Final acceptance:	27 July 2020

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

Review History

RSPB-2020-0581.R0 (Original submission)

Review form: Reviewer 1

Recommendation
Major revision is needed (please make suggestions in comments)

Scientific importance: Is the manuscript an original and important contribution to its field?
Excellent

General interest: Is the paper of sufficient general interest?
Good

Quality of the paper: Is the overall quality of the paper suitable?
Good

Is the length of the paper justified?
Yes

Should the paper be seen by a specialist statistical reviewer?
No

Do you have any concerns about statistical analyses in this paper? If so, please specify them explicitly in your report.
Yes

It is a condition of publication that authors make their supporting data, code and materials available - either as supplementary material or hosted in an external repository. Please rate, if applicable, the supporting data on the following criteria.

> **Is it accessible?**
> No
>
> **Is it clear?**
> N/A
>
> **Is it adequate?**
> N/A

Do you have any ethical concerns with this paper?
No

Comments to the Author
Really interesting paper leveraging an extensive tracking dataset over a decade long. The manuscript is extremely well written with good structure and flow making it easy to understand. The study nicely shows that changes in SIA signatures (particularly 13C) are not related to a shifting foraging distribution, but wider ecosystem change. However, links to phytoplankton communities and productivity remain quite speculative, and relationships between female foraging areas and pup weaning mass are based on some assumptions that may not be valid.

The analysis seems quite sophisticated, however I think results/interpretation are based on a number of assumptions that should have been explicitly tested given the very large dataset available. First, the authors assume a correlation between female and pup 13C signatures. They provide a reference showing this from the same colony but in a single year. Given the current study found a year effect over time in the data, it would be more appropriate to do this analysis on the larger dataset available, particularly as the cited study found a unimodal distribution in 13C, while this study (assumes?) a bimodal distribution corresponding to differing foraging regions.

Secondly, there is an assumption that differences in 13C values represent either Antarctic or subantarctic foraging. The authors cite a reference that 13C values are bimodal in SES and that lower 13C value must have come from Antarctic waters. However, the cited reference (Bailleul et al., 2010) doesn't provide any SIA data, and the previously cited reference that established the link between pup and mother SIA signatures (from the same location) noted a unimodal distribution in female 13C values and suggested that there were no contrasted foraging areas within the population. So there seems to be a lack of evidence for a bimodal distribution in 13C that is the basis for assigning pups to differing female foraging areas.

I think it would be appropriate to look at the distribution of the 13C values in the larger dataset spanning multiple years (showing bimodality), and then explicitly link 13C values of tracked females to the extensive tracking data before assuming differences relate to foraging area.

The current study seems to show significant differences in weaning mass related to assumed mother foraging locations which is quite interesting and could have large knock-on effects for the population over time. I would just be aware of potential confounding factors that can't be accounted for in the analysis when assigning pups to a female foraging location based on 13C values alone. For example, there seems to be quite a range in seal lengths, and if larger females wean larger pups, and larger females have a different diet due to increased aerobic dive limits for example, this may affect 13C values? This could be important given that the study showing a correlation between pup and mother 13C signatures found no relationship between pup weaning mass and 13C signature indicating no link between female foraging areas and pup success. Given the extensive SIA and tracking dataset now available, perhaps a good sample size of pups with known mother 13C values and known foraging locations might be available to establish this relationship between female forging area and pup mass at weaning as I think the current relationship is based on too many unvalidated assumptions.

Such large datasets over so many years are really valuable and has provided an opportunity to highlight an important finding that could have implications for a range of top predators in antarctic ecosystems, so I think its well worth addressing the comment above as I think this can make a significant contribution to the field.

Review form: Reviewer 2

Recommendation
Major revision is needed (please make suggestions in comments)

Scientific importance: Is the manuscript an original and important contribution to its field?
Good

General interest: Is the paper of sufficient general interest?
Acceptable

Quality of the paper: Is the overall quality of the paper suitable?
Excellent

Is the length of the paper justified?
Yes

Should the paper be seen by a specialist statistical reviewer?
No

Do you have any concerns about statistical analyses in this paper? If so, please specify them explicitly in your report.
No

It is a condition of publication that authors make their supporting data, code and materials available - either as supplementary material or hosted in an external repository. Please rate, if applicable, the supporting data on the following criteria.

> **Is it accessible?**
> Yes
>
> **Is it clear?**
> Yes
>
> **Is it adequate?**
> Yes

Do you have any ethical concerns with this paper?
No

Comments to the Author
In this manuscript titled: "Decadal changes in blood δ 13C values, at-sea distribution and weaning mass of elephant seals from Kerguelen.", the authors assessed decadal (2004-2018) environmental regime shifts in the foraging habitat of an increasing population of southern elephant seals from Kerguelen Islands using blood δ 13C values and bio-logging. The influence of foraging habitat on pup weaning mass was also assessed. The authors found no significant shift in seals at-sea distribution between 2004 and 2017 or changes in the proportion of females foraging in either sub-Antarctic or Antarctic habitats. Adult females foraging in sub-Antarctic conveyed a fitness advantage to their offspring and led to increased weaning weights compared to females foraging in Antarctic habitats. Aside from this interesting observation, the main finding was that blood δ 13C values decreased by 0.1‰ per year. This led the authors to suggest that a "large-scale ecological shift is currently underway within the Indian sector of the Southern Ocean with direct consequences on the foraging performances of southern elephant seals". Similar findings have already been discussed by Hobson et al. (2004) with samples collected from seals and birds sampled in the 1960s -1980s. The study provides interesting findings, but I am not convinced that the available combination of data were entirely compatible with addressing the proposed aims. Indeed, the conclusion that an environmental regime shift might occur is not supported by the presented data in light of other potential drivers. The authors needs to better explain the relevance of a 0.1‰ annual decrease in the δ 13C values mean for upper-trophic level marine predator before claiming that the change will have "direct consequences on the foraging performances of southern elephant seals".

Major comments:
The authors discussed various physical (change in oceanic fronts), biogeochemical (incl. Seuss effect), and/or ecological factors that could explain the 0.1 ‰ per year decrease in the δ 13C values, and through the process of elimination, concluded that change in the baseline δ 13C values likely relates to a change in the "composition of phytoplankton communities". The conclusion that "…large-scale ecological shift is currently underway" is extrapolation beyond what the data can support. The authors are conscious of this, hence the conclusion that "Changes in the composition of phytoplankton communities should be a research priority…". As stated, "Earlier studies revealed temporal variation in the δ 13C values of metabolically inert issues…", of which baleen and teeth provide longer records more suitable for these analyses (up to 30 yrs).

- Changes in dissolved inorganic carbon (δ 13CDIC) reflect changes in the δ 13C of atmospheric CO2, which are decreasing due to the Suess Effect. For example, the rate of decrease in the baseline δ 13C values ranges from −0.023 to −0.029‰ ·yr−1 based on coral reefs (Pereira et al. 2018; https://doi.org/10.1016/j.palaeo.2018.02.007). The decrease of δ 13C values of 0.1‰ per year is therefore, higher than expected, but lower than a comparable study that assessed the decrease in the δ 13C values during 2000 to 2015, which declined by 0.8‰–2.5‰ in three tuna species (Lorrain et al. 2019, https://doi.org/10.1111/gcb.14858; study briefly mentioned in line 322-324 of the discussion). Lorrain et al. (2019) came to the same conclusion: "We suggest a global shift in phytoplankton community structure, for example, a reduction in 13C-rich phytoplankton such as diatoms, and/or a change in phytoplankton physiology during this period, although this does not rule out other concomitant changes at higher levels in the food webs". De la Vega et al. (2019; DOI: 10.1111/gcb.14832) present similar conclusions where they also describe a "decadal decline in δ 13C-[particulate organic carbon in the water] values (1987–2013) [which] was more than 10 times larger than the trend in δ 13C values of CO2 (or DIC)...".
Although cited in the present study, I believe more consideration could have been given to the existing body of knowledge on this topic, and incorporated better in the conclusions.

- Is a change in the δ 13C of up to 1.4‰ considered biologically significant enough to claim that "large-scale ecological shift is currently underway"? The authors should elaborate on what a change in δ 13C of up to 1.4‰ means for the ecosystem (changes of ~10 ‰ can occur when diatom species composition changes, Henley et al. 2012; Fischer 1991;

https://doi.org/10.1016/S0304-4203(09)90044-5). We know salps might be increasing at the higher latitudes, replacing sub-Antarctic krill species. Could this be changing the δ 13C values? If a larger ecosystem shift is underway/happening and there is no change in the δ 15N values (proxy for trophic level), how would this have "direct consequences on the foraging performances of southern elephant seals" (sensitivity of food webs)? Nonetheless, when framed along the lines of, i.e. changes in δ 13C values of dissolved organic matter (DOC) on an ocean-wide scale, then a change of ~ 1.0‰ might be noteworthy; but the authors need to better clarify what their findings might mean within the broader literature.

- It is noted that "a 303 km southward shift in 13 years" occurred. The authors state "such latitudinal shift would not be sufficient to explain the decrease in the δ 13C values". The authors are urged to provide the data/elaborate on why this is the case. Could small changes in the foraging latitude (albeit not statistically significant) explain the 0.1‰ δ 13C decrease per year given the δ 13C isoscape in the Southern Ocean? How much change in the foraging range (degrees) should occur per year to explain a change of δ 13C decrease of 0.1‰? Perhaps the authors can provide some sort of sensitivity analyses in this regard?
- What is the lag effect of the change in terms of "…large-scale ecological shift is currently underway"? "Equilibration timescale for the isotopic ratios 13C/12C in the ocean mixed layer is on the order of a decade" (Pereira et al. 2018). Also, consider the influence of changes in sea ice cover and the associated "biological pump" in the Southern Ocean. The "CO2 uptake by the Southern Ocean (<35◦S) varies substantially on all timescales and is a major determinant of the variations of the global ocean carbon sink" (Gruber et al. 2019; https://doi.org/10.1146/annurev-marine-121916-063407) and could have decadal effects on the δ 13C values without major ecosystem shift consequences (?).
- Changes in ocean productivity are also known to affect oceanic 13C-POC (persistent organic matter) values (some phytoplankton species). As with many studies before, the lack of baseline 13C values continues to hinder identification of the drivers of the temporal decrease of δ 13C in both hemispheres, which in marine mammals, are often larger than the Suess effect (Vega et al. 2019). Essentially, the δ 13C values can change without necessarily having a "large-scale ecological shift". The noted "increase in surface chlorophyll-a biomass" which likely occurs to enhanced thermal stratification in the South Ocean could lead to the incorporation of more 13C over time and explain the decreasing δ 13C values. "The baleen records reveal a consistent decrease in the δ 13C values (over 2.7‰) for the Bering and Chukchi phytoplankton, which Schell suggests reflects a decrease in phytoplankton growth rates" (Freeman, 2001).
- The authors account for the poleward potential "migration of targeted preys" seeing that the "distribution of these mesopelagic fish is mostly ruled by the temperature of water masses". However, I did not notice a discussion on the potential change in the vertical (depth) used by SES and their prey in relation to vertical 13C baseline gradients (see e.g., McIntyre et al. 2013; DOI: https://doi.org/10.1017/S0954102012000570).

Minor comments
Line 65: refs cited are not relevant to all the mentioned locations. Perhaps add MCMahon et al. 2005 (Mamm Rev) and Pistorius et al. 2011 (https://doi.org/10.2989/1814232X.2011.637357)
Methods: Where were the isotopic analyses conducted (laboratory) and how many laboratory standards were used? Also need information on which laboratory standards were used (biochemical composition should be similar to blood).
Lines 337-339: See McIntyre et al. 2017 (https://doi.org/10.1016/j.anbehav.2017.03.006) where mention of this is made. Also relevant in line 93.
Results, Fig 1 – Seeing that the pup δ 13C C values are presented at an annual resolution, would it be sensible to colourize the tracks for each year?

Decision letter (RSPB-2020-0581.R0)

29-Apr-2020

Dear Ms Mestre:

I am writing to inform you that your manuscript RSPB-2020-0581 entitled "Decadal changes in blood δ 13C values, at-sea distribution and weaning mass of elephant seals from Kerguelen Islands." has, in its current form, been rejected for publication in Proceedings B.

This action has been taken on the advice of referees, who have recommended that substantial revisions are necessary. With this in mind we would be happy to consider a resubmission, provided the comments of the referees are fully addressed. However please note that this is not a provisional acceptance.

The resubmission will be treated as a new manuscript. However, we will approach the same reviewers if they are available and it is deemed appropriate to do so by the Editor. Please note that resubmissions must be submitted within six months of the date of this email. In exceptional circumstances, extensions may be possible if agreed with the Editorial Office. Manuscripts submitted after this date will be automatically rejected.

Please find below the comments made by the referees, not including confidential reports to the Editor, which I hope you will find useful. If you do choose to resubmit your manuscript, please upload the following:

1) A 'response to referees' document including details of how you have responded to the comments, and the adjustments you have made.
2) A clean copy of the manuscript and one with 'tracked changes' indicating your 'response to referees' comments document.
3) Line numbers in your main document.

To upload a resubmitted manuscript, log into http://mc.manuscriptcentral.com/prsb and enter your Author Centre, where you will find your manuscript title listed under "Manuscripts with Decisions." Under "Actions," click on "Create a Resubmission." Please be sure to indicate in your cover letter that it is a resubmission, and supply the previous reference number.

Sincerely,
Dr Daniel Costa
mailto: proceedingsb@royalsociety.org

Associate Editor
Board Member: 1
Comments to Author:
Two thorough reviews have been received and are both generally positive, but address a range of assumptions and issues that the authors should address. One reviewer focuses on what they consider to be some untested assumptions which they consider it should be possible to address in the larger multiyear dataset. The other asks for more detail in a number of specific areas. Particular value is emphasised in the value of using of a rare long term dataset such as this, something that I very strongly agree with.

Reviewer(s)' Comments to Author:
Referee: 1
Comments to the Author(s)
Really interesting paper leveraging an extensive tracking dataset over a decade long. The manuscript is extremely well written with good structure and flow making it easy to understand. The study nicely shows that changes in SIA signatures (particularly 13C) are not related to a shifting foraging distribution, but wider ecosystem change. However, links to phytoplankton communities and productivity remain quite speculative, and relationships between female foraging areas and pup weaning mass are based on some assumptions that may not be valid.

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Referee: 2

Comments to the Author(s)
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Major comments:
The authors discussed various physical (change in oceanic fronts), biogeochemical (incl. Seuss effect), and/or ecological factors that could explain the 0.1 ‰ per year decrease in the δ 13C values, and through the process of elimination, concluded that change in the baseline δ 13C values likely relates to a change in the “composition of phytoplankton communities”. The conclusion that “…large-scale ecological shift is currently underway” is extrapolation beyond what the data can support. The authors are conscious of this, hence the conclusion that “Changes in the composition of phytoplankton communities should be a research priority…”. As stated, “Earlier studies revealed temporal variation in the δ 13C values of metabolically inert issues…”, of which baleen and teeth provide longer records more suitable for these analyses (up to 30 yrs).
- Changes in dissolved inorganic carbon (δ 13CDIC) reflect changes in the δ 13C of atmospheric CO_2, which are decreasing due to the Suess Effect. For example, the rate of decrease in the baseline δ 13C values ranges from −0.023 to −0.029‰ ·yr−1 based on coral reefs (Pereira et al. 2018; https://doi.org/10.1016/j.palaeo.2018.02.007). The decrease of δ 13C values of 0.1‰ per year is therefore, higher than expected, but lower than a comparable study that assessed the decrease in the δ 13C values during 2000 to 2015, which declined by 0.8‰–2.5‰ in three tuna species (Lorrain et al. 2019, https://doi.org/10.1111/gcb.14858; study briefly mentioned in line 322-324 of the discussion). Lorrain et al. (2019) came to the same conclusion: “We suggest a global shift in phytoplankton community structure, for example, a reduction in 13C-rich phytoplankton such as diatoms, and/or a change in phytoplankton physiology during this period, although this does not rule out other concomitant changes at higher levels in the food webs”. De la Vega et al. (2019; DOI: 10.1111/gcb.14832) present similar conclusions where they also describe a “decadal decline in δ 13C-[particulate organic carbon in the water] values (1987–2013) [which] was more than 10 times larger than the trend in δ 13C values of CO_2 (or DIC)...”.
Although cited in the present study, I believe more consideration could have been given to the existing body of knowledge on this topic, and incorporated better in the conclusions.
- Is a change in the δ 13C of up to 1.4‰ considered biologically significant enough to claim that “large-scale ecological shift is currently underway”? The authors should elaborate on what a change in δ 13C of up to 1.4‰ means for the ecosystem (changes of ~10 ‰ can occur when diatom species composition changes, Henley et al. 2012; Fischer 1991; https://doi.org/10.1016/S0304-4203(09)90044-5). We know salps might be increasing at the higher latitudes, replacing sub-Antarctic krill species. Could this be changing the δ 13C values? If

a larger ecosystem shift is underway/happening and there is no change in the δ15N values (proxy for trophic level), how would this have "direct consequences on the foraging performances of southern elephant seals" (sensitivity of food webs)? Nonetheless, when framed along the lines of, i.e. changes in δ13C values of dissolved organic matter (DOC) on an ocean-wide scale, then a change of ~ 1.0‰ might be noteworthy; but the authors need to better clarify what their findings might mean within the broader literature.
- It is noted that "a 303 km southward shift in 13 years" occurred. The authors state "such latitudinal shift would not be sufficient to explain the decrease in the δ13C values". The authors are urged to provide the data/elaborate on why this is the case. Could small changes in the foraging latitude (albeit not statistically significant) explain the 0.1‰ δ13C decrease per year given the δ13C isoscape in the Southern Ocean? How much change in the foraging range (degrees) should occur per year to explain a change of δ13C decrease of 0.1‰? Perhaps the authors can provide some sort of sensitivity analyses in this regard?
- What is the lag effect of the change in terms of "…large-scale ecological shift is currently underway"? "Equilibration timescale for the isotopic ratios 13C/12C in the ocean mixed layer is on the order of a decade" (Pereira et al. 2018). Also, consider the influence of changes in sea ice cover and the associated "biological pump" in the Southern Ocean. The "CO2 uptake by the Southern Ocean (<35◦S) varies substantially on all timescales and is a major determinant of the variations of the global ocean carbon sink" (Gruber et al. 2019; https://doi.org/10.1146/annurev-marine-121916-063407) and could have decadal effects on the δ13C values without major ecosystem shift consequences (?).
- Changes in ocean productivity are also known to affect oceanic 13C-POC (persistent organic matter) values (some phytoplankton species). As with many studies before, the lack of baseline 13C values continues to hinder identification of the drivers of the temporal decrease of δ13C in both hemispheres, which in marine mammals, are often larger than the Suess effect (Vega et al. 2019). Essentially, the δ13C values can change without necessarily having a "large-scale ecological shift". The noted "increase in surface chlorophyll-a biomass" which likely occurs to enhanced thermal stratification in the South Ocean could lead to the incorporation of more 13C over time and explain the decreasing δ13C values. "The baleen records reveal a consistent decrease in the δ13C values (over 2.7‰) for the Bering and Chukchi phytoplankton, which Schell suggests reflects a decrease in phytoplankton growth rates" (Freeman, 2001).
- The authors account for the poleward potential "migration of targeted preys" seeing that the "distribution of these mesopelagic fish is mostly ruled by the temperature of water masses". However, I did not notice a discussion on the potential change in the vertical (depth) used by SES and their prey in relation to vertical ��13C baseline gradients (see e.g., McIntyre et al. 2013; DOI: https://doi.org/10.1017/S0954102012000570).

Minor comments
Line 65: refs cited are not relevant to all the mentioned locations. Perhaps add MCMahon et al. 2005 (Mamm Rev) and Pistorius et al. 2011 (https://doi.org/10.2989/1814232X.2011.637357)
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Results, Fig 1 – Seeing that the pup δ13C C values are presented at an annual resolution, would it be sensible to colourize the tracks for each year?

Author's Response to Decision Letter for (RSPB-2020-0581.R0)

See Appendix A.

RSPB-2020-1544.R0

Review form: Reviewer 2

Recommendation
Accept as is

Scientific importance: Is the manuscript an original and important contribution to its field?
Excellent

General interest: Is the paper of sufficient general interest?
Excellent

Quality of the paper: Is the overall quality of the paper suitable?
Excellent

Is the length of the paper justified?
Yes

Should the paper be seen by a specialist statistical reviewer?
No

Do you have any concerns about statistical analyses in this paper? If so, please specify them explicitly in your report.
No

It is a condition of publication that authors make their supporting data, code and materials available - either as supplementary material or hosted in an external repository. Please rate, if applicable, the supporting data on the following criteria.

> **Is it accessible?**
> Yes
>
> **Is it clear?**
> Yes
>
> **Is it adequate?**
> Yes

Do you have any ethical concerns with this paper?
No

Comments to the Author
The authors have done well to revise the manuscript according to earlier review suggestions. I have no further concerns or queries, aside from a few very minor editorial errors which I presume will be sorted out during proof stages. Well done on an excellent piece of work.

Decision letter (RSPB-2020-1544.R0)

21-Jul-2020

Dear Ms Mestre

I am pleased to inform you that your manuscript RSPB-2020-1544 entitled "Decadal changes in blood δ 13C values, at-sea distribution, and weaning mass of southern elephant seals from Kerguelen Islands." has been accepted for publication in Proceedings B.

The referee(s) have recommended publication, but also suggest some minor revisions to your manuscript. Therefore, I invite you to respond to the referee(s)' comments and revise your manuscript. Because the schedule for publication is very tight, it is a condition of publication that you submit the revised version of your manuscript within 7 days. If you do not think you will be able to meet this date please let us know.

To revise your manuscript, log into https://mc.manuscriptcentral.com/prsb and enter your Author Centre, where you will find your manuscript title listed under "Manuscripts with Decisions." Under "Actions," click on "Create a Revision." Your manuscript number has been appended to denote a revision. You will be unable to make your revisions on the originally submitted version of the manuscript. Instead, revise your manuscript and upload a new version through your Author Centre.

When submitting your revised manuscript, you will be able to respond to the comments made by the referee(s) and upload a file "Response to Referees". You can use this to document any changes you make to the original manuscript. We require a copy of the manuscript with revisions made since the previous version marked as ‘tracked changes’ to be included in the ‘response to referees’ document.

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2) A separate electronic file of each figure (tiff, EPS or print-quality PDF preferred). The format should be produced directly from original creation package, or original software format. PowerPoint files are not accepted.

3) Electronic supplementary material: this should be contained in a separate file and where possible, all ESM should be combined into a single file. All supplementary materials accompanying an accepted article will be treated as in their final form. They will be published alongside the paper on the journal website and posted on the online figshare repository. Files on figshare will be made available approximately one week before the accompanying article so that the supplementary material can be attributed a unique DOI.

Online supplementary material will also carry the title and description provided during submission, so please ensure these are accurate and informative. Note that the Royal Society will not edit or typeset supplementary material and it will be hosted as provided. Please ensure that the supplementary material includes the paper details (authors, title, journal name, article DOI). Your article DOI will be 10.1098/rspb.[paper ID in form xxxx.xxxx e.g. 10.1098/rspb.2016.0049].

4) A media summary: a short non-technical summary (up to 100 words) of the key findings/importance of your manuscript.

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

In order to ensure effective and robust dissemination and appropriate credit to authors the dataset(s) used should be fully cited. To ensure archived data are available to readers, authors should include a 'data accessibility' section immediately after the acknowledgements section. This should list the database and accession number for all data from the article that has been made publicly available, for instance:
• DNA sequences: Genbank accessions F234391-F234402
• Phylogenetic data: TreeBASE accession number S9123
• Final DNA sequence assembly uploaded as online supplemental material
• Climate data and MaxEnt input files: Dryad doi:10.5521/dryad.12311
NB. From April 1 2013, peer reviewed articles based on research funded wholly or partly by RCUK must include, if applicable, a statement on how the underlying research materials – such as data, samples or models – can be accessed. This statement should be included in the data accessibility section.

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Once again, thank you for submitting your manuscript to Proceedings B and I look forward to receiving your revision. If you have any questions at all, please do not hesitate to get in touch.

Sincerely,
Dr Daniel Costa
mailto: proceedingsb@royalsociety.org

Associate Editor
Board Member
Comments to Author:
Thank you for the revisions, which have satisfied the reviewer.

Reviewer(s)' Comments to Author:

Referee: 2

Comments to the Author(s).
The authors have done well to revise the manuscript according to earlier review suggestions. I have no further concerns or queries, aside from a few very minor editorial errors which I presume will be sorted out during proof stages. Well done on an excellent piece of work.

Decision letter (RSPB-2020-1544.R1)

27-Jul-2020

Dear Ms Mestre

I am pleased to inform you that your manuscript entitled "Decadal changes in blood δ 13C values, at-sea distribution, and weaning mass of southern elephant seals from Kerguelen Islands." has been accepted for publication in Proceedings B.

You can expect to receive a proof of your article from our Production office in due course, please check your spam filter if you do not receive it. PLEASE NOTE: you will be given the exact page length of your paper which may be different from the estimation from Editorial and you may be asked to reduce your paper if it goes over the 10 page limit.

If you are likely to be away from e-mail contact please let us know. Due to rapid publication and an extremely tight schedule, if comments are not received, we may publish the paper as it stands.

If you have any queries regarding the production of your final article or the publication date please contact procb_proofs@royalsociety.org

Your article has been estimated as being 10 pages long. Our Production Office will be able to confirm the exact length at proof stage.

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Thank you for your fine contribution. On behalf of the Editors of the Proceedings B, we look forward to your continued contributions to the Journal.

Sincerely,
Proceedings B
mailto: proceedingsb@royalsociety.org

Appendix A

29-Apr-2020

Dear Ms Mestre:

I am writing to inform you that your manuscript RSPB-2020-0581 entitled "Decadal changes in blood δ13C values, at-sea distribution and weaning mass of elephant seals from Kerguelen Islands." has, in its current form, been rejected for publication in Proceedings B.

This action has been taken on the advice of referees who have recommended that substantial revisions are necessary. With this in mind we would be happy to consider a resubmission, provided the comments of the referees are fully addressed. However please note that this is not a provisional acceptance.

The resubmission will be treated as a new manuscript. However, we will approach the same reviewers if they are available and it is deemed appropriate to do so by the Editor. Please note that resubmissions must be submitted within six months of the date of this email. In exceptional circumstances, extensions may be possible if agreed with the Editorial Office. Manuscripts submitted after this date will be automatically rejected.

Please find below the comments made by the referees, not including confidential reports to the Editor, which I hope you will find useful. If you do choose to resubmit your manuscript, please upload the following:

1) A ‘response to referees’ document including details of how you have responded to the comments, and the adjustments you have made.

2) A clean copy of the manuscript and one with ‘tracked changes’ indicating your ‘response to referees’ comments document.

3) Line numbers in your main document

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Sincerely,

Dr Daniel Costa

mailto: proceedingsb@royalsociety.org

Associate Editor
Board Member: 1

Comments to Author:

Two thorough reviews have been received and are both generally positive, but address a range of assumptions and issues that the authors should address. One reviewer focuses on what they consider to be some untested assumptions which they consider it should be possible to address in the larger multiyear dataset. The other asks for more detail in a number of specific areas. Particular value is emphasised in the value of using of a rare long term dataset such as this, something that I very strongly agree with.

We did our best to complete the present study with additional analyses and answer reviewers' questions. Modifications are listed in the present document and highlighted in the tracked changes document.

ESM1 and ESM2 were completed with additional analyses (ESM1 part2 and ESM2 part2). All figures numbers in ESMs have been updated because of previously mentioned additions, as well as reference numbers in the main document. The first figure of ESM3 (Figure S5) has been modified to display empirical distribution and probability density functions for each study year.

We also conducted modifications on a range of specific formulations or typos or reformulations and updated the acknowledgment section, all indicated in the tracked changes document.

Provided lines numbers correspond to line numbers in the main document (i.e. clean copy).

Reviewer(s)' Comments to Author:

Referee: 1

Comments to the Author(s)

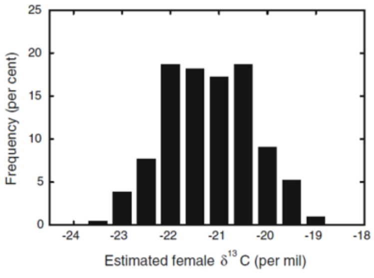
Really interesting paper leveraging an extensive tracking dataset over a decade long. The manuscript is extremely well written with good structure and flow making it easy to understand. The study nicely shows that changes in SIA signatures (particularly 13C) are not related to a shifting foraging distribution, but wider ecosystem change. However, links to phytoplankton communities and productivity remain quite speculative, and relationships between female foraging areas and pup weaning mass are based on some assumptions that may not be valid.

Assumptions linking seal blood $\delta^{13}C$ values to phytoplankton productivity and communities have been redrafted to temper our conclusions and ensure cautious interpretation by the reader (lines 30-35 and lines 304-329).

Relationships between females foraging areas and pup weaning mass have been clarified (part 2 of the discussion, ESM1 and ESM2) as mentioned in the following subsections.

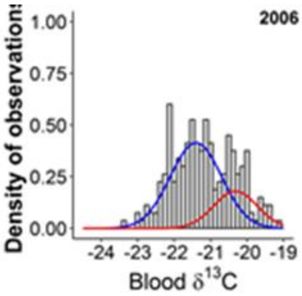
The analysis seems quite sophisticated, however I think results/interpretation are based on a number of assumptions that should have been explicitly tested given the very large dataset available. First, the authors assume a correlation between female and pup 13C signatures. They provide a reference showing this from the same colony but in a single year. Given the current study found a year effect over time in the data, it would be more appropriate to do this analysis on the larger dataset available, particularly as the cited study found a unimodal distribution in 13C, while this study (assumes?) a bimodal distribution corresponding to differing foraging regions.

• *The authors of the cited study (Ducatez et al., 2008) effectively found what they qualify as "a single broad mode", stating that the frequency distribution of pup $\delta^{13}C$ values was not bimodal. However, the unimodal distribution they observed (n = 209) seems to be graphically assessed (upper Figure 3. of their paper*



), and authors acknowledge that "elephant seals show a large range in $\delta^{13}C$ values indicating foraging grounds encompassing a wide latitudinal isotopic gradient". We do believe that more complex statistical analyses (i.e. mixture of two Gaussian distributions fitted in a Bayesian framework) would have highlighted a bimodal distribution. We reproduced the same graphical representation

with available blood $\delta^{13}C$ values for the same year (n = 214 pups, year = 2006) with more classes and superimposed probability density functions of our mixture model



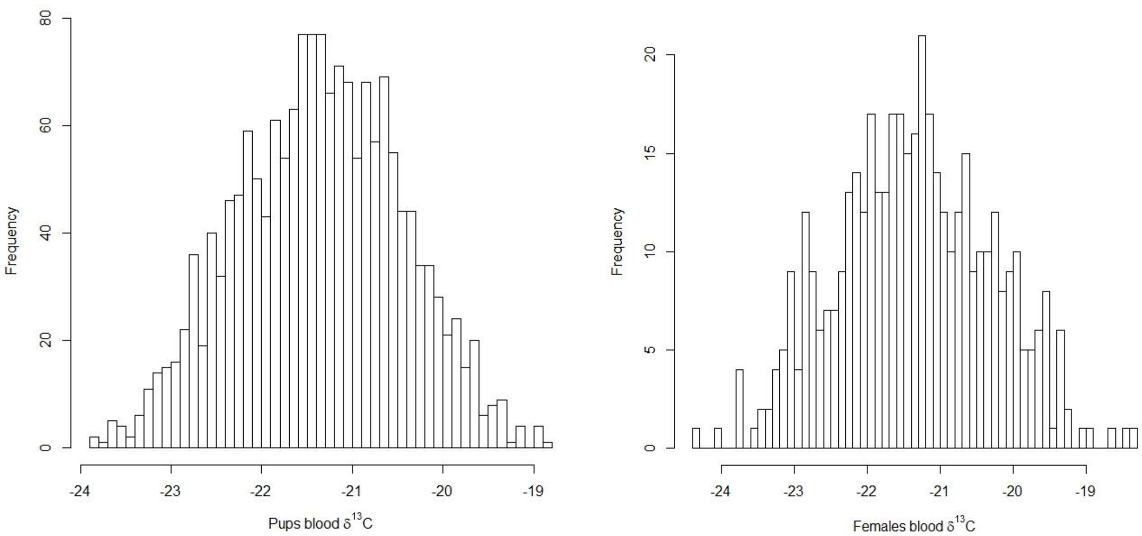
. Our plot and statistical analyses display a bimodal distribution, with two groups of individuals very likely to correspond to the two foraging strategies known from the literature. We added the corresponding plot in Electronic Supplementary Material (ESM) 3. Previous version of ESM3 displayed examples for years 2008 and 2010 only. Hence, we replaced the corresponding plot with another one showing pup blood $\delta^{13}C$ frequency distribution and associated density probability functions for each year, from 2006 to 2018. We will further discuss bimodality into the next section as it is the main subject of the next comment.

• *Regarding the relationship between pups and females $\delta^{13}C$ values, Ducatez et al. (2008) conducted their analyses on 17 pairs of individuals sampled in 2006. They got a very good correlation (linear model: $\delta^{13}C = 1.04x + 0.45$, $R^2 = 0.87$, $P < 0.0001$). The isotopic relationship between pup and their mothers $\delta^{13}C$ values is a physiological one, independent of the seal foraging ecology. Hence, we found no theoretical background that could change this relationship. Since, a few other pairs were investigated over time (8 more in 2006, 1 in 2008, 1 in 2015, 5 in 2016 and 11 in 2017). We updated the Ducatez et al. analysis, and got the following linear model: $\delta^{13}C = 0.9x - 2.3$, $R^2 = 0.76$, p-value < 0.0001. Spearman's rank correlation test revealed a strong correlation between mother and pup blood $\delta^{13}C$ values (rho = 0.86), confirming the relationship between pups and mothers seals blood $\delta^{13}C$ values over time. Model and plot with details for each available study year have been added in ESM 2 part 2. We added a sentence referring to it in the ms (line 196).Note that all our analyses were conducted on raw pup blood $\delta^{13}C$ values (as expressed in line 195 of the main document), and that our discussion refers to adult females as an extrapolation, but that we did not transform measured pups values into females estimated ones to prevent comparison between measured and estimated values.*

Secondly, there is an assumption that differences in 13C values represent either Antarctic or subantarctic foraging. The authors cite a reference that 13C values are bimodal in SES and that lower 13C value must have come from Antarctic waters. However, the cited reference (Bailleul et al., 2010) doesn't provide any SIA data, and the previously cited reference that established the link between pup and mother SIA signatures (from the same location) noted a unimodal distribution in female 13C values and suggested that there were no contrasted foraging areas within the population. So there seems to be a lack of evidence for a bimodal distribution in 13C that is the basis for assigning pups to differing female foraging areas.
I think it would be appropriate to look at the distribution of the 13C values in the larger dataset spanning multiple years (showing bimodality), and then explicitly link

13C values of tracked females to the extensive tracking data before assuming differences relate to foraging area.

• We could not assess bimodality in the distribution of blood $\delta^{13}C$ values within our dataset, neither for pups (2006-2018, n = 1684) nor for adult females (2004-2017, n = 469), without taking the year of sampling into account. We previously discussed above the unimodality in Ducatez et al. (2008), showing that it is an artefact due to a too simple statistical analysis.



Werner Heisenber stated in 1958: "What we observe is not nature itself, but nature exposed to our method of questioning", and we do believe that bimodality does exist as shown with the mixture model we fitted on an annual basis (see ESM3, Figure S5). Numerous studies based on tracking data have highlighted the two foraging strategies (i.e. Antarctic versus Sub-Antarctic) displayed by adult female southern elephant seals from the Kerguelen population (Bailleul et al., 2010, Guinet et al., 2014, Hindell et al., 2016).

• We did not understand Referee #1 comment in a first place because there are some significant SIA in Bailleul et al. (2010) paper (p6 and p8): "For both sexes, the distribution of $\delta^{13}C$ for large individuals was bimodal, while that of small individuals was unimodal (Fig.3). We therefore modelled $\delta^{13}C$ in light of this pattern". We then realized that we mistakenly put the wrong citation in the reference section, as we cited Bailleul et al. paper published in 2010 in MEPS (doi: 10.3354/meps08560) instead of the paper published the same year in Ecography (doi: 10.111/j.1600-0587.2009.06034). We apologize for the gross error that we corrected in the references section (ref [33]).

The current study seems to show significant differences in weaning mass related to assumed mother foraging locations which is quite interesting and could have large knock-on effects for the population over time. I would just be aware of potential confounding factors that can't be accounted for in the analysis when assigning pups to a female foraging location based on 13C values alone. For example, there seems to be quite a range in seal lengths, and if larger females wean larger pups, and larger females have a different diet due to increased aerobic dive limits for example, this may affect 13C values? This could be important given that the study showing a correlation between pup and mother 13C signatures found no relationship between pup weaning mass and 13C signature indicating no link between female foraging areas and pup success. Given the extensive SIA and tracking dataset now available, perhaps a good sample size of pups with known mother 13C values and known foraging locations might be available to establish this relationship between female foraging area and pup mass at weaning as I think the current relationship is based on too many invalidated assumptions.

1) Females carbon isotopes ratio and thus foraging location is a strong predictor of pup weaning mass (Authier et al., 2012a). However, some other intrinsic and extrinsic covariates that we discussed but were not accounted for in the present study may impact pup weaning mass. For example, environmental variables such as sea-ice extent (Clausius et al., 2017b) and primary production (Authier et al., 2012a, Oosthuizen et al., 2015) are susceptible to impact females' fitness and ultimately the weaning mass of their pups (Desprez 2015). We did refer to those studies in the ms (lines 338-340), and added the concept of "fitness" (line 335) and more references (e.g. [19] and [44]) which may help to better explain the link between environmental conditions, females foraging success/fitness, and pup weaning mass.

Maternal size and the number of females ashore are susceptible to further impact pups condition (as illustrated in Clausius et al. (2017b), were 7276 weaners across 7 cohorts and for which mother size (categorized by eye at parturition as either small, medium or large) was available were studied, but without corresponding $\delta^{13}C$ values). However, it is important to keep in mind that those intrinsic factors can, except for age -and related body length- and the unknown importance of genetic transmission, be considered as a feedback of environmental conditions and population status; see the end of the discussion (p481) in Arnbom et al. (1997), related to the link between ecosystems productivity, size and recruitment age of female seals, and the related pup weaning mass. We referred to Arnbom's concept in lines 361-364 of the manuscript but did not explicitly mentioned females size, which we added lines 364 and 366. Figure 3 in McMahon et al. 2005 (Mammal Review) also highlights the concomitant impacts of maternal age and maternal foraging success on maternal size and ultimately pup weaning mass.

No further data related to Kerguelen southern elephant seals population diving physiology are yet available, but previous work showed that yearling elephant seals develop their diving availabilities during post weaning fast (Somo et al., 2015) and their first trip at sea (Orgeret et al., 2018). However, elephant seals develop fidelity to their foraging zones (demonstrated with four years of consecutive tagging of females from Macquarie population in Bradshaw et al., 2004, and through SIA for Kerguelen males in Authier et al., 2012b, see also McIntyre et al., 2017 – doi: 10.1016/j.anbehav.2017.03.006). As female seals perform pelagic dives, and because we focus on reproductive females (i.e. mature adult females), we assume that they use consistent foraging areas, and that their blood $\delta^{13}C$ values cannot be *impacted either by the $\delta^{13}C$ benthic/pelagic gradient (France, 1995), nor by the coastal/offshore one (France, 1995; Cherel et Hobson, 2007) on an inter-annual basis. We thus assume that female seal size cannot impact their blood $\delta^{13}C$ values, but reckon that individual size and related diving physiology might impact quality and energetic values of accessible preys, which cannot be assessed through SIA. Furthermore, female size was available for 435 individuals blood-sampled during either the breeding or moulting period. We checked the distribution of female blood $\delta^{13}C$ values according to their size, and there was no relationship.*

2) We acknowledge that Ducatez et al. (2008) found no relationship between pup weaning mass and blood $\delta^{13}C$ signature. However, we do believe it is due once again to different statistical approaches. Indeed, this was demonstrated since in Authier et al. (2012a): "We augment the work of Ducatez et al. [17] using more data and an explicit mixture modelling approach. Specifically, we modelled weaned pups as a mixture of two groups depending on their isotope ratio, then compared their respective proportions with those of maternal foraging behavior estimated from tracking data".

Thus, we estimate that our statistical approach, based on best suited analyses (i.e. mixture models fitted in a Bayesian framework), does enable inferring a link between female foraging areas and pup weaning mass. This indeed does not rule out other concomitant factors impacting pup weaning mass. Please note that Authier et al. (2012) fitted a mixture model to model pup weaning mass, whereas we fitted our model on blood $\delta^{13}C$ values. This earlier study concluded that "carbon isotope ratio was a strong predictor of weaning mass". We choose a different approach, aiming to determine the foraging strategies of females based on the isotopic values of their pups. We then assessed if pup weaning mass was influenced by the estimated foraging strategy of their mothers, the latter assigned based on pup isotopic values.

3) The link we established between females SIA and tracking dataset (lines 218-225 in the main document) is based on 60 individuals. We unfortunately do not have more individuals with complete post-moulting tracks which were blood-sampled on their return ashore. Among those 60 females, none has a known pup during the following breeding period. This lack of concomitant information is explained on one hand by the difficulties to record a complete post-moulting trip and to be able to recover the tag and blood-sample the tagged individuals on their return ashore at the study site. On the other hand, this is due to the protocols and sampling design at Kerguelen Islands, were no mark recapture programs are conducted on marked individual due to logistical issues (very large island and elephant seal population) requiring a too large effort for tag monitoring by the team in the field.

Our study focusses on the foraging strategies displayed by female SES during the post-moult foraging trips, and their potential impacts on their pups during the following breeding season. Such inferences appear as relevant as they were mentioned in previous studies conducted at South Georgia and Macquarie Islands:

Fedak et al., 1996	*"maternal investment is influenced by prey availability and female foraging success during the eight-month long pre-breeding migration"*

Arnbom et al., 1997	*"the foraging success of females over the pre-partum period (a function of foraging conditions over the winter months) strongly influences the energy expended on their pups over the lactation period and consequently the size of pups at weaning"*
McMahon et al., 2017	*"environmental conditions in the preceding winter would have a profound effect on female reproduction in terms of their pup's wean mass and subsequent survival"*
Clausius et al., 2017b	*"our study highlights how short-term environmental variability affects the life-history traits of marine predator populations, including reproductive performance, first-year survival rates and recruitment into the breeding population"*

Despite the absence of "complete" datasets (i.e. relying on the same individuals), we do believe our extensive dataset enables addressing key questions relative to the relationship between females' foraging strategies and pup weaning mass, through a step by step procedure. We first considered the link between SIA and tracking data in 60 females (i.e. we inferred their strategies during the previous post-moult foraging trip). Please note that we added a second part in ESM1, relative to the relationship between females' latitudinal distribution and blood $\delta^{13}C$ values, since our first submission. We then based our analyses on an extensive dataset (1684 pup blood-sampled at weaning among which 1543 were weighed, 2006-2018). The 1684 blood-samples conducted on pups highlighted a decrease in $\delta^{13}C$ values through time, result which was confirmed with an independent sample of 396 adult females from 2004-2017. Simultaneously, this multiple years dataset has enabled us to link pup weaning mass to the estimated foraging strategies of their mothers (assessed through pups SIA), thanks to the physiological isotopic relationship between blood $\delta^{13}C$ values in pups and their mothers' (see updated ESM2, part 2).

We acknowledge the missing direct link between mother and pups southern elephant seals in our study (i.e. tracked females and blood-sampled pups are independent), but recall that samplings were conducted on the same study site and over the same study period. We are confident that our stepwise design and extensive dataset, combined with available literature, enables us to address such questions. We agree with thorough review and do not question the relevance of suggested analyses which would undoubtedly promote tougher conclusions, but the present dataset unfortunately does not enable conducting such analyses.

Moreover, we aim to link female estimated foraging strategies with the weaning mass of their pups, but are aware that some confounding factor are very likely to complexify interpretations (e.g. importance of females size and maternal investment ; mentioned in the discussion). This is the reason why we advise to be careful with extrapolation from individual reproductive success to population trends, question which requires biggest datasets and longer time series, and usually rely on mark-recapture studies. Indeed, this is a female lifetime reproductive success that will influence the persistence of a particular strategy, and the average weaning mass values should be investigated over several generations to determine the relative importance (and future) of foraging strategies within a population. More than pup *weaning mass, resultant survival (McMahon et al., 2000) is key factor impacting seals recruitment into the breeding population (Pistorius et al., 2004, Oosthuizen et al., 2017). Individual seal weaning mass would likely impact population growth rate through recruitment around the age of four (McMahon et al., 2017; Clausius et al., 2017b), so it might be interesting to study the link between pup weaning mass and population census with a lag of few years.*

Such large datasets over so many years are really valuable and has provided an opportunity to highlight an important finding that could have implications for a range of top predators in antarctic ecosystems, so I think its well worth addressing the comment above as I think this can make a significant contribution to the field.

Referee: 2

Comments to the Author(s)

In this manuscript titled: “Decadal changes in blood δ13C values, at-sea distribution and weaning mass of elephant seals from Kerguelen.”, the authors assessed decadal (2004-2018) environmental regime shifts in the foraging habitat of an increasing population of southern elephant seals from Kerguelen Islands using blood δ13C values and bio-logging. The influence of foraging habitat on pup weaning mass was also assessed. The authors found no significant shift in seals at-sea distribution between 2004 and 2017 or changes in the proportion of females foraging in either sub-Antarctic or Antarctic habitats. Adult females foraging in sub-Antarctic conveyed a fitness advantage to their offspring and led to increased weaning weights compared to females foraging in Antarctic habitats. Aside from this interesting observation, the main finding was that blood δ13C values decreased by 0.1‰ per year. This led the authors to suggest that a “large-scale ecological shift is currently underway within the Indian sector of the Southern Ocean with direct consequences on the foraging performances of southern elephant seals”. Similar findings have already been discussed by Hobson et al. (2004) with samples collected from seals and birds sampled in the 1960s -1980s. The study provides interesting findings, but I am not convinced that the available combination of data were entirely compatible with addressing the proposed aims. Indeed, the conclusion that an environmental regime shift might occur is not supported by the presented data in light of other potential drivers. The authors needs to better explain the relevance of a 0.1‰ annual decrease in the δ13C values mean for upper-trophic level marine predator before claiming that the change will have “direct consequences on the foraging performances of southern elephant seals”.

We understand Reviewer #2 comment and modified the manuscript accordingly. Substantial modifications were conducted in the abstract (lines 30-35) and discussion (lines 304-329) to ensure tempered interpretation, and are detailed in our answers to following comments.

We did not mention Hobson et al. (2004) study in the previous version of the manuscript, and now refer to it line 332 (ref [61]).

Major comments:

The authors discussed various physical (change in oceanic fronts), biogeochemical (incl. Seuss effect), and/or ecological factors that could explain the 0.1 ‰ per year decrease in the δ13C values, and through the process of elimination, concluded that change in the baseline δ13C values likely relates to a change in the “composition of phytoplankton communities”. The conclusion that “…large-scale ecological shift is currently underway” is extrapolation beyond what the data can support. The authors are conscious of this, hence the conclusion that “Changes in the composition of phytoplankton communities should be a research priority…”. As stated, “Earlier studies revealed temporal variation in the δ13C values of metabolically inert issues…”, of which baleen and teeth provide longer records more suitable for these analyses (up to 30 yrs).

We agree that the conclusion that “a large-scale ecological shift is currently underway” was too strong regarding the available dataset and compared to studies conducted on arctic marine mammals over several decades (that we refer to in lines 88-94 and which were already mentioned in the previous version of the manuscript). This sentence could be confusing so we chose to rewrite it (lines 30-35). We tempered our discussion accordingly (lines 304-329), specify which concomitant ecological changes might occur as hypotheses are non-exclusive (lines 312-315 and previous paragraphs) and better referred to the existing body of knowledge on this topic (some references were mentioned in the introduction lines 88-94, but we now further discuss those references in the discussion lines 304-329 by reorganizing some ideas and adding more references).

- Changes in dissolved inorganic carbon (δ13CDIC) reflect changes in the δ13C of atmospheric CO2, which are decreasing due to the Suess Effect. For example, the rate of decrease in the baseline δ13C values ranges from −0.023 to −0.029‰·yr−1 based on coral reefs (Pereira et al. 2018; https://doi.org/10.1016/j.palaeo.2018.02.007). The decrease of δ13C values of 0.1‰ per year is therefore, higher than expected, but lower than a comparable study that assessed the decrease in the δ13C values during 2000 to 2015, which declined by 0.8‰–2.5‰ in three tuna species (Lorrain et al. 2019, https://doi.org/10.1111/gcb.14858; study briefly mentioned in line 322-324 of the discussion). Lorrain et al. (2019) came to the same conclusion: “We suggest a global shift in phytoplankton community structure, for example, a reduction in 13C-rich phytoplankton such as diatoms, and/or a change in phytoplankton physiology during this period, although this does not rule out other concomitant changes at higher levels in the food webs”. De la Vega et al. (2019; DOI: 10.1111/gcb.14832) present similar conclusions where they also describe a “decadal decline in δ13C-[particulate organic carbon in the water] values (1987–2013) [which] was more than 10 times larger than the trend in δ13C values of CO2 (or DIC)...”. Although cited in the present study, I believe more consideration could have been given to the existing body of knowledge on this topic, and incorporated better in the conclusions.

As previously mentioned, we have modified the discussion in order to better take into account and discuss the results of studies we already referred to (lines 304-329). However, please note that none of those studies was conducted in the Southern Ocean. Pereira et al. (2018) focusses on coral species $\delta^{13}C$ (tropical South Atlantic), giving an insight into the $\delta^{13}C$ DIC fluctuation which in turn reflects changes in atmospheric CO_2 $\delta^{13}C$ and thus Suess effect. Hirons et al. (2001), Schell (2001), Hobson et al. (2005), Newsome et al. (2007), Matthews and Ferguson (2018) and De La Vega et al. (2019) refer to marine mammals and some seabirds species occurring in the Arctic/north Pacific Ocean and present results similar to the present study despite some differences in interpretation, whereas to our knowledge none study focusses in $\delta^{13}C$ trends in the southern polar hemisphere.

Lorrain et al. (2019) assessed trends in a time series (2000 to 2015) of stable isotopes values in three species of tuna collected in the Pacific, Indian and Atlantic Ocean, between ~50°N and ~50°S. They stated that "mean annual $\delta^{13}C$ values decreased by 0.8‰ to 2.5‰ within species and ocean basins from 2000 to 2015". However, they obtained no data south to 30°S in the Indian Ocean which does not enable to draw conclusions in our study site. We nevertheless agree with Reviewer #2 suggestion, and have modified the discussion (lines 304-329) to better refer on one hand to the studies spanning longest time series (e.g. De La Vega et al., 2019), and on the other hand to Lorrain et al. (2019) work which is particularly relevant in the corresponding study field (similar investigations, and process of elimination supported by models and sensitivity analyses - synthesised in Fig.4).

- Is a change in the δ13C of up to 1.4‰ considered biologically significant enough to claim that "large-scale ecological shift is currently underway"? The authors should elaborate on what a change in δ13C of up to 1.4‰ means for the ecosystem (changes of ~10 ‰ can occur when diatom species composition changes, Henley et al. 2012; Fischer 1991; https://doi.org/10.1016/S0304-4203(09)90044-5). We know salps might be increasing at the higher latitudes, replacing sub-Antarctic krill species. Could this be changing the δ13C values? If a larger ecosystem shift is underway/happening and there is no change in the δ15N values (proxy for trophic level), how would this have "direct consequences on the foraging performances of southern elephant seals" (sensitivity of food webs)? Nonetheless, when framed along the lines of, i.e. changes in δ13C values of dissolved organic matter (DOC) on an ocean-wide scale, then a change of ~ 1.0‰ might be noteworthy; but the authors need to better clarify what their findings might mean within the broader literature.

We do not believe that an increase in Southern Ocean salps biomass could impact neither the $\delta^{13}C$ values which are dependent of location, nor the d15N values. Indeed, whether consumed or not by elephant seals -which seems unlikely-, salps are gelatinous tunicates. Abundance of gelatinous organisms is known to globally increase (Richardson et al., 2009; doi: 10.1016/j.tree.2009.01.010), and more than impacting isotopic values, we assume that an increase in salps abundance (and *more generally gelatinous organisms such as Cnidaria and Ctenophora) may induce some changes in the functioning of Southern Ocean ecosystems. Indeed, energy flow pathways vary between several mid-trophic levels according to the food web structure. Gelatinous organisms are sometimes considered as "a trophic dead-end and loss-pathway for zooplankton production", and this was for example highlighted in Ruzicka et al., 2012 (doi: 10.1016/j.pocean.2012.02.002). Their study demonstrated that gelatinous organisms were the biggest consumers among three modelled mid-trophic groups (i.e. jellyfish, forage fish and euphausiids), and transferred very little energy upwards in the Northern California Current food web during the 2003-2007 upwelling seasons.*

In phytoplankton species, the $\delta^{13}C$ values are susceptible to change simultaneously with e.g. cells size and abundance due to several physiological processes (see discussion lines 316-315). Previous work showed that changes in diatoms species composition can induce a ~10‰ isotopic shift in $\delta^{13}C$ POC (particulate organic carbon) values (Fischer, 1991; Henley et al., 2012). We thank Reviewer #2 for providing those relevant references that complete our discussion regarding possible changes in phytoplankton communities, and which we added in the discussion (lines 317-319). Further than the 1.4‰ decadal decrease we observe in elephant seals blood $\delta^{13}C$ values, which was larger than expected, we want to draw attention to the uninterrupted decrease in isotopic values observed from one year to another over a decade. This decrease cannot solely be explained by a change in seals latitudinal distribution (see ESM1 part 2) or by SUESS effect (see discussion lines 297-299), suggesting a progressive modification in the Southern Ocean's $\delta^{13}C$ isoscapes. Because we preclude modification in seals trophic position (see results relative to $\delta^{15}N$ lines 231-235, ESM2 part1, and mentioned in discussion lines 286-290), decrease in seals $\delta^{13}C$ values may reflect changes in Southern Ocean primary productivity and/or phytoplankton communities' composition, but this requires further multidisciplinary investigation.

As illustrated with gelatinous organisms, such food web modifications (organisms' size and abundance, which can be linked to $\delta^{13}C$ values in phytoplankton) may impact energy transfer and ultimately elephant seals prey abundance and/or quality. However, such assumptions are speculative, and this is the reason why we did not further discuss this point in the paper. Available datasets and statistical analyses conducted on isotopic values lead us to suspect a modification in primary productivity and/or a change in phytoplankton communities through a process of elimination, but this does not rule out other concomitant explanations, and conclusions related to ensuing energy transfer cannot be drawn without ecosystem modelling and is beyond what the present dataset can support. As mentioned above, we modified the misleading "large ecological shift" expression in the abstract (lines 30-35) and developed the discussion accordingly to ensure balanced and non-hastily interpretation (lines 304-329).

- It is noted that "a 303 km southward shift in 13 years" occurred. The authors state "such latitudinal shift would not be sufficient to explain the decrease in the δ13C values". The authors are urged to provide the data/elaborate on why this is the case.

Could small changes in the foraging latitude (albeit not statistically significant) explain the 0.1‰ δ13C decrease per year given the δ13C isoscape in the Southern Ocean? How much change in the foraging range (degrees) should occur per year to explain a change of δ13C decrease of 0.1‰? Perhaps the authors can provide some sort of sensitivity analyses in this regard?

We thank Reviewer #2 for his/her relevant comment. We added a section in ESM1 (i.e. part 2- Relationship between females latitudinal distribution and blood δ13C values) to address the corresponding questions. To fully explain a -1.4 ‰ blood $\delta^{13}C$ decrease over the study period (2004-2017), female seals should have moved ~ 9.33° (corresponding to 1036 km) southward, which is obviously not the case.

We are aware our study may not represent the whole Southern Ocean ecosystem as isoscapes are not precisely determined (our additional analysis displayed in ESM1 relies on 32 individuals sampled during the austral summer). Hence, we went further by comparing our results with those obtained by Quillfeldt et al. (2005) (doi:10.3354/meps295295) which studied Wilson's storm-petrel but also gathered δ13C values from numerous species obtained from the literature. They fitted two linear regressions:

(1) $\delta 13C_{seabird\_chicks} = -10.24 - 0.21 * latitude$

(2) $\delta 13C_{crustaceans+fish+squids+seabirds} = -8.52 - 0.26 * latitude$

Using their regressions to estimate latitude from δ13C values, equation (1) would imply that elephant seals should have moved 6.66° (740 km) southward over a 13-years period for their blood δ13C values to decrease of 1.4 ‰. Equation (2) would correspond to a 5.38° (597 km) southward shift in their latitudinal distribution over the study period. Those additional equations corroborate the fact that a latitudinal shift in elephant seals distribution could contribute to the decrease in δ13C values but cannot be the sole explanation.

- What is the lag effect of the change in terms of "…large-scale ecological shift is currently underway"? "Equilibration timescale for the isotopic ratios 13C/12C in the ocean mixed layer is on the order of a decade" (Pereira et al. 2018). Also, consider the influence of changes in sea ice cover and the associated "biological pump" in the Southern Ocean. The "CO2 uptake by the Southern Ocean (<35◦S) varies substantially on all timescales and is a major determinant of the variations of the global ocean carbon sink" (Gruber et al. 2019; https://doi.org/10.1146/annurev-marine-121916-063407) and could have decadal effects on the δ13C values without major ecosystem shift consequences (?).

There is indeed a lag between the atmospheric increase in isotopically light CO_2 released during anthropogenic fossil fuel burning, which dilutes atmospheric $^{13}C/^{12}C$, and the decrease in marine $\delta^{13}C$ values. We won't further detail the underlying processes which are detailed in Quay et al. (1992). However, we want to draw attention on the fact that no change in DIC $\delta^{13}C$ values has been detected south of the Polar Front in the Indian sector of the Southern Ocean over the last decade (as mentioned in lines 301-303). Hence, it suggests that the decrease in blood $\delta^{13}C$

values obtained in elephant seals reflects biological changes occurring in lower trophic levels. This decrease in $\delta^{13}C$ values was observed for the whole elephant seals population, whenever the attributed foraging strategies (i.e. seals foraging or not under sea ice edge).

Moreover, the isotopic integration time in seals blood is of few months, so data resolution is probably not sufficient (and fine-scale physical/chemical oceanographic data not available for the entire Southern Ocean) to conduct comparisons and infer the possible influence of oceanographic parameters (i.e. sea-ice, but also water temperature and mixed-layer depth, sub-mesoscale features, Fe or Si availability,…) on primary producers and ultimately seals blood $\delta^{13}C$ values.

Decadal effects on $\delta^{13}C$ may occur without major ecosystem shift consequences, but further multidisciplinary investigations are needed to assess the extent to which ongoing environmental changes may affect elephant seals and more generally all Southern Ocean's food web species. We further discuss this point in our answer to next Reviewer #2 's comment, and added a sentence referring to it in lines 326-329 of the discussion. However, we recall that the available dataset does not enable answering such questions and that southern elephant seals studied in the present manuscript offer some information regarding possible environmental shifts and so may act as environmental sentinels. More than deciphering undoubtly complex underlying mechanisms explaining the decadal decrease in seals blood $\delta^{13}C$, the present study opens up new prospects relative to the oceanography of the Indian sector of the Southern Ocean, and the structure and functioning of associated ecosystems.

- Changes in ocean productivity are also known to affect oceanic 13C-POC (persistent organic matter) values (some phytoplankton species). As with many studies before, the lack of baseline 13C values continues to hinder identification of the drivers of the temporal decrease of δ13C in both hemispheres, which in marine mammals, are often larger than the Suess effect (Vega et al. 2019). Essentially, the δ13C values can change without necessarily having a "large-scale ecological shift". The noted "increase in surface chlorophyll-a biomass" which likely occurs to enhanced thermal stratification in the South Ocean could lead to the incorporation of more 13C over time and explain the decreasing δ13C values. "The baleen records reveal a consistent decrease in the δ13C values (over 2.7‰) for the Bering and Chukchi phytoplankton, which Schell suggests reflects a decrease in phytoplankton growth rates" (Freeman, 2001).

We agree with the first part of Reviewer #2's comment. Sharp specific studies relative to baseline $\delta^{13}C$ values, ecological network modelling and food web energetics are needed to decipher the impacts of oceans' productivity and change in $\delta^{13}C$ values on intermediate trophic levels and ultimately top marine predators. This is the reason why we mentioned that such questions require multidisciplinary investigations (line 327) and composition of phytoplankton communities should be a research priority (line 325). Longest time-series should also be beneficial. However, the present study is intended as a step towards a better understanding of current modifications occurring in Southern Ocean's ecosystems. It is to our knowledge the first study *highlighting a decrease in the $\delta^{13}C$ values of a marine top predator over a decade in such a latitudinal range in the Southern Ocean. Tracking data are usually lacking in previous studies investigation $\delta^{13}C$ trends in marine species, preventing authors from disentangling the relative importance of possible explanation factors, but thanks to our multidisciplinary approach (tracking + SIA), we were able to discount seals latitudinal migration as the possible explanation of the decrease in $\delta^{13}C$ values. We showed concomitant changes in seals' pup weaning mass, and the elephant seals population from Kerguelen Islands is currently increasing (Laborie et al., unpublished data). Some recent studies highlighted an increase in primary productivity over the past 20 years in the Southern Ocean (Del Castillo et al., 2019) and we share the interpretation of a possible shift in phytoplankton community structure with De La Vega et al. (2019) and Lorrain et al. (2019). Despite not precisely assessed, there is no doubt that some changes are currently happening in Southern Ocean ecosystems, and those changes (either increase in primary productivity or modification in communities structure) are likely to impact upper trophic levels. As stated above, we updated the abstract to remove the "large-scale ecological shift is currently underway" misleading affirmation (line 30-35) and conducted changes in the ms accordingly in order to temper our conclusions (lines 304-329).*

We do believe the present study can represent a significant contribution to the field, but opens prospect for various other essential questions that should be answered to offer a better and global understanding of Southern Ocean ecosystems, the current modifications occurring therein, and their consequences. Some non-exhaustive research avenues would consist in (i) sampling of planktonic and mid-trophic level organisms to ensure their identification, assess their abundance and conduct SIA, (ii) investigating SeaWiFS satellite images of water colour (see Séverine Alvain's publications) to assess dominant phytoplankton groups over a complete annual cycle and conduct comparisons on an inter-annual basis to evaluate the evolution of phytoplankton community structure, (iii) investigating southern elephant seals foraging behaviour, energy expenditure/gain over the same study period, and (iv) conducting demographic studies on several species simultaneously and assessing energy flow pathways in order to model Southern Ocean ecosystems.

- The authors account for the poleward potential "migration of targeted preys" seeing that the "distribution of these mesopelagic fish is mostly ruled by the temperature of water masses". However, I did not notice a discussion on the potential change in the vertical (depth) used by SES and their prey in relation to vertical ��13C baseline gradients (see e.g., McIntyre et al. 2013; DOI:

https://doi.org/10.1017/S0954102012000570).

McIntyre et al. (2012) study focusses on male southern elephant seals satellite tagged at Marion Island. They highlighted that male seals forage in pelagic waters and do not target areas of shallow bathymetry close to Marion Island contrary to previously thought (and contrary to males from the Kerguelen population). They also demonstrated that male seals tend to follow the diurnal vertical migration of their preys. This phenomenon has been shown in female elephant seals from Kerguelen

Island (Guinet et al., 2014), and there is to our knowledge no link between diel vertical migration and δ^{13}C values. Benthic food webs are indeed more enriched in ^{13}C than pelagic food webs (France, 1995), but prey of female elephant seals from the Kerguelen Islands are pelagic anyway. Moreover, McIntyre's study does not rely on SIA.

Seals diving depth is impacted by the water masses and depth their prey are located in, and is influenced by water temperature and light attenuation (Guinet et al., 2014). As elephant seals main prey, myctophids vertical distribution may be impacted by climate change (Freer al., 2019). However, we believe a change in the vertical distribution of their prey won't influence δ^{13}C values (also note that no change in the vertical distribution of abiotic carbon has been detected over the last decade, see lines 301-303), but may surely impact seals energy expenditure and fitness. This is the reason why we chose not to discuss vertical δ^{13}C gradients in the present paper, but plan to study seals foraging behavior and energy expenditure/gain over the same time-series in the future.

Minor comments

Line 65: refs cited are not relevant to all the mentioned locations. Perhaps add MCMahon et al. 2005 (Mamm Rev) and Pistorius et al. 2011

(https://doi.org/10.2989/1814232X.2011.637357)

We added those references in the manuscript (line 67, refs [19] and [22]).

Methods: Where were the isotopic analyses conducted (laboratory) and how many laboratory standards were used? Also need information on which laboratory standards were used (biochemical composition should be similar to blood).

Precisions were added in the ms (lines 170-171 and 178).

Lines 337-339: See McIntyre et al. 2017 (https://doi.org/10.1016/j.anbehav.2017.03.006) where mention of this is made. Also relevant in line 93.

We corrected this omission and added a citation relative to McIntyre et al. (2017) study (ref [43], line 344).

Results, Fig 1 – Seeing that the pup δ13C C values are presented at an annual resolution, would it be sensible to colourize the tracks for each year?

Figure 1 and corresponding legend (lines 639-643) were updated as suggested.