



Research

Cite this article: Mestre J, Authier M, Chérel Y, Harcourt R, McMahon CR, Hindell MA, Charrassin J-B, Guinet C. 2020 Decadal changes in blood $\delta^{13}\text{C}$ values, at-sea distribution, and weaning mass of southern elephant seals from Kerguelen Islands. *Proc. R. Soc. B* **287**: 20201544.
<http://dx.doi.org/10.1098/rspb.2020.1544>

Received: 29 June 2020

Accepted: 27 July 2020

Subject Category:

Ecology

Subject Areas:

ecology, behaviour, environmental science

Keywords:

foraging habitat, stable isotopes, bio-logging, population strategies, decadal change, Indian sector of the Southern Ocean

Author for correspondence:

Julie Mestre

e-mail: julie.mestre@cebc.cnrs.fr;

j.mestre@hotmail.fr

Electronic supplementary material is available online at <https://doi.org/10.6084/m9.figshare.c.5082874>.

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

Julie Mestre^{1,2}, Matthieu Authier^{3,4}, Yves Chérel¹, Rob Harcourt⁵, Clive R. McMahon^{5,6,7}, Mark A. Hindell⁷, Jean-Benoît Charrassin⁸ and Christophe Guinet¹

¹Centre d'Etudes Biologiques de Chizé (CEBC), UMR 7372 du CNRS-La Rochelle Université, 79360 Villiers-en-Bois, France

²Sorbonne Université, Collège Doctoral, F-75005 Paris, France

³Observatoire PELAGIS, UMS 3462 La Rochelle Université and CNRS, La Rochelle, France

⁴ADERA, Pessac Cedex, France

⁵Department of Biological Sciences, Macquarie University, North Ryde, NSW, Australia

⁶IMOS Animal Tagging, Sydney Institute of Marine Science, Sydney, NSW, Australia

⁷Institute for Marine and Antarctic Studies, University of Tasmania, Hobart, TAS, Australia

⁸LOCEAN/IPSL, Sorbonne Université-CNRS-IRD-MNHN, UMR 7159 Paris, France

JM, 0000-0003-3020-8921; MA, 0000-0001-7394-1993; YC, 0000-0001-9469-9489; RH, 0000-0003-4666-2934; CRM, 0000-0001-5241-8917; MAH, 0000-0002-7823-7185; J-BC, 0000-0003-1679-6974; CG, 0000-0003-2481-6947

Changes in the foraging environment and at-sea distribution of southern elephant seals from Kerguelen Islands were investigated over a decade (2004–2018) using tracking, weaning mass, and blood $\delta^{13}\text{C}$ values. Females showed either a sub-Antarctic or an Antarctic foraging strategy, and no significant shift in their at-sea distribution was detected between 2004 and 2017. The proportion of females foraging in sub-Antarctic versus Antarctic habitats did not change over the 2006–2018 period. Pup weaning mass varied according to the foraging habitat of their mothers. The weaning mass of sub-Antarctic foraging mothers' pups decreased by 11.7 kg over the study period, but they were on average 5.8 kg heavier than pups from Antarctic foraging mothers. Pup blood $\delta^{13}\text{C}$ values decreased by 1.1‰ over the study period regardless of their sex and the presumed foraging habitat of their mothers. Together, these results suggest an ecological change is occurring within the Indian sector of the Southern Ocean with possible consequences on the foraging performance of southern elephant seals. We hypothesize that this shift in $\delta^{13}\text{C}$ is related to a change in primary production and/or in the composition of phytoplankton communities, but this requires further multidisciplinary investigations.

1. Introduction

Global climate change triggers deep modifications in a broad range of terrestrial and marine ecosystems, and across a great variety of species [1,2]. Of particular concern are polar environments as climate change models predict that ocean warming should be especially intense at high latitudes with some likely large-scale consequences on the related marine ecosystems [3–5]. In the Southern Ocean (water masses south of the Subtropical Front), these predictions are supported by an increasing number of empirical observations, related to the melting of coastal glaciers [6,7], a reinforced wind regime modifying nutrient vertical advection and therefore influencing primary production [3,8], and an increase in surface chlorophyll-a biomass [9]. Quantifying and integrating the behaviour of top and wide-ranging predators is an especially informative way to monitor ecosystem changes. Due to their upper trophic

position, their vital rates integrate spatial and temporal variation of the underlying trophic levels—from phytoplankton to their prey that are generally difficult to monitor—across broad ocean basins [10]. Consequently, these animals can act as environmental sentinels by providing critical information about ongoing changes in components of the ecosystem that cannot otherwise be measured [10–12] and this is particularly true for the remote and poorly sampled Southern Ocean [13–16].

Among such upper predators, southern elephant seals (*Mirounga leonina*, hereafter SES) have been extensively studied. Adult females haul-out twice a year for approximately one month each time [17], to breed during the austral spring (September–October), and again to moult during summer (December–January). They can be monitored and sampled during these two terrestrial phases to quantify their at-sea performance by measuring mass and equipped with instruments to study their at-sea behaviour including distribution, foraging behaviour, and success. Because of their large body mass and abundant populations, SES are important consumers of resources in the Southern Ocean [18]. Therefore, variations in their vital rates and demography are likely to reflect large-scale changes in food availability. In that context, the Kerguelen, Crozet, and Marion Islands populations from the Indian sector of the Southern Ocean are now recovering following a marked decrease in numbers between the 1960s and early 1990s [19–22], suggesting that foraging conditions have been improving over the last decades. On the other hand, the population on Macquarie Island from the Pacific sector of the Southern Ocean is still decreasing, presumably because of a lack of available resources [10,19]. The status of the largest population of South Georgia is currently unknown [10]. Poor foraging efficiency by a female results in a decrease in pup weaning mass and first-year survival [23,24], ultimately leading to lower recruitment into the reproductive population [25,26]. Therefore, monitoring simple parameters such as pup weaning mass provides information on the foraging performance of their mother [25,27].

Biotelemetry tags provide critical information for monitoring animals' at-sea movements and identifying foraging habitats [11,12,28], but are generally deployed on a small number of individuals due to their cost. They enable the detection of possible changes over time in the at-sea distribution of marine predators. Complementary to biotelemetry, stable isotope analysis from individual tissues provide an indication of diet/trophic levels ($\delta^{15}\text{N}$ [29,30]) and foraging habitat ($\delta^{13}\text{C}$), and can be easily conducted on a large number of individuals. A Southern Ocean latitudinal gradient in $\delta^{13}\text{C}$ values [29,31] enables the delineation of broad-scale latitudinal foraging habitats of female SES according to their blood $\delta^{13}\text{C}$ values [32,33]. Long-term monitoring of the $\delta^{13}\text{C}$ values can be a powerful way to quantify longitudinal foraging distribution and/or environmental conditions. If changes in $\delta^{13}\text{C}$ values take place over time without a change in where individuals are distributed at-sea, this suggests that physical, biogeochemical, and/or ecological changes are taking place at the ecosystem scale.

Earlier studies revealed temporal variation in the $\delta^{13}\text{C}$ values of metabolically inert tissues in a range of Arctic marine mammals including Steller sea lions [34], bowhead whales [35], northern fur seals [36], beluga whales, and killer whales [37]. The lack of $\delta^{13}\text{C}$ baseline information and animal movement data prevented these authors from disentangling the driving mechanisms of trends in $\delta^{13}\text{C}$ values. However, they suggested that $\delta^{13}\text{C}$ variations were linked to changes in

primary productivity, combined with the release of anthropogenic CO_2 [38,39]. Isotopically light CO_2 released during anthropogenic fossil fuel burning causes a dilution of atmospheric $^{13}\text{C}/^{12}\text{C}$ and ultimately decreases marine $\delta^{13}\text{C}$ values. This process is referred to as the 'Suess effect'.

As adult SES display fidelity to their foraging sites [40–43], SES are likely to be affected by ongoing environmental changes at their foraging grounds propagated through the food web. This will be reflected in population-level demographic responses to environmental variations [23,44,45]. As part of a long-term study, the Kerguelen SES population has been censused annually since the late 1950s, and recent analyses reveal a 20% increase in the size of the Kerguelen SES population (J Laborie 2019, *et al.*, unpublished data). At-sea movement data are available from satellite tracking studies since 2004 as well as the blood $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values of tracked individuals. In addition, weaning mass of pups and their $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values have been monitored every year since 2006. Because pups exclusively feed on their mother's milk until weaning, pup blood isotopic values indicate the isotopic values of their mothers [46]. The concomitant study of foraging performance indices (such as pup weaning mass) and isotopic values may highlight regional differences in foraging performances with potential demographic consequences.

The first and main objective of this study was to investigate if a change in seal $\delta^{13}\text{C}$ values took place over the study period and whether this variation reflects a change in the at-sea foraging distribution of female SES or changing $\delta^{13}\text{C}$ isoscapes in the Indian sector of the Southern Ocean. We assessed whether this shift in $\delta^{13}\text{C}$ values reflects environmental changes such as the Suess effect and/or other broad-scale ecological mechanisms [38]. The second objective of this study was to determine if pup weaning mass varied according to the estimated foraging habitat of their mothers and over the study period. Such changes could be used as an index of female breeding success and have implications for population size and growth at Kerguelen Islands. Finally, we discuss the observed changes in the Kerguelen SES population over the last 15 years and the underlying potential environmental drivers of such changes.

2. Material and methods

Fieldwork took place on Kerguelen Islands from 2004 to 2018, as part of long-term scientific programs led by CEBC. All animals used were cared for in accordance with the French Polar Institute Paul Emile Victor (IPEV) ethics committee guidelines. Data processing and statistical analyses were performed under the R v. 3.6.1 software [47], and the *ggplot2* package was used for graphical representations [48].

(a) Satellite telemetry

From 2004 to 2017, 154 post-moult adult female elephant seals were captured and anaesthetized with an intravenous injection of Zoletil100 (1:1 combination of tiletamine and zolazepam; [49,50]). They were equipped with a glued head-mounted satellite-relayed-data-logger (CTD-SRDL, $10.5 \times 7 \times 4$ cm, Sea Mammal Research Unit, St Andrews, UK). Individual seals were measured from snout to tail and tagged on land during the breeding (austral spring) or moulting period (austral summer). Seals carrying such devices were not affected in either the short-term (growth rates) or long-term (survival) [51]. Seals at-sea movements were determined using the ARGOS satellite tracking system (<http://www.argos-system.org>).

The raw tracking data were filtered by first removing class Z locations (the lowest location quality index provided by the ARGOS service). Then the McConnell *et al.* [18] speed filter was applied to remove successive locations implying an unrealistic speed (20 km h⁻¹; [52]). The resulting tracks were mapped to identify the main foraging habitats and used to investigate changes in mean latitudinal distribution. A mixture model set up on the density of satellite locations with respect to latitude using the Rmixmod R package [53] was used to determine the main latitudinal foraging habitats. Only locations for the months of May, June, and July were retained to calculate the trip's mean latitude of each individual and allow for inter-annual comparisons. Those three months were chosen as they are included in the core foraging area of SES during their post-moult trip, and are the best correlated to the blood $\delta^{13}\text{C}$ isotopic values of SES sampled during the breeding period [32]. Linear models of the mean latitude of each individual trip (for May, June, and July) according to the year were performed for each foraging habitat.

(b) Pup weaning mass

Each year from 2006 to 2018, between 57 and 275 pups were tagged at birth with a flipper-tag set in the interdigital space of the hind-flipper. This tag allowed pup identification for recapture at weaning approximately three weeks later, when it moved out of the harem. These known-age pups were weighed to the nearest 0.1 kg before removing the flipper-tags. Pup data collected in 2017 were excluded from the analyses to remove spatial variability because they were sampled at another sub-colony. Females from that sub-colony foraged in a different location compared to females from the east Courbet sub-colony (C Guinet 2019, unpublished data).

(c) Stable isotope analyses

Blood samples were taken from the extradural intervertebral venous sinus for all elephant seals regardless of their age and sex. All pups were sampled at weaning, whereas adult females were sampled when satellite tags were deployed and recovered. Whole blood samples (hereafter blood) were stored in 70% ethanol until laboratory analyses. Females were considered sexually mature if they were longer than 1.89 m (i.e. the length of the smallest female observed with a pup within our dataset). Female seals of unknown length or those smaller than 1.89 m were excluded from stable isotope analyses.

Prior to isotopic analyses, blood samples were stood in a fume hood to evaporate ethanol, and then freeze-dried for 48 h. The resulting blood powder was weighed (0.3–0.5 mg) into tin cups before combustion in an elemental analyser (Flash 2000, Thermo Scientific, Milan, Italy) coupled to a continuous flow mass spectrometer (ConFlo IV, Thermo Scientific, Bremen, Germany). Isotopic analyses were conducted in LIENSs Stable Isotope Facility (La Rochelle, France). Carbon to nitrogen (C:N) mass ratios were carefully checked because lipids are depleted in ¹³C relative to proteins and carbohydrates [54]. When C:N ratios were above 3.7, lipids were extracted from blood using cyclohexane and new stable isotope analyses were conducted. Stable isotope values are presented in the usual δ notation with units expressed as parts per thousand (‰) relative to Vienna Pee Dee Belemnite and atmospheric N₂ for $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$, respectively. Precisions for isotopic measurement were 0.15‰ for $\delta^{13}\text{C}$, and 0.20‰ for $\delta^{15}\text{N}$, respectively. In addition to C:N mass ratios, replicate measurements of laboratory standards (USGS-61 and USGS-62) were checked to ensure that inter-annual comparisons of stable isotopes measurements would not be skewed.

Stable isotope values were compared inter-annually for monitored pups and tagged adults in order to detect any trends in foraging habits over the study period. Proportions of individuals using either the Antarctic or sub-Antarctic habitats were studied

using mixture models, which are typically used to determine hidden groups of individuals inside a population of some known parameters. SES blood $\delta^{13}\text{C}$ values follow a bimodal distribution [33]. We thus assumed that a $\delta^{13}\text{C}$ bimodal distribution reflects the two foraging strategies of female SES (i.e. lower blood $\delta^{13}\text{C}$ values in the Antarctic zone versus higher $\delta^{13}\text{C}$ values in the sub-Antarctic zone). Mixture models were run for $\delta^{13}\text{C}$ values of blood-sampled pups, taking into account the effect of year and a potential trend in $\delta^{13}\text{C}$ to avoid any bias in the formation of groups through time. We modelled $\delta^{13}\text{C}$ as a mixture of two Gaussian distributions:

$$\delta^{13}\text{C} = p(\delta^{13}\text{C}_{\text{sub-Antarctic}} + \varepsilon_{\text{sub-Antarctic}}) + (1 - p)(\delta^{13}\text{C}_{\text{Antarctic}} + \varepsilon_{\text{Antarctic}}),$$

where p is the probability of seals having foraged in the sub-Antarctic zone, ε the residuals, and $\delta^{13}\text{C}_{\text{sub-Antarctic}} > \delta^{13}\text{C}_{\text{Antarctic}}$. Models were fitted in a Bayesian framework (see electronic supplementary material S3 for model specification) with the R package rstan [55], which runs Stan software [56] through R. Unless specified, blood isotopic values were raw values of pups. Because pup stable isotope values reflect those of their mothers ([46], updated in electronic supplementary material S2), the two groups of pups assigned according to their $\delta^{13}\text{C}$ value enabled a comparison of weaning mass according to the estimated foraging habitat targeted by their mother (i.e. sub-Antarctic versus Antarctic). Those two habitats relate to broad-scale foraging zones, and do not correspond to the water masses the SES passed through.

3. Results

(a) Satellite telemetry to investigate at-sea distribution

From 2004 to 2017, 64 complete post-moult foraging trips (approx. 180 days) were collected from the 154 equipped adult females. Most females travelled southeast of Kerguelen Islands (figure 1). A mixture model of the number of latitudinal satellite locations suggested that a threshold at 58°S could be used to split individuals according to their foraging habitat (sub-Antarctic north of 58°S, and Antarctic south of 58°S; electronic supplementary material S1, figure S1). No significant shifts in the latitudinal distribution of female SES was found for any of the foraging habitats (lm: mean latitude_{[May–July], sub-Antarctic habitat} = $-0.21 \times \text{year} + 363.83$, $n = 38$, $p\text{-value} = 0.12$, $R^2 = 0.07$; lm: mean latitude_{[May–July], Antarctic habitat} = $0.10 \times \text{year} - 271.26$, $n = 22$, $p\text{-value} = 0.37$, $R^2 = 0.04$).

(b) Insights into the foraging habitat through stable isotopes

Linear models were established for adult females that were blood-sampled during tag deployment or on retrieval (during either the moult, $n = 244$ or breeding period, $n = 153$). The blood $\delta^{13}\text{C}$ values of adult females decreased significantly with time ($\delta^{13}\text{C} = -0.11 \times \text{year} + 206$; $n = 396$, $p\text{-value} < 0.001$, $R^2 = 0.12$), highlighting a mean overall decrease of -1.4‰ over the 2004–2017 period.

A multiple linear model on females which were fitted with satellite tags and blood-sampled on their return ashore following their post-moulting trip ($\delta^{13}\text{C} = 0.13 \times \text{mean latitude} - 0.09 \times \text{year} + 181.10$; $n = 60$, $p\text{-value} < 0.001$, $R^2 = 0.59$) revealed a significant effect of year (negative effect) and mean latitude of trips from May to July (positive effect) on the blood $\delta^{13}\text{C}$ values of female SES. As expected, the $\delta^{13}\text{C}$ value of a female was also strongly correlated to the mean

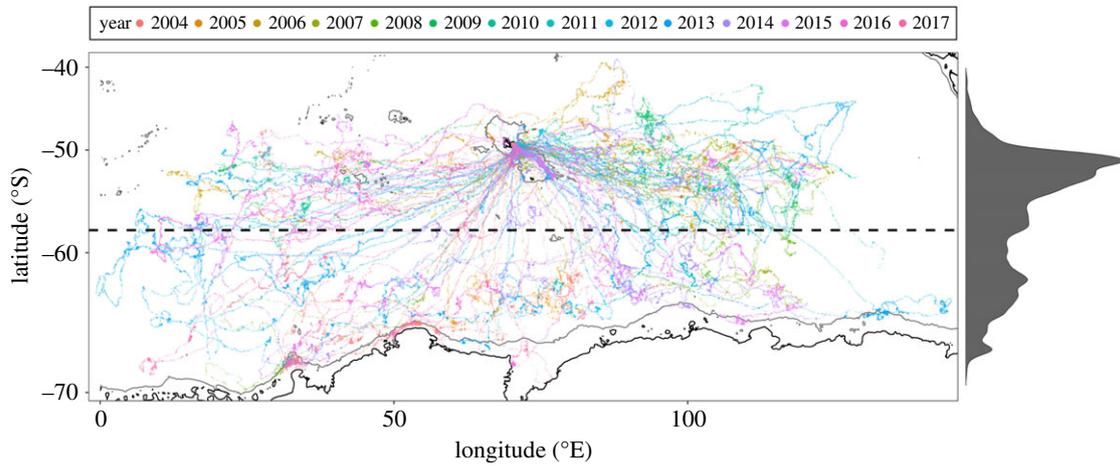


Figure 1. Satellite tracking of 64 complete post-moult foraging trips of adult female southern elephant seals from Kerguelen Islands. Trip colours represent the year of tracking. Black lines indicate the coastline of adjacent landmasses (Antarctica, Kerguelen Islands, and Australia), and grey lines the 1000 m isobath. The marginal plot depicts the density of satellite locations, and the dashed black line the -58°S latitudinal threshold. (Online version in colour.)

Table 1. Blood $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values of southern elephant seal pups from 2006 to 2018 at Kerguelen Islands. Female-predicted values after [46] are displayed in the last row.

	year	n	blood $\delta^{13}\text{C}$ (‰)			blood $\delta^{15}\text{N}$ (‰)		
			min	mean \pm s.d.	max	min	mean \pm s.d.	max
pup raw values	2006	214	-23.4	-21.2 ± 0.9	-18.9	10.3	11.3 ± 0.4	12.6
	2007	57	-23.6	-20.9 ± 0.9	-19.0	10.4	11.1 ± 0.4	12.3
	2008	231	-23.0	-20.9 ± 0.8	-19.1	10.2	11.5 ± 0.5	12.8
	2009	275	-23.9	-21.3 ± 0.9	-18.8	10.1	11.4 ± 0.4	12.7
	2010	204	-23.2	-21.1 ± 0.9	-19.2	10.5	11.4 ± 0.4	12.8
	2011	110	-23.7	-21.5 ± 0.8	-19.0	10.7	11.4 ± 0.3	12.6
	2012	96	-23.4	-21.7 ± 0.8	-19.9	10.8	11.5 ± 0.4	12.7
	2013	85	-23.1	-21.5 ± 0.7	-19.9	11.0	11.5 ± 0.3	12.6
	2014	112	-23.6	-21.6 ± 0.8	-20.0	10.8	11.5 ± 0.3	12.6
	2015	123	-23.3	-21.7 ± 0.8	-19.8	9.4	11.3 ± 0.5	12.8
	2016	77	-23.3	-21.8 ± 0.7	-20.0	9.7	11.3 ± 0.4	12.0
	2018	100	-23.9	-22.1 ± 0.9	-20.2	10.5	11.2 ± 0.3	12.2
	2006–2018	1684	-23.9	-21.4 ± 0.9	-18.8	9.4	11.4 ± 0.4	12.8
female estimated values	2006–2018	1684	-24.4	-21.8 ± 0.9	-19.2	9.2	10.2 ± 0.2	10.9

latitude of its trip for the months of May, June, and July ($\rho = 0.69$, p -value < 0.0001 , Spearman's rank correlation). Importantly, blood $\delta^{13}\text{C}$ values decreased over the study period for a given latitude visited by female SES.

Pup blood $\delta^{13}\text{C}$ values range from -18.8‰ to -23.9‰ , with annual means between -20.9‰ and -22.1‰ . Pup blood $\delta^{15}\text{N}$ values are less scattered, ranging from 9.4‰ to 12.8‰ with average annual means between 11.1‰ and 11.5‰ (table 1).

From 2006 to 2018, an annual decrease in $\delta^{13}\text{C}$ was found (linear model: $\delta^{13}\text{C} = -0.09 \times \text{year} + 160$; $n = 1684$, p -value < 0.001 , $R^2 = 0.11$) resulting in an overall 1.08‰ decrease in the mean $\delta^{13}\text{C}$ value of pups (figure 2). A second linear model applied on $\delta^{15}\text{N}$ values suggested a decrease over time ($\delta^{15}\text{N} = -0.006 \times \text{year} + 23$; $n = 1684$, p -value $= 0.04$, $R^2 = 0.002$). Considering the poor significance of the linear model

for $\delta^{15}\text{N}$, and because a β coefficient of -0.006 is irrelevant regarding the precision of isotopic measurements and biological meaning, only $\delta^{13}\text{C}$ values were kept for further analyses (see electronic supplementary material S2, figure S3).

The probability that a pup was born from a mother which foraged in sub-Antarctic or Antarctic waters was estimated using a mixture model on pup $\delta^{13}\text{C}$ values between 2006 and 2018. The $\delta^{13}\text{C}$ trend of -0.09‰ per year was included in the model (electronic supplementary material S3, §§1 and 2). No change in the distribution of probability to belong to either group (sub-Antarctic versus Antarctic) was detected over the study period (linear model, p -value > 0.05 ; electronic supplementary material S3, figure S5), suggesting that the balance between the two foraging habitats remained stable from 2006 to 2018 (figure 3). From 40.2% to 63.1% of individuals were attributed to the Antarctic strategy, whereas

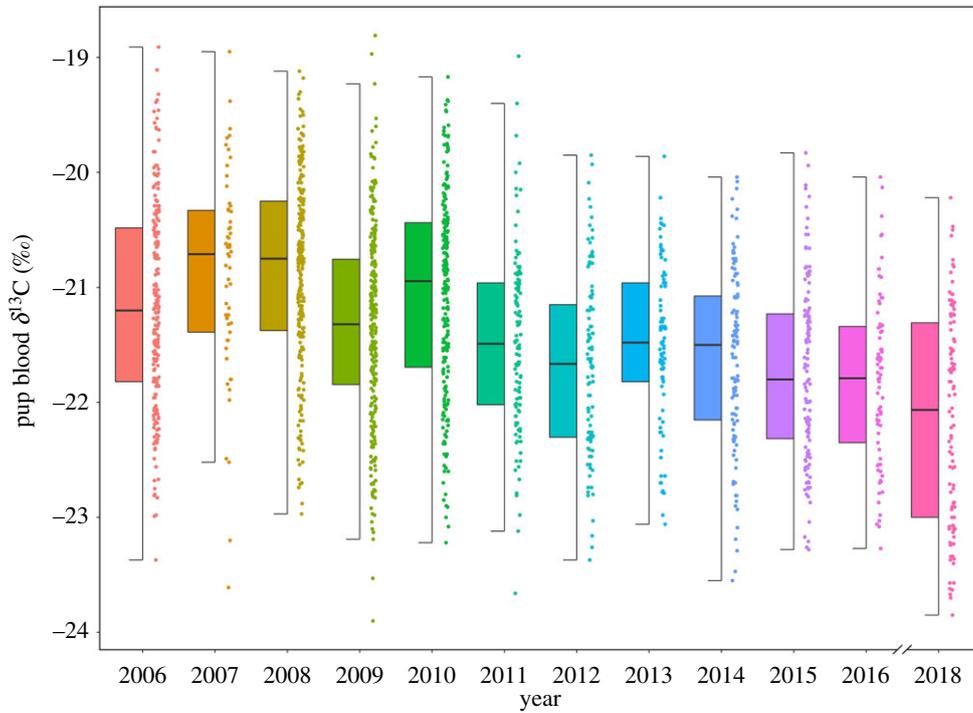


Figure 2. Hybrid box- and scatterplot of inter-annual blood $\delta^{13}\text{C}$ values of southern elephant seal pups at Kerguelen Islands. (Online version in colour.)

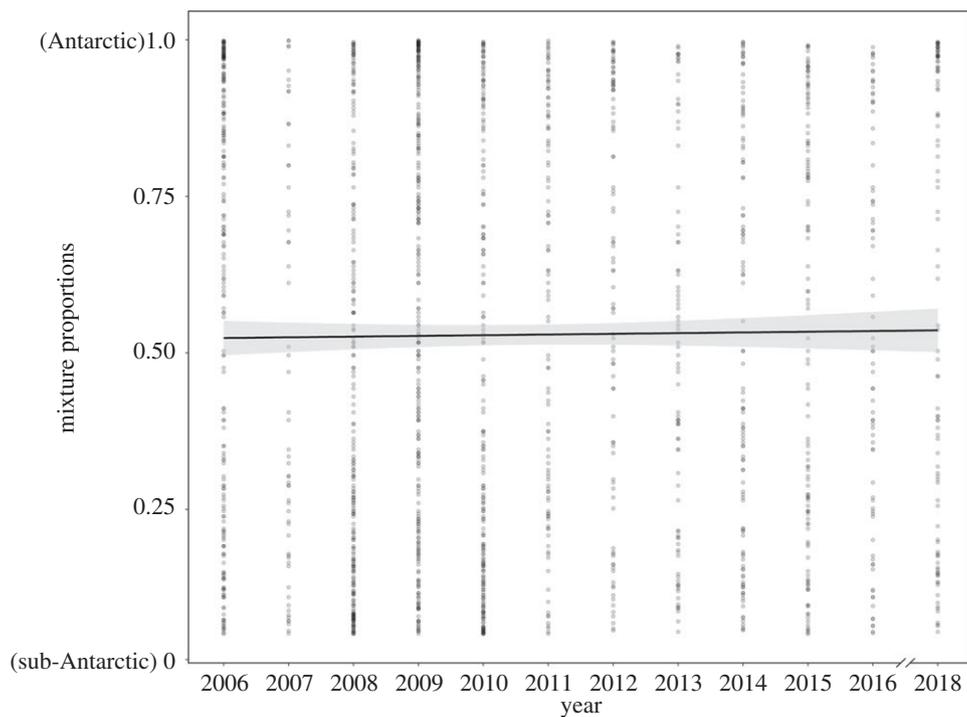


Figure 3. Marginal probabilities of southern elephant seal pups to be assigned to the Antarctic or sub-Antarctic group. Each dot represents a pup. A pup with a posterior mean of 1 is assigned to the Antarctic habitat with 100% confidence, whereas a posterior mean of 0 means that the pup belongs to the sub-Antarctic group. Pups whose probability is higher than 0.5 were assigned to the Antarctic group, whereas those with a probability lower than 0.5 were assigned to the sub-Antarctic group. The straight line represents the linear regression of the mixture proportions through years, and the shaded area highlights the 0.95% confidence interval.

36.5% to 61.5% were assigned to the sub-Antarctic one (electronic supplementary material S3, figure S6).

(c) Pup weaning mass

Of the 1684 pups in the study, 1550 were weighed and of these, 1543 were sexed. The mixture model based on pup $\delta^{13}\text{C}$

value indicated a sub-Antarctic group of 826 individuals whose mean weaning mass was 105.9 ± 23.0 kg. By contrast, the mean weaning mass of the 858 pups assigned to the Antarctic group was 100.1 ± 22.3 kg. Pups assigned to the sub-Antarctic group (i.e. with less negative $\delta^{13}\text{C}$ values) were significantly heavier (+5.8 kg) at weaning than their conspecifics (linear model: weaning mass = $100.1 + 5.8 \times$

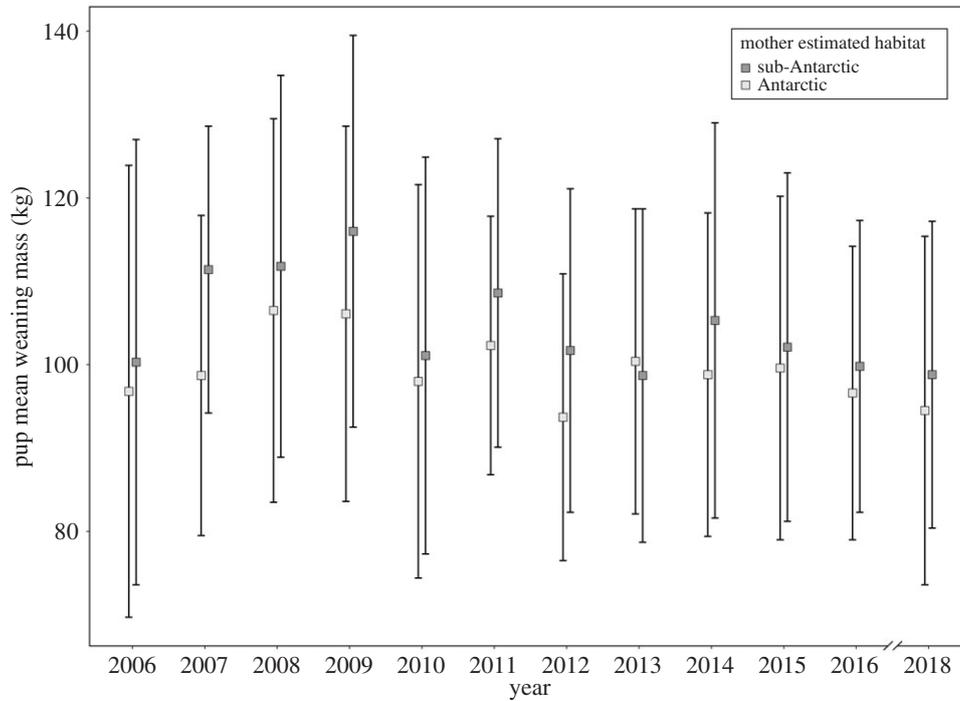


Figure 4. Mean \pm standard deviation of pup weaning mass through time. Dark grey squares correspond to mean weaning mass of pups assigned to the sub-Antarctic group, and light grey ones represent pups assigned to the Antarctic group.

foraging habitat; $n = 1550$, p -value < 0.0001 , $R^2 = 0.016$; figure 4). A linear model revealed a decrease in pup weaning mass with time (weaning mass = $-0.9 \times \text{year} + 1821$; $n = 826$, p -value < 0.0005 , $R^2 = 0.015$) in the sub-Antarctic habitat, corresponding to a mean decrease of 11.7 kg over the 2006–2018 period. No significant trend was detected in the Antarctic group.

Those results were confirmed by a multiple linear model ($p < 0.0001$, $R^2 = 0.04$, $n = 1543$) revealing that pup weaning mass was significantly influenced by their birth year ($p < 0.0001$; negative effect), the probability of being assigned to a foraging group ($p < 0.0001$; pups assigned to the sub-Antarctic group being on average heavier at weaning), and sex ($p < 0.0005$; with male pups being on average heavier than females).

4. Discussion

(a) Towards shifting foraging strategies or environmental-driven changes?

This study aimed to investigate female SES foraging strategies over 14 years, in order to detect any changes in behaviour. A mean annual decrease of -0.09% in the blood $\delta^{13}\text{C}$ values of pups was detected over the 2006–2018 period, corresponding to -1.2% in 13 years. Smaller datasets obtained from blood-sampled adult females at moulting and breeding corroborated the values from pups with a mean blood $\delta^{13}\text{C}$ decrease of -1.4% over the 2004–2017 period. We explore several possible hypotheses to explain this decrease in seal blood $\delta^{13}\text{C}$ values.

First, and perhaps most obviously, this decrease could have been related to an increase in the proportion of female SES using the Antarctic habitat compared to the sub-Antarctic one, and/or a global southward shift of their at-sea distribution. However, our findings do not support this hypothesis. A decrease in $\delta^{13}\text{C}$ values with increasing latitude is well-documented in the Southern Ocean [29,31]. If females travelled further south

to forage, this would lead to a decrease in their $\delta^{13}\text{C}$ values and those of their pups. The latitudinal distribution of adult females suggests two main habitats during their post-moult foraging trip (i.e. the Antarctic and the sub-Antarctic habitats), confirming earlier observations [32,33]. We found no change in the proportion of individuals foraging in the Antarctic versus the sub-Antarctic habitat over the study period. Inter-annual comparisons of the mean latitude of females' post-moulting tracks for the months of May, June, and July revealed a non-significant annually -0.21° trend in the distribution of sub-Antarctic foraging females which corresponds to a 300 km southward shift in 13 years. However, a minor latitudinal shift such as this would not be sufficient to explain the decrease in the $\delta^{13}\text{C}$ values (see electronic supplementary material S1, §2).

As the clear decrease in blood $\delta^{13}\text{C}$ values cannot be explained by a change in SES at-sea distribution, it may be due to changes in abiotic conditions and/or other biotic components in the Indian sector of the Southern Ocean. Blood $\delta^{15}\text{N}$ values strongly suggest that adult female SES from the Kerguelen Islands feed primarily on mesopelagic fish, including myctophids [57] with no indication of significant dietary shifts over the study period. Hence, the decrease in blood $\delta^{13}\text{C}$ values is most likely unrelated to a change in SES foraging ecology, but rather to changes in the environment itself.

An alternative explanation of the observed $\delta^{13}\text{C}$ decrease is a depletion in ^{13}C at the base of the food web ($\delta^{13}\text{C}$ baseline). Oceanic dissolved inorganic carbon (DIC) $\delta^{13}\text{C}$ relies on atmospheric CO_2 composition [58] and may be influenced by the Suess effect [39], whose magnitude varies with latitude and ocean basins [59]. Previous studies investigating metabolically inert tissues in Arctic marine mammals and seabirds, and in coral species in tropical ecosystems imputed a decrease in $\delta^{13}\text{C}$ values to the Suess effect [37,60] at times combined with changes in primary productivity [35,38,39,61]. However, the Southern Ocean's Suess effect accounts for only approximately

−0.01‰ per decade [59,62], whereas our dataset showed a tenfold greater decrease in blood $\delta^{13}\text{C}$ values (i.e. −1‰ per decade). DIC $\delta^{13}\text{C}$ may also be influenced by remobilization of deep ^{12}C because of the benthic-pelagic $\delta^{13}\text{C}$ gradient [63], implying processes such as wind strengthening or upwelling. However, no changes in the vertical distribution of abiotic carbon have been detected south of the Polar Front over the last decade in the Indian sector of the Southern Ocean (N Metzl 2019, personal communication).

Population declines in a number of top predator species across several oceans, including the Southern Ocean and over the past few decades have been attributed to decreases in primary productivity of these ecosystems (e.g. Steller sea lions [34]; rockhopper penguins [64]). It was recently revealed that primary productivity has increased over the past 20 years in the Southern Ocean [9] and is supported by a change in phenology with blooms starting earlier in spring [65]. Changes in Southern Ocean productivity and/or in the composition of phytoplankton communities could contribute to the observed decrease in seal $\delta^{13}\text{C}$ values. Photosynthesis drives $\delta^{13}\text{C}$ baseline fluctuation for a given location through many biotic processes, and $\delta^{13}\text{C}$ values then vary little throughout the food web [30,31]. The food chain $\delta^{13}\text{C}$ value is mostly affected by primary producers through the rate of C incorporation [66], cell surface/volume ratio and cell growth rate [67–69], the timing of phytoplankton blooms, and phytoplankton types [70,71]. A change in the proportion of ^{13}C -rich phytoplankton species such as diatoms versus ^{13}C -depleted nano- and picophytoplankton could for example lead to a decrease in the observed $\delta^{13}\text{C}$ values in our study [70]. Changes in diatom species composition can induce an approximately 10‰ isotopic shift in particulate organic carbon $\delta^{13}\text{C}$ values [72,73], hence investigating the evolution of phytoplankton biomass and composition of the communities seems a promising line of investigation.

Interestingly, a recent study using scenario modelling and investigating $\delta^{13}\text{C}$ trends and their causal links in three tuna species also supports the hypothesis of a global shift in the structure of pelagic phytoplankton communities [74]. Our study suggests that investigating changes in primary productivity and the composition of phytoplankton communities should be a research priority to help understand the functional links between physical oceanography and primary producers in the Indian sector of the Southern Ocean. Moreover, further multidisciplinary investigation across multiple species is needed to assess to what extent a decrease in food web $\delta^{13}\text{C}$ baseline and associated changes may impact upper trophic levels in the context of global change.

(b) From foraging habitat to reproductive success

Linking foraging behaviour to reproductive success in wide-ranging species, including SES, remains challenging. Between 1970 and 1987, the Kerguelen SES population underwent a significant decrease in the number of breeding females of 3.6% per annum [20]. Earlier studies suggested that this decline was due to poor female foraging conditions [20], implying a drop in maternal fitness and investment, leading to an overall decrease in pup weaning mass, survival, and subsequent recruitment [19,32]. It did identify that female foraging strategies (i.e. Antarctic versus sub-Antarctic habitat) are of critical importance for their pups' survival rate, and ultimately for the future of the population [44,75,76].

The influence of some abiotic factors such as sea ice extent and chlorophyll-a concentration on pup weaning mass has been suggested for SES breeding on Kerguelen, Macquarie, and Marion Islands [23,32,77–79]. A similar strong positive relationship was found between annual primary production in an Antarctic polynya and pup production in Weddell seals (*Leptonychotes weddellii*) [80]. This raises the question of the viability of SES foraging strategies in the context of global change, and the potential consequences for the SES population from Kerguelen Islands [43].

Numerous studies have revealed the existence of distinct foraging strategies among individuals from the same population (e.g. loggerhead turtles, [81]; Antarctic fur seals, [82]; northern fur seals, [83]). Adult SES display fidelity to their foraging site [40,41], and no significant change in the annual proportion of seals assigned to the two foraging strategies was detected over the study period. We suggest that both strategies may persist in the population because current environmental conditions in sub-Antarctic and Antarctic habitats provide sustainable foraging grounds. However, SES foraging success varies between individuals and with environmental conditions for a given foraging zone [84], hence generalizing the relationship between pup weaning mass and the foraging habitat of their mothers may be overly simplistic.

We found that pups born from mothers foraging in the sub-Antarctic habitat were on average 5.8 kg heavier than their conspecifics at weaning. Weaners that are 5 kg heavier could spend 10 more days fasting at-sea during their first foraging trip due to their higher energy stores [85,86], suggesting a benefit to sub-Antarctic foraging. However, we observed a decrease in pup weaning mass only in the sub-Antarctic group (−11.7 kg over the study period). A continuous decrease in pup weaning mass should impact population recruitment through reduced survival [19,26,85,86] and lead to a differing recruitment age [24]. However, density dependence predicts that weaning mass should decrease in growing populations inhabiting rich foraging areas, as individuals should breed at a younger age and thus be smaller [25]. A strong link between demographic trends and pup weaning mass has been found in multiple studies [75,77,79], and a link between pup weaning mass, the number and size of females ashore, and even harem size was demonstrated for SES at Marion [79] and Macquarie Islands [77]. The Kerguelen SES population is now increasing (J Laborie 2019, *et al.*, unpublished data) raising the question of the consequences of increased intraspecific competition.

The present work does not allow partitioning the variance to explain whether the decrease in weaning mass (only observed in pups from the sub-Antarctic group) is a consequence of a density dependence mechanism alone, or a density dependence mechanism combined with ecosystem changes. Hence, it is important to explore further the relationships between foraging strategies and reproductive success by maintaining this monitoring over a longer time scale.

Ethics. All animals used were cared for in accordance with the French Polar Institute Paul Emile Victor (IPEV) ethics committee guidelines.

Data accessibility. The tracking data were collected and made freely available by the International MEOP Consortium and the national programs that contribute to it (<http://www.meop.net>).

The SIA data underlying this study are available as part of the electronic supplementary material.

Authors' contributions. C.G., M.A.H., and R.H. designed data collection and provided the dataset. J.M. and C.G. conceived the study. J.M. and M.A. performed SIA and Y.C. helped with data validation. J.M. performed data analysis with substantial contributions from M.A. and C.G. J.M. wrote the paper and all authors contributed to the paper review, read and approved the final manuscript.

Competing interests. We declare we have no competing interests.

Funding. This study contributes to SENTinels of the SEa Ice program funded by the BNP Paribas Foundation. It benefited from a discussion held in the framework of the KER-TREND project supported by the French National program LEFE (Les Enveloppes Fluides et l'Environnement). The marine mammal data were sourced from the International MEOP Consortium and the national programs that contribute to it (<http://meop.net>), including the French National Observatory Mammals as samplers of the Ocean Environment (SNO-MEMO) data and the Integrated Marine Observing System (IMOS) for the Australian data. The French satellite tagging program was financially supported by the program Terre, Océan, Surfaces Continentales, Atmosphère (TOSCA) of the Centre National d'Etudes

Spatiales - over the whole study period -, the Agence Nationale de la Recherche and the Total Foundation. IMOS is a national collaborative research infrastructure, supported by the Australian Government. It is operated by a consortium of institutions as an unincorporated joint venture, with the University of Tasmania as lead agent. We finally thank the Institut Polaire Français Paul Emile Victor (IPEV) programs 109, H. Weimerskirch, and 1201, C. Gilbert) for providing logistical and financial support.

Acknowledgements. We thank all the fieldworkers who collected data in Kerguelen Islands since 2002, and Adélie Krellenstein and numerous students who prepared blood samples in the laboratory from 2006 to 2013. We are very grateful to Gaël Guillou from the Plateforme Analyses Isotopiques de LIENSs (La Rochelle Université) for running the stable isotope analyses. We thank Baptiste Picard for his help with the database, and Karine Heerah for her advice on the cleaning of low resolution tracking data. We also thank Nicolas Metzl for information on $\delta^{13}\text{C}_{\text{DIC}}$ vertical distribution in the Indian sector of the Southern Ocean. We finally thank two anonymous reviewers and the associate editor, Daniel Costa, for constructive comments that improved the manuscript.

References

- Sadykova D, Scott BE, Dominicus MD, Wakelin SL, Wolf J, Sadykov A. 2020 Ecological costs of climate change on marine predator-prey population distributions by 2050. *Ecol. Evol.* **10**, 1069–1086. (doi:10.1002/ece3.5973)
- Kowalczyk ND, Chiaradia A, Preston TJ, Reina RD. 2014 Linking dietary shifts and reproductive failure in seabirds: a stable isotope approach. *Funct. Ecol.* **28**, 755–765. (doi:10.1111/1365-2435.12216)
- Constable AJ *et al.* 2014 Climate change and Southern Ocean ecosystems I: how changes in physical habitats directly affect marine biota. *Glob. Change Biol.* **20**, 3004–3025. (doi:10.1111/gcb.12623)
- De La Mare WK. 1997 Abrupt mid-twentieth-century decline in Antarctic sea-ice extent from whaling records. *Nature* **389**, 57–60. (doi:10.1038/37956)
- Meijers AJS, Shuckburgh E, Bruneau N, Sallee J-B, Bracegirdle TJ, Wang Z. 2012 Representation of the Antarctic Circumpolar Current in the CMIP5 climate models and future changes under warming scenarios. *J. Geophys. Res. Oceans* **117**, C12008. (doi:10.1029/2012JC008412)
- Holland PR, Bracegirdle TJ, Dutrieux P, Jenkins A, Steig EJ. 2019 West Antarctic ice loss influenced by internal climate variability and anthropogenic forcing. *Nat. Geosci.* **12**, 718–724. (doi:10.1038/s41561-019-0420-9)
- Williams GD *et al.* 2016 The suppression of Antarctic bottom water formation by melting ice shelves in Prydz Bay. *Nat. Commun.* **7**, 1–9. (doi:10.1038/ncomms12577)
- Gregg WW, Conkright ME, Ginoux P, O'Reilly JE, Casey NW. 2003 Ocean primary production and climate: global decadal changes. *Geophys. Res. Lett.* **30**, 1809. (doi:10.1029/2003GL016889)
- Del Castillo CE, Signorini SR, Karaköylü EM, Rivero-Calle S. 2019 Is the Southern Ocean getting greener? *Geophys. Res. Lett.* **46**, 6034–6040. (doi:10.1029/2019GL083163)
- Hindell MA *et al.* 2016 Circumpolar habitat use in the southern elephant seal: implications for foraging success and population trajectories. *Ecosphere* **7**, e01213. (doi:10.1002/ecs2.1213)
- Harcourt R *et al.* 2019 Animal-borne telemetry: an integral component of the ocean observing toolkit. *Frontiers in Marine Science* **6**, Article 326. (doi:10.3389/fmars.2019.00326)
- Heylen BC, Nachtsheim DA. 2018 Bio-telemetry as an essential tool in movement ecology and marine conservation. In *YOUMARES 8 – oceans across boundaries: learning from each other* (eds S Jungblut, V Liebig, M Bode), pp. 83–107. Cham, Switzerland: Springer International Publishing.
- Barreau E, Ropert-Coudert Y, Delord K, Barbraud C, Kato-Ropert A. 2019 Scale matters: sea ice and breeding success of Adélie penguins. *Polar Biol.* **42**, 1405–1410. (doi:10.1007/s00300-019-02531-2)
- Bost CA *et al.* 2015 Large-scale climatic anomalies affect marine predator foraging behaviour and demography. *Nat. Commun.* **6**, 1–9. (doi:10.1038/ncomms9220)
- Le Guen C *et al.* 2018 Reproductive performance and diving behaviour share a common sea-ice concentration optimum in Adélie penguins (*Pygoscelis adeliae*). *Glob. Change Biol.* **24**, 5304–5317. (doi:10.1111/gcb.14377)
- Siniff DB, Garrott RA, Rotella JJ, Fraser WR, Ainley DG. 2008 Opinion: projecting the effects of environmental change on Antarctic seals. *Antarct. Sci.* **20**, 425–435. (doi:10.1017/S0954102008001351)
- Condy PR. 1979 Annual cycle of the southern elephant seal *Mirounga leonina* (Linn.) at Marion Island. *South Afr. J. Zool.* **14**, 95–102. (doi:10.1080/02541858.1979.11447655)
- McConnell BJ, Chambers C, Fedak MA. 1992 Foraging ecology of southern elephant seals in relation to the bathymetry and productivity of the Southern Ocean. *Antarct. Sci.* **4**, 393–398. (doi:10.1017/S0954102092000580)
- McMahon CR, Bester MN, Burton HR, Hindell MA, Bradshaw CJA. 2005 Population status, trends and a re-examination of the hypotheses explaining the recent declines of the southern elephant seal *Mirounga leonina*. *Mammal. Rev.* **35**, 82–100. (doi:10.1111/j.1365-2907.2005.00055.x)
- Guinet C, Jouventin P, Weimerskirch H. 1999 Recent population change of the southern elephant seal at Îles Crozet and Îles Kerguelen: the end of the decrease? *Antarct. Sci.* **11**, 193–197. (doi:10.1017/S0954102099000255)
- Authier M, Delord K, Guinet C. 2011 Population trends of female elephant seals breeding on the Courbet Peninsula, îles Kerguelen. *Polar Biol.* **34**, 319–328. (doi:10.1007/s00300-010-0881-1)
- Pistorius PA, De Bruyn PJN, Bester MN. 2011 Population dynamics of southern elephant seals: a synthesis of three decades of demographic research at Marion Island. *Afr. J. Mar. Sci.* **33**, 523–534. (doi:10.2989/1814232X.2011.637357)
- McMahon CR, Harcourt RG, Burton HR, Daniel O, Hindell MA. 2017 Seal mothers expend more on offspring under favourable conditions and less when resources are limited. *J. Anim. Ecol.* **86**, 359–370. (doi:10.1111/1365-2656.12611)
- Oosthuizen WC, Altwegg R, Nevoux M, Bester MN, de Bruyn PJN. 2018 Phenotypic selection and covariation in the life-history traits of elephant seals: heavier offspring gain a double selective advantage. *Oikos* **127**, 875–889. (doi:10.1111/oik.04998)
- Arnbom T, Fedak MA, Boyd IL. 1997 Factors affecting maternal expenditure in southern elephant seals during lactation. *Ecology* **78**, 471–483. (doi:10.1890/0012-9658(1997)078[0471:FAMEIS]2.0.CO;2)
- McMahon CR, Burton HR, Bester MN. 2003 A demographic comparison of two southern elephant seal populations. *J. Anim. Ecol.* **72**, 61–74. (doi:10.1046/j.1365-2656.2003.00685.x)
- Fedak MA, Arnbom T, Boyd IL. 1996 The relation between the size of southern elephant seal mothers, the growth of their pups, and the use of maternal energy, fat, and protein during lactation.

- Physiol. Zool.* **69**, 887–911. (doi:10.1086/physzool.69.4.30164234)
28. Ropert-Coudert Y, Wilson RP. 2005 Trends and perspectives in animal-attached remote sensing. *Front. Ecol. Environ.* **3**, 437–444. (doi:10.1890/1540-9295(2005)003[0437:TAPIAR]2.0.CO;2)
 29. Cherel Y, Hobson KA. 2007 Geographical variation in carbon stable isotope signatures of marine predators: a tool to investigate their foraging areas in the Southern Ocean. *Mar. Ecol. Prog. Ser.* **329**, 281–287. (doi:10.3354/meps329281)
 30. McCutchan JH, Lewis Jr WM, Kendall C, McGrath CC. 2003 Variation in trophic shift for stable isotope ratios of carbon, nitrogen, and sulfur. *Oikos* **102**, 378–390. (doi:10.1034/j.1600-0706.2003.12098.x)
 31. Jaeger A, Connan M, Richard P, Cherel Y. 2010 Use of stable isotopes to quantify seasonal changes of trophic niche and levels of population and individual specialisation in seabirds. *Mar. Ecol. Prog. Ser.* **401**, 269–277. (doi:10.3354/meps08380)
 32. Authier M, Dragon A-C, Richard P, Cherel Y, Guinet C. 2012 O' mother where wert thou? Maternal strategies in the southern elephant seal: a stable isotope investigation. *Proc. R. Soc. B* **279**, 2681–2690. (doi:10.1098/rspb.2012.0199)
 33. Bailleul F, Authier M, Ducatez S, Roquet F, Charrassin J-B, Cherel Y, Guinet C. 2010 Looking at the unseen: combining animal bio-logging and stable isotopes to reveal a shift in the ecological niche of a deep diving predator. *Ecography* **33**, 709–719. (doi:10.1111/j.1600-0587.2009.06034.x)
 34. Hirons AC, Schell DM, Finney BP. 2001 Temporal records of $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ in North Pacific pinnipeds: inferences regarding environmental change and diet. *Oecologia* **129**, 591–601. (doi:10.1007/s004420100756)
 35. Schell DM. 2001 Carbon isotope ratio variations in Bering Sea biota: the role of anthropogenic carbon dioxide. *Limnol. Oceanogr.* **46**, 999–1000. (doi:10.4319/lo.2001.46.4.0999)
 36. Newsome SD *et al.* 2007 The shifting baseline of northern fur seal ecology in the northeast Pacific Ocean. *Proc. Natl. Acad. Sci. USA* **104**, 9709–9714. (doi:10.1073/pnas.0610986104)
 37. Matthews CJ, Ferguson SH. 2018 Validation of dentine deposition rates in beluga whales by interspecies cross dating of temporal $\delta^{13}\text{C}$ trends in teeth. *NAMMCO Sci. Publ.* **10**. (doi:10.7557/3.3196)
 38. De La Vega C, Jeffreys RM, Tuerena R, Ganeshram R, Mahaffey C. 2019 Temporal and spatial trends in marine carbon isotopes in the Arctic Ocean and implications for food web studies. *Glob. Change Biol.* **25**, 4116–4130. (doi:10.1111/gcb.14832)
 39. Quay PD, Tilbrook B, Wong CS. 1992 Oceanic uptake of fossil fuel CO_2 : carbon-13 evidence. *Science* **256**, 74–79. (doi:10.1126/science.256.5053.74)
 40. Authier M, Bentaleb I, Ponchon A, Martin C, Guinet C. 2012 Foraging fidelity as a recipe for a long life: foraging strategy and longevity in male southern elephant seals. *PLoS ONE* **7**, e32026. (doi:10.1371/journal.pone.0032026)
 41. Bradshaw CJA, Hindell MA, Sumner MD, Michael KJ. 2004 Loyalty pays: potential life history consequences of fidelity to marine foraging regions by southern elephant seals. *Animal Behaviour* **68**, 1349–1360. ISSN 0003-3472 (doi:10.1016/j.anbehav.2003.12.013)
 42. McConnell B, Fedak M, Burton HR, Engelhard GH, Reijnders PJH. 2002 Movements and foraging areas of naïve, recently weaned southern elephant seal pups. *J. Anim. Ecol.* **71**, 65–78. (doi:10.1046/j.0021-8790.2001.00576.x)
 43. McIntyre T, Bester MN, Bornemann H, Tosh CA, De Bruyn PJN. 2017 Slow to change? Individual fidelity to three-dimensional foraging habitats in southern elephant seals, *Mirounga leonina*. *Anim. Behav.* **127**, 91–99. (doi:10.1016/j.anbehav.2017.03.006)
 44. Hindell MA, Sumner M, Bestley S, Wotherspoon S, Harcourt RG, Lea M-A, Alderman R, McMahon CR. 2017 Decadal changes in habitat characteristics influence population trajectories of southern elephant seals. *Glob. Change Biol.* **23**, 5136–5150. (doi:10.1111/gcb.13776)
 45. McMahon CR *et al.* 2019 Finding mesopelagic prey in a changing Southern Ocean. *Sci. Rep.* **9**, 1–11. (doi:10.1038/s41598-019-55152-4)
 46. Ducatez S, Dalloyau S, Richard P, Guinet C, Cherel Y. 2008 Stable isotopes document winter trophic ecology and maternal investment of adult female southern elephant seals (*Mirounga leonina*) breeding at the Kerguelen Islands. *Mar. Biol.* **155**, 413–420. (doi:10.1007/s00227-008-1039-3)
 47. R Core Team. 2019 *R: A language and environment for statistical computing*. Vienna, Austria: R Foundation for statistical Computing. See <https://www.R-project.org/>.
 48. Wickham H. 2016 *Ggplot2: elegant graphics for data analysis*. New York, NY: Springer.
 49. Field IC, McMahon CR, Burton HR, Bradshaw CJA, Harrington J. 2002 Effects of age, size and condition of elephant seals (*Mirounga leonina*) on their intravenous anaesthesia with tiletamine and zolazepam. *Vet. Rec.* **151**, 235–240. (doi:10.1136/vr.151.8.235)
 50. McMahon CR, Burton H, McLean S, Slip D, Bester M. 2000 Field immobilisation of southern elephant seals with intravenous tiletamine and zolazepam. *Vet. Rec.* **146**, 251–254. (doi:10.1136/vr.146.9.251)
 51. McMahon CR, Field IC, Bradshaw CJA, White GC, Hindell MA. 2008 Tracking and data-logging devices attached to elephant seals do not affect individual mass gain or survival. *J. Exp. Mar. Biol. Ecol.* **360**, 71–77. (doi:10.1016/j.jembe.2008.03.012)
 52. Heerah K, Hindell M, Andrew-Goff V, Field I, McMahon CR, Charrassin J-B. 2017 Contrasting behavior between two populations of an ice-obligate predator in East Antarctica. *Ecol. Evol.* **7**, 606–618. (doi:10.1002/ece3.2652)
 53. Langrognet F, Lebrez R, Poli C, Iovleff S, Auder B. 2019 Rmixmod: classification with mixture modelling. R package version 2.1.2.2. See <https://CRAN.R-project.org/package=Rmixmod>.
 54. DeNiro MJ, Epstein S. 1977 Mechanism of carbon isotope fractionation associated with lipid synthesis. *Science* **197**, 261–263. (doi:10.1126/science.327543)
 55. Stan Development Team. 2019 RStan: the R interface to Stan. R package version 2.19.2. See <http://mc-stan.org/>.
 56. Carpenter B *et al.* 2017 Stan: a probabilistic programming language. *J. Stat. Softw.* **76**, 1–32. (doi:10.18637/jss.v076.i01)
 57. Cherel Y, Ducatez S, Fontaine C, Richard P, Guinet C. 2008 Stable isotopes reveal the trophic position and mesopelagic fish diet of female southern elephant seals breeding on the Kerguelen Islands. *Mar. Ecol. Prog. Ser.* **370**, 239–247. (doi:10.3354/meps07673)
 58. Gruber N *et al.* 2019 The oceanic sink for anthropogenic CO_2 from 1994 to 2007. *Science* **363**, 1193–1199. (doi:10.1126/science.aau5153)
 59. Tagliabue A, Bopp L. 2008 Towards understanding global variability in ocean carbon-13: variability in ocean carbon-13. *Glob. Biogeochem. Cycles* **22**, GB1025. (doi:10.1029/2007GB003037)
 60. Pereira NS *et al.* 2018 Carbon stable isotope record in the coral species *Siderastrea stellata*: a link to the Suess effect in the tropical South Atlantic Ocean. *Palaeogeogr. Palaeoclimatol. Palaeoecol.* **497**, 82–90. (doi:10.1016/j.palaeo.2018.02.007)
 61. Hobson KA, Sinclair E, York A, Thomason J, Merrick R. 2004 Retrospective isotopic analyses of stellar sea lion tooth annuli and sea-bird feathers: a cross-taxa approach to investigating regime and dietary shifts in the gulf of Alaska. *Mar. Mammal Sci.* **20**, 621–638. (doi:10.1111/j.1748-7692.2004.tb01183.x)
 62. Racapé V, Monaco CL, Metz N, Pierre C. 2010 Summer and winter distribution of $\delta^{13}\text{C}_{\text{DIC}}$ in surface waters of the South Indian Ocean [20°S–60°S]. *Tellus B* **62**, 660–673. (doi:10.1111/j.1600-0889.2010.00504.x)
 63. France R. 1995 Carbon-13 enrichment in benthic compared to planktonic algae: foodweb implications. *Mar. Ecol. Prog. Ser.* **124**, 307–312. (doi:10.3354/meps124307)
 64. Hilton GM, Thompson DR, Sagar PM, Cuthbert RJ, Cherel Y, Bury SJ. 2006 A stable isotopic investigation into the causes of decline in a sub-Antarctic predator, the rockhopper penguin *Eudyptes chrysocome*. *Glob. Change Biol.* **12**, 611–625. (doi:10.1111/j.1365-2486.2006.01130.x)
 65. Henson SA, Cole HS, Hopkins J, Martin AP, Yool A. 2018 Detection of climate change-driven trends in phytoplankton phenology. *Glob. Change Biol.* **24**, e101–e111. (doi:10.1111/gcb.13886)
 66. Goericke R. 1994 Physiology of isotopic fractionation in algae and cyanobacteria. *Stable Isot. Ecol. Environ. Sci.* **0**, 187–221.
 67. Bidigare RR *et al.* 1997 Consistent fractionation of ^{13}C in nature and in the laboratory: growth-rate effects in some haptophyte algae. *Glob. Biogeochem. Cycles* **11**, 279–292. (doi:10.1029/96GB03939)
 68. Laws EA, Popp BN, Bidigare RR, Kennicutt MC, Macko SA. 1995 Dependence of phytoplankton carbon isotopic composition on growth rate and $[\text{CO}_2]_{\text{aq}}$: theoretical considerations and experimental results. *Geochim. Cosmochim. Acta* **59**, 1131–1138. (doi:10.1016/0016-7037(95)00030-4)

69. Popp BN, Laws EA, Bidigare RR, Dore JE, Hanson KL, Wakeham SG. 1998 Effect of phytoplankton cell geometry on carbon isotopic fractionation. *Geochim. Cosmochim. Acta* **62**, 69–77. (doi:10.1016/S0016-7037(97)00333-5)
70. Deuser WG. 1970 Isotopic evidence for diminishing supply of available carbon during diatom bloom in the Black Sea. *Nature* **225**, 1069–1071. (doi:10.1038/2251069a0)
71. Hansman RL, Sessions AL. 2016 Measuring the *in situ* carbon isotopic composition of distinct marine plankton populations sorted by flow cytometry. *Limnol. Oceanogr. Methods* **14**, 87–99. (doi:10.1002/lom3.10073)
72. Fischer G. 1991 Stable carbon isotope ratios of plankton carbon and sinking organic matter from the Atlantic sector of the Southern Ocean. *Mar. Chem.* **35**, 581–596. (doi:10.1016/S0304-4203(09)90044-5)
73. Henley SF *et al.* 2012 Factors influencing the stable carbon isotopic composition of suspended and sinking organic matter in the coastal Antarctic sea ice environment. *Biogeosciences* **9**, 1137–1157. (doi:10.5194/bg-9-1137-2012)
74. Lorrain A *et al.* 2019 Trends in tuna carbon isotopes suggest global changes in pelagic phytoplankton communities. *Glob. Change Biol.* **26**, 458–470. (doi:10.1111/gcb.14858)
75. Burton HR, Arnborn T, Boyd IL, Bester M, Vergani D, Wilkinson I. 1997 Significant differences in weaning mass of southern elephant seals from five sub-Antarctic islands in relation to population declines. In *Antarctic communities: species, structure and survival* (eds B Battaglia, J Valencia, DWH Walton), pp. 335–338. Cambridge, UK: Cambridge University Press.
76. McMahon CR, Hindell MA, Burton HR, Bester MN. 2005 Comparison of southern elephant seal populations, and observations of a population on a demographic knife-edge. *Mar. Ecol. Prog. Ser.* **288**, 273–283. (doi:10.3354/meps288273)
77. Clausius E, McMahon CR, Harcourt R, Hindell MA. 2017 Effect of climate variability on weaning mass in a declining population of southern elephant seals *Mirounga leonina*. *Mar. Ecol. Prog. Ser.* **568**, 249–260. (doi:10.3354/meps12085)
78. McMahon CR, Burton HR. 2005 Climate change and seal survival: evidence for environmentally mediated changes in elephant seal, *Mirounga leonina*, pup survival. *Proc. R. Soc. B* **272**, 923–928. (doi:10.1098/rspb.2004.3038)
79. Oosthuizen WC, Bester MN, Altwegg R, McIntyre T, De Bruyn PJN. 2015 Decomposing the variance in southern elephant seal weaning mass: partitioning environmental signals and maternal effects. *Ecosphere* **6**, 1–22. (doi:10.1890/ES14-00508.1)
80. Paterson JT, Rotella JJ, Arrigo KR, Garrott RA. 2015 Tight coupling of primary production and marine mammal reproduction in the Southern Ocean. *Proc. R. Soc. B* **282**, 20143137. (doi:10.1098/rspb.2014.3137)
81. Zanden HBV, Tucker AD, Bolten AB, Reich KJ, Bjørndal KA. 2014 Stable isotopic comparison between loggerhead sea turtle tissues. *Rapid Commun. Mass Spectrom.* **28**, 2059–2064. (doi:10.1002/rcm.6995)
82. Arthur B, Hindell M, Bester MN, Oosthuizen WC, Wege M, Lea M-A. 2016 South for the winter? Within-dive foraging effort reveals the trade-offs between divergent foraging strategies in a free-ranging predator. *Funct. Ecol.* **30**, 1623–1637. (doi:10.1111/1365-2435.12636)
83. Jeanniard du Dot T, Trites A, Arnould J, Speakman J, Guinet C. 2018 Trade-offs between foraging efficiency and pup feeding rate of lactating northern fur seals in a declining population. *Mar. Ecol. Prog. Ser.* **600**, 207–222. (doi:10.3354/meps12638)
84. Jonsen ID, McMahon CR, Patterson TA, Auger-Méthé M, Harcourt R, Hindell MA, Bestley S. 2019 Movement responses to environment: fast inference of variation among southern elephant seals with a mixed effects model. *Ecology* **100**, e02566. (doi:10.1002/ecy.2566)
85. McMahon CR, Burton HR, Bester MN. 2000 Weaning mass and the future survival of juvenile southern elephant seals, *Mirounga leonina*, at Macquarie Island. *Antarct. Sci.* **12**, 149–153. (doi:10.1017/S095410200000195)
86. Postma M, Bester MN, de Bruyn PJN. 2013 Age-related reproductive variation in a wild marine mammal population. *Polar Biol.* **36**, 719–729. (doi:10.1007/s00300-013-1298-4)